Environmental changes in a Mediterranean river: implications for the fish assemblage

Javier Sánchez-Hernández[1*] and Andy D. Nunn[2]

[1]Department of Zoology and Physical Anthropology, Faculty of Biology. University of Santiago de Compostela. Campus Sur s/n, 15782 Santiago de Compostela, Spain

[2]Hull International Fisheries Institute, School of Biological, Biomedical and Environmental Sciences, University of Hull, Hull, UK

Javier Sánchez-Hernández (javier.sanchez@usc.es)

Andy D. Nunn (a.d.nunn@hull.ac.uk)

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[*]Author to whom correspondence should be addressed. Tel.: +34 630 156 186; e-mail: javier.sanchez@usc.es

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Abstract

This study examined the impacts of climate change on hydrology and fish population dynamics in a river in central Spain. The objectives were to: (i) contextualise long-term trends in the hydrology (1943–2012) and climate (1985–2011) of the study area, and (ii) identify the environmental factors driving fish population dynamics (1998–2012). Air and water temperatures progressively increased over the study period, whereas there were substantial reductions in mean spring river discharges but increases in peak-flow discharges during the spawning and early larval period of endemic cyprinids in recent decades. In particular, the changes in spring river discharges could have fundamental implications for the future status of the endemic cyprinids because this study revealed a positive influence of stable and low flow conditions during the spawning and early larval period (in late spring) on recruitment success (young-of-the-year densities). The density of young-of-the-year *Salmo trutta* appeared most influenced by flow conditions during fry emergence and the early larval period (in early spring), with the highest densities associated with low peak-flow hydrological pulses. Overall, fish abundances were significantly influenced by the frequency and duration of high and low hydrological pulses, but there were interspecific and ontogenetic differences in their influence. We conclude that although it is widely accepted that global warming should favour cyprinid over salmonid species, future shifts in hydrology due to climate change could negatively affect some cyprinids, including endemic species.

Keywords: abundance, endemic species, flow, threatened species, water temperature, climate change

Introduction

The study of changes in the fish assemblages of freshwater systems has received considerable attention over the last two decades. Fish communities are structured by a wide range of abiotic factors, including water quality, physical habitat and hydrological regime (e.g. Jackson *et al*. 2001; Bernardo *et al*. 2003; Kiernan and Moyle 2012), as well as biotic factors, such as density-dependent mechanisms, intra- and interspecific competition and predator-prey interactions (e.g. Abrams 2000; Forrester *et al*. 2006; Vincenzi *et al*. 2012). Thus, fish population dynamics in the wild are established as a consequence of the interactions among biotic and abiotic factors.

Of all these factors, water temperature and hydrology have been considered as key variables affecting the dynamics of fish populations (e.g. Elliott 1994; Taniguchi *et al*. 1998). Water temperature may affect fish directly, through its effects on survival, feeding and growth, or indirectly, through its effects on both prey and predator populations (e.g. Elliott 1994). Overall, the negative effects of temperature increases on fishes are well documented and much attention has been paid by many researchers (Elliott and Elliott 2010 and references therein). High water temperatures and low dissolved oxygen during summer droughts are pivotal factors in fish summer survival (e.g. Closs and Lake 1996; Matthews and Marsh-Matthews 2003). In addition, interannual differences in river discharge during fish hatching may cause variations in recruitment success, and thereby in fish population dynamics (e.g. Cattanéo *et al*. 2002; Nunn *et al*. 2007; Cowx *et al*. 2012). The effects of flow conditions may vary among sympatric species, for example some cyprinids are vulnerable to droughts, whereas others are more sensitive to floods (Magalhães *et al*. 2007). Similarly, Cattanéo *et al*. (2001) found that high flow conditions during the spawning period could lead to an increase in the abundance of some cyprinid species, but a decrease in other sympatric cyprinids. Most

studies in running waters have examined the influence of flow and temperature on fish growth and recruitment success, but few have assessed their influence on the density and size structure of fish assemblages. However, shifts in both flow conditions and water temperatures through climate change will produce a scenario in which it is reasonable to expect that some fish species will be negatively affected, whereas others, such as warm-water species at high latitudes or altitudes, could be enhanced.

Substantial changes in both flow conditions and water temperatures are predicted to occur in the next few decades as a consequence of climate change (e.g. Gómez-Navarro *et al*. 2011; Vautard *et al*. 2014), and it is expected that freshwater fish assemblages will undergo considerable changes in structure and diversity as a result (e.g. Tisseuil *et al*. 2012; Buisson *et al*. 2013; Tedesco *et al*. 2013). Fish have species-specific optimal and tolerance ranges (Matthews and Maness 1979; Beitinger *et al*. 2000), and climate change scenarios predicting higher water temperatures in the future are likely to give an advantage to thermophilic species, such as some cyprinids, in comparison with salmonid species (e.g. Daufresne *et al*. 2003; Matulla *et al*. 2007; Almodóvar *et al*. 2012). It should be noted, however, that the majority of studies on the impacts of climate change on fishes have focused on salmonids as model species (e.g. Jonsson and Jonsson 2009; Elliott and Elliott 2010; Santiago *et al*. 2016), and that little is known about the possible effects on cyprinids –the largest vertebrate family in the world– because how most species will respond to new environmental conditions is unknown (Jackson and Mandrak 2002; Daufresne *et al*. 2003; Graham and Harrod 2009; Nunn *et al*. 2010).

A particular concern for the Mediterranean region is the lack of information on the possible consequences of climate change for endemic cyprinid populations (see Magalhães *et al.* 2007; Tedesco *et al.* 2013), even though warming predictions under climate change in this region are well documented (Giorgi and Lionello 2008 and references therein). As a consequence of climate change, Mediterranean rivers are suffering important reductions in winter and spring river discharges, but also increases in peak-flow discharges in recent decades because of extreme weather events (e.g. Zanchettin *et al.* 2008; Morán-Tejeda *et al.* 2010). This is important because some endemic fish species are already under immediate threat of extinction (Freyhof and Brooks 2011), which could be exacerbated by changes in hydrology. Indeed, a recent study predicted a significant increase in fish extinctions in Mediterranean rivers due to climate change, and that such regional extinctions will involve a global net biodiversity loss because riverine fish assemblages in those territories are characterized by a high level of endemism (Tedesco *et al.* 2013 and references therein).

This study examined the impacts of climate change on hydrology and fish population dynamics in a Mediterranean river. The objectives were to: (i) contextualise long-term trends in the hydrology and climate of the study area, and (ii) identify the environmental factors driving fish population dynamics. The rationale was that the effects of climate change on water temperature and hydrology (e.g. Zanchettin *et al.* 2008; Vautard *et al.* 2014) could have adverse implications for fish population dynamics, especially of endemic species. The hypotheses were thus that: (i) environmental conditions have changed in recent decades due to climate change, and (ii) changes in fish population dynamics can be explained by shifts in environmental variables, particularly during egg incubation and the early larval period. The possible implications of environmental changes for fish assemblages in Mediterranean

climate regions (i.e. areas surrounding the Mediterranean Sea and parts of America, Australia, Africa and Asia) are discussed.

Materials and methods

Study area

The study area was located in the headwater of the Tormes basin, central Spain (Figure 1). The area has a typically continental Mediterranean climate, with extreme differences between temperatures in summer and winter. The hydrology is characterised by a snow–rainfall regime, with the highest annual flows occurring during spring (Ceballos-Barbancho and Morán-Tejeda 2006), and there are no significant flow regulation structures (Alonso-González *et al*. 2008). The fish community is composed by native fish species: brown trout *Salmo trutta* L. (hereafter trout), northern straight-mouth nase *Pseudochondrostoma duriense* (Coelho, 1985) (hereafter nase), northern Iberian chub *Squalius carolitertii* (Doadrio, 1988) (hereafter chub), and Iberian barbel *Luciobarbus bocagei* (Steindachner, 1864) (hereafter barbel), the latter three of which are endemic. A recent decline in the chub population has been documented, but the populations of trout and nase appear stable (Sánchez-Hernández *et al*. 2015). The situation for the barbel is critical and local extirpations in the study area could now be occurring (Sánchez-Hernández *et al*. 2015).

Abiotic parameters

Daily flow records for the River Tormes were compiled from gauging station number 02006 (UTM 30T 314785E 4468115N, altitude: 1377 m; catchment area: 88 km^2). Four hydrological parameters (m^3/s) were compiled from October 1943 to September 2012: mean daily flow for each month (Q_{med}), mean minimum daily flow for each month (Q_{min}), mean maximum daily flow for each month (Q_{max}) and maximum peak-flow for each month (Q_{peak}).

Hydrological studies generally standardise streamflow characteristics for use as indicators of hydrologic alteration (IHA), with the 75th percentile (high pulse) and 25th percentile (low pulse) considered of particular ecological relevance (e.g. Richter *et al*. 1996; Nicola *et al*. 2009; Knight *et al*. 2014). The frequency (no.) and duration (days) of high (daily discharge >2.150m^3/s) and low (daily discharge <0.300 m^3/s) hydrological pulses during specific periods (see below) were therefore calculated. In addition, the rate of change in discharge was calculated as the mean of both positive (increasing) and negative (decreasing) changes in discharge between consecutive days, and the number of reversals was measured as the number of times river discharge switched between 'positive' and 'negative' periods (Nicola *et al*. 2009; Bejarano *et al*. 2010).

Monthly mean water temperature data (ºC, January 1996 to December 2012) were obtained from El Barco de Ávila gauging station (UTM 30T 288835E 4466575N), and climatic data (mean air temperature and total precipitation per month, 1985 to 2011) were obtained from meteorological station number 2444 (UTM 30T 357980E 4502279N, altitude: 1130 m).

Biotic parameters

Fish surveys were conducted at six sites from 1998–2002 (Alonso-González 2003; Alonso-González et al. 2008) and 2006–2012 (this study) (Figure 1), except in 2010 when only four of the sites were surveyed (70 surveys in total). The fish populations were surveyed in summer by three-pass removal electrofishing using a 2200-W generator. Fishes were identified to species level, counted, measured for fork length (FL; nearest 1 mm) and returned to the river. The low prevalence and abundance of barbel prevented their inclusion in the study.

The density (fish/m^2) of each fish species was calculated using the Zippin multiple-pass depletion method (Zippin 1956); when no depletion in catches was achieved (e.g. chub in some surveys), a minimum density per unit area was calculated. Young-of-the-year (YOY) of each species were identified using Petersen's length frequency analysis (LFA) method (Petersen 1982) to explore differences in the annual recruitment, and chub, nase and trout larger than 100, 150 and 175 mm, respectively, were considered sexually mature (Lobón-Cerviá and Elvira 1981; Lobón-Cerviá *et al.* 1986; Nicola and Almodóvar 2002; Maia *et al.* 2006; Sánchez-Hernández and Cobo 2012). Thus, fish abundance was studied at three levels: (i) YOY, (ii) sub-adults (immature individuals, excluding YOY) and (iii) adults (sexually mature individuals).

Timing of spawning and hatching

Trout spawning and fry emergence in the River Tormes usually take place in December and March-April, respectively (Alonso-González 2003). The spawning seasons of nase and chub may overlap, usually extending from May to June (Doadrio *et al.* 2011 and references therein), but their hatching periods are largely unknown and no specific studies have yet been conducted. Their incubation periods are likely to be shorter than in trout and fry emergence is likely to occur in late spring (May and June) as in other cyprinid species (see Herzig and Winkler 1986; Carrapato and Ribeiro, 2012). Overall, three critical periods in the fish life-cycle were considered in the present study: (i) winter (December-February), coinciding with the trout spawning season, (ii) spring, coinciding with the emergence of trout (early spring, March-April) and spawning and hatching of the cyprinids (late spring, May-June), and (iii)

summer (July-September). Dividing the spring into early and late seasons was intended to increase the biological relevance of any relationships between species-specific life-history characteristics and the environmental variables.

Statistical analysis

The non-parametric Kruskal–Wallis test was used to analyze differences in hydrological parameters (Q_{med}, Q_{max}, Q_{min} and Q_{peak}) and water temperature among years. Non-parametric Mann–Kendall (*MK*) tests and Sen's slope estimator methods were used to test for common temporal trends in the hydro-meteorological variables (Q_{med}, Q_{max}, Q_{min}, Q_{peak}, water temperature, air temperature and precipitation) and fish densities (Worku *et al*. 2014; Adarsh and Janga Reddy 2015; Ayllón *et al*. 2015). The *MK* test checks the null hypothesis of no trend versus the alternative hypothesis of the existence of a decreasing or increasing trend, whereas Sen's slope estimator measures the slope for linear rate of change. Here, the *MK* test and Sen's slope estimator were computed using the package *trend* through the functions *mk.test* and *sens.slope*, respectively (see Pohlert *et al*. 2015 for further details).

Canonical correspondence analysis (CCA) was performed using the *vegan* package for R program (Oksanen *et al*. 2015) to examine associations between fish densities (dependent variables) and environmental conditions (independent variables); a suite of 11 environmental variables (water temperature, Q_{med}, Q_{max}, Q_{min}, Q_{peak}, number of reversals, rate of change and frequency and duration of high and low hydrologic pulses) was used for each season (winter, early spring, late spring and summer, and all seasons combined). The most significant environmental variables for each species were identified using Akaike's information criteria (AIC) (see Oksanen *et al*. 2015 for further details), and CCA was conducted to test for associations between the environmental variables and the abundance of YOY, sub-adult and

adult trout, nase and chub. In the resulting ordination diagrams, sampling occasions are represented by dots and environmental variables are represented by arrows, with the length of the arrows indicating the importance of the environmental variables (Ter Braak, 1986). Finally, the strength of association between fish densities and each environmental variable was tested using Pearson's rank correlation. These analyses allowed us to test for associations between fish densities and environmental conditions during fry emergence, the first summer and winter. Additionally, annual recruitment (YOY abundance) was compared with adult abundance using correlation analyses in order to determine the influence of spawning stock size on recruitment success. It was anticipated that, due to the timing of fish sampling (summer) and spawning (winter for trout and late spring for cyprinids), adult abundance in the previous year would have an influence on YOY abundance, but the abundance of adult cyprinids in the same year could also be influential. In all analyses, a significance level of $P = 0.05$ was used. Statistics and graphical outputs were performed using R 3.2.2 (R Core Team 2012).

Results

Abiotic parameters

Analyses of 69 years (1943–2012) of hydrological parameters (Q_{med}, Q_{min}, Q_{max} and Q_{peak}) revealed substantial and significant variations among years (Kruskal–Wallis test; $P < 0.05$ in all cases). For instance, the frequency of high Q_{peak} values (e.g. above 10 m^3/s) was higher over the fish data series (46.7%) than previously (29.4%). Long-term trends in hydro-meteorological variables showed some significant trends (Table I), Q_{med} in early spring and Q_{max} in early and late spring have declined; there were no statistically significant trends for Q_{min} and Q_{peak} (Table I and Figure 2). Air temperature has increased significantly in all

seasons except winter, whereas an apparent increasing trend in annual precipitation was not statistically significant.

The River Tormes' flow conditions were typical of snow–rainfall regimes, with peak flows in spring (mainly in March and April) and autumn (mainly in November and December). However, substantial inter-annual differences in the hydrological regime occurred (Figure 3). For example, there was a noticeable lack of peak-flow discharges from July 1998 to October 1999 and from June 2008 to January 2009, with the flow regime relatively stable but very low (Figure 3). In contrast, flows were considerably higher in December 2000 (Q_{max} = 37.4 m^3/s), October 2006 (Q_{max} = 28.4 m^3/s), April 2008 (Q_{max} = 20.3 m^3/s), February 2010 (Q_{max} = 19.1 m^3/s) and December 2010 (Q_{max} = 16.5 m^3/s). Two seasons with remarkably sudden variations in daily flow conditions were identified, one from October to December and the other coinciding with the cyprinid spawning and larval periods (hatching, fry emergence and early life-stages) in the spring. By contrast, no notable peak-flow discharges occurred in January, February or the summer, with the exception of in 2001, when flow from December to February was very changeable (Figure 4). High-amplitude flows sometimes occurred in a short time period; for example, in April 2008, the mean daily flow (Q_{med}) increased almost three-fold in 24 hours (from 7.3 m^3/s to 20.3 m^3/s) and decreased to a similar value 24 hours later (from 20.3 m^3/s to 9.3 m^3/s). Likewise, in December 2000, Q_{med} increased from 4.1 m^3/s to 37.4 m^3/s in 24 hours and then took 3 days to fall (from 37.4 m^3/s to 4.55 m^3/s).

Annual mean water temperatures ranged from 9.5ºC to 12.5ºC, but no statistically significant inter-annual differences were found (Kruskal–Wallis test; $P > 0.05$) and the apparent increasing trend in the annual mean water temperature time series was not statistically significant (Table I). By contrast, there was a significant increasing trend in late spring water

temperatures over the study period (Table I). A similar pattern was observed in all years; minima were recorded in January, with maxima recorded in August or September (except in 2006, when the maximum temperature occurred in July).

Biotic parameters

Substantial temporal variations in fish densities were observed during the study (Figure 5). Moreover, there was a significant reduction in the densities of YOY chub and nase over the study period (Table II). The frequency and duration of high and low hydrological pulses, as well as Q_{min}, Q_{peak} and Q_{med}, had the greatest influence on fish abundance, but there were interspecific and ontogenetic differences in their influence (Figure 6); chub seemed most sensitive to changes in summer flows, whereas nase were most influenced by flow in spring, and trout by flow in spring and winter (Table III). Specifically, Q_{min} (winter) and Q_{peak} (early spring) had a strong negative influence on trout densities, whereas all environmental variables seemed of equal importance to nase (Figure 6). For chub, the most important environmental variables were Q_{max} and the duration and frequency of high hydrological pulses during summer (with a positive influence on chub densities), but other variables were also influential (Figure 6 and Table III). Species-specific correlations between fish densities of each developmental period and environmental variables are provided as supplementary material (Appendix I).

The density of YOY trout appeared to be influenced by flow conditions during fry emergence and early larval period, with the highest densities associated with low Q_{peak} values in early spring ($R = -0.241$; $P = 0.044$) and a high frequency of low hydrological pulses in late spring ($R = 0.250$; $P = 0.040$); no significant correlations with summer environmental conditions were found (Appendix I). The density of YOY nase was negatively correlated with the

number of flow reversals during the spawning and early larval period (late spring) ($R = -0.294$; $P = 0.045$). A number of correlations between the density of YOY chub and environmental conditions in late spring and summer was found (Appendix I). For example, density of YOY chub was positively correlated with the duration of low hydrological pulses during the spawning and early larval period ($R = 0.321$; $P = 0.028$). There were also positive correlations between the densities of adult chub and flow conditions (the duration of high hydrological pulses, Q_{max} and Q_{med}) in summer (Appendix I).

Recruitment success (YOY density) of trout tended to increase with increasing spawning stock size (adult density in the previous year) ($R = 0.374$; $P = 0.005$). By contrast, no statistically significant relationships between recruitment success and the density of adults in the previous year were found for the cyprinid species. However, the density of YOY chub was positively correlated with adult density in the same year ($R = 0.709$; $P < 0.001$). Densities of YOY nase were highly correlated with sub-adult, but not adult, density in the same year ($R = 0.610$; $P < 0.001$).

Discussion

This study demonstrates that discharge, especially the timing and magnitude of peak-flows, in the River Tormes is highly variable among years. Moreover, the study corroborates previous observations that the hydrology has changed considerably in recent decades, with substantial reductions in mean spring river discharge but increases in peak-flow discharges (Ceballos-Barbancho and Morán-Tejeda 2006; Ceballos-Barbancho *et al*. 2008). These changes have been attributed to shifts in precipitation and air temperature due to climate change (Ceballos-Barbancho *et al*. 2008; Morán-Tejeda *et al*. 2010, 2011). In this study, the temporal analysis of air temperature data revealed that a gradual warming of the area has occurred, but the

increase in water temperature was statistically significant only during late spring. The latter result should therefore be interpreted with caution, as the length of the data series (17 years) may not be sufficient to ascertain whether or not water temperature is increasing as a consequence of increases in air temperature. Although the increase in air temperature over the study period was gradual, significant changes in hydrology could have occurred before the start of the fish data series. Notwithstanding, inter-annual flow variation during the fish time series was high, thereby facilitating assessments of the influence of hydrology on both fish community structure and population dynamics.

Fish abundances were significantly influenced by the frequency and duration of high and low hydrological pulses, but there were interspecific and ontogenetic differences in their influence. For example, chub seemed most sensitive to changes in summer flows, whereas nase were most influenced by flow in spring, and trout by flow in spring and winter. The shifts in environmental conditions in the headwater of the River Tormes basin could therefore have negative consequences for the fish populations. Several studies have demonstrated that changes in fish communities are related to abiotic or biotic shifts in ecosystems, such as droughts or floods, habitat degradation, the introduction of exotic species, and human alterations of river channels or flow regimes (Jackson *et al*. 2001; Bernardo *et al*. 2003; Gido *et al*. 2010). Habitat degradation, flow regulation and exotic species do not affect the fish assemblage in this study, because the headwater of the River Tormes basin is oligotrophic and not polluted, the habitat has not been modified, no significant flow regulation has been implemented (González del Tánago and García de Jalón 1984; Alonso-González *et al*. 2008), and the fish community is composed entirely of four native species. By contrast, the present study supports the hypothesis that interannual variations in fish populations may be linked to changes in environmental conditions, especially the frequency and duration of high and low

hydrological pulses in spring. Despite the growing interest in the role of biotic factors, such as intra- and interspecific competition on fish assemblages (e.g. Jackson *et al*. 2001; Forrester *et al*. 2006), we did not find any relationship between trout and cyprinid abundance. Thus, the present study suggests hydrology as the most important factor influencing fish assemblage structure.

Although difficult to separate the key factors influencing the recruitment success of fishes, flow conditions during the spawning season, egg incubation and/or fry emergence may be important (e.g. Nicola *et al*. 2009; Piffady *et al*. 2010; Cowx *et al*. 2012). The sudden variations in the daily flow of the River Tormes during spring as a consequence of snow melt may therefore have negative consequences for the recruitment success of fishes, especially if high daily peak-flow discharges occur during egg incubation and/or fry emergence. Indeed, YOY trout abundance was negatively correlated with high peak-flows (Q_{peak}) during fry emergence and the early larval period (in early spring; Alonso-González 2003; Nicola *et al*. 2009). Therefore, congruent with observations elsewhere (e.g. Alonso-González *et al*. 2008; Nicola *et al*. 2009), our results suggest that, in addition to the timing of spring floods associated with snow melt, the *frequency* and *magnitude* of fluctuations pulses (here measured as daily flow) can also have an influence on recruitment success. Additionally, there was a positive influence of the *duration* of low hydrological pulses during the spawning and early larval period (in late spring) on the recruitment success of chub, whereas the density of YOY nase was negatively correlated with the number of flow reversals during the early larval period. The YOY cyprinids may be indirectly affected by sudden variations in daily flow conditions during spring as high peak-flow discharges coincided with the spawning and egg incubation seasons of these species, although YOY nase seemed more vulnerable than chub to daily variations. This suggests that cyprinid recruitment should be

enhanced when flows are relatively stable (no sudden daily variations) and low (here measured as the duration of low hydrological pulses) during spring. However, extreme flow reductions between late spring and early summer could have a negative impact on the recruitment success of the cyprinid species because of their spawning preferences, i.e. lithophilic spawners using shallow nests close to the shore (e.g. Balon 1975; Melcher and Schmutz 2010). For example, eggs could dry out, be exposed to predators or even damaged by anglers walking on spawning habitats, but also YOY cyprinids can be isolated in areas that dry in late summer (J. Sánchez-Hernández personal observation).

Our study highlights the importance of the combination of environmental factors and spawning stock size in understanding temporal variations in fish populations through recruitment success. The relationship between spawning stock size and subsequent recruitment has the potential to play a major part in fish population dynamics (e.g. Elliott 1994; Brodziak *et al*. 2001). Our results only partially supported the hypothesis that spawning stock size (adult abundance) and subsequent recruitment (YOY abundance in the following year) are highly connected as the relationship was only statistically significant for trout. However, as anticipated due to the timing of fish sampling (summer) and cyprinid spawning (late spring), the abundance of adult cyprinids in the same year can also be influential. Our results thus highlight the possibility that the density of YOY fish can be influenced by the synergistic effects of spawning stock size and flow conditions. Regarding the latter point, an important issue is the capacity of fish to retreat to appropriate refugia when flow conditions are adverse, for example downstream movements in response to low-flow periods in summer (Alexandre *et al*. 2016) or movement to deep areas (pools) in response to severe droughts (Magoulick and Kobza 2003). Moreover, it seems reasonable to posit that local abundance of potamodromous cyprinid species (here estimated in summer) could be influenced by previous

fish movements, as their dispersal is highly influenced by flow conditions during spring and early summer (Alexandre *et al*. 2016). The upstream spawning migration of potamodromous cyprinid species usually begins in mid-late March and ends in June (e.g. Rodriguez-Ruiz and Granado-Lorencio 1992; Encina *et al*. 2006). Despite nase being considered a good swimmer (Romão *et al*. 2012), hydrology during the upstream spawning migration might have an influence on the abundance of adult nase, as we found a positive correlation between low hydrological pulses (Q_{med}) in late spring and adult abundance in summer. These findings are in agreement with Alexandre *et al*. (2016), who found that the dispersal of a potamodromous cyprinid species during late spring and early summer can be positively linked to a decrease in the number of flow falls.

Consideration of the effects of environmental conditions on fish populations should include non-spawning periods in areas where climatic impacts are important. Low dissolved oxygen and high temperatures in Mediterranean running waters during natural summer droughts may have a direct effect on fish populations via mortality (Pires *et al*. 1999; Bernardo *et al*. 2003, Magalhães *et al*. 2007). High water temperatures should be more problematic for trout than the cyprinid species because the upper thermal tolerance is lower in trout than cyprinids (e.g. Elliott 1994; Souchon and Tissot 2012). Elliott (1981) determined 24.7°C (up to 7 days) as the upper incipient lethal temperature for trout, but a narrower thermal niche has been described in central Spain (Santiago *et al.* 2016). The thermal tolerances of nase and chub are unknown (see Elliott 1981; Souchon and Tissot 2012) but, considering the thermal tolerances of closely related species (e.g. *Squalius cephalus* (L.) and *Chondrostoma toxostoma* (Vallot, 1837); reviewed by Souchon and Tissot 2012), it may be expected that the upper critical temperatures of chub and nase are higher than that of trout. The upper lethal temperature for adult *S. cephalus* is 30 °C, and the optimal temperature range of adult *C. toxostoma* varies

between 16 °C and 25 °C (Souchon and Tissot 2012 and references therein). In the present study, mean water temperatures exceeded the upper thresholds for trout in central Spain (between 18.1 and 18.7 °C; Santiago *et al.* 2016) in July (1999, 2005 and 2006), August (1996, 1999, 2001, 2002, 2004, 2006, 2008, 2009 and 2011) and September (2009 and 2010). Although it is possible that water temperatures in the fish sampling area were lower than at the gauging station (downstream), such conditions are nonetheless likely to be more problematic to trout than cyprinids. For example, thermal habitat losses, leading to decreases in the trout population, could occur if there are significant increases in summer temperatures. Thermal tolerance is generally higher in cyprinids than salmonids (e.g. Elliott 1994; Souchon and Tissot 2012), but species-specific information on the thermal requirements of endemic cyprinids is required to predict the impacts of climate change. Although we have some knowledge of how natural summer droughts affect Mediterranean ichthyofauna (e.g. Magalhães *et al*. 2007), our study aimed to assist in filling this knowledge gap and enhance the understanding of the impacts of summer environmental conditions on the cyprinid species. Our results are in agreement with Magalhães *et al*. (2007), who reported that chub abundance declined after droughts. Moreover, this study revealed a positive influence of the duration of high hydrological pulses during the summer on the abundance of adult and YOY chub. However, hydrology may not have the same effect on all developmental periods or in all seasons. For example, whereas unusual high-flow conditions during the summer appeared to be a significant indicator for different developmental periods (YOY and adults) of chub, the recruitment success of the chub appeared to be favoured by low-flow conditions during late spring.

Understanding the influence of environmental conditions on fish populations in the wild is challenging, but essential to improve our knowledge of freshwater ecosystem functioning and predictions of the impacts and implications of future climate scenarios. The present study demonstrated that fish populations can be affected by short-term changes in flow regimes, but such relationships cannot easily be used to extrapolate the likely effects of long-term changes in environmental conditions. Notwithstanding, the study identified important environmental trends in the river system as a consequence of climate change, which may affect fish populations directly or indirectly, and help to understand the fate of these species in the near future. It is widely accepted that global warming should favour cyprinids in comparison with salmonid species (e.g. Daufresne *et al*. 2003; Matulla *et al*. 2007; Almodóvar *et al*. 2012). By contrast, even though projected hydro-climatic changes could lead to increases in local species richness through colonization by warm-water species (Tisseuil *et al*. 2012 and references therein), future shifts in flow conditions, especially during the spawning and early larval periods, via climate change could have detrimental impacts on riverine cyprinid fish species. More studies are needed, however, because the attention allocated to endemic fish species in the Mediterranean region has been insufficient.

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Table I. Trend analyses of hydro-meteorological variables in the River Tormes basin (Spain) over the study period. Significant results are marked in bold.

	Mann–Kendall (*MK*) test		Sen's slope
	z	*P*	
Annual			
Q_{med}	-2.10	**0.033**	-0.011
Q_{max}	-3.00	**0.003**	-0.059
Q_{min}	0.60	0.517	0.002
Q_{peak}	1.50	0.126	0.124
Air temperature	4.00	**<0.001**	0.070
Precipitation	0.30	0.802	0.533
Water temperature	1.60	0.117	0.082
Winter			
Q_{med}	-0.70	0.508	-0.005
Q_{max}	-1.40	0.154	-0.035
Q_{min}	1.80	0.071	0.006
Q_{peak}	-0.60	0.569	-0.029
Air temperature	1.60	0.103	0.033
Precipitation	-0.30	0.752	-0.207
Water temperature	-0.50	0.621	-0.043
Early Spring			
Q_{med}	-2.50	**0.011**	-0.029
Q_{max}	-2.90	**0.003**	-0.089
Q_{min}	-0.70	0.475	-0.004
Q_{peak}	-0.10	0.911	-0.006
Air temperature	3.90	**<0.001**	0.100
Precipitation	0.80	0.441	0.612
Water temperature	0.10	0.934	0.014
Late Spring			
Q_{med}	-1.60	0.111	-0.010
Q_{max}	-3.10	**0.002**	-0.042
Q_{min}	0.20	0.807	0.001
Q_{peak}	-1.50	0.131	-0.053
Air temperature	3.50	**0.001**	0.125
Precipitation	-0.50	0.621	-0.622
Water temperature	2.40	**0.019**	0.203
Summer			
Q_{med}	0.70	0.506	0.001
Q_{max}	-0.80	0.432	-0.002
Q_{min}	1.90	0.063	0.001
Q_{peak}	-0.80	0.398	-0.007
Air temperature	2.70	**0.007**	0.059
Precipitation	-0.90	0.343	-0.882
Water temperature	1.50	0.127	0.124

Table II. Trend analyses of fish density in the River Tormes basin (Spain) over the study period. Data are displayed for each species and developmental period. Significant results are marked in bold.

		Mann–Kendall (*MK*) test		Sen's slope
		z	*P*	
	Trout			
YOY		0.50	0.582	0.010
Sub-adults		1.80	0.072	0.006
Adults		1.60	0.099	0.003
	Nase			
YOY		-2.30	**0.023**	-0.003
Sub-adults		-1.30	0.193	-0.031
Adults		-1.40	0.157	-0.001
	Chub			
YOY		-2.20	**0.027**	-0.003
Sub-adults		-1.90	0.064	-0.015
Adults		-1.60	0.115	-0.004

Table III. Environmental variables used in canonical correspondence analysis (CCA) after variable selection based on the forward selection method. Akaike's information criterion (AIC).

| Fish species	Description of the variables	Code	AIC	*F*	*P*
Trout					
	Mean minimum daily flow (total)	V1	-102.093	4.996	0.020
	Mean minimum daily flow (winter)	V2	-101.769	4.659	0.025
	Duration of high hydrological pulses (total)	V3	-101.680	4.566	0.030
	Frequency of low hydrological pulses (late spring)	V4	-101.306	4.180	0.030
	Maximum peak-flow (early spring)	V5	-100.929	3.792	0.035
	Maximum peak-flow (total)	V6	-100.847	3.708	0.035
	Mean daily flow (total)	V7	-100.803	3.664	0.040
	Duration of low hydrological pulses (late spring)	V8	-100.637	3.494	0.050
Nase					
	Frequency of low hydrological pulses (early spring)	V9	-24.316	6.970	0.020
	Duration of low hydrological pulses (early spring)	V10	-24.316	6.9703	0.020
	Frequency of low hydrological pulses (winter)	V11	-21.065	3.564	0.045
	Mean daily flow (late spring)	V12	-20.089	2.586	0.050
Chub					
	Mean maximum daily flow (summer)	V13	-134.05	10.582	0.005
	Duration of high hydrological pulses (summer)	V14	-133.69	10.152	0.010
	Frequency of high hydrological pulses (summer)	V15	-133.15	10.105	0.010
	Mean maximum daily flow (total)	V16	-131.01	7.094	0.015
	Mean daily flow (summer)	V17	-130.84	6.913	0.015
	Maximum peak-flow (total)	V6	-130.25	6.907	0.020
	Maximum peak-flow (summer)	V18	-130.10	6.903	0.020
	Duration of high hydrological pulses (late spring)	V19	-129.30	5.232	0.020
	Mean daily flow (total)	V7	-129.75	5.719	0.025
	Duration of low hydrological pulses (total)	V20	-127.85	3.705	0.045
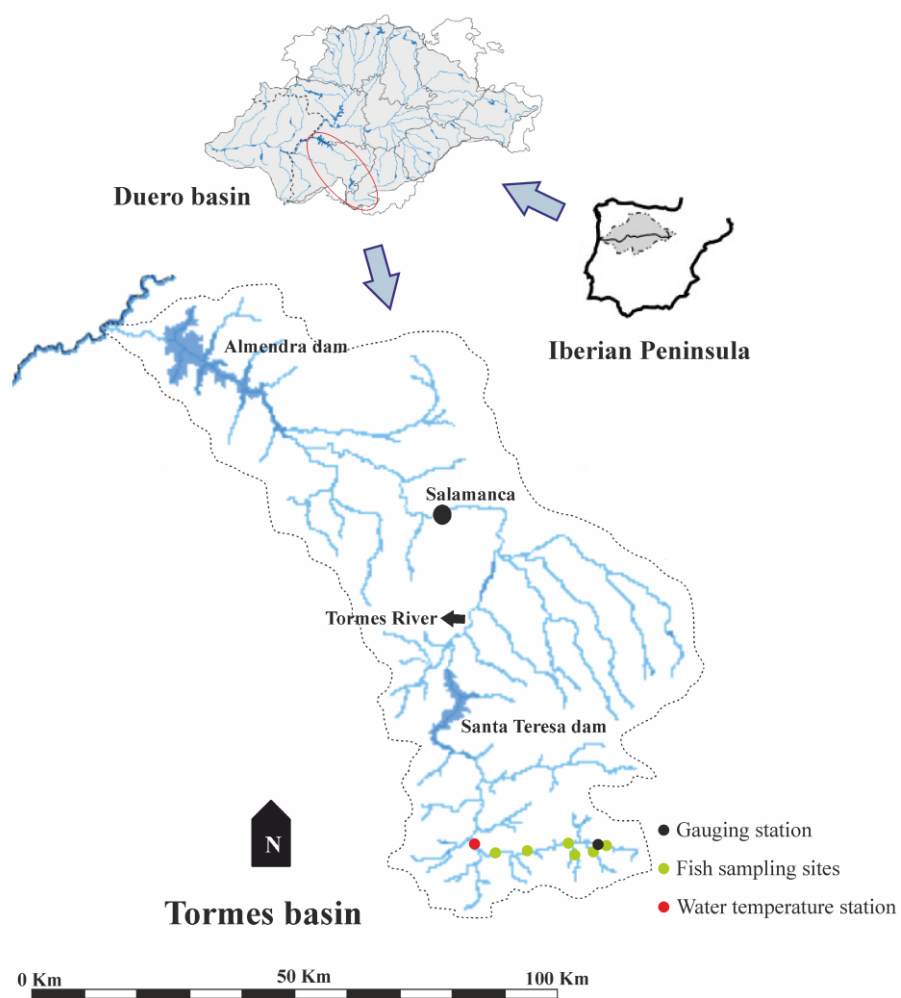
Figure 1. Map of the Iberian Peninsula and Duero basin showing the fish sampling sites, water temperature station and gauging station in the River Tormes basin, Spain.
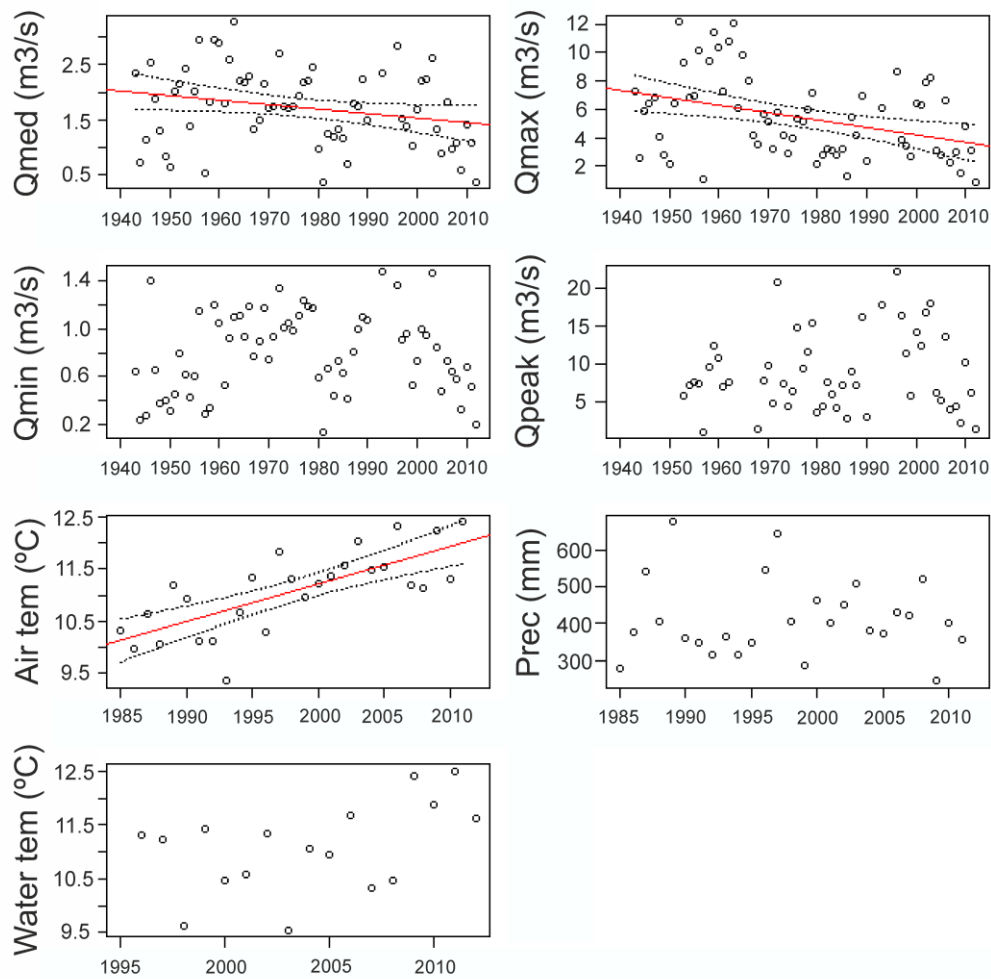
Figure 2. Long-term changes in hydrology, climate (air temperature and precipitation) and water temperature in the River Tormes basin (Spain). Linear trends with 95% confidence limits are shown only for statistically significant relationships based on Mann–Kendall test (Table I). The hydrological dataset had a gap from 1990–1995 (with the exception of the 1992–1993 hydrological year), and no Q_{peak} data were available from 1943–1953 and 1963–1968.
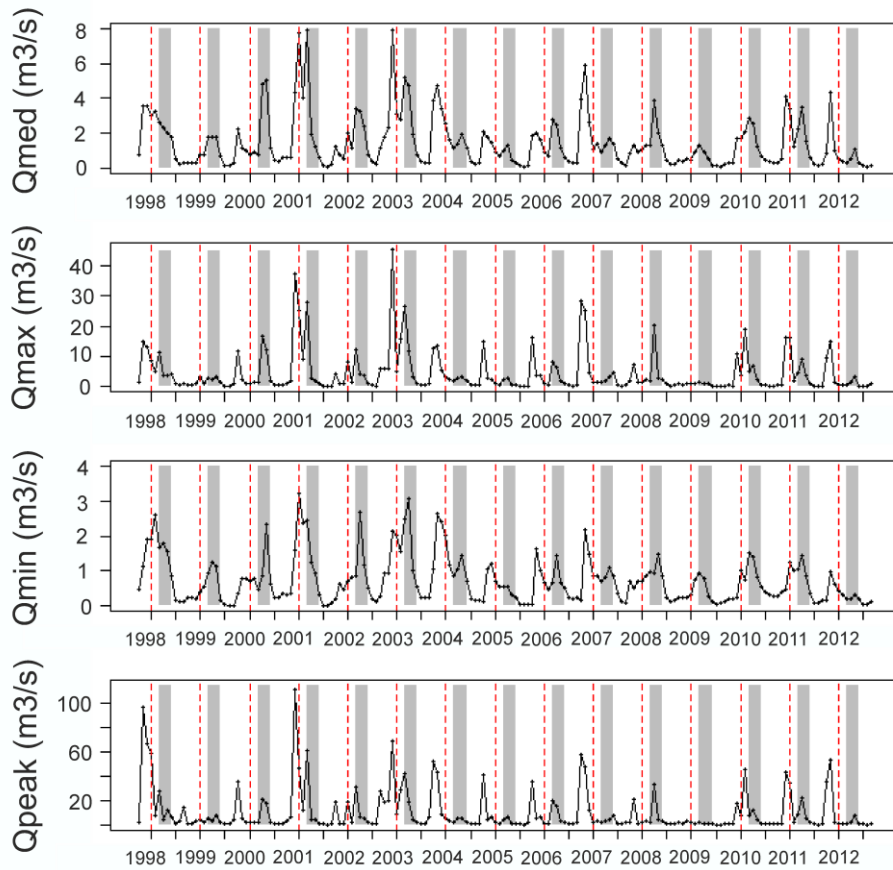
Figure 3. Mean monthly flow (m^3/s) in the River Tormes (Spain). Red broken lines show the year turn (1 January) and grey rectangles show the potential fry emergence season (March-June) during the fish sampling period (1 October 1997 to 30 September 2012).
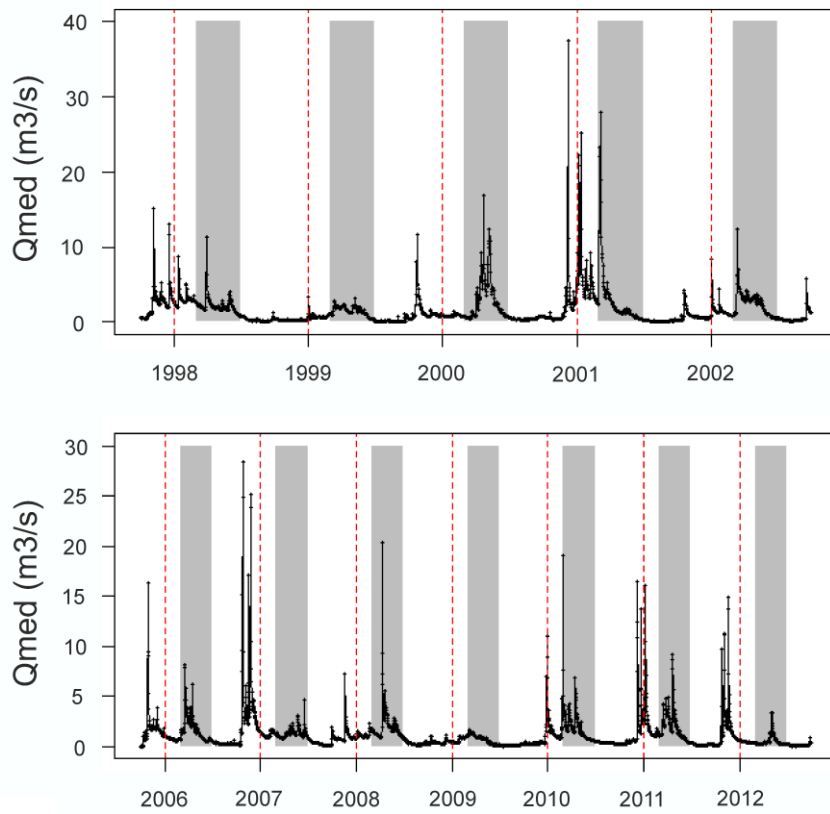
Figure 4. Mean daily flow (m^3/s) in the River Tormes (Spain) during the fish sampling period (1 October 1997to 30 September 2012). Red broken lines show the year turn (1 January) and grey rectangles show the potential fry emergence season (March-June).
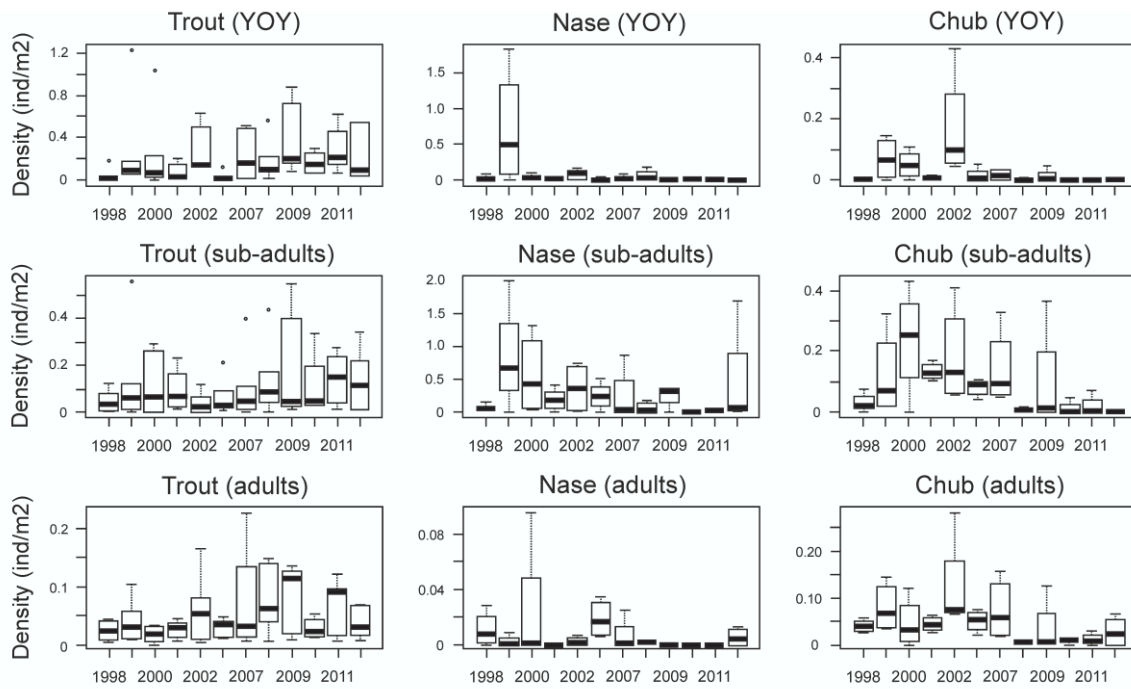
Figure 5. Density (fish/m^2) of the fish assemblage in the River Tormes (Spain) over time (1998–2012). The boxes show 25th to 75th percentiles and the median (the inner horizontal line in each box). Whiskers above and below the box indicate the 90th and 10th percentiles.
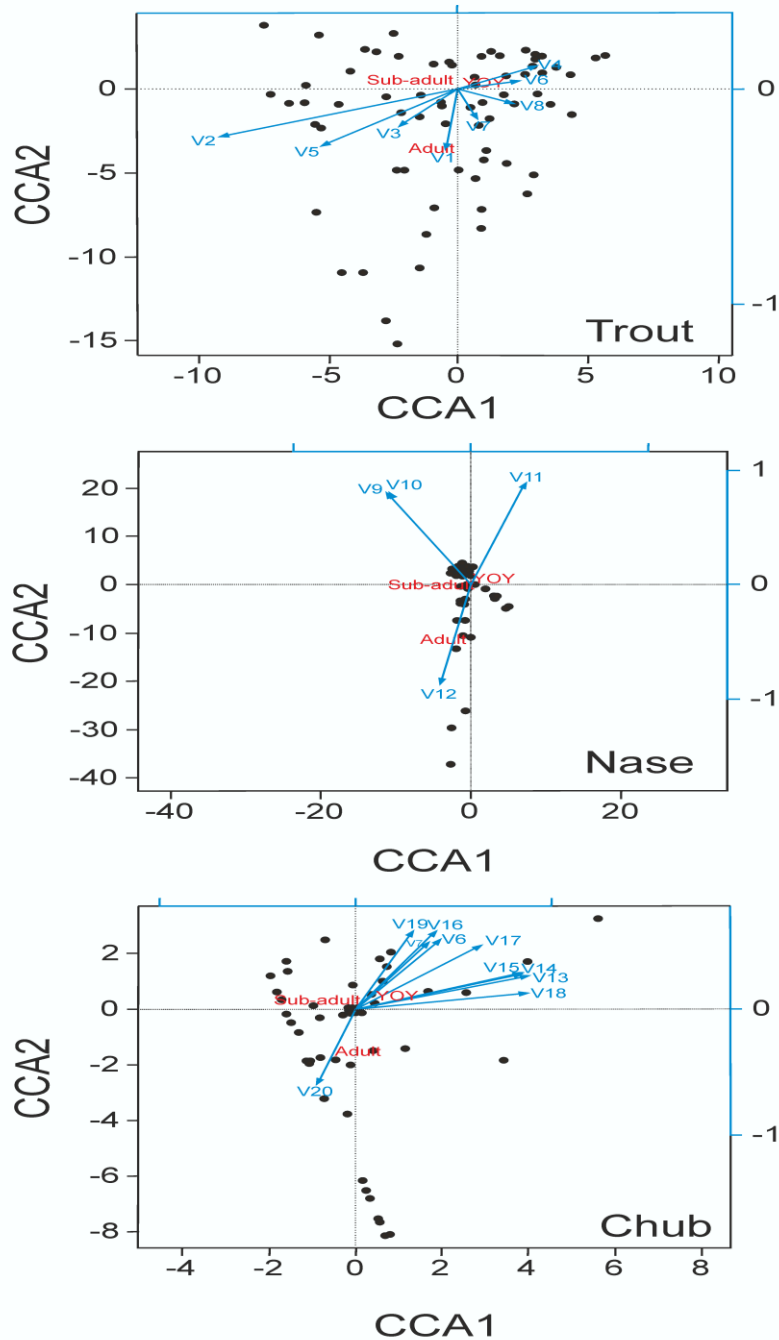
Figure 6. Canonical correspondence analysis (CCA) plot after stepwise forward selection based on fish abundances and selected environmental variables from 1998–2012. Descriptions of the abbreviations are given in Table III. The first two axes of the CCA accounted for 99.9, 100 and 100% of the total variance for trout, nase and chub, respectively. The length of the arrow is a measure of the importance of the environmental variable and the arrow heads point in the direction of increasing influence.

Supporting Information

Appendix I. Pearson's rank correlations between fish abundance and environmental variables. Only significant results are shown. D25 = duration of low hydrological pulses, D75 = duration of high hydrological pulses, F25 = frequency of low hydrological pulses, F75 = frequency of high hydrological pulses and Temp = water temperature. Definitions of rate, reversals, Q_{med}, Q_{max}, Q_{min}, Q_{peak} and Q_{flow} are given in "Materials and methods".