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FLOW VARIABILITY AND MACROINVERTEBRATE COMMUNITY RESPONSE WITHIN RIVERINE SYSTEMS

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ABSTRACT

River flow regimes, controlled by climatic and catchment factors, vary over a wide range of temporal and spatial scales. This hydrological dynamism is important in determining the structure and functioning of riverine ecosystems; however, such hydroecological associations remain poorly quantified. This paper explores and models relationships between a suite of flow regime predictors and macroinvertebrate community metrics from 83 rivers in England and Wales. A two-stage analytical approach was employed: (1) classification of 83 river basins based upon the magnitude and shape (form) of their long-term (1980 – 1999) average annual regime to group basins with similar flow responses; and (2) examination of relationships between a total of 201 flow regime descriptors identified by previous researchers and macroinvertebrate community metrics for the whole data set and long-term flow regime classes over an 11-year period (1990 – 2000). The classification method highlighted large-scale patterns in river flow regimes, identifying five magnitude classes and three shape classes. A west–east trend of flow regime magnitude (high-low) and timing (early-late peak) was displayed across the study area, reflecting climatic gradients and basin controls (e.g. lithology). From the suite of hydrological variables, those associated with the magnitude of the flow regime consistently produced the strongest relationships with macroinvertebrate community metrics for all sites and for the long-term regime composite classes. The results indicate that the classification (subdivision) of rivers into flow regime regions potentially offers a means of increasing predictive capacity and, in turn, better management of fluvial hydrosystems.

INTRODUCTION

River flow regimes, driven by climate and basin controls, demonstrate variability over a range of temporal and spatial scales (Poff, 2002; Bower*, et al.*, 2004). River flow is a valuable predictor of the instream physical environment, and a significant factor in understanding riverine ecosystems (e.g. Statzner and Higler, 1986; Poff and Allan, 1995; Poff*, et al.*, 1997; Lancaster and Mole, 1999; Naiman*, et al.*, 2002; Matthaei*, et al.*, 2003; Olden and Poff, 2003; Wood and Armitage, 2004; Wright*, et al.*, 2004). Recent research has begun to assess potentially ecologically important components of the flow regime (Jowett and Duncan, 1990; Biggs, 1995; Wood*, et al.*, 1999; Poff, 2002; Boulton, 2003; Lake, 2003; Lytle and Poff, 2004). A number of different methodological approaches have been proposed, including the Indicators of Hydrologic Alteration (IHA) procedure of Richter *et al.* (1996), which identified five facets of the flow that may be ecologically relevant: (i) magnitude of monthly water conditions; (ii) magnitude and duration of extreme water conditions; (iii) timing of annual extreme water conditions; (iv) frequency and timing of high and low pulses; and (v) rate and frequency of water condition changes. The IHA methodology has recently been modified and expanded by Olden and Poff (2003) to incorporate over 200 hydrological indices, which may influence riverine communities. However, there is a lack of critical knowledge regarding the selection of the most appropriate hydrological parameters and many have not been tested as predictors of ecological response.

Baseline data collected as part of biomonitoring programmes for water quality provides an opportunity to develop methodologies for evaluating the ecological integrity of riverine systems over a range of time scales (Davies, 2000; Wright, 2000). However, attempts to integrate hydrological variability with baseline ecological data have been relatively limited due to the absence of appropriate medium- and long-term hydrological and, to a greater extent, biological data sets for analysis (notable exceptions include: Richter, *et al.*, 1997; Wood, *et al.*, 2000; Woodward, *et al.*, 2002; Wright, *et al.*, 2004). In addition, few studies have attempted to quantify the relationship between hydrological indices and instream communities, metrics or indicator organisms (notable exceptions include: Jowett and Duncan, 1990; Wright, 2000; Gibbins, *et al.*, 2001; Wood, *et al.*, 2001).

The Lotic-invertebrate Index for Flow Evaluation (LIFE) is based upon known requirements of riverine benthic macroinvertebrate species and families to particular flow velocity ranges (Extence, *et al.*, 1999). Thus, the LIFE score provides a potentially valuable metric to assess changes in aquatic faunal communities in relation to hydrological variability. The LIFE methodology has been used to evaluate the influence of river flow on benthic macroinvertebrates at a range of sites in England and Wales (Extence, *et al.*, 1999) and represents one of the first metrics specifically designed to reflect faunal responses to 'flow conditions' and their change over time.

This paper aims to examine the relationship between river flow regimes, hydrological descriptors (indices) and instream benthic macroinvertebrate communities using a long-term data set collected by the statutory environmental monitoring organisation for England and Wales (The Environment Agency). A two-stage approach is employed, involving: (1) classification of 83 river basins based upon the shape (form) and magnitude (size) of their long-term average annual regime to group basins with similar flow responses; and (2) examination of relationships between a suite of 201 flow regime descriptors and family-level benthic macroinvertebrate community data (expressed as ecological metrics) for the entire data set and long-term flow regime classes (yielded by stage 1) over an 11-year period (1980 – 1999). Thus, this study is the first attempt to examine hydroecological relationships between family-level instream macroinvertebrate community metrics and flow regimes for multiple sites across England and Wales.

DATA SET AND SITE SELECTION

The Environment Agency LIFE paired data set provides the basis for analysis. This database comprises 291 rivers across England and Wales, for which daily discharge measurements from an Environment Agency gauging station have been paired with adjacent biomonitoring sites. To be included within the dataset, sites had to be unaffected by water quality issues and largely unregulated. A total of 7,981 macroinvertebrate samples have been collected at these sites as part of routine monitoring programmes (Balbi, 2001). All macroinvertebrate samples were collected with a Freshwater Biological Association pond net using a three-minute kick sample (<1 mm mesh net) with an additional one-minute hand search, requiring collectors to sample instream habitats in proportion to their occurrence (Murray-Bligh, 1999). All taxa were identified to family level and relative abundance recorded within five $\log_{10}$ categories (A = ≤ 9, B = 10 – 99, C = 100 – 999, D = 1000 – 9999, E = ≥10000 individuals per family).

The hydrological and biotic components of the paired sites were individually evaluated prior to site selection for analysis. For each river gauging site, a benchmark period of twenty years (1980 – 1999) of data was set for river flow time-series. This twenty-year period was considered sufficient to reflect the range of flow conditions experienced in England and Wales, including extreme events (floods and droughts) (Figure 1). Furthermore, selection of a longer flow reference period would have significantly reduced the spatial coverage of observations due to a lack of overlapping records between many sites. Sites with <10% data missing in any one year were interpolated using long-term mean daily values, while sites with a greater percentage of missing values were rejected.

A key pre-requisite for analysis was the availability of at least one biological sample per year between 1990 and 2000, and/or at least two per year between 1995 and 2000 unaffected by water quality issues. These criteria resulted in 83 river sites, paired with 719 autumn (September, October or November) macroinvertebrate samples, being identified for analysis (Figure 2). Autumn macroinvertebrate samples were selected as this period corresponds to one of two standard Environment Agency macroinvertebrate sampling seasons and corresponds to a period of low flow prior to the annual rise of the hydrograph within rivers throughout England and Wales. However, following application of data selection criteria, the resultant geographical distribution of sites was uneven with Wales and southwest England being poorly represented compared to other regions (Figure 2).

METHODOLOGY

A two-stage process was employed to examine flow regime variability between river sites and, subsequently, the influence of hydrological descriptors on the instream macroinvertebrate communities. First, a classification methodology was used to group rivers based upon their long-term flow regime (1980 – 1999), independent of biological data. Second, the potential ecological significance of the flow regime classes was explored through correlation analysis and development of stepwise multiple linear regression models for a suite of flow regime descriptors based upon those initially proposed by Richter *et al.* (1996) and expanded by Olden and Poff (2003).

Flow regime classification

A classification method for flow regime regionalisation (identification of hydrologically homogenous areas) was applied to group rivers with similar long-term (1980 – 1999) average annual magnitude or seasonality of flows (developed by Hannah, *et al.*, 2000; modified by Harris, *et al.*, 2000; and evaluated by Bower, *et al.*, 2004). This classification technique uses hierarchical, agglomerative cluster analysis (Ward's method) to separately group rivers according to the two ecologically relevant flow regime attributes, namely magnitude and shape (form). The classification allows these components to be analysed separately, in addition to allowing for their interaction in the form of composite (magnitude – shape) classes. The flow regime magnitude element is based upon four annual flow descriptors (mean, maximum, minimum and standard deviation) derived from monthly mean observations for each station, regardless of their timing; the shape element identifies stations with a similar form of annual hydrograph, regardless of absolute magnitude.

Exploratory analysis indicated that classification based upon the raw discharge time-series was strongly biased by catchment area. Thus, monthly averages of daily discharge records (m^3s^{-1}) were expressed as runoff (mm month^{-1}) to standardise for differences in catchment area. The runoff time-series for each site was divided into hydrological years commencing in August, as July was identified as the most frequent month of minimum runoff across England and Wales. This timeframe ensured the rising limb, annual peak and flow recession were included within the same 12-month period. The four magnitude indices were derived from the long-term regime for each river gauging station and standardised to remove differences in relative values between indices prior to cluster analysis. The shape classes were identified independently of magnitude by separately standardising the 12 monthly observations for each station using z-scores (mean = 0, standard deviation = 1).

Biotic scores

Family-level macroinvertebrate community data, collected for the biomonitoring of water quality provided the biotic metrics analysed. Three scores were determined as dependent variables: (i) LIFE score; (ii) BMWP score (Biological Monitoring Working Party score: Armitage*, et al.*, 1983); and (iii) the ASPT (Average Score Per Taxon: Armitage*, et al.*, 1983). The LIFE score provides a semi-quantitative description of the structure of the macroinvertebrate community based on mean flow velocities (Extence*, et al.*, 1999). The BMWP score and the ASPT are widely used in the UK and are sensitive to organic pollution. The BMWP score and the ASPT were included in the analysis since the sites within the dataset were unaffected by water quality issues and the use of both metrics to assess flow variability has been questioned in previous research (e.g. Clarke*, et al.*, 2002), although not extensively analysed to date. The BMWP score and the ASPT are not independent; but research has demonstrated that the ASPT is a more temporally robust measure of the community variability (Armitage*, et al.*, 1983). In addition, multivariate analysis techniques (ordination techniques) were used to derive samples scores for sites by: (i) correspondence analysis (CA); (ii) detrended correspondence analysis (DCA); and (iii) non-metric multidimensional scaling (nMDS). Samples scores were extracted for the first four axes, which explain the majority of the statistical variation in the data set, and these axes scores were used in analysis. Other macroinvertebrate metrics were considered (e.g., diversity metrics, and taxa traits), although their application was limited due to the records being comprised of family level log-abundance classes. Preliminary analysis indicated that intercorrelations between hydrological indices and both ordination axis scores and the BMWP score were consistently weaker (lower correlation ceofficients) than those recorded for the LIFE score and the ASPT. As a result, only the latter two metrics were utilised in further detailed analysis and are presented herein.

Comparison of ecological indices between flow regime classes

Results of the Levene's test of the homogeneity of variances were highly significant for all three flow regime classes ($p < 0.001$). Therefore, the nonparametric Kruskal-Wallis test was applied to explore if significant differences between- and within- flow regime shape, magnitude and composite classes, and biotic occurred. This allowed classes with significantly high or low values of any of the biotic metrics scores to be clearly identified.

Correlation and regression analysis

Pearson's correlation was used to examine the relationship between flow variables and ecological metrics (LIFE score and the ASPT) prior to development of stepwise multiple linear regression models. The ecological metrics were paired with the flow time-series from the previous 12 months (e.g. a macroinvertebrate sample from September 1990 was paired with flow data between August 1989 and July 1990).

A total of 201 hydrological variables were derived and used in analysis, representing ecologically relevant aspects of the flow regimes. The 'ecologically-relevant' hydrological variables were identified from previous research reported within 15 hydrological and ecological journal papers (see Appendix I, Hughes and James, 1989; Poff and Ward, 1989; Richards, 1989; Biggs, 1990; Jowett and Duncan, 1990; Poff, 1996; Richter*, et al.*, 1996; Clausen and Biggs, 1997; Richter*, et al.*, 1997; Puckridge*, et al.*, 1998; Richter*, et al.*, 1998; Clausen and Biggs, 2000; Clausen*, et al.*, 2000; Wood*, et al.*, 2000; Wood*, et al.*, 2001). Flow variables were assigned to one of five hydrological regime facets, as originally proposed in the Indicators of Hydrologic Alteration methodology (Richter*, et al.*, 1996) and its derivatives (Poff*, et al.*, 1997; Olden and Poff, 2003). Hydrological variables were derived using daily and/or monthly mean data, as appropriate, to form monthly and/or annual indices describing flow characteristics for the hydrological year before the macroinvertebrate sampling date. Where two or more similar flow descriptors existed, the most widely used form in the literature was employed to avoid unnecessary redundancy (Olden and Poff, 2003). All hydrological variables were assessed in raw and standardised (in the form of zscores) form.

Stepwise multiple linear regression models were developed to examine the ability of flow variables to account for variation in the benthic macroinvertebrate communities. Analysis was undertaken using (1) all sites (global model) and stratified by: (2) flow regime magnitude; (3) flow regime shape; and (4) flow regime composite classes. Autocorrelation and redundancy between variables was examined as many parameters used by previous authors are interrelated (Clausen*, et al.*, 2000; Olden and Poff, 2003). Redundancy between variables was identified using Pearson's correlation coefficients, coefficient of determination and scatter plots examining both the nature of the hydroecological relationships and degree of multicollinearity between variables. Where redundancy did occur, the variable accounting for least variation in the biotic metric was excluded from the model. This resulted in only one or two hydrological variables being incorporated in to any model.

RESULTS

Flow regime classification

Flow regime shape and magnitude were classified using long-term (1980 – 1999) mean monthly runoff data for 83 stations in England and Wales. Composite classes (magnitude – shape) were produced and provided structure for further analysis (correlation and regression).

Five flow regime magnitude classes (RM_1 – RM_5) were identified from an inspection of the cluster dendrogram and agglomeration schedule (scree plot). Summary statistics and Box and Whisker plots indicate that flow regime magnitude classes were distinct (Table 1 and Figure 3):

Class RM_1 – Low with the lowest values for all indices (42 rivers);

Class RM_2 – Relatively low with the second lowest values for all indices (29 rivers);

Class RM_3 – Intermediate with mean and maximum runoff values between classes RM_2 and RM_4, and higher values for standard deviation and minimum runoff (5 rivers);

Class RM_4 – Moderately high runoff with high values for mean and maximum runoff and relatively low values for minimum and standard deviation of runoff (5 rivers, including the single site in Wales); and

Class RM_5 – High with high mean, minimum and standard deviation of runoff with intermediate maximum value (2 rivers).

Three distinct flow regime shape classes (RS_A – RS_C) were identified providing a classification of the timing of peak(s) runoff and rising and falling limbs as illustrated in Figure 4:

Class RS_A – Extended December to January peak with secondary March peak (11 rivers);

Class RS_B – January peak with relatively steep rising and falling limbs (51 rivers); and

Class RS_C – Late March peak with prolonged rising limb (21 rivers).

A west-east gradient of decreasing regime magnitude is observed; sites with higher flow regime magnitude classes (RM_3 – RM_5) are largely located in the northwest of England and the site in Wales, while lower flow regime magnitude classes (RM_1 and RM_2) are situated in central and eastern England. Sites with an extended December – January peak and secondary March peak (class RS_A) are predominantly located on upland catchments in northwest England and the single site in Wales. Sites with a dominant January peak (class RS_B) exhibit an even distribution across England, whereas rivers characterised by a late March peak (class RS_C) are distributed across the south and east of England (Figure 2).

Composite flow regime classes

The five flow regime magnitude and three flow regime shape classes were combined to form composite classes (i.e. regime shape was scaled by regime magnitude). However, only ten of the 15 possible composite classes were present within the dataset (Table 2). The composite classes have a clear spatial distribution with a west – east pattern that reflects both flow regime shape and magnitude components (described above); for example high flow regime magnitude sites with a December – January peak (Class RC_{5A}) are located in northwest England while the low flow regime magnitude sites, with a late peak (Class RC_{1C}) are situated in east and central southern England. The absent composite classes equate to low flow regime magnitude sites, with a December – January peak (Class RC_{2A}) and intermediate/high flow regime magnitude sites, with predominantly late peaks (Classes RC_{3C}, RC_{4C}, RC_{5B} and RC_{5C}). Three clusters (RC_{1A}, RC_{3B} and RC_{4B}) contained only a single river site (but for multiple occasions 1990-

2000) and care should be exercised when extrapolating the results of these rivers to others due to lack of between site replication.

Between flow regime class differences in biotic metrics

Results of the Kruskal-Wallis test indicated that there were significant differences between flow regime magnitude, shape and composite classes, and the LIFE score ($p <$ 0.001) and ASPT ($p < 0.001$) (Figure 5). Pairwise analysis of the flow regime composite classes using the Kruskal-Wallis test indicated that of the 45 between group comparisons, significant differences occurred between 33 for the LIFE score and 34 for the ASPT. For the LIFE score, comparisons between low flow regime magnitude composite classes (i.e. classes RC_{1A}, RC_{1B}, RC_{1C}, RC_{2B} and RC_{2C}) resulted in significant differences. However, there were fewer significant differences between intermediate and high flow regime magnitude composite classes (i.e. classes RC_{3A}, RC_{3B}, RC_{4A}, RC_{4B} and RC_{5A}) (Figure 5a). This reflects the overlapping LIFE score values particularly for the intermediate and high flow regime magnitude composite classes, which contained a small number of sites within a limited geographical area. The ASPT displayed a similar pattern to that of the LIFE score, although the level of statistical significance was more variable (Figure 5b).

Correlation analysis

The five highest values of Pearson's correlation coefficients between hydrological variables and the LIFE score and the ASPT are presented for the whole data set and by composite flow regime class in Table 3. Correlations between standardised hydrological variables and biotic indices were consistently lower than unstandardised versions of the same variables and the former were excluded from further analysis. Median annual flow divided by the catchment area (SMED) yielded the strongest relationship with the LIFE score when all rivers (global model) were included (Figure 6a). Significant relationships ($p < 0.01$) were also recorded for individual flow regime shape and magnitude classes (e.g. Figure 6b) as well as for all composite classes (e.g. Figure 6c), although these were generally stronger (higher correlation coefficients) when fewer sites were included in the composite classes (Table 3). The LIFE score yielded the strongest correlation coefficients for six of the ten flow regime composite classes while ASPT yielded the strongest relationships for four composite classes (RC_{1C} and RC_{2B}, RC_{2C} and RC_{5A}) (Table 3). Hydrological variables describing the magnitude component of the flow regime ('Group 1 – magnitude of monthly water conditions' and 'Group 2 – magnitude and duration of annual extreme water conditions' of the Indicators of Hydrologic Alteration: Richter, *et al.,* 1996, 1998) consistently produced the most significant ($p < 0.01$) correlations with the LIFE score when compared with any of the flow regime facets (i.e. frequency, duration, timing and rate of change) (Table 3). These magnitude variables also had the strongest association with the ASPT when the entire dataset was examined. The ASPT was not employed in the regression analysis (below) because it consistently yielded weaker correlations (lower correlation coefficients) than the LIFE score for the majority of flow regime shape, magnitude and composite classes and, therefore, the ASPT was considered to be less sensitive to flow.

Regression Models

Stepwise multiple linear regression models using flow regime indices as predictors were developed for the LIFE score. Models were developed for all sites (global model), and for regime shape, magnitude and composite classes (Table 4). The global model incorporated a single magnitude variable (SMED; median annual flow divided by the catchment area) and yielded an adjusted R^2 = 0.381. Across the composite classes, the adjusted R^2 values varied between 0.151 and 0.755. With the exception of classes RC_{1B}, RC_{1C} and RC_{2C}, only one variable was included in the models for the composite classes following assessment of redundancy and multicollinearity (Table 4). Magnitude variables were consistently incorporated into all of the models (total number of variables = 23, which include 20 = magnitude; 0 = frequency; 1 = duration; 1 = timing; and 1 = rate of change).

DISCUSSION

This study represents the first attempt to examine the relationship between river flow regimes (as characterised by classification of annual regime 'types' and 201 indices using an expanded set of variables based on the Indicators of Hydrologic Alteration methodology) (Richter, *et al.*, 1996; Poff, *et al.*, 1997; Richter, *et al.*, 1998; Olden and Poff, 2003) and benthic macroinvertebrate communities at multiple sites. Additionally, this paper is the first analysis of hydroecological relationships at the scale of England and Wales. The two-stage analytical process used clearly demonstrates the value of modelling benthic community response to river flow at nested scales, especially where clear differences between flow regime (river) types are observed. The flow regime classification procedure allows rivers with distinct average annual hydrological patterns to be identified. The results presented clearly demonstrate the influence of the flow regime upon benthic communities (Table 4). The approach(es) presented herein may be reproduced using standard spreadsheet and software packages and, therefore, they have the potential for wider application to other localities, assuming similar hydroecological data are available.

To date, a major limitation to the analysis of hydroecological linkages has been an absence of appropriate medium- to long-term ecological time-series. Previous studies have demonstrated limited application of ecological data following environmental classification (e.g. Snelder*, et al.*, 2005). Detailed long-term hydrological observations are available for many locations across Europe and North America, in particular, and long-term river flow records have been reconstructed based on climatological data and other proxies (for example Jones and Lister, 1998). In comparison, relatively few comparably long ecological data sets exist. The family-level macroinvertebrate data used in this study is one of the most extensive and detailed data sets available for rivers in England and Wales. Most of the macroinvertebrate families recorded have a cosmopolitan distribution thus facilitating comparisons between different river classes; although care should be exercised for composite classes comprised of single rivers.

The flow regime magnitude, shape and composite classes identified in this investigation are similar to those reported in other studies of UK rivers (Harris*, et al.*, 2000; Bower and Hannah, 2002; Bower*, et al.*, 2004). The emergent shape, magnitude and composite classes have a clear spatial structure reflecting known hydroclimatological gradients (west – east) across the UK and basin modifiers such as geology (Bower*, et al.*, 2004). These studies, in common with the present investigation, indicate that a distinct set of flow regimes exist for rivers throughout England and Wales, and suggests that attempts to manage all sites in a similar fashion is not best practice because a 'global' approach cannot account for spatial heterogeneity in hydrological response. The flow regime groups identified offer a framework for further detailed investigations of river biotic response and a starting point for the development of resource management criteria for different river types.

Detailed examination of the regime magnitude, shape and composite classes using pairwise Kruskal-Wallis analysis demonstrates that rivers characterised by different flow regimes support macroinvertebrate communities with significantly different LIFE scores. This was most evident for low flow regime composite classes (Classes RC_{1A} – RC_{2C}) where there was very little overlap in the unstandardised LIFE score values compared with intermediate and high flow regime classes (Classes RC_{3A} – RC_{5A}) (Figure 5). This reinforces the need to understand the spatial and temporal hydrologic variability (Richter*, et al.*, 1996; Poff*, et al.*, 1997; Hannah*, et al.*, 2000; Bower and Hannah, 2002; Bower*, et al.*, 2004) and plan to structure analyses accordingly (i.e. between- and within-regions), even within relatively limited geographical areas, before consideration of its influence upon instream ecology.

The LIFE score and the ASPT consistently yielded stronger relationships with hydrologic parameters than the BMWP or any of a variety of multivariate analysis (ordination) axis sample scores. This reflects the fact that the LIFE methodology has been specifically developed to examine faunal response to flow velocity (Extence*, et al.*, 1999). Additionally, previous research has demonstrated the increased temporal stability of the ASPT compared to the BMWP score (Armitage*, et al.*, 1983). This is reflected in the highly variable pattern demonstrated by the relationships with the BMWP score and hydrological parameters. The ASPT is clearly responsive to changes in flow regime for most composite classes, composed of rivers unaffected by water quality issues, used in this research. However, it has also been demonstrated that invertebrate taxa associated with higher flow velocities are generally the most sensitive to organic pollution (Extence and Ferguson, 1989). Therefore the LIFE score should be used to assess flow variability wherever possible, and the BMWP score and the ASPT should only be considered at sites unaffected by water quality issues.

Stepwise multiple linear regression modelling indicated that a significant proportion of the variance in the LIFE score of 83 rivers in England and Wales could be explained by one or two hydrological indices. This suggests a very high level of redundancy among hydrologic parameters (Olden and Poff, 2003) and, perhaps most notably, the robustness of the methodology employed in this study to overcome multicollinearity. Up to 38% of the variance in the LIFE score could be explained for all sites (global model) by one variable (specific median flow; SMED). The flow regime classification procedure allowed between 18% and 72% of the ecological variance to be explained for sites pooled within the regime magnitude classes, 14% and 41% within the shape classes, and 15% and 76% within the composite classes. The results of this linear regression are comparable to those reported by Clausen and Biggs (1997) for rivers in New Zealand, where a single flow variable (FRE3 – frequency of high flow events greater than three times the median discharge) accounted for between 41% and 52% of the variance in periphyton communities (25 sites), and between 14% and 36% of the variance in the macroinvertebrate communities (62 sites). In marked contrast to previous studies, the results of this study indicate that the flow magnitude (‘Group 1 – magnitude of monthly water conditions’ and ‘Group 2 – magnitude and duration of annual extreme water conditions’ of the Indicators of Hydrologic Alteration: Richter, *et al.,* 1996, 1998) were the ‘best’ predictors of macroinvertebrate community response to flow. The predominance of these variables within hydroecological models may reflect the variable temperate maritime climate of England and Wales and the absence of intermittent and snowmelt dominated riverine systems within the dataset reported in other investigations (Poff, 1996; Clausen and Biggs, 1997; Poff*, et al.*, 1997; Clausen and Biggs, 2000; Olden and Poff, 2003).

CONCLUSION

It is increasingly recognised that an understanding of hydroecological interactions is required as the basis for development of sustainable river management strategies (Zalewski, 2002). In addition, the need for baseline hydrological and ecological data, and a knowledge of natural variability, is imperative to understand the impacts on riverine systems if significant shifts occur to flow regimes as a result of human activities and/or climate change (Arnell and Reynard, 1996; Environment Agency, 2001; Lytle and Poff, 2004). However, the absence of long-term data sets of floral or faunal communities coupled with high quality hydrological time-series remains a major limitation to achieving this in many parts of the world.

Hydrological classification is now widespread (Hannah*, et al.*, 2000; Snelder and Biggs, 2002) although the integration with ecological data is rare but an essential process for true hydroecological investigations (Hannah, *et al.*, 2004). The results of this research demonstrate the importance of recognising rivers with different hydrological regimes and the dominance of flow magnitude (monthly and annual extremes) in shaping instream communities in England and Wales. The methodological approach outlined provides a simple and easily replicated approach applicable to a range of scales for water resource management.

The temporal variation and persistence of instream communities associated with environmental variability in now widely acknowledged (e.g. Woodward, *et al.*, 2002; Brown, *et al.*, In Press). In addition, the potential ecological importance of climate variability and large scale climatic diagnostic indices, such as the North Atlantic Oscillation (NAO), have been demonstrated in previous studies (Bradley and Ormerod, 2001). However, caution should be exercised when developing models of benthic community variability since the changes observed in abundance, structure and composition do not necessarily imply causality (Bunn and Davies, 2000). The influence of flow variability can be masked by other factors, such as anthropogenic disturbances (for example Englund and Malmqvist, 1996; Bunn and Arthington, 2002; Lytle and Poff, 2004) and the natural heterogeneity of the local-scale physical and biotic environment (for example Karr, 1991; Weigel, *et al.*, 2003). It is important that future research examines these external influences and intrinsic controls on a site-by-site basis because they may exert overriding controls on some riverine systems.

This study was confined to macroinvertebrates; other ecological groups may respond to other hydrologic indices. This would suggests that at a larger geographical scale and for other taxonomic groups, variables from any of the five groups of hydrological parameters identified in the Indicators of Hydrologic Alteration methodology (Richter, *et al.*, 1996; Richter, *et al.*, 1997) may be ecologically relevant. In addition, future research is required to examine inter-annual flow regime variability (i.e. seasonality and magnitude of flows over the hydrological year) on both individual rivers and groups of sites.

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Appendix I – Summary of hydrological variables used in this study.

Table 1 – Average values of the magnitude indices (mm month^{-1}) for each of the five flow regime magnitude classes.

	Cluster Average					Average
	RM_1	RM_2	RM_3	RM_4	RM_5	
R_{mean} (mm month^{-1})	13.96	32.01	71.46	119.55	129.53	32.88
R_{max} (mm month^{-1})	53.67	102.57	171.92	383.65	274.39	103.08
R_{min} (mm month^{-1})	1.95	7.26	13.09	8.98	32.66	5.64
$R_{std\ dev}$ (mm month^{-1})	4.00	9.56	51.33	17.26	80.50	11.44
Mean catchment area (km^2)	223.56	313.24	321.08	295.00	99.250	262.08
N (number of rivers) (n = 83)	42	29	5	5	2	
Number of samples (n = 719)	387	252	30	38	12	

R_{mean} = long-term mean runoff; R_{max} = long-term maximum runoff; R_{min} = long-term minimum runoff; $R_{std\ dev}$ = long-term standard deviation of runoff.

Table 2 – Summary of the distribution and characteristics of flow regime composite classes.

Composite flow regime	Number of rivers (number of macroinvertebrate samples)	Geographical distribution and catchment geology
1A*	1 (9)	Situated in northwest England on a very wet impervious, high relief catchment.
1B	28 (267)	Predominantly located on pervious rural catchments in east and southeast England.
1C	13 (111)	Mainly permeable groundwater-dominated rural catchments (largely chalk) in east and central southern England.
2B	22 (193)	Located in central, northeast and southern England draining a mixture of impervious/semi-permeable geologies.
2C	7 (59)	Predominantly located in south and southeast of England with rural catchments (chalk).
3A	4 (20)	Located in northwest England and the one site in Wales draining moderate relief, rural catchments, on impermeable geologies.
3B*	1 (10)	Predominantly rural catchment draining the Pennines in northeastern England with a mixed geology.
4A	4 (29)	Cluster of catchments in northwest England on predominantly impervious mixed geologies.
4B*	1 (9)	Predominantly rural catchment in northeastern England with a mixed geology.
5A	2 (12)	Located in northwest England on impervious catchments supporting rough pasture, moorland and grassland.

* Indicates compositeclasses composed of multiple samples (years) for a single river.

*Table 3 –Pearson's correlation coefficients for all sites and composite flow regime classes (only the five strongest for each class are presented). **** p < *0.001; *** p < *0.01; ** p < *0.05;* NS *Not significant. See Appendix I for definitions of variables.*

	LIFE		ASPT	
ALL SITES				
	SMED	0.604 ***	MAR	0.446 ***
	MAR	0.584 ***	SMED	0.444 ***
	SMIN	0.546 ***	SMAX	0.426 ***
	SMAX	0.527 ***	QNOV	0.395 ***
	QOCT	0.427 ***	Q25	0.390 ***
COMPOSITE CLASSES				
1A*	STDMAXJD	0.779 *	D30CVMIN	-0.683 *
	MAXDF	0.775 *	MINJUNE	-0.663 *NS*
	DFRANGE	0.774 *	Q5DF	-0.646 *NS*
	MINJD	-0.681 *	MAX3	0.603 *NS*
	CVMINDF	-0.661 *NS*	DFMESEPT	-0.592 *NS*
1B	SMED	0.480 ***	SMED	0.409 ***
	MAR	0.442 ***	MAR	0.397 ***
	PORRYR	-0.384 ***	SMAX	0.357 ***
	PORR	-0.383 ***	NERR	0.263 ***
	SMAX	0.363 ***	NERRYR	0.262 ***
1C	SMAX	0.402 ***	SMAX	0.534 ***
	MAR	0.383 ***	D7MAX50	0.510 ***
	SMED	0.373 ***	Q1DFQ50	0.508 ***
	STDEVQ	0.360 ***	D3MAX50	0.504 ***
	QJAN	0.344 ***	NERR	0.500 ***
2B	DFQ95MEAN	-0.459 ***	BFV	-0.457 ***
	MAR	0.451 ***	STDEVDF	0.433 ***
	SMED	0.445 ***	MAXDF	0.431 ***
	Q1090DF	0.438 ***	DFRANGE	0.430 ***
	SMAX	0.432 ***	Q10	0.429 ***
2C	SMIN	0.299 *	Q90DFQ50	-0.444 ***
	SMED	0.298 *	Q80DFQ50	-0.434 **
	MEDMAX	0.283 *	Q95DFQ50	-0.409 **
	NERR	-0.273 *	Q75DFQ50	-0.404 **
	MAR	0.272 *	D30MIN50	-0402 **
3A	MINJULY	-0.701 **	MAXOCT	-0.600 **
	DAY3MIN	-0.689 **	MAXNOV	-0.569 **
	MINDF	-0.687 **	DFMENOV	-0.564 **
	QFEB	-0.686 **	MINSEPT	-0.564 *
	DAY7MIN	-0.685 **	MINNOV	-0.563 *
3B*	Q95	0.847 **	FRE3YR	0.730 *
	Q90	0.840 **	FRE3	0.729 *
	Q75	0.816 **	DFMENOV	-0.727 *
	QJUNE	0.769 **	Q5	0.700 *
	Q99	0.763 **	MAXNOV	-0.697 *
4A	SMIN	0.613 ***	MEMAXJD	-0.487 **
	MAX9	-0.603 **	Q1	-0.485 **
	DFMEJAN	-0.597 **	STDEVQ	-0.480 **
	MAXAPR	-0.594 **	PORR	-0.461 *
	MAX6	-0.562 **	PORRYR	-0.460 *
4B*	QSEPT	0.886 **	Q25Q50	0.762 *
	MAXJUNE	0.872 **	D3CVMIN	0.727 *
	DFMEJUNE	0.844 **	D7CVMAX	0.721 *
	MINDEC	0.817 **	Q10Q90	0.695 *
	D30CVMIN	0.813 **	STDEVQ	0.692 *
5A	Q50DF	-0.861 ***	Q50DF	-0.868 ***
	MAXAUG	-0.823 **	MAXAUG	-0.815 **
	Q75DF	-0.749 **	Q75DF	-0.719 **
	Q10Q90	0.726 **	MDF	-0.708 **
	Q80DF	-0.715 **	TOTALVOL	-0.707 *

* Indicates composite classes composed of multiple samples (years) for a single river.

Table 4 – Stepwise multiple linear regression models for the LIFE index using hydrological variables for all sites and by shape, magnitude and composite flow regime classes. See Appendix I for definitions of variables. *** p*<0.001;* ** p*<0.01;* * p<0.05

Model	Adjusted R^2	F	Number of rivers (samples)	Predictor variables plus sign
(a) All sites				
	0.381	442.622 ***	83 (719)	+ SMED
(b) Magnitude				
RM_1	0.357	214.115 ***	(42) 387	+ SMED
RM_2	0.209	67.249 ***	(29) 252	+ Q1090DF
RM_3	0.259	11.136 **	(5) 30	– CVDF
RM_4	0.183	9.291 **	(5) 38	+ NERRYR
RM_5	0.716	28.722 ***	(2) 12	– Q50DF
(c) Shape				
RS_A	0.300	30.544 ***	(11) 70	– QFEB
RS_B	0.411	334.010 ***	(52) 479	+ SMED
RS_C	0.137	14.452 ***	(20) 170	+ SMED – CVDF
(d) Composite				
RC_{1A}*	0.551	10.830 *	(1) 9	+ STDMAJD
RC_{1B}	0.431	100.119 ***	(28) 267	+ SMED – Q50DF
RC_{1C}	0.231	17.538 ***	(13) 111	+ SMAX – Q80
RC_{2B}	0.204	50.297 ***	(22) 193	– DFQ95MEAN
RC_{2C}	0.151	6.172 **	(7) 59	+ SMIN + MEDMAX
RC_{3A}	0.463	17.389 **	(4) 20	– MINJULY
RC_{3B}*	0.683	20.389 **	(1) 10	+ Q95
RC_{4A}	0.353	16.250 ***	(4) 29	+ SMIN
RC_{4B}*	0.755	25.636 **	(1) 9	+ QSEPT
RC_{5A}	0.716	28.722 ***	(2) 12	– Q50DF

* Indicates composite classes composed of multiple samples (years) for a single river.

Appendix I - Summary of hydrological variables calculated for this study.

Identification code	N	Hydrological variables	Units	References [1]
Magnitude of flow events				
Average flow conditions				
CVANN / CVDF / CVANNQ	3	Coefficient of variation of annual discharges – average standard deviation of discharge divided by the annual mean discharge.	–	8, 12, 13, 1, 5, 6, 3
DFRANGE	1	Maximum annual discharge minus minimum annual discharge.	m^3s^{-1}	This study
MAR	1	Mean annual runoff $= \frac{\text{Mean annual discharge}}{\text{Catchment area}}$	$m^3s^{-1}km^{-2}$	4, 1, 5, 6, 3
MAD / MMD / MDF	3	Mean annual discharge.	m^3s^{-1}	8, 12, 13, 5, 6, 3
Q(*M*) / DFME(*M*)	24	Mean discharge for month, *M* (August, September, October, …). The relative hydrological constancy is reflected by the similarity of monthly means over the hydrological year.	m^3s^{-1}	13, 7, 9, 11, 14, 15
Q1…Q99 / Q1DF…Q99DF	20	Percentile flow with the discharge exceeded 99%…1% of the time.	m^3s^{-1}	This study
Q10Q90…Q25Q75 / Q10Q90DF…Q25Q75DF	6	Ratios of annual discharges of $10^{th}/90^{th}$, $20^{th}/80^{th}$ and $25^{th}/75^{th}$ percentiles.	–	2
Q1Q50, Q25Q50, Q75Q50 / Q1Q50DF, Q25Q50DF, Q75Q50DF	6	Percentile discharges Q1, Q25 and Q75 divided by median discharge.	–	13
Q10Q50, Q10Q50DF, Q20Q50, Q20Q50DF, Q90Q50, Q90Q50DF	6	Percentile discharges Q10, Q20 and Q90 divided by median discharge.	–	8, 12, 13
Q5Q50, Q80Q50, Q95Q50, Q99Q50 / Q5Q50DF, Q80Q50DF, Q95Q50DF, Q99Q50DF	8	Percentile discharges Q5, Q80, Q95 and Q99 divided by median discharge.	–	This study
Q50 / Q50DF	2	Median annual discharge.	m^3s^{-1}	8, 12, 13, 5
S100 / S100DF	2	$\text{S100} = \frac{\text{Range}}{\text{Q50}}$	m^3s^{-1}	10
S50	1	$\text{S50} = \frac{\text{Interquartile range}}{\text{Q50}}$	m^3s^{-1}	10
S80	1	$\text{S80} = \frac{\text{(90th - 10th percentile range}}{\text{Q50}}$	m^3s^{-1}	10
SK1 / SKDF	2	$\text{Skewness} = \frac{\text{Mean discharge}}{\text{Q50}}$	–	4, 8, 12, 13
SK2 / SKDFQ50	2	$\text{Skewness} = \frac{(\text{Mean discharge - Q50})}{\text{Q50}}$	m^3s^{-1}	10
SMED	1	Specific median discharge $= \frac{\text{Q50}}{\text{Catchment area}}$	$m^3s^{-1}km^{-2}$	4
STDEVQ / STDEVDF	2	Standard deviation of annual discharge.	m^3s^{-1}	This study
TOTALVOL	1	Total discharge for that hydrological year.	m^3s^{-1}	This study

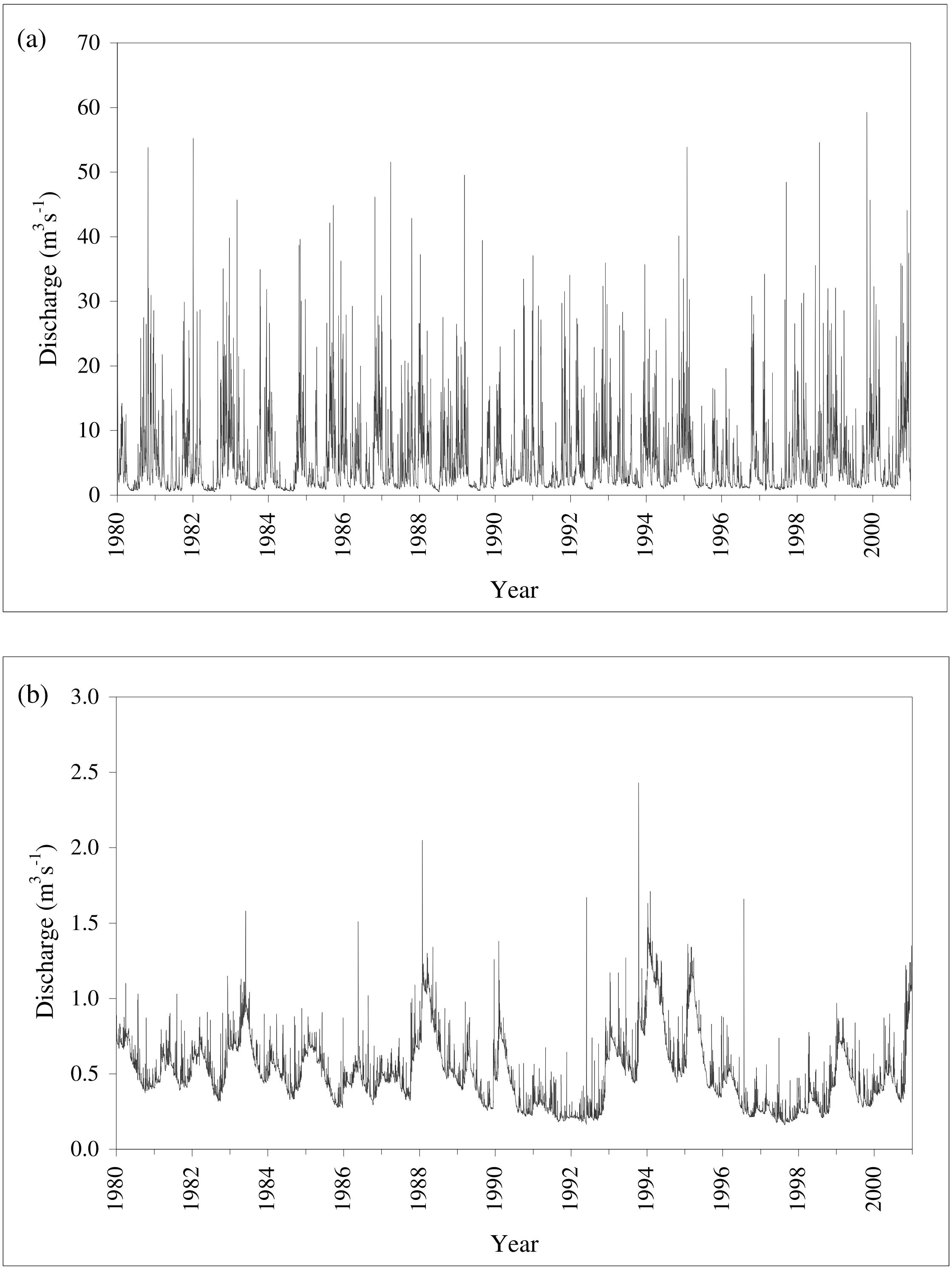
High flow conditions				
AMAX / AMAXDF	2	Annual maximum = $= \frac{\text{Maximum annual discharge}}{\text{Q50}}$	–	This study

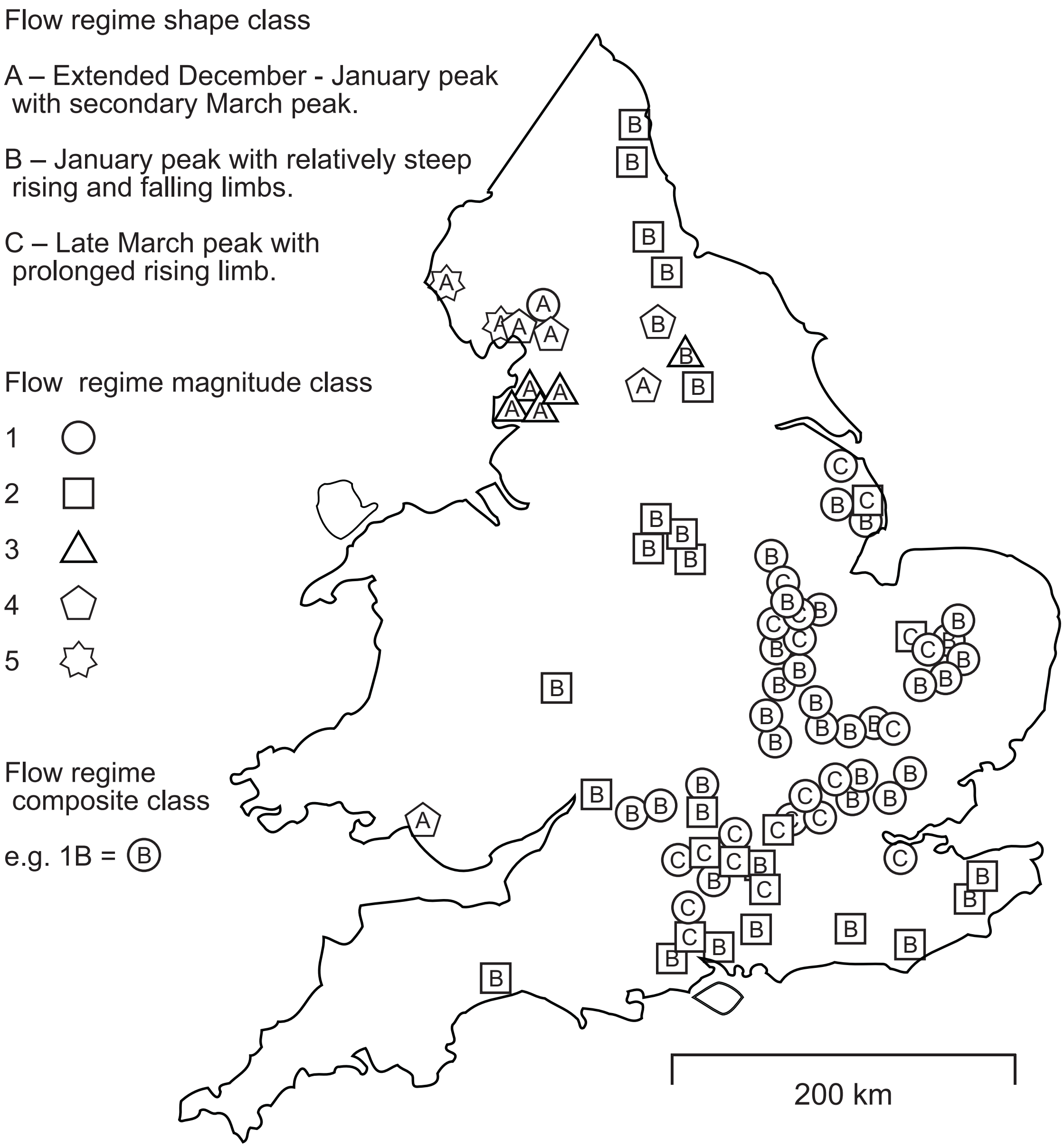
CVANNMA / CVMAXDF	2	Coefficient of variation of MMAD and MAX(*M*).	–	1, 5
DFMEDMAX	1	$=\frac{\text{Median maximum annual discharge}}{\text{Q50}}$	–	13
HF	1	High flow volume $=\frac{\text{Average monthly maximum discharge}}{\text{Q50}}$	–	This study
MAX(*M*)	12	Maximum discharge for month, *M* (August, September, October,…).	m^3s^{-1}	14, 15
MAX3…MAX9	3	Maximum discharge in the previous 3months / 6 months / 9 months.	m^3s^{-1}	14, 15
MEDMAX	1	$=\frac{\text{Median annual maximum discharge}}{\text{Mean annual maximum discharge}}$	–	This study
MAXQ / MMAD / MAXDF	3	Mean annual maximum discharge.	m^3s^{-1}	4, 1, 5 (1-day maximum – 7, 9, 11)
SMAX	1	Specific maximum discharge $=\frac{\text{Annual maximum discharge}}{\text{Catchment area}}$	$m^3s^{-1}km^{-2}$	1
STDEVMA	1	Standard deviation of the annual maximum discharge.	m^3s^{-1}	This study
Low flow conditions				
AMIN / AMINDF	2	Annual minimum = $=\frac{\text{Minimum annual discharge}}{\text{Q50}}$	–	8, 12, 5
BASEFLOW	1	Seven-day minimum discharge divided by the mean annual daily discharge.	–	11
BFV / BFI / DFBFI	3	Baseflow index, i.e. average annual ratio of the lowest daily discharge to the mean daily discharge.	–	12, 13, 5
CVANNMI / CVMINDF	2	Coefficient of variation of MMID and MIN(*M*).	–	1, 5
DFMEDMIN	1	$=\frac{\text{Median minimum annual discharge}}{\text{Q50}}$	m^3s^{-1}	13
MEDMIN / MEDDF	2	$=\frac{\text{Median annual minimum discharge}}{\text{Mean annual minimum discharge}}$	–	This study
MIN(*M*)	12	Minimum discharge for month, *M* (August, September, October, …).	m^3s^{-1}	14, 15
MINQ / MMID / MINDF	3	Mean annual minimum discharge.	m^3s^{-1}	4, 5, (1-day minimum – 7, 9, 11)
SMIN	1	Specific minimum discharge $=\frac{\text{Annual minimum discharge}}{\text{Catchment area}}$	$m^3s^{-1}km^{-2}$	4, 1
STDEVMI	1	Standard deviation of the annual minimum discharge.	m^3s^{-1}	This study
Frequency of flow events				
High flow conditions				
FRE1…FRE3	2	Number of high flow events using a threshold of 1 and 3 times the median.	–	This study
FRE1YR…FRE3YR	2	Mean number of high flow events per year using a threshold of 1 and 3 times the	yr^{-1}	8, 12, 13

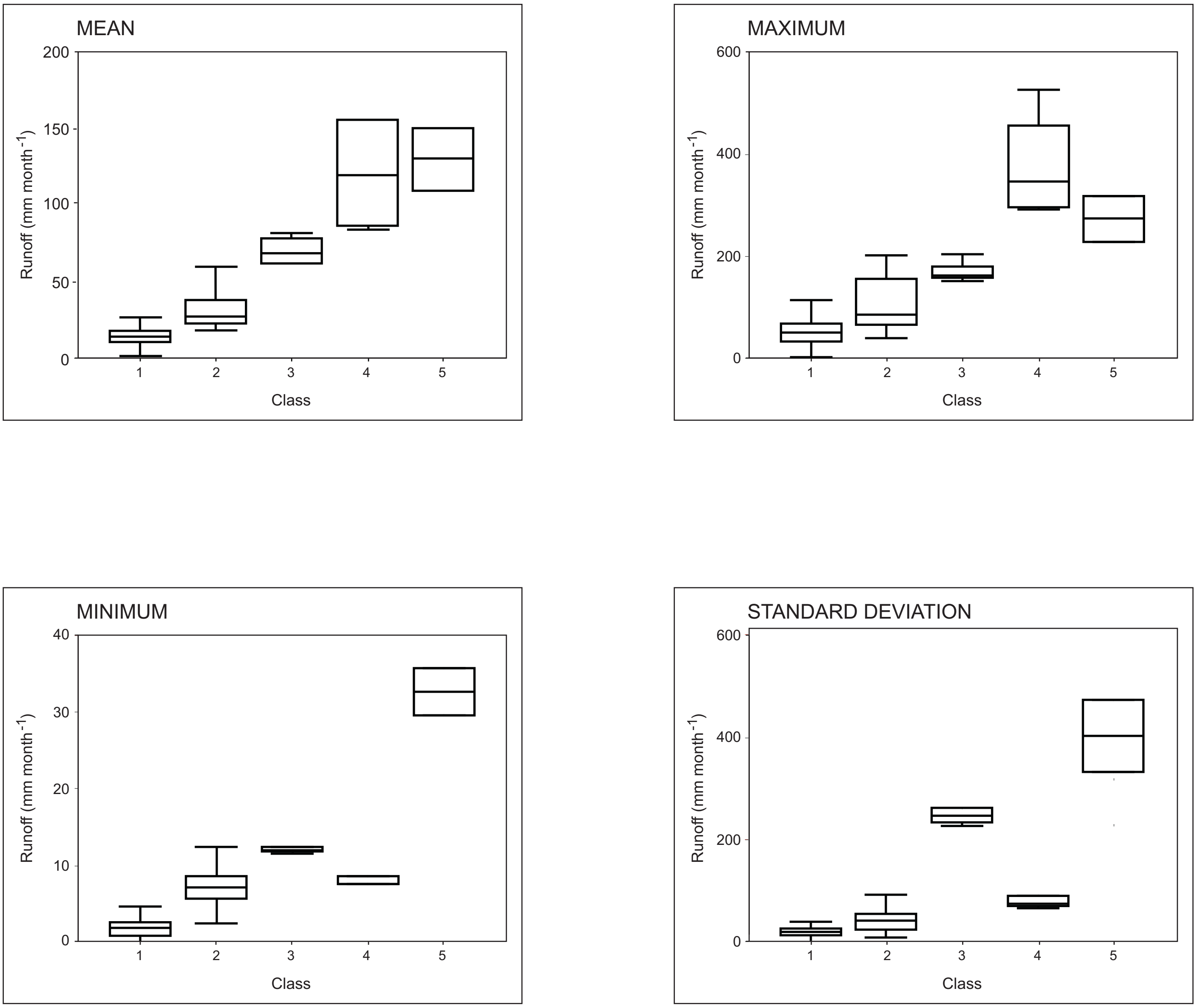
		median.		
HAMAX	1	High pulse count, where a high pulse is defined as an event greater than Q25 per year.	–	7, 9, 11
Low flow conditions				
LPC	1	Low pulse count: number of low pulses in the sample year, where a low pulse is defined as less than Q75.	–	7, 9, 11
LPCYR	1	Mean number of LPC per year.	yr^{-1}	7, 9, 11
Duration of flow events				
High flow conditions				
D3CVMA…D90CVMA	4	Coefficient of variation of the average annual 3-day/7-day/30-day/90-day maximum.	–	This study
D3MAX50…D30MAX50	4	Average annual 3-day/7-day/30-day/90-day maximum discharge divided by Q50.	–	13 (90-day – this study)
DAY3MAX…DAY90MAX	4	Average annual 3-day/7-day/30-day/90-day maximum discharge.	m^3s^{-1}	7, 9, 11
FFI	1	Flood Flow Index i.e. ratio of flood volumes to baseflow volumes $= \frac{(1-\mathrm{BFI})}{\mathrm{BFI}}$	–	8
Q5MEAN / DFQ5ME	2	Monthly flow duration index i.e. $= \frac{\mathrm{Q5}}{\text{Mean discharge}}$	–	1
Low flow conditions				
D3CVMI…D90CVMI	4	Coefficient of variation of the average annual 3-day/7-day/30-day/90-day minimum.	–	This study
D3MIN50…D90MIN50	4	Average annual 3-day/7-day/30-day/90-day minimum divided by Q50.	–	13 (90-day – this study)
DAY3MIN…DAY90MIN	4	Average 3-day/7-day/30-day/90-day minimum.	m^3s^{-1}	7, 9, 11 (7-day – 14, 15)
Q95MEAN / DFQ95MEAN	2	$= \frac{\mathrm{Q95}}{\text{Mean discharge}}$	–	This study
ZERODAY	1	The extent of intermittence i.e. the average number of days with zero discharge.	–	6, 3, 11
ZEROMON	1	Percentage of all months with zero discharge.	%	10
Timing of flow events				
High flow conditions				
CV7JDMA	1	Coefficient of variation of the Julian date of the seven 1-day maximum discharges in the hydrological year.	–	This study
MAXJD	1	The Julian date of the 1-day annual maximum discharge.	–	13, 7, 9, 11
MEMAXJD	1	Average Julian date of the seven 1-day maximum discharges in the hydrological year.	–	This study
STDMAJD	1	Standard deviation of the Julian date of the seven 1-day maximum discharges in the hydrological year.	–	This study

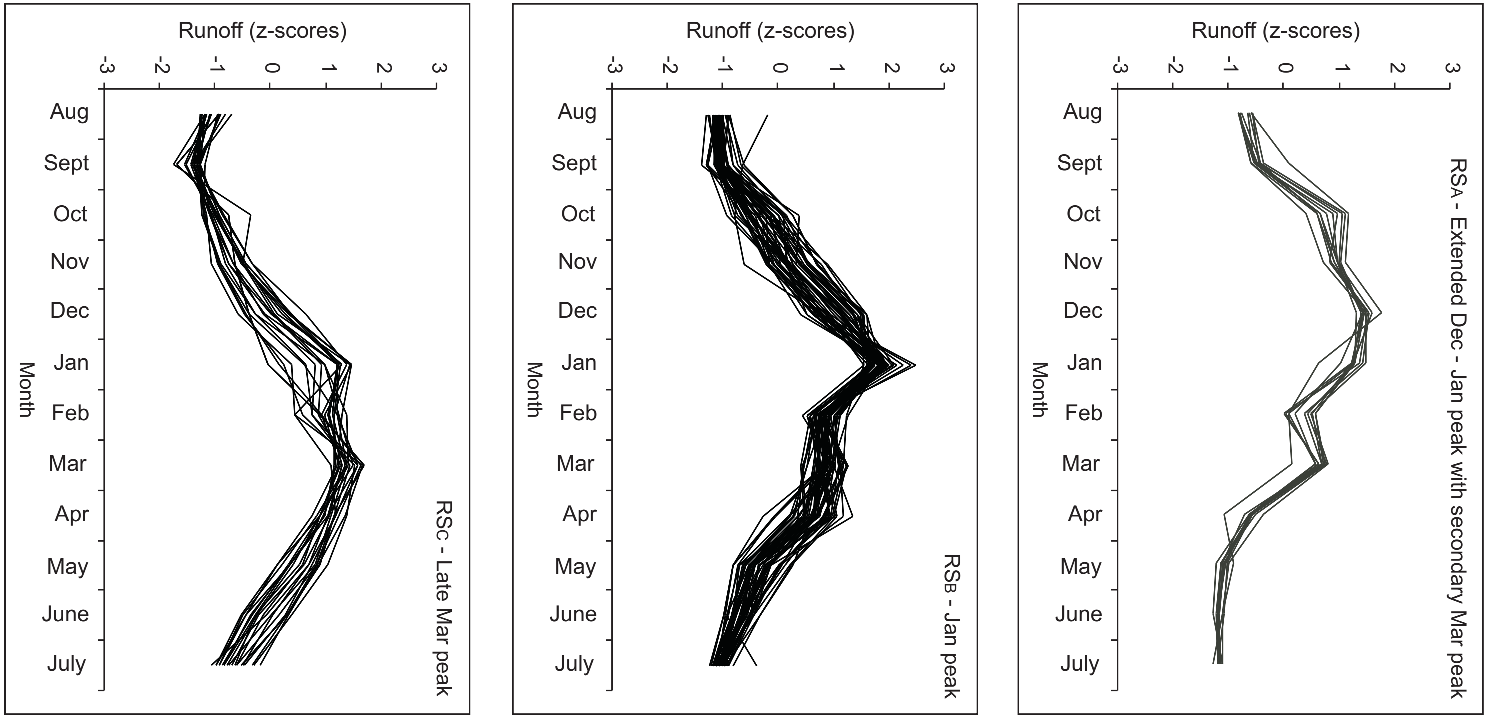
Low flow conditions				
CV7JDMI	1	Coefficient of variation of the Julian date of the seven 1-day minimum discharges in the hydrological year.	–	This study
MEMINJD	1	Average Julian date of the seven 1-day minimum discharges in the hydrological year.	–	This study
MINJD	1	The Julian date of the 1-day annual minimum discharge.	–	13, 7, 9, 11
STDMIJD	1	Standard deviation of the Julian date of the seven 1-day minimum discharges in the hydrological year.	–	This study
Rate of change of flow conditions				
Average flow conditions				
MEDIFF	1	Mean of difference between the annual positive and negative changes in water conditions.	m^3s^{-1}	This study
NCRR	1	Number of days of constant discharge from one day to the next.	–	This study
NCRRYR	1	Number of days of constant discharge per year from one day to the next.	yr^{-1}	This study
NERR	1	Number of negative changes in discharge from one day to the next.	–	7, 9, 11
NERRYR	1	Number of negative changes per year in discharge from one day to the next.	yr^{-1}	This study
PORR	1	Number of positive changes in discharge from one day to the next.	–	7, 9, 11
PORRYR	1	Number of positive changes per year in discharge from one day to the next.	yr^{-1}	This study
STDDIFF	1	Standard deviation of differences between the annual positive and negative changes in water conditions.	m^3s^{-1}	This study

[1] *Codes for references: 1. Hughes and James (1989); 2. Richards (1989); 3. Poff and Ward (1989); 4. Biggs (1990); 5. Jowett and Duncan (1990); 6. Poff (1996); 7. Richter* et al. *(1996); 8. Clausen and Biggs (1997); 9. Richter* et al. *(1997); 10. Puckridge* et al. *(1998); 11. Richter* et al. *(1998); 12. Clausen and Biggs (2000); 13. Clausen* et al. *(2000); 14. Wood* et al. *(2000); and 15. Wood* et al. *(2001).*

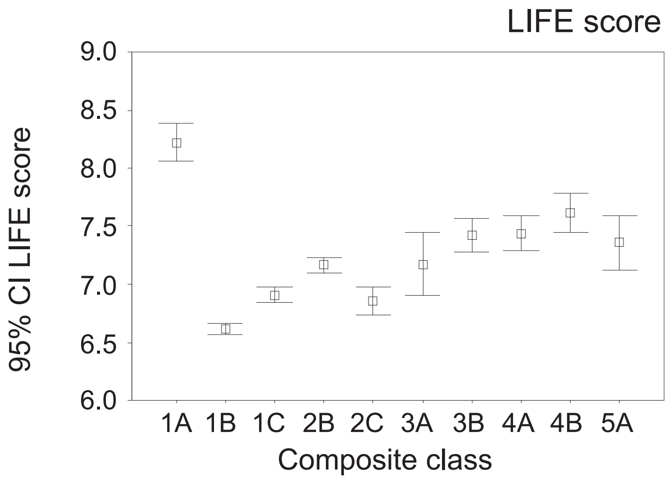

(a)
Discharge (m^3s^{-1})
Year
(b)
Discharge (m^3s^{-1})
Year


Flow regime shape class
A – Extended December - January peak with secondary March peak.
B – January peak with relatively steep rising and falling limbs.
C – Late March peak with prolonged rising limb.
Flow regime magnitude class
1
2
3
4
5
Flow regime composite class
e.g. 1B = B
200 km

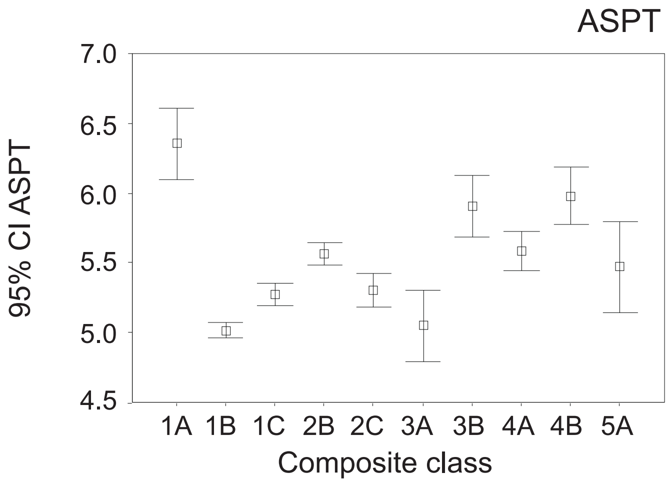

MEAN
Runoff (mm month-1)
0
50
100
150
200
1
2
3
4
5
Class
MAXIMUM
Runoff (mm month-1)
0
200
400
600
1
2
3
4
5
Class
MINIMUM
Runoff (mm month-1)
0
10
20
30
40
1
2
3
4
5
Class
STANDARD DEVIATION
Runoff (mm month-1)
0
200
400
600
1
2
3
4
5
Class



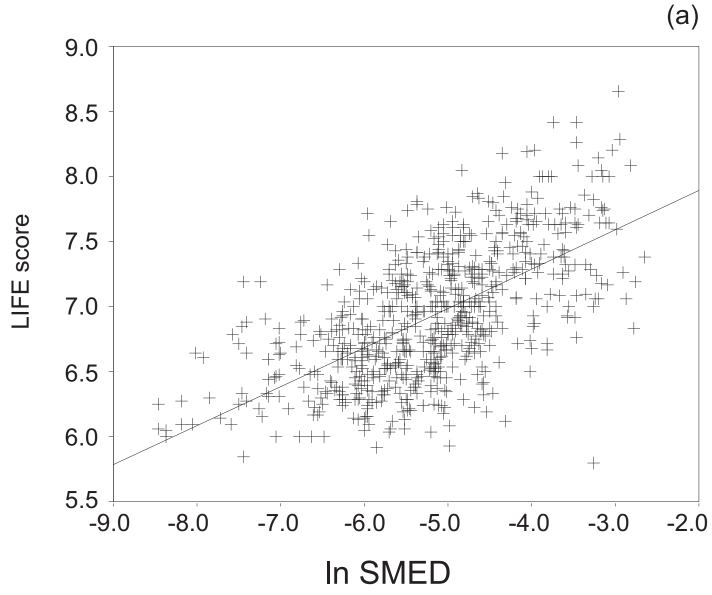
Runoff (z-scores)
-3 -2 -1 0 1 2 3
Month
Aug
Sept
Oct
Nov
Dec
Jan
Feb
Mar
Apr
May
June
July
RSc - Late Mar peak
RSB - Jan peak
RSA - Extended Dec - Jan peak with secondary Mar peak

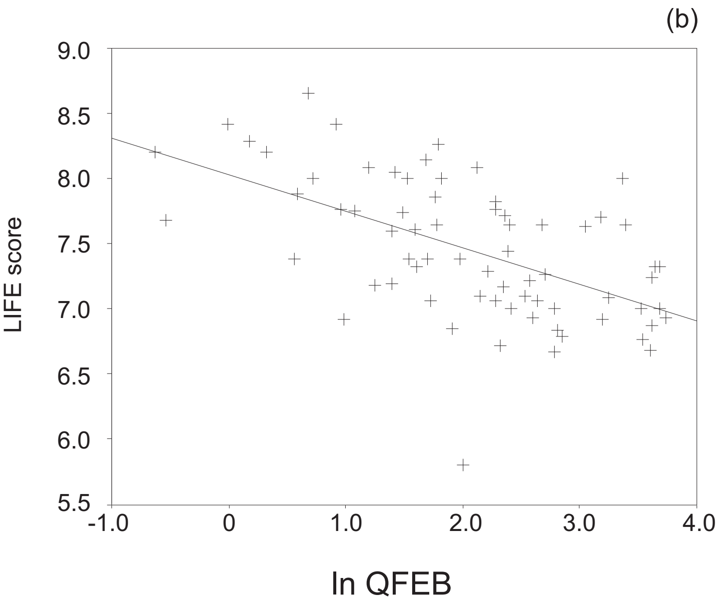


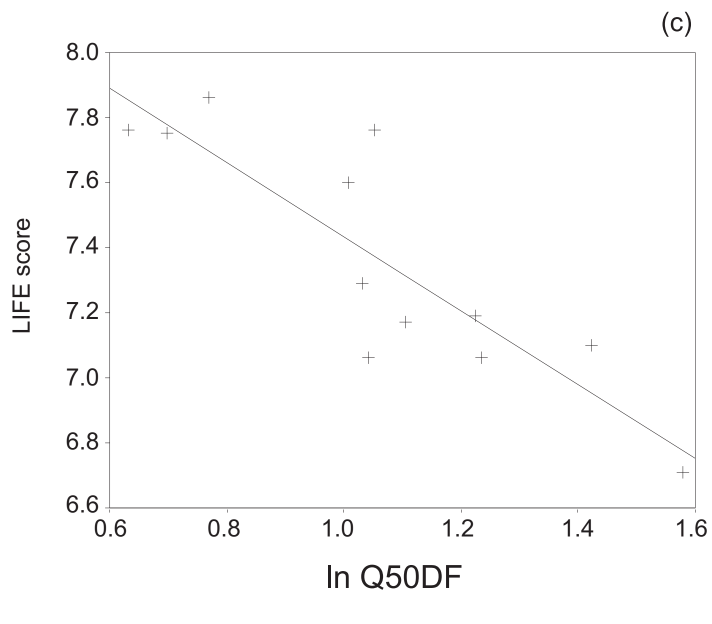
	RC_{1A}	RC_{1B}	RC_{1C}	RC_{2B}	RC_{2C}	RC_{3A}	RC_{3B}	RC_{4A}	RC_{4B}
RC_{1B}	***								
RC_{1C}	***	***							
RC_{2B}	***	***	***						
RC_{2C}	***	***	NS	***					
RC_{3A}	***	***	*	NS	*				
RC_{3B}	***	***	***	NS	***	NS			
RC_{4A}	***	***	***	**	***	*	NS		
RC_{4B}	***	***	***	**	***	*	NS	NS	
RC_{5A}	***	***	***	NS	**	NS	NS	NS	NS



	RC_{1A}	RC_{1B}	RC_{1C}	RC_{2B}	RC_{2C}	RC_{3A}	RC_{3B}	RC_{4A}	RC_{4B}
RC_{1B}	***								
RC_{1C}	***	***							
RC_{2B}	***	***	***						
RC_{2C}	***	***	NS	**					
RC_{3A}	***	NS	NS	***	NS				
RC_{3B}	*	***	***	NS	***	***			
RC_{4A}	***	***	**	NS	**	**	*		
RC_{4B}	*	***	***	*	***	***	NS	**	
RC_{5A}	***	**	NS	NS	NS	*	*	NS	**


(a)
LIFE score
9.0
8.5
8.0
7.5
7.0
6.5
6.0
5.5
-9.0 -8.0 -7.0 -6.0 -5.0 -4.0 -3.0 -2.0
ln SMED


(b)
LIFE score
9.0
8.5
8.0
7.5
7.0
6.5
6.0
5.5
-1.0 0 1.0 2.0 3.0 4.0
ln QFEB


(c)
LIFE score
8.0
7.8
7.6
7.4
7.2
7.0
6.8
6.6
0.6 0.8 1.0 1.2 1.4 1.6
ln Q50DF