

Comparing fish assemblages and trophic ecology of permanent and intermittent reaches in a Mediterranean stream

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Abstract Mediterranean streams are characterised by seasonal droughts, the frequency and intensity of which vary spatially and are expected to increase with global change. We studied the potential effects of drought and climate change on the fish assemblage and its trophic ecology in a Mediterranean stream by comparing an intermittent tributary with two more permanent neighbouring reaches. Although the three sites were dominated by the same two fish species, Mediterranean barbel (*Barbus meridionalis*) and chub (*Squalius laietanus*), the intermittent tributary had a lower overall fish density and fewer eel (*Anguilla anguilla*). The intermittent tributary had macroinvertebrates with lower density, smaller taxa and higher

diversity. Fish in the intermittent tributary had significantly lower biomasses in their gut contents (adjusted for fish length) and more negative electivities than those in the permanent reaches, as well as significantly lower taxonomic diversity. These results indicate that there was reduced resource availability in the intermittent tributary, which resulted in significantly lower condition and gonadal weight (adjusted for length) of barbel and chub. The data obtained in this Mediterranean stream support the observation that reduced water flow may affect fish at both individual and assemblage levels.

Keywords Mediterranean streams · Intermittent stream · Drought · Fish condition · Diet · Resource availability

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Introduction

Mediterranean stream ecosystems are characterised by strong variations in stream flow and water temperature throughout the year (Gasith & Resh, 1999; Acuña et al., 2004). These streams also dry out, mostly often during the summer. Therefore, organisms in Mediterranean streams as well as other intermittent streams need to be adapted to highly variable physicochemical factors and biotic interactions (Williams, 1996). The severity of drought is an important determinant of the magnitude of these

environmental changes and thus the effects on the local biota (Golladay et al., 2004; Dewson et al., 2007). Flow decrease diminishes both wetted width and depth and consequently reduces habitat availability (Lake, 2003). In addition, habitat suitability may also be altered by reduced water velocity, increased sedimentation, lower resource availability, changes in nutrient concentrations, reduced dissolved oxygen levels or increased water temperatures (e.g. Butturini et al., 2003; Dewson et al., 2007). Drought can affect streams indirectly through effects on connected ecosystems such as riparian zones (Sabater et al., 2001; Acuña et al., 2005). Severe drought can cause local extinctions of the taxa unable to adapt to drought, either through behavioural or life-history strategies (Lytle & Poff, 2004), particularly if water flow is completely interrupted and the stream bed dries out completely.

In current predictions of climate change, both the intensity and frequency of droughts are likely to increase, reducing discharge in many European rivers (Arnell, 1999a, b; IPCC, 2007). Summer precipitation would decrease over Europe, the frequency, severity and duration of heat waves would increase (and consequently evapotranspiration), and therefore runoff would decrease. Overall, a 'mediterranealisation' of many temperate streams would occur (Arnell, 1999a, b; Giorgi et al., 2004; Beniston et al., 2007; IPCC, 2007). Since earlier and longer droughts may occur in the Mediterranean area (Beniston et al., 2007), the seasonal drought effects would be exacerbated, especially in small- and middle-sized streams. In these systems, permanent riffle habitats could dry in summer and intermittent reaches might dry out completely. These effects on riverine ecosystems may be worsened by increasing urbanisation and more intensive irrigation, as both would enhance water abstraction (Arnell, 1999a; IPCC, 2007; Sabater & Tockner, 2010). Temporality would thus extend from Mediterranean ecosystems to other temperate river systems. Therefore, understanding how the stream biota reacts to drought conditions is essential for predicting and mitigating potential effects of increasing water scarcity.

Flow intermittency affects fish populations in several ways (Matthews & Marsh-Matthews, 2003). During dry periods, fish are confined to refugia (i.e. pools), where they reach high densities. In these pools, abiotic (increased water temperature, reduced stream

flow and lower oxygen concentration) and biotic interactions (predation and competition for space and food) are intense (Spranza & Stanley, 2000; Lake, 2003; Magoulick & Kobza, 2003). However, the rapid recovery of populations after droughts (Gasith & Resh, 1999; Matthews & Marsh-Matthews, 2003; Vasiliou & Economidis, 2005) points out that many fish species may have developed adaptations to survive in such harsh ecosystems (Labbe & Fausch, 2000; Humphries & Baldwin, 2003). Nevertheless, the existence of behavioural, anatomical and physiological adaptations to small warm-water streams undoubtedly requires some energy investment (Grossman et al., 1998; Spranza & Stanley, 2000). Although adaptations may allow fish survival in these systems, they may not completely prevent fitness consequences (Lake, 2003).

Physiological stress resulting from harsher abiotic conditions or increased competition for resources (either habitat or food) should impact individual fish. Consequently, individuals in intermittent streams might present stress symptoms derived from their higher energy investment, such as a lower condition or reproductive success than others inhabiting permanent river systems. Increased drought frequency and intensity will produce negative effects on habitat quantity (i.e. the occurrence of smaller and shallower pools) and quality (increased temperature, reduced oxygen levels and changes in resource availability) and will thus reduce community stability and persistence (Magoulick, 2000; Oberdorff et al., 2001). Consequently, the effects on fish will increase with drought severity, and the time needed for communities to recover will be longer. Therefore, both the existence of fish adaptations and the severity of drought would determine the necessary time lag for fish to overcome the effects of drought.

A final effect on fish assemblages may be related to the quality and availability of prey under drought conditions. Similarly to fish assemblages, the macro-invertebrate community structure can recover rapidly from drought (Boulton, 2003; Lake, 2003). However, the extension of drought may influence community development during the following year. Surface water disappearance in intermittent streams represents a critical stage that negatively affects survival and next-year recruitment of taxa that have limited mobility, those whose aquatic stage is longer than 1 year, as well as those lacking desiccation-resistant stages (Boulton & Lake, 1992; Boulton, 2003; Acuña et al., 2005;

Bêche et al., 2006; Bêche & Resh, 2007). Compared to permanent rivers, intermittent streams have macroinvertebrate assemblages with lower densities, biomasses and productions, as well as smaller individuals for a given taxon and smaller-bodied taxa with shorter generation times (del Rosario & Resh, 2000; Muñoz, 2003; Halwas et al., 2005; Chadwick & Huryn, 2005, 2007; Bonada et al., 2007). Optimal foraging theory predicts that prey selection is determined by the relative profitability of particular types and sizes of prey (Pyke, 1984). Therefore, the effects of drought on macroinvertebrate fauna may reduce both optimal and overall prey availability, causing shifts in fish diets towards less nutritious prey.

Despite the existence of studies proving the effects of drought on fish populations and their rapid recovery, studies considering delayed effects (such as those arising from changes in food availability) are still rare (Matthews & Marsh-Matthews, 2003), particularly in Mediterranean streams (Magalhães et al., 2007). In this study, we aimed to compare the differences in fish condition and trophic ecology between an intermittent Mediterranean stream and neighbouring permanent reaches. The studied reaches supported the same native fish assemblage typical of the Mediterranean basin (Aparicio et al., 2000; Benejam et al., 2008). Although intermittent and permanent reaches differ in a number of factors, such as basin size, river flow, productivity and connectivity (Nilsson et al., 1994; Taylor et al., 1996; Bonada et al., 2006), comparing them provides large scale, realistic information on how natural or artificial droughts affect overall community structure and functioning. The study was conducted in the spring, a season that allowed maximum recovery from the preceding drought and that is the period prior to the start of the next seasonal drought. We hypothesised that stronger cumulative effects of drought in the intermittent stream would alter macroinvertebrate assemblages and thereby cause changes in fish trophic ecology as well as a reduction in the abundance and individual condition of fish.

Materials and methods

Study site

The study was performed in La Tordera and one of its tributaries, Fuirosos (NE Iberian Peninsula; Fig. 1).

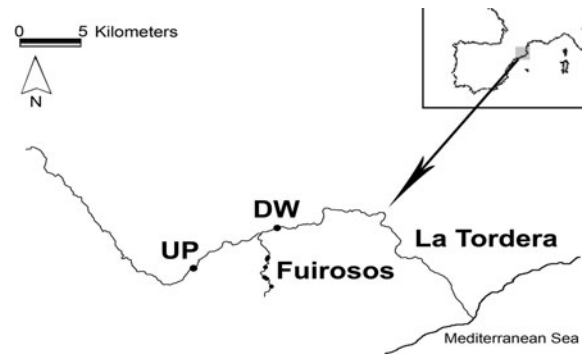


Fig. 1 Location of sampling sites (filled circle) at the mainstream, La Tordera, and its Fuirosos tributary

This catchment is characterised by a typical Mediterranean climate with mild, humid winters and warm, dry summers. Seasonal rainstorms occur during the autumn and spring, and they usually cause spates that increase stream base-flow. Summer drought can highly reduce stream flow, causing streambed drying in the Fuirosos tributary (Acuña et al., 2005; Benejam et al., 2008; Artigas et al., 2009). The study sites are <10 km apart within the Tordera catchment, and thus subject to very similar weather conditions. Therefore, differences in flow among sites were not caused by short term weather-related differences, but by differences in their drainage areas.

La Tordera drains a siliceous catchment with a total area of 895 km². The studied permanent reaches (UP and DW) are located midstream (Fig. 1). Land uses in the catchment are heterogeneous: while most headwater valleys (including Fuirosos subcatchment) are protected and remain forested with little human activity, the main valley plain is also occupied by both agricultural and urban areas. These activities diminish the water quality in the mainstream, mainly with respect to the high nutrient concentrations (Table 1).

During the study period, both streams were similar in habitat. All reaches alternated between riffles and pools and had similar substrate composition. Reaches were flanked by riparian vegetation, mainly hazel-nut (*Corylus avellana* L.), plane (*Platanus acerifolia* Aiton-Willd.) and cottonwood (*Populus* sp.). The mean stream width was 5.5–8 m in La Tordera and 3–5 m in Fuirosos. During the study period, none of the reaches were light limited since leaf emergence had not yet occurred. Differences in hydrology were remarkable, and the effect of summer drought

Table 1 Physical and chemical characteristics and fork length values from the fish captured at the sampling sites

	Fuirosos (F)	Tordera upstream (UP)	Tordera downstream (DW)
Sub-drainage area (km ²)	15.6	152.54	315.04
Flow (l s ⁻¹)			
Mean/median (range)	49.57/11.49 (0–5,000)	350/60 (0.005–9,690)	–
Physical and chemical characteristics			
Temperature (°C)	8.4	12.8	14.5
O ₂ (mg l ⁻¹) (%)	10.1 (90.6)	7.5 (87)	8.25 (80)
Conductivity (µS cm ⁻¹)	223	308	340
Phosphate (µg l ⁻¹)	3.76	340	340
NH ₄ ⁺ (µg l ⁻¹)	2.84	360	530
Mean fork length (mm) (range)			
<i>Barbus meridionalis</i>	86.81 (45–159)	92.17 (39–197)	82.83 (60–114)
<i>Squalius laietanus</i>	152.21 (86–246)	107.52 (54–252)	114.80 (71–154)

Physico-chemical data from Fuirosos corresponds to the sampling date, while data from La Tordera is the mean value from Spring 2007. The flow data from both streams correspond to the period of 2000–2009. The flow and chemical data from La Tordera were obtained from the Catalan Water Agency (<http://aca.gencat.net:2020/sdim/fillForm.do>)

on the remaining flow varied between the streams. Base-flow in the study sites in La Tordera ranged from 350 to 660 l s⁻¹ but could be highly reduced due to summer drought. Pool isolation does not occur within the reaches studied in La Tordera (Benejam et al., 2010), whereas the effects of summer drought on the Fuirosos hydrology were more severe. Base-flow in the study reaches (5–20 l s⁻¹) could be reduced to complete streambed drying in the Fuirosos, which can last from July/August to September/October (Sabater et al., 2001).

Field study

In spring 2007, we sampled two 100-m reaches in La Tordera, one upstream (UP) and another downstream (DW) from the confluence with Fuirosos (Fig. 1). Fish were sampled by electrofishing with a Smith-Root backpack engine (200–350 V, 2–3 A fully rectified triphasic DC). Due to low fish occurrence, six reaches (885 m in total) were sampled in Fuirosos (F) (Fig. 1) and they were used as replicates to estimate fish abundance but were pooled as a single sample for other statistical analyses. In the field, fish were preserved on ice to avoid digestion of the gut contents and were later frozen in the laboratory. Subsequently, they were measured (fork and total lengths to the nearest 0.5 mm), eviscerated, sexed

and weighed (total, eviscerated and gonadal weight to the nearest 0.1 mg), and the entire gut was preserved in 70% alcohol until analysis. Gut contents were examined under a dissecting microscope. All the prey present in the gut were sorted, usually to the family level, counted, and a minimum of 30 individuals (if available) of each prey taxon were measured with an ocular micrometer. Measurements were converted to dry mass according to published length–dry mass relationships (mainly Meyer, 1989; Stead et al., 2003). Other food categories (e.g. detritus and plant debris) were dried until constant weight and weighed to the nearest 0.1 mg.

Quantitative samples of benthic macroinvertebrates were also taken from the different sites. We took three replicate samples from riffles and pools at the two sites in La Tordera using a 0.1-m² and 250-µm mesh size surber. In Fuirosos, five samples were taken from the dominant substrates, leaves (which accumulated in pools) and rock substrata (dominant in riffles) in two of the study reaches. A cylinder of 115 cm² was used to sample leaf substrata. Entire cobbles were sampled, and the surface area was calculated after an empirical relationship using the three maximum dimensions of the cobbles (Acuña et al., 2005). All samples were sieved through a 250-µm sieve and immediately fixed in 4% formalin. The differences in macroinvertebrate sampling

methods were motivated by the need to maximise sampling efficiency given the different hydraulic conditions of the streams. In the laboratory, organisms were sorted and usually identified to the genus or species level under a dissecting microscope. Benthic macroinvertebrate biomass was obtained following prey biomass measurements (see above).

Data analysis

Differences between sites in total macroinvertebrate density, biomass and individual weights were analysed by means of one-way analyses of variance (ANOVA) and differences between sites controlling for taxon with a two-way ANOVA (with taxon and site as factors). Quantitative variables were log-transformed for the analyses to improve the homoscedasticity and linearity of the data. Macroinvertebrate diversity was assessed using Simpson's index (D):

$$D = \sum_i \frac{n_i(n_i - 1)}{N(N - 1)},$$

where n_i is the number of individuals of macroinvertebrate type i and N is the total number of macroinvertebrates (Hurlbert, 1971).

Differences in fish assemblage composition among the three sites were tested by a χ^2 test of independence. Differences in overall density and mean length of the fish species between sites were also analysed by one-way ANOVA. Analysis of covariance (ANCOVA) was used to compare fish weight, gonadal weight and ingested gut biomass between the sites, using fish length as a covariate. Differences in mean prey weight between the sites were also analysed with ANCOVA, using fish length as a covariate. We started with the most complex model, introducing all possible interactions (including interactions of covariates and factors, following García-Berthou & Moreno-Amich, 1993). The general linear model was then simplified by removing non-significant interactions ($P > 0.10$). When the covariate was not significant, it was also removed from the model and ANOVA was used. All factors were considered as fixed effects.

We also measured diet diversity (for each fish) using Simpson's index. In order to compare diet composition versus resource availability, we used

Vanderploeg & Scavia's (1979) relativised electivity index (E^*):

$$E_i^* = \frac{W_i - (1/N)}{W_i + (1/N)}; \quad \text{where} \quad W_i = \frac{r_i/p_i}{\sum r_i/p_i},$$

where r_i is the relative abundance of prey i in the diet, p_i is the relative abundance of prey i in the environment and N is the number of prey types included in the analysis. This index ranges from +1 (positive selection or preference for a certain prey type in relation to its abundance or availability in the environment) to -1 (negative selection or avoidance of a certain prey consumption); values near zero indicate neutral electivity. The E^* index was arcsine transformed ($\arcsin \sqrt{[(E_i^* + 1)/2]}$) for statistical analysis, as the homoscedasticity and normality were clearly improved. To test whether electivity significantly deviated from 0, a one-sample Student's t test was used. Both electivity and diet diversity were further analysed with ANCOVA (see above), using fish length as a covariate.

The statistical analyses of fish data follow our previous work (e.g. García-Berthou & Moreno-Amich, 2000; Alcaraz & García-Berthou, 2007) and focused on the two most abundant species, *Barbus meridionalis* (Risso) and *Squalius laietanus* (Doadrio, Kottelat & de Sostoa), which are also dominant in middle reaches throughout NE Catalonia (Aparicio et al., 2000). All statistical analyses were performed with SPSS 15.

Results

Environmental conditions in streams

The different location of the studied reaches within the catchment resulted in large differences in their drainage areas (10 and 20 times larger in UP and DW than F, respectively). Consequently stream flow was 86% lower in F than in UP. Different predominant land uses at the studied sites were probably related to physico-chemical parameters in the reaches. Higher oxygen concentration, as well as lower temperature and conductivity characterised the intermittent stream, which is forested and located in a natural reserve (Table 1). The largest differences between sites corresponded to their nutrient concentrations,

phosphorus being 90 times lower, and ammonia 120–185 times lower in Fuirosos than in the others.

Structure of the fish assemblage

The fish assemblages in all the sites were dominated by the Mediterranean barbel (*Barbus meridionalis*) and chub (*Squalius laietanus*). However, there was a significant variation in species composition ($\chi^2_6 = 50.3$, $P < 0.0005$) between the sites. Eels (*Anguilla anguilla* L.) were less abundant in the intermittent stream, and minnows (*Phoxinus sp.*) were only present in the UP site (Fig. 2). Single individuals of common carp (*Cyprinus carpio* L.) and largemouth bass (*Micropterus salmoides* (Lacepède)) were detected in the intermittent stream. The total fish density was significantly greater in permanent sites than in the intermittent site (ANOVA using the different transects in Fuirosos as replicates; $F_{2, 9} = 9.41$, $P = 0.006$, Fig. 2).

The mean lengths for most of the fish species were similar between the sites (ANOVAs, $P > 0.05$), except chub which were larger in the intermittent stream ($F_{2, 87} = 14.36$, $P < 0.0005$) (Table 1). The condition (ANCOVA of total weight with length as a covariate) of the barbel was significantly lower in the intermittent stream for both male and female individuals (Table 2). The condition of the chub was significantly lower in intermittent stream (Fig. 3). The same patterns in condition were observed when eviscerated weight was used instead of total weight.

The gonadal weight (adjusted for length with ANCOVA) of the chub was the lowest in individuals

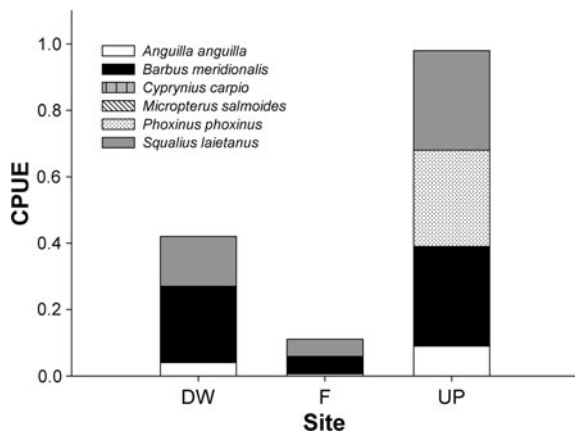


Fig. 2 Catch per unit effort (CPUE, individuals per meter of electrofishing transect) of fish at the three sampling sites

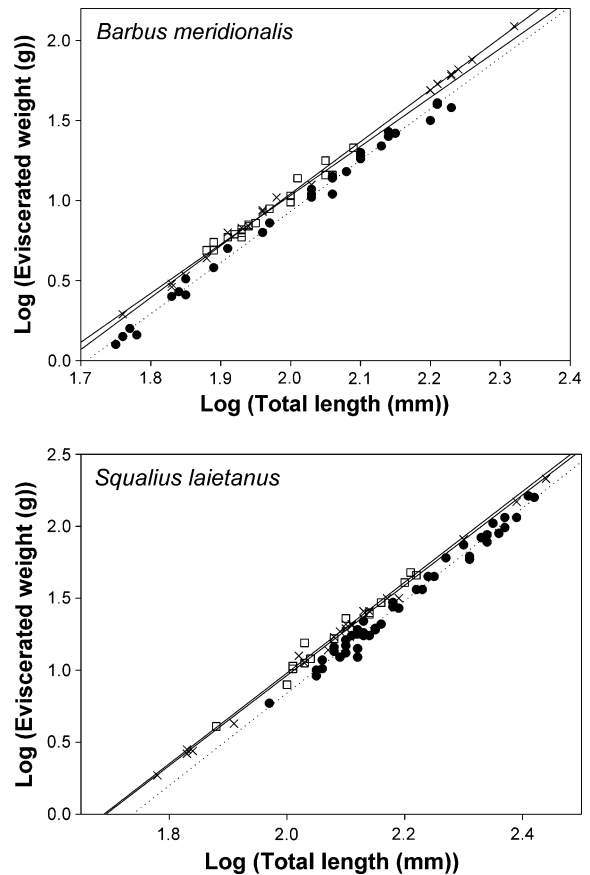


Fig. 3 Eviscerated weight–length relationship (log scales) of barbel (top) and chub (bottom) for the F (filled circle), DW (open square) and UP (times) sites. Linear regressions are shown for each site: for barbel, the r^2 were 0.994, 0.966 and 0.997 at F (dotted line), DW and UP, respectively; for chub, the respective r^2 were 0.987, 0.978 and 0.995

from the intermittent stream, especially in the females (Table 2, Fig. 4). Lower gonadal weights were also found in male barbels from Fuirosos (Table 2, Fig. 4). Barbel females were too scarce for analysis. The total biomass of material in guts (adjusted for fish length with ANCOVA) was significantly lower in fish from Fuirosos than in those from La Tordera. This was true both for barbel and chub (Table 2, Fig. 5).

Resource availability

Although the total macroinvertebrate density did not differ significantly between the sampling sites (ANOVA, $F_{2, 29} = 2.16$, $P = 0.13$), the overall densities at the UP and DW sites were, respectively, 39.0

Table 2 Analyses of covariance of total, eviscerated and gonadal weight and total gut biomass with site and sex (factors) and fish length (covariate)

	Site			Sex			Site × sex			Log (total length)		
	df	F	P	df	F	P	df	F	P	df	F	P
<i>Barbus meridionalis</i>												
Total weight	2, 63	3.218	0.047	1, 63	5.584	0.021	1, 63	11.688	0.001	1, 63	1784.83	<0.001
Eviscerated weight	2, 62	1.831	0.169	1, 62	4.65	0.035	1, 62	6.796	0.011	1, 62	2199.62	<0.001
Female gonadal weight	1, 16	1.309	0.269	–	–	–	–	–	–	1, 16	16.116	0.001
Male gonadal weight	2, 47	10.61	<0.001	–	–	–	–	–	–	1, 47	27.126	<0.001
Total gut biomass	2, 472	25.026	<0.001	–	–	–	–	–	–	1, 472	62.97	<0.001
<i>Squalius laietanus</i>												
Total weight	2, 76	72.812	<0.001	1, 76	0.311	0.578	1, 76	0.986	0.986	1, 76	5124.776	<0.001
Eviscerated weight	2, 77	73.038	<0.001	1, 77	2.384	0.127	1, 77	0.035	0.852	1, 77	6026.533	<0.001
Female gonadal weight	1, 35	5.097	0.03	–	–	–	–	–	–	1, 35	257.497	<0.001
Male gonadal weight	2, 38	3.082	0.058	–	–	–	–	–	–	1, 38	145.666	<0.001
Total gut biomass	2, 437	81.598	<0.001	–	–	–	–	–	–	1, 437	55.961	<0.001

All quantitative variables were log₁₀ transformed

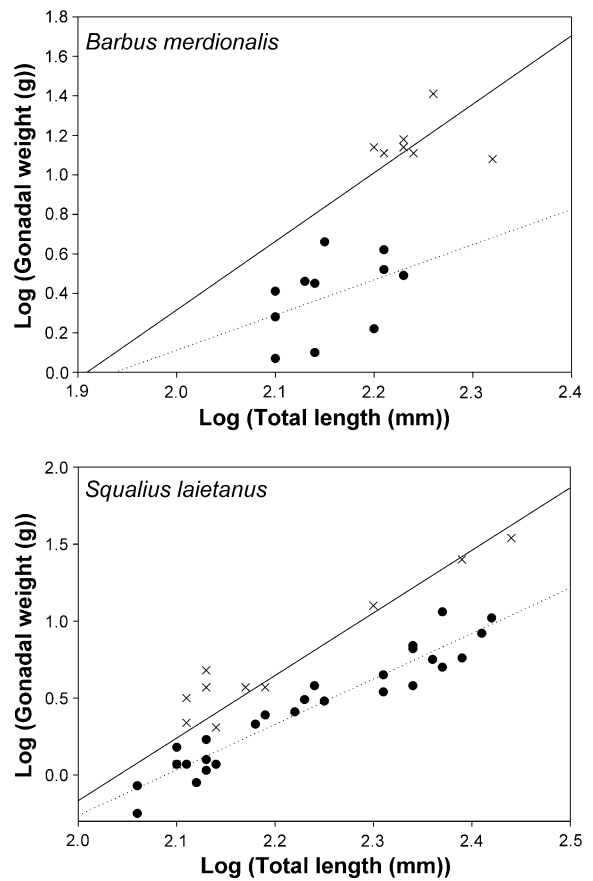


Fig. 4 Gonadal weight–length relationship (log scales) of female barbel (top) and chub (bottom) for the F (filled circle) and UP (times) sites. No female individuals for these species were found in DW. Linear regressions are shown for each site: for barbel, the r^2 were 0.183 and 0.855 at F (dotted line) and UP, respectively; for chub, the respective r^2 were 0.913 and 0.925

and 50.6% higher than those in the intermittent stream (Fig. 6). Similarly, the macroinvertebrate biomass was lower in the intermittent stream, despite differences only being significant between the F and DW sites (Fig. 6, ANOVA, $F_{2, 29} = 12.1, P < 0.0005$). Moreover, an analysis of taxonomic groups showed significant differences in both density and biomass among the sites (two-way ANOVA, $F_{100, 1473} = 13.0, P < 0.0005$ and $F_{90, 1334} = 12.0, P < 0.0005$, respectively). Oligochaeta and especially baetid ephemeropterans were more abundant in the permanent reaches, while chironomid larvae dominated in Fuirosos.

The highest contribution to the biomass in the permanent sites was derived either from ephemeropteran larvae or from the crustacean isopod

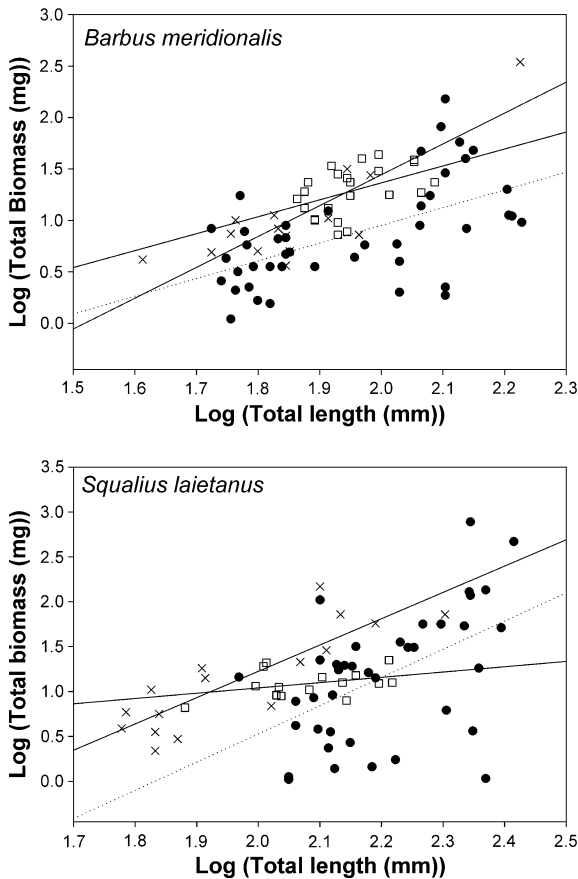


Fig. 5 Total biomass in the gut–length relationship (log scales) of barbel (top) and chub (bottom) for the F (filled circle), DW (open square) and UP (times) sites. Linear regressions are shown for each site: for barbel, the r^2 were 0.315, 0.213 and 0.709 at F (dotted line), DW and UP, respectively; for chub, the respective r^2 were 0.259, 0.139 and 0.720

Proasellus sp., which was only present in the permanent sites. Terrestrial invertebrates were also important in terms of biomass in the permanent site, UP. Despite the lower mean biomass per macroinvertebrate individual in Fuirosos (Table 3), differences were not significant between the sites

Table 3 Weight of macroinvertebrate individuals and overall macroinvertebrate diversity (Simpson’s index) found at the three sampling sites

Site	Macroinvertebrate weight (mg)			Macroinvertebrate diversity (<i>D</i>)	
	Mean	SEM	Range (minimum–maximum)	Mean	SEM
F	0.87	0.18	(2.13×10^{-5} –14.9)	0.86	0.01
Dw	2.80	0.63	(1.50×10^{-6} –40.5)	0.84	0.01
Up	1.41	0.43	(9.85×10^{-4} –24.9)	0.79	0.03

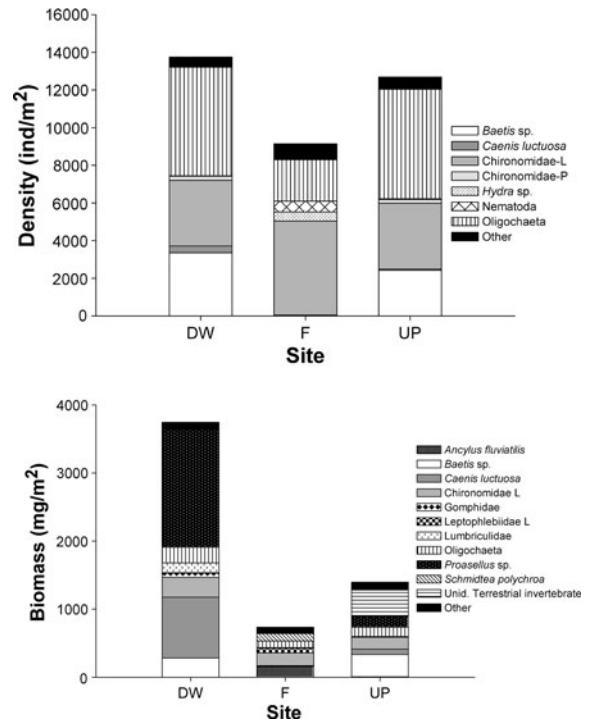


Fig. 6 Mean macroinvertebrate density (top) and biomass (bottom) at the three sampling sites. L = larvae, P = pupae, A = adult, Unid = unidentified. Taxa that accounted for <1% of the total density or biomass have been pooled into ‘Other’

(ANOVA, $F_{2, 403} = 0.199$, $P = 0.820$). Small-sized individuals were present in the two streams, although the largest individuals were found in La Tordera (Table 3). The macroinvertebrate diversity (Simpson’s index) was significantly higher in Fuirosos than in the other sampling sites ($F_{2, 8} = 5.32$, $P = 0.034$; Table 3).

Trophic ecology

Overall, the diet diversity in both barbel and chub did not significantly depend on fish length (ANCOVA,

$F_{1, 67} = 3.21$, $P = 0.078$) and was significantly lower in the intermittent stream (ANOVA, $F_{2, 79} = 7.10$, $P = 0.001$ and $F_{2, 67} = 8.45$, $P = 0.001$ for barbel and chub, respectively; Fig. 7). The mean prey electivity was not significantly related to barbel length (ANCOVA, $F_{1, 1710} = 1.26$, $P = 0.261$) and did not differ significantly between the sites (ANOVA, $F_{2, 1711} = 1.96$, $P = 0.14$), although the mean value was lowest in the intermittent stream (Fig. 8). Similarly, the electivity in chub showed no significant relation to fish length (ANCOVA, $F_{1, 1516} = 0.85$, $P = 0.357$) and was significantly lower in Fuirosos (ANOVA, $F_{2, 1517} = 22.40$, $P < 0.0005$; Fig. 8). At all the sites, fish showed significantly negative mean electivities (t tests, $P < 0.001$) for benthic macroinvertebrate

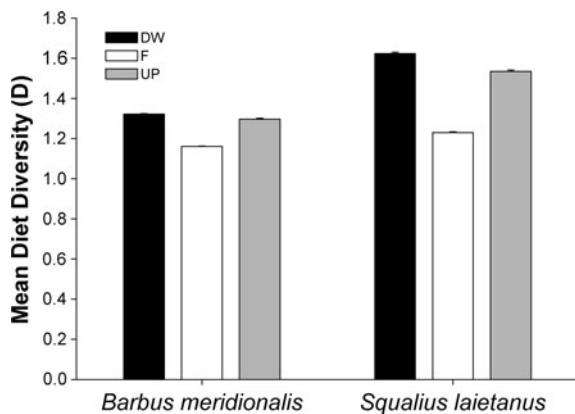


Fig. 7 Mean diet diversity (Simpson's index) for barbel and chub at the three sites. Error bars show the standard error

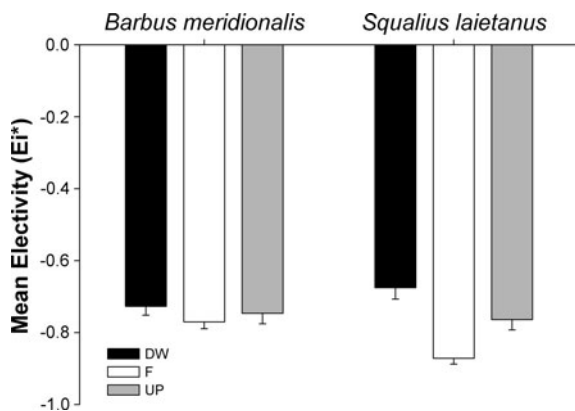


Fig. 8 Mean electivity values (Vanderploeg and Scavia's index) by number for barbel and chub at the three sampling sites. Error bars show the standard error

species, indicating that the consumption of most of the potential prey was avoided. Barbel and chub mainly fed on detritus and chironomid larvae in both streams. However, a higher proportion of ephemeropterans, *Proasellus* and prey from terrestrial origin were also found in the guts of the permanent stream fish.

Despite the lower mean electivity in Fuirosos, the mean prey weight for prey consumed by the barbel was higher in Fuirosos (ANCOVA, $F_{2, 282} = 4.07$, $P = 0.018$) ($1.42 \text{ mg} \pm \text{SD} = 6.38$) than in La Tordera ($0.72 \text{ mg} \pm \text{SD} = 1.21$ and $0.62 \text{ mg} \pm \text{SD} = 1.87$ for the DW and UP sites, respectively). However, these differences were not statistically significant for chub (ANCOVA, $F_{2, 187} = 0.54$, $P = 0.58$), probably due to the high variability in the mean prey weight caused by the occasional presence of large prey such as salamanders or Oligochaeta (Lumbricidae). The mean prey weight increased significantly with fish size in both barbel and chub at all sites (ANCOVA, $F_{1, 282} = 4.51$, $P = 0.035$ and $F_{1, 187} = 6.87$, $P = 0.009$ for barbel and chub, respectively).

Discussion

Comparing intermittent and permanent reaches

The effects of natural- or human-induced reduction on water flow and fish communities were analysed by comparing two permanent reaches and a neighbouring intermittent tributary. The analysis assumed that a permanent reach would turn into intermittent because of hydrological alterations as a result of climate change or water withdrawal. All the reaches supported the same autochthonous Mediterranean fish assemblage, and were close enough to minimise climatic and geologic differences between them. There were substantial differences in fish condition and trophic ecology between the fish communities in the intermittent Mediterranean stream and those in the neighbouring permanent reaches. The intermittent stream had lower water flow and dried up in summer with only a few pools remaining. This stream also had lower drainage area, temperature or nutrient concentrations (Table 1). These differences result from the covariance of many abiotic factors along environmental gradients in rivers. Intermittent tributaries occur at higher altitude, show lower temperature, conductivity, and nutrients, and have lower

hydraulic connectivity than perennial streams (e.g. Nilsson et al., 1994; Taylor et al., 1996; Ostrand & Wilde, 2002; Bonada et al., 2006).

Although differences in fish community could be related to drought intensity, alternative hypothesis such as the relevance of decreased habitat or nutrient availability for fish in the intermittent reaches cannot be ruled out as regulating factors. Even though the specific mechanisms that cause the observed differences between the permanent and intermittent reaches are ambiguous and would require of an experimental approach, the comparative results benefit from the large scale and realism of observational studies (Keddy, 1989) and results are consistent with changes expected from drought stress.

Differences in the fish assemblage

Fish density was significantly lower in the intermittent stream, even well after drought had ceased. Davey & Kelly (2007) and Magalhães et al. (2007) found that fish density declined with decreasing flow permanence. Fish population recovery depends on the rate and extent of recolonisation from refugia upon rewetting, the distance from refugia, and the species-specific behaviour (Magoulick & Kobza, 2003; Davey & Kelly, 2007; Albanese et al., 2009). We could not isolate water intermittency as the only cause of diminished fish density in the intermittent stream. However, a previous study in Fuirosos (Aparicio & Vargas, 2004) found that despite the availability of long reaches that were suitable for colonisation, there was no significant expansion of the fish population during the wet period after drought. That study highlighted that although the fish population started to recover during the flow period, the recovery was interrupted by the arrival of a new summer drought. Periods between droughts were insufficiently long for the fish population to recover from disturbance, causing the fish density to remain low. It might be assumed that greater effects on fish populations can be expected (Nicola et al., 2009) if more intense and frequent droughts occur in the future. Fish are long-lived organisms that are sensitive to variations in the intensity, frequency and timing of drying. Fish may show a decrease in survival rates due to mismatches between life-history adaptations (e.g. spawning and hatching periods) and the intervals in water flow.

Differences in species composition between the intermittent and the permanent sites were not due to the most abundant species (Mediterranean barbel and chub), but were due to the presence of minnows in one of the permanent sites and, secondarily, to the lower density of eels in the intermittent stream. These results contrast with others, which found similar fish species composition during and after a drought period (Matthews & Marsh-Matthews, 2003; Aparicio & Vargas, 2004; Magalhães et al., 2007). Our results may be partly explained because the minnow is an introduced species in La Tordera that has expanded in recent years (Benejam et al., 2010) but has not yet reached Fuirosos. The long-lasting disconnection between the intermittent and the permanent streams would have impeded eel migration upstream towards Fuirosos.

We observed lower fish condition (chub, barbel) in the intermittent stream than in the permanent reaches. These results are consistent with others that observed that fish condition decreased with either lower flow or intermittent waters (Torralva et al., 1997; Vila-Gispert & Moreno-Amich, 2001; Oliva-Paterna et al., 2003; but see Spranza & Stanley (2000) for the opposite pattern). Our results also show that the minimum summer flow values do not only affect fish autumnal condition (Oliva-Paterna et al., 2003; Vasiliou & Economidis, 2005), but also effects of seasonal drought prevail until the following spring. Therefore, despite the initial recovery in fish condition in autumn (Oliva-Paterna et al., 2003; Vasiliou & Economidis, 2005), the repeated seasonal drought in Mediterranean regions prevents the complete recovery of fish condition in the favourable wet period that precedes the subsequent drought.

Even though the major resource allocation for reproductive strategies is a plausible cause for the reduction in fish condition (Aparicio & de Sostoa 1998; Oliva-Paterna et al., 2003), as the lower gonadal weight-length relationship obtained in the intermittent stream suggests, reproduction investment may not be the only cause of lower fish condition. Low flow periods lead to decreased fecundity and shorter reproductive period in barbel (Aparicio & de Sostoa 1998). Similarly, recruitment can fail in dry years (Magalhães et al., 2003, 2007; Matthews & Marsh-Matthews, 2003) even if high levels of reproduction occur during an unusually high-flow year (Labbe & Fausch, 2000; Lake, 2003). Drought may cause delayed

reproductive effects on fish assemblages, leading to lower abundance in the following year (Matthews & Marsh-Matthews, 2003). Moreover, if drying occurs annually (which is the case for Mediterranean streams), droughts may have cumulative effects expressed in low fish densities and limited population recovery. Because a higher investment in reproduction was not causing the lower fish condition in the intermittent stream, indirect mechanisms must be responsible, at least to some extent, for the low condition.

Stream size differed among permanent and intermittent reaches, the former being ~ 1.7 times wider than the latter. Although such a difference did not result in different habitat availability among reaches during the study period, it could have an indirect effect through increased drought intensity in the intermittent stream. Smaller streams are more prone to flow fluctuations (Medici et al., 2008), and susceptible to suffer more severe droughts (Sabater & Tockner, 2010). Fuirosos experienced pool disconnection and almost complete bed drying (Acuña et al., 2005), while a decreased water flow during the dry season was never intermittent in La Tordera reaches. Intermittent streams experience reduced habitat availability and suitability (Lake, 2003; Dewson et al., 2007) under drought, which might have negative effects on fish condition.

The increased fish condition in the permanent reaches could also respond to the higher nutrient availability in these reaches. Whole stream fertilization resulted in increased fish and insect growth via autochthonous primary production (Deegan & Peterson, 1992; Peterson et al., 1993). However, effects on insect secondary production were only important for some grazers (the caddisfly *Brachycentrus* and the mayfly *Baetis*) and were not general to the overall insect community (Peterson et al., 1993). Deegan et al. (1997) also observed that stream nutrient addition caused a fivefold increase in chlorophyll levels but not to total insect abundance, fish growth being more related with per capita insect availability than with per capita algal standing stock. Neither whole stream fertilization experiments conducted in Fuirosos intermittent stream had bottom-up effects in its detritus based food web (Sabater et al., 2005). Although higher macroinvertebrate density and biomass could result from flow permanence (del Rosario & Resh, 2000; Muñoz, 2003; Halwas et al., 2005) and nutrient availability (Cross et al., 2006), macroinvertebrates from intermittent streams possess life traits

that enable them to cope with streambed drying (Bonada et al., 2007).

Trophic ecology: effects of drought through food availability

There was a lower macroinvertebrate density and biomass in the intermittent stream, as well as a lower abundance of the more frequently consumed prey items in the permanent river. These patterns of lower macroinvertebrate densities and biomass in intermittent streams and after severe droughts have been described elsewhere (Feminella, 1996; Gasith & Resh, 1999; del Rosario & Resh, 2000; Muñoz, 2003; Acuña et al., 2005; Halwas et al., 2005; Bêche et al., 2006). In addition, macroinvertebrate taxa were generally smaller in the intermittent reach (e.g. *Oulimnius* and chironomid larvae, nematodes and *Hydra* sp.) than in the permanent ones (e.g. baetid larvae, *Proasellus* and lumbriculids). This finding is consistent with the observations of Chadwick & Huryn (2007). The combination of the small size and the lower density of invertebrates likely indicate resource limitation for predators (Zaret & Rand, 1971; Oliva-Paterna et al., 2003; Nunn et al., 2007). This possibility was confirmed by the lower ingested biomass in guts of both barbel and chub from the intermittent stream.

Proasellus individuals were only found in the permanent reaches, and their absence in the intermittent stream might be due to the life-history traits. *Proasellus* lacks aerial stages, and its life-cycle lasts for more than a year (Tachet et al., 2000); streambed drying would have excluded them from the intermittent stream. This taxon was an important prey item as indicated by their high biomass in the fish gut contents. Confounding effects derived from increased nutrient availability in the permanent reaches on macroinvertebrate structure cannot be ruled out. However, the indirect effects of drought (i.e. elimination of certain prey) are certainly likely determinants for the diminished fish condition in the intermittent reach.

Although macroinvertebrates had the highest diversity in the intermittent stream, fish diets were the least diverse, suggesting that many of the potential trophic resources available were not actually used by the fish. Despite mean electivity indices being negative in the permanent and intermittent

streams, the lower values in the latter indicate that fish either rejected more food categories or that they had a lower ability to select the available prey.

Rapid changes in macroinvertebrate abundance follow changes in habitat, food or hydrologic disturbance (Bêche & Resh, 2007). However, seasonal droughts will also affect assemblage composition. Increased consumer effects with longer drought duration (Ludlam & Magoulick, 2009) suggest that the increased drought duration and intensity resulting from global change may increase pool isolation and streambed drying. There is therefore a hydrological threshold for some invertebrate species, either directly, through a mismatch between species life-cycle and hydrology (Lytle & Poff, 2004; Statzner et al., 2004), or indirectly, through increased competition for resources or predation.

In the predicted scenarios of climate change, with reduced summer precipitation and increased temperatures over Europe, droughts in Mediterranean regions are expected to start earlier in season and increase in duration (Beniston et al., 2007). Direct pressures of climate change on river intermittency will probably be exacerbated by human water demand (Arnell, 1999a; Benejam et al., 2010), and therefore many permanent streams could become more intermittent. The observed differences between intermittent and permanent streams provide insight about larger-scale impacts of global change on the inhabiting biota. In this study, the intermittent reach exhibited a significantly lower fish density, as well as reduced condition and reproductive investment, than the permanent river reaches. Further, there was lower prey availability and significantly lower food biomass in the gut of fishes inhabiting the intermittent stream. Diminished prey availability may be responsible for the lower fish condition in the intermittent stream. Therefore, not only would the direct effects of drought on fish condition be important, but also the indirect bottom-up effects resulting from changes in resource availability and suitability.

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