Macroinvertebrate community response to inter-annual and regional river flow regime dynamics

Wendy A. Monk[1], Paul J. Wood[2*], David M. Hannah[3] and Douglas A. Wilson[4]

[1] Canadian Rivers Institute, Department of Biology, P.O. Box 4400, University of New Brunswick, Fredericton, New Brunswick, E3B 6E1, Canada.

[2] Department of Geography, Loughborough University, Loughborough, Leicestershire, LE11 3TU, UK.

[3] School of Geography, Earth and Environmental Sciences, University of Birmingham, Edgbaston, Birmingham, B15 2TT, UK.

[4] Monitoring, Assessment and Reporting, The Environment Agency of England and Wales, Rio House, Waterside Drive, Aztec West, Bristol, BS32 4UD, UK.

* Author for Correspondence:

Dr Paul J. Wood. Department of Geography, Loughborough University, Loughborough, Leicestershire, LE11 3TU, UK.

Phone: ++ 44 (0)1509 223012; Fax: ++ 44 (0)1509 223930

Email: p.j.wood@lboro.ac.uk

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Abstract

Spatio-temporal variability in river flow is a fundamental control on instream habitat structure and riverine ecosystem biodiversity and integrity. However, long-term riverine ecological time-series to test hypotheses about hydrology-ecology interactions in a broader temporal context are rare, and studies spanning multiple rivers are often limited in their temporal coverage to less than five years. To address this research gap, a unique spatio-temporal hydroecological analysis was conducted of long-term instream ecological responses (1990-2000) to river flow regime variability at 83 sites across England and Wales. The results demonstrate clear hydroecological associations at the national scale (all data). In addition, significant differences in ecological response are recorded between three 'regions' identified (RM1-3*) associated with characteristics of the flow regime. The effect of two major supra-seasonal droughts (1990-1992 and 1996-1997) on inter-annual variability of the LIFE scores is evident with both events showing a gradual decline before and recovery of LIFE scores after the low flow period. The instream community response to high magnitude flow regimes (1994 and 1995) is also apparent, although these associations are less striking. The results demonstrate classification of rivers into flow regime regions offers a way to help unravel complex hydroecological associations. The approach adopted herein could easily be adapted for other geographical locations, where data sets are available. Such work is imperative to understand flow regime-ecology interactions in a longer-term, wider spatial context and so assess future hydroecological responses to climate change and anthropogenic modification of riverine ecosystems.

Keywords

Lotic-invertebrate Index for Flow Evaluation (LIFE); river regime variability; environmental flows; Indicators of Hydrologic Alteration (IHA); hydroecology.

Introduction

Temporal and spatial variability in river flow is recognised as a fundamental control on instream habitat structure and availability, and riverine ecosystem biodiversity and integrity (Naiman et al., 2002; Richter *et al.*, 2003; Arthington *et al.*, 2006; Dudgeon *et al.*, 2006). Instream faunal communities are adapted to the 'natural' flow regime and the variability in magnitude, frequency, timing and duration of high, low and intermediate flow events (e.g., Jowett and Duncan, 1990; Lytle and Poff, 2004; Monk *et al.*, 2006). As a result, there is a growing interest in the identification of ecologically relevant hydrological descriptors, which may be used to characterise and quantify 'natural', semi-natural, and anthropogenic modifications to river flow regimes (e.g. Clausen and Biggs, 1997; Jowett and Duncan, 1990; Monk *et al.*, 2006; Olden and Poff, 2003; Richter *et al.*, 1998; Sheldon and Thoms, 2006). When combined with biological data, these hydrological descriptors can be used as a basis for the development of ecologically sustainable management strategies that balance anthropogenic demands on water resources against protecting, conserving and even enhancing, instream habitat and communities (Petts *et al.*, 2006; Poff *et al.*, 2003; Richter *et al.*, 2006; Tharme, 2003).

The critical importance of long-term hydroecological time-series in understanding and managing riverine ecosystems has been highlighted recently (e.g., Hannah *et al.*, 2004; 2007; Holmes 2006; Jackson and Fűreder, 2006). Hydrological and hydroclimatological studies, including palaeohydrology, have long recognised that both short- and long-term variations in precipitation and river flow occur, and that analyses of extended time-series are essential to place extreme events (floods and droughts) within an appropriate historical context (e.g., Barker *et al.*, 2004; Jones *et al.*, 2006; Macklin and Rumsby, 2007). Long-term hydroclimatological time-series can provide a benchmark against which recent and predicted future changes (natural or anthropogenic) may be gauged (Marsh *et al.*, 2007). However, in contrast to the hydrological sciences, there are few long-term ecological time-series for riverine ecosystems (Jackson and Fűreder, 2006, Monk *et al.*, 2006; Reid and Ogden 2006). The vast majority of ecological time-series are limited in duration, perhaps reflecting the resource intensive nature of generating species-level ecological data (Holmes 2006). Longer duration ecological datasets are almost invariably confined to individual rivers or catchments, where data have been collected in targeted studies of response to ecosystem change or disturbances such as acidification, drought and water transfer schemes, or as part of community change/ persistence studies (e.g. Bradley and Ormerod, 2002; Wagner and Schmidt, 2004; Wood and Armitage, 2004; Woodward *et al.*, 2002). Hence, there is a pressing need for hydroecological studies using long-term data that span a wider geographical range to assess the nature, dynamics and representativeness of river hydrology-ecology relationships (Monk et al., 2007a).

Results from the available long-term hydroecological studies indicate that instream communities are influenced by variations in both the climatological (Bradley and Ormerod, 2001; Daufresne *et al*., 2003; Scarsbrook *et al.*, 2003) and hydrological regimes (e.g., Lamouroux et al., 2006; Monk *et al.*, 2006, Scarsbrook, 2002; Wagner and Schmidt, 2004; Wood *et al.*, 2001). However, attempts to quantify macroinvertebrate community response to river flow variability, and in particular high and low flows, are currently limited in terms of their temporal (typically <5 years study period) and/or geographical coverage (e.g., Caruso 2002; Clausen and Biggs, 1997; Sheldon and Thoms, 2006; Suren and Jowett, 2006).

Given this context, this paper aims to examine macroinvertebrate community response to inter-annual hydrological variability using a national scale long-term paired hydrological (1980 - 2000) and ecological dataset (1990 - 2000). The specific objectives are: (1) to identify temporal (between year) and spatial patterns in the hydrological regimes using a statistical river classification scheme applied over a 21-year period (1980 - 2000) and, more specifically, define 'regions' with similar flow regime magnitudes (RM); and (2) to assess temporal (between-year) and spatial (between-region) dynamics in instream macroinvertebrate community response to inter-annual regime variability, and in particular periods of high and low flow, over an 11-year period (1990–2000). This study provides a synchronous and wider temporal and spatial perspective on river hydroecological associations than hitherto undertaken and, in so doing, reveals important, more robust information about macroinvertebrate community response to inter-annual and spatial river flow regime dynamics.

Methodological approach

Dataset

The LIFE paired dataset (version 1.03), developed by the Environment Agency of England and Wales, provided the basis for analysis. The data set combines long-term river gauging records with adjacent routine biomonitoring (benthic macroinvertebrate) stations for 291 sites across England and Wales. The LIFE data set includes sites that are largely unaffected by water quality issues and other confounding factors (i.e., close proximity to an impoundment) that may mask and/or modify the influence of flow regime variability on instream communities. Preliminary screening of data was undertaken to ensure that only sites with the most complete and comprehensive records were included.

To be included in our analysis, each site required a minimum of 21 years discharge data (1980 - 2000) to characterise the range of hydrological conditions typically experienced by UK rivers (Bower *et al.*, 2004). For sites with <10% missing data in any one year, data gaps were interpolated using long-term mean daily flows; whereas, sites with ≥10% missing data were excluded from the analysis. In addition, a minimum of 10 macroinvertebrate samples were required at each site during the study period (1990-2000). Sampling of rivers by the Environment Agency usually occurs during two standard survey periods each year (spring and autumn) although samples may not be collected on every occasion due to a variety of reasons (e.g., local flooding or site access problems associated with agricultural activity). Following preliminary analysis, the autumn sampling period was selected for detailed analysis since it contained a greater number of samples and corresponds to the end of the annual period of low flow prior to the rise of the hydrograph for most rivers throughout England and Wales (Bower *et al.*, 2004). All macroinvertebrate samples were collected using the Environment Agency's standard macroinvertebrate sampling protocol (3-minute kick sample with an additional 1-minute hand search), covering instream habitats in proportion to their occurrence (Murray-Bligh, 1999). This provides a semi-quantitative sample (Furse *et al.*, 1981), which has proved effective in detecting temporal changes in previous English and Welsh research (Bradley and Ormerod, 2002; Davy-Bowker at al., 2006). All taxa were identified to at least family level and recorded within five relative abundance ($\log_{10}$) categories (A = ≤ 9, B = 10 – 99, C = 100 – 999, D = 1000 – 9999, E = ≥10000 individuals per family). Our screening criteria resulted in 83 river sites, paired with 721 autumn (September, October or November) macroinvertebrate samples, being available for analyses.

Data analyses

Hierarchical agglomerative cluster analysis (Ward's method) was used to examine spatial and temporal variability in the annual hydrological regimes of the 83 rivers, yielding a total of 1660 station-years for analysis. The approach used was developed by Hannah *et al.* (2000), modified by Harris *et al.* (2000) and evaluated by Bower *et al.* (2004). The method produces a flow regime regionalisation through the identification of hydrologically homogeneous areas. The classification scheme was applied using a two-stage procedure to separately identify: (1) hydrologically homogenous regions (spatially) based on long-term magnitude (size) of flow regimes (1980-2000) and (2) individual years with similar annual magnitude of flow regimes. This dual classification forms the basis for the subsequent hydroecological analysis and allows both the long term 'average' and the year-to-year variability of the flow regime of individual sites and regions to be characterised, and its influence on the instream macroinvertebrate community to be assessed. In both applications, the magnitude of the hydrological regime was quantified by four indices: mean, maximum, minimum and standard deviation of the annual (single year) or long-term (1980 – 1999) discharge time-series. Prior to classification of the flow regime, discharges (m^3s^{-1}) were converted to runoff (mm $month^{-1}$) and transformed to *z*-scores (mean = 0; standard deviation = 1) to remove any statistical bias associated with catchment area (Monk *et al.*, 2006). The hydrological time-series for each site was divided into hydrological years commencing in August, since July was identified as the most frequent month of minimum runoff across the selected rivers. This timeframe ensured the rising limb, annual peak and flow recession were included within the same 12-month period. Long-term regions and temporal changes in the inter-annual flow regime magnitude classes (IA) were plotted in ArcMap (ESRI Inc., 2005), a Geographical Information System (GIS), allowing spatial structure to be readily visualised.

Each benthic macroinvertebrate sample was quantified using the Lotic-invertebrate Index for Flow Evaluation (LIFE) score (Extence *et al*., 1999). The LIFE methodology was developed to facilitate the assessment of environmental flows by linking semi-quantitative changes in instream macroinvertebrate communities with river flow regimes. The LIFE score assigned to taxa is based on published quantified preferences and expert opinion regarding the sensitivity of benthic macroinvertebrates, at both species and family level, to flow velocity. Previous research has demonstrated the utility of the LIFE methodology compared to other metrics (e.g., total abundance, number of taxa and diversity indices) when using data recorded in $\log_{10}$ abundance categories at the family level; and that the LIFE score is a more appropriate and statistically powerful metric compared to other macroinvertebrate biotic indices (e.g., BMWP and ASPT) when examining the ecological response to flow regime variability (Monk *et al.*, 2006). Other research has shown the LIFE score to be sensitive to both natural river flow variability and anthropogenic modification (Extence *et al.*, 1999; Dunbar and Clarke, 2004). LIFE scores are now routinely used by the Environment Agency and public water companies in the UK to identify sites subject to hydrological stress, for water resources planning, and for Catchment Abstraction Management Strategies (CAMS). For further details regarding the derivation of LIFE, and the scores for individual macroinvertebrate families and species, see Extence *et al.*, (1999).

A total of 201 hydrological variables were derived for each site from the raw river flow time-series based on the Range of Variability Approach (RVA) and Indicators of

Hydrological Alteration (IHA) methodology and its derivatives (Richter et al., 1996; Richter et al., 1997; Olden and Poff, 2003). These variables were derived from the raw daily, monthly or annual series (as appropriate) independently of the regime classification outlined above and were only transformed if required to comply with the underlying assumptions of parametric statistical tests (e.g., a normal distribution). In the current application, only two of the three hydrological indices used required transformation using natural logarithms (ln) prior to analysis. The hydrological variables were used to examine how macroinvertebrate communities responded to inter-annual flow regime variability at the national scale and for the long-term regime magnitude (RM) regions. The hydrological descriptors identified previously by Monk *et al.* (2006; 2007b) demonstrating the strongest statistical association with LIFE scores for the long-term RM classes are presented herein to explore the relationship between 'flow' and instream macroinvertebrates over the 11-year biological record. Hereafter these variables are described as the 'most significant hydrological descriptors'. One-way analysis on variance (ANOVA) was used to examine differences in standardised LIFE scores (sample LIFE score minus the long-term average for the site) between inter-annual (IA) regime classes following the application of the Levene's test to confirm that homogeneity of variances were not significant. Differences between the IA classes were examined using Tukey's post-hoc multiple comparisons test to identify where significant differences occurred.

Results

Long-term regime magnitude regionalisation

Five distinct long-term (1980-2000) flow regime magnitude (RM) groups were identified for the 83 sites across England and Wales based on inspection of the cluster dendrogram and agglomeration schedule (scree plot). Based on the four magnitude indices, the flow regimes were characterised thus (Table 1): (1) RM1 - low magnitude regimes (with the lowest mean, maximum, minimum and standard deviation of runoff) and predominately located on pervious geologies located in southern and eastern England (42 sites); (2) RM2 low-intermediate magnitude regime (with the second lowest mean, maximum, minimum and standard deviation of runoff) and were widely distributed across southern, central and northern England on a mixture of geologies (29 sites); (3) RM3 -intermediate magnitude (5 sites); (4) RM4 intermediate-high magnitude (5 sites); and (5) RM5 - high magnitude (2 sites). The latter three groups (RM3-RM5) contained only 12 sites (with the highest overall mean, maximum, minimum and standard deviation of runoff) in total and so they were combined in the current analysis (referred to as RM3*) because of their clustered geographic distribution in northern England (except a single site in Wales) and association with largely impervious basin geologies (Figure 1). Combining these three groups into RM3* increased the number of replicates within this 'higher' magnitude group. In addition to broad hydrogeological zones, the west-east pattern of decreasing regime magnitude also maps onto the known deceasing northwest to southeast precipitation gradient across England and Wales (Bower *et al.*, 2004).

Inter-annual regime variability

The inter-annual (IA) flow regime magnitude classification identified three distinct classes (Table 1 and Figure 2), which may be arranged in ascending magnitude order:

(1) ***Class IA1*: *Low***, with the lowest values for all four magnitude indices (407 station-years).

(2) ***Class IA2*: *Intermediate***, yielding intermediate (i.e. between IA1 and IA3) values for mean, maximum and standard deviation of runoff but with relatively high minimum runoff (762 station-years).

(3) ***Class IA3*: *High***, exhibiting the highest values for mean, maximum and standard deviation of runoff with intermediate minimum runoff values (491 station-years).

When the results were mapped clear spatial patterns in the inter-annual runoff regimes were observed (only flow regimes maps for 1990-2000 are presented in Figure 3 as this periods overlaps with available biological data). The flow regimes for the year ending in July 1990 indicated a mixture of runoff regimes across the country (Figure 3a). However, for the following two hydrological years, flow regimes were dominated by low runoff magnitude (Figure 3b-c). This dominance was most marked in 1992 when, with the exception of eight sites in north-west England and one site in the south, all sites were characterised by low runoff magnitude (Figure 3c). 1993 illustrated a marked transition, with the majority of the sites in northern England characterised by intermediate regimes, and central, southern and eastern sites comprising intermediate and high magnitude regimes. Only four sites in eastern England were characterised by low runoff magnitude (Figure 3d). During the subsequent two hydrological years (1994-1995), the majority of sites experienced high magnitude regimes with only four (1994) and six sites (1995) being characterised by intermediate magnitude regimes (Figure 3e and 3f) and just a single site in 1995 being characterised by a low magnitude regime. The next year (1996) showed another (cf. 1993) marked transition with the majority of sites (except six sites in southern England and one high magnitude regime site in south-west England) displaying low magnitude regimes (Figure 3g). Similarly, 1997 was dominated by low magnitude regimes with the exception of two sites in southern England, one on the east coast and a group of 14 sites in northern England characterised by intermediate (11 sites) and high (three sites) magnitude regimes (Figure 3h). The following year (1998) illustrated a mosaic of regimes across England (Figure 3i). The final two years of the study period, (1999-2000) were dominated by high and intermediate magnitude regimes, respectively (Figure 3j and 3k). Notably, there is a distinct geographical division in the distribution of classes for 1999 with northern sites characterised by intermediate and the rest of the study area characterised by high magnitude regimes (Figure 3j), whereas during 2000 the pattern is reversed (Figure 3k).

Inter-annual hydroecological variability

Examination of standardised LIFE scores for all sites over the entire study period indicated a clear inter-annual pattern, with low values at the start of the study period (1990-1992) prior to a marked rise and peak in 1994. This was followed by a clear reduction in the subsequent two years (1995-1996) and an increase in LIFE scores from 1996-2000 (Figure 4a). The inter-annual variability of LIFE scores (Figure 4a) displayed a similar pattern to that of the 'most significant hydrological descriptor', the Specific Median Discharge [lnSMED - median discharge (Q_{50}) divided by the catchment area (km^{-2})] adjusted $R^2 = 0.381$, $p < 0.001$ (Figure 5a). One-way analysis of variance (ANOVA) indicated a significant difference between the three inter-annual regime classes when all sites were considered (F= 19.58, p<0.001). Tukey's post-hoc multiple comparisons indicated a significant difference in the LIFE scores between the low and high IA regime classes (p<0.001), and that a significant difference between the low and intermediate IA regime classes also occurred (p<0.001) (Figure 6a)

The long-term regime magnitude classification (RM1-RM3*) provided the basis for structuring analysis of inter-annual regime patterns and their association with macroinvertebrate data. Examination of RM1 rivers indicated similar inter-annual patterns of LIFE scores and the 'most significant hydrological descriptor' (lnSMED – adjusted $R^2 = 0.357$, $p < 0.001$) (Figure 4b and Figure 5b). However, in contrast to the pattern recorded for all sites, LIFE scores were lower in 1997 before increasing over the following two years (1998-1999). ANOVA indicated that significant differences occurred between IA regime classes ($F = 13.99$, $p<0.001$). Tukey's post-hoc multiple comparisons indicated significant differences between low and high IA regime classes ($p<0.001$), and low and intermediate IA regime classes ($p<0.001$) (Figure 6b).

The inter-annual pattern of LIFE scores for RM2 sites reflected a similar, although more subdued, general inter-annual pattern to that shown for all sites and RM1. However, within-year variance was greater for RM2, particularly 1994 (Figure 4c). ANOVA indicated that significant differences occurred between the IA classes ($F = 4.72$, $p<0.05$). Tukey's post-hoc multiple comparisons indicated significant differences between low and high IA regime classes ($p<0.05$), and low and intermediate IA classes ($p<0.05$) (Figure 6c). The inter-annual pattern of the LIFE scores and the 'most significant hydrological descriptor' (lnQ1090DF - ratio of daily discharges Q_{10}/Q_{90} of percentile flows) displayed little correspondence (adjusted $R^2 = 0.209$, $p < 0.001$) with the exception of 1990 - 1993 (Figure 4c and Figure 5c).

The inter-annual pattern of standardised LIFE scores for RM3* displayed the most variability of any of the regions (Figure 4d). The final year in the series (2000) has been excluded from the analysis because floods during the early autumn prevented the collection of macroinvertebrate samples from ten of the 12 sites in this region. In marked contrast to the other regions, the highest LIFE scores were recorded during 1993 (Figure 4d) compared to 1994 for all sites, RM1 and RM2. Analysis of variance (ANOVA) indicated there was no significant difference among IA regime classes (F = 2.18, p = 0.120) (Figure 6d). When the inter-annual pattern of LIFE scores were compared with the 'most significant hydrological descriptor', the Positive Rise Rate (PORR – Number of positive changes in discharge from one day to the next – adjusted $R^2 = 0.096$, $p < 0.01$), little similarity in the pattern was observed (Figure 4d and Figure 5d).

Discussion

This research provides a spatially and temporally unique hydroecological analysis of the long-term instream ecological responses to flow regime variability at multiple sites. The results provide new evidence of the influence of flow regime variability on instream communities, and support the findings of some previous longer-term studies of single river basins/ sites (e.g., Wood *et al.*, 2001; Wagner and Schmidt, 2004) and short-term research at larger (national) spatial scales (e.g., Clausen and Biggs, 1997). The methodological approach employed demonstrates the value of identifying distinct river regime types, which may be grouped into physically-interpretable hydrological regions (e.g. Buttle, 2006; Kingston *et al.*, 2006; Wagener *et al.*, 2007). The results also clearly indicate that significant inter-annual regime variability occurs and that this can be clearly detected at a national and regional scale (Figure 3 and Table 2).

Inter-annual river regime variability during the study period (1990 - 2000) reflected climatological patterns recorded for England and Wales (Bower *et al.*, 2004; Marsh *et al.*, 2007). The 11-year period for which macroinvertebrate data are available includes two major droughts events (1990-1992 and 1996-1997). A pattern of declining flow and extended periods of low flow can be clearly identified within the inter-annual magnitude classes between 1991-1992 and 1996-1997 (Figure 3). These events correspond to major droughts and constitute 'supra-seasonal events' (Lake, 2003), extending over more than one season or year, and resulted in significant impacts on river flows (e.g. Burt *et al.*, 1998; Peters *et al.*, 2006) and instream ecology (Wood and Armitage, 2004; Wright et al., 2004). Years associated with higher regime magnitudes can also be clearly identified (1994 - 1995 and 1999 - 2000) (Figure 3). These years represent the highest monthly mean, maximum, minimum and standard deviation in runoff (recorded during the study period - 1980-2000). However, in contrast to low magnitude regime years that generally correspond to national-scale drought events, years characterised by high regime magnitude do not necessarily correspond to patterns of flooding at a national- or regional-scale. Although the notable exception to this was that the ecological samples for RM3* during autumn 2000 could not be collected due to regional flooding.

The long-term (1980-1999) regime magnitude regionalisation highlighted that distinct regime types (regions) can be identified across England and Wales, and perhaps more significantly, inter-annual regime variability differed between-regions. RM1 and RM2 had wide and overlapping geographical distributions. Rivers comprising RM1 generally mirror the 'national' pattern of flow regime variability (Figure 4a and Figure 4b). Those sites comprising RM2 displayed greater within-year variance and as a result little inter-annual variability could be discerned beyond the years representing the 'extremes' (i.e. low and high years) in the series. In contrast to the other regions, RM3* had a clear geographical focus in north-western England (Figure 1). The majority of the sites comprising RM3* were characterised by a different inter-annual regime classes (IA) to those of RM1 and RM 2 sites during 1992, 1997, 1999 and 2000 (Figure 3c, h and j-k). This spatial pattern reflects a west-east hydroclimatological gradient across the UK (Bower *et al.*, 2004). The hydrological response of RM3* rivers is also strongly modified by the impervious geologies dominating these catchments, which results in limited water catchment storage and no hydrological buffering by major aquifers (Bower *et al.*, 2004; Monk *et al.*, 2006). To qualify this discussion, it should be noted that parts of England and Wales are underrepresented within the data set, particularly Wales, south-west England and upland sites in general (Figure 2). Only a limited number of sites from these areas were used in the analysis due to the volume of missing data. This paucity of data reflects the difficulties of maintaining long-term gauging stations and the collection of biological samples within predefined time windows for riverine systems with 'flashy' hydrographs.

Examination of the long-term LIFE scores for rivers at the national scale clearly indicated that the inter-annual pattern (1990-2000) closely tracked, or corresponded with, the 'most significant hydrological descriptor' (lnSMED = specific median discharge; Figure 4a and Figure 5a) identified from 201 flow descriptors (Monk et al., 2006; Monk et al., 2007b; Olden and Poff, 2003). This flow index provides an annual measure of river flow (discharge) scaled by catchment area. This variable is one of a sub-set of flow descriptors of 'magnitude of average conditions' (part of the magnitude of flow events category) within the Indicators of Hydrologic Alteration methodology (Richter et al., 1996; Olden and Poff, 2003). Although lnSMED was identified at the national scale, at the regional scale other hydrological descriptors were identified as the 'most significant hydrological descriptors' for two RM groups. This suggests that an approach which incorporates a suite of variables from the IHA methodology may be the most appropriate to characterise the way in which instream ecology responds to changes in the flow regime. Redundancy methods have been suggested as a means of reducing the range of hydrological predictors of ecological response. However such an approach may overlook more subtle ecological associations (Monk et al., 2007b).

RM1 displayed a similar pattern of inter-annual regime variability to that identified at the national scale, except the year of lowest flow and mean LIFE scores was 1997 opposed to 1996, and the same hydrological descriptor (lnSMED) best characterised the ecological response (RM1; Figure 4b and Figure 5b). Region RM1 comprised just over half of the sites examined (42 stations) and corresponds with the location of permeable geologies (primarily chalk) in southern and eastern England. The high baseflow component of these rivers probably acts as a 'filter' and so serves as a buffer for any rapid response (rise and/or fall) of the hydrograph.

Examination of the 'most significant hydrological descriptors', for the other long-term regime magnitude groups (RM2 and RM3*) did not display such a high degree of concordance with inter-annual ecological time-series (Figure 4 and Figure 5). This demonstrates that the hydrology and ecology of different river 'types' interact in a variety of ways and also that additional factors (i.e. other than the flow regime such as climatology, catchment characteristics, habitat availability, water chemistry and biological interactions) may be important in structuring instream macroinvertebrate communities (Allan et al., 1997; Doisy and Rabeni, 2001; Hughes and James, 1989; Poff and Ward, 1989; Rabeni and Doisy, 2000; Richards *et al.*, 1997; Richards and Minshall, 1992; Sponseller *et al.*, 2001). In the case of RM2, the 'region' is widely distributed across the study area and the variable LIFE scores recorded and high variance of the 'most significant hydrological descriptor ($\ln Q_{10}/Q_{90}$ – from the magnitude of flow events category within the IHA methodology) (Figure 4c) may reflect these 'additional' factors. In the case of RM3*, the rivers are characterised by 'flashy' regimes with relatively rapid rises and falls of the hydrograph. The 'most significant hydrological descriptor' of the macroinvertebrate community response to regime variability was the positive rise rate (PORR - from the rate of change of flow conditions category within the IHA methodology) and, although this provides a strong indication of the ecological importance of a 'flashy' regime, it displayed little concordance with the ecological time-series. It is likely that local site specific factors may be particularly important for these rivers because storage of water within the catchment may be limited and as a result channel morphology and riparian habitat characteristics may become of primary importance in determining the volume and timing of delivery of water downstream.

The significance of the preceding hydrological conditions for instream ecological response has been demonstrated in other studies of individual catchments (e.g. Clausen and Biggs, 1997; Wagner and Schmidt, 2004; Wood *et al.*, 2001). The inter-annual variability of the LIFE scores, at the national scale and for the largest regime magnitude group (RM1), indicated that the response to the two major droughts recorded within the series (summer 1990-1992 and summer 1995-1997) were clearly detectable with both events showing a gradual decline before and recovery in the LIFE score after the events. Previous research from other locations across the globe has reported relatively rapid recovery times associated with hydrological disturbances such as floods (e.g. Collier and Quinn, 2003; Robinson *et al.*, 2004) and short duration droughts (e.g. Hynes, 1958; Extence 1981; Ledger and Hildrew 2001; Lake, 2003). However, the recovery pattern associated with supra-seasonal droughts has not been widely reported (Lake 2003) and data demonstrating the extended duration of faunal recovery over two years were limited to a small number of sites until now (e.g., Wood *et al.*, 2000; Wood and Armitage 2004; Wright et al., 2004).

The results also demonstrate that instream communities respond to flow regimes of high magnitude (such as 1994 and 1995; Figure 4). However, the influence of higher flows on the autumn ecological data is less clear and more variable at both the national and regional scale, probably reflecting the predominance of higher flows during the late autumn and winter periods (12 to 9-months prior to the 'autumn' biological sample collection). This lag between high flow events and biological sample collection may allow recovery of the community to occur and act as a filter during the intervening period, so that it may not be possible to detect the influence of winter and spring spates by examination of the subsequent 'autumn' biological samples alone. However, it may be possible to address this in future research by utilising both spring (6-3 months prior to sample collection) and autumn biological samples, and through detailed site-by-site analyses. Further refinement (i.e. finer scale) of the long-term regime magnitude classification may also be required for RM2 and RM3* rivers to fully explore the influence of biogeographical factors and site specific influences.

Conclusions

Temporal and spatial variability of river flow regimes are recognised as a fundamental control on instream habitat structure and availability and, in turn, riverine ecosystem biodiversity and integrity. However long-term riverine ecological time-series (usually focused on single rivers) to test hypotheses about hydrology-ecology interactions in a broader temporal context are rare (Jackson and Fűreder, 20006; Reid and Ogden, 2006). Conversely, such research over a wider spatial domain (i.e. multiple rivers) is often limited in its temporal dimension to less than five-years (Clausen and Biggs, 1997; Sheldon and Thoms, 2006). The research presented herein represents a unique spatio-temporal hydroecological analysis of long-term instream ecological responses to river flow regime variability at 83 sites across England and Wales. The research aimed to: (1) identify temporal (inter-annual) and spatial (define regions) patterns in flow regime magnitude using a statistical river classification applied over a 20-year period (1980-2000); and (2) assess temporal (between-year) and spatial (between-region) dynamics in instream macroinvertebrate community response (characterised using LIFE scores) to flow regime variability over an 11-year period (1990–2000). The results clearly demonstrates that inter-annual regime variability can be identified at both the national and regional level, and that the influence of periods of low magnitude (1990-1992 and 1996-1997) and higher magnitude flow (1994-1995) can be identified within the ecological series.

The methodological approach used could be applied to other locations and biological groups with relative ease, provided that hydrological and ecological time-series are available. The research demonstrates the value of long-term biomonitoring programmes where a range of river types, including pristine/semi-natural are sampled. The LIFE methodology and metric (derived for the sites largely unaffected by water quality issues) used in this study has demonstrated its sensitivity to flow variability and its value for instream research. It is currently the only metric of its type and could be relatively easily adapted for other geographical locations.

Further research examining biological samples collected during the spring seasonal surveys within the LIFE paired dataset would be particularly useful to aid understanding of the ecological legacy of higher flows on instream ecology. In addition, other factors influencing ecosystem responses, such as site specific channel morphology, riparian habitat characteristics, and regional biogeography, need to be considered so that they can be controlled for in future models of ecological response to flow variability. A greater understanding of the influence of regional and site specific factors may ultimately enable the inter-annual variability of the instream community to be placed into the longer-term context of changing hydroclimatological patterns (e.g. under climate change) and future responses to climate change and anthropogenic modification of riverine ecosystems.

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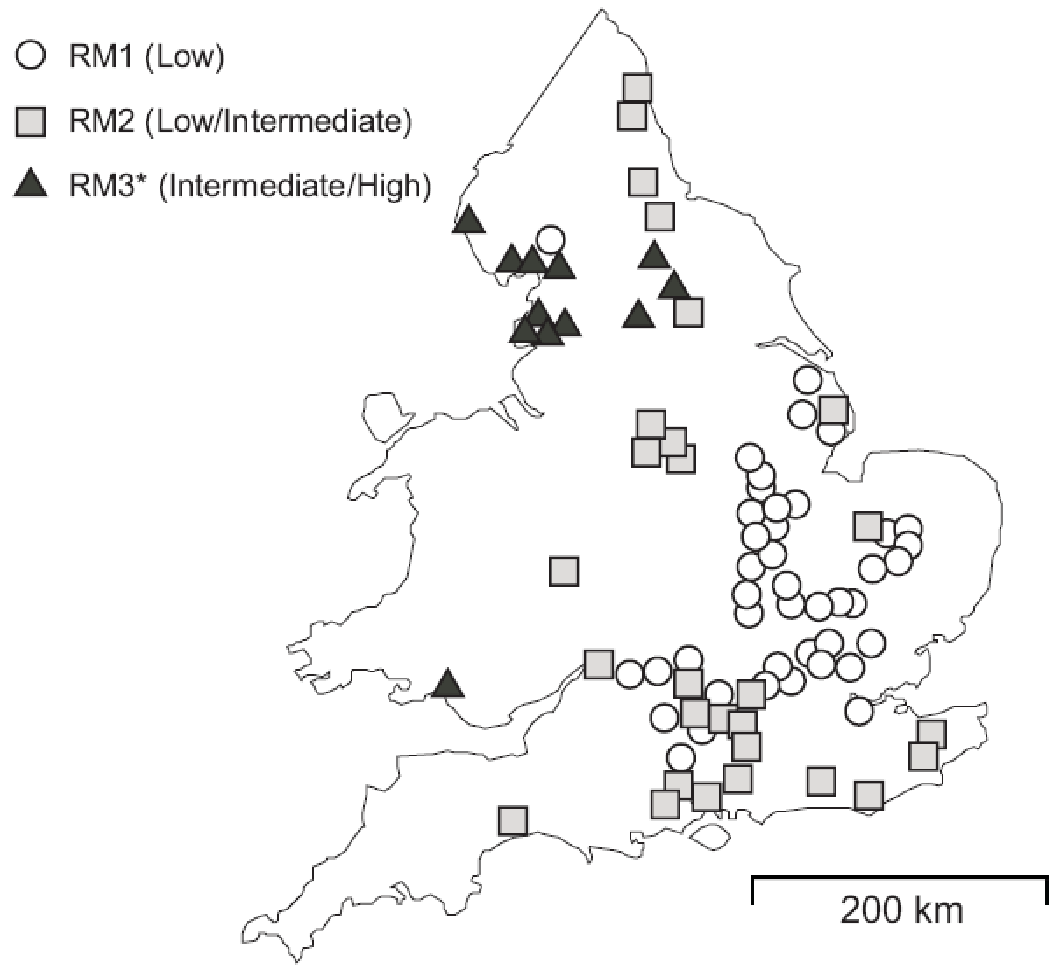
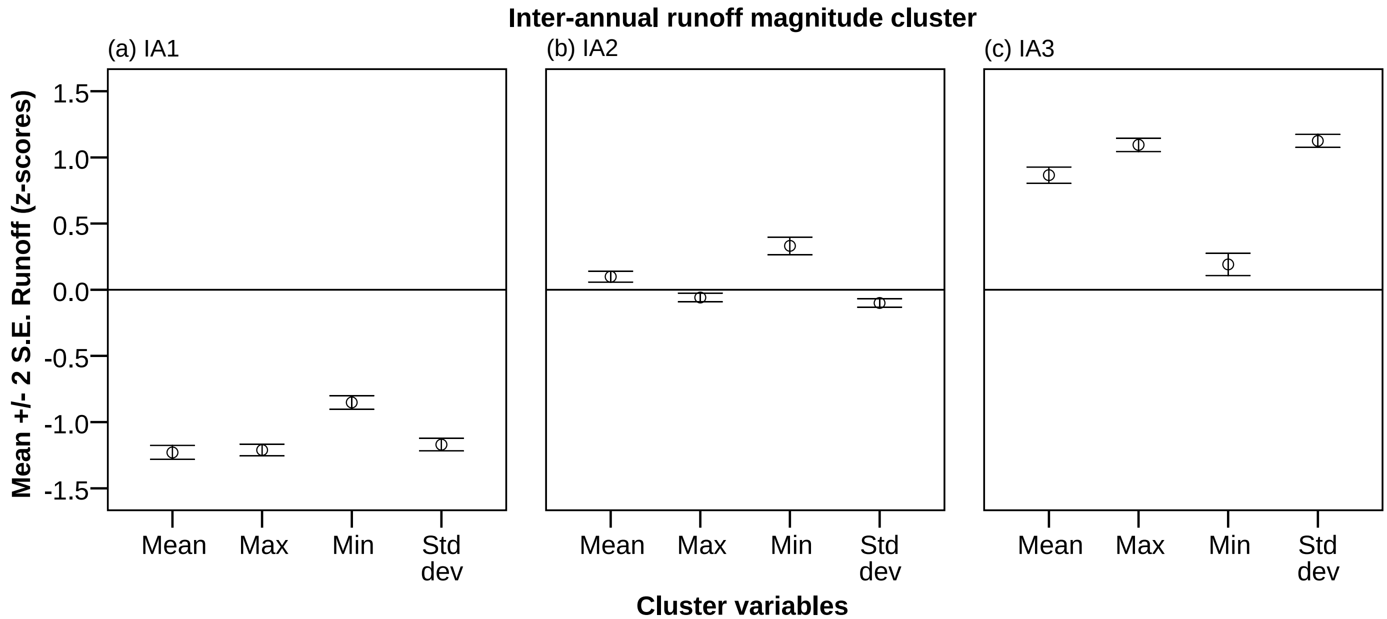
Table 1 – Summary of the runoff (mm month^{-1}) characteristics (standard deviation) of the mean, maximum, minimum and standard deviation for the (i) long-term regional magnitude (RM) and (ii) inter-annual (IA) magnitude clusters.

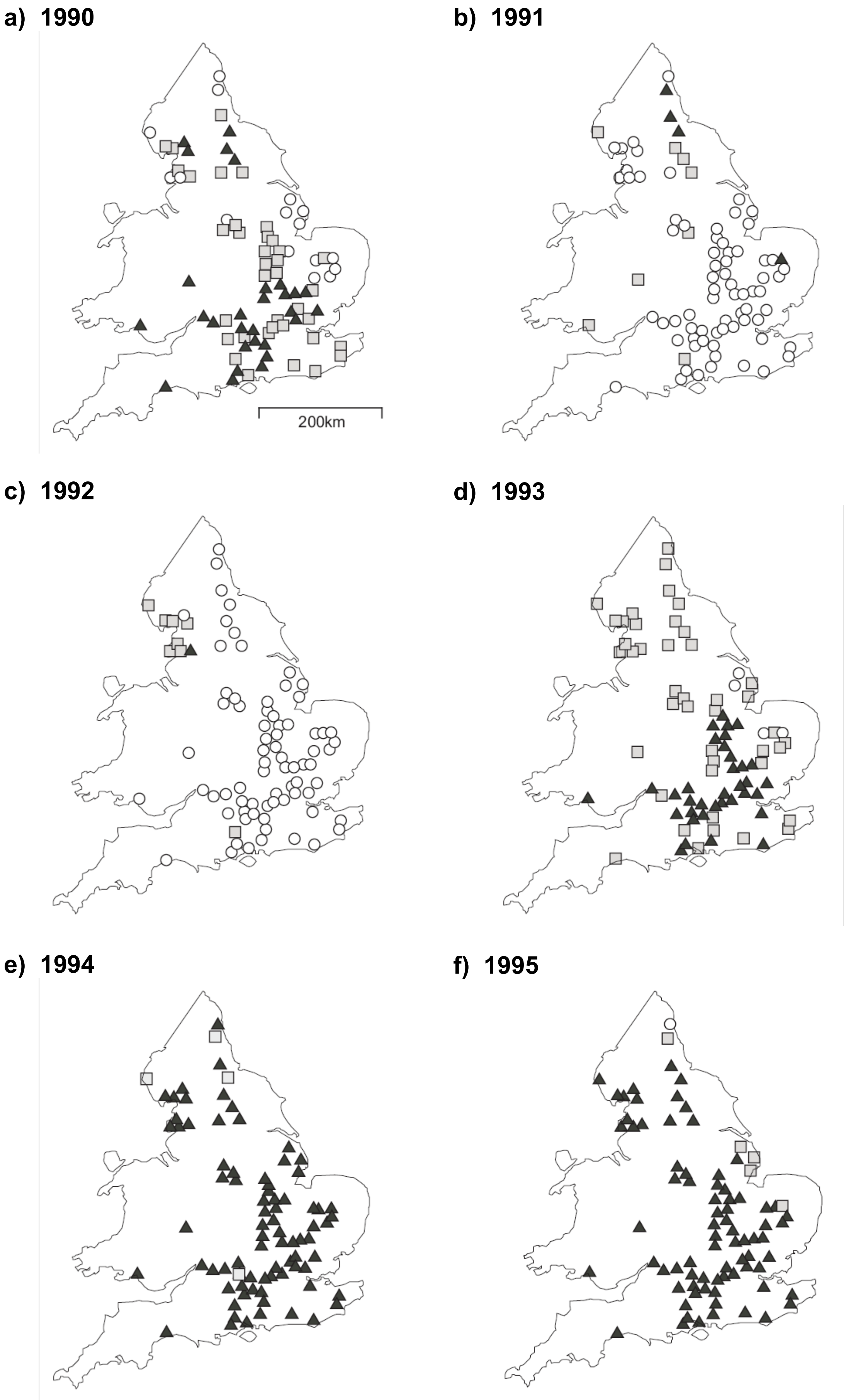
Regime group	Number of stations or station years	Class average (standard deviation) (mm month^{-1})			
		Mean	Maximum	Minimum	Standard deviation
(i) Regionalisation					
RM1	42	13.96 (5.29)	53.67 (24.48)	1.95 (1.35)	4.00 (1.89)
RM2	29	32.01 (13.48)	102.57 (49.77)	7.26 (2.43)	9.56 (7.20)
RM3*	12	101.17 (35.49)	277.22 (120.97)	14.64 (9.52)	42.00 (25.50)
(ii) Inter-annual					
IA1	407	20.96 (26.70)	45.75 (58.34)	6.31 (5.98)	12.63 (17.40)
IA2	762	34.62 (33.78)	75.93 (75.99)	10.39 (9.53)	21.63 (23.39)
IA3	491	40.03 (38.65)	98.58 (95.12)	9.81 (8.80)	28.88 (28.67)

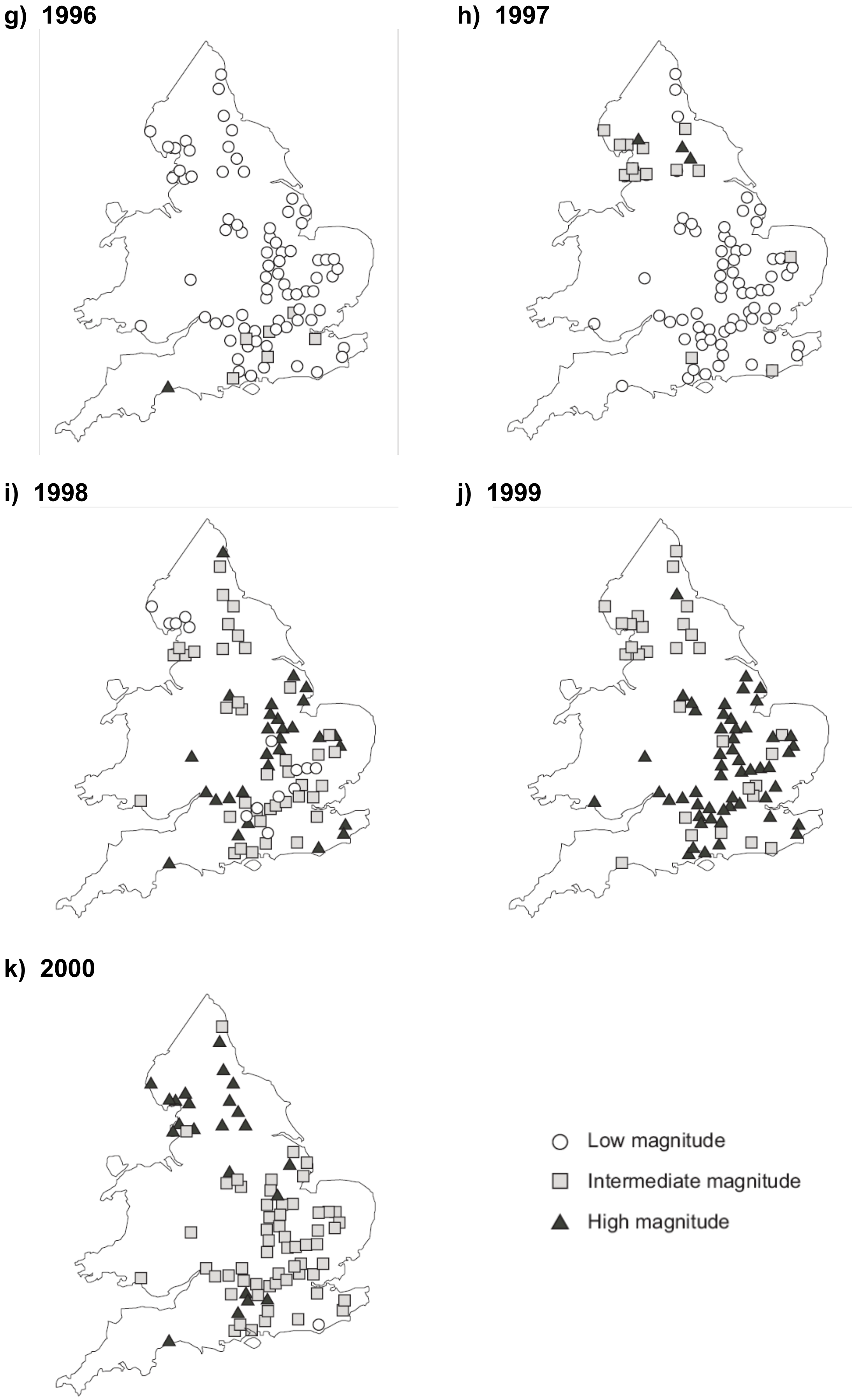


RM1 (Low)
RM2 (Low/Intermediate)
RM3* (Intermediate/High)
200 km

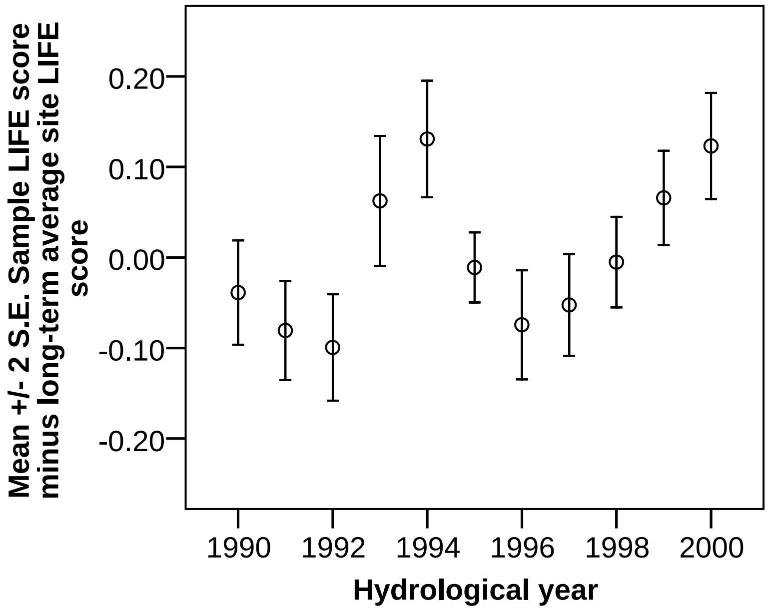


Inter-annual runoff magnitude cluster
(a) IA1
(b) IA2
(c) IA3
Mean +/- 2 S.E. Runoff (z-scores)
1.5
1.0
0.5
0.0
-0.5
-1.0
-1.5
Mean
Max
Min
Std dev
Cluster variables

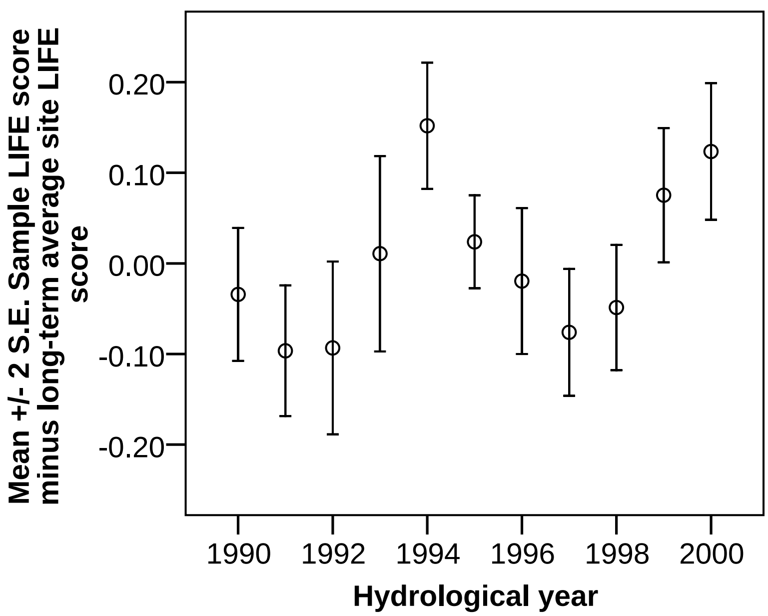

a) 1990
200km
b) 1991
c) 1992
d) 1993
e) 1994
f) 1995


g) 1996
h) 1997
i) 1998
j) 1999
k) 2000
Low magnitude
Intermediate magnitude
High magnitude

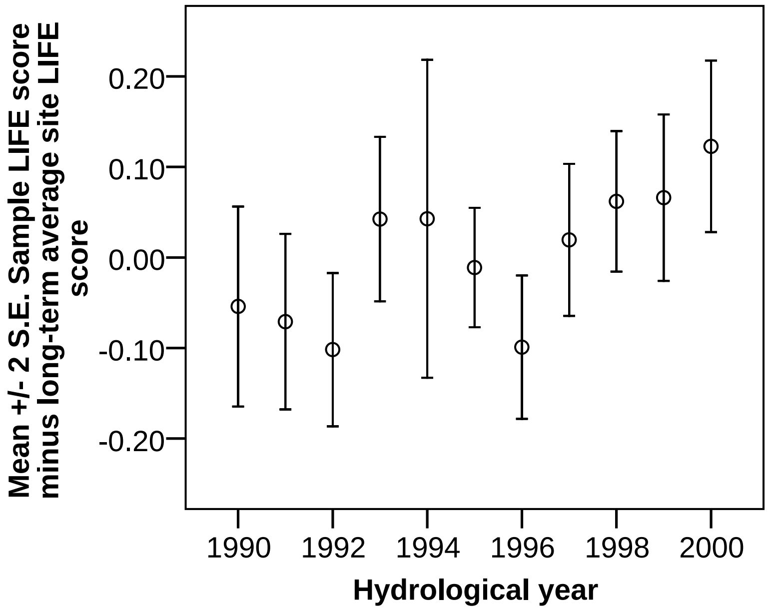
(a) All sites



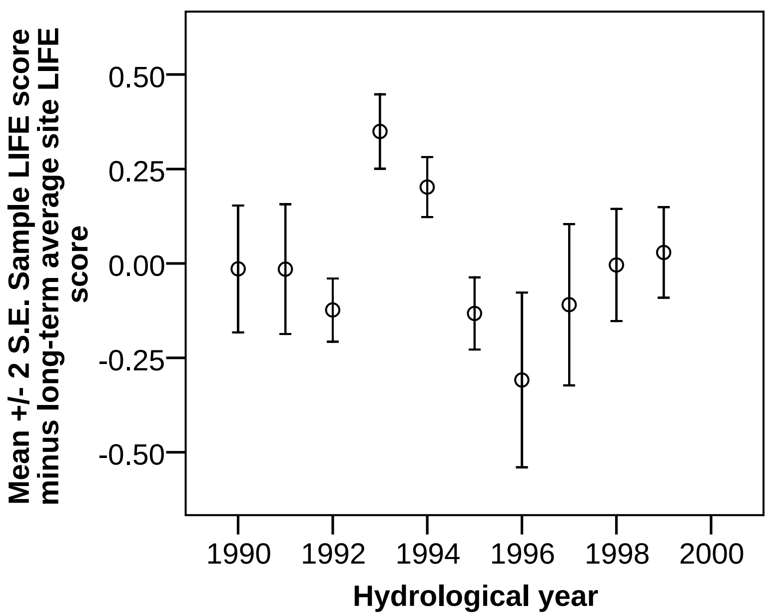
(b) RM1



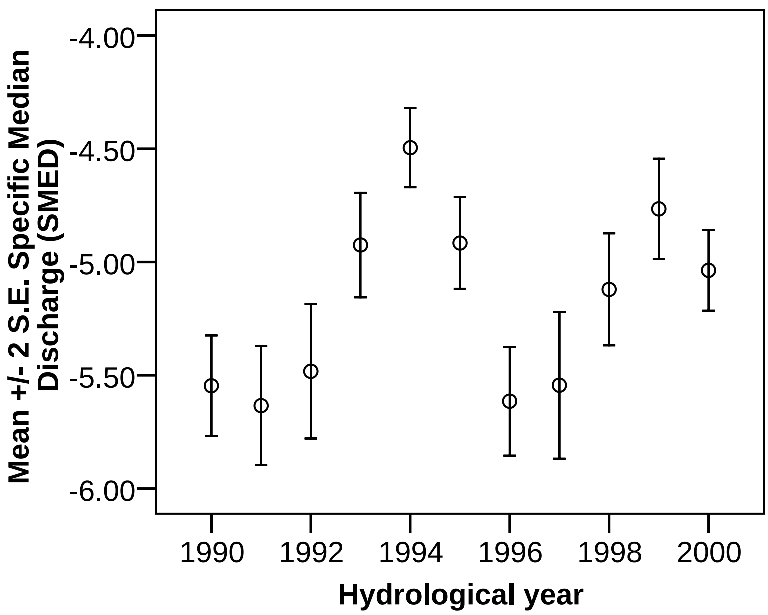
(c) RM2


Mean +/- 2 S.E. Sample LIFE score minus long-term average site LIFE score
0.20
0.10
0.00
-0.10
-0.20
1990
1992
1994
1996
1998
2000
Hydrological year

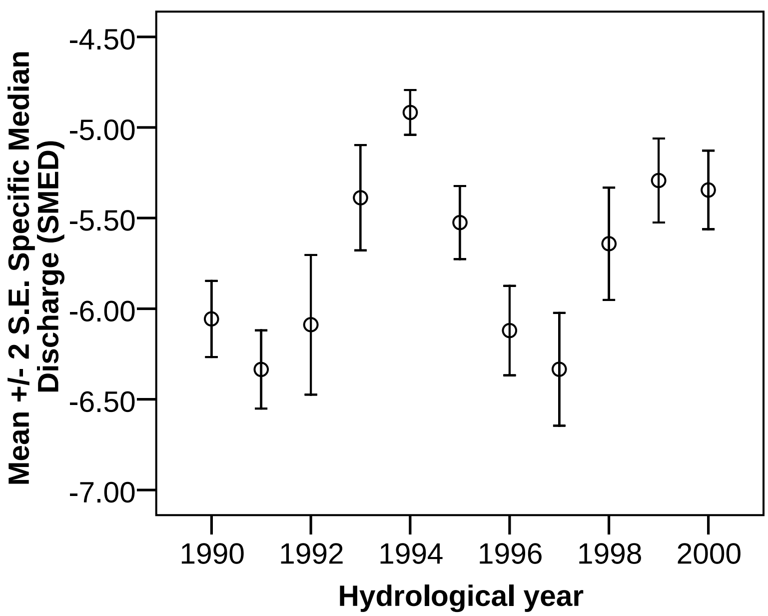
(d) RM3*


Mean +/- 2 S.E. Sample LIFE score minus long-term average site LIFE score
0.50
0.25
0.00
-0.25
-0.50
1990
1992
1994
1996
1998
2000
Hydrological year

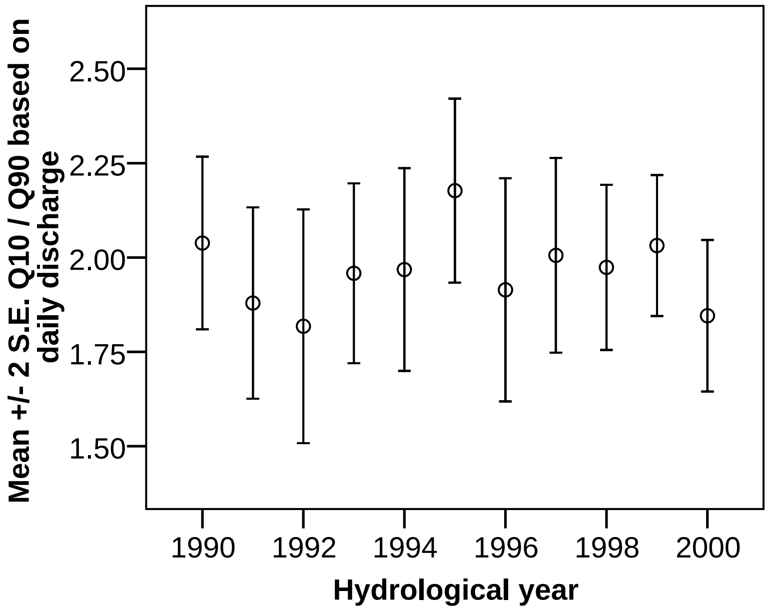
(a) All sites



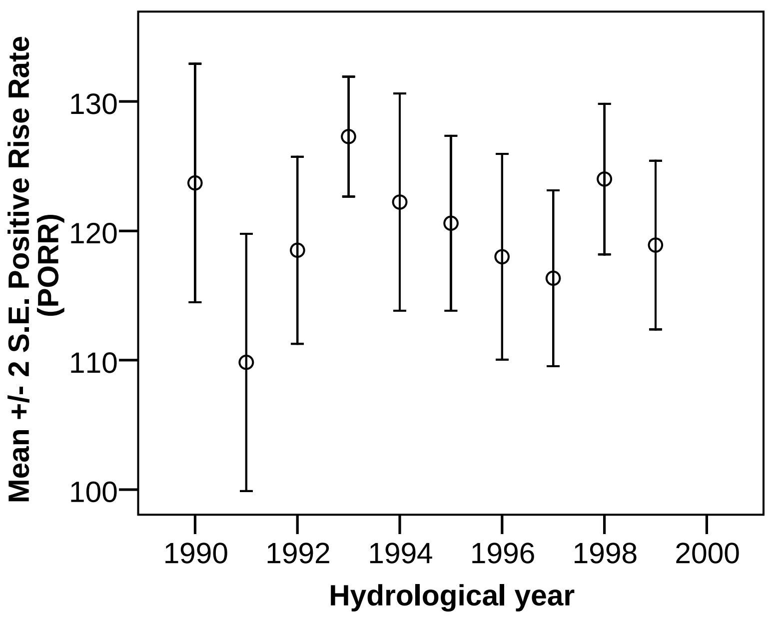
(b) RM1



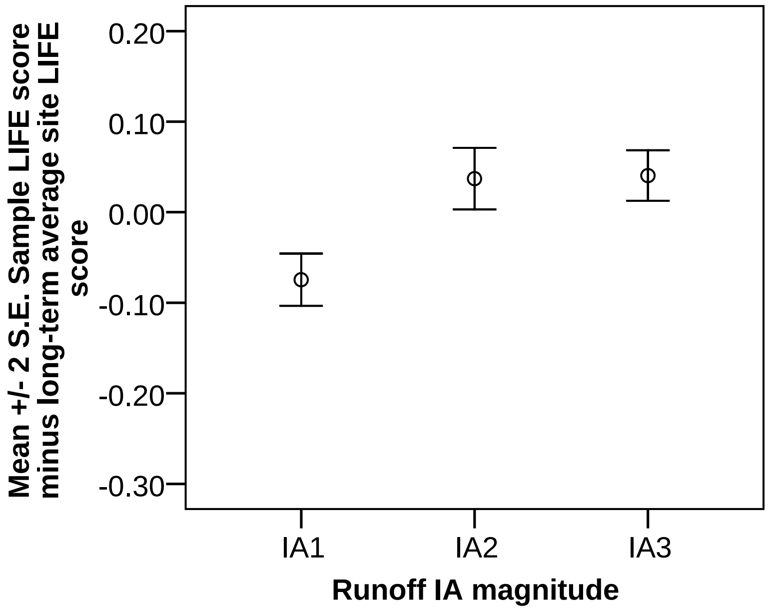
(c) RM2


Mean +/- 2 S.E. Q10 / Q90 based on daily discharge
2.50
2.25
2.00
1.75
1.50
1990
1992
1994
1996
1998
2000
Hydrological year

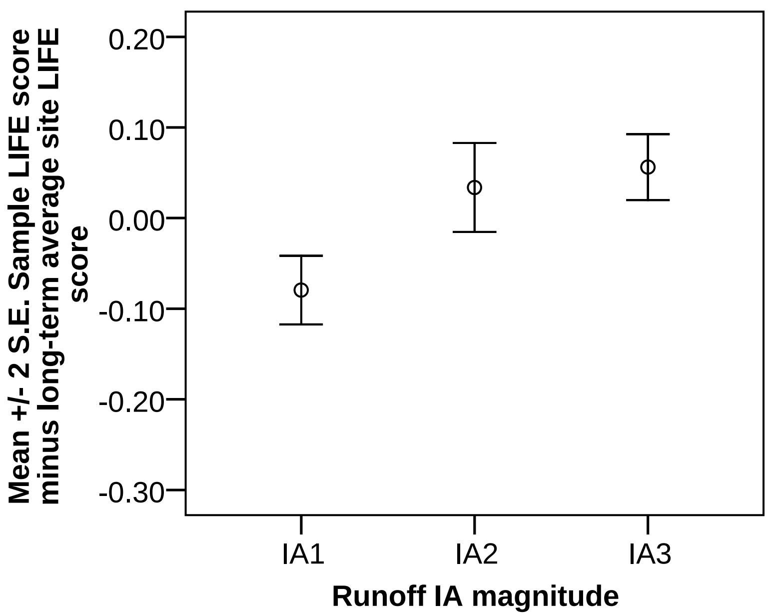
(d) RM3*


Mean +/- 2 S.E. Positive Rise Rate (PORR)
130
120
110
100
1990
1992
1994
1996
1998
2000
Hydrological year

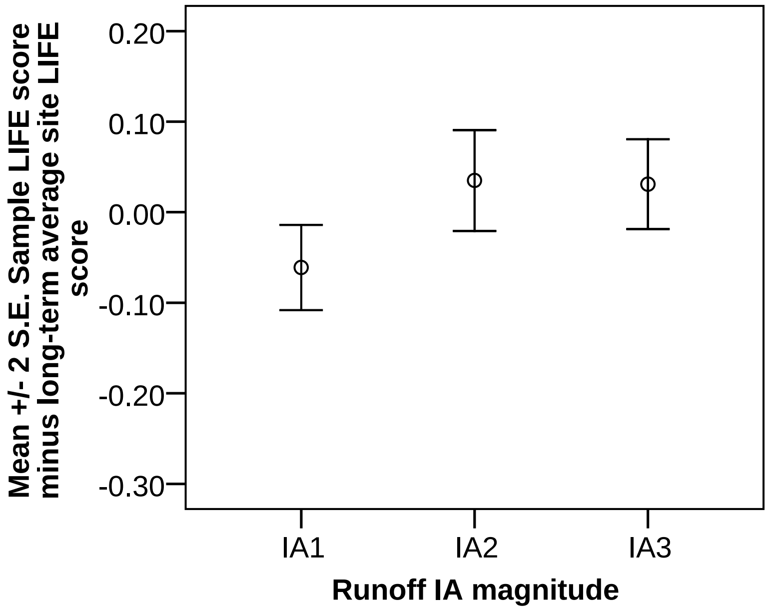
(a) All sites



(b) RM1

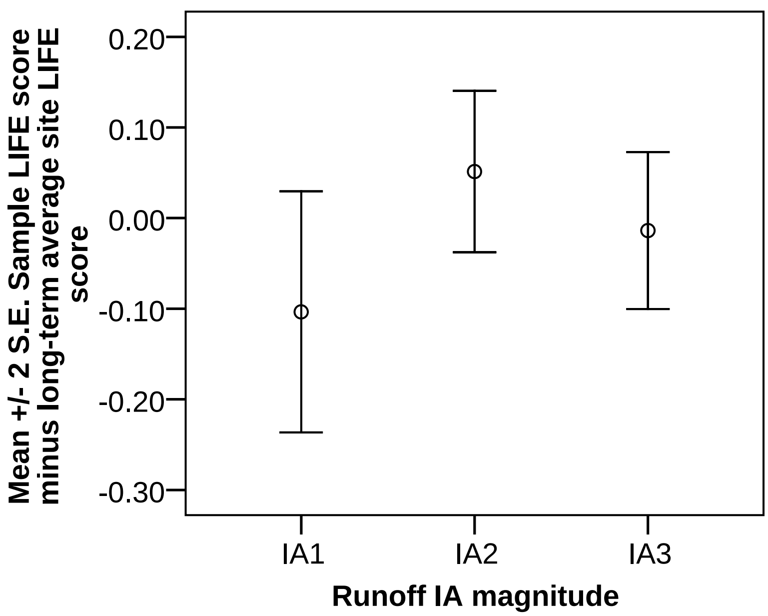


(c) RM2



Mean +/- 2 S.E. Sample LIFE score minus long-term average site LIFE score
0.20
0.10
0.00
-0.10
-0.20
-0.30
IA1
IA2
IA3
Runoff IA magnitude

(d) RM3*



Mean +/- 2 S.E. Sample LIFE score minus long-term average site LIFE score
0.20
0.10
0.00
-0.10
-0.20
-0.30
IA1
IA2
IA3
Runoff IA magnitude