Hydrol. Earth Syst. Sci., 16, 3165–3182, 2012
www.hydrol-earth-syst-sci.net/16/3165/2012/
doi:10.5194/hess-16-3165-2012

Hydrology and Earth System Sciences

A novel approach to analysing the regimes of temporary streams in relation to their controls on the composition and structure of aquatic biota

F. Gallart[1], N. Prat[2], E. M. García-Roger[2,*], J. Latron[1], M. Rieradevall[2], P. Llorens[1], G. G. Barberá[3], D. Brito[4], A. M. De Girolamo[5], A. Lo Porto[5], A. Buffagni[6], S. Erba[6], R. Neves[4], N. P. Nikolaidis[7], J. L. Perrin[8], E. P. Querner[11], J. M. Quiñonero[3], M. G. Tournoud[8], O. Tzoraki[7], N. Skoulikidis[9], R. Gómez[10], M. M. Sánchez-Montoya[10], and J. Froebrich[11]

[1]IDAEA, CSIC, Jordi Girona 18, 08034 Barcelona, Spain
[2]FEM, D. Ecologia, UB, 08028 Barcelona, Spain
[3]CEBAS, CSIC, 30100 Murcia, Spain
[4]IMAR, 3004-517 Coimbra, Portugal
[5]IRSA, CNR, 70132 Bari, Italy
[6]IRSA, CNR, 20861 Brugherio MB, Italy
[7]EED, TUC, 73100 Chania, Greece
[8]Université Montpellier 2, 34095 Montpellier, France
[9]HCMR, 19013 Anavissos, Athens, Greece
[10]Dept. Ecología e Hidrología, UMU, 30100 Murcia, Spain
[11]Alterra, 6708 PB, Wageningen, The Netherlands
[*]present address: ICBIBE, UV, 46980 Paterna, València, Spain

Correspondence to: F. Gallart (francesc.gallart@idaea.csic.es)

Received: 14 October 2011 – Published in Hydrol. Earth Syst. Sci. Discuss.: 31 October 2011
Revised: 14 August 2012 – Accepted: 14 August 2012 – Published: 6 September 2012

Abstract. Temporary streams are those water courses that undergo the recurrent cessation of flow or the complete drying of their channel. The structure and composition of biological communities in temporary stream reaches are strongly dependent on the temporal changes of the aquatic habitats determined by the hydrological conditions. Therefore, the structural and functional characteristics of aquatic fauna to assess the ecological quality of a temporary stream reach cannot be used without taking into account the controls imposed by the hydrological regime. This paper develops methods for analysing temporary streams' aquatic regimes, based on the definition of six aquatic states that summarize the transient sets of mesohabitats occurring on a given reach at a particular moment, depending on the hydrological conditions: *Hyperrheic, Eurheic, Oligorheic, Arheic, Hyporheic* and *Edaphic*. When the hydrological conditions lead to a change in the aquatic state, the structure and composition of the aquatic community changes according to the new set of available habitats. We used the water discharge records from gauging stations or simulations with rainfall-runoff models to infer the temporal patterns of occurrence of these states in the Aquatic States Frequency Graph we developed. The visual analysis of this graph is complemented by the development of two metrics which describe the permanence of flow and the seasonal predictability of zero flow periods. Finally, a classification of temporary streams in four aquatic regimes in terms of their influence over the development of aquatic life is updated from the existing classifications, with stream aquatic regimes defined as *Permanent, Temporary-pools, Temporary-dry* and *Episodic*. While aquatic regimes describe the long-term overall variability of the hydrological conditions of the river section and have been used for many years by hydrologists and ecologists, aquatic states describe the availability of mesohabitats in given periods that

determine the presence of different biotic assemblages. This novel concept links hydrological and ecological conditions in a unique way. All these methods were implemented with data from eight temporary streams around the Mediterranean within the MIRAGE project. Their application was a precondition to assessing the ecological quality of these streams.

1 Introduction

Temporary streams are water courses whose flow regime is characterized by the recurrent interruption of flow or even the complete drying of their channel. This type of water course is not only widespread in dry climate areas (e.g. Rossouw et al., 2005; Levick et al., 2008), but also constitutes the first-order stream network in many drainage basins in wetter climates (Fritz et al., 2006). The frequency of these streams is expected to increase in the near future because of both climate warming and rising water consumption due to human activities (Tooth, 2000; Larned et al., 2010). The interruption of the aquatic conditions in temporary streams plays a determinant role in their ecological communities (Boulton, 1989; Arscott et al., 2010), so much so that temporary streams should be considered a distinct class of ecosystems instead of simply hydrologically challenged permanent streams (Larned et al., 2010). Indeed, the traditional perception among managers that a "healthy" stream must flow all year round can no longer be sustained (Boulton et al., 2000), though there are still severe gaps in our knowledge of these streams that affect their sound management.

As extreme states, large floods are considered to be short but important disturbance events on aquatic biota, as they imply an indiscriminate "washing" effect of most species (Boulton and Lake, 1992; pulse disturbances in Lake, 2003). Only the most resilient and resistant species are found just after a major flood event. This diminishes ecological quality metrics if sampling is done soon after a flood. In the reverse situation, no aquatic invertebrates – except in resistant forms (e.g. cysts, cocoons, diapausing eggs) – are present when there is no surface water (Boulton, 1989). Even when only disconnected pools are present, biotic communities are not representative of the actual ecological status of the stream, since conditions may vary among and within pools over time, even under reference conditions. These depend on many factors (e.g. pool size, pool water temperature and quality, stochastic assemblage of refugees, etc.) (Boulton, 1989; Buffagni, et al., 2009; press disturbance in Lake, 2003). Only when flow is present (in either the Eurheic or Oligorheic states defined below) are the diversity of habitats and the environmental conditions sufficient to sustain a biological aquatic community representative of biological quality. The current metrics used to establish ecological status in permanent streams can only be applied in these two cases (e.g. Munné and Prat, 2009, 2011).

Many hydrological and ecological studies, using diverse metrics, have been devoted to the hydrological characterization of temporary streams. The frequency of zero-flow periods (or its complement, flow permanence) is the first criterion for most of them (e.g. Hedman and Osterkamp, 1982; Poff, 1996). The seasonality of these periods is also used in some classifications (Uys and O'Keeffe, 1997; Rossouw et al., 2005; Kennard et al., 2010). A few authors also take into account the occurrence of isolated pools during periods without flow (Uys and O'Keeffe, 1997; Boulton et al., 2000). In fact, in ecological terms, the more relevant characteristics of the water regime in temporary streams are not flow values, but the temporal and spatial patterns of occurrence or disappearance of the features of the aquatic habitats that depend on the presence and flow of water (hereafter called mesohabitats sensu Salo, 1990), such as riffles and pools as well as the connectivity of water flow between them (e.g. Lake, 2007; Bonada et al., 2007; Chaves et al., 2008). While the information recorded at network gauging stations consists of water discharges, the occurrence of the diverse habitats and particularly of pools above and below the station during periods of zero discharge is not recorded, despite their prominent ecological role (e.g. Uys and O'Keeffe, 1997; Bond and Cottingham, 2008).

If predictability hypotheses concerning the hydrological controls on aquatic life are constructed for temporary streams, robust methods for measuring the ecological status of these streams and rivers, mainly based on the biological conditions (primary producers, macro-invertebrates and fish), need to be developed. According to the Water Framework Directive (WFD; European Communities, 2000), the current regulations for the management of waters in Europe, the ecological status (ES) is the key condition of streams to be evaluated. This is a term equivalent to "biological integrity" or similar concepts used in other parts of the world (Karr, 1981). When the ES of a stream is assessed to be less than "good", the water authorities are committed to establish measures within a river basin management plan to return the stream to that status. However, biological sampling to determine the ES of temporary streams needs to accommodate different mesohabitats that are present and change over time, unlike sampling designed for perennial streams. Such strategies need to be adapted if water is not present on the sampling date or if aquatic life is reduced to those animals found in isolated pools. When there are only pools, the biological communities found (even if they are pristine) may be significantly poorer in taxa or lower in diversity than the reference ones living in permanent streams. The importance of pools for establishing ES in Mediterranean streams was highlighted by Buffagni et al. (2009), who suggested that pool mesohabitat may give a better indication of biological quality than riffles during the riffle or connected pool phase, when sampled separately, but that the presence of pools alone always ends in an impoverished community, which gets poorer as the time elapsed after the disconnection of pools from riffles increases. This has been highlighted recently by Sheldon et al. (2010); in their Fig. 3 they depicted how the assemblage of organisms in a long-lasting disconnected pool is dominated by generalist species with lower diversity, a conclusion similar to the results found formerly in Bonada et al. (2007). For this reason the ecological status of the streams should not be measured during the disconnected pools phase.

How biological metrics defining ES using macroinvertebrates may change from wet to dry periods was investigated recently by Munné and Prat (2011), who showed that in dry periods in Mediterranean streams there is always less richness than in wet years, although in another study (Rose et al., 2008) the comparison of spring samples when riffles are present gave similar values between years despite the hydrological conditions of the year (dry or wet).

In temporary streams, only when the hydrological controls on aquatic life are completely understood, the impact of human changes on biota and the ES can be appropriately assessed. For fish studies, pools should remain the entire year round if they are intended to be used for biomonitoring (not necessarily for macroinvertebrates and algae) and it is clear that the fish community would be very dependent on the changes of water quality of pools over time (Magalhäes et al., 2007; Benejam et al., 2010; Dewson et al., 2007; see also the review of Williams, 2006). In these cases (based on fish studies), the dependence of fish characteristics on the water quality of pools is clear. Thus, for temporary rivers, before the evaluation of the biological condition of streams for calculating ES, hydrological conditions (and their influence on mesohabitat composition) should be studied.

In this context, the present study puts forward a composite approach for analysing the hydrological conditions of temporary streams on the basis of their controls of the occurrence of aquatic mesohabitats relevant to the development of aquatic life at the reach scale. This approach is designed for both research and management purposes and consists of four closely-related aspects:

The first aspect consists of the characterisation of the diverse states of a stream aquatic system when the hydrological conditions change. Boulton (2003) outlined the existence of "critical stages" in macroinvertebrate aquatic systems, defined by critical thresholds of discharge or water level at which mesohabitats become isolated or dry during a drought. Later on, Fritz et al. (2006), in an outstanding field manual, defined five hydrologic conditions that describe the diverse levels of connectivity or fragmentation of the aquatic phase in headwater streams from "no surface water" (0) to "surface flow continuous" (4). Here, the concept of aquatic state (AS) is introduced; it summarizes the set of aquatic mesohabitats occurring on a given reach at a particular moment, depending on the hydrological conditions. Six ASs are defined: *Hyperrheic, Eurheic, Oligorheic, Arheic, Hyporheic and Edaphic* (definitions provided below). The AS concept is consistent with the two earlier definitions and the relationships between them are analysed below along with their definition. The set of aquatic mesohabitats that occurs on a temporary stream reach is known to be crucial for the presence and abundance of aquatic fauna. Pools act as refuges for fish, providing places of survival during the absence of flow (Magoulick and Kobza, 2003) or influencing their vigour (Spranza and Stanley, 2000), while riffles are necessary for filter-feeder organisms that need the current for their nourishment. The effect of the mesohabitat conditions on the community of macroinvertebrates has been studied in some detail (Feminella, 1996; Bonada et al., 2006; Acuña et al., 2005), as well as the interactions between different trophic levels (Lundlam and Magoulick, 2009). Comparing communities before and following multi-year droughts (Magalhäes et al., 2007) or the comparison between communities in temporary and permanent streams (Rieradevall et al., 1999; Mas-Martí et al., 2010) emphasized the importance of knowing both the present AS and its evolution over time. It is known that fauna in temporary streams are more complex and taxa richness may even be higher than in permanent ones; the replacement of different ASs through the year gives opportunities to a succession of species typical of riffles and then of ponds, making their final richness greater than in many permanent streams (e.g. Bonada et al., 2006; García-Roger et al., 2011; Puntí et al., 2007). The EPT index (Number of taxa of Ephemeroptera, Plecoptera and Trichoptera) and EPT versus OCH (Taxa of Odonata, Coleoptera and Heteroptera) are good indicators of changes in mesohabitat conditions (Bonada et al., 2006). The importance of mesohabitats and the heterogeneity they give the river (microhabitat conditions) has been highlighted recently in temporary streams by García-Roger et al. (2011, 2012).

The second aspect of the approach aims to analyse the temporal patterns of occurrence of ASs in stream reaches using available flow records or simulations. Indeed, at present there are almost no data on the presence, duration and interannual variability of different mesohabitat changes in temporary streams and, therefore, of the presence of the different AS, and it is unlikely that this kind of data will be observed operationally in the near future. Boulton's (2003) "critical stages" in macroinvertebrate aquatic systems are more conceptual than measurable in terms of flow, whereas the 'hydrological conditions' defined by Fritz et al. (2006) need field or specific instruments for their determination. If water discharge thresholds separating the ASs in a stream reach can be defined, the available flow statistics may be transformed into AS statistics. A similar procedure is commonly used to assess the chronicle of mesohabitats for fish from water discharge data in permanent streams (e.g. Capra et al., 1995). The complex temporal patterns of occurrence of ASs is then to be analysed for two purposes that correspond to two temporal scales: the actual succession of ASs during sampling periods, on the daily scale, and the long-term seasonal occurrence pattern, pooled on the monthly scale. The first is done using adapted hydrographs and the second, through the development of the Aquatic States Frequency Graph (ASFG), which shows the annual variation in the occurrence of the diverse aquatic states. These graphic methods enable the temporal patterns of occurrence of the ASs of a temporary stream to be seen quickly, but do not allow the quantitative assessment of the stream regime that is necessary versus biological metrics and for comparisons between stream reaches.

Therefore, the third aspect of the approach develops some metrics for the efficient characterisation, ranking and comparison of stream regimes, as well as for analysing the relationships with biological indices or metrics. In the present study, only metrics focusing on the analysis of the statistics of zero flow were considered, as cessation of flow is the only flow discharge feature directly linked to some major change in the ASs available from flow records, and it may be considered the key feature defining the aquatic regime in a temporary stream (Boulton, 1989). Indeed, although many studies are devoted to characterizing the flow regime of streams for ecological or management purposes with diverse metrics, most of these metrics are conceived for permanent flow. For example, the Richards-Baker flashiness index (Baker et al., 2004) assigns zero flashiness values during the periods without flow because there is no change in the discharge values within them; subsequently but inconsistently, the longer the annual period without flow in a stream, the lower the flashiness index is.

The fourth and last aspect addresses a classification of the aquatic regimes (ARs) of temporary streams, based on the existing ones. The AR refers here to the long-term aggregated temporal schedule of flow and no-flow periods, which characterizes the general hydrological conditions of a stream, but only indirectly its mesohabitat or microhabitat conditions. There is some agreement on the main terminology used for classifying temporary stream regimes, but the criteria used to establish the limits between the classes vary between different authors (Uys and O'Keeffe, 1997; Boulton et al., 2000; Rossouw et al., 2005; Levick et al., 2008). We propose a conceptual classification that tries to summarize the main types of temporal hydrological discontinuities relevant to the occurrence of aquatic mesohabitats, paying less attention to the limits between the types. Nevertheless, to be operational, this classification needs to be applicable to streams using recorded or modelled hydrological data. For this purpose, the use of the metrics developed in the former aspect for classifying stream ARs is attempted.

Overall, this approach is intended to be used for three main purposes: (i) improved investigation of the hydrological restrictions on the development of aquatic life; (ii) the characterisation and classification of aquatic stream mesohabitat conditions (aquatic states), which helps managers to define the ES of streams; and (iii) the design of biological sampling calendars (i.e. scheduling biota sampling at the more ecologically significant moments: see Bond and Cottingham, 2008). The ultimate goal is the development of tools for characterising the hydrological controls on the development of aquatic life in stream reaches for both research and management applications. In fact, this method is being developed within the European MIRAGE project, which addresses the improvement of the WFD by regulating the inclusion of temporary streams.

2 Methodological approach

The approach developed consists of four steps, two on the definition and analysis of the ASs and two on the ARs, as introduced above. Though the data necessary for determining ASs and ARs are the same, they use different approaches and metrics. In the first step, the ASs, establishing the mesohabitat conditions relevant to the growth of aquatic life in temporary streams, are defined. In the second step, the flow thresholds between ASs are assessed using field observations and the flow duration curve, allowing us to investigate the temporal patterns of occurrence for the 5 wetter ASs at the reach scale, using hydrographs and the ASFG. In the third step, as the periods with zero flow are the key identifiable hydrological driver of biological communities, the metrics that best characterize the frequency and predictability of these periods are developed and analysed. Finally, the fourth step consists of the updated classification of the ARs of temporary streams and its implementation using the metrics developed. The first and second steps are sequential; the third and fourth steps can follow in any order.

The data used here for implementing the AS and AR methods come from the records from gauging stations at several sites around the European Mediterranean (Fig. 1). Table 1 shows the location and main hydrological characteristics of these sites. These gauging stations are located on streams with discharges that are not influenced by human activities, or only slightly, except for the Vène S station where summer flows are sustained by effluents from urban sewage systems (David et al., 2011). The Vallcebre and Vène streams are research basins where flow data were directly recorded by the teams involved in the MIRAGE project (Latron and Gallart, 2008; Perrin and Tournoud, 2009), whereas the flow data from the other stations were obtained from the respective basin authorities.

The time scale used through the different steps is the month, although a daily scale was used for analysing the history of the AS during the months before the sampling campaigns. The monthly scale was selected for long-term analyses because it is easier to manage and to obtain from records or models and it is usually sufficient for the development of the aquatic fauna. A finer temporal scale would result in too spiky data, because short occasional events would not be pooled unless the series lasted for many years.

The spatial scale was the stream reach (50–100 m long), which is the scale of gauging station measurements and usual field observations in relatively small streams (Buffagni et al., 2006), whereas longer reaches may be necessary in large or low-gradient streams. The analysis of spatial patterns along stream courses or networks would need the use of distributed

Table 1. Main characteristics of the studied basins. Catchment area in km^2; MAP = mean annual precipitation (mm); ETP = mean annual reference evapotranspiration (mm); MAR = mean annual runoff (mm), Length = available record length in years.

Operational basin	Stream	Station	X	Y	Area	MAP	ETP	MAR	Length
Thau lagoon	Vène	Karst (K)	3°41′42″ E	43°32′02″ N	1.4*	668	1336	590*	8
Thau lagoon	Vène	Sanglier (S)	3°41′55″ E	43°29′44″ N	35*	668	1336	332*	8
Candelaro	Celone	S. Vincenzo	15°21′51″ E	41°24′13″ N	85.8	723.6	1024	176	31
Guadiana	Cobres	Entradas	8°00′36″ W	37°45′58″ N	51	500	1080	116	37
Segura	Minateda	Minateda	1°36′36″ W	38°28′47″ N	1166*	316	770	9.6*	45
Llobregat	Vallcebre	Can Vila	1°49′24″ E	42°11′52″ N	0.56	823	862	260	13
Muga	Manol	S. Llogaia	2°56′03″ E	42°12′35″ N	163	748	794	118	9
Evrotas	Evrotas	Vrontamas	22°36′21″ E	36°57′50″ N	2418*	802	980	47*	34

* karstic areas with uncertain real groundwater recharge area.

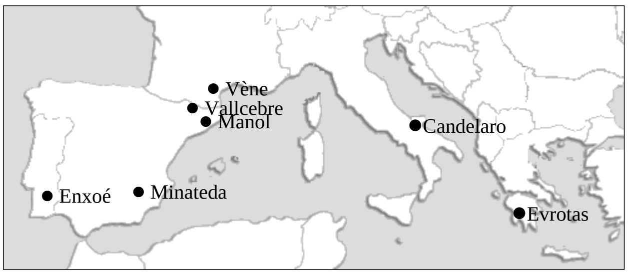

Fig. 1. Location of the main streams studied.

field observations or the simulations made with a model designed for this purpose (e.g. Arscott et al., 2010).

2.1 Defining the ecologically relevant aquatic states (AS)

The ASs summarize the transient sets of aquatic mesohabitats occurring on a given stream reach at a particular moment, depending on the hydrological conditions. From a review of the literature (Hawkins et al., 1993; Gasith and Resh, 1999; Boulton, 2003; Fritz et al., 2006; Lake, 2007) and the expertise of some of the authors (e.g. Rieradevall et al., 1999; Bonada et al., 2006, 2007; García-Roger et al., 2011), the following ASs may be defined as relevant in the ecology of temporary stream reaches, in a sequence from wetter to drier (see Table 2). The terms were selected in a way similar to the widely accepted grades in aquatic ecology for nutrient availability (i.e. Eutrophic, Mesotrophic, Oligotrophic) or pollution (i.e. Oligosaprobic, Mesosaprobic) that grade from the highest (hyper-) to the lowest condition (A-, Hypo-), using here the Greek suffix "-rheos" as indicating flowing water:

– Hyperrheic: infrequently high water (flood) causes major movement of stream bed alluvium and the drift of most of the aquatic fauna in the reach. In permanent streams, this state corresponds to flow above bankfull discharge, but temporary streams may not show distinct channel banks. Observations of temporary streams suggest that floods cause a strong but short-lived disturbance (pulse disturbances in Lake, 2003) in aquatic communities (Boulton and Lake, 1992; Lake, 2000; Arscott et al., 2010), whereas their occurrence is considered highly relevant to the health of river systems (Junk et al., 1989). In low gradient rivers of dry areas, overbank floods may be the periods of the highest biological productivity due to the release of nutrients from sediments and detritus in the alluvial plain (e.g. Walker et al., 1995). This state is not differentiated from the following one in the schemes of both Fritz et al. (2006) and Boulton (2003).

– Eurheic: water discharge is high enough to allow the occurrence of all the available aquatic habitats in the reach, including the abundant presence of riffles, and to allow optimum hydraulic connectivity between the diverse habitats. This is the habitual state in permanent streams and the one with the widest range of discharges in temporary streams; a succession of riffles and pools (macrohabitats) is the rule, with great variability in microhabitat conditions (García-Roger et al., 2012). This state corresponds to the "surface flow continuous (4)" condition defined by Fritz et al. (2006), whereas Boulton (2003) differentiated two intermediate states above or below the critical step of the water body's "isolation from the littoral vegetation", suggesting the existence of a subsequent state that we could call *Mesorheic*. Nevertheless, we decided not to use this intermediate state here because, as already mentioned by this author, the associated loss of species is rather low and it might be relevant only for certain particular conditions, such as large rivers or wetlands in low-gradient areas.

– Oligorheic: water discharge is low but sufficient to connect most pools in the reach through water rivulets. Riffles are absent or limited to scarce rapid flow areas between main pools (Bonada et al., 2006). This state corresponds to the "flow only interstitial (3)" condition of Fritz et al. (2006), and is below Boulton's (2003) critical step of "loss of riffle". When few riffles persist, the riffle macroinvertebrate community can be still effective for bio-monitoring, but it tends to resemble that of pools and edges, due to decreased flow and increased lentic habitats (e.g. Bonada et al., 2006; Rose et al., 2008).

– Arheic: surface discharge is null or close to zero, but a number of water pools remain in the stream bed. If this is alluvial, some sub-surface connectivity of water may occur, allowing the preservation of the physico-chemical quality of the water in the pools for some time at least. If the stream bed is impervious, the pool waters are vulnerable to undergoing quality deterioration trends or cycles. The ecological importance of pools remaining after the cessation of flow has been highlighted in many papers (e.g. Boulton, 1989), but when the disconnection lasts for many weeks, the pools tend to disappear (through evaporation) and water quality may deteriorate rapidly. In large dryland rivers, persistent pools (usually named waterholes in Australia) play a primary role in river ecology as refugia of many species during the long periods between flow events (Sheldon et al., 2010). This state corresponds to both "surface water present but no visible flow (2)" and "surface water in pools only (1)" conditions defined by Fritz et al. (2006), whereas it is just mentioned but not differentiated in a critical step from the former state in Boulton (2003).

– Hyporheic: most of the stream bed is devoid of surface water in the reach, although alluvium may remain wet enough to allow hyporheic life (alluvium water content is higher than the field capacity point). Only terrestrial fauna may be observed on the surface of the stream bed, but since the hyporheic zone may be a refuge for many animals when surface water is absent (Boulton, 1989; Boulton et al., 1998), it should also be considered an aquatic mesohabitat. This state is included within the "no surface water (0)" condition defined by Fritz et al. (2006), and below the "loss of surface water" critical step defined by Boulton (2003).

– Edaphic: the entire stream bed is devoid of surface water in the reach and alluvium is dry enough to impede active hyporheic life (alluvium water content is lower than field capacity and similar to the surrounding soils in terrestrial locations). The active life in the alluvium is similar to the edaphic life in the interfluvial soils, but some invertebrates may survive in desiccation-resistant stages in dry substrata for some time (Boulton, 1989). This state is also included within the "no surface water (0)" condition of Fritz et al. (2006), and mentioned as "drying hyporheic zone" but not separated from the former state by any critical step by Boulton (2003). Only terrestrial fauna exist on the surface and, if the state lasts for many weeks, the river bed may be invaded by terrestrial plants, creating a quite different ecosystem.

Most of these adjectives are already in use: Hyperrheic, Oligorheic and Arheic illustrate regional water drainage levels, so there is no possible confusion with the terms defined in this work. Hyporheic designs the ground zone below the stream bed saturated with some proportion of water coming from the stream and Edaphic is an adjective used for soil life and overall properties and processes; we used the same terms for the ASs when these environments are dominant, making it easier to understand them.

2.2 Time patterns of occurrence of aquatic states

Although temperature and electrical conductivity of either water or bed sediments may be used for recording the timing of hydrological conditions in the absence of flow (Constantz et al., 2001; Blasch et al., 2003; Fritz et al., 2006), the only information currently available on stream water regimes is from flow discharge records, coming from either measurements at gauging stations or simulations using rainfall-runoff models. Flow records at gauging stations are the most commonly obtained ones and are usually managed on a daily basis, but the monthly time scale is also commonly used to obtain estimates of flows from climatic data, particularly in scarce data conditions.

Flow data from a gauging station may be used to obtain the statistics of the occurrence of the wetter ASs (Hyperrheic, Eurheic, Oligorheic) following the procedure shown in Fig. 2, for which the ASFG.xls spreadsheet is available in the Supplement to assist readers. Alternatively, flow simulations obtained with a rainfall-runoff model may be used, but as most models cannot simulate zero water discharges, the identification of a discharge threshold equivalent to zero will be necessary. Once flow thresholds between the AS were assessed (as in Fig. 3), we used both daily values, to analyse the regime during a sampling season (Fig. 4), and monthly values to analyse long-term seasonal patterns of occurrence of ASs (Fig. 5).

The most demanding step in the procedure shown in Fig. 2 is the selection of the threshold flow values that separate the occurrence of the various ASs. This can be done with the help of the shape of the flow duration curve (distribution function of flow discharges, Fig. 3). To identify these thresholds correctly, field observations on the ASs synchronous with discharge measurements are needed. However, in the absence of these observations, thresholds can be provisionally calculated by taking into account the width and regularity of the stream bed reach near the gauging station. The limitations of this method will be analysed in the Discussion section.

The AS corresponding to minimum recorded discharge values (close to zero) depends on the design of the gauging station and the characteristics of the reach. For reaches over alluvial sediments with gauging stations designed to impede sub-surface flow below them, very low flow may be expected to correspond approximately to the threshold between the Hyporheic and Arheic states. In contrast, for stream reaches

Table 2. Characterisation of the aquatic states in terms of hydrological and ecological features and comparison with two former schemes.

Aquatic state	Hydrology	Mesohabitats	Hydrological conditions Fritz et al. (2006)	Critical drought steps Boulton (2003)
Hyperrheic	flood, overbank flow	drift of bedload and fauna	surface flow continuous (4)	isolation from littoral vegetation loss of riffle
Eurheic	abundant riffles	all mesohabitats available and connected		
Oligorheic	pools connected by thin water threads	lentic fauna with most of lotic species present	flow only interstitial (3)	
Arheic	disconnected pools	only lentic fauna	surface water present but not visible flow (2) surface water in pools only (1)	drying pool loss of surface water
Hyporheic	no surface water but alluvium close to saturation	only hyporheic and terrestrial fauna active	no surface water (0)	drying refuges drying hyporheic zone
Edaphic	alluvium moisture as in interfluves	terrestrial fauna and some resistant phases of aquatic fauna		

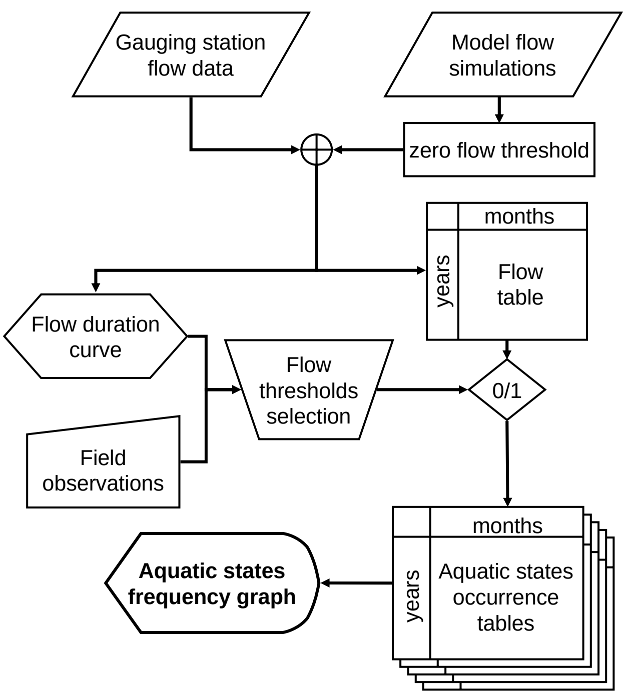

Fig. 2. Schematic flow chart for the procedure developed to estimate the temporal patterns of occurrence of the aquatic states from the available water flow data. The final products are the ASFGs (Fig. 4).

over impervious bedrock or alluvial ones with gauging stations allowing the bypass of sub-surface flow, minimum recorded flow may be expected to represent the threshold between Arheic and Oligorheic states. Consequently, discharge data cannot be used to derive information on the occurrence of the Edaphic AS in the first case and of the Hyporheic and Edaphic ASs in the second. Once the discharge thresholds between ASs are defined, they are used to convert the table of monthly discharges into the tables of occurrence of these ASs.

When a biological sampling campaign of a stream reach was designed for determination of the ES (see Sect. 2.5 below) and the subsequent results were to be analysed in comparison with the stream regime, the occurrence of the diverse ASs was calculated for the days before and during the sampling campaign. The flow hydrograph and the respective ASs corresponding to the sampling campaign held in 2009 at Can Vila (Vallcebre), using a daily temporal unit, is shown in Fig. 4. Note that the arrows indicate the dates when the sampling was done.

Then, for a long-term analysis of the seasonal patterns of occurrence of the ASs, the monthly frequencies obtained for the diverse ASs are obtained and plotted on an Aquatic States Frequency Graph (ASFG), with the frequencies accumulating from drier to wetter states for every month. In this study, data from 10 yr of daily flows were used, whenever available. Figure 5 shows the examples of ASFGs obtained for

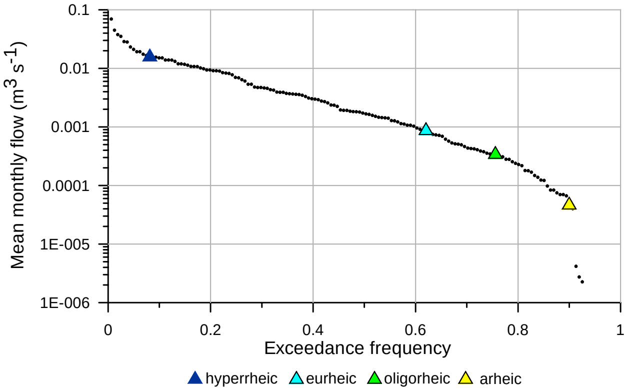

Fig. 3. Flow duration curve for the Vallcebre stream at Can Vila station, with identification of the minimum discharge thresholds that separate the diverse aquatic states.

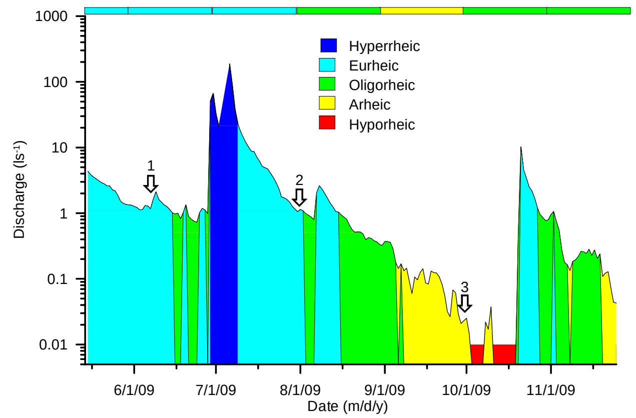

Fig. 4. Hydrograph and aquatic states during the 2010 biological sampling campaign at Vallcebre, Can Vila.

the various study sites. The discharge threshold values between ASs were assessed whenever possible with some field observations, using the expertise of the authors, and minimum measured flows were taken as the threshold between Hyporheic and Arheic states in the interim.

2.3 Metrics for characterizing the aquatic regime in temporary rivers

The ASFG method given above allows appraisal of the AR of the reach, as it describes the mean annual prevalence and timing of ASs for a stream reach by month. Nevertheless, the information shown is too complex to be synthesised in a few metrics and it depends on the somewhat subjective selection of flow thresholds. To circumvent these limitations, it may be hypothesized that the cessation of flow is the key feature defining the AR in a temporary stream (Boulton, 1989) and, therefore, the statistics of its metrics will summarize the main characteristics of the regimes of its ASs, as seen in its ASFG. Therefore, we selected the metrics that synthesize the two main hydrological parameters that are relevant to river ecology: the duration and predictability of periods with and without flow.

The relative time with or without water flow is usually the metric used for identifying temporary streams (e.g. Hedman and Osterkamp, 1982; Hewlett, 1982). Among regional flow regime studies, Poff (1996), in a widely used approach, employed only the mean number of days with zero flow per year; Kennard et al. (2010) used both the mean and the coefficient of variation of the number of days with zero flow per year, although there are no studies analysing the ecological significance of this latter metric. In an ecological study of a single stream in New Zealand, Arscott et al. (2010) characterised the aquatic regime at several points by using flow permanence (long-term annual average of the percentage of time a given site had flowing water), flow duration (days of flow at a site prior to each sample date) and drying frequency (average number of drying transitions per year). Arscott's results showed that flow permanence and duration correlated closely, with the former being well related to ecological features (see also Larned et al., 2010).

From these studies, it can be concluded that two metrics deserve to be retained for further investigation here: a measurement of flow permanence (a concept less ambiguous than flow duration), as the long-term mean annual relative number of months with flow, Mf (taking values between 0 and 1), and the drying frequency, Df, as in Arscott et al. (2010).

Besides these flow permanence and drying frequency metrics, several authors point to the relevant ecological role of the predictability of wetting or drying periods, because this predictability allows the development of taxa specialized in living in temporary conditions (e.g. Williams, 2006; Wissinger et al., 2008). As no suitable specific metrics were found in the literature, the predictability of the zero-flow periods was analysed using the P, C and M predictability metrics of Colwell (1974), and a new measurement, seasonality of drying (Sd_6), was developed below.

Colwell (1974), on the basis of Shannon's entropy, defined three metrics adequate for analysing the periodicity of the qualitative states of a system. These metrics were first defined on the basis of monthly system states for analysing seasonal periodicity during the year, but other time scales may be used. Following this author, seasonal predictability (P) of the monthly states of a system may be attained by two separable additional components: constancy (C), a measurement of state permanence, and contingency (M), a measurement of the repeatability of the time pattern in successive years. Here, the two system states considered are zero and positive values of discharge in the records of the gauging stations.

In addition to these metrics, the six-month seasonal predictability of dry periods (Sd_6) defined in Eq. (1) is here proposed as a new metric for characterizing the seasonality of the dry (zero-discharge values) conditions on a stream reach:

$$\mathrm{Sd}_6 = 1 - \left(\sum_1^6 \mathrm{Fd}_i / \sum_1^6 \mathrm{Fd}_j\right) \quad (1)$$

where Fd_i represents the multi-annual frequencies of 0-flow months for the contiguous 6 wetter months of the year and Fd_j represents the multi-annual frequencies of 0-flow months for the remaining 6 drier months. Wet and dry 6-month periods mean here those with fewer and more zero-flow frequencies, respectively. The calculation of this metric is also made easier for the reader through use of the ASFG.xls spreadsheet available in the Supplement.

This variable is dimensionless and takes the value of 0 when zero flows occur equally throughout the year in the long run and 1 when all the zero flows occur in the same 6-month period every year. When the regime is fully permanent, this metric cannot be computed, so the value of 1 is set to indicate full predictability. It should be mentioned that Sd_6 is defined at the 6-month scale, whereas the Colwell (1974) metrics were applied at the monthly scale. This was done to investigate the full capacity of these metrics, although the potential role of changing temporal scale was tested as stated below.

Redundancy between these six metrics (Mf, Sd_6, Df, P, C and M) was analysed by calculating the linear correlation coefficients when applied to the eight basins studied here (Table 3). All three of Colwell's (1974) predictability metrics (P, C and M) correlated significantly with flow permanence (Mf) and the first two correlated negatively with drying frequency (Df), whereas Sd_6 only correlated significantly with predictability (P). The possible role of the time scale in the use of P, C and M metrics was analysed by calculating them on the same 6-month periods used for the Sd_6 metric; the resulting 6-month values had correlation coefficients higher than 0.98 of the monthly values, showing that negligible information was added with this change of scale.

Given the high correlation coefficients between the other metrics, only flow permanence (Mf) and the seasonal predictability of dry periods (Sd_6) were selected for the subsequent analyses. The former (or its conversion into the number of days with zero-flows) has been widely used and found to be significant for explaining aquatic fauna, whereas the latter is the more orthogonal of the metrics tested and is easy to put into plain words in interviews when information from instruments is not available. This does not mean that the other metrics tested might not be useful for other analyses or for the investigation of ARs in other types of climate.

2.4 Classifying temporary stream aquatic regimes

Although the ASFG and regime metrics shown in the preceding sections are fully informative for analysing and comparing temporary stream regimes, a classification of temporary streams within the perspective of the present paper is necessary for operational purposes, as different stream regimes will need different sampling strategies and standards for

Table 3. Linear correlation coefficients between the metrics tested to analyse the statistics of zero flow periods in the basins studied. Values in bold are significant at the $p < 0.05$ level.

	Mf	Sd_6	Df	P	C	M
Mf	1	0.50	**−0.82**	**0.77**	**0.89**	**−0.74**
Sd_6	0.50	1	**−0.72**	**0.80**	0.58	0.11
Df	**−0.82**	**−0.72**	1	**−0.95**	**−0.92**	0.45
P	**0.77**	**0.80**	**−0.95**	1	**0.93**	−0.38
C	**0.89**	0.58	**−0.92**	**0.93**	1	−0.69
M	**−0.74**	0.11	0.45	−0.38	−0.69	1

defining the biological quality of stream waters (e.g. Bond and Cottingham, 2008), which is one of the most important objectives of the MIRAGE project. Although there is some agreement on the main terminology for classification of temporary stream regimes, the criteria used to establish the limits between regime classes vary between different authors (Rossouw et al., 2005; Levick et al., 2008). On the basis of the above considerations and the classifications proposed by Uys and O'Keeffe (1997) and Boulton et al. (2000), four main conceptual types of streams were defined by the MIRAGE project in function of the controls imposed by the time patterns of occurrence of aquatic mesohabitats on biological communities and their relevance for monitoring purposes:

- P (permanent or perennial): no relevant recurrent controls imposed on biological communities by lack of flow. Monitoring methods have already been defined (e.g. Hering et al., 2006).

- IP (intermittent-pools): stream's AR allows every year the development of biological communities similar to those in permanent streams, but afterwards the wet season flow is discontinued and only pools with impoverished communities remain. Ecological quality may be assessed as for permanent streams, though the biological sampling calendar may need adaptation to the hydrological regime. Sampling has to be done during the period with the more persistent flow.

- ID (intermittent-dry): streams usually cease to flow and dry out in summer, but in the wet season biological communities similar to those of permanent streams can be found, even if these may vary from year to year. Biological quality assessment needs to be measured with specific biological metrics somewhat different from those of permanent streams and (very important) a calendar adapted to the hydrological regime.

- E (episodic-ephemeral): water flow and pools are short-lived and occasional. Therefore, most of the organisms found are opportunistic, adapted to a quick development of their biological cycle. Biological quality assessment needs other methods beyond the customary

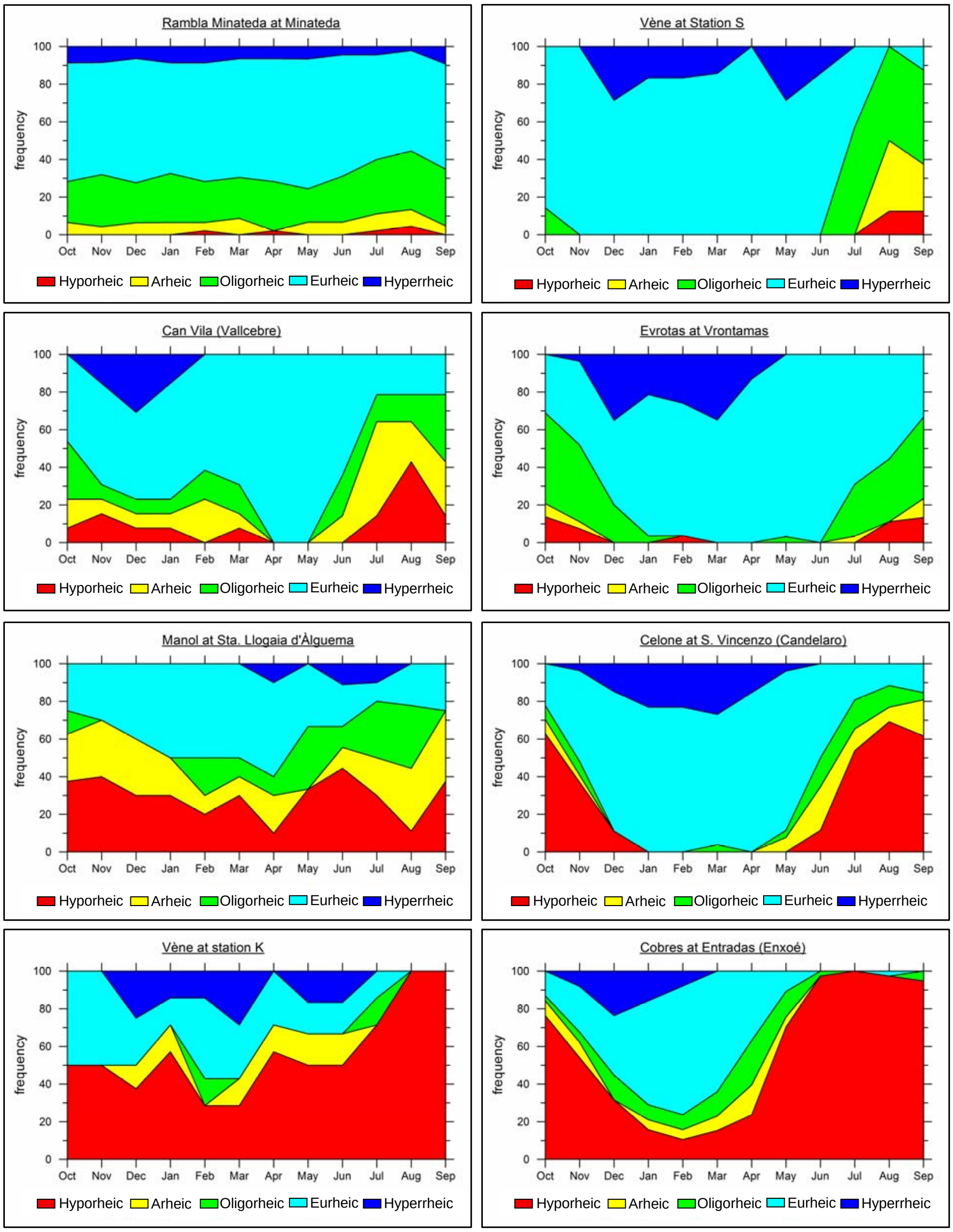

Fig. 5. Aquatic states frequency graphs for the eight main stream gauging stations in Fig. 1 and Table 1.

study of aquatic fauna (e.g. desiccation-resistant stages of aquatic fauna or terrestrial fauna).

The above classification does not permit any flow statistics for defining the boundaries between the classes for two reasons: usually there are no data on the occurrence of pools when flow is zero, and the values of flow statistics may vary between the different regime classes defined, depending on several other variables like temperature regime and characteristics of the stream bed. Nevertheless, in order to make the classification usable, we attempted to define the threshold values of the hydrological metrics defined in the former section for operationally classifying a stream reach on the basis of the statistics of zero-flow occurrence. Some interim trials, reported in the Results section, were attempted. The definition of these thresholds allowed the operational use of this classification for assisting the biological sampling strategy, as well as the interpretation of the biological communities found in terms of the ecological quality of the stream waters.

2.5 Measuring the stream's ecological status

Although the determination of ES is beyond the scope of this paper, some results are given below to show how the approach developed above can be applied.

The ESs of the streams in the MIRAGE project were measured by a standardized protocol (García-Roger et al., 2011, 2012) that provides the same information as the AQEM methodology (Buffagni et al., 2004) and thus the same metrics for characterizing the ES with which this methodology may be used. As these streams are located in the Mediterranean Region, we used metrics designed for these kinds of streams (Munné and Prat, 2009). As both are multimetric indices and use the reference condition approach, the EQR value (the ratio between the site value and the value at the reference condition sites) was determined (values close to 1 are good quality; close to 0, bad quality).

The measurement of ecological status (ES) was completed in the MIRAGE streams in 2010 and in Vallcebre in 2009. In each geographical area several sites were studied. If possible, one permanent site was sampled together with an intermittent one during the Arheic state. In both cases, a reference station was selected to check whether there was a disturbed station. This was variable in each basin according to the availability of the reference/disturbed or the permanent/intermittent stream pairs.

3 Results

3.1 Defining the threshold flow values between aquatic states

Using a few direct observations in the field and the support of the flow duration curve, when available, the interim flow thresholds between ASs were defined for the sites sampled for biological analysis in the MIRAGE project, as shown in Table 4. The thresholds varied according to different river characteristics, especially the size of the basin and the characteristics of the stream bed (if it is more or less impervious). Small basins tend to have lower thresholds, which is coherent with that, for connecting pools or developing riffles, more flow is needed in a large stream than in a small one. Note also that threshold values were very high in relation to the basin area in one case (Vène K), which is attributable to this site being a Karstic resurgence whose effective catchment area is much larger than the surface area of the topographic basin. The thresholds for the other stations shown in Fig. 5, not sampled for biological analysis, were assessed only from the flow duration curve without field observations.

Of course, differences along the river may be observed in AS occurrence: while upstream the river may be in Eurheic state, downstream it may be in Oligorheic or Arheic states. However, the idea is not to describe in detail the AS of the stream but the conditions at the site that will be sampled for biological analysis. In the case of MIRAGE data from Table 4, these were in the vicinity of the gauging stations, because they are relevant for the assemblage of macroinvertebrates that were to be sampled.

3.2 Temporal patterns of occurrence of the aquatic states

Once the water discharge threshold values between the ASs were assessed, the statistics of their occurrence were used for two main purposes: biological sampling design and interpretation, and overall regime assessment.

A biological sampling campaign was carried out in 2009 at Can Vila (Vallcebre). Figure 4 shows the hydrograph and the respective ASs during this campaign. Arrows show the biological sampling moments that were scheduled to assess the characteristics of the aquatic macroinvertebrates in the following conditions: after a sustained Eurheic state (arrow 1), during an Eurheic state that followed a short Hyperrheic period (arrow 2), and when pools started to dry out at the end of an Arheic state that followed the same drying sequence (arrow 3). The methods and results of the sampling of macroinvertebrate assemblages fall outside the scope of this paper and can be found in Garcia-Roger et al. (2011), which describes them in detail. It is worth emphasizing here that the first sample was discarded for biological analysis and the establishment of ES, because the temperature at this time was low and many of the animals were very small, making identification difficult. Therefore, the second sample was used for further studies. The monitoring of the daily flow of the site made it possible to establish the sampling date in springtime at least two weeks after the last flow peak (four days of Hyperrheic state by early April, not shown). Also note that the Arheic state period was very late in summer 2009 (September), so a sample taken in June would not be representative (in this year) of the dry conditions when only pools remain.

The analysis of the occurrence of ASs during this period using a monthly scale (colour bar at the top of Fig. 4) did not reflect the occurrence of the Hyperrheic and Hyporheic events, because of their short duration, which is attributable to the smallness of this basin. Nevertheless, with the flow records and the thresholds from Table 4 we can know the number of days in each AS for every sampling point close to the gauging station. This information is given in Table 5, where we calculated the daily ASs at each site during the three months preceding the sampling date. As can be seen in this table, 2010 was very wet and nearly all the streams remained in Eurheic or Oligorheic states. With this data we can analyse the effect of river intermittency on aquatic biota.

As explained in the Methods section, the ASFGs for the eight gauging stations were obtained at the monthly scale, as shown in Fig. 5. The relative importance of wet and dry states throughout the year and the degree of seasonality of the regime may be assessed at a glance from these graphs. These simple criteria were used to order the graphs in the figure,

Table 4. Flow thresholds between aquatic states in $\mathrm{l\,s^{-1}}$ defined in different streams studied in different basins of the MIRAGE project.

Stream	Vène	Vène	Celone	Celone	Enxoé	Taibilla	Vallcebre	Vallcebre
Station	K	S	P	S	Enxoé	Rogativa	CV	CR
Area (km^2)	1.4	35	72	24	61	77	0.56	4.17
Hyperrheic	> 800	> 1000	> 1000	> 200	> 100	> 1000	> 20	> 128
Eurheic	100–800	10–1000	30–1000	15–20	10–100	10–1000	1–20	6.4–128
Oligorheic	50–100	3–10	10–30	8–15	1–10	3–10	0.35–1	2.24–6.4
Arheic	10–50	1–3	1–10	1–8	0.1–1	0.05–3	0.05–0.35	0.32–2.24
Hyporheic	< 10	< 1	< 1	< 1	< 0.1	< 0.05	< 0.05	< 0.32

placing the wetter basins at the top and the more seasonal ones on the right-hand side. The ASFG was designed to view the changes of the AS over time and to obtain a first insight into how the sampling calendar should be defined for each basin.

3.3 The aquatic regime of the streams

The results obtained with the metrics of flow permanence, Mf, and seasonal predictability of dry periods, Sd_6, are shown in Fig. 6. Here, the stations with the highest flow permanence are plotted on the right and those with higher seasonal predictability at the top. The boundaries between the regime types are tentative, because more sites need to be analyzed.

The wetter streams, Rambla Minateda and Vène at station S, are both at the outlets of karstic systems and have near-permanent regimes. Nevertheless, the Vène stream had occasional dry periods in some summers, whereas, in the Rambla de Minateda, dry periods were more scattered throughout the year. Therefore, the respective Sd_6 metrics had different values for these streams and are clearly separate in Fig. 6. The quality of aquatic communities found in these streams should be no different from those living in perennial streams in the region (*Permanent* type).

At Vallcebre, the regime followed the equinoctial regime of precipitation: flow is more frequent in spring, whereas short-term droughts may be scattered over 9 months of the year. The Evrotas stream showed somewhat higher flow permanence and a more regular seasonal pattern, with a higher value in the Sd_6 metric in Fig. 6. It may be expected that the aquatic communities in both streams will be similar to those in perennial streams (*Permanent* type), whereas at Vallcebre the communities might be expected to be temporarily affected by the cessation of flow and eventually by the complete drying of the stream. However, they are expected to be similar to those living in perennial streams if sampled after sufficiently sustained Eurheic states (*Intermittent-pools* type).

Both the Manol and Celone streams had similar flow permanence, but the graphs in Fig. 5 show much greater regularity for the Celone stream, where continuous flow normally occurs from January to April. Indeed, the Celone stream had

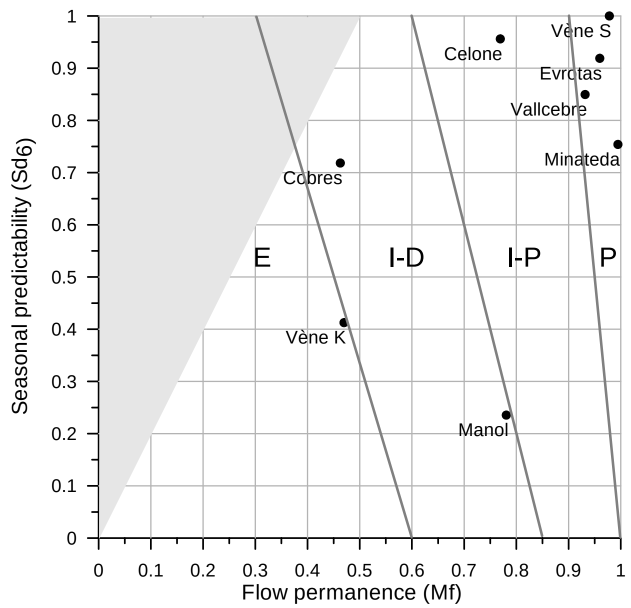

Fig. 6. Plot of the stations studied using the two regime metrics tested: flow permanence (Mf) and seasonal predictability of the zero-flow months (Sd_6). The oblique grey lines show the approximate interim separation between the four regime types: P (Permanent), I-P (Intermittent-pools), I-D (Intermittent-dry), E (Episodic-ephemeral). The grey triangle shows a field where the metric values are incompatible.

greater seasonality, as shown by the higher value of the Sd_6 metric in Fig. 6. It is worth noting that the features shown for the Manol stream in Fig. 5 and the low Sd_6 metric are linked to the occurrence of some sporadic periods of flow every year, but that are seasonally irregular in diverse years (low predictability). This may also be seen by analysing the drying frequency Df metrics for these streams, which gives 1.17 annual drying sequences for the Manol, but only 0.92 for the Celone. The characteristics of the aquatic communities living in these stream reaches may be expected to differ in spite of the similar value of their flow permanence, due to the differences in flow predictability. Indeed, as habitat conditions are very predictable in the Celone stream, during the wet season (from December to May) aquatic fauna are likely to be

Table 5. Frequency of occurrence of aquatic states during the 3 months before the sampling data together with community and biological water quality metrics for macro-invertebrates at several sites studied in the MIRAGE project. H, E, O, A, Ho = percent time occurrence of the Hyperrheic, Eurheic, Oligorheic, Arheic and Hyporheic states respectively; S = number of taxa; EPT = number of families of Ephemeroptera, Plecoptera and Trichoptera; OCH = Number of families of Odonata, Coleoptera and Heteroptera; H' = Shannon-Wiener diversity Index. IASPT and IMMi T indexes are biological quality indexes expressed in EQR.

Sites	H	E	O	A	Ho	S	EPT	OCH tax	H'	IASPT	IMMi T
Vène K	25	50	0	0	25	4	0	0	0.41	0.11	0.08
Vène S	25	75	10	0	0	7	0	0	0.84	0.00	0.02
Celone	2	97	0	0	0	39	16	7	1.70	1.21	1.39
Enxoé	33	17	17	33	0	23	4	5	1.22	0.66	0.75
Vallcebre	0	100	0	0	0	28	10	5	1.67	0.71	0.88
Evrotas	0	100	0	0	0	21	8	5	1.65	0.78	0.81

similar in richness and variety to those in perennial streams (*Intermittent-pools* type). On the contrary, as aquatic habitats are much less predictable in the Manol stream, aquatic fauna living in this stream are likely to be always less abundant and diverse, yielding low values of the biological metrics due to the hydrological constraints (*Intermittent-dry* type).

Finally, both the Vène stream at station K and the Cobres stream show the lowest frequency of flow occurrence, although the Cobres stream had higher predictability of flow (during winter), as shown in Fig. 5, and a much higher value of the Sd_6 metric, as shown in Fig. 6. This difference is also shown here by the drying frequency Df metric, which is as high as 1.63 for the Vène at station K, but only 0.95 for the Cobres. As in the former example, the characteristics of the aquatic fauna living in these streams are likely to differ because of the large difference in habitat predictability: the aquatic communities living in the Cobres stream may be well adapted to a dry but predictable regime (*Intermittent-dry* type), whereas those living in the Vène K are expected to be rather opportunistic (*Ephemeral* type).

3.4 Ecological status

The EQR values (the ratio between the site value and value at the reference conditions site) obtained for the ES analysis are provided in the two last columns of Table 5 (good quality are values close to 1, bad quality close to 0). Only data for spring are provided here (this was a wet period). As can be seen, we found values of very good (IMMi T-values higher than 0.85) or good (between 0.7 and 0.85) in Candelaro, Enxöe and Vallcebre. As 2010 was a wet year in the Mediterranean area, most of these streams were in Eurheic state at this time. However, data from the Vène stations show that their ESs were not good (site S) or even very bad (site K). Site S is in a stream reach where, as shown by chemical analyses, water quality is highly disturbed because of the spill of effluents from urban waste water-treatment plants (David et al., 2011). Site K is an unimpacted karstic resurgence that was naturally dry for at least 25 % of the time in this period. Therefore, the poor quality of the EQR value for this stream must be attributed to its AR hindering the presence of an aquatic macroinvertebrate community similar to those in permanent streams, which is consistent with the location of the Vène K site on the Fig. 6 graph.

4 Discussion

4.1 Working with aquatic states

The definition of the AS and the use of the ASFG made easier the comparison of the diverse sites studied in the MIRAGE project, the communication among the participants and the design and interpretation of the biological sampling campaigns. Nevertheless, we are aware that the main weak point of the method shown above is the possible subjectivity of the determination of the flow thresholds between the ASs.

This is not, however, a particular problem of our approach because the other published approaches that define comparable states (Boulton, 2003; Fritz et al., 2006) are similarly subjective and much less quantitative when defining the boundaries between the states or conditions. We went further than these approaches in trying to link qualitative states with flow water measurements, but the relationships between flow discharge and ASs are very site-dependent, so exact rules cannot be established. Thresholds are dependent on local conditions for each site and have to be calculated on the basis of local characteristics. Given present methods, ASs are only identifiable by field surveys and can only be associated with measured water discharges by direct comparison. Nevertheless, we hope that emerging technologies (e.g. LIDAR, RADAR) will make the remote identification of these transient states in extensive drainage systems possible in the near future.

Aware of these limitations, we used the information on the occurrence of the ASs only as a diagram in the ASFG and decided not to use this information for more quantitative or classification purposes. If a 10-yr flow record is used for building an ASFG, as the resolution of the monthly frequencies cannot be greater than 10 %, these statistics cannot be used more rigorously.

Notwithstanding, even though only a diagram was used and the thresholds were estimated without field observations or with very few, the ASFG was very informative about the main conditions of the streams and helped set up the sampling campaigns. Figure 5 shows clearly that, in a stream like Manol (that may become dry at any month of the year), it is not possible to measure ES using the current methods. On the other hand, in a typical intermittent stream like Celone, the likelihood of finding at least three months of Eurheic state in springtime is very high: thus, evaluation of ES by using the methods suitable for permanent streams is possible.

Along with the visualisation of the ASFGs, the use of flow permanence Mf and seasonal predictability of dry periods Sd_6 metrics provided a clear and nuanced analysis of the establishment of ASs and regimes that were relevant for ecological assessment and management purposes on the gauged reaches. When more field information is available on the threshold discharges that define the ASs on these reaches, the boundaries between states may be refined in the ASFGs, but their general shape will not change much because they are driven by the statistics of the objective zero flow values.

4.2 Limitations of the graphs and metrics used

The analysis of the ASFG suggests that the duration of the states might be calculated for every month directly from the graph. However, as this graph is a long-term probability analysis, the actual duration (in any given year) must be analysed directly from the data series using other metrics. Here, although only the mean annual frequency of drying transitions Df has been tested, other annual or monthly metrics could be used to characterize the statistics of periods with or without flow. Indeed, at the test gauging stations the two metrics on flow permanence and predictability were sufficient to characterise and compare the ARs. However, if this kind of analysis is to be applied to temporary streams in other climates, some other metrics may be needed, such as the timing of the drying period if its predictability is high.

This is the case of the Sd_6 metric, which uses a 6-month period to analyse the predictability of the period without flow. Because of its definition, its maximum possible values decrease for decreasing values of flow permanence when the latter are lower than 0.5, say less than 6 months of flow (there are no possible values within the upper left signalled area in Fig. 6). Shorter periods might be used for the definition of a similar metric, when streams that normally have less than 6 months of flow are to be analysed.

Another case when other metrics may be necessary is when thermal conditions are another control on aquatic life, superimposed on hydrological controls. The examples used in the present paper come from Mediterranean low- or medium-altitude areas, where the lack of flow is caused by a negative water balance and low temperatures were a marginal limitation for aquatic life (only found at Vallcebre in spring 2009).

4.3 Data availability

Nevertheless, since most temporary streams are ungauged or poorly gauged, the methodology described above will only be applicable to the relatively rare existing records from gauging stations. Rainfall-runoff models were used within the MIRAGE project to obtain simulated flow series for some sites on a monthly scale, but there are two main difficulties even for good performing models: first, most models will not be able to simulate zero water discharges, so the identification of a discharge threshold equivalent to zero will be necessary to use the above-defined metrics (see also Kirkby et al., 2011); and second, simulated values will be natural instead of actual discharges if these are affected by human activities. An exercise on how the metrics change over the years at several sites in the Evrotas basin, depending on the water abstractions, using the SIMGRO model, was performed recently (Cazemier et al., 2011). It is a good basis for studying the change of the river's AR over time and the differences from year to year in the duration of each AS.

Beyond the use of flow data and models, the permanence of flowing water in headwater streams has been operationally calculated from field surveys or topographic map data (Svec et al., 2005; Fritz et al., 2008). The presence of water at the pool scale has also been monitored by using temperature or electrical conductivity observations (Constantz et al., 2001; Blasch et al., 2003; Fritz et al., 2006) or, at the basin scale, remote sensing (Marcus and Fonstad, 2008). It is hoped that emerging technologies (e.g. LIDAR, RADAR) will make possible in the near future the remote identification of some of the ASs in extensive drainage systems, which will help us to understand the differences in the extent of each AS in the basin. However, for the purposes of monitoring ES, knowledge of the AS of the site at which the biological sample will be taken is the crucial issue. Of course, detailed knowledge of the AS of the entire basin would give us an idea of the representativeness of such a sample for this basin. The estimates of flow permanence obtained through some of these methods might be used to find the zero discharge threshold of a model. Furthermore, the relatively simple meaning of Mf and Sd_6 metrics may also allow the working classification of a stream's AR to be assessed from interviews with people living near the streams, when there are no data available.

Finally, the drier ASs, particularly the Edaphic state, cannot be analysed suitably from flow discharge records or simulations. The statistics of these states need other types of data beyond the water discharges usually measured or modelled in scientific or operational hydrology. Nevertheless, the examination of the ASFG may provide some insight into the possibilities of occurrence of these states over the course of the year and, when seasonality is high, it shows when pool occurrence or alluvium moisture needs to be tested for their recognition.

It is true that the occurrence of these dry states is very relevant for the characteristics of the aquatic fauna, particularly in the stream beds where aquatic communities are replaced by terrestrial communities. But in terms of establishing the ES of the stream, these states are not relevant because no method using terrestrial invertebrates has yet been defined. The MIRAGE project has worked on this topic, but no definitive results are available.

4.4 Ecological implications

As the six ASs and the subsequent analyses developed above were designed on the basis of preceding ecological studies in temporary waters, they can be expected to be useful for analysing the controls of the AR in aquatic biological communities.

The first results obtained in the European MIRAGE project do indeed suggest this. As shown in the Results section, all the sites sampled after sustained Eurheic and Oligorheic states provided biological metrics corresponding to good ES, except the Vène S site, which is known to be affected by water quality deterioration. On the other hand, the Vène K site, which had shorter Eurheic and Oligorheic states and is known to have a regime that is hard to predict, provided biological metrics corresponding to very bad ES in spite of the good quality of the waters.

Many authors (e.g. Townsend and Riley, 1999) demanded scientific investigation to define if current indices are robust enough with respect to detecting real changes in river health and avoiding the incorrect indication of changes. In this regard, the approach proposed here offers a framework for categorizing river stretches so that biological indices can be more suitably selected and sampling strategies set. This is done by providing an estimation of the AS based on historical data, which is assumed to well represent how the actual flow conditions were obtained over time, i.e. accounting for a component of predictability of biological community. This way, a relevant part of overall history behind community structure is taken into account. On the other hand, the amount and character of habitats actually present at the moment when the sample is taken are crucial also when establishing ES. As far as flow-related habitat assessment is concerned, the observed ratio between lentic and lotic in-channel habitats is known to be extremely relevant (Buffagni et al., 2010) and potentially accounts for the most part of community variance in Mediterranean rivers (Buffagni et al., 2009, 2010). An increase in lentic conditions is often associated with a decrease in metrics used to assess ecological quality, thus possibly causing a serious underestimation of ecological quality. Hence, if the presence of lentic conditions is due to natural processes, interannual variation or season, the obtained ES classification can be partly unsubstantiated (Buffagni et al., 2009). In such cases, adaptations or corrections to assessment systems are unquestionably needed (Buffagni et al., 2009). Both the quantification of the actual habitat present in the river at the moment of sampling – not under the scope of the present paper – and the definition of present and antecedent ASs, which provides hydrology-based evidence, should be contemplated in future assessment systems for temporary streams.

The methods described in this paper offer the possibility of extending the biological methods used in permanent streams to the range of temporary stream types if an adequate scheduling of the sampling period is made. The recovery of the community is highly dependent not only on the duration of the dry period, but also on the predictability of such a period over years. However, if flow is present in the wet period for several months (usually spring), riffles offer the opportunity of measuring biological quality using macroinvertebrates with methods defined for permanent streams (Rose et al., 2008). Nevertheless, the time of sampling must be determined by the hydrological conditions rather than the time of year because, as demonstrated by Munné and Prat (2011), wet summers and springs give higher values of metrics than dry springs do. Therefore, the moment when the sample is taken is crucial in establishing ES and should not be linked to a specific time of the year, but to a specific condition of the hydrograph. This was a key issue in the MIRAGE project and data in Table 5 were collected following this rule. From these data and the work of Rose et al. (2008) and Munné and Prat (2009), we can conclude that in temporary streams, if samples are taken at the appropriate stage of the hydrograph (after flow has resumed in the stream and been present in it for at least a month), ES may be measured by the same methods as in permanent streams if the values of the Mf and SD_6 metrics are high enough.

Despite the fluctuations in community assemblages described in Feminella (1996), Bonada et al. (2006, 2007) and Bêche and Resh (2007) and despite the changes from riffle-dominant species (EPT) to pool-dominant species (OCH), consistency of ES may be measured in both Eurheic (riffle-dominant mesohabitat, but with presence of pools) and Oligorheic (connected-pool mesohabitat conditions) states (Bonada et al., 2007; Rose et al., 2008).

Nevertheless, in streams with low flow permanence Mf and/or low seasonal predictability Sd_6, such as the Vène at K station, the hydrological controls on biological communities are so high that ecological quality must be measured by either standards specifically designed for them or other alternative methods (e.g. desiccation-resistant stages of aquatic fauna, terrestrial fauna, riparian environment, etc.). These methods are not yet available to managers.

Researchers with data on biological water quality metrics in temporary streams are invited to test the methods described above, in order to investigate how temporary stream ARs control aquatic fauna. The ASFG can be prepared and the Mf and Sd_6 metrics from flow data can be calculated with the ASFG.xls spreadsheet available in the Supplement.

Supplementary material related to this article is available online at: http://www.hydrol-earth-syst-sci.net/16/3165/2012/hess-16-3165-2012-supplement.zip.

Acknowledgements. The research leading to these results received funding from the European Community's Seventh Framework Programme (FP7/2007-2011) under grant agreement 211732 (MIRAGE project), as well from the Spanish Government under the RespHimed project (CGL2010-18374) and a research contract (Ramón y Cajal programme) granted to J. Latron. The authors are indebted to M. J. Kirkby, C. Campana, D. von Schiller and V. Andréassian for their comments. The editing work of P. Passalacqua and the recommendations of C. Smith and four anonymous reviewers helped to improve the quality of the paper significantly.

Edited by: P. Passalacqua

References

Acuña, V., Muñoz, I., Giorgi, A., Omella, M., Sabater, F., and Sabater, S.: Drought and postdrought recovery cycles in an intermittent Mediterranean stream: structural and functional aspects, J. N. Am. Benthol. Soc., 24. 919–933, 2005.

Arscott, D. B., Larned, S., Scarsbrook, M. R., and Lambert, P.: Aquatic invertebrate community structure along an intermittence gradient: Selwyn River, New Zealand, J. N. Am. Benthol. Soc., 29, 530–545, 2010.

Baker, D. B., Richards, R. P., Loftus, T. T., and Kramer, J.: A new flashiness index: Characteristics and applications to Midwestern rivers and streams, J. Am. Water Resour. As., 40, 503–522, 2004.

Bêche, L. A. and Resh, V. H.: Short-term climatic trends affect the temporal variability of macroinvertebrate in California Mediterranean streams, Freshwater Biol., 52, 2317–2339, 2007.

Benejam, L., Angemeier, P. L., Munné, A., and García-Berthou, E.: Assesing effects of water abstraction on fish assemblages in Mediteranean streams, Freshwater Biol., 55, 628–644, 2010.

Blasch, K. W., Ferre, T. P. A., Christensen, A. H., and Hoffmann, J. P.: New field method to determine streamflow timing using electrical resistance sensors, Vadose Zone J., 1, 289–299, 2003.

Bonada, N., Rieradevall, M., Prat, N., and Resh, V. H.: Benthic macroinvertebrate assemblages and macrohabitat connectivity in Mediterranean-climate streams of northern California, J. N. Am. Benthol. Soc., 25, 32–43, 2006.

Bonada, N., Rieradevall, M., and Prat, N.: Macroinvertebrate community structure and biological traits related to flow permanence in Mediterranean river network, Hydrobiologia, 589, 91–106, 2007.

Bond, N. R. and Cottingham, P.: Ecology and hydrology of temporary streams: implications for sustainable water management, eWater Technical Report, Canberra, available at: http://www.ewater.com.au/uploads/files/Bond_Cottingham-2008-Temporary_Streams.pdf (last access: 2 September 2012), 2008.

Boulton, A. J.: Over-summering refuges of aquatic macroinvertebrates in two intermittent streams in central Victoria, T. Roy. Soc. South. Aust., 31, 23–34, 1989.

Boulton, A. J.: Parallels and contrasts in the effects of drought on stream macroinvertebrate assemblages, Freshwater Biol., 48, 1173–1185, 2003.

Boulton, A. J. and Lake, P. S.: The ecology of two intermittent streams in Victoria, Australia. III. Temporal changes in faunal composition, Freshwater Biol., 27, 123–138, 1992.

Boulton, A. J., Findlay, S., Marmonier, P., Stanley, E. H., and Valett, H. M.: The functional significance of the hyporheic zone in streams and rivers, Annu. Rev. Ecol. Syst., 29, 59–81, 1998.

Boulton, A. J., Sheldon, F., Thoms, M. C., and Stanley, E. H.: Problems and constraints in managing rivers with variable flow regimes, in: Global perspectives on river conservation: science, policy and practice, edited by: Boon, P. J., Davies, B. R., and Petts, G. E., John Wiley & Sons, London, 415–425, 2000.

Buffagni, A., Erba, S., Cazzola, M., and Kemp, J. L.: The AQEM multimetric system for the southern Italian Apennines: assessing the impact of water quality and habitat degradation on pool macroinvertebrates in Mediterranean rivers, Hydrobiologia, 516, 313–329, 2004.

Buffagni, A., Erba, S., Cazzola, M., Murray-Bligh, J., Soszka, H., and Genoni, P.: The Star common metrics approach to the WFD Inter-calibration Process: a full application across Europe for small, lowland rivers, Hydrobiologia, 566, 379–399, 2006.

Buffagni, A., Armanini, D. G., and Erba, S.: Does the lentic-lotic character of rivers affect invertebrate metrics used in the assessment of ecological quality?, J. Limnol., 68, 95–109, 2009.

Buffagni, A., Erba, S., and Armanini, D. G.: The lentic-lotic character of Mediterranean rivers and its importance to aquatic invertebrate communities, Aquat. Sci., 72, 45–60, 2010.

Capra, H., Pascal, B., and Souchon, Y.: A new tool to interpret magnitude and duration of fish habitat variations, Regul. River, 10, 281–289, 1995.

Chaves, M.L., Rieradevall, M., Chainho, P., Costa, J. L., Costa, M. J., and Prat, N.: Macroinvertebrate communities of non-glacial, high altitude intermittent streams, Freshwater Biol., 53, 55–76, 2008.

Cazemier, M. M., Querner, E. P., van Lanen, H. A. J., Gallart, F., Prat, N., Tzoraki, R., and Froebrich, J.: Hydrological analysis of the Evrotas basin, Greece; Low flow characterization and scenario analysis, Wageningen, Alterra, Alterra-report 2249, 2011.

Colwell, R. K.: Predictability, constancy and contingency of periodic phenomena, Ecology, 55, 1148–1153, 1974.

Constantz, J., Stonestrom, D., Stewart, A. E., Niswonger, R., and Smith, T. R.: Analysis of streambed temperature in ephemeral channels to determine stream flow frequency and duration, Water Resour. Res., 37, 317–328, 2001.

David, A., Perrin, J. L., Rosain, D., Rodier, C., Picot, B., and Tournoud, M. G.: Implication of two in-stream processes in the fate of nutrients discharged by sewage effluents in a temporary river, Environ. Monit. Assess., 181, 491–507, doi:10.1007/s10661-010-1844-2, 2011.

Dewson, Z. S., James, A. B. W., and Death, R. G.: Invertebrate community responses to experimentally reduced discharge in small streams of different water quality, J. N. Am. Benthol. Soc., 12, 197–200, 2007.

European Communities: Directive 2000/60/EC of the European Parliament and of the Council of 23 October 2000 establishing a framework for Community action in the field of water policy, O.J. L 327, 22 December 2000, 1–73, 2000.

Feminella, J. W.: Comparison of benthic macroinvertebrate assemblages in small streams along a gradient of flow permanence, J. N. Am. Benthol. Soc., 15, 651–668, 1996.

Fritz, K. M., Johnson, B. R., and Walters, D. M.: Field Operations Manual for Assessing the Hydrologic Permanence and Ecological Condition of Headwater Streams. EPA/600/ R-06/126, US Environmental Protection Agency, Office of Research and Development, Washington DC, available at: http://www.epa.gov/eerd/methods/headwater.html (last access: 2 September 2012), 2006.

Fritz, K. M., Johnson, B. R., and Walters, D. M.: Physical indicators of hydrologic permanence in forested headwater streams, J. N. Am. Benthol. Soc., 27, 690–704, 2008.

García-Roger, E. M., Sánchez-Montoya, M. M., Gómez, R., Suárez, M. L., Vidal-Abarca, M. R., Rieradevall, M., Latron, J., and Prat, N.: Do seasonal changes in habitat features influence aquatic macroinvertebrate assemblages in permanent vs temporary Mediterranean streams?, Aquat. Sci., 73, 567–579, 2011.

García-Roger, E. M., Sánchez-Montoya, M. M., Cid, I., Verkaik, I., Karaouzas, I., Vardakas, L., Skoulikidis, N., Demartini, D., Buffagni, A., Gómez, R., Suárez, M. L., Vidal-Abarca, M. R., Rieradevall, M., and Prat, N.: Effect of spatial scale on stream macroinvertebrate community structure and composition; an insight into Mediterranean intermittent streams, Freshwater Biol., in revision, 2012.

Gasith, A. and Resh, V. H.: Streams in Mediterranean climate regions: abiotic influences and biotic responses to predictable seasonal events, Annu. Rev. Ecol. Syst., 30, 51–81, 1999.

Hawkins, C. P., Kershner, J. L., Bisson, P. A., Bryant, M .D., Decker, L. M., Gregory, S. V., McCullough, D. A., Overton, C. K., Reeves, G. H., Steedman, R. J., and Young, M. K.: A hierarchical approach to classifying stream habitat features, Fisheries, 18, 3–12, 1993.

Hedman, E. R. and Osterkamp, W. R.: Stream flow characteristics related to channel geometry of streams in western United States, USGS Water-Supply Paper 2193, 17 pp., 1982.

Hering, D., Johnson, R. K., Kramm, S., Schmutz, S., Szoszkiewicz, K., and Verdonschot, P. F. M.: Assessment of European streams with diatoms, macrophytes, macroinvertebrates and fish: a comparative metric based analysis of organism response to stress, Freshwater Biol., 51, 1757–1785, 2006.

Hewlett, J. D.: Principles of Forest Hydrology, University of Georgia Press, Athens, Ga, 183 pp., 1982.

Junk, W. J., Bayley, P. B., and Sparks, R. E.: The flood pulse concept in river-floodplain systems, in: Proceedings of the International Large River Symposium, edited by: Dodge, D. P., Can. Spec. Publ. Fish. Aquat. Sci, 106, 110–127, 1989.

Karr, J. R.: Assessment of biotic integrity using fish communities, Fisheries 6, 21–27, 1981.

Kennard, M. J., Pusey, B. J., Olden, J. D., MacKay, S. J., Stein, J. L., and Marsh, N.: Classification of natural flow regimes in Australia to support environmental flow management, Freshwater Biol. 55, 171–193, 2010.

Kirkby, M. J., Gallart, F., Kjeldsen, T. R., Irvine, B. J., Froebrich, J., Lo Porto, A., De Girolamo, A., and the MIRAGE team: Classifying low flow hydrological regimes at a regional scale, Hydrol. Earth Syst. Sci., 15, 3741–3750, doi:10.5194/hess-15-3741-2011, 2011.

Lake, P. S.: Disturbance, patchiness, and diversity in streams, J. N. Am. Benthol. Soc., 19, 573–592, 2000.

Lake, P. S.: Flow-generated disturbances and ecological responses: Floods and droughts in: Hydroecology and Ecohydrology: Past, Present and Future, edited by: Wood, P. J., Hannah, D. M., and Sadler, J. P., John Wiley & Sons, London, 2007.

Lake, P. S.: Ecological effects of perturbation by drought in flowing waters, Freshwater Biol., 48, 1161–1172, 2003.

Larned, S. T., Datry, Th., Arscott, D. B., and Tockner, K.: Emerging concepts in temporary-river ecology, Freshwater Biol., 55, 717–738, 2010.

Latron, J. and Gallart, F.: Runoff generation processes in a small Mediterranean research catchment (Vallcebre, Eastern Pyrenees), J. Hydrol., 358, 206–220, 2008.

Levick, L., Fonseca, J., Goodrich, D., Hernandez, M., Semmens, D., Stromberg, J., Leidy, R., Scianni, M., Guertin, D. P., Tluczek, M., and Kepner, W.: The ecological and hydrological significance of ephemeral and intermittent streams in the arid and semi-arid American Southwest, US Environmental Protection Agency and USDA/ARS Southwest Watershed Research Center, EPA/600/R-08/134, ARS/233046, 116 pp., 2008.

Lundlam, J. P. and Magoulick, D. D.: Spatial and temporal variation in the effects of fish and crayfish on benthic communities during stream drying, J. N. Am. Benthol. Soc., 28, 371–382, 2009.

Magalhäes, M. F., Beja, P., Schlosser, J., and Collares-Pereira, M. J.: Effects of multi-year droughts on fish assemblages of seasonally drying Mediterranean streams, Freshwater Biol., 52, 1494–1510, 2007.

Magoulick, D. D. and Kobza, R. M.: The role of refugia for fishes during drought: a review and synthesis, Freshwater Biol., 48, 1232–1253, 2003.

Marcus, W. A. and Fonstad, M. A.: Optical remote mapping of rivers at sub-meter resolutions and watershed extents, Earth Surf. Proc. Land., 33, 4–24, 2008.

Mas-Martí, E., García-Berthou, E., Sabater, S., Tomanova, S., and Muñoz, I.: Comparing fish assemblages and trophic ecology of permanent and intermittent reaches in a Mediterranean stream, Hydrobiologia, 657, 167–180, 2010.

Munné, A. and Prat, N.: Use of macroinvertebrate-based multimetric indices for water quality evalution in Spanish Mediterranean rivers: an intercalibration approach with the IBMWP index, Hydrobiologia, 628, 203–225, 2009.

Munné, A. and Prat, N.: Effects of Mediterranean climate annual variability on stream biological quality assessment using macroinvertebrate communities, Ecol. Indic., 11, 651–662, 2011.

Perrin, J. L. and Tournoud, M. G.: Hydrological processes controlling flow generation in a small Mediterranean catchment under karstic influence, Hydrolog. Sci. J., 54, 1125–1140, 2009.

Poff, N. L.: A hydrogeography of unregulated streams in the United States and an examination of scale-dependence in some hydrological descriptors, Freshwater Biol., 36, 71–91, 1996.

Puntí, T., Rieradevall, M., and Prat, N. Chironomidae assemblages in reference condition Mediterranean streams: environmental factors, seasonal variability and ecotypes. Fundamental and Applied Limnology, 170, 149–165, 2007.

Rieradevall, M., Bonada, N., and Prat, N.: Community structure and water quality in Mediterranean streams of a Natural Park (Sant

Llorenç de Munt, NE Spain), Limnetica, 17, 45–56, 1999.

Rossouw, L., Avenant, M. F., Seaman, M. T., King, J. M., Barker, C. H., du Preez, P. J., Pelser, A .J., Roos, J. C., van Staden, J. J., van Tonder, G. J., and Watson, M.: Environmental water requirements in non-perennial systems, Water Research Commission, WRC Report No: 1414/1/05, available at: http://www.wrc.org.za/KnowledgeHubDocuments/ResearchReports/1414.pdf (last access: 3 September 2012), 2005.

Rose, P., Metzeling, L., and Catzikiris, S.: Can macroinvertebrate rapid bioassessment methods be used to assess river health during drought in south eastern Australia streams?, Freshwater Biol., 53, 2626–2638, 2008.

Salo, J.: External processes influencing origin and maintenance of inland water-land ecotones, in: The Ecology and Management of Aquatic-Terrestrial Ecotones, edited by: Naiman, R. J. and Decamps, H., UNESCO Man and the Biosphere Series, 4, Parthenon, Paris, France, 37–64, 1990.

Sheldon, F., Bunn, S. E., Hughes, J. M., Arthington, A. H., Balcombe, S. R., and Fellows, C. S.: Ecological roles and threats to aquatic refugia in arid landscapes: dryland river waterholes, Mar. Freshwater Res., 61, 885–895, 2010.

Spranza, J. J. S. and Stanley, E. H.: Condition, growth, and reproductive styles of fishes exposed to different environment regimes in prairie drainage, Environ. Biol. Fish., 59, 99–109, 2000.

Svec, J. R., Kolka, R. K., and Stringer, J. W.: Defining perennial, intermittent, and ephemeral channels in eastern Kentucky: application to forestry best management practices, Forest Ecol. Manag., 214, 170–182, 2005.

Tooth, S.: Process, form and change in dryland rivers: a review of recent research, Earth-Sci. Rev., 51, 67–107, 2000.

Townsend, C. R. and Riley, R.: Assessment of river integrity: Accounting for perturbation pathways in physical and ecological space, Freshwater Biol., 41, 393–406, 1999.

Uys, M. C. and O'Keeffe, J. H.: Simple words and fuzzy zones: early directions for temporary river research in South Africa, Environ. Manage., 21, 517–531, 1997.

Walker, K. F., Sheldon, F., and Puckridge, J. T.: An ecological perspective on large dryland rivers, Regul. River., 11, 85–104, 1995.

Williams, D. D.: The biology of temporary waters, Oxford University Press, New York, 2006.

Wissinger, S. A., Greig, H. S., and McIntosh, A.: Absence of species replacements between permanent and temporary lentic communities in New Zealand, J. N. Am. Benthol. Soc., 28, 12–23, 2008.