Do fish go with the flow? The effects of periodic and episodic flow pulses on 0+ fish biomass in a constrained lowland river

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Running head line: Flow pulses and 0+ fish biomass

Summary

The hydrological regime is a significant driver of fish population dynamics in rivers, but there is a dearth of information regarding the mechanisms behind its effects on temperate species, especially non-salmonids. This study investigated the effects of periodic and episodic flow pulses on 0+ fish biomass in a constrained lowland river. De-seasonalised cross-correlation analysis was used to examine time-lagged correlations in episodic signals, in isolation of seasonal periodicity, to identify the responses and response timings of 0+ fish production to abiotic variables, and whether apparent "pulse-depletions" in biomass occur instantaneously (e.g. due to fish displacement during high pulses) or after a time lag. As anticipated, 0+ fish biomass was highest during periods of low discharge and high temperatures in summer, but cross-correlation analysis revealed a negative impact of high pulses on 0+ fish biomass with a lag of 7 months. There was no evidence for an instantaneous pulse-depletion effect of discharge on 0+ fish biomass, suggesting that the indirect effects of high pulses, such as habitat or food-web modifications, are more influential.

Key words: 0+ fish biomass, fish production, hydroecology, river discharge, cross-correlation, time lag

Introduction

Disturbances, defined by Lake (2000) as "potentially damaging forces applied to a habitat space, population, community or ecosystem", can have a profound influence on the physical and biological characteristics of ecosystems and their functioning. Flow pulses (*sensu* Tockner *et al.*, 2000) and flood pulses (*sensu* Junk *et al.*, 1989), for example, can be considered to represent flow-generated disturbances (Lake, 2007), and are responsible for creating and structuring habitats and controlling biota in lowland rivers (Resh *et al.*, 1988; Junk *et al.*, 1989; Welcomme and Halls, 2001). Fishes are useful indicators of environmental disturbances in lowland rivers because the various guilds integrate a wide range of conditions over their life cycles that are linked to the habitat requirements of particular species and ontogenetic stages (Copp, 1989; Schiemer, 2000; Welcomme *et al.*, 2006). Larvae and 0+ juveniles are particularly applicable in this respect because tolerable habitat conditions are often much narrower for such fishes compared with older and larger individuals, owing to the strict physical and energetic constraints facing young fishes (Schiemer *et al.*, 1991, 2001a; Flore *et al.*, 2001; Jurajda *et al.*, 2010; Leclere *et al.*, 2012; Musil *et al.*, 2012). Morphological and behavioural limitations often restrict the early developmental stages of fishes to specific habitats, which, together with their small size and fragility, means that larval and 0+ juvenile fishes are more susceptible than adults to adverse changes in their environment (Copp *et al.*, 1991; Schiemer and Waidbacher, 1992; Sogard, 1997; Jones and Petreman, 2012). The effects of flow and extreme events, as well as habitat fragmentation and degradation, are therefore generally most easily observed in 0+ fishes (Harvey, 1987; Nunn *et al.*, 2003, 2007b, 2010; Jones and Petreman, 2012).

Numerous studies have suggested that the cause of fluctuations in a biological response can be attributed to episodic fluctuations in an environmental driver (e.g. Strange *et al.*, 1992;

Dixon *et al*., 1999) or to deterministic oscillations such as seasonal cycles (e.g. Broekhuizen and McKenzie, 1995; Lehodey *et al.,* 2006). In the context of fish populations, flow pulses outside the normal range are seen as potentially negative disturbances capable of depleting fish stocks through physical displacement (Cowx *et al.* 2012; Jones and Petreman, 2012). For simplicity, this is hereafter referred to as "pulse-depletion". Several studies have examined the biomass and production of larval and juveniles fishes in lowland rivers (e.g. Gerking, 1978; Welcomme, 1979; Penczak *et al*., 1982; Holčík, 1996), but the reported impacts of river discharge have been varied: some populations were reduced in size or extirpated by high discharges (e.g. Záleský, 1925; Onodera and Ueno, 1961; Čihar, 1976), whereas others were positively affected (e.g. Stanković and Yanković, 1971; Holčík and Bastl, 1977). However, most studies have focused on discharge impacts over short time periods (<1 year) and hence provide no evidence of longer-term impacts (Holčík, 1996). The negative impacts of elevated flow events on fish are often reported as acute and relatively instantaneous (a "pulse" response; Glasby and Underwood, 1996; Lake, 2000), with displacement-induced mortality, or "wash-out", widely cited as a key mechanism (e.g. Harvey, 1987; Bolland *et al*., 2015), especially in poorly structured or degraded habitats (Pearsons *et al*., 1992; Bischoff and Wolter, 2001); "wash-down" may also be important in highly fragmented systems, with displaced fishes sometimes unable to return upstream due to the presence of migration barriers. It is important to note, however, that elevated flow events are an integral component of natural hydrological regimes, and generally only become an issue in watercourses that have been degraded by anthropogenic modifications.

Much of the current evidence for the existence of a pulse-depletion paradigm in riverine ecology is based on simple correlations between discharge and a biological response (e.g. fish abundance, biomass). These analyses often demonstrate a negative relationship between the

response variable and discharge, and causation is assumed. However, conclusions may be erroneous if they have not considered the existence of time-lagged relationships or accounted for inherent seasonality from annual weather patterns and spawning cycles, which could generate coincidental driver-response relationships. Time lags between environmental drivers and biotic responses are common and have been reported in numerous aquatic studies (Olden and Neff, 2001). Examples include food-web interactions (e.g. Mateev, 1995; Olden, 2000), dynamics of phytoplankton (e.g. Duarte, 1990; Vaque *et al*., 1997), zooplankton (e.g. Broekhuizen and Mckenzie, 1995) and plant communities (e.g. Healy, 1997), and fish-environment relationships (e.g. Kim *et al*., 1997; Downton and Miller, 1998; Smith *et al*., 2000). Failure to recognise time-lagged relationships could lead to erroneous conclusions about the response and response timing of a biological indicator to a driver or disturbance and the mechanisms that underlay them. Walters and Collie (1988), for example, described a situation where an apparent negative stock-recruitment relationship can be observed when favourable environmental conditions cause stocks to increase, but with a lag such that peaks in stock size coincide with periods of deteriorating environmental conditions. It should also be borne in mind that fish habitat use and geographical distribution may change according to environmental conditions (Keckeis *et al*., 1997; Bolland *et al*., 2015), which could incorrectly be interpreted as pulse-depletion if sampling strategies are inadequate.

In this study, we present a method that examines time-lagged correlations in episodic signals, interpreted as aseasonal flow pulses, in isolation of obfuscating low-frequency oscillations representing seasonal periodicity (Figure 1). The specific definition of Trexler *et al*. (2005), whereby a disturbance is defined as "a process that removes biomass", was adopted. The aim

was to elucidate the influence of a suite of abiotic factors on the long-term productivity of 0+ fishes in a constrained lowland river, and determine if biomass is influenced most by instantaneous pulse-depletion or the indirect effects of high pulses, such as habitat or food-web modifications. It was hypothesised that an intra-annual, non-time-lagged relationship between fish biomass and discharge (strongest significant relationship at time = 0) would be detected, validating instantaneous pulse-depletion as the most significant driver of changes in larval and juvenile fish production.

Materials and methods

Study area

This study was carried out on the lower River Trent, England (Figure 2). The Trent is the third longest river in the UK (274 km), with a long-term mean discharge of 84 m^3s^{-1} and a catchment area of 10 500 km^2. The river is impounded by a number of large weirs and sluices, resulting in a relatively stable discharge regime (Nunn *et al*., 2007a, b).

Fish sampling

Larval and 0+ juvenile fishes were captured monthly from May 1999 to June 2010, inclusive, at three fixed sites (Attenborough, no. samples = 119; Trent Bridge, no. samples = 122; Dunham, no. samples = 128) along a 60-km length of the Trent using a micromesh seine net (25 m long, 3 m deep, 3 mm hexagonal mesh) (369 samples in total). This net captures fishes with a minimum size of 5 mm, and is a very effective method of catching large numbers of small-bodied individuals (Cowx *et al*., 2001). In all cases, sampling was carried out in still, marginal areas <2 m depth, where 0+ fish aggregated throughout the sampling period. All fishes were identified to species (Pinder, 2001), measured (standard length, nearest mm) and

sub-samples were weighed (wet weight, nearest g) to produce species-specific weight-length relationships ($W = aL^b$, where W = fresh weight (g), L = standard length (mm) and a and b are calculated from Log W = log a + log L, where a = y-axis intercept and b = regression slope); these were then used to calculate total 0+ fish biomass (Walton, 2013). A small number of short gaps in the 11-year dataset did not compromise its coverage of periodic and episodic hydrological events.

The frequency of occurrence and relative abundance of each fish species at each site were calculated (Hynes, 1950), and biomass (g m^{-2}) of 0+ fishes (all species combined) was calculated for each sample by dividing the biomass captured by the area netted (length × width of the rectangular area enclosed by the net). Biomass was calculated as it represents the total contribution of larval and juvenile individuals to fish production, is a useful measure of the amount of energy produced at the ecosystem level and thus available for ecological production at higher trophic levels, and is less susceptible than abundance to variations caused by fish hatching (Bagenal, 1978; Gerking, 1978; Penczak *et al*., 1982; Holčík, 1996; Sedgwick, 2006). Biomass estimates were then natural logarithm ($x + 1$) transformed to account for null catches, and median biomasses were compared between sites using Kruskal-Wallis and *post hoc* Mann-Whitney U-tests. A Principal Components Analysis (PCA) biplot was produced to visualise the contribution of species biomass to the total community biomass in each year using Brodgar software (http://www.brodgar.com/).

Characterisation of water temperature regime

Water temperature data (°C) were obtained from the Environment Agency gauging station at Holme Pierrepont, located between Attenborough and Trent Bridge, from 1999 until its closure in 2004, after which they were calculated using the relationship between the River

Trent at Holme Pierrepont and the Yorkshire Ouse at Cawood (Trent = Ouse (0.97) + 1.603, $P<0.001$, $r^2 = 0.94$). The data were used to calculate four variables, namely $C18$, $Cmax$, S_1 and S_2, during two "critical periods" in the development of 0+ fish; >12 °C-18 °C and >18 °C-annual maxima (Mills and Mann, 1985; Piffady $et\ al.$, 2010). $C18$ is the number of days between the first day to exceed 12 °C and the first to reach 18 °C, and $Cmax$ is the number of days >18 °C to the annual maximum temperature. S_1 and S_2, respectively, are the sums of the differences (positive and negative) between daytime temperature and the mean daily inter-annual temperature over each of the two periods (i.e. >12-18 °C, >18 °C-max. temperature), and express the difference in cumulative degree-days between a particular critical period and the average critical period, thereby indicating whether the periods are warmer or colder than the 11-year inter-annual mean (Piffady $et\ al.$, 2010). They were computed as follows:

$$S_1 = \sum_{j=C_{12}}^{C_{18}} \left(T_{ji} - \frac{\sum_{i=1}^{I} T_{ji}}{I}\right)$$

$$S_2 = \sum_{j=C_{18}}^{C_{max}} \left(T_{ji} - \frac{\sum_{i=1}^{I} T_{ji}}{I}\right)$$

where T_{ji} is the temperature of the day j for the ith year and I is the number of days in the according critical period.

Characterisation of river discharge regime

Mean daily discharge data ($m^3\ s^{-1}$) were obtained from the Environment Agency gauging station at Colwick (~4 km downstream of Trent Bridge and ~10 km downstream of Attenborough). The hydrograph was separated into ecologically relevant "Indicators of

Hydrological Alteration" (IHA) according to Richter *et al*. (1996, 1997, 1998) using the IHA software package (http://conserveonline.org/workspaces/iha/) (see Table 1). The hydrograph was also categorised into five "Environmental Flow Components" (EFCs; Richter and Thomas, 2007) to identify events that could cause a biological response. The EFC algorithm within the IHA software defines: (1) high flows as those exceeding the 75th percentile of all flows; (2) low flows as those not exceeding the 50th percentile; (3) extreme low flows as those not exceeding the 10th percentile; and (4) small and (5) large floods as flows with a return interval of 2 and 10 years, respectively.

In addition, the cumulative number of days above the mean discharge, the sum of the differences between the daily maximum discharge and the mean, and the maximum discharge were calculated to describe how 'wet' the two critical periods defined by the temperature variables $C18$ and $Cmax$ (i.e. >12 °C-18 °C, >18 °C-max. temperature) were in any given year compared to the inter-annual mean of critical periods. These were labelled $Q18$, $Qmax$, Q_1, Q_2, Q_{mean} (critical period) and Q_{max} (critical period), respectively.

Fish-temperature and fish-discharge relationships

Following correlation analysis to remove redundant correlated variables ($r_s = 0.7$), a reduced set of 21 explanatory variables, namely IHAs and critical period variables (Table 1), was explored for relationships with the response variable (0+ fish biomass, standardised by area and averaged over all sites) using a series of linear regressions (multivariate techniques were not suitable due to a low case-to-variable ratio). False discovery rate (FDR) control (Benjamini and Hochberg, 1995) was used to account for the cumulative type-1-error associated with multiple comparisons (Shaffer, 1995). PCA was carried out to examine the underlying dimensions composed of weighted combinations of variables (principal

components) and the interaction of these principal components with years. The results were displayed in a biplot using Brodgar software. In addition, a Pearson product-moment correlation was conducted to test for a relationship between mean daily water temperature and river discharge.

Secondly, the interdependence of the dynamics of biomass-temperature and biomass-discharge interactions were analysed using cross-correlation analysis of monthly mean values of 0+ fish biomass, river discharge and water temperature. The cross-correlation function quantifies the association between two variables, and is calculated for various positive and negative time lags and plotted on the x-axis, with the correlation coefficient (-1 to $+1$) on the y-axis (Zuur et al., 2007). Dotted lines representing the 95% upper and lower confidence intervals are then used to test the null hypothesis that the correlation between y_t and x_{t-k} is not significant; points outside this interval are significant cross-correlations with time lag k. Periodic components of the same frequency in both series lead to high cross-correlation values (peaks) at the corresponding lags; the height of the peaks can be considered a relative measure of connectivity between two variables (Scutareanu et al., 1999; Probst et al., 2012), and the positions of the peaks determine the phase shift (time lag) between the variables. In each analysis, the hypothesised influential variable (discharge, temperature), hereafter referred to as a "driver", was used as the input variable and the hypothesised "response" (biomass) as the output. The focus of this study was on relationships where peaks in the driver and response had positive time lags, as this could indicate causality; a positive correlation between driver and response would be represented by a significant peak in the top half of the output chart, whilst a negative correlation would be represented by a significant peak in the bottom half of the chart (Probst et al., 2012). Prewhitening removes spurious correlations based on temporal dependencies between adjacent values of the input (in this

case "driver") time series and removes these influences from the output time series (in this case the "response" time series) (Gröger and Fogarty, 2011; Shumway and Stoffer, 2011; Probst *et al.*, 2012). To prewhiten the input time series, an integrated auto-regressive moving-average (ARIMA) model was fitted to the input time series to remove significant autocorrelations therein. The p, d and q values of the input ARIMA model were determined by checking the autocorrelation of the model residuals; the model that included the lowest number of parameters while indicating no significant autocorrelation in the residuals was used to prewhiten the output time series (Supplementary Material Table 1). Prewhitening was used for cross-correlations of the trend and residual components in the biomass-discharge and biomass-temperature analyses, but not in seasonal components; the time series were absolutely regular in seasonal components, and seasonal autocorrelations cannot be removed by prewhitening. The potential error introduced by intra-multiplicity (Olden and Neff, 2001) was reduced by examining only a restricted number of lags (12) (Smith *et al.*, 2000). This was deemed a suitable timescale within which to observe ecologically meaningful driver-response relationships.

Seasonal effects can mask cross-correlations that potentially represent a biotic response (Chatfield, 1989; Jassby and Powell, 1990). A seasonal and trend decomposition using repeated locally weighted scatterplot smoothing (LOESS) was therefore conducted using the STL function in R (Zuur *et al.*, 2007). Repeated LOESS is an additive modelling technique that applies a smoothing curve to time series data. A large span width (width of periodic signal; 12 months) was used to provide an overview of long-term trends in biomass and environmental data in isolation of the influence of a seasonal periodic component. All time-series were standardized by z-transformation to facilitate visualization (Blanchard *et al.*, 2010).

Results

Fishes

Approximately 500,000 fish of 29 species and 12 families were recorded over the 11-year study period. Overall, roach (*Rutilus rutilus* (L.)), dace (*Leuciscus leuciscus* (L.)), chub (*Squalius cephalus* (L.)), gudgeon (*Gobio gobio* (L.)), common bream (*Abramis brama* (L.)), three-spined stickleback (*Gasterosteus aculeatus* L.), perch (*Perca fluviatilis* L.), bleak (*Alburnus alburnus* (L.)) and minnow (*Phoxinus phoxinus* (L.)) occurred most frequently and in the highest abundances (Supplementary Material Table 2).

The median 0+ fish biomass at Dunham (Med, IQR: 0.45, 0.02-2.99 g m^{-2}) was significantly lower than at Attenborough (1.21, 0.04-10.18 g m^{-2}; Mann-Whitney *U*-test: $Z = -2.05$, $n = 94$, $P = 0.040$) and Trent Bridge (1.98, 0.06-8.07 g m^{-2}; Mann-Whitney *U*-test: $Z = -2.28$, $n = 97$, $P = 0.02$), but there was no significant difference between Attenborough and Trent Bridge (Mann-Whitney *U*-test: $Z = 0.00$, $n = 94$, $P = 1.00$). Attenborough had the highest mean biomass (mean $\pm$ S.D = 29.95 $\pm$ 80.48 g m^{-2}), followed by Trent Bridge (6.48 $\pm$ 15.48 g m^{-2}) and Dunham (3.34 $\pm$ 8.13 g m^{-2}).

The biomass composition of the assemblages was very variable over time. Although roach was dominant in most years (mean biomass of all sites), dominance changed dramatically between some years. This is best illustrated by the shift in the contribution of bream (to annual community biomass) from 15% (the fourth highest contributor to overall biomass in the assemblage) in 2001 to 49% (dominant) in 2002. Mean 0+ fish biomass (all sites) peaked in 2005, with high biomasses also recorded in contiguous years, caused largely by high densities at Attenborough; biomasses at Trent Bridge and Dunham were relatively stable over

the study period. The biomass minimum occurred in 2008. Generally, biomasses were higher in the second half of the year, due to the larger size of 0+ fishes at that time. Roach, dace and gudgeon contributed high percentage biomasses to the annual total in the first few years of the study period, with a substantial percentage biomass of chub also in 2001. By contrast, common bream contributed little to the percentage biomass in the first 3 years of the study period, but dominated from 2002-2004. Roach was the dominant species in 2005, but 2006 onwards was generally mixed, with higher percentage biomass contributions from dace and chub more apparent in some years, whilst a substantial increase in the proportion of bleak in the fish assemblage occurred in 2009 (Figure 3).

River discharge

Over the 11-year period, the River Trent experienced one "large flood", in November 2000 (Figure 4). Five other events, mostly in the winter, were classed as "high flows" (>75th percentile) (Figure 4). "Low flows" were the dominant flow type, occurring ~62% of the time (Fig. 4). "Extreme low flows" occurred annually, almost exclusively in the summer, with the longest low-flow period occurring in 2003 (Figure 4). IHA values indicated that mean monthly summer (May-September) flows were roughly 50% of mean flows during the winter (November-February), demonstrating high seasonal variation. In addition, the range between the mean 1-day minimum and maximum flows was approximately 410 m^3s^{-1}, indicating a difference of almost 15-fold between extreme low and extreme high flows. The mean number of high pulses per year (~12) was higher than the number of low pulses per year (~10), but low pulses had a longer mean duration (~6 days) than did high pulses (~5 days).

There was considerable inter-annual variation in the number of days above the basal discharge rate (long-term mean) during the $C18$ critical period. The years 2000 and 2001 had relatively high numbers of wetter-than-average days during the Cmax period, whereas 2006 and 2007 had very few 'wet' days; the cumulative amount of discharge above the long-term mean (Q_1) followed a similar pattern, with approximately biannual cycles in both data sets (Figure 5a).

Water temperature

No similarities were observed in the patterns of water temperature during $C18$ and Cmax. The highest number of days in the $C18$ period was recorded in 2007 (43 days, mean $\pm$ S.D $=$ 18.8 $\pm$ 12.49 days), whereas the same year represented the period minimum for Cmax (4 days, 25.45 $\pm$ 17.65 days). Whilst there was no clear trend in the interannual variation of $C18$, values for Cmax from 2003-2006 were higher than the period mean, of which 2005 and 2006 had warmer than average S_1 and S_2 values (Figure 5b). There was a significant negative correlation between mean daily water temperature and river discharge (Pearson product-moment correlation: $r^2 = 0.15$, $P<0.001$).

Fish-temperature and fish-discharge relationships

Although there were no statistically significant annual-resolution relationships between 0+ fish biomass and biologically relevant indicators after accounting for the number of comparisons (Table 1), the PCA biplot revealed potentially influential drivers of 0+ fish biomass. The years 2003 and 2005, which had relatively high 0+ fish biomass, were associated with a high number of low-flow pulses (Figure 6). Mean discharge was found to have a significant negative effect and temperature a significant positive effect on 0+ fish biomass at a higher temporal resolution (Table 1).

The cross-correlation analyses between raw monthly biomass and monthly discharge revealed a noticeable annual periodicity with time lag. The cyclical association was weak (~0.3 max.) and relatively inconsistent, however, and likely to stem from a strong seasonal pattern in both series. A similar periodicity was revealed by the cross-correlation analysis between monthly biomass and monthly temperature. Seasonal decomposition was thus conducted on the time series using repeated LOESS, which revealed that peaks in biomass generally occurred with peaks in temperature and periods of low discharge (Figure 7). This was reflected in maximum cross-correlations for seasonal components of temperature, discharge and biomass at lags of 0-3 months (Figure 8A and B). A significant negative cross-correlation was found at a lag of 7 months between the trend components of discharge and biomass (Figure 8D). A similar lag was also observed in the "residual" components of discharge and biomass (8 months), whereas no significant cross-correlation was observed between the trends and residuals of temperature and biomass (Figure 8C and E).

Discussion

Fish recruitment success is determined by many factors, including the abundance and condition of spawners, trophic resources, the quality and quantity of spawning and nursery habitats, the duration of suitable spawning periods, predation and disease, and abiotic conditions in the larval and juvenile periods (Larkin, 1978). In particular, water temperature and river discharge are known to affect the growth and recruitment of many species (Mills and Mann, 1985; Schlosser, 1985; Nunn *et al*., 2003), and therefore their contribution to community biomass. In the current study, the peak in biomass coincided with a hydrologically stable period with few high flows; EFC analysis revealed that the period was characterised by low flows and extreme low flows. The association of the peak in biomass

with low-flow pulses was also demonstrated in a PCA analysis of IHA variables. This low-flow period was also well defined by the low number of discharge-days and the low cumulative difference between daily discharge and the long-term mean during the $C18$ period (between the first day to exceed 12 °C and the first to reach 18 °C). In addition, cumulative temperatures during the peak in biomass were higher than the long-term mean. This suggests, in accordance with the Inshore Retention Concept (Schiemer *et al*., 2001b), that warm periods (within species' physiological tolerance ranges) coinciding with sustained periods of low flow can be beneficial to 0+ fish biomass production in large European rivers by increasing the growth and survival of some, particularly warm-water cyprinid, species (Mills and Mann, 1985; Nunn *et al*., 2003; Wolter, 2007). By contrast, it is important to note that recruitment of cool-water species, such as salmonids, is known to respond negatively to sustained warm periods with low flows (Cowx *et al*., 1984; Riley *et al*., 2009).

Stochastic, episodic increases in river discharge can significantly influence the survival of 0+ fishes and may cause densities, species richness and species composition to fluctuate yearly (Schlosser, 1985; Schlosser and Angermeier, 1990; Pont and Nicolas, 2001). There were no statistically significant annual-resolution relationships between 0+ fish biomass and biologically relevant indicators (IHAs and critical period variables) in this study after accounting for the number of comparisons. In addition, although there were statistically significant higher temporal-resolution (monthly) relationships (Qmean and mean temp; see Table 1), they likely reflected only periodic seasonal relationships between driver and response i.e. evolved annual co-variation in spawning/growth cycles and seasonal flow periodicity, and contribute little to a mechanistic understanding of aseasonal environmental drivers and biotic responses. However, the cross-correlation analysis of the monthly resolution, biomass-discharge time series revealed significant lags of 7 months in the trend

and 8 months in the residuals, indicating that the episodic signals within the discharge time series, representative of flow pulses, have an observable long-term effect on fish biomass. If the effects of high discharges on 0+ fish biomass were only instantaneous (i.e. displacement-related population declines), the position of the maximum cross-correlation would be at zero months. Although a lag at zero months was observed in the cross-correlation of seasonal components, the possibility of seasonality-driven covariation with natural cycles and colinearity with confounding factors (e.g. temperature) cannot be ignored. There was no significant lag at zero months in the trend and residual components, however, thus there is no evidence for an instantaneous pulse-depletion effect of discharge on 0+ fish biomass, whereby high-flow events significantly reduce fish biomass through immediate displacement, in the regulated River Trent. Contrary to the influence of discharge, no long-term effect of temperature on fish biomass was observed. Temperature appears to have only an instantaneous, direct effect on fish biomass, presumably by increasing growth and survival in synchronisation with temperature increases.

The delayed biotic response demonstrated in this study suggests that discharge has a significant long-term influence on the stability of fish community biomass in the regulated River Trent. The specific mechanisms behind the delayed response are unclear, but the observed lag can be explained by one or both of the following hypotheses: (1) 0+ fish biomass increases occur 7 months after discharge decreases due to pre-spawning factors; and (2) 0+ fish biomass decreases occur 7 months after discharge increases due to indirect effects of high discharges. Given the timing of biomass peaks (generally in July) and that the earliest species (perch and dace) hatch in late April (Nunn *et al*., 2007c), hypothesis 1 would suggest that factors prior to spawning are influential on 0+ biomass. It is possible that discharges 7 months prior to a response in 0+ biomass affect adults prior to spawning, for example low

flows could enhance adult condition and survival, thereby increasing individual fitness and reproductive output. River discharge may also affect spawning and nursery habitats prior to spawning. Hypothesis 2, however, is perhaps the more likely explanation for the lag in biomass-discharge dynamics observed in this study. The environmental changes caused by high discharges may negatively affect habitat quality and/or prey availability, thereby reducing the growth and survival of 0+ fish. This is in accordance with Nunn *et al*. (2003), who suggested that, in most years, the indirect effects of high-discharge events, such as restricted growth caused by reductions in water temperature, discharge-associated increases in energy expenditure or a lack of suitable food, have more influence on year-class strength than does discharge-induced mortality by displacement; the exception is when floods occur during the early larval period. Similarly, Reichard and Jurajda (2004) found that periods of elevated flow had no effect on the numbers of 0+ cyprinid fishes displaced and, as in other studies (e.g. Pavlov, 1994; Pavlov *et al*., 2008; Schludermann *et al*., 2012; Lechner *et al*., 2014), suggested that the downstream movement of 0+ cyprinids is active, rather than purely passive.

Contrary to the potential (negative) impacts of pulse-depletion in modified systems, many studies have demonstrated the positive role of elevated flows, especially over-bank events, in enhancing fish production in natural lowland rivers by increasing useable habitat area, facilitating lateral movements for reproduction and refuge, and enabling the transfer of terrestrial resources (e.g. nutrients, woody debris and sediments) (e.g. Junk *et al*., 1989; Welcomme and Halls, 2001). This implies that habitat structure and connectivity play a crucial role in the dynamics of floodplain fish populations, and that fragmentation in constrained rivers is likely to influence the capacity of fishes to respond to high-flow events. Positive effects of elevated discharges on 0+ fish biomass were not observed in this study,

possibly due in part to the high degree of physical and hydrological modification of the River Trent; instream and floodplain rehabilitation would increase the diversity and area of habitats available to fishes, and potentially enhance production and survival during floods (Nunn *et al*., 2007b). It remains to be tested whether more natural or rehabilitated rivers demonstrate similar long- and short-term responses to high discharge events, but the results of this study support the view that high-flow events should not be seen exclusively as an acute disturbance to fish, which are generally adaptively resistant to flows of high magnitude, and chronic ecosystem alterations caused by high or low flows also appear to affect long-term resilience.

It is essential to distinguish between cause and effect when describing environmental perturbations, to allow any undesirable effects of flow alterations to be prevented or ameliorated. River discharge and water temperature are extrinsic master variables known to explain a significant proportion of the variation in fish populations (Poff and Ward, 1989) but, due to evolved annual synchronicity, seasonality represents a source of deterministic bias when examining the effects of stochastic flow events. Isolating episodic signals from time series in eco-hydrological investigations is therefore advantageous, to remove any underlying extraneous variables, unrelated to flow events, that could generate a biomass response. This study has demonstrated a method to decompose flow-response time series to better evaluate potential relationships and their causal mechanisms, through the removal of obfuscating signals and the consideration of time lags. Correlations of raw variables do not account for omitted variable bias, as discharge, temperature and biomass oscillations are confounding and temporal autocorrelations within each time series generate bias lags. By contrast, the 7-8 month lag between flow events and biomass observed in this study could only be generated by a genuine discharge-related effect, or improbable coincidence, rather than omitted variable bias. This study demonstrates both the value of long-term datasets in eco-hydrological

investigations (Bayley, 2002; Holmes, 2006; Nunn *et al*., 2010; Dodds *et al*., 2012; Lindenmayer *et al*., 2012) and the importance of recognising time-lagged relationships in the response of a biological indicator to a driver.

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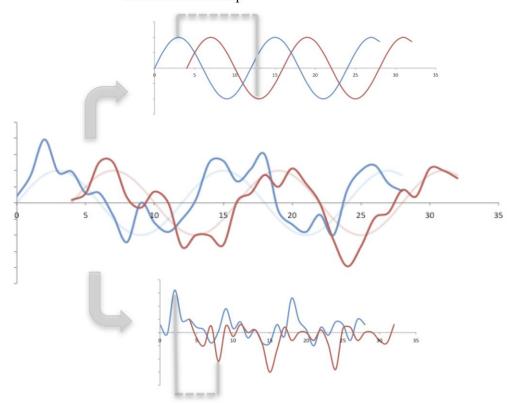
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Table 1. Relationships between 0+ fish biomass (g m^{-2}) in the River Trent and various hydrological and water temperature indices.

Annual resolution indicators	Mean	Correlation with biomass			
		r	R^2	Adj p	n
January mean flow	106.75				
February mean flow	101.51	−0.28	0.08	0.856	12
March mean flow	70.87	−0.26	0.07	0.856	12
April mean flow	73.48	−0.14	0.02	0.868	12
May mean flow	52.47				
June mean flow	50.22				
July mean flow	53.25	−0.33	0.11	0.771	12
August mean flow	47.24	−0.08	0.01	0.889	12
September mean flow	42.50	−0.24	0.06	0.856	12
October mean flow	66.42	0.10	0.01	0.889	12
November mean flow	98.70				
December mean flow	107.41	−0.40	0.16	0.771	12
1-day minimum flow	28.54				
3-day minimum flow	29.00				
7-day minimum flow	29.91				
30-day minimum flow	33.76				
90-day minimum flow	41.21				
1-day maximum flow	440.64				
3-day maximum flow	390.87				
7-day maximum flow	311.88				
30-day maximum flow	199.19				
90-day maximum flow	135.31				
Zero flow (days)	0				
Base flow	0.37	0.37	0.14	0.771	12
1-day minimum flow (Julian date)	220.67				
1-day maximum flow (Julian date)	191.08	0.16	0.02	0.868	12
Number of low pulses	10.58	0.50	0.25	0.771	12
Median duration of low pulses (days)	5.33	−0.37	0.13	0.771	12
Number of high pulses	12.42	−0.10	0.01	0.889	12
Median duration of high pulses (days)	4.54				
Rise rate (m^3/s/day)	7.49	−0.44	0.19	0.771	12
Fall rate (m^3/s/day)	-4.98				
Number of hydrologic reversals	112.17	0.14	0.02	0.868	12
Qmean	43.75	−0.33	0.11	0.771	12
Qmin	28.54	−0.59	0.35	0.771	12
Qmean (>12°C-18°C)	70.59				
Qmax (>12°C-18°C)	122.95				
Q18: no. days Q above LTM (>12°C-18°C)	12.40	−0.03	0.00	0.924	10
Q1: cum. deviation Q from LTM (>12°C-18°C)	0.09	−0.06	0.00	0.889	10
Qmean (>18°C-max. temp.)	43.75				
Qmax (>18°C-max. temp.)	100.90				
Qmax: no. days Q above LTM (>18°C-max. temp.)	16.09				
Q2: cum. deviation Q from LTM (>18°C-max. temp.)	1.09				
C18: no. days temp. above LTM (>12°C-18°C)	39.50	0.14	0.02	0.868	10
S1: cum. deviation temp. from LTM (>12°C-18°C)	-	−0.18	0.03	0.868	10
Cmax: no. days temp. above LTM (>18°C-max. temp.)	46.90				
S2: cum. deviation temp. from LTM (>18°C-max. temp.)	-				
Monthly resolution indicators		r	R^2	p	n
Qmean		−0.31	0.09	0.023*	55
Mean temperature (°C)		0.48	0.23	0.000**	55

Grey cells denote variables excluded due to high correlations with other predictors, LTM = long-term mean. Units are m^{3}s^{-1} unless stated otherwise. *Significant at the $\alpha= 0.05$ level **Significant at the $\alpha= 0.001$ level.

Lag in seasonal component of a discharge-biomass relationship

Lag in aseasonal pulses within discharge-biomass relationship

Figure 1. Example of hypothetical breakdown of Discharge-biomass time series (blue = discharge, red = fish biomass)
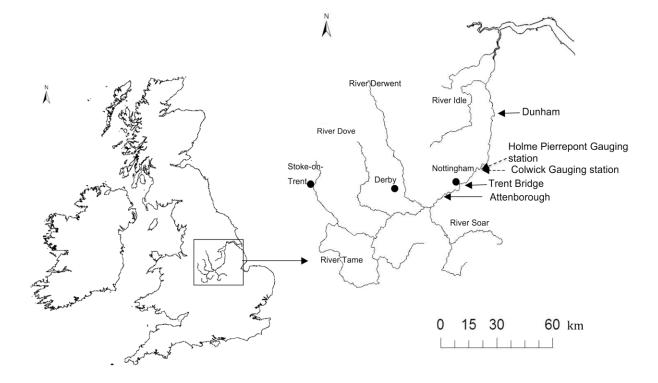
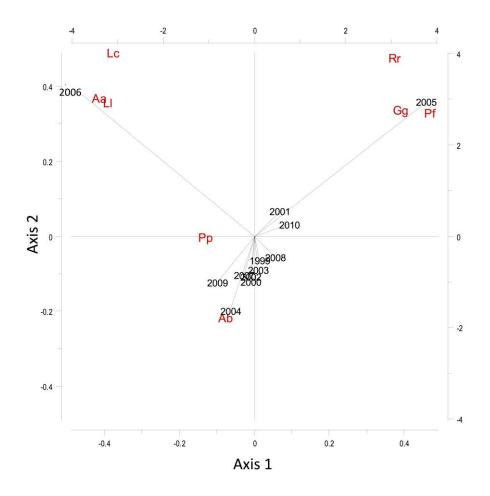Figure 2. Location of the River Trent and a map of site locations.

Figure 3. PCA biplot of the contribution of species biomass to total community biomass in each year. Species abbreviations according to Supplementary material Table 2. The first two axis explain 61.84% of the variance in the model. The angles between the lines represent the degree to which the years are related in terms of their biomass composition, the more acute the angle the higher the correlation. For example 2005 and 2009 differ the most and this difference is driven by the contribution of roach (Rr) and gudgeon (Gg) in 2005 and bream (Ab) to the total 0+ biomass in 2009, as indicated by their proximity to the years on the biplot.

Figure 4. Breakdown of the hydrograph for the River Trent at Colwick from 1999-2010 into "Environmental Flow Components" (Richter & Thomas, 2007). Red = extreme low flows (flows that do not exceed the 10th percentile), dark green = low flows (flows that do not exceed the 50th percentile), blue = high flows (flows that exceed the 75th percentile), light green = small floods (flows with a return interval of 2 years), orange = large floods (flows with a return interval of 10 years). Standardised average monthly temperature (grey line) and 0+ fish biomass (red bars) are overlaid.
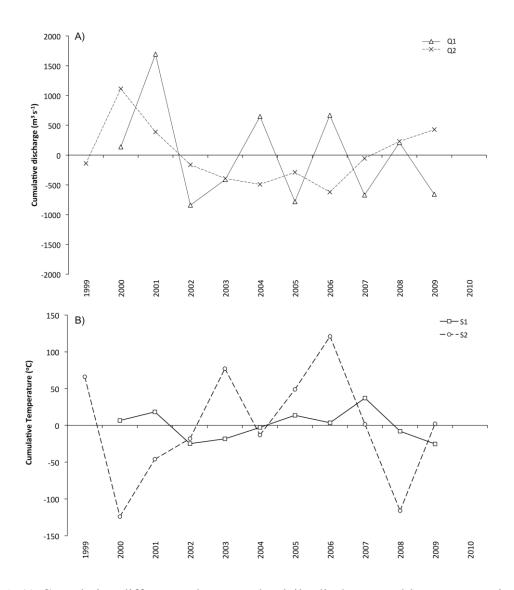
Figure 5. A) Cumulative differences between the daily discharge and long-term period mean of the River Trent at Colwick during the >12°C-18°C and >18°C-max periods, 1999-2010. B) Cumulative differences between the daily temperature and long-term period mean of the River Trent at Holme Pierrepont during the (a) >12°C-18°C and (b) >18°C-max periods, 1999-2010.
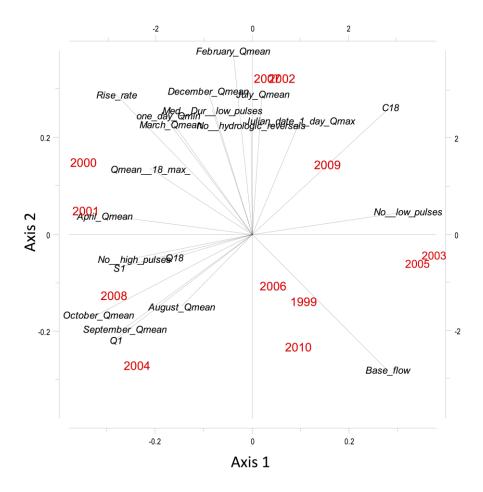
Figure 6. PCA biplot of a subset of 21 hydrological and temperature indices for the lower River Trent 1999- 2010. The two axis of the PCA biplot explain 45.33% of the variance in the model. In the scaling of this biplot, angles between lines (variables) represent correlations, with acute angles representing high correlations (see Jollife (2002)), the distances between years represents Mahanalobis distances and the projection of years over lines indicates whether the variable had high or low values in those years.
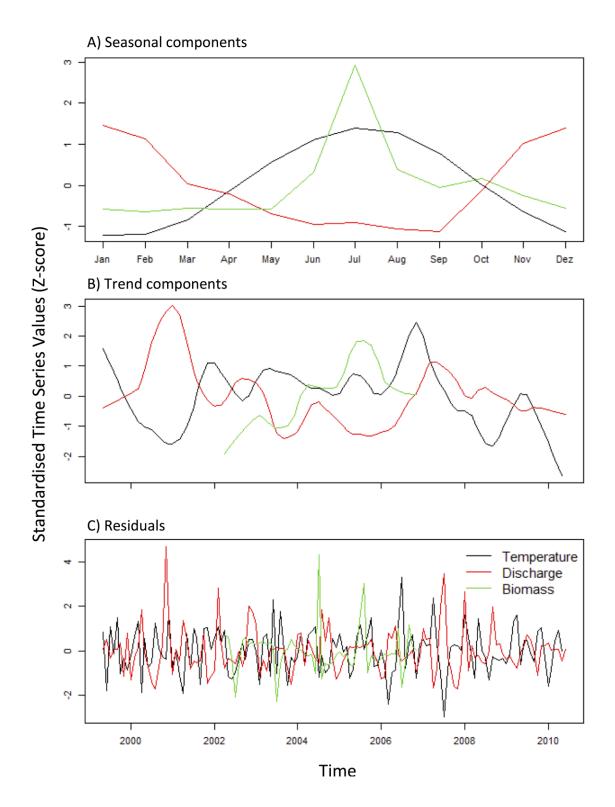
Figure 7. Overview of the seasonal component (A), long term trend component (B) and residuals of time series of monthly discharge (m3 s−1), temperature (°C) and 0+ fish biomass (g m−2) in the lower River Trent, 1999-2010.
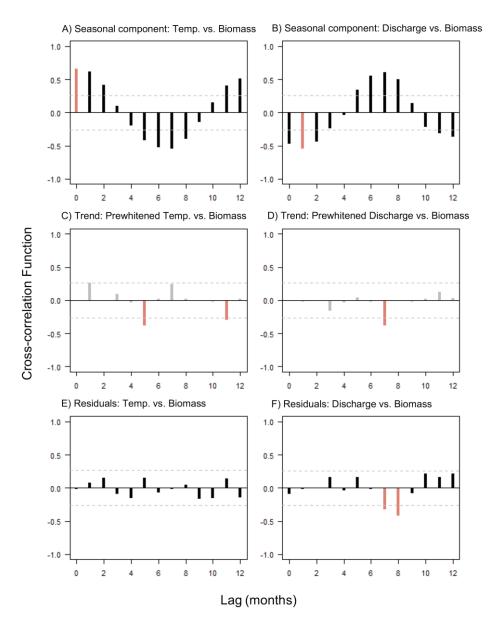
Figure 8. Cross-correlations between the seasonal components (A,B), the long-term trend components (C,D) and residuals (E,F) of monthly temperature (°C) and discharge (m3 s−1) vs. 0+fish biomass (g m-2) in the lower River Trent. Cross-correlations with prewhitening are plotted in grey, red bars indicate significant correlations at the according lags. The dashed line indicates the significance threshold at α=0.05.