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RESEARCH PAPER

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## Plasticity in life history traits of a cyprinid fish in an intermittent river

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**Abstract** – The extreme seasonal environmental variation of intermittent rivers has a profound effect on freshwater fish communities. Yet, few studies have examined the consequences of the seasonal cycles of flooding and drying to fish condition and reproduction in these ecosystems. In this study, we compared the body condition, reproduction and diet of two chub populations from two adjacent sites (a perennial and an intermittent site) on the main stem of a Mediterranean river (Evrotas River, S. Greece). The study was conducted in spring 2017, three months after flow resumption and before the onset of chub reproductive period. Condition (net weight adjusted for length) of fish did not differ significantly between the two sites, despite lower aquatic macroinvertebrate availability at the intermittent site. Fish at the intermittent site compensated for the lower aquatic prey availability by increasing their feeding intensity and by shifting to higher terrestrial prey consumption. In addition, chub liver weight (adjusted for length) and gonadal weight (adjusted for length) were significantly higher at the intermittent site, indicating higher somatic and reproductive investment. These results highlight the resilience of fish populations inhabiting streams with extreme variation in flow, due to natural and/or anthropogenic drought.

**Keywords:** fish condition / fish reproduction / trophic ecology / drought

**Résumé** – **Plasticité des traits d'histoire de vie d'un poisson cyprinidé dans une rivière intermittente.**

Les variations environnementales saisonnières extrêmes des rivières intermittentes ont un effet profond sur les communautés de poissons d'eau douce. Pourtant, peu d'études ont examiné les conséquences des cycles saisonniers d'inondation et d'assèchement sur la condition et la reproduction des poissons dans ces écosystèmes. Dans cette étude, nous avons comparé l'état corporel, la reproduction et le régime alimentaire de deux populations de chevesnes provenant de deux sites adjacents (un site pérenne et un site intermittent) sur le bras principal d'une rivière méditerranéenne (rivière Evrotas, Grèce du Sud). L'étude a été menée au printemps 2017, trois mois après la reprise du débit et avant le début de la période de reproduction du chevesne. La condition (poids net ajusté en fonction de la longueur) des poissons ne différait pas de façon significative entre les deux sites, malgré une disponibilité moindre de macroinvertébrés aquatiques sur le site intermittent. Les poissons au site intermittent ont compensé la faible disponibilité des proies aquatiques en augmentant leur intensité d'alimentation et en passant à une plus grande consommation de proies terrestres. De plus, le poids du foie de chevesne (ajusté pour la longueur) et le poids gonadique (ajusté pour la longueur) étaient significativement plus élevés au site intermittent, indiquant un investissement somatique et reproducteur plus élevé. Ces résultats mettent en évidence la résilience des populations de poissons vivant dans les cours d'eau avec des variations extrêmes du débit, dues à la sécheresse naturelle et/ou anthropique.

**Mots-clés :** condition des poissons / reproduction des poissons / écologie trophique / sécheresse

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## 1 Introduction

Intermittent rivers and streams are lotic ecosystems that seasonally exhibit partial or total flow cessation. These fluctuating aquatic ecosystems, with extreme high and low flow periods, are dominant in arid and semi-arid regions (Lamed *et al.*, 2010; Datry *et al.*, 2016), while future projections postulate an accelerated trend towards their expansion, attributed mainly to water over-abstraction and climate change (Datry *et al.*, 2018). Intermittent rivers and streams have drawn less attention in river research compared to perennial rivers (Lamed *et al.*, 2010; Datry *et al.*, 2014, 2016; Skoulikidis *et al.*, 2017) but they are increasingly recognized as unique environments that provide important ecosystem services (Datry *et al.*, 2018). Furthermore, they support a high biodiversity (Soria *et al.*, 2017), with many range-restricted endemic and threatened species, especially in the Mediterranean region (Hermoso and Clavero, 2011).

Flow variation is the defining critical component of all intermittent streams affecting a multitude of biogeochemical and ecological processes, thus successively affecting abiotic parameters and river biota (Cid *et al.*, 2017). Freshwater fish are particularly sensitive to water deprivation, but the existence of water is not the sole factor for fish to survive and fulfill their biological cycle, since other additional environmental requirements must also be met. Fish inhabiting intermittent streams are repeatedly forced to survive under adverse environmental conditions (Matthews, 1998). During the contraction phase, fish are confined to shrinking aquatic refugia, where they experience harsh abiotic conditions (*e.g.* high water temperatures, oxygen depletion, poor water quality due to lower dilution capacity), as well as increased competition for food and predation pressure (Lake, 2003; Magoulick and Kobza, 2003; Matthews and Marsh-Matthews, 2003). Contrastingly, during the high flooding season fish are forced to tolerate high torrential flows, low temperatures and lower food availability (Encina and Granado-Lorencio, 1997). Still, flow resumption provides the opportunity for aquatic organisms, such as fish and macroinvertebrates, to recolonize the drought affected areas (Detenbeck *et al.*, 1992; Skoulikidis *et al.*, 2011; Marshall *et al.*, 2016), dispersing passively or actively from the persistent refugia to the formerly desiccated areas; a significant process demonstrating population resilience that affects the recovery process of the desiccated areas (Hershkovitz and Gasith, 2013; Leigh *et al.*, 2016).

The evolution of life history patterns of fish species in natural ecosystems is a compound effect of various, often interacting, environmental and biotic selective factors, such as density-dependent regulation, resource availability, predation, competition and environmental variability (Winemiller and Rose, 1992; Reznick *et al.*, 2001, 2002; Tedesco *et al.*, 2008; Mims and Olden, 2013). Fish species inhabiting streams with high environmental variability require distinctive and adaptive life-history traits (*e.g.* short life span, rapid growth, high fertility, early sexual maturity and reproduction, and low food electivity, Magalhães *et al.*, 2003, 2007; Olden and Kennard, 2010; Mims and Olden, 2012; Filipe *et al.*, 2013).

Even though fish and other biota in streams of arid and semi-arid regions, such as the Mediterranean, are evolutionary able to adapt to harsh environmental conditions (Gasith and Resh, 1999; Filipe *et al.*, 2013; Hershkovitz and Gasith, 2013),

the accelerated climatic change coupled with the increasing anthropogenic water demand may create unfavorable abiotic settings that could bring species to the brink of extinction (Jaeger *et al.*, 2014; Knouft and Ficklin, 2017; Reid *et al.*, 2018).

Though several studies have explored the effects of the seasonal cycles of flooding and drying on fish assemblage structure (*e.g.* Magalhães *et al.*, 2007; Benejam *et al.*, 2010; Skoulikidis *et al.*, 2011), less attention has been given on the effects on fish condition and reproduction. Recent studies though have documented the lower condition and/or reproduction success of fish in intermittent streams, possibly related to lower prey availability (Rincón and Lobón-Cerviá, 1989; Oliva-Paterna *et al.*, 2003; Mas-Martí *et al.*, 2010). Other studies, however, have shown that populations at unstable environmental conditions may consist of robust individuals that benefit from variable local conditions, indicating life history plasticity (Spranza and Stanley, 2000).

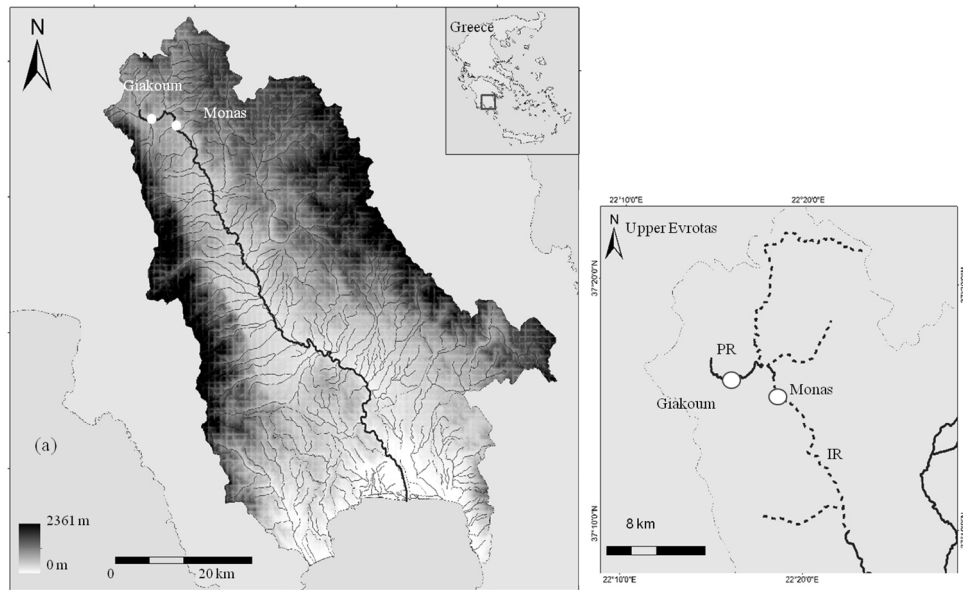
The aim of the current study was to assess differences in condition, reproduction and trophic ecology of a native chub species, between an intermittent reach and an adjacent perennial reach of a Mediterranean river. Based on previous studies, we assumed that the colonization of the intermittent reach was conducted by individuals from the resident population of the upstream perennial reach. In the current study, our working hypothesis was that the preceding drought would have negatively affected the macroinvertebrate community of the intermittent reach, with subsequent effects on condition, reproduction and trophic ecology of the colonizers of the intermittent reach.

## 2 Materials and methods

### 2.1 Study area and sampling site description

This study was conducted at the Evrotas River, a biogeographically isolated Mediterranean intermittent river, located in the Peloponnese (Southern Greece). The hydrological, topographical and ecosystem attributes of the Evrotas River have been described in detail in previous studies (for a review see Karouzas *et al.*, 2017). Anthropogenic pressures in the Evrotas basin include mainly hydromorphological alterations *i.e.* severe water abstraction, as well as channelisation and wetland and riparian zone reduction, and sparse diffuse pollution (Skoulikidis *et al.*, 2008; 2011). The intensity of the dry period fluctuates every year, as in other Mediterranean rivers (Gasith and Resh, 1999), but normally, every year during the low flow period, the Evrotas River is partially desiccated, with approximately 20% of its main channel and most of its tributaries, drying out. The over-abstraction of both surface and ground waters throughout the river valley, define the Evrotas River as an “artificially intermittent Mediterranean river” (Skoulikidis *et al.*, 2011).

The river hosts three range-restricted cyprinid species of high conservation concern: the Evrotas chub *Squalius keadicus* (Stephanidis, 1971), the Spartan minnowroach *Tropidophoxinellus spartiaticus* (Schmidt-Ries, 1943) and the Evrotas minnow *Pelasgus laconicus* (Kottelat & Barbieri, 2004). The current study focused exclusively on the Evrotas chub, endemic only to the Evrotas, since this species is more



**Fig. 1.** (a) the study area and the two sampling sites, “Giakoum” (perennial) and “Monas” (intermittent) in the Upper Evrotas main stem; (b) The location of the two sampling sites within the upper perennial reach of Evrotas (PR, solid line) and the more downstream intermittent reach (IR, dashed line) respectively.

likely to be affected from future water scarcity at the basin (Vardakas *et al.*, 2017).

This study was conducted at two 100 m riverine sites of the upper Evrotas main stem (Fig. 1a), sites Giakoum (37° 15' 57.83"N, 22° 15' 54.00"E) and Monas (37° 15' 30.88"N, 22° 18' 21.16"E) in late March 2017. The surrounding area of the upper Evrotas River is characterised by sparse rural settlements and scant riparian trees with low anthropogenic pressures (small scale agriculture and animal husbandry). Site Giakoum is located in the 8.5 km section of the uppermost Evrotas main stem that is characterised by perennial flow (PR, Fig. 1b), while site Monas is located in the subsequent 16 km downstream intermittent section of the river, that typically dries out from July to November each year (IR, Fig. 1b); for a description of the flow regime in Upper Evrotas see also Kalogianni *et al.* (2017) and Karaouzas *et al.* (2017, 2018). The two sampling sites at the Upper Evrotas were selected based mainly on three criteria: a) they should display a similar generic macro-habitat representativeness (all habitats present, *i.e.* riffles, runs, glides and pools), b) the two sites had to differ in their hydrology, *i.e.* a perennial *versus* an intermittent site, with a steady and recurrent pattern of intermittency and c) both sites should display low chemical degradation. No other sites further downstream the Evrotas main stem fulfilled these criteria, since they had different hydromorphological characteristics and higher pollution load. A single sampling campaign in early spring was opted for, considering the endangered status of the target species and in an effort to avoid capturing spawning fish.

During the field survey, a series of physical, chemical and habitat parameters were recorded at each sampling site. Specifically, conductivity ( $\mu\text{S cm}^{-1}$ ), dissolved oxygen ( $\text{mg L}^{-1}$ ), pH, and water temperature ( $^{\circ}\text{C}$ ) were recorded *in situ*

using a portable multiparameter Aquaprobe AP-200 with a GPS Aquameter (Aquaread AP 2000). Water flow and depth data were obtained using a water flow meter OTT C20. Other habitat characteristics determined were mean wetted width (m), shadedness (%) and substrate coarseness *i.e.*  $\geq 63$  mm (%), as well as the percentage of the dominant habitat type, *i.e.* pool, glide, run or pool, for each study site. In order to calculate days of desiccation at the intermittent site, water level data obtained from an automatic gauging station within the 16 km intermittent section of the upper Evrotas (approx. 11 km downstream from site Monas, Fig. 1) were used.

## 2.2 Fish sampling

Sampling was conducted in early spring 2017 (March), after flow resumption at the intermittent site and prior to the next spawning season of the Evrotas chub (mid April–May). Fish sampling was conducted using an EFKO electrofishing DC unit (Honda 7 kVA generator, 150 m cable, 1.5 m anode pole, 6 A DC output, voltage range 300–600 V) on the same day at both sites in the morning hours. The sampling team consisted of four members, one operator of the electrofishing device, two netters collecting the stunned fish and one data recorder. Electrofishing began at a shallow riffle and proceeded upstream in a meandering manner to adequately sample all types of habitats. Captured fish were identified to species level, counted and their size class recorded at 5 cm intervals. Evrotas chub specimens were immediately placed in ice to prevent digestion of the gut content and to euthanize them, and then were preserved in 4% formaldehyde for laboratory analysis. Fished area was also recorded in order to calculate fish CPUE values, *i.e.* catch per unit effort, expressed as number of fish caught/ $\text{m}^2$  fished area.

### 2.3 Macroinvertebrate sampling

Benthic macroinvertebrate samples were collected according to the AQEM method (AQEM Consortium, 2002) *i.e.* 20 “replicates” were collected from all the main microhabitat types of at least 5% coverage at each site. A total of 1.25 m<sup>2</sup> (0.25 × 0.25 m × 20 replicates) was sampled at each sampling site, using a hand net of 25 × 25 cm with a mesh size of 500 μm. Benthic samples were preserved in 70% ethanol before being transferred to the laboratory for quantification, identification to family level and weighing to the nearest 0.001 mg.

### 2.4 Laboratory analysis

Water samples obtained for nutrient analyses were filtered in the laboratory through 0.45 μm membrane filters. Nitrite (NO<sub>2</sub>, mg L<sup>-1</sup>), and orthophosphate (PO<sub>4</sub>, mg L<sup>-1</sup>) concentrations were determined by a Skalar San++ Continuous flow analyzer (Boltz and Mellon, 1948; Navone, 1964), whereas nitrate (NO<sub>3</sub>, mg L<sup>-1</sup>) concentration was determined using both Ion chromatography and a Skalar automatic analyzer. NH<sub>4</sub> (mg L<sup>-1</sup>) concentration was determined using a Skalar automatic analyzer. Ecological quality assessment based on nutrients was made following Skoulikidis *et al.* (2006).

Macroinvertebrate samples were sorted at the laboratory, identified down to family level, according to Tachet *et al.* (2000), counted and weighed to the nearest 0.001 mg. Fish samples (33 individuals from the perennial Giakoum site and 39 from the intermittent Monas site) were measured in length (total length TL and fork length FL); TL was used for the separation of juveniles from adults (juveniles < 10 cm TL, adults > 10 cm following Vardakas *et al.*, 2017), while FL was used in all subsequent analyses. They were then weighed before (total weight, TW) and after being eviscerated (net weight, NW) and sexed. Gonad weight (GW) and liver weight (LW) were also recorded, along with gut weight (GTW), before the removal of its content. Gut content was analysed under a dissecting stereoscope; animal prey items were identified down to the lowest taxonomic category possible (mostly at family level) according to Tachet *et al.* (2000), and counted. Gut content was then weighed (GCW) to the nearest 0.001 mg. Other food categories, such as plants and non-organic materials, were also recorded and weighed separately.

### 2.5 Data analysis

#### 2.5.1 Fish condition

Differences in fish length between sites were analyzed by independent samples *t*-test. Analysis of covariance (ANCOVA) was used to compare fish TW, NW, GW, LW, GTW, and GCW, with site and sex as factors, using fish fork length as a covariate. ANCOVA and independent samples *t*-test were performed on log(*x* + 1) transformed data to approximate normality and homogeneity of variances (Quinn and Keough, 2002), using the IBM SPSS 23.0 software package.

We estimated length-weight relationships of TW, LW, GW and GTW with FL, according to the formula:  $W = aL^b$  by the least squares method, through the transformed equation

(Tesch, 1971):  $\log W = \log a + b \cdot \log L$  where *a* is the intercept, *b* is the slope of the regression line and *L* is FL. The statistical significance level of the coefficient of determination (*r*<sup>2</sup>) for each relationship was also estimated. The estimated *b* values were used to check whether the growth of each species is isometric (*b* = 3), negative allometric (*b* < 3), or positive allometric (*b* > 3) (see Froese 2006; Oikonomou *et al.*, 2014).

#### 2.5.2 Food availability and diet

To assess the macroinvertebrate community structure of the two study sites, the following metrics were calculated: abundance, richness, Shannon's diversity, total biomass, EPT (Ephemeroptera, Plecoptera, Trichoptera) and COH (Coleoptera, Odonata, Heteroptera) taxa.

Feeding intensity was evaluated using the Vacuity index (VI, percentage of empty guts), the Fullness index (FI, estimated visually on a scale of 1 to 5), and the number of animal prey items consumed. To determine prey importance in the diet of the Evrotas chub, frequency of occurrence (Fi) and prey abundance (Ai) were calculated, according to Hyslop (1980). These indices are represented by the following equations:  $Fi = (Ni/N) \times 100$ , where Ni is the number of guts that contain prey *i*, and N is the total number of observed guts that were not empty;  $Ai = (Si/St) \times 100$ , where Si is the number of prey *i* in each gut, and St is the number of all ingested prey items in the entire sample (*i.e.*, seasonal, sex or age group sample). Fish diet diversity was estimated with Shannon's diversity index per individual and per site.

Differences between sites in fish diet diversity and number of consumed animal prey items were assessed by independent samples *t*-test. Mann–Whitney *U*-test was used to compare the relative abundance (%) of consumed terrestrial prey items *versus* aquatic prey items, as well as the Fullness Index between sites. All tests were performed on log(*x* + 1) transformed data. Pearson's chi-square test was used to assess between sites' differences in plant material consumption, using occurrence data. All analyses were performed using the IBM SPSS 23.0 software package.

To determine possible shifts in fish feeding strategy between the two sites, the modified Costello graphical method was used (Amundsen *et al.*, 1996). In this method, prey-specific abundance (Pi) is plotted against prey-specific frequency of occurrence (Fi), both expressed as a percentage, on a two-dimensional graph. Pi is the percentage a prey group comprises of all prey items consumed (only in those guts in which the actual prey occurred). Prey-specific frequency of occurrence (Fi) is the percentage of guts in which a prey was present. Information about prey importance and feeding strategy of the predator can be obtained by examining the distribution of points along the diagonals and the axes of the diagram.

## 3 Results

### 3.1 Environmental setting

Nitrite load and ammonia levels were low at both study sites, indicating low organic pollution (Tab. 1), and the quality based on these nutrients was high or good; phosphorous



**Table 1.** Physical, chemical and habitat parameters, nutrient load, Evrotas chub CPUE values and fork length values (mean  $\pm$  StD) at the two sampling sites.

	Giakoum	Monas
<b>Habitat/physical/chemical</b>		
Flow regime	Perennial	Intermittent
Flow velocity (mean, m/s)	0.60	0.17
Depth (mean, m)	0.13	0.29
Width (mean, m)	5	7
Substrate (%) > 63 mm	5	20
Shadedness (%)	10	5
Conductivity ( $\mu\text{S cm}^{-1}$ )	514	438
Diss. Oxygen ( $\text{mg L}^{-1}$ )	10.21	10.54
pH	7.97	8.12
T of water ( $^{\circ}\text{C}$ )	13.5	13.2
Dominant habitat type (%)	Glide 80%	Glide 80%
<b>Nutrients</b>		
Nitrates ( $\text{mg L}^{-1}\text{N-NO}_3^-$ )	0.79	0.58
Nitrites ( $\text{mg L}^{-1}\text{N-NO}_2^-$ )	0.001	0.002
Ammonium ( $\text{mg/l N-NH}_4^+$ )	0.007	0.043
Phosphates ( $\text{mg L}^{-1}\text{P-PO}_4^{3-}$ )	0.002	0.008
Total dissolved Nitrogen ( $\text{mg L}^{-1}\text{N}$ )	0.80	0.63
Total dissolved Phosphorous ( $\text{mg L}^{-1}\text{P}$ )	0.003	0.027
<b>Fish</b>		
Fished area ( $\text{m}^2$ )	212.2	189
CPUE ( $\text{ind/m}^2$ )		
Total sample	0.75	0.40
<i>S. keadicus</i>	0.17	0.26
<i>S. keadicus</i> juveniles	0.08	0.13
<i>S. keadicus</i> adults	0.08	0.08
<i>S. keadicus</i> fork length (cm)	9.53 (2.00)	8.00 (2.63)

concentrations (both as phosphate and TP) were also low, and the respective quality was found also high. Nitrate values were slightly elevated in the perennial site (Giakoum), with nitrate quality being moderate at this site; overall, however, the ecological quality based on nutrients was high at both sampling sites indicating low levels of pollution.

Overall, during the study period, the two sites were also similar in terms of habitat characteristics (Tab. 1). More specifically, both sites were dominated by glides (shallow, slow flowing, 80%) as a generic macro-habitat type and had fairly similar substrate composition, with substrate coarseness being low, at 5 and 20%, for the perennial and the intermittent site, respectively (Tab. 1). In addition, shadedness levels were low at both sites (5–10%), while helophytes and bottom vegetation were absent from both locations. However, the two sites differed in their hydrology, with flow being disconnected at the intermittent site (Monas) from June 17th 2016 to January 6th 2017, with only two brief rainfall episodes in September and November 2016. Flow had resumed in the intermittent site for almost three months (79 days) prior to fish sampling on March 26th 2017.

### 3.2 Fish abundance, condition and reproduction

During this study, a total of 160 and 75 fish were caught at the perennial (Giakoum) and the intermittent site (Monas) respectively (Tab. 1). Evrotas chub (*S. keadicus*) CPUE ranged from 0.17 inds  $\text{m}^{-2}$  at the perennial site to 0.26 inds  $\text{m}^{-2}$  at the intermittent site; juvenile chubs represented 48% of the total sample at the permanent site and 61.5% at the intermittent site. Chub FL varied from 5.8 to 14.2 cm at the perennial site, and from 3 to 12.9 cm at the intermittent site.

Evrotas chub FL was significantly higher at the perennial site ( $t=3.090$ ,  $p=0.003$ ). Chub TW (adjusted for length by ANCOVA) was significantly higher at the intermittent site (Tab. 2, Fig. 2a) and the same pattern was evident when examining female TW (Tab. 2, Fig. 2b) and adult TW (Tab. 2). Both the total sample and female chubs exhibited a positive allometric growth ( $b > 3$ , similar slopes, Fig. 2a and b). However, there was no significant difference in Evrotas chub NW between the two sites (Tab. 2).

LW of the Evrotas chub was also significantly higher at the intermittent site and the same was evident when examining the female LW (Tab. 2, Fig. 2c and d) and adult LW (Tab. 2). In the total sample of the intermittent site, there was lower liver growth rate (lower slope) than in the perennial site, whereas this trend was opposite in females (Fig. 2c and d).

GW of female chubs was also significantly higher at the intermittent site with similar slopes at both sites, indicating similar positive gonad growth (Tab. 2). GTW of the Evrotas chub was also significantly higher at the intermittent site, with GTW slope of the intermittent site lower than in the perennial (Tab. 2, Fig. 3b). GTW and GCW of juveniles from the intermittent site were also significantly higher, as well as GCW in male chubs (Tab. 2).

### 3.3 Macroinvertebrate community composition and food availability

The abundance and biomass of potential macroinvertebrate prey was 3 fold higher and 2.5 fold higher respectively in the perennial compared to the intermittent site (Tab. 3). The number and percentage of EPT taxa in the perennial site was also higher, while the reverse was evident for COH taxa. Diversity and Evenness had similar values (Tab. 3).

In terms of abundance, both samples were dominated by Ephemeroptera larvae (> 40%, Fig. 4a). The second most abundant category was Dipteran larvae (20–25%) (Fig. 4). These were followed by Trichoptera (15%) in the perennial site and by Coleoptera (19%) in the intermittent site. All other categories contributed less than 6%. In terms of biomass, at the perennial site the sample was dominated by Plecoptera (23%) followed closely by Ephemeroptera (21%, Fig. 4b). At the intermittent site, in contrast, the sample was dominated by Ephemeroptera (37%), followed by Odonata (28%, Fig. 4b).

### 3.4 Diet

At the intermittent site, less specimens with empty stomachs were found compared to the perennial site (%VI, Tab. 4). Also, the Fullness index (FI) increased significantly

**Table 2.** Analyses of covariance of total (TW), eviscerated (NW), Gonadal (GW), gut (GTW) and gut content (GCW) weight, with site and sex as factors and fish fork length as covariate. All variables were  $\log(x + 1)$  transformed.

	Log (fork length)		Site		Sex		Site $\times$ Sex	
	F	<i>p</i>	F	<i>p</i>	F	<i>p</i>	F	<i>p</i>
<b>All</b>								
TW	4480.088	< <b>0.001</b>	11.733	<b>0.001</b>	1.112	0.295	4.437	<b>0.039</b>
NW	4045.527	< <b>0.001</b>	2.870	0.095	0.045	0.833	4.316	<b>0.042</b>
LW	236.145	< <b>0.001</b>	19.842	< <b>0.001</b>	16.056	< <b>0.001</b>	3.151	<b>0.080</b>
GTW	291.778	< <b>0.001</b>	6.609	<b>0.012</b>	31.210	< <b>0.001</b>	0.091	0.764
GCW	9.265	<b>0.003</b>	2.323	0.132	4.322	<b>0.041</b>	2.808	0.098
<b>Juveniles</b>								
TW	842.230	< <b>0.001</b>	1.114	0.298				
NW	774.841	< <b>0.001</b>	0.108	0.744				
LW	77.844	< <b>0.001</b>	3.985	0.054				
GTW	111.237	< <b>0.001</b>	6.258	<b>0.017</b>				
GCW	5.325	<b>0.027</b>	4.665	<b>0.038</b>				
<b>Adults</b>								
TW	504.446	< <b>0.001</b>	15.388	<b>0.001</b>				
NW	465.393	< <b>0.001</b>	1.596	0.218				
LW	42.014	< <b>0.001</b>	8.767	<b>0.006</b>				
GTW	19.858	< <b>0.001</b>	0.376	0.545				
GCW	0.192	0.665	0.012	0.914				
<b>Females</b>								
TW	1713.060	< <b>0.001</b>	8.912	<b>0.005</b>				
NW	1570.028	< <b>0.001</b>	3.371	0.075				
GW	119.167	< <b>0.001</b>	7.302	<b>0.011</b>				
LW	131.119	< <b>0.001</b>	17.029	< <b>0.001</b>				
GTW	209.255	< <b>0.001</b>	3.957	0.055				
GCW	5.800	<b>0.022</b>	0.001	0.978				
<b>Males</b>								
TW	4024.873	< <b>0.001</b>	2.872	0.100				
NW	3838.644	< <b>0.001</b>	0.130	0.721				
GW	231.414	< <b>0.001</b>	1.180	0.285				
LW	104.509	< <b>0.001</b>	3.566	0.068				
GTW	91.254	< <b>0.001</b>	2.558	0.119				
GCW	3.063	0.089	5.033	<b>0.032</b>				

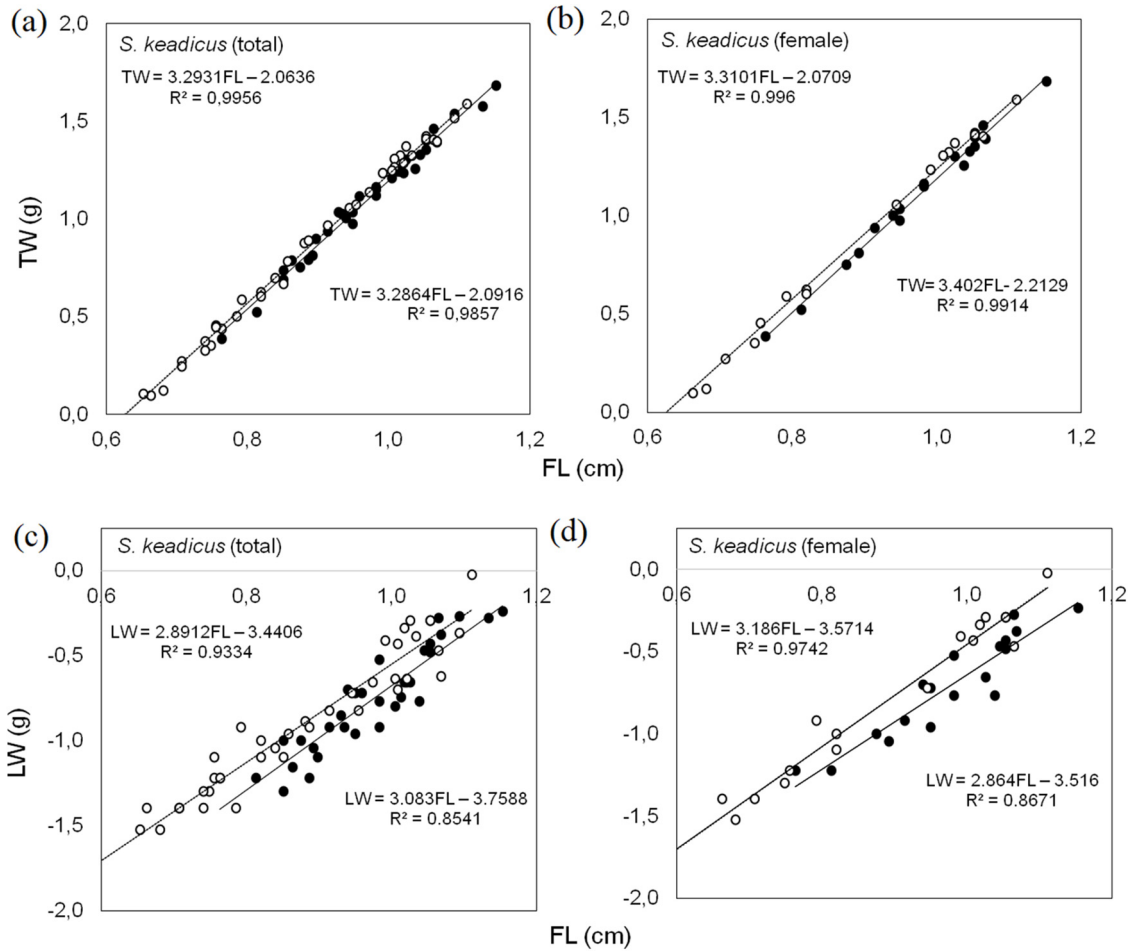
Note: Statistically significant *p* values are marked with bold.

(Mann-Whitney *U*-test,  $p = 0.014$ ), due to a significant increase in the FI of juveniles at the intermittent site (Mann-Whitney *U*-test,  $p = 0.035$ ). Mean number of animal prey items consumed also appeared to increase at the intermittent site (Tab. 4) though this was not statistically significant (*t*-test,  $p = 0.464$ ). Overall, these differences indicate that the individuals from the intermittent site demonstrated increased feeding intensity in comparison to the ones from the perennial site. Diet diversity *H'* did not differ significantly between the two sites (*t*-test,  $p = 0.732$ ).

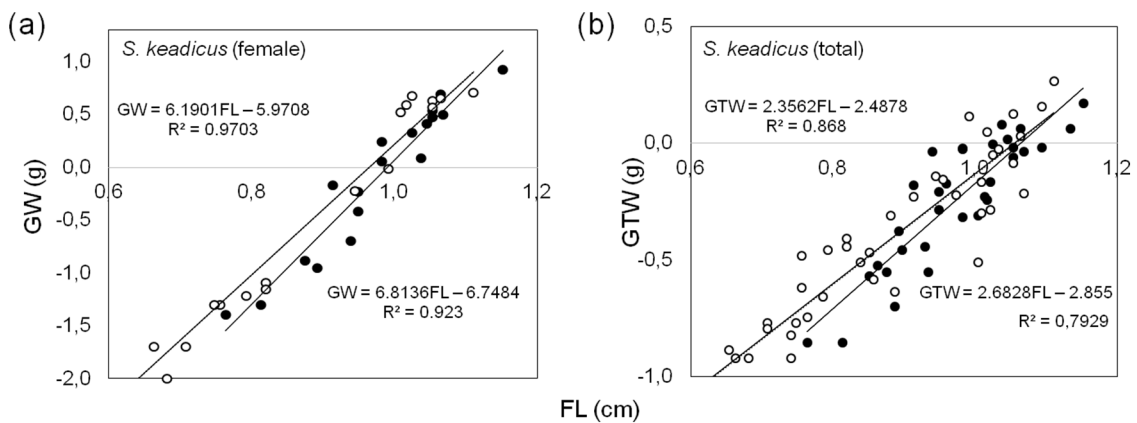
Consumed items were divided in three broad categories, *i.e.* aquatic prey, terrestrial prey (including all flying adult macroinvertebrate life stages) and plant material; both in terms of relative abundance (%Ai) and of frequency of occurrence (%Fo), aquatic prey was the dominant prey at both sites (Tab. 4). However, there was a significant decrease in aquatic

prey consumption (%Ai) and a concomitant increase in terrestrial prey consumption (%Ai, Mann-Whitney *U*-test,  $p = 0.019$ ) in the intermittent site. Plant material occurrence also increased in the intermittent site, but Pearson Chi-Square test did not reveal any statistically significant differences ( $p = 0.364$ ).

Qualitative and quantitative diet comparison indicates that the main forage base of the Evrotas chub at both sites consisted of a smaller subgroup of main prey items (Tab. 4). Most consumed prey in the perennial site were aquatic Leptoceridae larvae (Trichoptera, 43%), while in the intermittent site this was replaced by a terrestrial prey, Chironomidae adults (41%). Feeding strategy plots confirmed these observations, indicating overall a generalized diet in both sites with most preys consumed rarely (low Pi and Fi, points located mostly at lower left of the diagram in Fig. 5) with some preference for



**Fig. 2.** Total weight-fork length relationship (a, b) and liver weight-fork length relationship (c, d) of the Evrotas chub for the perennial reach (filled circles) and the intermittent reach (open circles). Linear regressions for the perennial (solid line) and the intermittent reach (dotted line) are also shown. All values log<sub>10</sub> transformed.



**Fig. 3.** Gonad weight-fork length relationship of female Evrotas chubs (a) and Gut weight-fork length relationship (b) of the Evrotas chub for the perennial (filled circles) and the intermittent reach (open circles). Linear regressions for the perennial (solid line) and the intermittent reach (dotted line) are also shown. All values log<sub>10</sub> transformed.

Leptoceridae larvae (aquatic prey) in the perennial site, *versus* a preference for Chironomidae adults (terrestrial prey) in the intermittent site (points located upper right of the diagram in Fig. 5), indicating a shift in the dominant prey from the perennial to the intermittent site.

## 4 Discussion

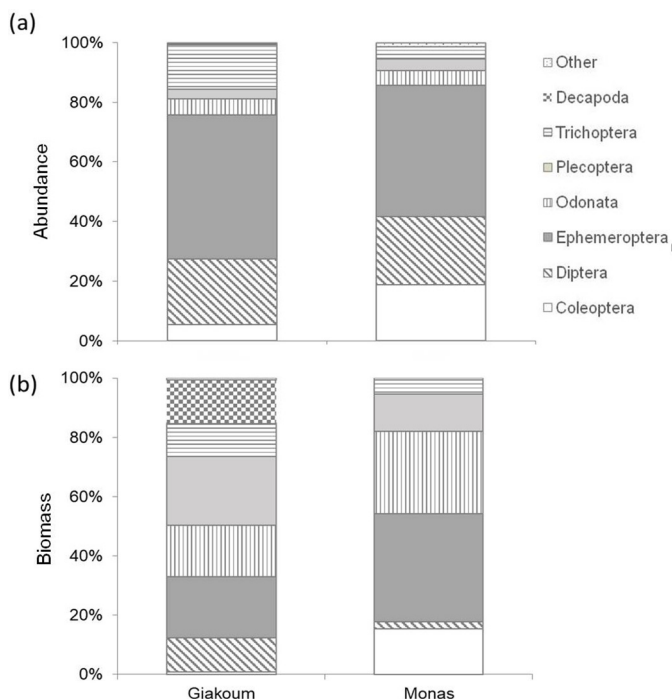
### 4.1 Fish condition and reproduction

In the current study, there were no significant differences in fish condition between the perennial and the intermittent site, three months after flow resumption. These results contrast with other studies that indicate lower condition of

various freshwater species in intermittent river sections, obtained from field observations (Oliva-Paterna *et al.*, 2003; Mas-Martí *et al.*, 2010) and manipulative experiments (Harvey *et al.*, 2006). More specifically, a study conducted in the south-eastern Iberian Peninsula (Segura river basin) indicated lower fish condition of the benthic species Sclater's barbel (*Barbus sclateri* Gunther, 1868) upon flow resumption, associated with lower flow or intermittency (Oliva-Paterna *et al.*, 2003). Another study conducted in La Tordera River and its intermittent tributary Fuirosos showed that the negative effects of seasonal drought on the condition of the chub *Squalius laietanus* (Doadrio, Kottelat & de Sostoa, 2007) and the Mediterranean barbel *Barbus meridionalis* (Risso, 1827) could prevail until next spring, preventing complete recovery (Mas-Martí *et al.*, 2010). Comparing the life histories of red roach *Rutilus arcasii* (Steindachner, 1866) inhabiting an intermittent and a perennial tributary of river Duero (Spain), Rincón and Lobón-Cerviá (1989) also reported that the condition of adult fish from the intermittent tributary did not recover after spawning, compared to the population at the perennial tributary. Our findings are, however, coincident with those of Spranza and Stanley (2000) that reported similar or higher condition of cyprinids in drought-impacted segments of an Oklahoma prairie stream. Similarly, Vasiliou and Economidis (2005) reported an increase in late autumn condition of two barbel species, upon flow recovery, in two intermittent streams of Northern Greece, while Merciai *et al.* (2018) also reported the higher condition (weight-length relationship) of barbel inhabiting the intermittent sites of an Iberian stream. They postulated that this was due to reduced competition upon rewetting or to colonisation by better fitted individuals. A higher somatic investment of the fish at the intermittent Evrotas site was also evident, as indicated by their higher liver weight, implying higher energy reserves. Fish inhabiting unstable environments, such as intermittent streams, may require higher levels of energy reserves, an investment that may increase reproductive success (Merciai *et al.*, 2018). This may account for the higher reproductive investment of the fish in the Evrotas intermittent site, indicated by their higher gonadal weight, prior to spawning. Spranza and Stanley (2000) also reported higher gonadosomatic index (GSI) values and a more protracted spawning period for cyprinid fish inhabiting an intermittent river segment, compared to their conspecifics at the perennial segment. Recently, Rezende (2018 and personal communication), conducting a comparative study of life history traits' variation in guppies from an intermittent and a permanent stream, reported the larger body size of guppies at the permanent stream and the higher female fecundity of their conspecifics of the intermittent stream, which agree with the findings of the current study. Çek *et al.* (2001) reported that changes in the gonadal (GSI) and liver (HIS) indices of the cyprinid *Puntius conchoni* (Hamilton, 1822) followed a similar pattern during gametogenesis in females, with both increasing with increasing mean body weight and length confirming similar finding in other species (Htun-Han, 1978; Delahunty and de Vlaming, 1980). It had been suggested that the correlation of liver weight with gonadal activity depends on the energetic requirements for recrudescence (gonadal growth), feeding habits and food availability for the species in question (Delahunty and de Vlaming, 1980), which may also apply in the case of the Evrotas chub.

**Table 3.** Macroinvertebrate fauna attributes at the perennial (Giakoum) and the intermittent (Monas) site.

	Perennial	Intermittent
Abundance	790	278
Biomass (mg)	5159	2027
Richness	31	28
Shannon's diversity $H'$	2.69	2.38
Evenness $J'$	0.79	0.71
EPT taxa	14	8
EPT taxa %	67	52
COH taxa	9	10
COH taxa %	11	24



**Fig. 4.** Abundance (a) and biomass (b) of invertebrate taxa at the two sampling reaches. Category “Other” includes all taxa accounting for less than 1% of total abundance and biomass respectively.



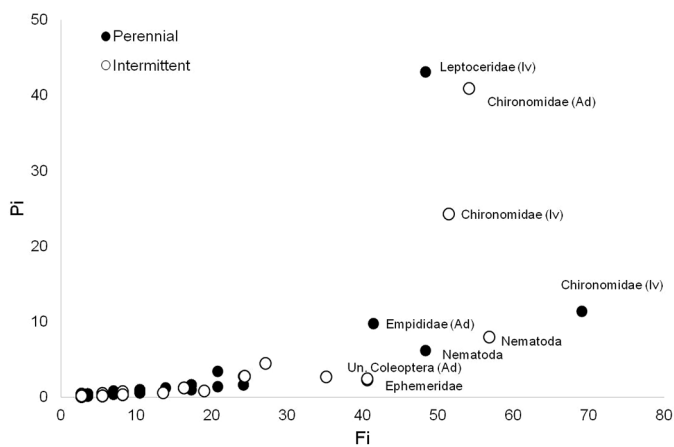
**Table 4.** Dietary composition of the Evrotas chub from the perennial and the intermittent site, displayed as frequency of occurrence (Fo, %) and numeric abundance (Ai, %) from non-empty guts. Pooled data for aquatic prey and terrestrial prey (including all adult invertebrate forms) are also presented. L: larvae; P: pupa; A: adult.

Prey Categories		Perennial		Intermittent	
		Fo%	Ai%	Fo%	Ai%
			(n=29)		(n=37)
	<i>Aquatic prey</i>				
Acari	Hydrachnidae			2.70	0.20
Coleoptera	Elmidae (A.)	3.45	0.20	2.70	0.10
	Elmidae (L.)	3.45	0.20		
Diptera	Helophoridae (A.)			2.70	0.10
	Athericidae (L.)			5.41	0.20
	Ceratopogonidae (L.)	3.45	0.20	5.41	0.20
	Chironomidae (L.)	68.97	<b>11.38</b>	51.35	<b>24.26</b>
	Chironomidae (P.)	3.45	0.40	5.41	0.51
	Dixidae (L.)	3.45	0.20	8.11	0.31
	Limonidae (L.)	20.69	1.40	18.92	0.82
	Simulidae (L.)	24.14	2.79	8.11	0.51
	Stratiomyidae (L.)	6.90	0.40	5.41	0.20
	Tipulidae (L.)	3.45	0.40		
	Anthomyidae (L.)			27.03	4.50
	Unidentified Diptera (P.)	13.79	1.20		
	Ephemeroptera	Baetidae (L.)	24.14	2.79	35.14
Baetidae (P.)		3.45	0.20		
Ephemeridae (L.)		17.24	1.60	40.54	2.25
Ephemerillidae (L.)		10.34	0.60		
Heptagenidae (L.)		24.14	1.60	16.22	1.23
Leptophlebiae (L.)		10.34	1.00	5.41	0.51
Unidentified Ephemeroptera (L.)		17.24	1.00		
Lepidoptera		Lepidoptera (L.)	6.90	0.40	2.70
Nematoda	Nematoda	48.28	6.19	56.76	7.98
Odonata	Calopterygidae (L.)	3.45	0.20		
	Gomphidae (L.)			5.41	0.20
Oligochaeta	Oligochaeta	10.34	0.60		
Plecoptera	Perlidae (L.)			8.11	0.72
	Perlodidae (L.)	6.90	0.80	24.32	2.76
	Unidentified Plecoptera (L.)	3.45	0.20		
Trichoptera	Hydropsychidae (L.)	17.24	1.60	13.51	0.61
	Hydroptilidae (L.)	24.14	1.60	8.11	0.31
	Leptoceridae (L.)	48.28	<b>43.11</b>	2.70	0.10
	Philopotamidae (L.)	3.45	0.20		
	Polycentropodidae (L.)			2.70	0.31
	Psychomyidae (L.)			2.70	0.10
	Unidentified Trichoptera (L.)	10.34	0.80		
	Unidentified Trichoptera (P.)	6.90	0.40		
	<i>Total Aquatic prey</i>	93.10	83.63	89.19	51.79
	<i>Terrestrial prey</i>				
Aranea	Aranea	3.45	0.40	8.11	0.31
Chilopoda	Chilopoda	3.45	0.20		
Coleoptera	Staphylinidae (A.)	6.90	0.40		
	Unidentified Coleoptera (A.)			40.54	2.46
Diptera	Ceratopogonidae (A.)			2.70	0.41
	Chironomidae (A.)	20.69	3.39	50.05	<b>40.94</b>
	Empididae (A.)	41.38	9.78	24.32	2.76
	Unidentified Diptera (A.)	6.90	0.40		
	Baetidae (A.)			2.70	0.10
Hymenoptera	Hymenoptera (A.)	3.45	0.40		
Trichoptera	Unidentified Trichoptera (A.)	3.45	0.40		

**Table 4.** (continued).

		Perennial		Intermittent	
Unidentified items	Unidentified items	10.34	1.00	16.22	1.23
	<i>Total Terrestrial prey</i>	55.17	16.37	78.38	48.21
	Algae and plants	17.24		27.03	
	Total prey	501		977	
	% VI ( <i>n</i> total fish examined)	12.12 (33)		5.13 (39)	
	FI (mean)	2.48		3.10	
	Mean <i>n</i> items consumed	17.28		26.41	
	Number of prey categories	39		33	
	Shannon's diversity <i>H'</i>	2.31		2.02	

Note: The dominant categories in the diet of the two species are in bold.



**Fig. 5.** Feeding strategy plots of the Evrotas chub from the perennial site (filled circles) and the intermittent site (open circles), indicating a generalist feeding strategy.

#### 4.2 Trophic plasticity

Both abundance and biomass of macroinvertebrate prey, as well as EPT richness, were lower at the intermittent site. This has been shown also in other studies (Bonada *et al.*, 2007; Bêche *et al.*, 2009; Mas-Martí *et al.*, 2010) and indicates a resource limitation for predators that may lead to lower gut content biomass in fish (Mas-Martí *et al.*, 2010). In the latter study, the lower condition of fish in the intermittent stream was partly attributed to bottom up effects of stream desiccation on the food web. Similarly, Lobón-Cerviá and Rincón (1994), in their study of red roach diet at the same intermittent river that they had reported lower fish condition (Rincón and Lobón-Cerviá, 1989), showed a shift to a detritus-based diet, and attributed the lower condition of the fish inhabiting the intermittent tributary to the low nutritional and energetic value of detritus. In our study, chubs at the intermittent site had, however, higher feeding intensity as indicated by their lower vacuity index, higher fullness index and higher mean number of items consumed. Gut weight and gut content weight were significantly higher in (juvenile) chub at the intermittent site, also indicating higher feeding activity. Furthermore, the decrease in the consumption of aquatic prey, possibly due to resource limitation at the intermittent site, was coupled with

an increase in terrestrial prey consumption. Generally, prey consumption is the result of a dynamic equilibrium between the energy required for the capture of prey and the benefit of its intake for the fish; thus, the shift at the intermittent Evrotas site, that is characterized by lower aquatic invertebrate availability, to higher terrestrial prey consumption, *i.e.* adult forms of aquatic prey, is maybe related also to their lower mobility and consequently to the lower energy required for their capture. Magalhães (1993) reported a seasonal switch to terrestrial prey consumption (Formicidae and dipteran adults) by roach and to temporarily abundant Ephemeropteran adults by chub, also attributed to fluctuations in aquatic invertebrate abundance and diversity. Overall, our results indicate that chubs at the intermittent site exhibited a feeding plasticity that enabled them to retain their body condition, as well as to increase both liver and gonad weight, as opposed to their counterparts in the perennial site. Similarly, though Santos *et al.* (2013) found no significant variation in the diet of the ruivaco *Achondrostoma oligolepis* (Robalo, Doadrio, Almada & Kottelat, 2005), a Portuguese endemic cyprinid, among three medium-sized rivers representing a gradient of temporality, they reported that the species' diet presented the highest seasonal variation in the intermittent Arunca River compared to the two other rivers. The opportunistic feeding behavior of cyprinids inhabiting highly fluctuating environments has been indicated by several studies, with resource limitation and interspecific interactions believed to shape fish diet during periods of food repression (Magalhães, 1993; Lobón-Cerviá and Rincón, 1994; Santos *et al.*, 2013).

In the current study, liver growth of females at the intermittent site was higher than their counterparts in the perennial site indicating more rapid growth, whereas gonad growth rate was higher at females of the perennial site, possibly reflecting the interplay between somatic and reproductive investment. The above support Spranza and Stanley (2000) postulation that areas with the largest environmental fluctuations may produce more robust individuals, and that at least some resident taxa have sufficient life history plasticity to exploit the opportunities generated by these environments. They contrast, however, to Rincón and Lobón-Cerviá (1989) findings that reported lower growth of red roach at the intermittent Duero tributary, as well as to those of Mas-Martí *et al.* (2010) that reported lower gonadal weight of chub and barbell inhabiting the intermittent Fuirosos

tributary. These may represent long-term adverse effects of intermittency, as opposed to our findings that indicate that the Evrotas chub compensate for lower trophic availability the period after the prolonged drought and prior to the species reproductive period with life history and trophic adaptations.

Finally, though chub abundances were similar in the two sites, chub population structure differed, with juvenile chubs being more abundant at the intermittent site; younger age classes of fish do tend to be more mobile, and repopulation after fish eradication has been noted to be accomplished primarily by immature individuals (Olmsted and Cloutman, 1974). Previous studies in the Evrotas basin have provided evidence of recolonisation of intermittent sites along the river's main stem mainly through downstream displacement and, also partially, by active movement from nearby perennial reaches, upon flow resumption (Skoulikidis *et al.*, 2011). In our intermittent site, however, recolonisation from downstream refugia is highly unlikely, due to the long distance (approx. 15 km) from the next downstream perennial section of the river (Skoulikidis *et al.*, 2011; Vardakas *et al.*, 2017) thus passive downstream displacement of mostly younger individuals appears to be the mechanism of recolonization of the intermittent site of the current study. The difference in the age structure of the two Evrotas populations may partly be responsible for the lower mean body length of fish from the intermittent site upon its recolonization after flow resumption. Similarly, Merciai *et al.* (2018) showed that two local cyprinids in the intermittent reaches of a Mediterranean stream were less abundant and with fewer large individuals.

## 5 Conclusions

The aim of the current study was to assess differences in condition and reproduction of a chub population inhabiting a perennial reach of a Mediterranean river ("source population") and of a population of colonizers at an adjacent intermittent reach, three months after flow resumption and prior to the species reproductive period. Our results indicate that life history and trophic adaptations of the colonizers seem to compensate, at least in the short term, for lower food availability at the intermittent reach. Though temporarily and spatially limited, our results are comparable to other studies using data obtained also during a single season (*e.g.* Oliva-Paterna *et al.*, 2003; Vasiliou and Economidis, 2005; Mas-Martí *et al.*, 2010). The current study highlights the resilience of a cyprinid species following a prolonged drought in a Mediterranean river; in conditions of lower aquatic food availability, chubs at the intermittent site exhibited, after flow resumption, higher somatic and reproductive investment compared to the perennial site, coupled to diet modification. Densities of the Evrotas chub were similar in the two sites, thus this higher investment could not be attributed to reduced intraspecific competition, though this cannot be excluded (Merciai *et al.*, 2018). The Evrotas chub appears to be relatively adapted to recurrent hydrological disturbance; however, under current climate change scenarios, the increased frequency and duration of drought events, combined with increasing anthropogenic water demand, could upset this precarious balance and reduce stream biota resistance and resilience to desiccation

(Filipe *et al.*, 2013). The resulting negative effects on both the macroinvertebrate fauna, as well as on stream fish distribution, community structure and life histories evidently will have important implications at the level of the management of these freshwater systems.

## Supplementary Material

Table S1. Relative abundance (%Ai) and biomass (%Bi) of the various aquatic macroinvertebrate categories.

The Supplementary Material is available at <https://www.kmae-journal.org/10.1051/kmae/2019015/olm>.

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