High frequency variability of environmental drivers determining benthic community dynamics in headwater streams.

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Abstract

Headwater streams are an important feature of the landscape, with their diversity in structure and associated ecological function providing a potential natural buffer against downstream nutrient export. Phytobenthic communities, dominated in many headwaters by diatoms, must respond to physical and chemical parameters that can vary in magnitude within hours, whereas the ecological regeneration times are much longer. How diatom communities develop in the fluctuating, dynamic environments characteristic of headwaters is poorly understood. Deployment of near-continuous monitoring technology in sub-catchments of the River Eden, NW England, provides the opportunity for measurement of temporal variability in stream discharge and nutrient resource supply to benthic communities, as represented by monthly diatom samples collected over two years. Our data suggest that the diatom communities and the derived Trophic Diatom Index, best reflect stream discharge conditions over the preceding 18 - 21 days and Total Phosphorus concentrations over a wider antecedent window of 7 – 21 days. This is one of the first quantitative assessments of long-term diatom community development in response to continuously-measured stream nutrient concentration and discharge fluctuations. The data reveal the sensitivity of these headwater communities to mean conditions prior to sampling, with flow as the dominant variable. With sufficient understanding of the role of antecedent conditions, these methods can be used to inform interpretation of monitoring data, including those collected under the European Water Framework Directive and related mitigation efforts.

Key words

Headwater streams, Diatoms, Ecological status assessments, Antecedent conditions.

Environmental Impact

Headwater streams are a central feature of the landscape, with their diversity in structure and associated ecological function providing a potential natural buffer against downstream nutrient export. Assessment of these systems through their dominant biota, the phytobenthos, is critical given the key role of headwaters within catchments. By understanding the responses of benthic diatoms to antecedent conditions we can begin to determine key physical and chemical drivers of these communities, which could then be used to inform stream and wider catchment mitigation and monitoring efforts.

Introduction

Headwater streams, of first and second order, drain up to 80% of catchments yet pose daunting challenges to the assessment of ecological status using indicator organisms [1-3], necessary for meeting the objectives of the European Water Framework Directive (WFD)[4]. The dynamic nature of dicharge in many headwater catchments is attributed to their small catchment areas and therefore short residence times of precipitation. This results in frequent disturbance and resetting of community structure by high discharge events and episodic nutrient fluxes [5]. To understand the biodiversity and ecology of headwater systems it is important to recognise that the natural flow regime of headwaters is dynamic [6] and that this dynamism plays a central role in determining and maintaining ecosystem integrity [7-11]. Traditional biomonitoring approaches are typically based on single season sampling of relatively long-lived organisms such as fish or macrophytes, or multi-season sampling of invertebrates [12-15], providing only snap-shots of a community and not capturing the natural variability that defines headwaters.

Headwater ecosystems are often dominated by benthic communities [16] forming biofilms comprising a mixture of algae and microbial components[17, 18]. Foremost amongst the algae in terms of biomass are diatoms; siliceous unicellular algae with strong environmental affinities, which are widely used in monitoring[19-23]. Benthic diatoms have the most rapid turnover of organisms used in stream monitoring and readily respond to changes in discharge and nutrient availability[24-27], making them useful proxies of temporally-rapid ecosystem change and one of the few that can capture the dynamics of headwaters. Understanding ecological sensitivities is important if adequate baselines are to be established from which to assess attempts to mitigate diffuse pollution, in headwaters specifically and within wider river systems more generally.

The dynamic hydrological environment of headwaters ensures that nutrient resources are also highly temporally variable [28, 29]. In small headwater catchments, nutrients enter streams through varied hydrological pathways [30-32], where event-driven processes predominate, rather than the damped, baseflow-influenced hydrological regime within larger, lowland catchments [33]. This generates considerable variability across diverse temporal scales in nutrient concentration and nutrient availability to the benthic community in these systems [34, 35]. Community structural variability can be captured using nutrient-sensitive metrics such as the Trophic Diatom Index (TDI) [36]. The TDI is an index used for classifying ecological status in the UK [37] based on the ecological sensitivity of diatoms to water quality, and especially to total phosphorus concentration (TP) [36, 38]. Therefore, event-driven discharge patterns and nutrient delivery processes are particularly important in understanding benthic diatom community dynamics [39], which are in a continuous mode of re-set and response. It has long been established through temporal studies that benthic diatom communities are a function of not only the nutrient loading on the system but also the hydrological regime [40]. Further studies [41] conducted over 15 months in 12 New Zealand gravel-bed streams have demonstrated through monthly sampling that diatom taxonomic richness is influenced by interaction between annual flood frequency and nutrient concentrations. Despite these observations, understanding of the temporal impacts of flow-nutrient transfer relationships on community dynamics in headwaters over an extended period of time remains limited. However, advances in monitoring technology have led to the opportunity for near-continuous measurements of environmental variables such as water chemistry and discharge [42-47] to better determine the salient drivers of ecological communities and crucially their response period.

This paper aims to evaluate the influence of temporal variability in discharge and TP concentration on benthic headwater communities, and therefore the reliability of ecological status assessments based on infrequent sampling of these organisms. Twenty five months of diatom community data from two headwater streams in the River Eden catchment, England, were investigated to address the hypothesis that, at any given point in time, the benthic diatom community will reflect the accumulated effect of a critical period of antecedent temporal dynamics in discharge and nutrient conditions. Hence, the calculated metrics used in ecological assessments will be skewed toward these antecedent conditions, rather than reflecting the spot water samples often collected as part of monitoring. For the first time, we attempt to define the duration of diatom community representivity and response periods in headwater streams. This evaluation will contribute to the interpretation of the ecological monitoring of water quality in headwater ecosystems, and give greater insights into diversity and species interactions that condition the resilience and dynamics of headwater phytobenthos and, ultimately, down-stream function [48-50].

Methods

Study area

Data were collected from two small rivers, Newby Beck (54°35'N, 02°962'W) which drains the headwaters of the Morland catchment, and Pow Beck (54°50'N, 02°57'W) which drains the Pow catchment, with areas of 12.5 and 10.5 km^2 respectively, within the wider River Eden catchment, NW England. These sub-catchments (Figure 1) form part of the Defra (Department for the Environment and Rural Affairs)-funded Demonstration Test Catchments (DTC) programme, a catchment-scale research platform testing measures for addressing the effects of diffuse pollution from agriculture on stream ecosystems [42, 43, 47, 51-54].

Automatic weather stations in each catchment measure rainfall at intervals of 15 minutes [45]. Fixed monitoring stations, designed by NWQIS and built by AT Engineering [55], are located no more than 3 m from stream channels, adjacent to biological sampling areas providing *in-situ* water quality measurements. A Hach Lange combined Sigmatax SC sampling and homogenisation unit and Phosphax Sigma wet chemistry analyser, is used to measure phosphorus concentration. A sample is taken from the watercourse using an intake pipe located mid-stream, via a peristaltic pump, which fills a flow cell located inside the monitoring station. The pump runs for five minutes every 30 minutes, allowing the flow cell to overflow with stream water. The Sigmatax draws a sample from the flow cell into a glass chamber, where it is homogenised by ultrasonication for 3 minutes. A 10 ml aliquot of the homogenised sample is delivered to a glass cuvette inside the Phosphax Sigma. Therefore, within the 30 minute sampling time, a single measurement of TP is made before the flow cell is re-filled. Due to asynchrony between pump timing and Sigmatax sampling frequency, the Hach Lange data is reported at hourly frequency [42, 44, 47].

Flow measurements are derived by applying stage-discharge relationship to 15 minute water level readings recorded by a pressure transducer. The stage-discharge relationship was developed through the collection of manual current metering measurements and extrapolated beyond the gauged range using assumptions for the stage-velocity relationship and the hydrological water balance[56]. To identify major errors in the high-resolution rainfall, discharge and TP time series, each dataset was visually assessed to identify anomalies. Evident outliers for periods where the readings clearly demonstrated instrument drift were removed. Missing value replacement, based on averaging of neighbouring values, was undertaken when three days or less of missing data were observed, gaps greater than three days were left blank.

From March 2011 to March 2013 mid-monthly diatom samples were taken from submerged stones in riffle areas (10-15cm water depth) [57]. Clean frustule suspensions were obtained by oxidizing organic matter with hot hydrogen peroxide (30% v/v). Permanent slides were then prepared using Naphrax high resolution diatom mountant. Three hundred diatom valves were identified and counted along transects at 1000x magnification, under oil immersion, with a Zeiss Axioskop microscope. Valves were identified using standard floras (primarily

Krammer and Lange-Bertalot, 1986, 1988, 1991, 1991)[58]. Margalef Index of community diversity was calculated for each monthly diatom assemblage. Calculation and interpretation of TDI v3 and Ecological Quality Ratio (EQR) followed the WFD protocol under the classification tool DARLEQ (Diatom Assessment of River and Lake Ecological Status) [59, 60]. The TDI developed by Kelly and Whitton [36] and subsequently revised [61], is based on the weighted average equation:

$$\frac{\sum_{j=1}^{n} a_j \times s_j}{\sum_{j=1}^{n} a_j}$$

where a_j = abundance of valves of species j in sample, s_j = pollution sensitivity of species j. Values of diatom sensitivity range from 1 (indicating low nutrient conditions) to 5 (indicating very high nutrient conditions). This equation provides the weighted mean sensitivity (WMS) of taxa present in a given sample. TDI is the WMS expressed on a scale of 0 – 100, with 0 indicating low nutrient condition and 100 indicating high nutrient condition. TDI is calculated as (WMS*25)-25. EQR is calculated based on the observed TDI value for a particular river system and that expected under reference conditions (see WFD UK TAG for specific details)[59].

Daily average rainfall, discharge and TP data were used to explore relationships with TDI and chlorophyll-a. Monthly TDI values are based on scrapes from 5 cobbles taken from riffles which are pooled to form a composite sample. Benthic chlorophyll-a measurements were taken using *in-situ* fluorometry (ISF), through a hand-held probe, the BenthoTorch© [62]. Three cobbles were taken at random from the same riffle zones and benthic chlorophyll-a of each was measured. Results were then averaged. Calculations of antecedent forcing periods of TDI and ISF chlorophyll-a to rainfall were based on daily averaged data over 18 months for Pow, and 25 months for Newby Beck. Daily averages for discharge and TP for Newby Beck are based over 23 and 16 months, and for Pow 18 and 10 months, respectively.

Pearson's r statistic was calculated between monthly TDI and chlorophyll-a against mean discharge for Pow Beck and Newby Beck, and TP for Newby Beck. The quasi-continuously sampled discharge and TP data were averaged over periods from zero to 21 days.

Results

High temporal variability in the benthic communities of the two River Eden sub-catchments was anticipated as an ecological response to rainfall and associated discharge characteristics (Table 1) and nutrient transfer processes. The flashy hydrological regime is clearly revealed by the tight coupling between daily precipitation and discharge over a 24-month period for Newby Beck, and over a 20 month period for Pow Beck (Figure 3). Correlations between rainfall and discharge are significantly positively correlated (Newby Beck: $r = 0.74$, $p < 0.01$; Pow Beck: $r = 0.63$, $p < 0.01$). TP concentrations are also significantly positively correlated with discharge (Newby Beck: $r = 0.74$, $p < 0.01$; Pow Beck: $r = 0.54$, $p < 0.01$). In Pow Beck, high TDI and low biomass periods are generally associated with high discharge events and corresponding peaks in TP concentration (Figure 3). During these periods fast growing pioneer diatom species, such as *Achnanthidium minutissimum* and *Amphora pediculus*, which have optimal colonisation rates on the scoured cobble substrate, are seen to dominate up to 68 % of the diatom assemblage (Figure 2). In spring of both years *Achnanthidium minutissimum* is particularly dominant comprising more than 50 % of the diatom assemblage. *Amphora pediculus* becomes dominant throughout autumn and winter. In 2011 *Amphora pediculus* reaches a maximum of 27 % in September, while in 2012 a maximum of 48 % is reached in December (Figure 2b).

Periods of higher biomass are generally associated with an increase in abundance of *Achnanthidium minutissimum*, as observed in May 2012, and *Cocconeis placentula var euglypta*, as typified in October 2011 and September 2012. In Newby Beck, key pioneer species also dominate community structure on an annual cycle with *Achnanthidium minutissimum* dominating the species assemblage in spring and early summer. *Amphora pediculus* becomes dominant from September to February, reaching maximum percentage abundance in December of both years (Figure 2a). In Pow Beck, values of Margalef species richness demonstrated greater variation in species and assemblage heterogeneity, ranging from 1.92 to 5.08, than Newby Beck which ranged from 2.63 to 4.2(Figure 2).

Figure 3 illustrates the monthly development of two measures related to the headwater diatom communities, namely the calculated TDI water quality measure and the ISF benthic chlorophyll-a. For Newby Beck (Figure 3a), two distinct quasi-cyclic periods can be distinguished in the diatom community structure. TDI values, used here as a proxy for community structure, are higher between September and February than March to August (t (10df), = -16.07, $p<0.05$), with a peak in December in both years, indicating a higher level of nutrient-tolerant taxa and thus, more nutrient-enriched conditions. This is supported by generally higher TP concentrations during these months. These patterns in TDI are partly tracked by benthic chlorophyll-a, which is used as a surrogate for benthic productivity. Within relatively quiescent hydrological periods, e.g. January to May 2012, broadly positive relationships between benthic productivity and community structure are observed, where lower TP concentrations and improved water quality, as inferred from the TDI, is matched by an increase in benthic chlorophyll-a. However, Figure 3a demonstrates near anti-phasing of chlorophyll-a with TDI during high discharge episodes, such as December 2012 and January 2013. Considerable resilience of these diatom communities is highlighted by the stability of the inter-monthly TDI scores against the highly variable hydrological regime, and even the benthic chlorophyll-a. However, the annual range of TDI values is high, spanning 'high' to 'poor' EQR status and chlorophyll-a values from 1.73 to 10.35 µg/cm^2.

Similar quasi-cyclic periods are observed in the Pow catchment for TDI (Figure 3b) with TDI values indicative of poorer water conditions from September to March in both years. While monthly values of TDI across Morland and Pow catchments are correlated over the study periods ($r = 0.72$, $p < 0.05$), the range of TDI values in Pow (41 to 79) is less than that observed in Morland (32 to 83). Inter-monthly variations are again relatively small in Pow, but as in Newby Beck, the range is significant in terms of classification, spanning 'high' to 'poor' EQR classes. However, chlorophyll-a values range from 0.14 to 7.92 µg/cm^2 in Pow Beck, which is generally lower than in Newby Beck. Unlike in Newby Beck, there is usually an inverse relationship between the TDI and benthic chlorophyll-a. When values of TDI are high in Pow from October to March in both years, benthic chlorophyll-a was seen to be less than

1 μg/cm^2, which is lower than chlorophyll-a in the Morland catchment. Similar to Newby Beck, there is a non-significant relationship between water temperature and chlorophyll-a (Newby Beck: $r = 0.24$, $p > 0.05$; Pow Beck: $r = 0.18$, $p > 0.05$). Clusters of high rainfall events and associated high stream discharges correlate with high TDI values and low chlorophyll-a, suggesting that unlike in Newby Beck, physical rather than nutrient factors dominate. Extreme examples of this inverse response in the ecological community structure and function to high discharge occurred in December 2011 and October 2012. Similarly to the case study at Newby Beck in the Morland catchment, the resilience of the communities in the Pow is evidenced by their overall stability in key species *Achnanthidium minutissimum, Amphora pediculus* and *Cocconeis placentula var euglypta*, and associated productivity.

Discussion

Increases in discharge in these study catchments can occur rapidly with timescales of hours to days, and recovery from peaks to baseline conditions also occurs quickly (Figure 3). Within the Morland catchment, these flashy hydrographs are due to the steepness of the terrain and shallow soils overlying bedrock. As clay-rich glacial till is widespread in the Pow catchment, surface runoff can quickly be generated following rainfall. Similarly in other catchments this flashy hydrological response has been shown to contribute to extremely variable nutrient concentrations[46, 63, 64], which benthic communities, with longer regeneration times, must respond to. Key questions in in-stream ecological assessment are how these benthic communities respond and recover from event-driven disturbances, and how sensitive they are to antecedent nutrient and discharge conditions.

Despite the dynamic nature of the physical environment, strong similarities in the overall structural and functional benthic ecosystem changes in these two headwater streams are observed. The primary control appears to be rainfall and associated discharge, which is coherent between these geographically related sites. For both Newby Beck and Pow Beck, TDI increases as discharge increases, indicating delivery of nutrients to the streams during high rainfall and associated discharge events. Conversely, chlorophyll-a values tend to be lower during high discharge events. This is most likely a combination of high bed shear stress scouring the biofilms, probably enhanced by sediment abrasion, and lower light levels restricting photosynthesis under deep water with high turbidity levels [65-67]. Our data suggest that yearly biomass of the community can change 10-fold, whereas month-on-month community composition remains relatively stable within the annual cycle. The TDI does mask some internal variation in assemblage diversity of more specialist species, but the value is largely controlled by the ratio of aforementioned key pioneer species that are both present and abundant all year round in the benthic assemblage, and have the ability to withstand changes in their habitat associated with discharge including shear stress, light and nutrient concentration. From a community perspective, these flow related habitat characteristics can be significant in terms of succession stage [68-70], with successional state having a direct result on metric scores and WFD classification[71] .

This lends to the hypothesis that at any point in time the benthic diatom community will represent a critical time period which reflects the accumulative impact of antecedent temporal dynamics in discharge-nutrient condition. The continuous water chemistry, rainfall, flow data and levels collected by the EdenDTC project enables the critical antecedent period determining the diatom community structure (using TDI as a surrogate) and biomass (ISF benthic chlorophyll-a) to be investigated. Figure 4 shows that the TDI is positively correlated with mean discharge and the strength of the correlation increases according to the antecedent period. For Newby Beck an initial correlation is found between TDI and mean discharge on the day of diatom sampling ($p < 0.05$, $r = 0.54$), which strengthens to a maximum after 18 days ($p < 0.05$, $r = 0.7$). Significant correlations are also observed between TDI and TP after 15 days ($p < 0.05$, $r = 0.53$), but this increases further to a maximum after 21 days ($p < 0.05$, $r = 0.66$). A similar correlation with discharge is observed in Pow Beck, although with lower coefficients and a maximum is reached later (21 days; $p < 0.05$; $r = 0.63$). For Pow Beck, significant correlations are observed between TDI and TP between 7-12 days ($p < 0.05$, $r = - 0.6$). Overall, this indicates that at-a-point community composition is a product of factors related to discharge over the preceding 15-21 days. Given the positive relationship between discharge and TP in the Morland catchment, it is possible the relationship between TDI and discharge is partly mediated by nutrient concentration.

In Newby Beck and Pow Beck, a non-significant relationship is found between benthic chlorophyll-a and antecedent discharge-TP conditions, thus indicating that antecedent conditions over the preceding 21 days are not key determinands of benthic productivity, which may be due to disturbance frequency [5]. While non-significant relationships are observed between benthic productivity and antecedent discharge-TP conditions, a clear response to high discharge conditions is evident in Figure 3. This is consistent with community structure being defined by nutrient supply and retention within benthic biofilms [72], whereas physical controls on productivity, especially damage to biofilms through scouring, may be expected to have a more immediate influence [40]. This analysis demonstrates that aspects of community structure and ecological functional processes, such as chlorophyll-a production, respond differently to antecedent discharge and nutrient conditions, and that this may be dependent on catchment specific factors such as geology and land use which may be equally important determinands of these benthic communities as climate [73-75].

Our results confirm temporal coupling between benthic algal biomass and nutrient concentrations in the two streams through the monthly sampling period, although the relationship between these variables differs in its strength and direction. The near-cyclical patterns observed in the two years of ecological data from both Eden sub-catchments suggest that variability linked to rainfall patterns on an almost seasonal basis is an inherent part of these systems. Note, these are not true seasonal cycles, but rather are linked to clusters in the incidence of precipitation and nutrient delivery. The ability of the community to recover from event-driven disturbances to their underlying equilibrium with water quality implies considerable resilience [76] . Moreover, sustained differences in the magnitude of the TDI and chlorophyll-a levels between Newby Beck and Pow Beck highlights the importance of catchment specific factors, as well as temporal changes in physical and chemical variables. The two similarly sized catchments have comparable rainfall and discharge characteristics, yet local influences on the stream ecology are likely, including geology, water flow, residence times and most importantly, farming practices [77-80].

Due to the inherent variability of headwater streams it is important that ecological monitoring is conducted at an appropriate temporal resolution, and employs the appropriate community measures [81]. These data imply that a single season sampling monitoring frequency, such as those suggested under the WFD, is inadequate and is unlikely to give results representative of the full annual cycle. At the other extreme, the benthic diatom community structure will not reflect single events, but rather an accumulated average of the preceding two to three weeks of stream physical and chemical condition. This finding is beneficial to studies of baseline water quality conditions and highlights the time-integrating property of water quality assessments based on benthic community structure [82].

Conclusion

The opportunities provided by near-continuous environmental measurements within the DTC programme, have revealed the time-scale of response and sensitivities of benthic ecosystems in headwaters. The data indicate that assessment tools and metrics developed under the WFD for lower order rivers can be applied to headwater streams despite their dynamic nature, and that they can discriminate nutrient pressures between catchments. Nevertheless, it is essential to understand the importance of the impact of precipitation on these streams, and therefore both climate change [83] and land use management [84] have to be considered in parallel when planning for the future. Both of these factors can only be evaluated against long term data sets and an understanding of catchment processes across all seasons for several years. An appropriate temporal approach of multi-annual duration that encompasses both short term events and seasonal variability would provide particular value in terms of informing mitigation efforts to reduce diffuse pollution. Future research should be focused on improving understanding of benthic community composition and productivity in appropriate temporal frameworks, and environmental decision-making must accommodate event-driven physical and chemical processes, as only by understanding the real-time dynamics of headwaters can we fully understand the ecology of these streams.

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