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The Effects of Hydropeaking on Lotic Benthic Macroinvertebrate Assemblages

Andrew L. Garey

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by

Andrew L. Garey,

M.S., Virginia Commonwealth University, May, 2008

B.S., Virginia Tech, May, 2000

Directors: Dr. Leonard A. Smock, Professor and Director, VCU Rice Rivers Center, Interim Vice Provost for Life Sciences and Research

Dr. Paul A. Bukaveckas, Professor, Department of Biology and Center for Environmental Studies

Virginia Commonwealth University

Richmond, Virginia

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Dedication

This dissertation is dedicated to my parents, Ms. Patricia and Mr. Louis Garey, sister, Ms. Katey Garey, father- and mother-in-law, Ms. Ellie and Mr. Mike Griffiths, sister-in-law Lowri Griffiths, aunt and uncle, Ms. Brenda and Mr. Chip Booth, cousins Ashley, Stacey and Kelli Booth, and most of all, to my loving wife, Ms. Rachael Griffiths.

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Chapter I

Effects of Hydropeaking on Lotic Benthic Macroinvertebrate Assemblages: General Introduction

Abstract

The term hydropeaking refers to anthropogenically induced, short-duration, high-magnitude discharge pulses that are generated in lotic systems for electricity production. The practice of hydropeaking produces the largest source of renewable energy worldwide, and its use is projected to increase through the year 2040. The primary objective of this work was to evaluate the effects of hydropeaking on benthic macroinvertebrate assemblages, which are important components of lotic ecosystems. Results of this work show that, across a wide range of impacted systems worldwide, the consistently observed patterns of elevated benthic macroinvertebrate drift in response to hydropeaking pulses are primarily related to the rate at which discharge is increased (i.e., ramping rate) and secondarily to the time between pulses. In addition, it was shown that taxa inhabiting depositional habitat patches (i.e. fine substrates and slow water velocities) were most susceptible to peaking-induced drift, and that these taxa were also those most prevalent in hydropeaking-impacted systems. Collectively, these results suggest that increased pulse ramping rate and the resulting elevated macroinvertebrate drift may be positive selective forces, which benefit populations adapted for life in hydropeaking-impacted lotic ecosystems. These results provide a greater understanding of the factors that are most important for governing the effects of hydropeaking on benthic assemblages.

Flow Modification and hydropeaking

The flow regimes of lotic systems greatly affect biological and physicochemical structure and functioning (Marchetti and Moyle, 2001). The magnitude, frequency, duration, timing, and rate of change of flow events largely govern ecological integrity (Poff *et al.*, 1997). Richter (2010) asserted that a focus on flow management is essential to maintaining healthy river ecosystems. Haxton and Findlay (2008) described detailed relationships between flow modifications and aquatic animals, including reduced macroinvertebrate abundance associated with dewatering, reduced fish and macroinvertebrate abundance caused by hypolimnetic water releases from impoundments, and reduced abundance of fluvial specialist fishes associated with damming. In a global scale review, Poff and Zimmerman (2010) showed that altered flow regimes consistently resulted in ecological community alterations, but that the magnitude of these effects was not generalizable across community types or for different types of flow modification. In order to better elucidate quantitative relationships between flow modification and biotic assemblages, analyses that focus on specific types of flow modification, specific aspects of altered hydrology caused by these modifications, and specific ecological responses to this altered hydrology are needed.

Hydroelectric power is the nation's largest renewable source for electricity and is projected to increase through 2040 (EIA, 2015). Hydropower generation is most often achieved through rapid, high-magnitude discharge increases over short time periods, commonly referred to as hydropeaking (discharge increases of 2-35 fold over several hours occurred in events reviewed for this work). There is a growing body of work on hydropeaking events created both for power generation and for scientific experimentation. Many such works link changes in benthic macroinvertebrate assemblages to pulsed-flow events (Troelstrup and Hergenrader, 1990, Moog, 1993, Englund and Malmqvist, 1996, Cortes *et al.*, 2002, Xiaocheng *et al.*, 2008, Carolli *et al.*, 2010,). Assemblage changes caused by hydropeaking events have been ascribed to a variety of mechanisms, including water temperature shifts (Carolli *et al.*, 2012), reduced chemical water quality (Cortes *et al.*, 2002), benthic habitat degradation (Englund and Malmqvist, 1996) and catastrophic drift caused by mechanical dislodgement during rapid discharge increases (Mochizuki *et al.*, 2006). Previous investigations, however, have generally focused on simple *no effect* null hypotheses, wherein significant differences in benthic assemblages between control and hydropeaking systems are cited, without explicit quantification of the factors most responsible for the observed differences. Despite the wide variation in mechanisms implicated in benthic community degradation within hydropeaking-impacted systems, the ultimate driver of these impacts is flow, which exerts a governing influence on all of the physicochemical factors assessed in the studies discussed above (*sensu* Poff *et al.*, 1997).

Studies displaying quantitative relationships between hydrologic variables and macroinvertebrate response metrics in hydropeaking systems are largely lacking (but see Mochizuki *et al.*, 2006). McMullen and Lytle (2012) showed that flood magnitude is negatively correlated with benthic macroinvertebrate density, though they included few flood events where flow dynamics were similar to hydropeaking for hydropower generation and did not assess the effects of other hydrologic characteristics (e.g., rate of change, timing and duration of flood events). The effects of pulsed flow events on macroinvertebrate assemblages differ depending on the hydrologic characteristics of the events, for example, patterns of drift differ between abrupt flow increases and stepwise, incremental increases (Imbert and Perry, 2000, Carolli *et al.*, 2010). Assemblage responses to hydropeaking events have not been quantified in a manner that allows for a determination of which hydrologic factors are most important for affecting benthic biota. Determining the manner in which flow variables (duration, frequency, magnitude and rate of change in flow) affect ecological communities is essential for effective management of regulated rivers. A determination of the hydrologic characteristics of systems modified by hydropeaking that most affect benthic assemblages would aid system managers in determining the manner in which hydrologic variables might be manipulated to minimize deleterious effects.

Short-term hydropeaking effects: macroinvertebrate drift

Increased macroinvertebrate drift is the most commonly observed short-term effect of hydropeaking on benthic assemblages (e.g. Lagarrigue *et al.*, 2002, Mochizuki *et al.*, 2006, Marty *et al.*, 2009, Bruno *et al.*, 2010, Miller *et al.*, 2014). Similar, unimodal patterns of elevated drift during hydropeaking events occur across systems. Drift typically increases rapidly at the onset of the hydropeaking pulse, exhibits a distinct maximum, and then declines rapidly while discharge remains high in the system (e.g., see time-drift density curves in Bruno *et al.*, 2010 and Robinson, 2012). Previous works have indicated that the rate of change in discharge during hydropeaking (ramping rate) is more important for affecting drift than the maximum discharge attained (pulse magnitude) (Imbert and Perry, 2000, Patterson and Smokorowski, 2011), though none have included comprehensive across-system comparisons of the hydrologic characteristics of hydropeaking events and their effects on drift.

In addition, it remains unclear as to whether peaking-induced drift is deleterious to the long-term survival of affected populations. Drift provides a mechanism of dispersal. Therefore, drifting benthic macroinvertebrates may benefit by recolonizing new habitats. Furthermore, those that remain on the benthos may benefit from population reductions and the corresponding alleviation of competition-induced stress caused by losses to the drift (Townsend and Hildrew, 1976, Brittain and Eikeland, 1988, Anholt, 1995). In contrast, drifting individuals may be at increased risk of predation by drift-feeding fishes (Flecker, 1992, Miller *et al.*, 2014), or may become stranded in the riparian zone and desiccate (Robinson *et al.*, 2004).

Physical habitat factors: hydrology and substrate

In lotic ecosystems, habitat-related investigations often focus on hydrology and the benthic substrate because of the overarching importance of these factors in shaping aquatic assemblage structure and functioning (e.g., Horrigan and Baird, 2008, Statzner and Beche, 2010 and below). The force that water flow exerts on resident organisms is often highlighted as the major determinant of population distributions in space and time (Lancaster and Hildrew, 1993, Szczerkowska-Majchrzak *et al.*, 2014). Substrate composition governs the amount of habitat space available and selects for those organisms with the best physical adaptations for occupying substrate surfaces or interstices (Cover *et al.*, 2008, Gayraud and Philippe, 2003). Substrate and hydrology are closely interactive in their effects and exert critical indirect effects on biota by governing organic matter, nutrient and dissolved oxygen cycling (Rabeni and Minshall, 1977, Wilcock, 1993, Dittrich and Schmedtje, 1995, Valett *et al.*, 1997, Negishi and Richardson, 2003, Malcolm *et al.*, 2004, Greig *et al.*, 2007).

Anthropogenic flow modifications cause extensive changes to the physical habitats and biological assemblages of lotic systems (Poff *et al.*, 1997, Richter, 2010). Therefore, information on the affinities of biota for different habitat conditions are important for assessing the manner in which flow modifications affect riverine ecosystems, as well as how such effects might vary among habitat types (Freeman *et al.*, 2001, Hart and Finelli, 1999).

Macroinvertebrate traits

Characteristics that describe the interactions of species with the environment are referred to as functional traits, or, as is the convention in this work, simply as traits (Frimpong and Angermeier, 2009, Frimpong and Angermeier, 2010, Menezes *et al.*, 2010, Poff *et al.*, 2006, Van den Brink *et al.*, 2011). Southwood (1988) postulated that: “habitat provides the templet on which evolution forges characteristic life-history strategies”. This habitat templet concept (Southwood, 1977, Southwood, 1988) forms the theoretical foundation of traits-based research. Studies on the effects of anthropogenic stressors on traits are commonly based on the assumption that natural selection should favor traits conferring resistance or resilience to stressors (Culp *et al.*, 2011).

Traits have been used effectively to evaluate the effects of a wide range of environmental factors in aquatic ecosystems (Blocksom *et al.*, 2002, Hughes *et al.*, 1998, Johnson and Ringler, 2014, Pan *et al.*, 2000). Because of the widespread effectiveness of traits-based approaches, a number of comprehensive databases have been developed to compile trait information for aquatic taxa over large geographic regions (Frimpong and Angermeier, 2009, Schmidt-Kloiber and Hering, 2015, Tachet et al. 2002, Vieira *et al.*, 2006).

In traits databases, quantitative trait information is coded in a manner that allows for ambiguity with regard to the trait status of organisms. This is achieved through the use of multiple categories (often referred to as modalities) for a given trait. The values assigned to each modality, which provide quantitative descriptions of organisms’ trait characteristics, are referred to as trait states. For example, in the traits database of Tachet *et al.* (2002), five different feeding strategies are listed as modalities for the trait feeding. Odonata are obligate predators, therefore, for the odonate *Progomphus genei*, the feeding trait modality predator was assigned a trait state of 3, whereas all other modalities received trait states of 0, indicating that the taxon does not employ other modes of feeding. In contrast, crayfish typically employ multiple feeding strategies, therefore, the crayfish *Orconectes limosus* was assigned scores of 2 for the modalities shredder, scraper and predator, indicating a quantitative trait state of 33% for each modality (see Chevenet *et al.*,1994 for a further description of this process).

It has been postulated that traits-based evaluations of specific environmental stressors should be less confounded by temporal and spatial variability than taxonomy-based approaches (Culp *et al.*, 2011, Van den Brink *et al.*, 2011). This postulate is based on the principle that the taxonomic structures of assemblages are influenced not only by current environmental conditions, but also those acting over evolutionary time scales, and because taxonomic assemblages are constrained by the biogeographic limits imposed by the regional species pool available for colonization. In contrast, and in keeping with Southwood's Habitat Templet concept (1977, 1988) and the River Habitat Templet concept of Townsend and Hildrew (1994), traits should respond primarily to variations in the abiotic environment and, therefore, similar environmental stressors acting in different locations and at different times should elicit similar responses, in terms of the traits expressed by the affected biota, regardless of their taxonomy.

Broadly, traits can be divided into two categories: 1) biological: those that directly describe the physiology, morphology, life history or life cycle characteristics of specific organisms (e.g., feeding strategy, body size, voltinism, pupation) and 2) ecological: those that describe the environmental conditions with which organisms are associated (e.g. food type and physical habitat preferences; see Vieira *et al.*, 2006 for further discussion).

Interdependence among traits, that is, a decreased or increased likelihood of one trait state, given another, is common. Such interdependence is problematic because it confounds the clear determination of which trait states represent causative associations between the assemblage and the environment (Statzner and Beche, 2010, Van den Brink *et al.*, 2011).

Statistically significant associations among trait states have been attributed to two causes: 1) trait syndromes, wherein associations among traits result from phylogenetic relationships among taxa, rather than causative links between traits and the environment (Carlisle and Hawkins, 2008, Culp *et al.*, 2011, Horrigan and Baird, 2008, Poff *et al.*, 2006) and 2) multiple life history strategies, wherein multiple traits may confer fitness in response to the same suite of environmental stressors (Charvet *et al.*, 1998, Haddad *et al.*, 2008).

Poff et al. (2006) postulated that biological traits would be more likely to be confounded by trait syndromes, because they are more likely to be associated with phylogeny. This seems plausible, as related taxa often share physiological and morphological characteristics, but less commonly share ecological characteristics. For example, all Trichoptera produce silk, eat with mandibles adapted for chewing, and are holometabolous (biological traits), however trichopteran species vary widely with respect to the current regimes and substrate compositions of their habitats and the food resources they consume (ecological traits). Poff et al. (2006) provide strong empirical evidence supporting their postulate of stronger phylogenetic links for biological, rather than ecological traits, but do not include a direct comparison of the prevalence of among-trait associations between the two categories. It also seems plausible that biological traits are more likely to be confounded by multiple life history strategies than ecological traits, because ecological traits (e.g., substrate affinity) are often the result of multiple biological traits (e.g., claws, ability to produce silk, body morphology).

Some authors have criticized the use of traits databases because collected trait information within them is generalized from many literature sources and therefore encompasses large spatial and long temporal time scales (Culp *et al.*, 2011, Orlofske and Baird, 2014). These authors contend that, whenever possible, system-specific trait information should be developed which reflects the condition of taxa observed specifically for the systems under investigation and that such system-specific information is better suited to evaluating assemblage responses to environmental variations.

Specific aims and chapter organization

The remainder of this dissertation is divided into four chapters. Chapters 2-4 are primary research studies, and Chapter 5 contains synthetic conclusions derived from the collective results of these studies.

The primary objective of Chapter 2 was to determine what hydrologic factors associated with hydropeaking pulses exert the strongest influences on hydropeaking-induced drift. It was hypothesized that pulse ramping rate (i.e., the rate of discharge increase) would be positively correlated with drift and would be more closely associated with drift than pulse magnitude (i.e., the maximum discharge attained). In addition, it was hypothesized that the effects of increased ramping rate would be increased for systems wherein longer periods between hydropeaking events occurred. A secondary objective of the chapter was to determine whether drift responses were taxon-specific. It was hypothesized that drift responses among taxa would be highly synchronous, with similar patterns of drift density variation occurring for each taxon observed during a given hydropeaking event.

The objective of Chapter 3 was to determine what habitat characteristics were most important for influencing the susceptibility of benthic macroinvertebrate taxa to hydropeaking-induced drift. It was hypothesized that taxa with high affinities for coarse substrate with abundant interstitial space, low embeddedness with fine sediment and high water velocities would show reduced susceptibility to entrainment in the drift during hydropeaking, whereas those associated with fine substrates or those lacking interstitial spaces and those having low water velocities would show increased drift susceptibility.

The primary objective of Chapter 4 was to determine whether relationships existed between hydropeaking and benthic macroinvertebrate traits which were consistent across a wide geographic distance and for systems which differed substantially with respect to their natural settings (Mid-Atlantic region of the US and French Pyrenees). It was hypothesized that ecological traits associated with physical substrate composition and hydrology would exhibit such consistent relationships. Furthermore, it was hypothesized that these traits would indicate clearer distinctions between hydropeaking-impacted and non-impacted sites than would a similar analysis conducted based on taxonomic composition.

The results of Chapter 4 are integral to those of Chapters 2 and 3 (Figure 1). If the prevalent habitat-related traits observed in hydropeaking-impacted systems (as indicated in Chapter 4) are those that reduce susceptibility to drift (as indicated in Chapter 3), then hydropeaking-induced drift is most probably a detrimental factor to benthic macroinvertebrate assemblages. Following this scenario, those hydrologic variables most associated with increased drift (as indicated in Chapter 2) should be viewed as negative selective forces, and expected to reduce the proportional abundances of populations of the most-affected taxa. In contrast, if the assemblages inhabiting hydropeaking-impacted systems show increased affinities for habitat characteristics associated with increased drift susceptibility, then the opposite conclusion should be drawn. That is, hydropeaking-induced drift, and the hydrologic factors that most influence it, should be viewed as positive selective forces, which benefit the assemblages adapted for life in hydropeaking-impacted river systems.

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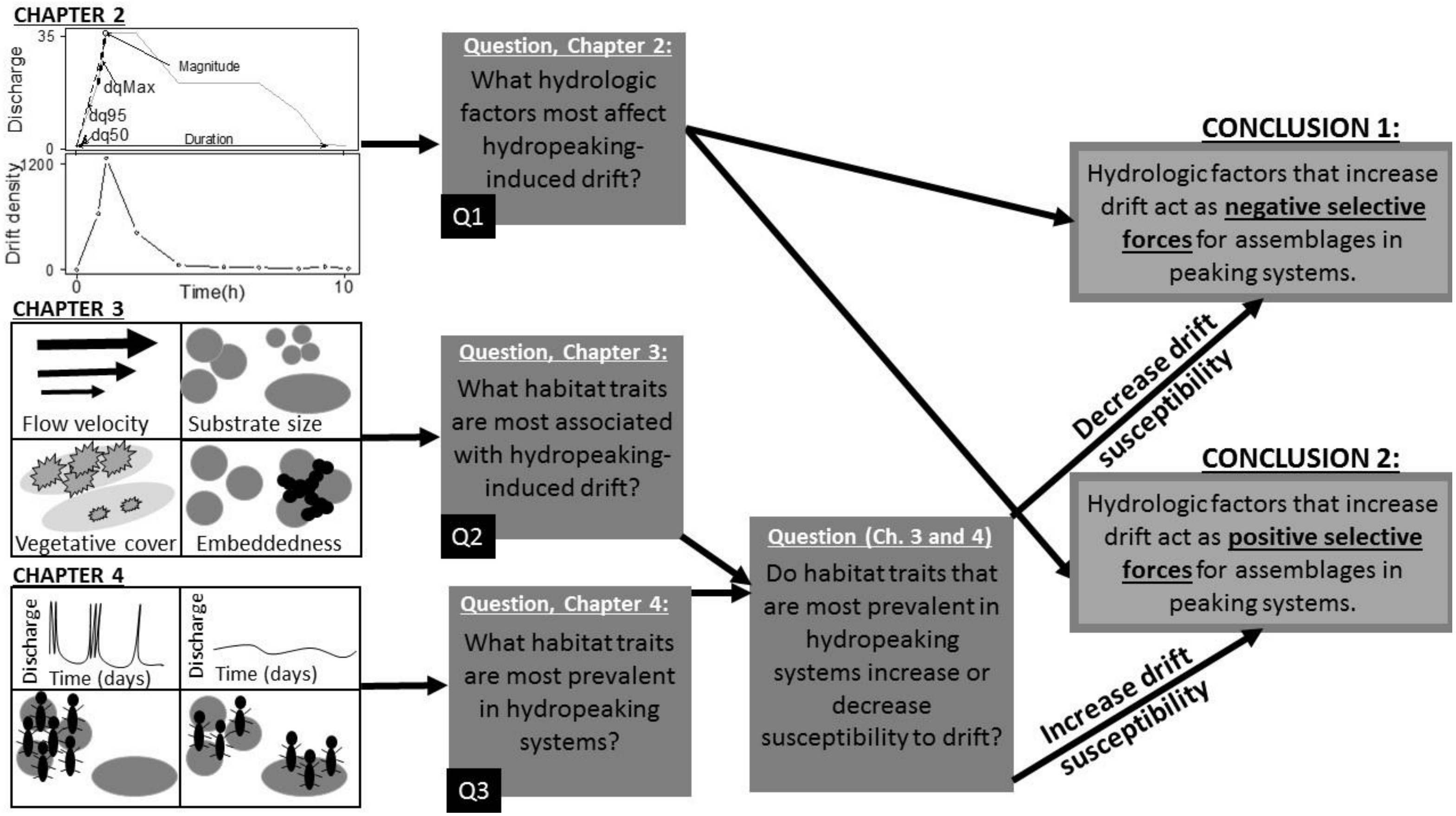

Figure 1.1: Study overview: Chapters 2-4. The Chapter 2 diagram (top left) shows a typical discharge hydrograph during a hydropeaking pulse and the corresponding macroinvertebrate drift response (data are from the River Spöl, Switzerland [Robinson et al. 2004]). Hydrologic variables shown are: the rate of discharge increase (i.e. ramping rate), from base flow to twice base flow (dq50), ramping rate from baseflow to 95% of maximum discharge (dq95) and maximum ramping rate (dqMax), as well as maximum discharge attained (Magnitude) and pulse duration. Each of these flow variables was evaluated to answer research question 1 (Q1). The Chapter 3 diagram illustrates the major environmental variables considered in the development of macroinvertebrate trait affinities, and evaluation of which characteristics were most related to hydropeaking-induced drift (Q2). The Chapter 4 diagram illustrates the evaluation of whether habitat-related traits differ between hydropeaking and non-hydropeaking systems (Q3). Collectively, these studies were conducted to determine whether hydrologic factors associated with hydropeaking pulses which increase drift susceptibility serve as negative (**Conclusion 1**) or positive **(Conclusion 2)** selective forces.

Chapter II

The effects of hydropeaking-induced flow events on benthic macroinvertebrate drift: a global-scale meta-analysis.

Abstract

Invertebrate drift is commonly used for assessing the short-term effects of hydrologic modifications. The objective of this study was to develop a quantitative explanation for the qualitatively similar drift responses that occur in systems that experience artificially-induced flow pulses generated for electricity generation (i.e. hydropeaking). A meta-analysis of data reported from pulsed-flow events in both naturally formed and constructed stream systems was conducted. Results of this investigation showed that, in comparison to other hydrologic factors, maximum pulse ramping rate (e.g., the maximum rate of change in discharge) was the most important factor for explaining peaking-induced drift. During each event, taxa were relatively concordant with respect to their patterns of drift, providing indirect evidence that drift during pulsed flow is catastrophic in nature and not related to variable behavioral responses among taxa. This work shows mechanistic links between drift and river hydrology and provides important information regarding the variability in drift responses among taxonomic groups during pulsed flow events.

Introduction

Hydropeaking is the artificial generation of rapid discharge pulses (typically 2-10 fold above baseflow) for electricity generation. This method provides the world's largest source of renewable energy and its use is projected to increase in the coming decades 2040 (EIA, 2015) Flow modifications associated with hydropeaking have wide-ranging effects on lotic ecosystems which extend to physicochemical water quality, physical habitat structure, and ultimately to the composition and functioning of biotic assemblages (Troelstrup and Hergenrader, 1990, Moog, 1993, Englund and Malmqvist, 1996, Cortes *et al.*, 2002, Xiaocheng *et al.*, 2008, Carolli *et al.*, 2010).

The most commonly observed short-term effect of hydropeaking on benthic macroinvertebrates is elevated drift density (Lagarrigue *et al.*, 2002, Robinson *et al.*, 2004, Mochizuki *et al.*, 2006, Marty *et al.*, 2009, Bruno *et al.*, 2010, Robinson, 2012, Miller *et al.*, 2014), which has been shown to increase by two orders of magnitude above typical baseflow densities (Mochizuki *et al.*, 2006). Similar, unimodal patterns of elevated drift during hydropeaking events occur across systems. Drift typically increases rapidly at the onset of the hydropeaking pulse, exhibits a distinct maximum, and then declines rapidly while discharge remains high in the system (e.g., see time-drift density curves in Bruno *et al.*, 2010, Robinson, 2012). Previous works have indicated that the rate of change in discharge during hydropeaking (ramping rate) is more important for affecting drift than the maximum discharge attained (pulse magnitude; Imbert and Perry, 2000, Patterson and Smokorowski, 2011), though none have included comprehensive across-system comparisons of the hydrologic characteristics of hydropeaking events and their effects on drift.

This investigation was focused on determining and quantifying the most important hydrologic drivers of the relatively consistent macroinvertebrate drift responses observed in hydropeaking-impacted systems. Here, drift density (individuals m^{-3}) is used to represent the potential magnitude of the drift response on other ecosystem components and on downstream habitats. Drift-feeding fishes are dependent on drift density as it governs the number of invertebrates encountered within their finite foraging ranges and hydropeaking-induced drift has been associated with increased feeding by such fishes (Hayes *et al.*, 2000). In addition, drift has often and long been understood as a major mechanism of colonization of benthic habitat and as a major factor governing the degree of similarity among benthic communities within river networks (Townsend and Hildrew, 1976, Williams and Hynes, 1976, Williams, 1980, Wilson and McTammany, 2014). Therefore, underutilized benthic habitats encountering high drift densities are likely to encounter high rates of colonization and organisms in densely-populated habitats are likely to encounter increased competition from immigrants when drift density is high.

This study is a meta-analysis of both published and unpublished datasets from both hydropeaking-impacted river systems and experimental flumes. The objective was to determine what hydrologic factors associated with hydropeaking events most affect drift. Hydrologic factors investigated included pulse magnitude, ramping rate, pulse duration and the time between each pulse and the previous pulse that occurred in each system. Analyses were conducted at two distinct scales of observation: 1) among events, where relationships between hydrologic variables and drift were assessed across the entire dataset and 2) within events, wherein datasets from each hydropeaking event were analyzed individually. A subset of events for which taxon-specific data were available were analyzed to determine the degree to which patterns of drift density of different orders were temporally synchronous over each event. High temporal synchrony among orders would indicate that drift responses during pulsed flow are not governed by differences in behavioral or physiological characteristics among taxa and that different taxa are largely affected by the same hydrologic changes that occur during pulsed flow events.

It was hypothesized that ramping rate would show stronger relationships with drift than pulse magnitude or pulse duration and that systems experiencing long periods between hydropeaking events would exhibit greater drift responses than those with less time between events. Strong correlations between drift flux and discharge were not expected at the within-systems scale as it was hypothesized that flux rates were driven primarily by elevated drift densities during hydropeaking events, rather than by discharge. It was also hypothesized that invertebrate drift responses would be highly synchronous among taxa and that the drift synchrony would be independent of drift density.

Methods

Data collection and development

A global-scale literature review focused on studies of benthic macroinvertebrate drift during hydropeaking events was conducted. To be included in the meta-analysis dataset, drift data had to be expressed as, or convertible to, drift density (individuals/m^3). In order to ensure that sampling adequately described each included event, the dataset included only hydropeaking events where 6 or more samples were obtained during the flow pulse and which included samples taken on the day of the event before pulsed flow began, during the rising leg of the discharge hydrograph, and during peak flow. All studies had to include sub-hourly discharge data over each hydropeaking event. The compilation yielded data from 24 hydropeaking events (n = 6 to 31 samples per event; Table 2.1).

The corresponding authors of each study were contacted to request raw data and to ensure that all useable data were included. In instances where authors did not reply or could not provide data, they were extracted from figures using Data Thief III, Version 1.6 (Tummers, 2006). Unpublished data from the River Spöl, a hydropeaking-impacted alpine system in Punt Dal Gal, Switzerland, was provided by C. Robinson (pers. comm.) and supplementary, taxon-specific data were provided by C. Robinson and M. Bruno (pers. comm.). The final dataset included three natural river systems (those that existed as perennial lotic systems before flow modification) and five artificial flumes. The latter group consisted of artificially constructed channels flooded by diverted river water, with introduced substrate and biota to emulate the benthic assemblages of nearby streams and rivers.

Natural river systems included the River Spöl, the Noce Bianco Stream, a third order alpine stream in Trentino, Italy and the Roanoke River, a mid-Atlantic river in North Carolina, USA. The alpine systems are similar in size, with base flow (pre-peaking) discharges of 1.0 and 1.4 m^3/s on sampling days for the Noce Bianco Stream and the Spöl River, respectively. The Roanoke River is considerably larger, with baseflow discharges ranging from 61 to 96 m^3/s on sampling days. The River Spöl had experienced relatively infrequent hydropeaking pulses (1-4 per year from 1999 to 2012). Those pulses were experimental in nature and intended to restore hydrodynamic features of the system that were lost when snowmelt pulses were eliminated by flow regulation beginning in 1970 (see Fig. 1 in Robinson, 2012). In contrast, the Noce Bianco Stream and Roanoke River often experienced multiple hydropeaking pulses per week in response to demand for hydroelectric power. Data from one event in the River Spöl were excluded because observed drift density before the onset of pulsed flow was 61 % of the maximum drift density observed on that date and was greater than five-fold higher than for the eight events included in the dataset from that system. The cause of this elevated baseflow drift is not known, but this atypical condition may indicate the effects of an unmeasured confounding factor affecting the system preceding the hydropeaking event.

The artificial flumes were constructed to assess the effects of flow peaking on invertebrate drift. They included two channel systems in Trentino, Italy, two systems in Minnesota, USA and one system in Gifu, Japan. The artificial systems were all considerably smaller than the natural systems, with base flow discharges on sampling days varying from 1.2E-03 to 3.0E-01 m^3/s (Table 2.1).

Drift nets, suspended in the water column, were used to sample macroinvertebrates in all systems except for artificial flumes 1-3. The entire water column of flumes 1 and 2 was passed through sampling nets (Carolli *et al.*, 2010) and a vacuum pump was used to sample flume 3 (Mochizuki *et al.*, 2006).

All artificial flume experiments included a single drift sample at each sampling time, whereas most samples from natural rivers were replicated (2 samples per time period for Roanoke River events, 3 samples for Noce Stream events and 1-5 samples for River Spöl events). In each case where sampling was replicated, mean values for drift density and flux (as described below) were used in the analyses.

Data analysis was restricted to taxa whose members are typically considered benthic macroinvertebrates, including all aquatic insect orders as well as Nematoda, Oligochaeta, Amphipoda, Isopoda, Gastropoda and Hydracarina. Smaller-bodied and typically planktonic taxa, including Ostracoda, Copepoda and Cladocera, were excluded from the analysis. These groups were inconsistently reported and, due to variability in the mesh size used to collect drift samples, quantitative comparisons of these groups across studies was not possible.

Datasets are referred to hereafter as follows: BRU; data from the Noce Bianco Stream and artificial flumes, Trentino, Italy (Bruno *et al.*, 2010, Carolli *et al.*, 2010) ; MOCH; data from an artificial flume, Gifu, Japan (Mochizuki *et al.*, 2006) ; IMB data from two artificial flumes, Minnesota, USA (Imbert and Perry, 2000) ; GAR; data from the Roanoke River, N.C. USA (Garey and Smock 2009, Garey *et al.* 2012) ; and ROB; data from the River Spöl, Punt Dal Gall, Switzerland (Robinson *et al.*, 2004, Robinson, 2012). All analyses described below were conducted using the R Statistical Programming Language (R Core Team 2014).

Among-events analyses

Among-events analyses were conducted using the entire dataset (with the exceptions described below). Six explanatory variables were calculated in order to summarize each hydropeaking event, including the time (days) since the last hydropeaking pulse, and five hydrologic variables: pulse duration (hours of elevated discharge), pulse magnitude (maximum discharge) and three expressions of ramping rate: the rate of change in discharge from baseflow discharge to 200% of baseflow discharge (*doubling rate*, hr.$^{-1}$), the maximum rate of change in discharge (*maximum ramping rate*, hr^{-1}), the rate of change in discharge from baseflow to 95% of maximum discharge (*overall ramping rate*, hr^{-1}) (Fig. 2.1). The 95th percentile of discharge was used to calculate overall ramping rate because small increases in flow above the initial peak occurred in the later stages of some hydropeaking cycles, causing an underrepresentation of the overall rate of increase in flow when maximum discharge was used. Pulse magnitude and the three ramping rate variables were expressed as proportions of baseflow discharge to control for the effects of variations in system size on overall rates of invertebrate drift.

The response variable at the among-events scale was the mean drift density (ind. m^{-3}) observed over each event. An alternative potential response variable was the volume-weighted mean drift density. However, because the simple arithmetic mean density and the volume weighted mean were highly correlated ($p<0.001$, $r^2= 0.91$) the latter was considered unnecessary for further analysis.

To ensure that the capture of invertebrates was not affected by the variation in net mesh size that occurred across the dataset, thr simple linear correlation of mesh size with mean drift density was calculated. The correlation was weak, and not statistically significant ($r^2= 0.17$, $p > 0.10$) indicating no effect of this methodological variable.

Few events included samples taken through the entire period of elevated flow. In most cases, sampling ended before discharge returned to baseflow levels, most probably because the focus of the studies was to determine how drift was affected by elevated flow, and subsequent samples were of lesser interest. Therefore, linear extrapolation was used to estimate drift densities during the unsampled portion of incomplete events. To ensure that such extrapolations yielded reliable estimates of each drift response, only events where drift density reached or declined below 10 % of peak flux were included (n= 14 events, Table 2.1). To assess the error associated with these estimates, the six datasets that included sampling throughout hydropeaking events were evaluated by comparing extrapolated estimates of mean drift densities to actual values calculated using all samples. The differences between actual and estimated values were 5.2 % or less for all six datasets (mean difference= 3.0 %, range= -1.4 to 5.2%), indicating that the extrapolation provided accurate estimates of drift density.

Pulse duration and each of the five hydrologic variables were included in separate simple, linear correlation analyses to determine the relative strengths of each explanatory variable with mean drift density. In addition, multiple, linear regression models were constructed that included the additive and interactive effects of each hydrologic variable with time since previous pulse to determine if hydrologic stability, as estimated by the duration of time between hydropeaking events, affected relationships between the hydrologic characteristics and invertebrate drift. The best model for explaining mean drift density was selected as that yielding the lowest value of Akike's Information Criterion, corrected for small sample size (AICc; Akike, 1973, Hurvich and Tsai, 1989). Models including interactions between hydrologic variables and time since previous pulse did not improve explanatory power and, therefore, these models are not discussed further. The linear model assumptions of homoscedasticity, uncorrelatedness among explanatory variables, linearity and normality were evaluated using the Global Validation of Linear Model Analysis package in R (GVLMA; Peña and Slate 2014, R Core Team 2014). Unlike individual tests of each assumption, the global test statistic produced by the GVLMA package accounts for interdependence among assumptions via a simultaneous test of all (Peña and Slate, 2006). In addition, the data distributions were examined to determine if outliers existed with respect to the response variables that might have disproportionately affected model fit (values above the third quartile or below the first quartile by 1.5 times the interquartile range).

Within-event analyses

Within-event analyses were conducted using each dataset individually to determine the nature and magnitude of relationships between river hydrology and invertebrate drift. Explanatory variables were discharge magnitude, expressed as mean discharge occurring over the time of each drift sample (m^3 s^{-1}), and ramping rate, calculated as the change in discharge over each sampling time interval (m^3 $s.^{-2}$, Fig. 2.1). To account for time delays between the gauging station and drift sampling location in the GAR dataset, HOBO model U20 pressure loggers (Onset Computer Corp., Bourne, MA.) were installed at the gauging station and drift sampling point, and set to record at 30-second intervals. Discharge was time- corrected in the ROB dataset using measured water velocities at the drift sampling point (C. Robinson, pers. communication). Discharge in the artificial flume systems (BRU, IMB and MOCH datasets) was measured at the sampling point and therefore time correction was unnecessary. Response variables at the within-events scale were drift density (individuals m^{-3}) and instantaneous flux of invertebrates (ind/s), calculated as the product of pulse magnitude and drift density for each sample. For each of the 24 datasets, simple linear correlations were calculated between each hydrologic explanatory variable and each invertebrate drift response variable. Instantaneous flux and discharge magnitude are partially mathematically dependent, as the latter is used in the calculation of the former. Despite this mathematical relationship, strong correlations between drift flux and pulse magnitude were not expected because it was hypothesized that drift flux rates were driven primarily by elevated drift densities during hydropeaking events, rather than by river discharge. To test this hypothesis, simple linear correlations between instantaneous flux and drift densities were also calculated and compared to those between flux and pulse magnitude.

Taxon-specific drift responses

Taxon-specific drift density data were available for three studies: Noce Bianco Stream and two artificial stream channels in Italy (M. Bruno, *pers. comm;* BRU dataset); the River Spöl in Switzerland (C. Robinson, *pers. comm;* ROB dataset) and the Roanoke River in North Carolina (Garey and Smock, 2009; Garey *et al.*, 2012; GAR dataset). These data were analyzed to compare the relative drift responses of different taxonomic groups to hydropeaking. All data were analyzed at the taxonomic level of order to provide consistency among sampling events and datasets.

To determine the degree to which the drift of individuals of each order was in synchrony with overall drift, linear correlations of the drift density of each order (response variable) with total drift density (explanatory variable) were calculated for each event. To preserve statistical independence between explanatory and response variables in this analysis, the drift densities of each analyzed order were subtracted from the total densities in each sample before the correlations were calculated. Only orders that occurred in at least three samples from a given peaking event were included in the analysis for that event. The orders Amphipoda, Diptera, Ephemeroptera, Gastropoda, Hydracarina, Oligochaeta, Plecoptera and Trichoptera were included in the taxon-specific analysis. Other orders, including Coleoptera and Odonata, were rare in drift samples and therefore, to achieve sufficient replication, these were combined together in an Other Invertebrates category.

T-tests between all pairwise combinations of orders were conducted to determine if drift synchrony (r-values for correlations of taxon-specific drift with total drift densities) was significantly different among orders. The comparisons were blocked according to sampling date using paired T-tests to control for variability among hydropeaking events. Both uncorrected p-values as well as p-values corrected for multiple comparisons (via the Holm-Bonferroni method;Holm, 1979) were conducted, thus providing a balance between protecting against Type I errors while increasing the risk of Type II errors (corrected p-value approach) and vice-versa (uncorrected approach).

Simple linear regressions were conducted to determine whether the drift synchrony of each order was correlated with its drift density. For this analysis the occurrences of each order on each sampling date were used as replicates and drift synchrony (r-values calculated as above) was regressed against mean, order-specific, proportional drift density. All analyses associated with the taxon-specific drift responses were conducted separately for each dataset (BRU, GAR and ROB datasets).

Results

Macroinvertebrate drift among systems

Simple regression models indicated that the single best predictor of drift density was the maximum ramping rate occurring over each hydropeaking event (r^2=0.85; $p<0.01$), followed closely by mean ramping rate (r^2=0.71; $p<0.01$). Correlations of drift density with pulse magnitude, doubling rate, pulse duration, and the time since the last pulse occurred were each weak and non-significant (r^2=0.01-0.26; $p>0.05$, Table 2.2). The model that best explained mean drift density (lowest AICc value) included time since last pulse and maximum ramping rate (r^2=0.92, both parameters significant at $p<0.01$, Fig 2.2). This model explained the majority of variation across the wide-ranging drift density values in the dataset, and considerably more than all other multiple regression models evaluated (r^2=0.13-0.72). The global test of the linear assumptions was not significant ($p > 0.05$), indicating that the assumptions were met, however, the analysis included one outlier that may have influenced model fit (event observed by Mochizuki *et al.*, 2006 in July 2001; Fig. 2.2). After removal of this point and re-analyzing with the 13 remaining datasets, the model that included maximum ramping rate and time since previous pulse remained the best explanatory model for mean drift density (r^2= 0.73, Table 2.2, Fig. 2.3).

Macroinvertebrate drift within events

Analysis of each pulsed flow event indicated that instantaneous flux was consistently and positively correlated with drift density (r= 0.48-1.00, mean: 0.88). In contrast, there was little correlation between flux and discharge in most cases (r= -0.14- 0.86, mean: 0.34) and correlations of drift flux with drift density were stronger than correlations of flux with discharge in 23 of 24 cases (Fig. 2.4). These results indicate that, in most cases, increased drift flux during hydropeaking is driven by elevated drift densities, rather than simply being a function of increased discharge.

Positive correlations between hydrologic explanatory variables and invertebrate drift response variables occurred for most events; however, the relative strengths of such correlations were highly variable across the dataset with no consistent patterns of temporal concordance between hydrology and invertebrate drift at the within-events scale (Figs. 2.5 and 2.6). The sign and magnitude of correlations between pulse magnitude and drift density was largely dependent on the timing of peak drift density. Positive correlations between pulse magnitude and drift density occurred for some events, though negative correlations of considerable strength were also observed (occurring in 2 of 5 events in the GAR dataset and 3 of 4 events in the MOCH dataset; Fig. 2.5), indicating a dilution effect on drift density at least over some time periods within these hydropeaking pulses. In instances where such negative correlations occurred, drift density peaked and declined before discharge reached its maximum and low drift density was sustained for most of the pulsed flow duration while discharge remained elevated. Events exhibiting positive correlations between drift density and pulse magnitude also exhibited rapid increases and subsequent rapid declines in macroinvertebrate drift; however, in such cases the drift pattern was delayed such that maximum drift occurred during, or near, maximum discharge (e.g. compare June 2010 event from the GAR dataset to July 2001 event from the ROB dataset; Fig 2.6).

Taxon-specific drift responses

Correlations of order-specific drift densities with total drift density were generally high (most mean r-values > 0.60), with few differences among orders (Table 2.3, Fig. 2.7), supporting the hypothesis that taxa drifted in a synchronous manner during hydropeaking events. Holm-

Bonferroni-corrected t-tests yielded no significant differences in synchrony (r-values) between orders for any of the three datasets ($p>0.05$). When un-corrected T-tests were used, most pairwise differences among orders were not significant ($p>0.05$; Table 2.3). Oligochaeta exhibited significantly lower synchrony than Ephemeroptera and Diptera during the events described by the BRU data, and Oligochaeta exhibited significantly lower synchrony than all other orders in the GAR events (uncorrected $p<0.05$; Table 3). No significant differences in drift synchrony among orders occurred in the ROB events (uncorrected $p>0.05$; Table 2.3).

Drift synchrony was relatively similar among hydropeaking events for taxa such as Diptera, Ephemeroptera and Plecoptera, whereas for others, synchrony was variable among events. For example, Amphipoda were synchronous with overall drift during most events but exhibited low synchrony for two events described by the ROB dataset (Fig. 2.7, Panel 1). Oligochaeta and Hydracarina also exhibited highly variable levels of synchrony among events. Hydracarina exhibited high drift synchrony in 4 of 5 events in the GAR dataset and in 1 of 3 events in the ROB dataset, despite their low synchrony during other events. Oligochaeta exhibited relatively high synchrony in the BRU dataset (mean $r = 0.69$), but low synchrony in the ROB (mean $r = 0.34$) and GAR (mean $r = 0.25$) datasets (Table 2.3, Fig. 2.7).

As hypothesized, drift synchrony was not strongly related to drift density. Overall correlations between synchrony and density were statistically significant, yet weak for the BRU and ROB datasets ($r^2 = 0.22$ and 0.11, respectively, $p = 0.03$ and 0.02, respectively), and not significant for the GAR dataset ($r^2 = 0.05$, $p= 0.20$). High-density taxa (most notably Diptera) generally showed high drift synchrony ($r>0.60$) during most hydropeaking events. Some low-density taxa, notably, Oligochaeta in the GAR and ROB datasets exhibited relatively low synchrony (mean $r= 0.25$ and 0.34, respectively; Table 2.3). Most low-density orders, however exhibited relatively high synchrony. For example, Plecoptera exhibited high drift synchrony in the ROB and BRU datasets despite the low proportional abundance of this order in these studies (mean r= 0.82 and 0.75, respectively, mean proportional densities= 0.08 and 0.05, respectively; Table 2.3; Plecoptera are rare in the Roanoke River and did not occur in any GAR drift samples). Drift of Ephemeroptera was also synchronous with total drift among all three datasets (mean r > 0.80), though this order generally occurred at low proportional densities (Table 2.3). Overall, despite wide variations in drift densities, patterns of taxon-specific macroinvertebrate drift exhibit high temporal synchrony with total drift, suggesting that variations in drift responses are not strongly affected by behavioral or physiological differences among taxa and are driven by the same hydrologic factors.

Discussion

This investigation provides a greater understanding of the manner in which flow modifications affect benthic assemblages. Drift density was most strongly correlated with the maximum ramping rate observed during each pulse. Systems exhibiting the highest rates of peaking-induced drift were those exhibiting the most rapid discharge increases. The model that best explained drift density variations included both maximum ramping rate and the time since the previous hydropeaking event occurred in the system, which, collectively, explained 91% of the variation in drift observed among studies. Maximum ramping rate was considerably more important than the time period between events, as the slope coefficient on the former was greater than that of the latter by an order of magnitude (Table 2.1). These results suggest that the most effective way to affect peaking-induced drift is by altering the rate of discharge increase that occurs over a given pulse and that at a given ramping rate, longer time periods between pulses should result in greater drift responses.

Drift flux rates were strongly concordant with drift density at the within-events scale, indicating that elevated concentrations of invertebrates in the water column, rather than elevated discharge rates were most important in explaining the observed temporal patterns in drift. Consistent temporal concordance between hydrologic variables (discharge or ramping rate) and drift metrics (flux or density) would provide evidence of the most important causative mechanisms of drift, however, such consistent concordance was not observed among the studies. The lack of consistent correlations between hydrology and drift within events may be interpreted as a lack of causation, however, given the consistent and qualitatively similar drift responses observed among events, this interpretation seems implausible. Alternatively, there may be temporal delays between hydrologic causative factors and drift responses or, as postulated by

Poff *et al.*, (1997), hydrology may be acting indirectly on other physicochemical factors, which in turn are the mechanisms that directly affect drift. Indeed, elevated drift has been implicated as an ecological response to a wide range of environmental changes in lotic systems (Hall *et al.*, 1982, Brittain and Eikeland, 1988, James *et al.*, 2008). If such time lags or intermediate explanatory variables exist, the wide variation in the strengths of correlations between hydrologic variables and drift metrics observed indicates that these factors are highly variable among hydropeaking events.

Taxon-specific responses indicated that drift is synchronous among taxa. The drift density patterns of macroinvertebrate orders were consistent with the overall pattern of drift during hydropeaking. This suggests that the drift response to hydropeaking is not driven by differences in behavioral, morphological or physiological differences among orders and indicates that conclusions drawn here regarding the effects of variations in the management of pulsed-flow hydrology on macroinvertebrate drift are broadly generalizable across taxonomic groups.

The conclusion that different aspects of pulsed-flow hydrology are variable with respect to their relative importance for affecting benthic assemblages has important management implications. Managers seeking to reduce the displacement of macroinvertebrates during hydropeaking should reduce overall pulse ramping rate, whereas changes in pulse magnitude are less likely to affect the drift response. Understanding what factors most affect drift is important because this phenomenon affects not only the displaced organisms, but also affects downstream habitat patches and other ecosystem components. Drift density is a major controlling factor in the rate of dispersal of benthic organisms to new habitat patches (Waters, 1964, Townsend and Hildrew, 1976). In addition, hydropeaking-induced drift stimulates fish feeding (Lagarrigue *et al.*, 2002, Miller *et al.*, 2014). Given the importance of drift density in governing the growth and development of drift feeding fishes (Hayes *et al.*, 2000), and the results of the present study, pulse ramping rate and the time between hydropeaking pulses are the most important factors that should be considered in management strategies that prioritize effects on such fish populations. Pulse duration was uncorrelated with drift density, therefore, it may be possible for system managers to sustain a given water volume release that meets energy demands while minimizing effects on the benthos by reducing ramping rate and increasing pulse duration. Data from additional, long-duration, low-magnitude and low- ramping rate events are needed to fully evaluate this hypothesis.

Though beyond the scope of this work, it should be noted that the manner in which pulsed-flow systems are managed has economic implications that should be considered in addition to ecological impacts. For example, rapid ramping rates are often employed in hydropower systems in order to quickly meet peak energy demands. As discussed by Patterson and Smokorowski (2011), reduced ramping rates may reduce ecological impacts, but may also inhibit power generation at times when user demand is highest. Similarly, long-duration, lower-magnitude events might allow managers to achieve the total power generation needed over longer time scales (e.g., over one week) but might not be suitable for matching periods of maximum power generation with periods of peak demand over shorter time scales (e.g. during hours of the day when power demand for air conditioning is highest). Future work focused on valuing economic and ecological resources on a common scale is essential, not only for the management of hydropower systems, but also for the responsible management of environmental systems in general.

Additional evaluations that include precise, time-series measurements of drift, hydrology and physicochemistry would provide important information on the presence and nature of time lags between causative hydrologic factors and drift responses and on the underlying mechanisms of hydropeaking-induced drift. Given the myriad factors that affect drift and the benefit of controlled, replicated trials, artificial flume experiments seem especially suited for providing this information (e.g., see Carolli *et al.*, 2010).

In addition to the short-term effects assessed here, hydropeaking-induced drift may have additional effects on long-term population dynamics through depletive effects that are compounded over multiple events or by enhancing or inhibiting production. Imbert and Perry (2000) indicated that drift generally accounts for a relatively small proportion of total benthic abundance, though others have shown that pulsed flow events may cause substantial depletions of abundance (McMullen and Lytle, 2012, Robinson *et al.*, 2004) and these effects are compounded over multiple events (Irvine, 1985, Robinson, 2012). Future studies focused on the long-term impacts of hydropeaking should balance the deleterious effects of displacement and mortality with the additive effects of secondary production and recolonization.

Others have provided evidence of the effects of hydropeaking on drift within individual systems, however, this study is the first to provide an across-system assessment of the most important hydrologic drivers of macroinvertebrate drift responses to hydropeaking. This work provides much-needed information on the relative importance of different aspects of pulsed-flow hydrology on hydropeaking-induced drift. These results provide valuable new information for managing the impacts of hydropeaking on benthic macroinvertebrate assemblages in lotic ecosystems.

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Table 2.1: Hydropeaking events included in the analysis. * denotes events included in the among-events analysis. n denotes the number of drift samples collected during each hydropeaking event. Event numbers are used for reference in Figures 3 and 4. Dataset codes are included for reference in the text; BRU: artificial flume experiments and hydropeaking event in the Noce Bianco Stream, Trentino, Italy (Bruno *et al.*, 2010, Carolli *et al.*, 2010), MOC: artificial flume experiments, Gifu, Japan (Mochizuki *et al.*, 2006), IMB: artificial flume experiments, Minnesota, USA (Imbert and Perry, 2000), GAR: hydropeaking events in the Roanoke River, North Carolina, USA (Garey and Smock 2009, Garey *et al.* 2012) and ROB: hydropeaking events in the River Spöl, Switzerland (Robinson *et al.*, 2004, Robinson, 2012) and unpublished).

Event	System	Baseflow discharge (m^3/s)	Sampling method	n	Sample Date	Location	Dataset	Reference
1	Artificial Flume 1	2.2E-03	100 µm drift net	8	Sept. 2006	Italy	BRU	Carolli et al., 2010b
2	Artificial Flume 2 *	1.2E-03	100 µm drift net	8	Sept. 2006	Italy	BRU	Carolli et al., 2010b
3	Artificial Flume 3	3.0 E-01	Vacuum pump, 334 µm net	20	Dec. 2001	Japan	MOC	Mochizuki et al., 2006
4	Artificial Flume 3 *	8.0 E-02	Vacuum pump, 334 µm net	25	July 2001	Japan	MOC	Mochizuki et al., 2006
5	Artificial Flume 3	7.0 E-02	Vacuum pump, 334 µm net	31	Sept. 2001	Japan	MOC	Mochizuki et al., 2006
6	Artificial Flume 3	7.0E-02	Vacuum pump, 334 µm net	25	July 2002	Japan	MOC	Mochizuki et al., 2006
7	Artificial Flume 4	1.0E-02	356 µm drift net	11	Oct. 1991	USA	IMB	Imbert and Perry, 2000
8	Artificial Flume 4	1.3E-02	356 µm drift net	11	Nov. 1991	USA	IMB	Imbert and Perry, 2000
9	Artificial Flume 5	1.0E-02	356 µm drift net	10	Oct. 1991	USA	IMB	Imbert and Perry, 2000
10	Artificial Flume 5	1.3E-02	356 µm drift net	10	Nov. 1991	USA	IMB	Imbert and Perry, 2000
11	Noce Bianco Stream	1.0	100 µm drift net	7	Sept. 2006	Italy	BRU	Bruno et al., 2010
12	Roanoke River *	7.0E+02	500 µm drift net	9	July 2009	USA	GAR	Garey and Smock, 2009
13	Roanoke River *	9.6E+02	500 µm drift net	12	June 2010	USA	GAR	Garey et al., 2012
14	Roanoke River *	7.0E+02	500 µm drift net	12	July 2010	USA	GAR	Garey et al., 2012
15	Roanoke River *	6.1E+02	500 µm drift net	7	Aug. 2010	USA	GAR	Garey et al., 2012
16	Roanoke River *	6.1E+02	500 µm drift net	10	Aug. 2010	USA	GAR	Garey et al., 2012

Event	System	Baseflow discharge (m^3/s)	Sampling method	n	Sample Date	Location	Dataset	Reference
17	River Spöl *	1.4	400 µm drift net	6	June 2001	Switzerland	ROB	Robinson et al., 2004
18	River Spöl *	1.4	400 µm drift net	6	July 2001	Switzerland	ROB	Robinson et al., 2004
19	River Spöl *	1.4	400 µm drift net	13	Aug. 2001	Switzerland	ROB	Robinson et al., 2004
20	River Spöl	1.4	400 µm drift net	17	July 2002	Switzerland	ROB	Robinson et al., 2004
21	River Spöl *	1.4	400 µm drift net	13	July 2007	Switzerland	ROB	Robinson, unpublished
22	River Spöl *	1.4	400 µm drift net	18	Sept. 2007	Switzerland	ROB	Robinson, unpublished
23	River Spöl *	1.4	400 µm drift net	20	July 2010	Switzerland	ROB	Robinson, 2012
24	River Spöl *	1.4	400 µm drift net	20	Oct. 2011	Switzerland	ROB	Robinson, unpublished

Table 2.2: Regression models for predicting mean drift density among hydropeaking events. Explanatory variables used in each regression model were: dq50: doubling rate (hr^{-1}); dq95: mean ramping rate (hr^{-1}); dqMax: maximum ramping rate (hr^{-1}); Mag: pulse magnitude, tSinceDist: time between the observed hydropeaking event and the preceding event (days). Underlined text indicates the overall best-fit model. AICc: Aikaike's information criterion, corrected for small sample sizes (Akaike 1973, Hurvich and Tsai 1989). β: slope parameters for each explanatory variable. Only slope parameters significant at $p \leq 0.05$ are shown. NS: not significant ($p > 0.05$). Values in parentheses for the best-fit model explaining mean drift density are for the regression analysis using all 14 hydropeaking events, whereas those not in parenthesis are for the analysis with one outlier value excluded.

Model	AICc	r^2	p	β (hydrologic variable)	β (tsincedist)
Maximum ramping rate (dqMax)	190	0.85	<0.01	9.86	--
Overal ramping rate (dq95)	199	0.71	<0.01	2.70E+01	--
Pulse duration	210	0.19	0.12	NS	--
Pulse magnitude (Mag)	212	0.26	0.06	NS	--
Doubling rate (dq50)	214	0.11	0.25	NS	--
Time since previous pulse tSinceDist.	216	0.01	0.76	--	NS
dqMax + tSinceDist.	180	0.92 (0.73)	<0.01 (<0.01)	1.02E+01 (1.70E+01)	1.05 (0.92)
dq95 + tSinceDist.	202	0.72	<0.01	2.70 E+01	0.34
Mag + tSinceDist.	215	0.27	0.17	NS	NS
duration + tSinceDist.	216	0.24	0.21	NS	NS
dq50 + tSinceDist.	218	0.13	0.48	NS	NS

Table 2.3: Number of hydropeaking events (n), drift synchrony (mean and standard error r-values), and proportional density (mean and standard error) for orders included in the pairwise comparisons of drift synchrony. Values followed by the same lowercase letter are not significantly different (pairwise T-tests, un-corrected for multiple comparisons, $p<0.05$). Italicized, grey columns were not analyzed due to lack of replication. NA: not applicable because the taxon was not reported in the dataset. ROB: hydropeaking events in the River Spöl, Switzerland (Robinson *et al.* 2004, Robinson 2012 and unpublished); BRU: artificial flume experiments and hydropeaking event in the Noce Bianco Stream, Trentino, Italy (Bruno *et. al.* 2010, Carroli *et al.*, *2010*) and GAR: hydropeaking events in the Roanoke River, North Carolina, USA (Garey and Smock 2009, Garey *et al.* 2012).

Dataset	Amphipoda	Diptera	Ephemeroptera	Gastropoda	Hydracarina	Oligochaeta	Plecoptera	Trichoptera	Other Invertebrates
ROB									
n	8	8	8	NA	3	*2*	7	4	7
r (mean)	0.78^{a}	0.87^{a}	0.8^{a}	NA	0.36^{a}	*0.34*	0.82^{a}	0.59^{a}	0.51^{a}
r (std. error)	0.08	0.04	0.07	NA	0.32	*0.18*	0.09	0.19	0.18
Prop. density (mean)	0.21	0.63	0.05	NA	0.03	*0.01*	0.08	0.02	0.04
Prop. density (std. error)	0.05	0.07	0.01	NA	0.03	*0.01*	0.03	0.01	0.01
BRU									
n	NA	3	3	NA	3	3	3	3	3
r (mean)	NA	0.91^{a}	0.90^{a}	NA	0.49^{ab}	0.69^{b}	0.75^{ab}	0.34^{ab}	0.24^{ab}
r (std. error)	NA	0.04	0.04	NA	0.13	0.07	0.08	0.23	0.36
Prop. density (mean)	NA	0.76	0.14	NA	0.01	0.01	0.05	0.01	0.01
Prop. density (std. error)	NA	0.01	0.03	NA	0.00	0.00	0.03	0.01	0.00

Dataset	Amphipoda	Diptera	Ephemeroptera	Gastropoda	Hydracarina	Oligochaeta	Plecoptera	Trichoptera	Other Invertebrates
GAR									
n	*2*	5	5	5	5	5	NA	5	5
r (mean)	*0.69*	0.88^{a}	0.9^{a}	0.84^{a}	0.83^{a}	0.25^{b}	NA	0.78^{a}	0.86^{a}
r (std. error)	*0.24*	0.06	0.05	0.07	0.08	0.16	NA	0.13	0.04
Prop. density (mean)	*0*	0.53	0.07	0.07	0.03	0.02	NA	0.24	0.05
Prop. density (std. error)	*0*	0.06	0.02	0.02	0.01	0.01	NA	0.03	0.01

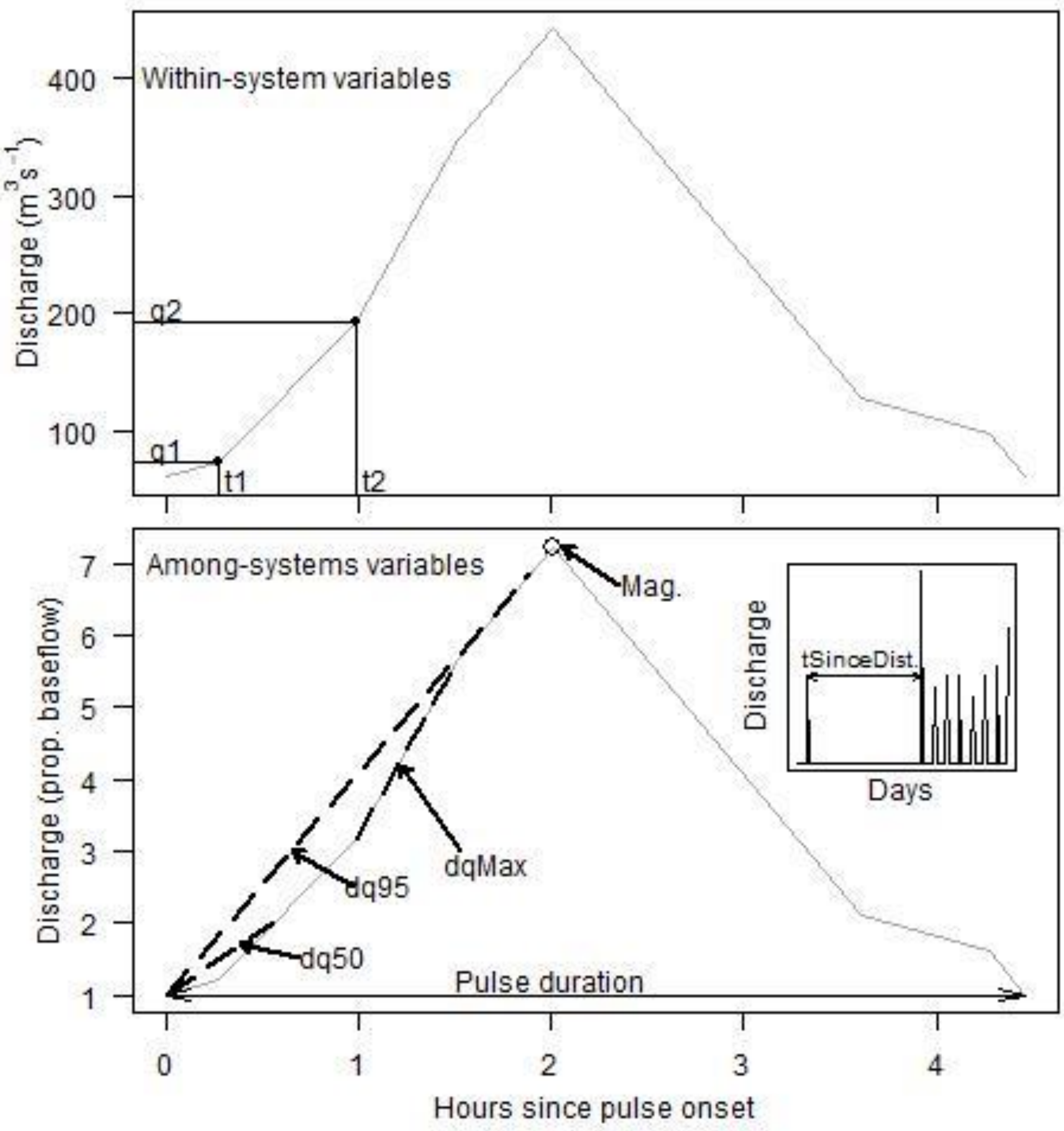

Figure 2.1: Explanatory variables used in the analysis. Grey line represents discharge during a hydropeaking event in the Roanoke River on 3 August, 2010, expressed in m^3/s (top panel) and in proportion to baseflow discharge (bottom panel). **Top panel:** within-system scale variables. q1 and q2: discharge measurements at the beginning and end of one drift sampling period, respectively. t1 and t2 represent beginning and end times of the sampling period. Discharge for the sample was calculated as the mean of q1 and q2. Ramping rate was calculated as the rate of change in discharge over the sampling period, via the equation: (q2-q1)/(t2-t1). **Bottom panel:** among-systems scale. dq50 denotes doubling rate: the rate of change in discharge from baseflow discharge to 200% of baseflow discharge. dq95 denotes overall ramping rate: the rate of change in discharge from baseflow to 95% of maximum discharge. dqMax denotes the maximum rate of change observed for each event. Mag. denotes pulse magnitude: the maximum discharge observed. tSinceDist denotes the time (number of days) between the observed hydropeaking event and the preceding event that occurred in the system.

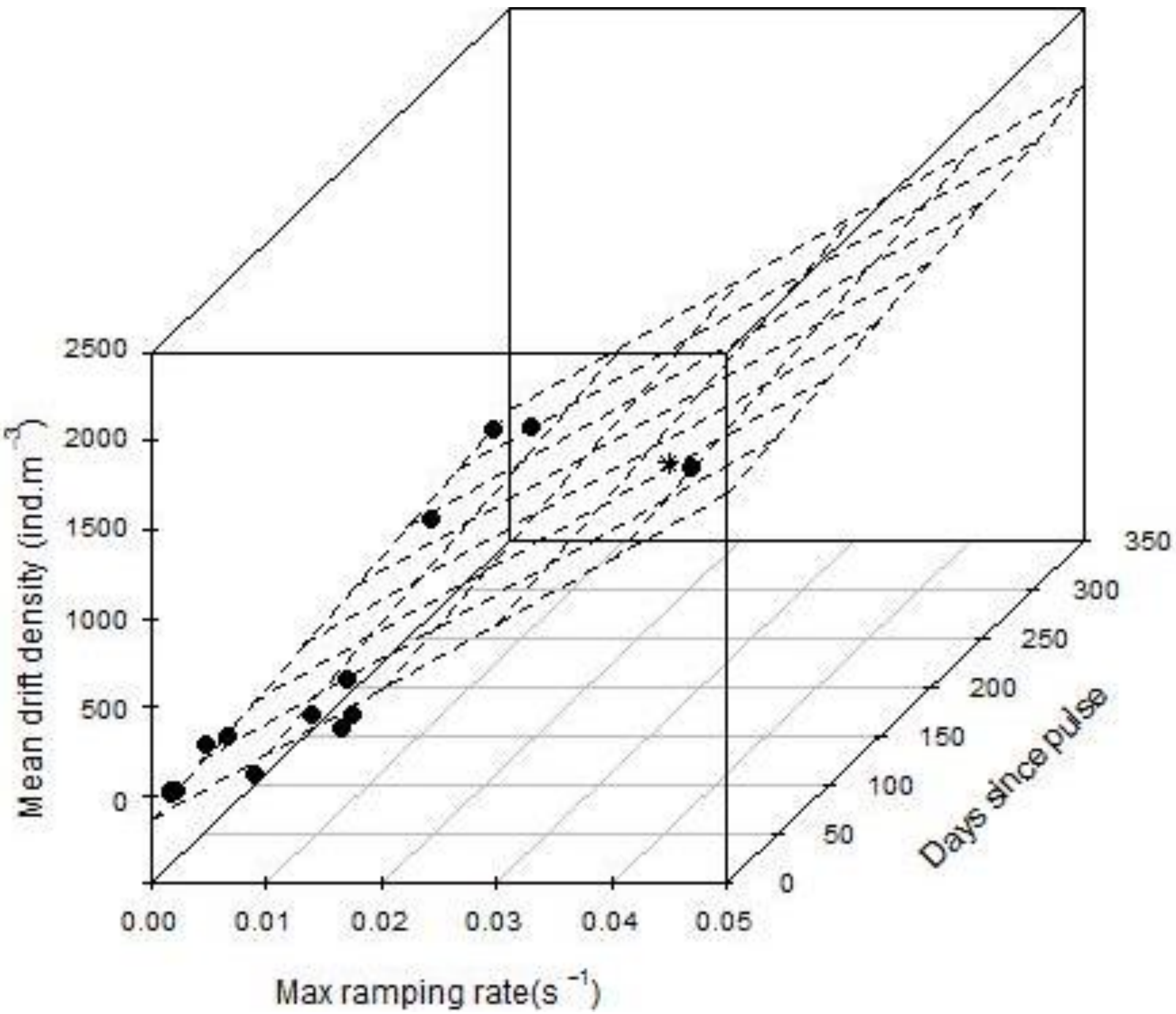

Figure 2.2: Best-fit linear model explaining mean drift density among the 14 hydropeaking events. Broken lines represent the 2-dimensional best-fit linear regression plane. Equation: **mean density = 3.67E+04(maximum ramping rate) + 1.05(time since previous pulse)- 1.37 E+02**. r^2: 0.92, $p < 0.01$. * denotes event exhibiting outlier value for mean density (event 15; MOC dataset, artificial flume experiment in July, 2001).

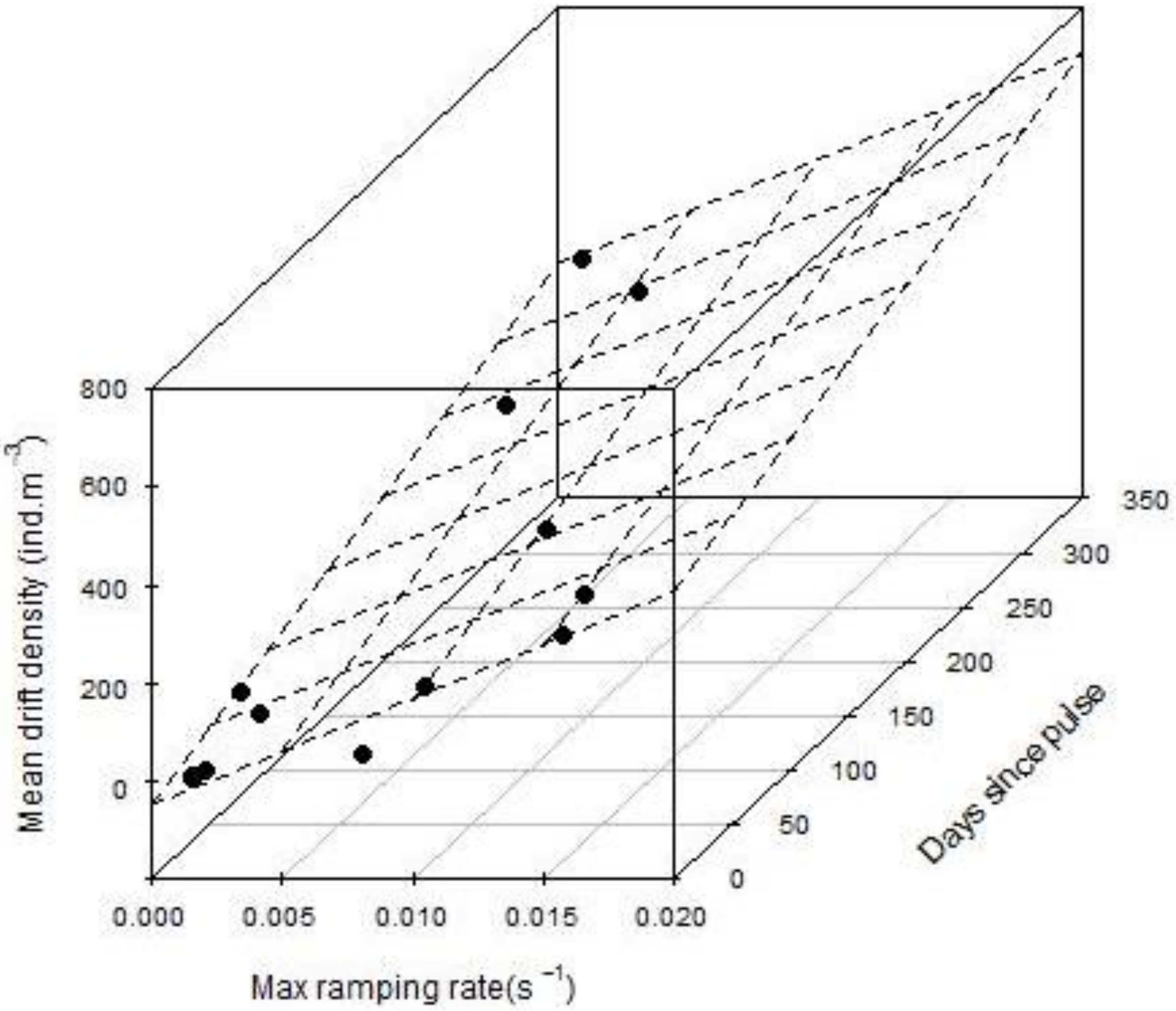

Figure 2.3: Best-fit linear model explaining mean drift density among the 13 hydropeaking events (outlier value from MOC dataset excluded). Broken lines represent the 2-dimensional best-fit linear regression plane. Equation: **mean density = 2.17E+04(maximum ramping rate) + 0.93(time since previous pulse) – 4.92E+01**. r^2: 0.73, $p < 0.01$.

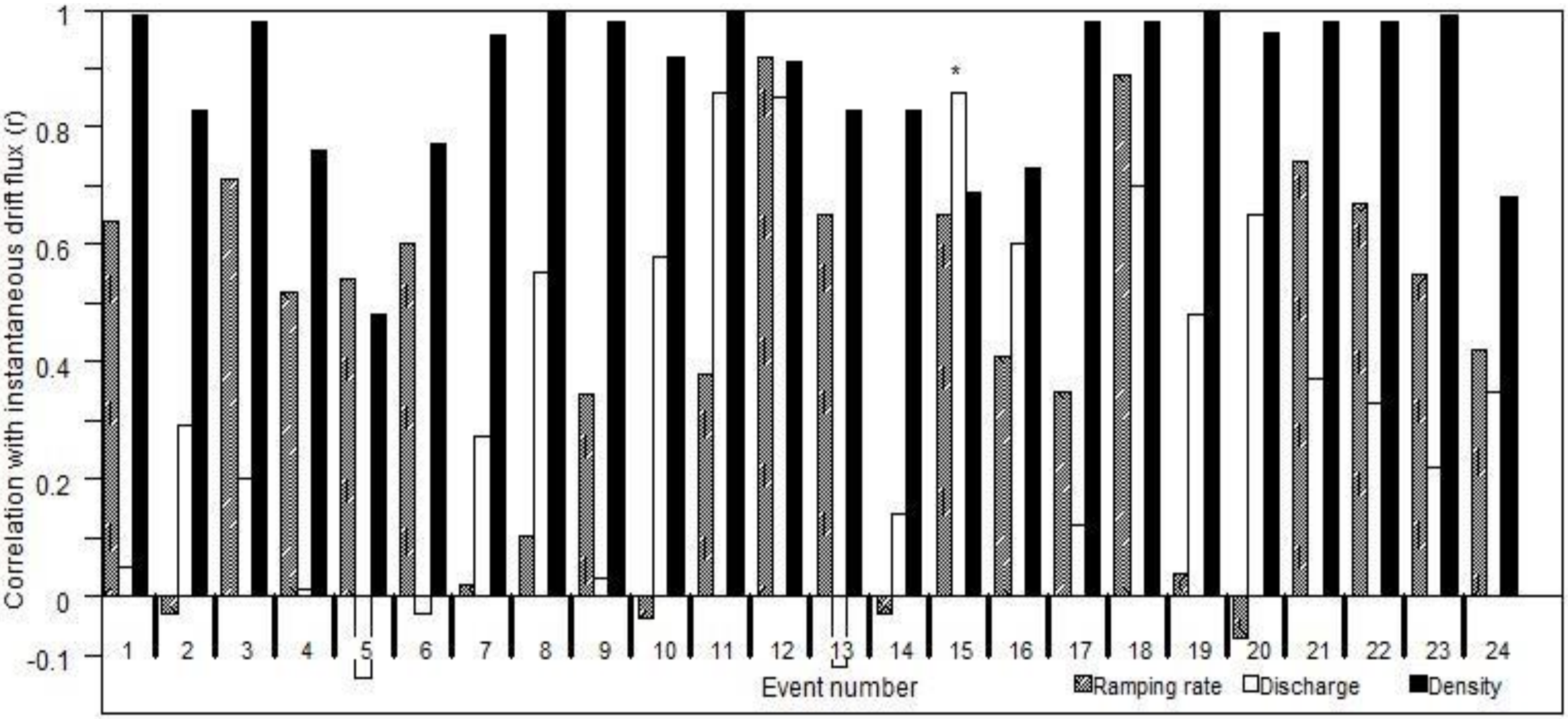

Figure 2.4: Correlations of ramping rate, discharge, and drift density with drift flux for each of the 24 hydropeaking events occurring in artificial flumes and natural river channels. * denotes single event for which the correlation of discharge with flux was greater than the correlation of density with flux. Event numbers correspond to those listed in Table 1.

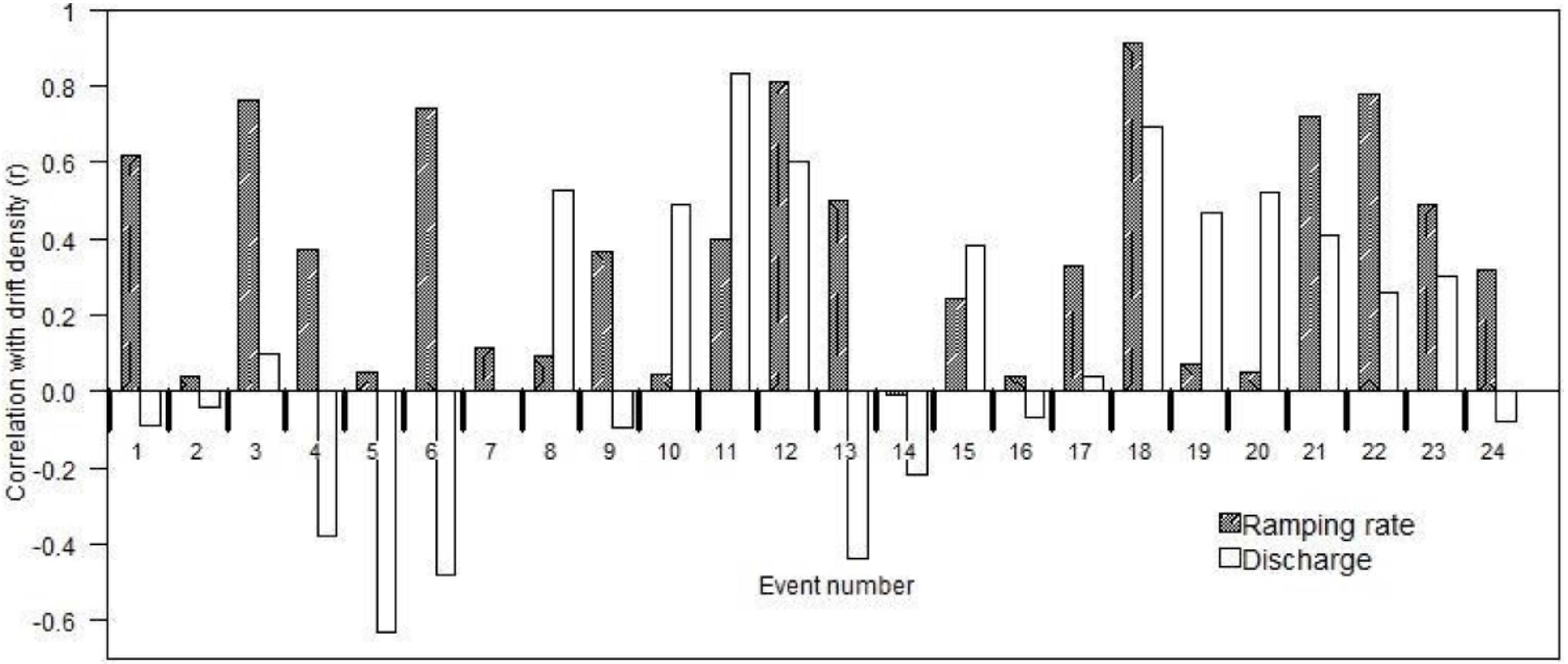

Figure 2.5: Correlations of ramping rate and discharge with drift density for each of the 24 hydropeaking events occurring in artificial flumes and natural river channels. Event numbers correspond to those listed in Table 1.

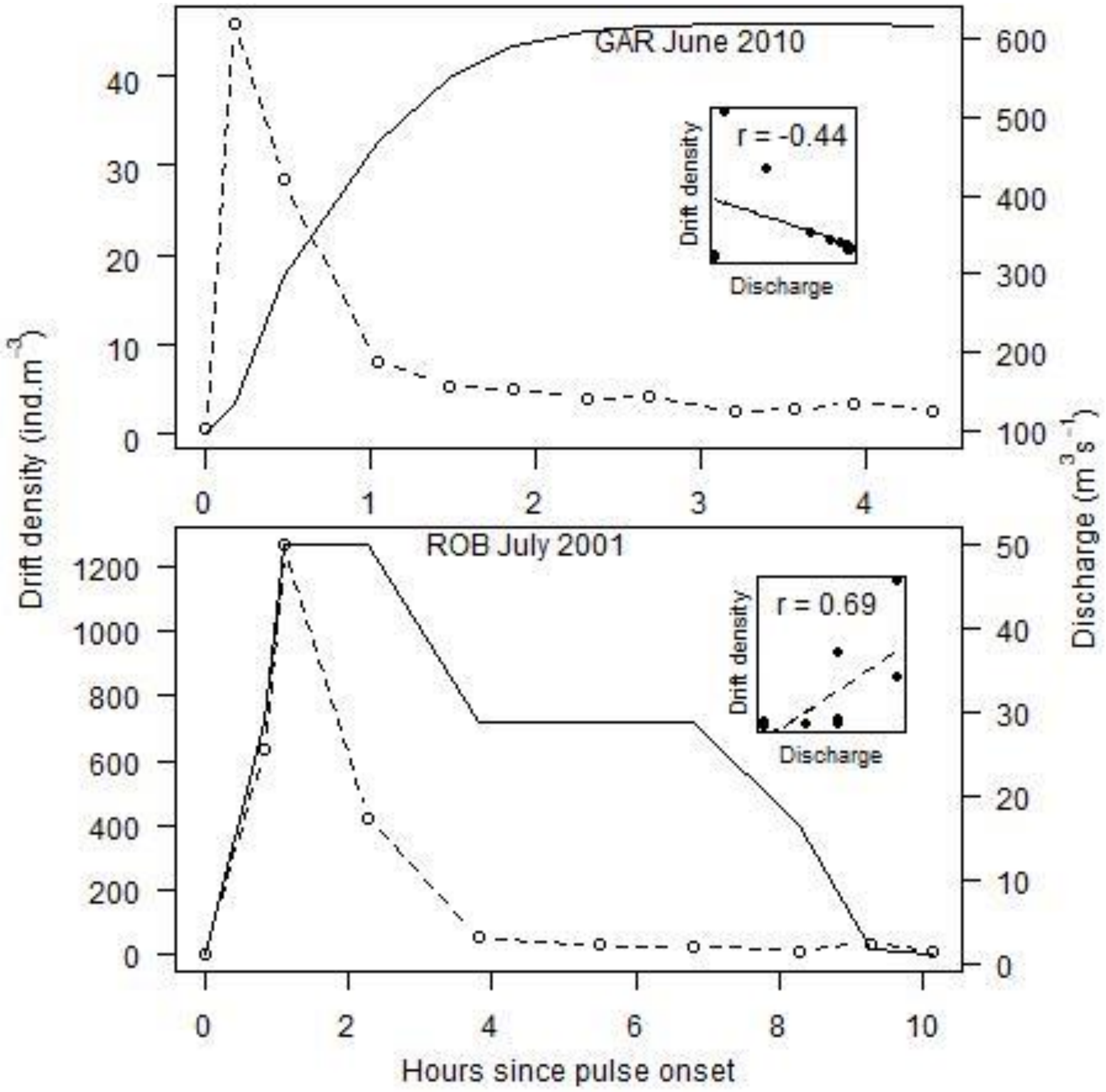

Figure 2.6: River hydrographs (solid line) and drift densities (broken line) in hydropeaking events in the Roanoke River and River Spöl. Inset figures show best-fit lines and correlations of river discharge with drift density.

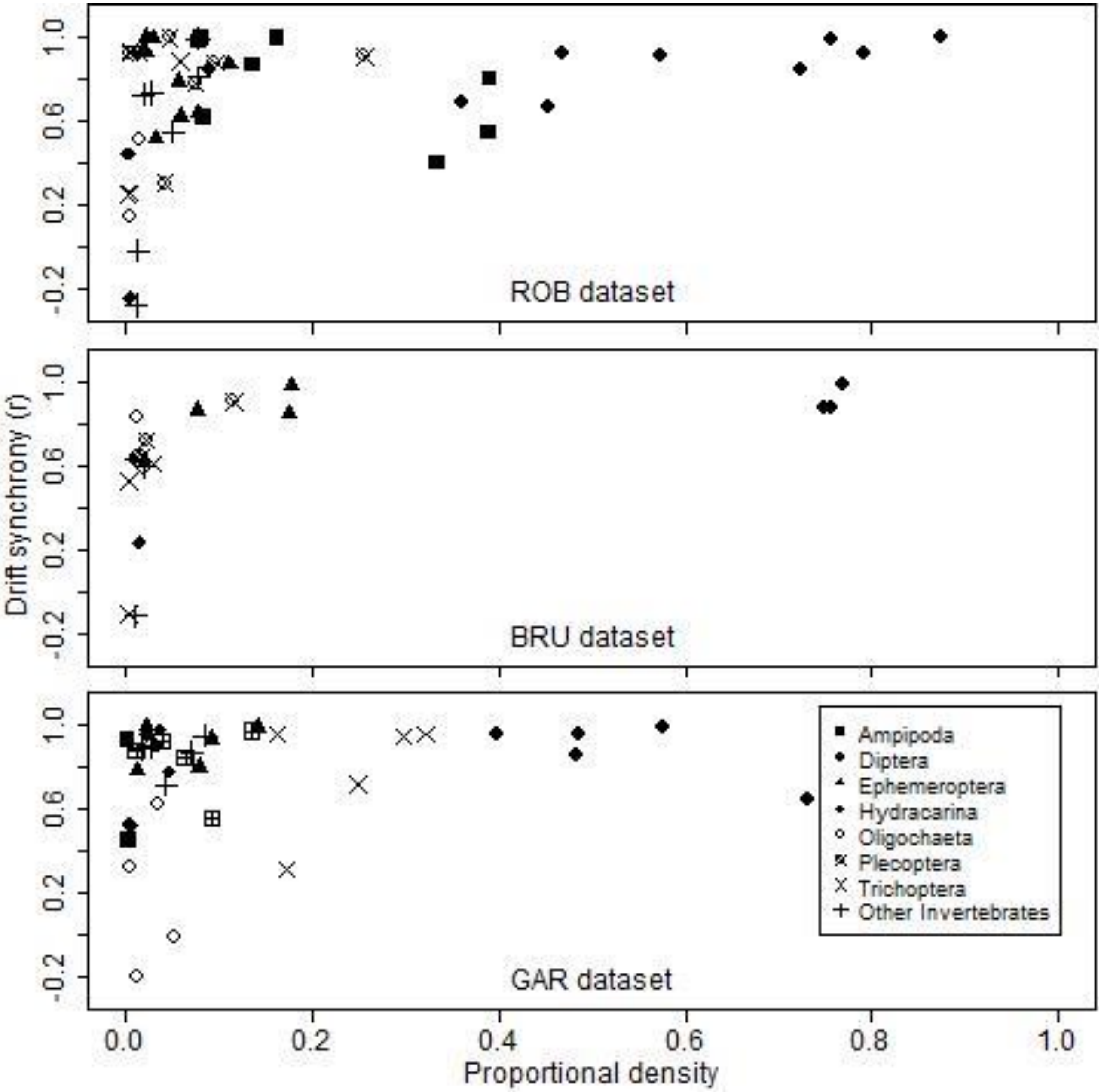

Figure 2.7: Order-specific drift synchrony for pulsed-flow events. Points represent the occurrence of each taxon during each hydropeaking event. ROB: hydropeaking events in the River Spöl, Switzerland (Robinson et al. 2004, Robinson 2012 and unpublished); BRU: artificial flume experiments and hydropeaking event in the Noce Bianco Stream, Trentino, Italy (Bruno et. al. 2010, Carroli et al, 2010b) and GAR: hydropeaking events in the Roanoke River, North Carolina, USA.

Chapter III

Influence of habitat patch characteristics on benthic macroinvertebrate drift responses to hydropeaking: a permutational null model approach.

Abstract

Anthropogenic flow modifications have markedly affected the structure and functioning of aquatic ecosystems worldwide. The alteration of discharge regimes to produce rapid, short-duration flow pulses for hydroelectric power generation (commonly known as hydropeaking) typically results in elevated drift of benthic macroinvertebrates. Here, I present a simple permutation-based model for evaluating the benthic habitat characteristics that are most associated with the susceptibility of macroinvertebrates to hydropeaking-induced drift. Taxa with propensities for slow-flow environments and for fine substrates (gravel-sized and smaller particles) are most susceptible to drift during hydropeaking events, whereas taxa with propensities for fast-flow environments and cobble-sized particles are least susceptible. The relative strength of associations between habitat factors and drift varies among hydropeaking events, and drift susceptibility is best explained by the combined effects of substrate and hydrology. These findings illustrate the ecological habits of taxa most susceptible to hydropeaking-induced drift, as well as the habitat types that are most affected.

Introduction

The flow regimes of rivers largely control ecosystem structure and function, and anthropogenic flow modifications cause extensive changes to the physical habitat, biochemical cycling and biological assemblage structure of these dynamic systems (Poff *et al.*, 1997, Richter, 2010). River flow and the physical structuring of habitat patches are strongly interactive in their effects on assemblages. Therefore, information on the affinities of biota for different habitat conditions (commonly referred to as ecological traits) are important for assessing the manner in which flow modifications affect riverine ecosystems, as well as how such effects might vary among habitat types (Hart and Finelli, 1999, Freeman *et al.*, 2001).

This study was conducted to determine the degree to which the affinities of benthic macroinvertebrates for different habitat characteristics affect their propensities to be entrained in the drift during high-magnitude (2-10 fold increases above baseflow), short-duration (several hours) flow pulses generated for electricity generation, which are commonly referred to as hydropeaking pulses. Hydropeaking is the world's leading source of renewable electricity generation (EIA, 2015). The effects of this type of flow modification on biotic assemblages comprise an important component of the overall anthropogenic impacts exerted on many lotic ecosystems (Meile *et al.*, 2011, Casas-Mulet *et al.*, 2015).

Many traits-based investigations focus on the physical habitat requirements of biota (Townsend *et al.*, 1997a, Townsend *et al.*, 1997b and below). The River Habitat Templet concept (Townsend and Hildrew, 1994) postulates that the physical structure of the habitat space, and the temporal and spatial variability in this space, determines the types of ecological traits expressed by inhabitants of riverine ecosystems. The seminal work of Resh *et al.* (1994) and the many supporting studies cited therein provided support for this theoretical construct, showing that, across a diverse array of taxonomic groups and at several scales of taxonomic resolution, the composition of assemblages inhabiting a river floodplain corresponded to their occurrences within distinct habitat patches. Therefore, because of the strong link between the habitat template and habitat-related traits, quantitative evaluations of the prevalence of such traits within assemblages should provide great utility for assessing the impacts of anthropogenic disturbances within aquatic ecosystems (Townsend et al. 1997b, Poff *et al.*, 2010)

Although traits-based approaches present a promising option for evaluating responses of biota to anthropogenic stressors, interdependences among traits are common and present a major challenge, as they confound the clear determination of which traits are causally linked to stressors (Resh *et al.*, 1994, Townsend and Hildrew, 1994, Poff *et al.*, 2006). As a result, taxa within assemblages may express multiple life history strategies consisting of different combinations of traits in response to the same environmental stressors (Charvet *et al.*, 1998, Haddad *et al.*, 2008). In addition, coevolution of multiple traits, commonly referred to as trait syndromes, may result in correlations among them due to phylogenetic relationships, when only some are causally linked to environmental stressors (Poff *et al.*, 2006, Carlisle and Hawkins, 2008, Horrigan and Baird, 2008, Culp *et al.*, 2011).

A second challenge of employing traits-based approaches is that many traits are system-specific. For example, voltinism may vary among populations of the same aquatic insect species inhabiting different systems (Corbet *et al.*, 2006). Although several robust, high-quality databases exist which contain extensive traits-based information for aquatic biota (Tachet *et al.* 2002, Vieira *et al.*, 2006, Frimpong and Angermeier, 2009, Schmidt-Kloiber and Hering, 2015), these databases generalize trait information across populations, leading investigators to call for the development of more system-specific trait information (Culp *et al.*, 2011, Orlofske and Baird, 2014).

A challenge for researchers focused specifically on habitat-related traits is that habitat characteristics commonly act as limiting, rather than controlling factors on species distributions, acting in concert with myriad other non-habitat factors (Thomson *et al.*, 1996). A result of this phenomenon is that functional responses between population abundance distributions and habitat factors are often wedge-shaped (Fig. 3.1). This is postulated to occur when a given habitat factor sets a conditional upper limit on abundance at all sites, but other, unmeasured factors are limiting at many sites. In such instances analysis techniques based on the conditional mean of abundance distributions often spuriously indicate weak relationships. Further, those that assume normality and homoscedasticity are inappropriate because wedge shaped distributions violate these assumptions (see further discussion in Cade and Noon, 2003). Alternatively quantile regression may be used to determine correlations between abundances and a given habitat condition at the extremes of the abundance distribution which is clearly beneficial for wedge-shaped habitat-abundance relationships (Cade *et al.*, 1999, Cade and Noon, 2003, Fornaroli *et al.*, 2015).

A second option, which is employed in this work, is to develop a permutation model to evaluate whether population abundances associated with particular habitat patches differ from abundances that would be expected if individuals were randomly distributed among habitat patches (see also Legendre *et al.*, 1997). Like quantile regression, the permutation model employed here is robust to violations of the assumptions of normality and homoscedasticity, and sensitive to non-linear, wedge-shaped responses of abundance distributions to habitat variables. This permutation technique has the added advantage of producing system-specific, quantitative descriptions of the affinities of taxa for habitat characteristics, expressed on a common and comparable numerical scale of 0-1, regardless of whether the assessed habitat characteristic is expressed as a continuous or binary variable (Fig 3.1).

This investigation had two primary objectives. The first was to quantify the affinities of benthic macroinvertebrate taxa to habitat patches based on varying flow velocities, substrate sizes and embeddedness, and vegetative cover. To achieve this objective, a permutational null model was developed to produce quantitative ratings of the affinities of each taxon for the habitat characteristics based on their abundance distributions.

The second objective was to determine whether the habitat affinities of each taxon were associated with the likelihood of its occurring in the drift during hydropeaking. For this objective, the permutation model was extended to assess relationships between the drift densities during hydropeaking and the affinity of each taxon for each habitat characteristic. To address the potential problem of interrelationships among traits, aggregate propensities were also included which encompassed multiple habitat characteristics. In contrast to previous studies, which have considered the conundrum of interrelated traits within the context of life history strategies or trait syndromes, this study considered whether multiple traits can decrease susceptibility to the same environmental stressor.

It was hypothesized that high propensities toward cobble (9-30-cm diameter) substrates, high flow velocities, low embeddedness, and low vegetative cover would be associated with lower peaking-induced drift than expected by chance. These characteristics are, therefore, referred to as stable habitat characteristics. Conversely, it was hypothesized that high propensities toward bedrock and gravel habitats would be associated with higher drift than expected by chance and these characteristics are referred to as unstable habitat characteristics. Gravel was considered unstable because these small-sized particles were often observed to shift during hydropeaking events. Bedrock was considered unstable because it lacked interstitial spaces which might serve as refugia that allow macroinvertebrates to resist entrainment in the drift. Because multiple habitat characteristics are expected to contribute to drift susceptibility, it was hypothesized that aggregate traits would exhibit stronger associations with drift than individual habitat characteristics.

Methods

Study site

The study was conducted on the Roanoke River, North Carolina, below the dam for the Roanoke Rapids Hydroelectric Power facility, which is operated for flood control and hydroelectric power generation. Sampling occurred over an 8 km reach of the river below the dam. The river at this point is 150-200 m wide, with depths over most of the reach ranging from 0.5-1.5 m. The benthic substrate consisted mostly of small cobbles (approximately 9 cm diameter) with deep interstitial spaces and covered to varying degrees by aquatic plants (primarily *Hydrilla* and *Podostemum*; Table 3.1). Rapid, turbulent flow predominated over most the study reach. Median discharge over the study period was 97 m^3/s. During base flow conditions, discharge was 60-230 m^3/s. The dam is operated such that stable flows are maintained below the dam from April 1 through June 14 each year to support anadromous fish spawning. Thereafter, summer hydropeaking begins, during which discharge pulses of 5-10 fold above baseflow levels and lasting several hours occur in order to meet high summer electricity demands (Fig. 3.2).

Macroinvertebrate sampling and processing

Macroinvertebrate drift samples were collected immediately preceding and during hydropeaking events on June 16 and July 7, 2010. Benthic macroinvertebrate sampling was conducted on June 3, June 24 and September 4, 2010. Data from these sampling events were used to evaluate the affinities of macroinvertebrate taxa for particular benthic habitat characteristics and to determine the proportional abundances of each taxon in drift during hydropeaking relative to their abundances on the benthos. Benthic data from June 3 were used to estimate taxon-specific abundances of the assemblage preceding the June 16 hydropeaking event and benthic data from June 24 were used to estimate abundances preceding the July 7 hydropeaking event. No hydropeaking events occurred between each benthic and drift sampling dates (Fig. 3.2).

During each benthic sampling event, transects were established in shallow-water areas (depth less than 1.2 m), selected as they were encountered along the study reach. The length of each shallow-water transect was measured with a laser range-finder, and a random-numbers table was used to select the locations of one sample per 10 m, with a maximum of three samples per transect. Benthic samples were collected using a Hess sampler (500-µm mesh; 0.09-m^2 sampling area).

Drift sampling was conducted from a boat by deploying two plankton nets (30-cm inner diameter; 500-µm mesh) suspended in tandem, from heavy nylon line and weighted at the bottom. Flow meters positioned at the mouth of each net allowed for measurement of the water volumes sampled. Nets were positioned at 0-0.5 m from the river bottom and at 0-0.5 m from the water’s surface and adjusted to account for changing water levels during each event. Neither drift density nor community composition were significantly different between top and bottom nets on either sampling date (paired T-test and Multiresponse Permutation Procedure [MRPP] used to assess density and composition, respectively; $p>0.05$). Therefore, top and bottom net samples were composited to produce one sample for each time period. Deployment times were between 30-45 minutes during base flow. Trial experiments indicated that nets became clogged during hydropeaking after 20-25 minutes; therefore, deployment times during hydropeaking were varied between 3 and 15 minutes depending on flow velocity and suspended solids loads such that no net clogging occurred during sampling.

Macroinvertebrate samples were preserved in 70% isopropyl alcohol with rose-Bengal stain, sorted in their entirety and organisms generally identified to genus, though some taxa were aggregated to higher taxonomic levels to facilitate comparisons among samples (see Appendix 3.1 for list of taxa). All organisms in the samples were identified except that those benthic samples with more than 400 individuals were sub-sampled by spreading the sample evenly over a gridded pan, and randomly selecting 25% of the grid cells for identification. Aquatic pupae were included in the analyses, whereas terrestrial organisms and life stages were excluded.

Benthic habitat variables

Benthic habitat variables used in the analyses were flow velocity, coarse substrate size, substrate embeddedness and vegetative cover. Velocity was measured using a Marsh-McBirney Flow Mate Model 2000 flow meter (Hach, Inc., Loveland, CO) placed directly over each benthic sampling location. In water depths ≥ 0.5 m, velocity was measured at 20% and 80% of the total depth, and velocity reported as the mean of the two measurements. In depths <0.5 m, velocity was measured at 60% of total depth. Coarse substrate size was estimated by first covering the sampling area with the Hess sampler and, before collecting the macroinvertebrate sample, measuring the longest dimension of the coarse substrate particle (>2 mm) that was closest to each of four points equidistant from the center and edges of the cylindrical Hess sampler, as well as at the center point of the sampler (n = 5 measurements per sample). The 50th percentile of the substrate measurements was used to classify substrates as cobble (≥9.3 cm) or gravel (<9.3 cm). Substrate larger than the 30-cm diameter of the Hess sampler was classified as bedrock. Substrate embeddedness was estimated as the mean percentage of surface area of each of the five coarse substrate particles that was covered by fine sediment (<2 mm). The percentage of vegetative cover over each sampling area was visually estimated as 0, 25, 50, 75 or 100 %.

Assemblage composition

The data were analyzed to evaluate whether macroinvertebrate assemblage composition differed between drift and benthic samples, between base flow and hydropeaking drift samples, or among sampling dates. Non-metric Multidimensional Scaling (NMS) Ordination and Multiresponse Permutation Procedures (MRPP) were conducted on a Sorenson Dissimilarity Matrix generated from the relative abundances of each taxon in each drift and benthic sample using PC-ORD, version 5.10 (McCune and Mefford, 2006). The NMS ordination was conducted using the default parameter settings of the slow and thorough mode, with the exception that Varimax rotation was applied to the ordination in order to maximize the loadings of among-sample distances with the ordination axes. MRPP yields a p-value, which represents the probability that differences among sample groups are significantly different than expected by chance, as well as the chance-corrected within-group agreement (*A*-value), which describes the effect strength of the groupings in the same manner that the r-value describes the strength of a correlation. *A*-values of 0.30 or greater indicate relatively strong groupings among samples (McCune *et al.*, 2002).

Habitat affinities

The habitat affinities of each taxon for each habitat characteristic were estimated using a simple permutation model as follows (see Appendix 3.2 for further details):

1) For a given taxon and habitat variable, the abundance-weighted mean value of the habitat variable was calculated for each of the three sampling dates.

2) After calculation of the actual weighted means, the abundance values were randomly permuted and a null value for the weighted mean was calculated. Permutations were restricted by sampling date to control for variations in taxon abundances and in the numerical ranges of

each habitat variable among dates. To maintain a balanced study design, twelve data points (the minimum number of samples obtained among the three dates) were randomly subsampled from the June 24 and Sept. 4 blocks after permutation and these subsets were used to calculate null weighted means.

3) This process was repeated 999 times for each date, producing a total of 3000 null weighted means and 3 actual weighted means for each taxon-environmental variable pair.

4) The habitat affinities were then calculated as the total proportion of instances where null weighted means were less than their respective abundance-weighted means.

Habitat affinities were developed for the conditions cobble, gravel, bedrock, high flow velocity, low embeddedness and low vegetation. Affinities for the conditions low velocity, high embeddedness and high vegetation were not used, as these were simply the complement (i.e. 1 minus the affinity) of the opposite condition and would therefore provide no new information.

To evaluate the hypothesis that multiple traits would be instrumental in determining each population’s overall susceptibility to drift, two trait aggregates were constructed. It was expected that the stable habitat characteristic for which a given taxon exhibited the lowest affinity would serve as the governing factor in its susceptibility to drift. For example, fast-flow adapted taxa, which might otherwise be expected to resist entrainment in the drift were expected to be highly susceptible to drift if they also predominated on unstable substrates, such as fine gravel, or bedrock. Aggregate affinity 1 was calculated as the harmonic mean of the affinities for cobble, high flow velocity, low embeddedness and low vegetation. Harmonic rather than arithmetic means were used to weight the aggregate traits toward the lowest affinity value (following Langhans *et al.*, 2013). Aggregate 1 was constructed before evaluation of the associations of each individual habitat affinity with drift. Following the evaluation, however, it was discovered that embeddedness and vegetation showed little association with drift, therefore, Aggregate affinity 2 was constructed *post-hoc* as the harmonic mean of the affinities for cobble and high flow velocity only.

Relationships between peaking-induced drift and habitat affinities

Because drift densities are driven not only by the magnitude of a given flow pulse, but also by abundance on the benthos (Kennedy *et al.*, 2014), the drift of each taxon was expressed as relative drift, that is, the ratio of relative abundance in the drift to relative abundance on the benthos (Tonkin and Death, 2013, 2014). The relative drift distributions of the observed taxa were plotted as functions of the habitat affinities to assess whether the distributions were consistent with the research hypotheses. Points on these plots represented each taxon observed, with y-axis positions indicating relative drift and x-axis positions representing trait affinities. Separate plots were produced for each date, as well as combined plots including data from both dates (and thus two data points for each taxon). For stable habitat characteristics, the hypothesis of reduced drift for taxa with high affinities would be supported by wedge-shaped distributions that are reversed from that shown in Figure 3.1, with the prevalence of high relative drift values increasing as the affinity for each characteristic decreases. In contrast, for unstable habitat characteristics, the wedge-shaped distributions should resemble Figure 3.1, with the prevalence of high relative drift values increasing as affinities for these habitat characteristics increase.

A second permutation analysis was conducted to evaluate whether relative drift was significantly associated with the habitat affinities. To maintain a balanced study design, only taxa observed in the drift on both drift sampling dates were included here. For each habitat characteristic, the relative drift of each taxon was multiplied by that taxon's habitat affinity and the mean of these values was then taken as the mean habitat-weighted relative drift for that characteristic. These actual weighted relative drift values were then compared to distributions of null mean values, derived from 1000 random permutations of the habitat affinities. To control for variations among the two hydropeaking events, permutations and weighted mean calculations were blocked within dates, producing 2000 null mean values and 2 actual weighted mean values for each habitat characteristic. One-sided tests were constructed to evaluate each research hypothesis (see Appendix 3.2 for additional explanation).

For the stable habitat characteristics (flow velocity, cobble and aggregates one and two), the statistics of interest were the proportions of null weighted means that were equal to, or less than, the actual weighted means for that trait. These proportions represent the probabilities below which the null hypotheses that affinities for these characteristics do not reduce drift may not be rejected. Conversely, for the unstable characteristics (embeddedness, bedrock, gravel and high vegetative cover) the statistics of interest were the proportions of null weighted means that were greater than, or equal to, the actual weighted means. To evaluate the overall relationships between habitat affinities and drift, global p-values were derived using data from both dates. In addition, to determine whether drift-habitat affinity associations differed between dates, separate p-values were also calculated for each of the two dates.

Results

Benthic Habitat Characteristics

Benthic habitat characteristics were highly variable, although the most common characteristics were relatively high velocity, high vegetative cover, low embeddedness and cobble substrate (Table 3.1). None of the habitat parameters was significantly different among the three sampling dates (ANOVA; $p > 0.50$ for all four parameters).

Macroinvertebrate assemblage composition

Macroinvertebrate assemblage composition was significantly different between dates as well as between drift and benthic samples (MRPP, Bonferroni-corrected $p < 0.01$). This temporal variation highlighted the importance of blocking by sampling date when deriving habitat affinities, and of conducting separate permutation analyses for each of the two sampling dates in the evaluation of drift-habitat affinity associations. Assemblage composition in the drift was also significantly different between periods of base flow and hydropeaking (MRPP, $A=0.05$, $p < 0.01$) and drift densities were highly elevated during hydropeaking on both sampling dates (46- and 31-fold increases on the two sampling dates). Moreover, the main focus of this work was on drift during hydropeaking. Therefore, only hydropeaking drift samples were included in the assessment of habitat-drift relationships discussed below.

The greatest difference in assemblage composition was between drift and benthic samples ($A=0.13$, $p < 0.01$) which was most apparent on the NMS plots (Fig. 3.3). Temporal variation among assemblages was overall weaker than variation between drift and benthic samples and was less apparent on the NMS plots ($p < 0.01$, $A=0.09$ and 0.05 for separations between drift dates and between benthic dates, respectively; Fig. 3.3). Pairwise comparisons between all four dates provided a similar result: within group agreements when comparing the two drift sampling dates (*A*: 0.09) and when comparing the two benthic sampling dates (*A*: 0.05) were weaker than for each comparison of a benthic date with a drift date (*A*: 0.14-0.18).

The NMS ordination produced a 3-dimensional solution with a final stress of 11.9, indicating an acceptably low amount of distortion of the original distance matrix (Clarke, 1993). The solution explained 90% of the variation in the original distance matrix ($r^2 = 0.33$, 0.31 and 0.26 for axes 1, 2 and 3, respectively, Fig. 3.3). Drift assemblages were separated from benthic assemblages mainly along axis 1 of the ordination plots. This separation was mainly driven by the relative abundances of Hydrobiidae (Gastropoda) and *Tricorythodes sp.* (Ephemeroptera), which were lower in the drift than on the benthos, and by the relative abundances of Simuliidae (Diptera) and Hydracarina, which were higher in the drift than on the benthos (Fig. 3). Temporal variation was apparent along axes 2 and 3 of the ordination. Axis 2 was correlated with the relative abundances of *Leptoxis sp.* (Gastropoda), Cambaridae (Decapoda), Hydracarina and *Hydroptila sp.* (Trichoptera), which varied primarily between the drift sampling dates. Axis 3 was correlated with the relative abundance of *Hydropsyche* and *Cheumatopsyche* sp. (Trichoptera), *Corbicula fluminea* (Veneroida) and Lumbriculidae (Oligochaeta) which varied primarily among the benthic sampling dates (Fig. 3.3).

Macroinvertebrate habitat affinities

Affinities for high-velocity and low-vegetation environments were not significantly correlated with each other, nor were they correlated with the affinities for cobble, gravel or bedrock ($p>0.05$). The affinities for low substrate embeddedness were significantly and positively correlated with the affinities for cobble and high velocity environments and negatively correlated with those for gravel, although all correlations were weak ($r= 0.42$, 0.41 and -0.37, respectively, $p<0.05$; Table 2). Therefore, the affinities for coarse substrate, embeddedness, velocity and vegetative cover each provided unique trait information for the benthic assemblage. The derived affinity values for cobble, gravel and bedrock were mathematically dependent and as a result significant negative correlations occurred between the affinities for cobble and those for bedrock, as well as between those for cobble and gravel ($r=-0.29$ and -0.79, respectively, $p<0.05$; Table 2). Therefore, it cannot be definitively determined whether high affinities for cobble represent preferences for the cobble or against gravel or bedrock. However, this ambiguity is inconsequential for evaluating the associations of the substrate categories and peaking-induced drift.

Taxa with the highest affinities for low-embeddedness environments included Simuliidae (Diptera), *Ferrissia* sp. (Gastropoda) and the trichopterans *Cheumatopsyche* sp., *Chimarra* sp. and *Orthotrichia* sp. (affinities= 0.89-0.97; Table 3.3; see Appendix 3.1 for complete list of affinities for all taxa). Few taxa exhibited high affinities for bedrock (median: 0.11) with only Simuliidae and *Campeloma* sp. (Gastropoda) exhibiting considerably higher affinities for the substrate than expected by chance (0.71 and 0.84, respectively). Taxa with high affinities for cobble habitats included erosional zone specialists such as *Brachycentrus* sp. (Trichoptera) and *Isonychia* sp. (Ephemeroptara, affinities 0.88 and 0.91, respectively), and the amphipods *Hyalella* sp. and *Crangonyx* sp. (affinities= 0.98 and 0.96, respectively), which occur primarily within substrate interstices. The observed correlations between the low embeddedness affinities and those for the substrate categories were again apparent here. Taxa with high affinities for cobble often exhibited high affinities for low embeddedness, whereas those with high affinities for gravel exhibited low affinities for low embeddedness habitats.

Taxa associated with high-velocity environments included many substrate clingers, including the trichopterans *Brachycentrus* sp., *Cheumatopsyche* sp., *Chimarra*, sp. and

Hydropsyche sp. and the dipteran Similiidae (high-velocity affinities 0.93-0.98) as well as the odonates *Boyeria* sp. and *Basiaeschna* sp., which are not substrate clingers (affinities= 0.93 for each). Taxa with affinities for low vegetative cover included the trichopterans *Hydroptila* sp. and *Hydropsyche* sp. (affinities= 0.91 and 0.81, respectively), the dipterans *Hemerodromia* sp. and *Atrichopogon* sp. (affinities= 0.95 and 0.75, respectively), and the gastropod *Ferrissia* sp. (affinity= 0.76).

Relationships between peaking-induced drift and habitat affinities

When both dates were analyzed together, associations between drift and the affinities of taxa for cobble and high-velocity habitats showed the expected wedge-shaped patterns (Fig. 3.4). Incidences of high relative drift, as well as variation in relative drift among taxa, generally increased as affinities toward cobble and high-velocity environments decreased. Mean relative drift, weighted by affinities for cobble, was significantly lower than expected by chance, providing evidence that susceptibility to drift was reduced for taxa with high affinities toward cobble and increased for those with low affinities toward cobble ($p=0.05$, blocked permutation analysis including both hydropeaking events). The association between relative drift and affinity for high-velocity habitats showed a similar trend, although this result was not significant at $p\leq0.05$ ($p=0.08$; Fig. 3.4).

The combined influence of substrate and hydrology was apparent from the associations of the habitat affinities with drift. Unexpectedly, some taxa with high affinities for cobble substrate (e.g. Pleuroceridae on June 16 and *Hemerodromia* sp. and *Caenis* sp. on July 7) showed high relative drift. However, these taxa also exhibited low affinities for high-flow environments and their relative drifts, plotted as functions of their velocity affinities, conformed to the expected wedge-shaped pattern (Figs 3.4-3.6). The conditional relationship between relative drift and

Aggregate 2 (harmonic mean of cobble and high velocity values) strongly conformed to the expected pattern. Mean relative drift weighted by Aggregate 2 was lower than expected by chance in the global analysis (Fig 3.4) and the weighted means for aggregate 2 were lower than for any other habitat characteristic on both dates (Fig. 3.5 and 3.6).

The observed associations between drift and habitat affinities were influenced by several high-density drifters (i.e. taxa exhibiting relative drift above the 90th percentile of the overall distribution). When the global analysis was repeated with high-density drifters excluded, none of the single habitat characteristics, nor Aggregate 1 (harmonic mean of affinities for low vegetation, low embeddedness, cobble and high velocity), were significantly associated with relative drift ($p \leq 0.05$). However, the relationship between Aggregate 2 (harmonic mean of cobble and high velocity values) and relative drift again exhibited the expected wedge-shaped pattern, and relative drift weighted by Aggregate 2 was again significantly lower than expected by chance ($p=0.03$, Fig. 3.4, bottom right panel).

For each of the two hydropeaking events analyzed individually, mean relative drift weighted by affinities for high velocity and cobble habitats was lower and mean relative drift weighted by bedrock was higher than their respective null means, supporting the hypotheses regarding these habitat characteristics. Associations between relative drift and individual habitat variables were often weak and in some cases not statistically significant. However, on both dates when high-density drifters were included as well as when they were excluded, Aggregate 2 showed the strongest and most consistently significant associations with relative drift (Figs 3.4-3.8).

On June 16, mean relative drift weighted by cobble affinities was significantly lower, and mean relative drift weighted by gravel affinities was significantly higher, than expected by chance (p= <0.01 and p= 0.04 for cobble and gravel, respectively, Fig. 3.5 and 3.7). Affinities for gravel and cobble were negatively correlated (r: -0.79; note that conditional plots for drift densities as functions of gravel and of cobble are near mirror images; Fig. 3.5, left panels). Therefore, the analysis did not provide conclusive evidence regarding whether cobble is a favorable habitat or gravel is an unfavorable habitat. However, the analysis does provide evidence that the substrate type inhabited by benthic taxa influences their susceptibility to peaking-induced drift. Relative drift on June 16 showed a weak association with affinity for high-velocity environments (p=0.10). Similar results were observed for the July 7 hydropeaking event. Affinities for cobble substrate and high water velocities showed weak associations with relative drift, whereas the strongest association was with the aggregate of these two characteristics (Aggregate 2), which contributed to significantly lower weighted mean relative drift than expected by chance when all taxa were included and when high-density drifters were excluded (p<0.05, Fig. 3.6 and 3.8).

Collectively the results of the permutation analysis support the hypotheses that taxa that exhibit high affinities toward cobble substratum and to high water velocities should exhibit reduced rates of drift during hydropeaking. The hypothesis that the aggregate of these traits would show stronger associations with drift than would single habitat characteristics was also supported. In contrast, relationships of drift with the affinities for low vegetative cover and low embeddedness were inconsistent and did not support the hypotheses that affinities for these habitat types would be associated with reduced drift.

Discussion

The analyses conducted for this work have provided quantitative, site-specific descriptions of the affinities of the observed macroinvertebrate taxa for a suite of benthic habitat characteristics. As demonstrated by others, site-specific trait information may provide improved utility for evaluating environmental conditions because literature-derived trait information is typically generalized over large geographic regions, although the traits exhibited by benthic species often vary over much smaller spatial scales (Orlofske and Baird, 2014). The approach employed here provides an added advantage in that the derived habitat affinities represent the probabilities that habit-taxon relationships are greater than expected by chance, thus providing a direct, quantitative basis for judging the strength of these taxon-habitat relationships.

The derived habitat affinities were generally consistent with expectations, based on the morphological adaptations and behavioral characteristics of the observed taxa. Those with high affinities for low-embeddedness environments, fast flow, and cobble substrates were erosional zone specialists, with mechanisms for active attachment to the substratum (e.g., trichopterans *Cheumatopsyche* sp. and *Brachycentrus* sp.). In contrast, taxa with high affinities for gravel (e.g., Lumbriculidae and Tubificidae [Oligochaeta], and *Palpomyia* sp. [Diptera]) and those with low affinities for low-embeddedness and fast-flow environments (e.g., the above taxa and the trichopteran *Nectopsyche* sp. and the dipteran *Hemerodromia* sp.) were those which are generally associated with depositional habitats and which burrow in, or sprawl atop loose substrate in low-flow areas. The overall low affinities of most taxa for bedrock habitat were also expected. Bare bedrock typically occurs in the most erosive areas in the system. The flat surfaces of these substrates lack interstitial spaces, which likely provide refuge from entrainment in the drift during flow pulses and retain the coarse particulate organic matter that is required as food for many taxa. The only taxa with high affinities for bedrock were Simuliidae (Diptera) and *Campeloma* sp. (Gastropoda), both of which are tenacious substrate clingers and do not require particulate organic matter for food (the former is an obligate filter-feeder on fine particulate material and the latter is an algae scraper).

Three notable exceptions where habitat affinities did not match theoretical expectations were observed. *Hydroptila* sp., which commonly feeds by piercing aquatic plant cells, exhibited a high affinity for habitat patches characterized by low vegetative cover. This apparent shortcoming of the model was likely due to viability at the microhabitat scale. Several samples for which vegetative cover was relatively low (25%) exhibited high abundances of *Hydroptila* sp., which were likely concentrated on the portions of these habitat patches that were covered by vegetation. Therefore, an alternative sampling strategy, focused on a finer spatial scale (i.e. < 0.09 m^2 per sample) is likely necessary to more precisely describe the affinity of *Hydroptila sp.* for vegetation. *Basiaeschna* sp. and *Boyeria* sp. exhibited high affinities for high-flow-velocity habitats, despite the general association of these odonates with low-flow, depositional environments. Both taxa were rare in the system (each observed only on 24 June, 2010). Rare taxa have sometimes been implicated as confounding factors, leading authors to call for their exclusion from predictive models designed to relate benthic assemblages to environmental characteristics (Hawkins *et al.*, 2000, Pond and North, 2013, Van Sickle *et al.*, 2007).

Of the habitat factors observed here, coarse substratum and flow velocity were the primary factors affecting the susceptibilities of benthic macroinvertebrates to peaking-induced drift. As hypothesized, taxa with high affinities for fast flow and for cobble substrate showed reduced susceptibilities to drift. Those most susceptible to peaking-induced drift were taxa typically associated with depositional areas and which exhibited low affinities for high-flow environments and cobble substrates (e.g., odonates and soft-bodied worms). The signs of the relationships between the habitat affinities and relative drift (i.e. greater than expected due to chance for bedrock and gravel and less than expected for cobble and fast flow) consistently supported the hypotheses on both dates. However, the associations between independent habitat factors and drift were often weak and the relative strengths of relationships varied between dates. For both hydropeaking events, the strongest association between habitat affinities and drift was for Aggregate 2 (the harmonic means of the fast flow and cobble substrate affinities). The consistent, negative associations of relative drift with Aggregate 2 supports the hypothesis that multiple trait affinities are important in determining susceptibility to peaking-induced drift and highlights the importance of interrelationships among traits for understanding how environmental stressors affect assemblages.

The hypotheses that affinities toward high vegetative cover and high substrate embeddedness would be associated with high peaking-induced drift were not supported. Biota in highly vegetated habitats were expected to exhibit increased drift susceptibility because increased drift of aquatic vegetation has been consistently observed during several hydropeaking events in the system and because aquatic vegetation has been shown to support high abundances of macroinvertebrates in similar river systems (Grubaugh *et al.*, 1997). However, it is plausible that the complex structure of the vegetation provided refuge for some organisms, partially counteracting the increased susceptibility to drift due to entrainment of vegetation during high flow. The affinities of taxa toward habitats with low substrate embeddedness were positively correlated with affinities toward fast flow and cobble substrate and negatively correlated with affinities toward gravel habitats. Coarse substrate type and flow velocity consistently showed stronger relationships with drift than embeddedness. Therefore, any perceived effects of substrate embeddedness on peaking induced drift may ultimately be the result of causative relationships of embeddedness with flow and coarse substrate composition, rather than the result of direct relationships between drift and embeddedness.

The approach of employing quantitatively-derived habitat affinities provides evidence as to which organisms as well as which habitats are most susceptible to anthropogenic stressors (see also Olsen *et al.*, 2014). For riverine benthic macroinvertebrates, habitat patches consisting of cobble substrates and exposed to fast flow appear to confer the least risk of entrainment in drift during hydropeaking, and those consisting of gravel substrate and low velocities appear to confer the most risk. The data and results produced here may be used to supplement future studies of habitat affinities across multiple hydropeaking-affected systems. Such work might allow for sufficient statistical replication to determine whether specific behavioral and morphological adaptations of individuals and populations (and combinations of these adaptations) are consistently related to peaking-induced drift across taxonomic groups and across systems. The Fourth-corner Method (Legendre *et al.*, 1997) is a permutation-based approach, similar to the model employed here, which could be used for this purpose. This future work would provide evidence on which adaptations and which assemblages are diagnostic indicators of hydropeaking impacts in river systems.

The observed synergistic effects of flow- and substratum-related traits on peaking-induced drift are a contribution to the theoretical understanding of functional traits and provide important evidence on the manner in which the Habitat Templet (*sensu* Southwood, 1977, Southwood, 1988) serves to structure benthic assemblages. These results provide an alternative viewpoint to others intended to explain the conundrum of interrelationships between traits, such as trait syndromes (i.e. phylogeny-driven interrelationships among traits; Poff *et al.*, 2006, Carlisle and Hawkins, 2008, Horrigan and Baird, 2008, Culp *et al.*, 2011) and multiple life history strategies (Nylin and Gotthard, 1998, Kneitel and Chase, 2004). Here a complementary perspective to the concept of multiple life history strategies is presented. This concept includes the general postulate that multiple combinations of traits should confer *increased* resistance and resilience to the same suite of stressors. This study shows that multiple traits may also confer *decreased* resistance to stressors, as taxa with affinities for either unstable substrates or slow flow velocities exhibited increased affinities toward hydropeaking-induced drift.

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Table 3.1: Water velocity, vegetative cover, embeddedness and coarse substrate size on benthic habitat patches sampled on June 3, June 24 and Sept. 3, 2010. Values are means (± 1 std. error).

	Velocity (m s^{-1})	Vegetative Cover (%)	Embeddedness (%)	Substrate size (cm)
June 3 (n=12)	0.46 (0.08)	0.58 (0.13)	9.79 (3.36)	15.17 (1.85)
June 24 (n=16)	0.35 (0.1)	0.52 (0.1)	15 (4.66)	7.04 (1.26)
Sept. 3 (n=15)	0.34 (0.1)	0.67 (0.09)	16.5 (6.62)	8.81 (1.85)
Grand Mean	0.35 (0.05)	0.59 (0.06)	14.23 (3.07)	9.82 (1.08)

Table 3.2: Correlations (r-values) between habitat propensities of each taxon. Embed: substrate embeddedness, veg: vegetation, Ag. 1, Ag 2: aggregate propensities 1 and 2. Ns: not significant (p>0.05).

	Bedrock	Cobble	Gravel	High velocity	Low veg.	Ag. 1	Ag. 2
Low embed.	ns	0.42	-0.37	0.41	ns	0.57	0.47
Bedrock		-0.29	ns	ns	ns	ns	ns
Cobble			-0.79	ns	ns	0.43	0.78
Gravel				ns	ns	ns	-0.49
High velocity					ns	0.41	0.51
Low veg.						0.46	ns
Ag. 1							0.64

Table 3.3: Relative abundances, relative drift, and habitat propensities of taxa with values exceeding the 90th percentile for at least 1 habitat propensity. Light grey cells: propensities above the 90th percentile for all taxa, dark grey cells: propensities above the 95th percentile for all taxa. Rel. abund: relative abundance, embed: substrate embeddedness, veg: vegetation, Ag.1, Ag. 2: aggregate propensities 1 and 2.

Taxon	Date observed	Rel. abund. benthos	Rel. abund. drift	Relative drift	Low embed.	Bedrock	Cobble	Gravel	High velocity	Low veg.	Ag. 1	Ag. 2
Baetidae	Both	0.71 ; 2.16	0.99 ; 4.10	1.40 ; 1.90	0.35	0.58	0.11	0.87	0.60	0.00	0.00	0.19
Brachycentrus	Both	1.03 ; 0.43	0.30 ; 0.40	0.29 ; 0.95	0.45	0.18	0.88	0.21	0.97	0.23	0.46	0.92
Ceraclea	Both	1.33 ; 0.67	0.66 ; 3.00	0.49 ; 4.51	0.78	0.01	0.80	0.55	0.89	0.24	0.51	0.85
Cheumatopsyche	Both	10.78 ; 4.96	0.89 ; 1.22	0.08 ; 0.25	0.89	0.36	0.37	0.71	0.96	0.69	0.63	0.54
Chimarra	Both	0.06 ; 0.02	0.15 ; 0.76	2.67 ; 30.87	0.96	0.26	0.36	0.68	0.93	0.37	0.52	0.52
Crangonyx	Both	0.23 ; 0.30	0.10 ; 0.05	0.43 ; 0.17	0.86	0.00	0.96	0.09	0.64	0.05	0.15	0.77
Elmidae	Both	0.17 ; 0.07	0.14 ; 0.11	0.83 ; 1.55	0.17	0.17	0.77	0.45	0.86	0.06	0.16	0.81
Enallagma	Both	0.01 ; 0.02	0.20 ; 1.56	28.01 ; 94.72	0.46	0.64	0.00	0.84	0.12	0.09	0.00	0.00
Hemerodromia	Both	0.06 ; 0.02	0.21 ; 1.80	3.67 ; 109.39	0.51	0.20	0.65	0.22	0.01	0.95	0.05	0.02
Hyalella	Both	0.62 ; 0.22	0.13 ; 0.42	0.22 ; 1.91	0.55	0.45	0.98	0.00	0.28	0.10	0.24	0.44
Hydropsyche	Both	4.65 ; 1.31	4.19 ; 1.70	0.90 ; 1.30	0.76	0.19	0.44	0.69	0.95	0.81	0.68	0.60
Hydroptila	Both	1.78 ; 1.28	5.76 ; 3.37	3.23 ; 2.63	0.70	0.04	0.16	0.99	0.49	0.91	0.37	0.24
Isonychia	Both	0.34 ; 0.06	0.00 ; 0.00	0.00 ; 0.00	0.59	0.20	0.91	0.24	0.81	0.11	0.31	0.86
Lumbriculidae	Both	0.41 ; 0.24	0.15 ; 0.00	0.36 ; 0.00	0.02	0.00	0.35	0.99	0.27	0.20	0.05	0.30
Orthotrichia	Both	0.03 ; 0.11	0.16 ; 0.46	5.57 ; 4.32	0.95	0.00	0.62	0.40	0.77	0.28	0.53	0.69
Placobdella	Both	0.01 ; 0.07	0.06 ; 0.03	8.23 ; 0.35	0.07	0.22	0.06	0.98	0.67	0.01	0.02	0.11
Simuliidae	Both	0.94 ; 0.34	2.68 ; 4.01	2.84 ; 11.90	0.93	0.84	0.03	0.90	0.98	0.52	0.12	0.06
Basiaeschna	7-Jul	1.00E-04	0.00	0.00	0.53	0.00	0.51	0.00	0.93	0.46	0.56	0.66
Boyeria	7-Jul	1.00E-04	0.00	0.00	0.54	0.00	0.55	0.00	0.93	0.47	0.58	0.69
Campeloma	7-Jul	1.00E-04	0.00	0.00	0.53	0.71	0.00	0.24	0.78	0.37	0.00	0.00
Ferrissia	7-Jul	7.00E-04	0.00	2.07	0.90	0.00	0.93	0.18	0.41	0.76	0.67	0.57
Nectopsyche	7-Jul	1.00E-03	0.01	5.70	0.05	0.57	0.02	0.96	0.06	0.06	0.04	0.03
Palpomyia	7-Jul	2.00E-04	0.00	8.83	0.07	0.00	0.03	0.97	0.08	0.07	0.05	0.04
Tubificidae	7-Jul	1.10E-03	0.00	0.00	0.05	0.43	0.04	0.98	0.50	0.20	0.08	0.08
Atrichopogon	16-Jun	8.00E-04	0.00	1.77	0.24	0.00	0.55	0.00	0.00	0.75	0.00	0.00

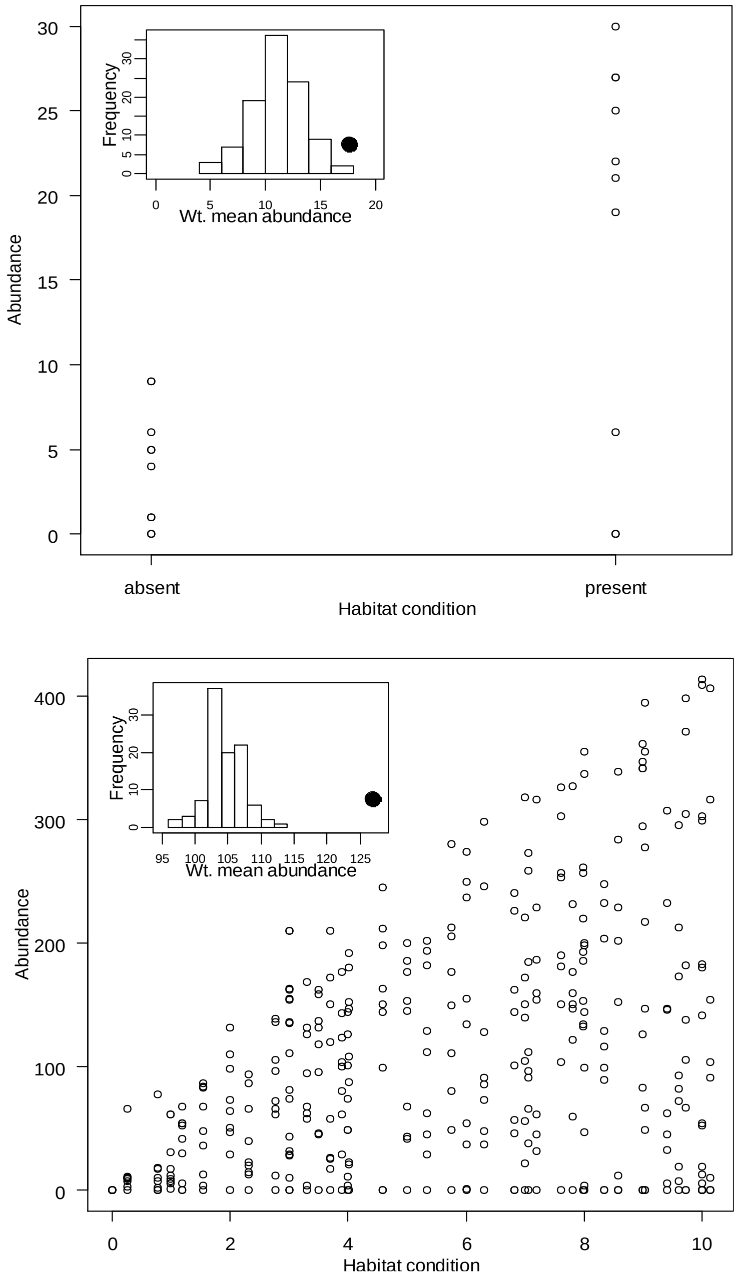

Figure 3.1: Typical (hypothetical) abundance distributions plotted as functions of a categorical (top panel) and a continuous (bottom panel) habitat factor. The main plot in the bottom panel is adapted from Cade et al. (1999). Inset plots show mean abundances, weighted by the habitat factors (solid circles: ●), and null weighted mean distributions derived from 1000 random permutations of the abundance distributions (histogram bars). Based on these distributions, the permutation model described in the text would indicate significant, positive associations of both habitat factors and abundance distributions of the hypothetical taxon ($p<0.01$).

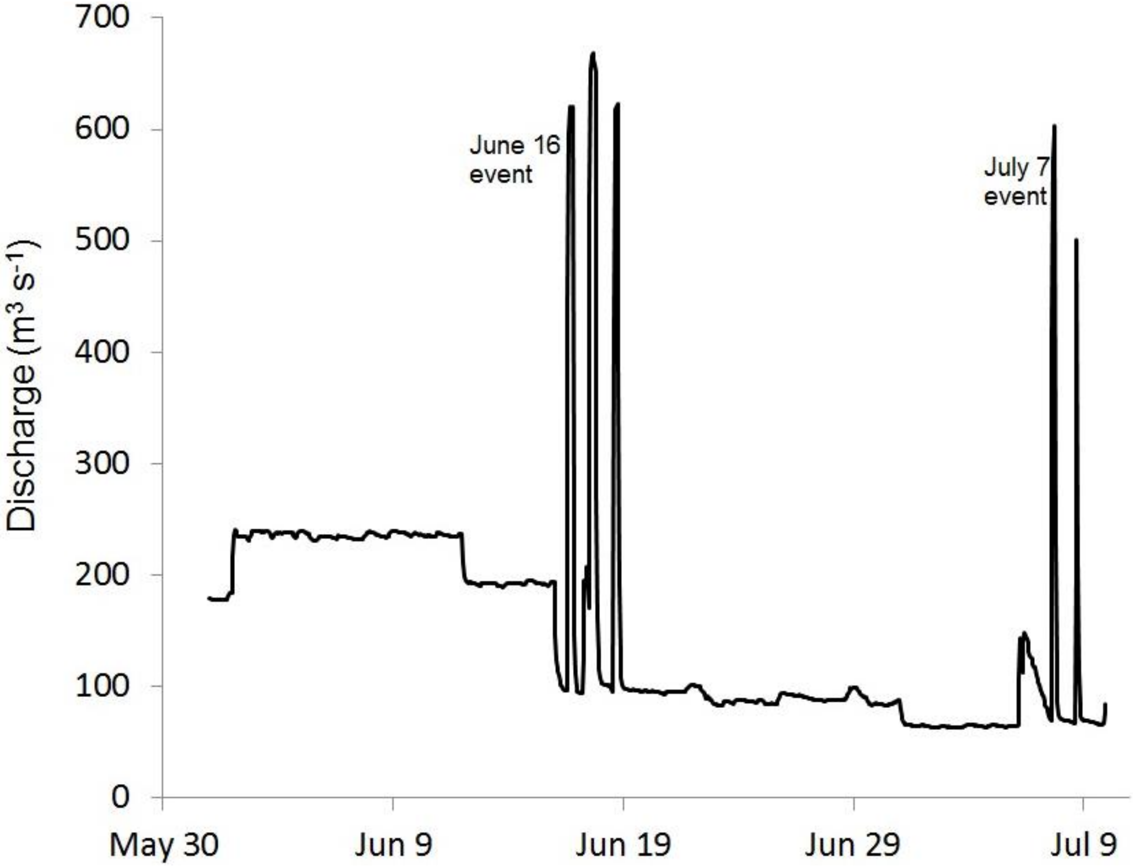

Figure 3.2: Discharge hydrograph from Roanoke Rapids, NC showing hydropeaking events on June 16 and July 7, 2010 during which drift dampling was conducted.

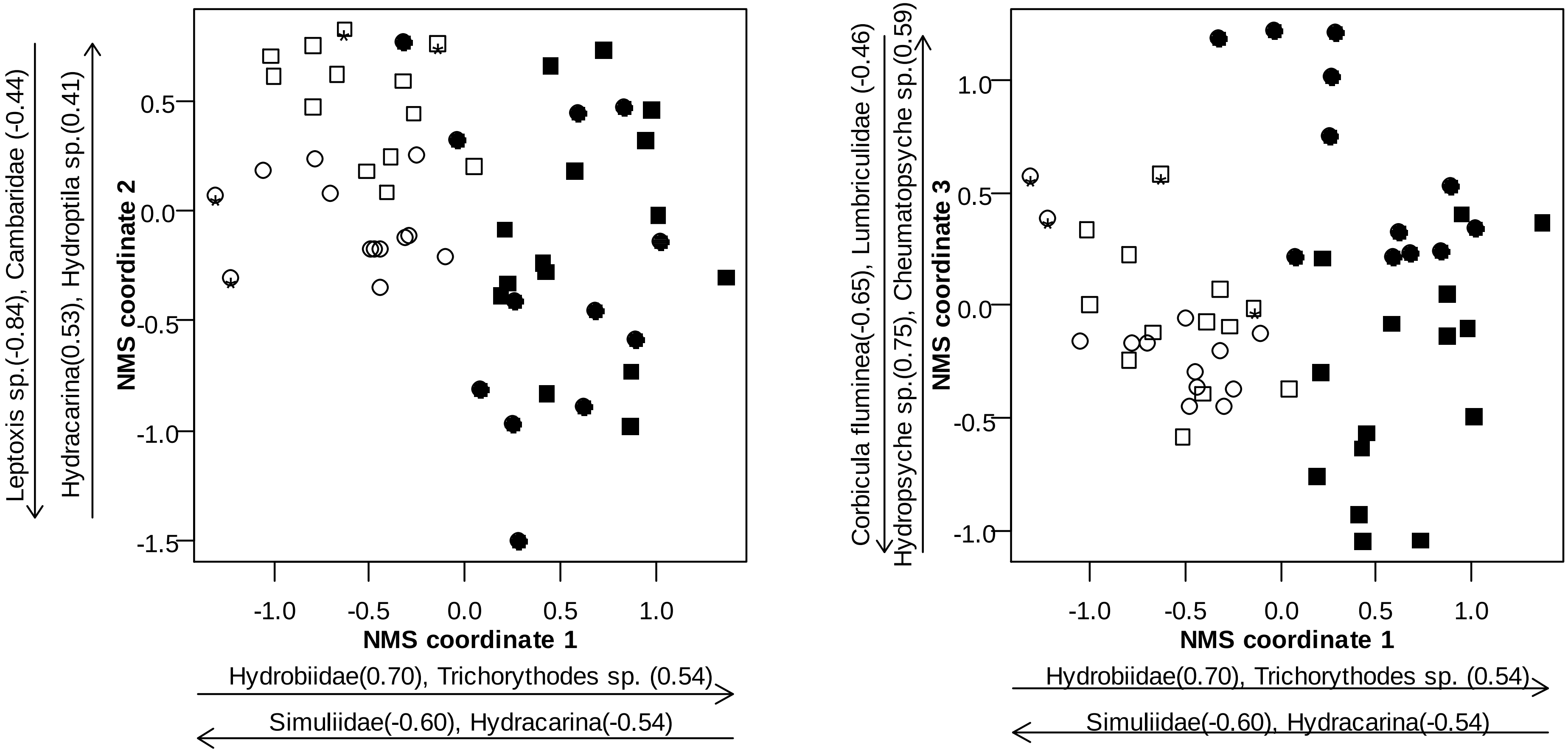

Figure 3.3: Non-metric multidimensional scaling ordination of benthic and drift samples in relative Sorenson distance space. Variance in original distance matrix explained by each axis: 33% (axis 1), 31% (axis 2) and 26% (axis 3). Final stress= 11.9. Taxa listed are those with strongest correlations with each axis (correlations listed in parentheses). Open symbools indicate drift samples and closed symbols indicate benthic samples. Open circle (○): June 16 drift samples, open square (□): July 7 drift samples, closed circle (●) : June 2 benthic samples and closed square (■): June 24 benthic samples. Asterisks (*) indicate drift samples obtained before the onset of hydropeaking.

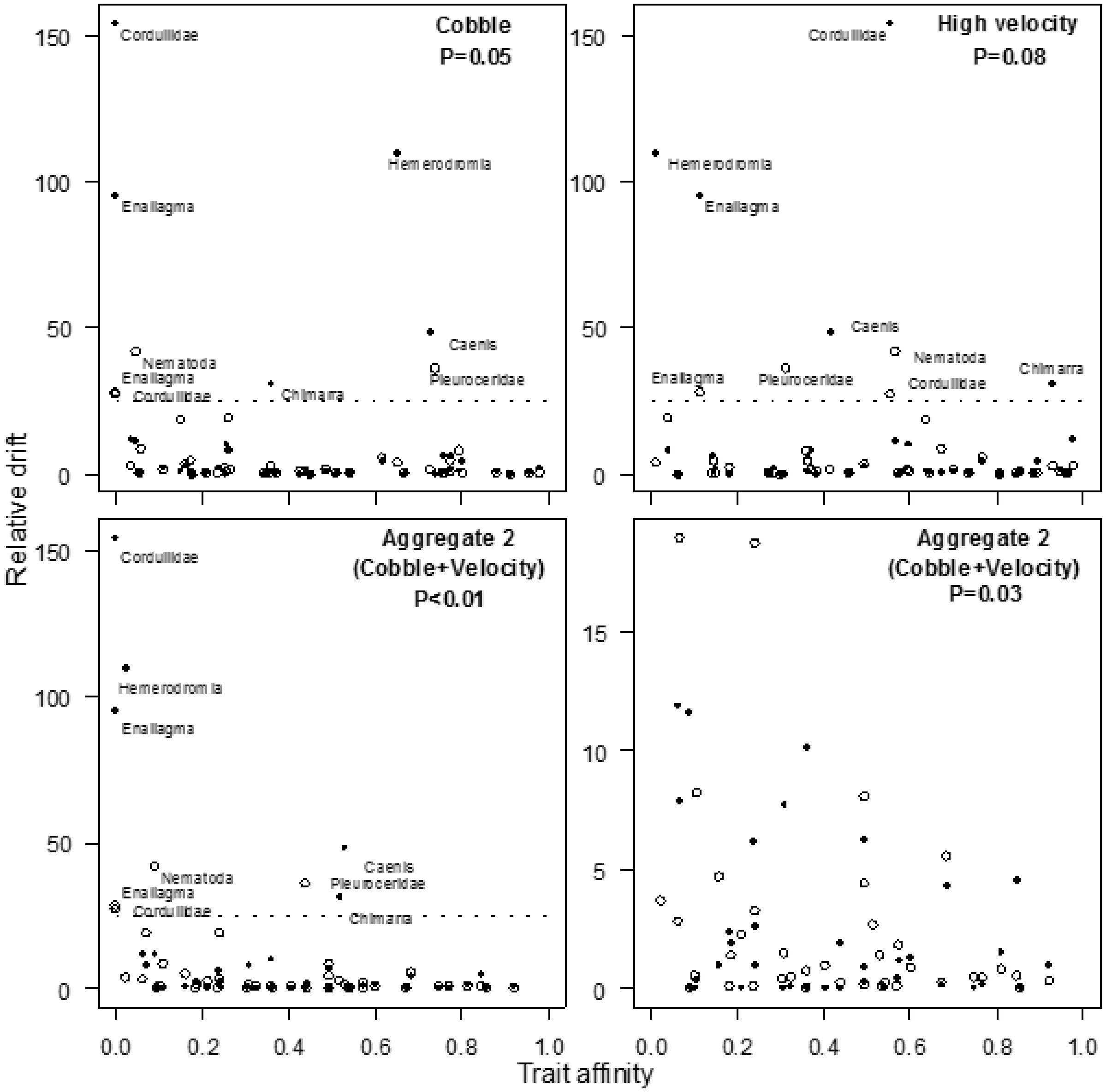

Figure 3.4. Relative drift of each taxon during hydropeaking events on June 16 (open circles: ○) and July 7, 2010 (open circles: ●), plotted against propensities of each taxon for cobble substrate, high flow velocity, and trait aggregate 2 (harmonic mean of propensities for cobble and high velocity). P-values indicate the probabilities that relative drift indices, weighted by each habitat propensity are lower than expected by chance (global analysis using data from both events, with permutations blocked by date). Broken line represents the 90th percentile of relative drift. Bottom right panel: plot showing only taxa with relative drift < 90th percentile. Additional taxa names are shown on Figs 7 and 8.

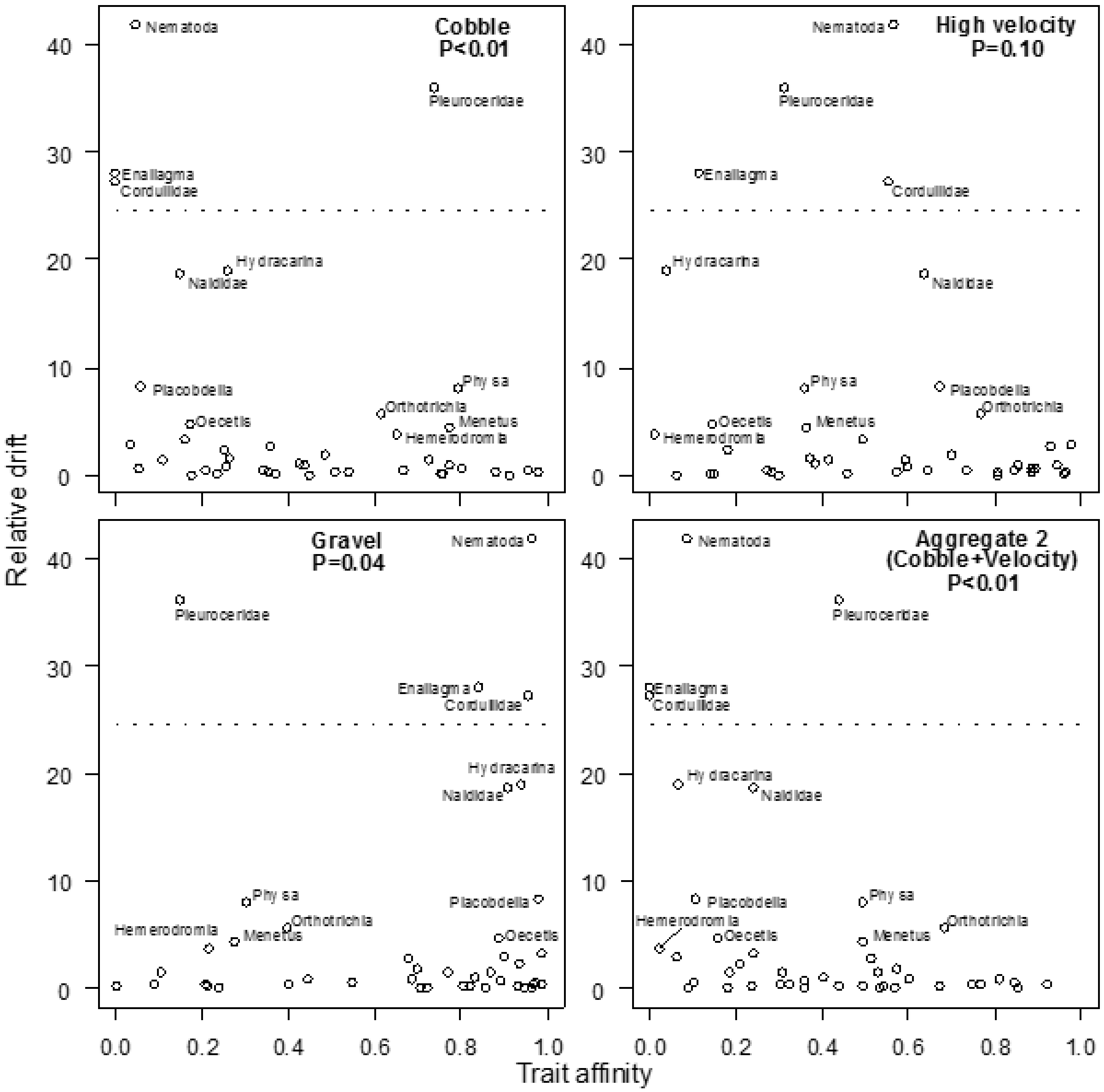

Figure 3.5. Relative drift of each taxon during hydropeaking events on June 16 2010, plotted against propensities of each taxon for cobble, high flow velocity, gravel and trait aggregate 2 (harmonic mean of propensities for cobble and high velocity). P-values indicate the probabilities that relative drift indices, weighted by each habitat propensity are lower than expected by chance. Broken line represents the 90th percentile of relative drift.

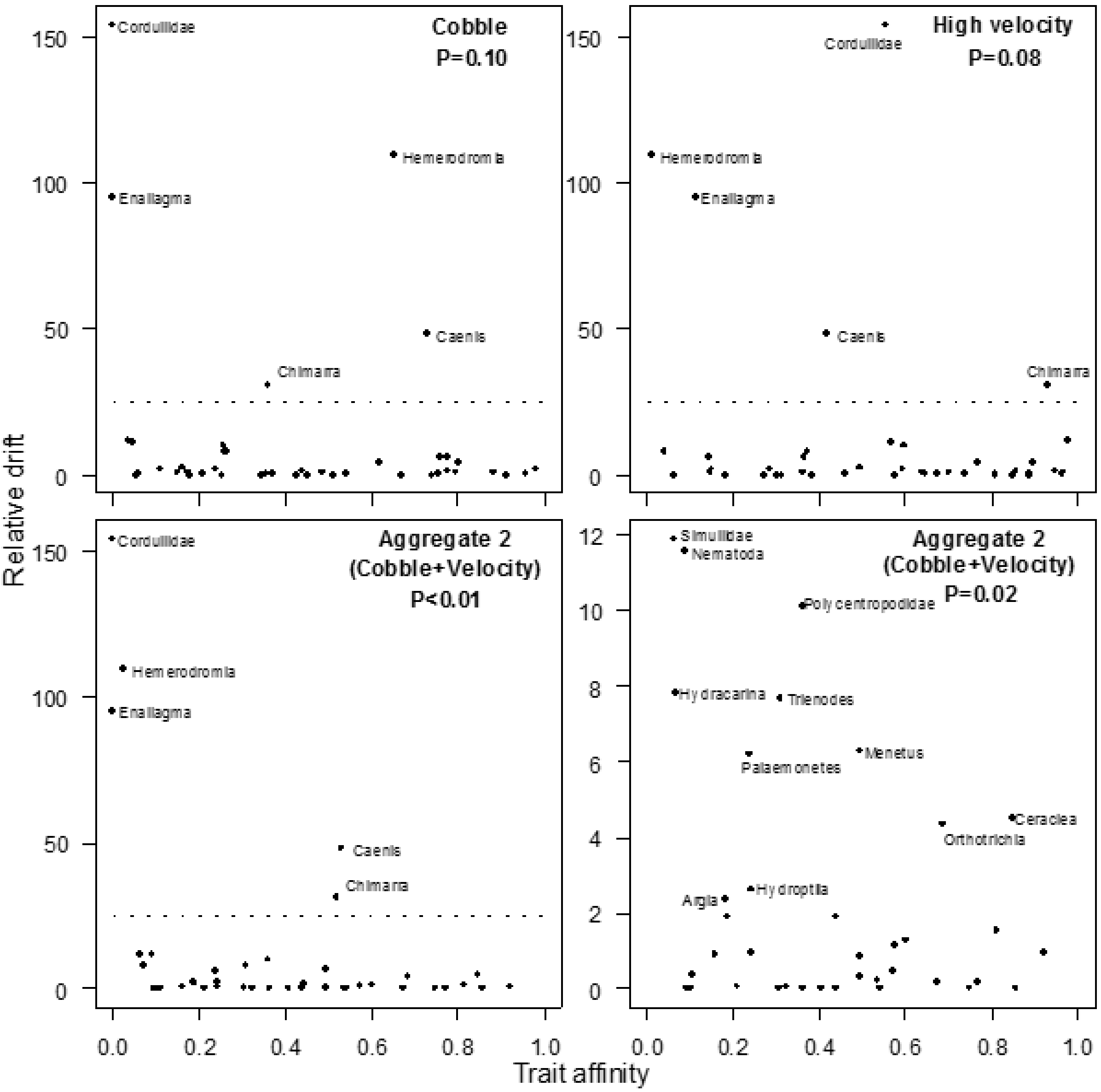

Figure 3.6. Relative drift of each taxon during hydropeaking events on July 7, 2010, plotted against propensities of each taxon for cobble, high flow velocity, and trait aggregate 2 (harmonic mean of propensities for cobble and high velocity). P-values indicate the probabilities that relative drift indices, weighted by each habitat propensity are lower than expected by chance. Broken line represents the 90th percentile of relative drift. Bottom right panel: plot showing only taxa with relative drift < 90th percentile.

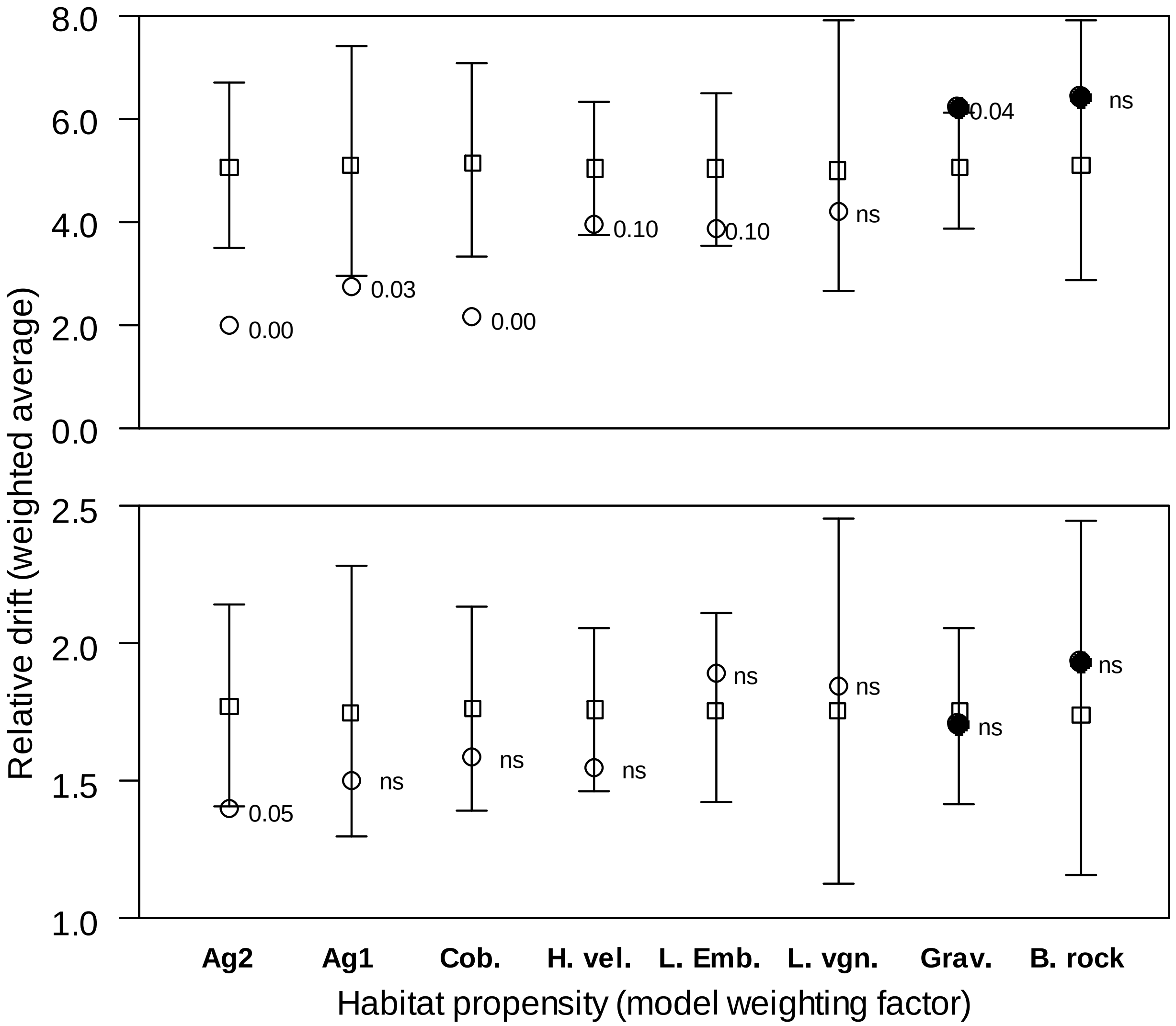

Figure 3.7: Mean relative drift densities during hydropeaking on June 16, 2010, weighted by habitat affinities. Ag 2: aggregate of affinities for cobble and high velocity, Ag 1: aggregate of affinities for cobble, high velocity, low embeddedness and low vegetative cover. Cob: cobble, H. vel: high velocity, L emb: low embeddedness, L. vgn: low vegetation, Grav: gravel, B. rock: bedrock. Open squares(□) null mean relative drift, calculated from 1000 random permutations of the habitat affinities. Error bars: 95% confidence intervals for the null distributions. Closed circles(●)affinities for which weighted average relative drift was hypothesized to be significantly higher than the null mean. Open circles (○)affinities for which weighted average relative drift was hypothesized to be significantly lower than the null mean. Numbers next to mean values are p-values associate with each one-tailed hypothesis test (ns: not significant, p>0.10).

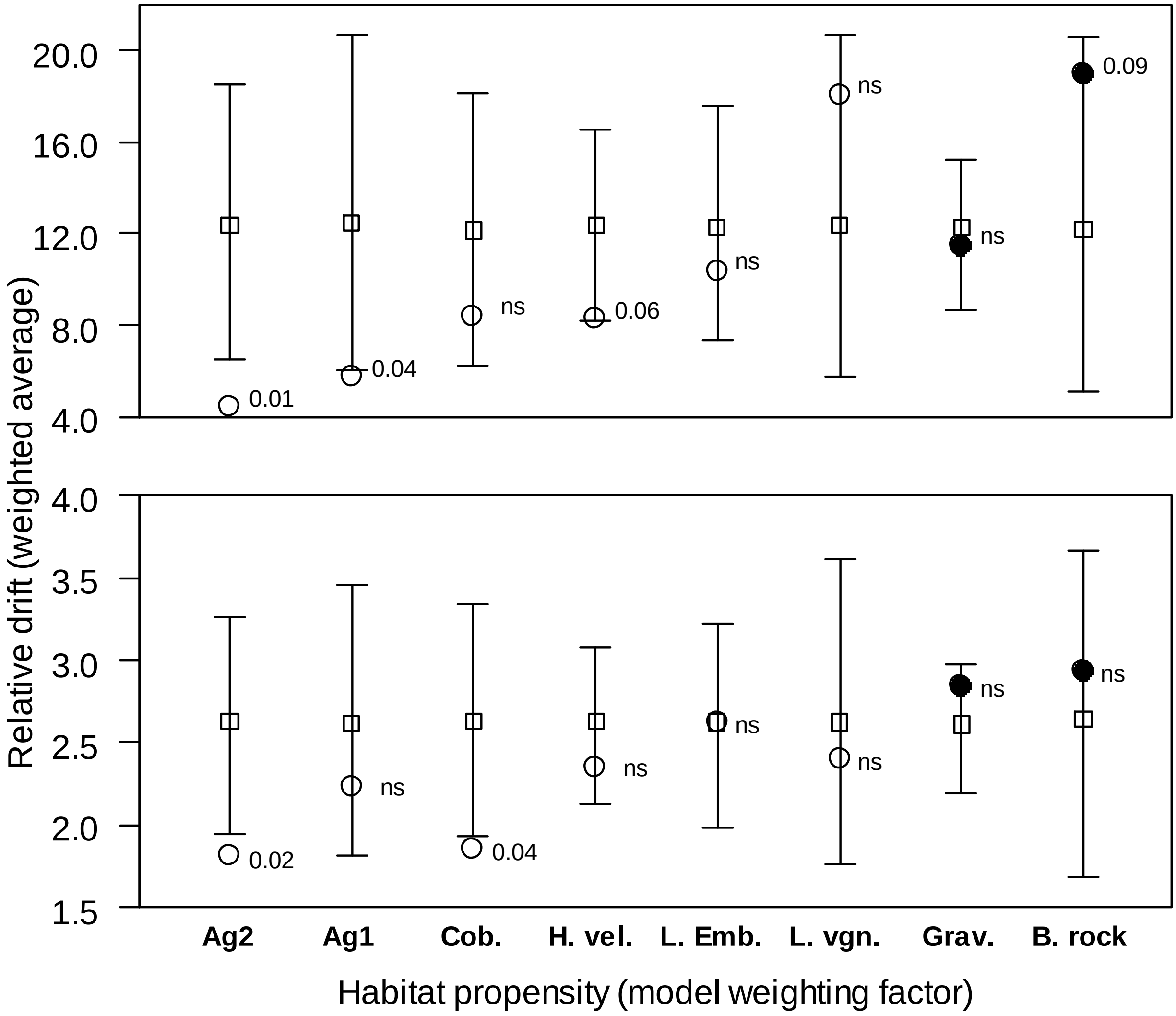

Figure 3.8: Mean relative drift densities during hydropeaking on July 7, 2010, weighted by habitat affinities. Ag 2: aggregate of affinities for cobble and high velocity, Ag 1: aggregate of affinities for cobble, high velocity, low embeddedness and low vegetative cover. Cob: cobble, H. vel: high velocity, L emb: low embeddedness, L. vgn: low vegetation, Grav: gravel, B. rock: bedrock. Open squares(□) null mean relative drift, calculated from 1000 random permutations of the habitat affinities, as described in Fig. 2. Error bars: 95% confidence intervals for the null distributions. Closed circles(●) affinities for which weighted average relative drift was hypothesized to be significantly higher than the null mean. Open circles (○) affinities for which weighted average relative drift was hypothesized to be significantly lower than the null mean. Numbers next to mean values are p-values associate with each one-tailed hypothesis (ns: not significant, p>0.10).

Chapter IV

The effects of hydropeaking on benthic assemblages: a traits-based approach

Abstract

Hydroelectric power generation is the world's largest source of renewable energy. Flow modifications for hydropower production have markedly affected the physicochemical and biological structure and functioning of lotic systems worldwide. Quantifiable characteristics of the physiology, morphology and ecological interactions (i.e. traits) of benthic macroinvertebrates are useful for evaluating the effects of anthropogenic disturbances to lotic ecosystems and provide conceptual links between environmental effects and assemblage responses. The primary objective of this investigation was to determine what ecological and biological traits were most prevalent in two river systems impacted by hydropower production: the Roanoke River in the Mid-Atlantic region of the United States and the River Oriège in the French Pyrenees. In both regions, taxa associated with depositional habitat characteristics (e.g., fine substrate, slow flow velocities and marginal habitat areas) were more prevalent at hydropower-impacted sites than at non-impacted sites, whereas those associated with erosional habitat characteristics were more prevalent at non-impacted sites. An analysis that included quantitatively defined trait states for the taxa observed in the systems showed greater distinctions between impacted and non-impacted sites than an analysis based on taxonomic composition. These results provide information on the ecological characteristics of taxa that are most (and least) likely to be impacted by flow modifications associated with hydropower production as well as on the benthic habitat types that are most likely to be affected. This information is useful for the design of future studies aimed at assessing the effects of such flow modification, as well as for the management of hydropower facilities.

Introduction

This study was conducted to determine whether macroinvertebrate assemblage characteristics associated with ecological interactions, morphology and life histories (collectively referred to as traits) are effective for assessing the effects of hydropeaking for hydroelectric power generation. For the purposes of this work, hydropeaking is defined as the modification of the natural flow regime (sensu Poff *et al.*, 1997) to include short-duration, rapid discharge pulses of 2-10 fold above baseflow levels and lasting several hours. Hydropeaking is a prevalent form of flow modification and has markedly affected the physicochemical and biological structure and functioning of lotic systems world-wide (Troelstrup and Hergenrader, 1990, Moog, 1993, Englund and Malmqvist, 1996, Mochizuki *et al.*, 2006, Xiaocheng *et al.*, 2008, Carolli *et al.*, 2012). Traits have been used effectively to evaluate the effects of a wide range of environmental factors in aquatic ecosystems (Blocksom *et al.*, 2002, Hughes *et al.*, 1998, Johnson and Ringler, 2014, Pan *et al.*, 2000). Here, associations between macroinvertebrate traits and hydropeaking are evaluated for impacted river systems on two continents: the River Oriège system in the French Pyrenees, and the Roanoke River in the Mid-Atlantic region of the eastern US.

This study focused on four major objectives. The first was to determine whether biological traits were more likely to exhibit among-trait associations for the macroinvertebrate taxa observed in the study systems than were ecological traits. This portion of the investigation was focused on traits for which there was information available for the majority of taxa observed in the dataset and on those that were judged to be most commonly used for the assessment of anthropogenic influences on aquatic systems. It was hypothesized that associations among biological trait modalities would be more common than those among ecological modalities.

The second objective was to compare the macroinvertebrate assemblages at hydropeaking-impacted and non-hydropeaking sites in order to determine whether, and which, trait states were influenced by hydropeaking. For this objective, a subset of the selected traits were used, specifically ecological traits related to the hydrologic and physical habitat preferences of each taxon and biological traits most directly related to interactions of organisms with hydrology and substrate conditions. These trait modalities were selected because of the strong relationships observed in previous works between flow modifications and the flow and substrate relations of macroinvertebrate assemblages and because of the overarching influences of flow and physical habitat structuring on riverine assemblages in general (Rabeni and Minshall, 1977, Hart and Finelli, 1999, Freeman *et al.*, 2001, McGarvey, 2011,).

The detection of traits with significant associations with hydropeaking status would provide important information for researchers assessing the effects of such flow modifications. Information on the *direction* of differences in these trait states, that is, on whether the utilization of specific habitat types or the expression of specific biological characteristics are likely to increase or decrease in response to hydropeaking, would aid future monitoring and management. If trait states associated with coarser (and thus more stable) substrate types and fast-flow environments are more prevalent in hydropeaking than in non-hydropeaking systems, then one might expect that future impacts would favor lotic-erosional taxa and that slow-flow habitats and the biota that inhabit them would be most imperiled by such flow modifications. In contrast, if hydropeaking systems exhibit increases in trait states associated with depositional conditions, then it would be expected that future hydropeaking impacts would be most detrimental to taxa inhabiting erosional flows and coarser substrates.

The third objective was to determine whether system-specific trait information could be used to more clearly distinguish the effects of hydropeaking than database-derived information, which was generalized based on information collected over larger geographic ranges and longer temporal extents. To address this objective, system-specific trait states were derived for taxa observed at the North American sites, based on measured environmental conditions at the sampling locations, as described in the previous chapter. It was hypothesized that these system-specific trait states would show larger differences between peaking and non-peaking sites than comparable database-derived values.

The fourth and final objective was to compare traits-based and taxonomy based approaches in their effectiveness for distinguishing between peaking and non-peaking systems. To address this objective, variation among the observed assemblages was partitioned into variation due to hydropeaking status, variation among sampling time periods, and variation among continents. Because of the myriad potential factors affecting taxonomic variation, it was expected that all sources of variation would be higher for the taxonomic approach than for the traits-based approach. However, it was hypothesized that variation based on hydropeaking status, expressed in proportion to temporal and continental variation, would be greater for the traits-based approach than for the taxonomy-based approach, indicating greater utility of the former for distinguishing the signal of the environmental variable of interest (hydropeaking) from the noise of additional temporal and spatial variation.

Methods

Study systems and field investigations

This study included two hydropeaking-impacted sites and two non-hydropeaking sites. The North American sites included the Roanoke River at Roanoke Rapids, North Carolina (a hydropeaking-impacted site) and the James River at Richmond, Virginia (a non-hydropeaking site), both in the mid-Atlantic region of the eastern U.S. Data from these North American sites are collectively referred to hereafter as the NA dataset. Two sites on the River Oriège in the French Pyrenees were also evaluated: one site located immediately above, and a second site immediately below, a hydropeaking outflow (see Fig. 1 in Céréghino *et al.*, 2002), Sites 1 and 2). Data from these sites are referred to hereafter as the EU dataset.

The benthic substrate compositions of the four sites were similar, consisting primarily of mineral material ranging from 20-200 mm (Céréghino *et al.*, 2002, Garey *et. al.* 2012). The hydrology of the North American sites was similar, with turbulent flow and mean velocities of 0.43 and 0.32 m/s for the James River and Roanoke River sites, respectively. The hydrology of the European sites was also was similar, but flow velocity was higher at these sites than at the North American sites (mean velocities of 0.60 and 0.52 for upstream and downstream sites; Céréghino *et al.,* 2002). Variations in the natural hydrologic regimes of mid-Atlantic rivers are driven primarily by evapotranspiration, with maximum flows typically occurring in winter, and minimum flows in summer. In contrast, natural hydrologic regimes in the Pyrenees are driven largely by snowmelt, with maximum flows typically occurring in spring (see Fig. 1 in Céréghino *et al.*, 2002).

The hydropeaking operations differed between the North American and European sites. On the Roanoke River, hydropeaking pulses were controlled at the Roanoke Rapids Dam, which allowed not only for rapid, increased flows during hydropeaking events, but also for stabilized flows that, except for hydropeaking events, were less variable than those in the James River (Fig. 4.1). In contrast, hydropeaking pulses on the River Oriège were supplied by a nearby reservoir that is not located along the main channel and therefore, does not affect flow inputs from the upstream portion of the river. Thus, the hydrograph in the hydropeaking-impacted portion of the River Oriège resembles that of the non-impacted section, but with short-duration flow spikes caused by hydropeaking events (Fig. 1 in Céréghino *et al.*, 2002).

Quantitative macroinvertebrate samples were collected at all sites, in shallow riffles and in approximate proportion to the relative prevalence of substrates of different size classes. Samples were collected at North American sites in spring (James River, 28 May, Roanoke River, 3 June 2010), early summer (James River, 22 June, Roanoke River, 24 June, 2010) and late summer (James River, 9 Sept., Roanoke River 4 Sept., 2010). During each sampling date and at each site, 3 samples were collected from bedrock habitat (>250 mm diameter) and 7 samples were collected from gravel-cobble substrate (20-200-mm diameter). Samples were collected by choosing random locations along pre-selected transects (Figs. 4.2 and 4.3) and using a Hess-style bottom sampler (0.09 m^2 per sample; total surface area = 9.0 m^2 per sampling event).

The River Oriège data were provided by R. Céréghino (pers. communication; see Céréghino *et al.* 2002 for further details). Samples were collected in the river in June and October 1991 and July and October 1993. During each of these four sampling events, five quantitative samples were collected in shallow riffle areas at both sites using a Surber sampler (0.1 m^2 per sample; total surface area = 5.0 m^2 per sampling event). Most macroinvertebrates were identified to genus, though some taxa were aggregated at higher taxonomic levels to facilitate comparisons among samples.

Macroinvertebrate traits

Macroinvertebrate trait information was compiled from the literature-derived European Traits Database of Tachet *et al.*, (2002; complete database provided by P. Usseglio-Polatera) and the North American database of Vieira *et al.*, (2006). Traits are broad aspects of the environmental conditions in which each taxon occurs (ecological traits) or characteristics of each taxon's morphology or physiology (biological traits). Each trait encompasses one or multiple trait categories. For each trait category a quantitative value, referred to as trait state, is assigned for each taxon. For example, the trait *feeding strategy* contains categories such as *collector-gatherer, shredder* and *predator*. Dragonflies are obligate predators and therefore all dragonfly taxa should be assigned a trait state of 1 for the category predator and trait states of 0 for all other categories. Seventeen traits and 61 categories from the EU database, and 16 traits and 57 categories from the NA database, were selected for analysis. Selected traits were those commonly used to assess environmental effects based on macroinvertebrate assemblage-level responses. These included biological traits associated with voltinism, body size, feeding strategy, movement, substrate relationships and external morphology, as well as ecological traits associated with food type consumed and substrate, flow and general habitat preferences (see Tables 4.1 and 4.2 for explanations of all trait categories). Of primary interest were those trait categories most directly related to physical substrate and flow preferences and those that could reasonably be considered equivalent between databases.

For most traits, quantitative, continuous trait state values were derived based on accounts in the literature as described in Viera et al. (2006). For each taxon and for each category, this process produced values ranging over a continuous scale from 0 (no evidence that the taxon occurs within the category), to 1 (all records indicating that the taxon occurs within the category). Complete genus-level information was included in the European database, and these data were used directly in this analysis. Genus-level summaries were lacking in the North American database for many taxa. In such cases, species-level records were used from studies conducted in close proximity to the James and Roanoke Rivers.

Some biological trait categories occurred as present or absent, including all of those associated with the trait *Shape*, the *Integument type* categories *Hard* and *Soft*, and the single-category traits *Silk* and *Case.* For the North American dataset, these were assigned binary (1/0) values based upon the majority of relevant records in the database. Values for the single-modality, binary trait *Hooks/claws* were not included, and was added based on the morphology of each of the North American taxa, as were all of the morphology-based, binary trait states for European taxa, as no such information was included in the database.

Some taxa in the two datasets were represented at the Family level. In such cases the mean (for continuous trait sates), or mode (for binary trait states) of all genus-level trait state values within each category were used. Further information on the derivation of the trait states is provided in Appendix 4.1.

In addition to the database-derived trait states, four site-specific traits were added, for which trait states were derived specifically for the North American sites. These included substrate *embeddedness* (affinities of taxa for high-embeddedness substrates), *gravel*, *cobble*, and *bedrock* (affinities of taxa for substrates with diameters of < 9.3cm, 9.3-30.0cm and > 30.0 cm), *velocity* (affinities toward high-velocity environments), and *vegetation* (affinities toward heavy vegetative cover). These traits were derived for the North American dataset by analyzing the relative abundance of each taxon in relation to each measured habitat characteristics, as described in Chapter 3. These trait states were developed to test the hypothesis that site-specific trait descriptors would better distinguish environmental responses of the assemblages to hydropeaking than the database-derived values that are generalized over larger geographic ranges.

Statistical Analysis

The Non-metric Multidimensional Scaling (NMS) ordinations discussed below were performed using PC-ORD, Version 5.0 (McCune and Mefford, 2006). All other data analyses were performed using R, Version 3.1.1 (R Core Team 2014).

Associations among trait states

For each of the two datasets, all pairwise comparisons between trait categories were evaluated for significant associations among categories, excluding categories for the same trait (which were mathematically dependent upon one another). For this evaluation test statistics were first calculated to express the magnitude of each association: the Jaccard dissimilarity index (j) for associations between pairs binary trait states, the Pearson Product-moment correlation (r) for associations between continuous states, and the Student's t-statistic (t) for associations between continuous and binary states. Once the proper test statistic was calculated for a given trait state pair, the trait state values were randomly permuted among taxa so that the actual test statistic could be compared to the same test statistic derived by chance, given the total taxa pool and distribution of trait states observed in the assemblages. One thousand random permutations were conducted for each trait category pair, and associations were considered significant at $p \leq 0.05$ (50 or fewer random test statistics that were all greater than, or all less than, the actual test statistic).

To determine whether biological and ecological traits differed with respect to the prevalence of among-category associations, Chi-squared tests were conducted to compare the proportions of significant associations between pairs of biological categories to those between pairs of ecological categories. Associations of ecological categories with biological categories not considered, as these would be equally confounding to both.

Evaluation of peaking effects on selected traits

Before this stage of the analysis was conducted a subset of the trait categories were selected to determine whether they differed significantly between hydropeaking and non-hydropeaking sites. The traits selected for this stage were those most associated with interactions of the taxa with flow and the physical composition of the substrate (Tables 3 and 4). Based on the results of Chapter 3, these characteristics appeared to affect the susceptibility of macroinvertebrates to hydropeaking effects. In addition, because of the strong links between flow-related and habitat-related traits and flow modification, it was judged that between-site differences in these trait states which consistently occurred at both the NA and EU sites could be reasonably attributed to hydropeaking effects and were less likely to be confounded by the effects of other environmental differences among sites. In contrast, other evaluated traits were considered more likely to be affected by myriad other between-site differences. To facilitate comparison between the Roanoke and Oriege Rivers, trait categories chosen for this stage were those that could reasonably be considered as equivalent between the EU and NA databases (see notation in Tables 4.3 and 4. 4).

To evaluate the effects of hydropeaking on each selected trait category, abundance-weighted average trait states were calculated for each site on each sampling date. The differences between weighted averages at peaking and non-peaking sites were then compared to null distributions of differences, which were created with the assumption of no difference in the assemblages between sites. Null samples were created by first blocking site pairs according to sampling date and continent (thus removing the effects of these variables from the analysis), pooling all individuals collected at each of the two sites in a pair, and then randomly selecting individuals from the pool to create pairs of null samples with the same total abundances as in the real dataset. For each site pair, 1000 permutations were conducted, creating a null distribution of 1000 between-site differences for each site pair and trait state. For each trait category, this process resulted in 3000 and 4000 null differences, corresponding to the 3 and 4 sampling dates in the NA and EU datasets, respectively. The probability of a significant difference for each trait state in each of the two datasets was taken as the proportion of null differences that were greater than the actual difference between sites. Differences were considered significant at $p<=0.05$ (i.e. <=150 and 200 null differences all greater than their respective between-site differences for the NA and EU datasets, respectively).

Comparison of traits-based and taxonomy-based approaches for evaluating hydropeaking effects

NMS plots were created based on Sorenson distance matrices derived from trait states, and (in separate plots) based on the relative abundances of the observed taxa. These plots allowed for a visual comparison of the potential sources of variation associated with traits and with taxonomic structure among sites and sampling dates.

To evaluate whether the evaluated traits could more clearly distinguish hydropeaking from non-hydropeaking sites than a taxonomy-based approach, the potential sources of variation among the observed assemblages were quantified and compared for both the taxonomic compositions and traits-based compositions of each assemblage. Possible sources of variation among assemblages included: 1) variation due to hydropeaking; differences between hydropeaking and non-hydropeaking sites, paired by continent and sampling date; 2) pure temporal variation (differences between the same sites on different sampling dates); and 3) continental variation (differences between sites from different continents, paired by hydropeaking status). These sources of variation were quantified by calculating the Sorenson dissimilarity index for all possible pairwise comparisons between sites, paired as described above using the taxonomic data, as well as dissimilarities using abundance-weighted average trait states. To determine the relative importance of each source of variation, Signal-to-Noise (S/N) ratios were calculated following Kaufmann et al. (1999). Dissimilarity based on hydropeaking status represents the *signal*, that is, the desired environmental effect to be measured. Large dissimilarities between hydropeaking and non-hydropeaking sites therefore indicate a stronger signal from the effect of interest. In contrast, dissimilarities based on temporal and continental variation represent noise or potential sources of variation that confound the clear indication of a hydropeaking effect. Therefore, large S/N ratios are desirable and indicate a clearer distinction between sites based on hydropeaking and less confounding effects from other sources of variation. Two S/N ratios were calculated for both the taxonomic and traits data: S/N_t, which is the ratio of Sorenson dissimilarity based on hydropeaking (variation source 1 above) to the dissimilarity based on different sampling times (source 2), and S/N_c which is the ratio of the Sorenson distance based on hydropeaking to those based on differences between sites on different continents (source 3 above). Support for the hypothesis that the traits-based approach provides a clearer distinction between sites based on hydropeaking than the taxonomy-based approach would be indicated by higher S/N_t and S/N_c values for dissimilarities based on traits than for those based on taxa.

Results

Associations among trait categories

Nearly all categories of the many traits included had multiple significant associations among categories. The biological trait category clinger exhibited the greatest number of significant associations among the NA traits, whereas the biological category crawler had the most associations among the EU traits (23 and 26 significant associations with other categories, respectively, Tables 4.1 and 4.2). Overall, 24% of possible pairwise comparisons between biological trait categories, and 25% of the comparisons based on ecological categories yielded significant associations. The hypothesis that biological traits would exhibit more between-category associations than would ecological traits was not supported, as the proportion of significant associations among the biological trait categories was not significantly different than that of the ecological categories for either dataset (χ^2_1 : 1.88 and 2.29 for NA and EU datasets, respectively, $p>0.10$).

Evaluation of peaking effects on selected traits

Ecological trait states more consistently showed differences between hydropeaking and non-hydropeaking sites than biological trait states. When ecological trait states exhibited significant differences between hydropeaking and non-hydropeaking sites, the directions of the differences (i.e. greater or less at hydropeaking sites) were the same for comparable categories in each dataset (Tables 4.3 and 4.4). The single exception was for the lateral habitat category *riffles* which was greater at NA peaking sites than non-peaking sites, whereas the comparable category *river channels* was not significantly different between peaking and non-peaking sites in the EU dataset.

In contrast, biological trait categories rarely showed differences in trait states that were consistent among datasets. Only the biological modalities *hooks/claws* and *burrowers* showed significant differences that were in agreement among datasets. The former was consistently higher at hydropeaking sites and the latter was consistently higher at non-peaking sites for both datasets (Tables 4.3 and 4.4).

Trait states associated with erosive conditions were more prevalent at non-peaking than at peaking sites, including the current category *fast current*, the substrate categories *coarse* and *flag/cobbles* and the biological category *hooks/claws* ($p<0.05$, Fig. 4.4 and 4.5). These results suggest a higher average affinity for erosional habitat patches for macroinvertebrates of non-peaking sites than for those at peaking sites.

Trait states associated with depositional conditions were higher at peaking sites than at non-peaking sites, including the current category *slow current*, the substrate categories *sand* and *mud* , the lateral habitat categories *banks/sidearms*, *lentic shores*, and *lotic margins* and the biological trait category *burrowers* (Fig. 4.4 and 4.5). This suggests a greater average affinity for depositional habitat patches at peaking sites than at non-peaking sites.

Evaluation of site-specific traits

The hypothesis that site specific traits would exhibit greater differences between hydropeaking and non-hydropeaking sites was not supported. Of the five site-specific categories evaluated, only *bedrock* and *velocity* showed significant differences between peaking and non-peaking sites and the magnitudes of these differences were less than for comparable database-derived trait states (state differences of 0.05 and 0.10 for the site-specific *bedrock* and *velocity* modalities, as compared to differences of 0.08 and 0.27 for the comparable database-derived categories *coarse substrate* and *fast current*, respectively, Table 4.1).

Comparison of traits-based and taxonomy-based approaches for evaluating hydropeaking effects

To limit the potential confounding effects of associations among multiple traits, three trait modalities were chosen to represent the overall ecological affinities of the macroinvertebrate assemblages based on substrate composition, hydrology and lateral habitat position: 1) *coarse substrate* (*coarse substrate* in the NA dataset combined with *flags/cobbles* in the EU dataset); 2) *fast current*; and 3) *margin habitat* (margins in the NA dataset and banks/sidearms in the EU dataset). This simplification was necessary to avoid including trait states from multiple categories within the same trait, which are mathematically dependent and, therefore inappropriate for inclusion in the same analysis.

Despite this simplification weak though statistically significant correlations among trait categories occurred. For the EU dataset, all three trait categories were weakly correlated ($r^2 =$ 0.24, 0.14 and 0.20 for *flags/cobbles* and *fast current*, *flags/cobbles* and *margin habitat*, and *fast current* and *margin habitat*, respectively). For the NA dataset, fast current was significantly correlated with margins ($r^{2\,=}$ 0.11, $p<0.05$) and coarse substrate was not significantly correlated with the other two modalities ($p>0.05$).

Both the NMS plot based on traits, and the plot based on taxa showed relatively clear separations among the invertebrate assemblages based on the presence or absence of hydropeaking, though some overlap occurred between peaking and non-peaking EU sites (Fig. 4.6). The widest separation in both plots appeared to be based on continent, though this separation was reduced in the traits-based plot relative to the taxa-based plot.

As expected, the mean between-site Sorenson distances based on peaking status, sampling time and continent were each greater for the taxonomic approach than for the traits-based approach (Fig. 4.7). For both approaches, among-continent variation was greater than temporal variation or variation due to hydropeaking. Overall, the hypothesis that the traits-based approach would more effectively distinguish the effects of hydropeaking than would the taxonomy based approach was supported. Both the S/N_t and the S/N_c ratios (which indicate the relative proportions of variation based on hydropeaking as compared to temporal and between-continent variation, respectively) were higher for traits than for taxa. However, neither approach provided a distinction between sites due to hydropeaking that was robust to among-continent variation. For the taxonomy-based approach, variation attributable to hydropeaking was only 65% of the amount attributable to continents, and for the traits-based approach, variation based on hydropeaking was 73% of that between continents (S/N_c: 0.65 and 0.75 for traits and taxa, respectively; Fig. 4.7). In contrast, the traits-based approach was considerably more robust to temporal variation than was the taxa-based approach, with nearly twice as much variation among traits associated with peaking as associated with time (S/N_t : 1.85), whereas variation due to hydropeaking and temporal variation were nearly equal for the taxonomic approach (S/N_t : 1.15).

Discussion

This work evaluates the interdependence among the categories of a suite of commonly studied biological and ecological traits of riverine macroinvertebrate assemblages. The study also evaluates the responses of habitat and hydrology related traits to hydropeaking in two environmentally distinct regions on two continents.

Others have postulated that, compared with ecological traits, the use of biological traits to assess environmental stressors may be more confounded by interdependences among trait states because biological traits are more closely linked to phylogeny (Poff *et al.*, 2006). This study represents the first direct test of the hypothesis that biological traits exhibit a greater degree of interdependence than do ecological traits. The results observed here indicate that interdependence among traits is relatively common, but that biological and ecological traits do not differ significantly with respect to the degree of interdependence between trait categories. Therefore, there appears to be no basis for favoring one trait type over the other (i.e. for choosing biological over ecological traits or vice-versa) based on the potential for interdependence among traits.

Despite differences in the natural settings of the study systems, as well as differences in the hydropeaking operations affecting them, consistent associations of hydropeaking with ecological trait categories related to physical habitat and hydrology were observed. Across both study regions, macroinvertebrate assemblages at hydropeaking sites showed greater affinities for fine substrates, depositional and marginal habitats and slow current, whereas assemblages at non-hydropeaking sites showed greater affinities for coarse substrates, erosional main-channel habitats and fast current. These results provide an important addition to those presented in Chapter 3. There, it was shown that macroinvertebrate taxa in the Roanoke River system with high affinities toward fine, unstable substrate and slow current environments showed the highest susceptibilities to hydropeaking-induced drift. Collectively, the results of this chapter and Chapter 3 suggest that hydropeaking may have a greater impact on, and thus select for, taxa with higher susceptibilities to drift due to their high affinity for unstable habitat patches. Given the many studies showing elevated drift during hydropeaking (Bruno *et al.*, 2010, Lagarrigue *et al.*, 2002, Marty *et al.*, 2009, Miller *et al.*, 2014, Mochizuki *et al.*, 2006, Robinson *et al.*, 2004, Robinson, 2012) and that macroinvertebrates persist in these systems, it is unlikely that the short-term impacts of elevated drift are detrimental to populations adapted for life in hydropeaking-impacted river systems. Drift provides a mechanism for colonizing new habitats for many taxa, and periodic population reductions caused by loss to drift have been postulated to alleviate competition-induced stress (Brittain and Eikeland, 1988). Therefore, it is plausible that hydropeaking-induced drift may confer increased fitness on some populations in these systems.

The traits-based approach employed here was more effective in distinguishing between hydropeaking and non-hydropeaking sites, and was less confounded by natural temporal and spatial variation, than an equivalent taxonomy-based approach. Variation based on trait states as well as that based on taxonomy were considerably greater between continents than between hydropeaking and non-hydropeaking sites. This suggests that a diagnostic suite of taxa, or of trait state values, which is indicative of hydropeaking effects in a manner that is generalizable across river systems at the global scale, is likely not attainable. However, trait-based variation between peaking and non-peaking sites was nearly twice that of variation among sampling dates, indicating that the trait-based approach was robust with respect to the temporal variation encompassed in the datasets (1-3 months in the NA study and 3-13 months in the EU study). This result is especially useful for river monitoring, as field work associated with the collection of macroinvertebrate samples is expensive and time-consuming, and conducting multiple site visits in close temporal proximity is often not feasible. This study shows that traits-based evaluations of hydropeaking effects should be less prone to errors associated with natural temporal variation of lotic assemblages than are taxonomy based approaches.

This study informs future investigations focused on diagnosing and monitoring the ecological effects of hydropeaking. Although potentially confounding associations among trait states are equally common for biological and ecological traits, the latter appear to more consistently indicate differences in the drift of macroinvertebrate assemblages between peaking and non-peaking systems. Ecological traits associated with current velocity and physical habitat structure provide great utility for this purpose and should be prioritized in investigations of hydropeaking effects on macroinvertebrate assemblages.

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Table 4.1: Mean abundance-weighted trait states and among-state associations for North American traits. Shaded cells with asterisks indicate significant differences between hydropeaking and non-hydropeaking sites (permutation test, p<0.05).

Trait and Modality	Ecol./biol.	Explanation	Mean trait states James River	Mean trait states Roanoke River	Associations Ecol.	Associations Biol.
Current	E					
Quiet current	E	Taxon resides in areas devoid of current	0.11	0.14	7	11
Fast current	E	Taxon resides in slow, moving current	0.63*	0.36	12	10
Slow current	E	Taxon resides in areas of fast current	0.23	0.30*	7	5
Current (system specific)	E					
Velocity	E	Propensity toward fast-flow environments	0.66*	0.56	8	5
Lateral habitat zone	E					
Hyporheic	E	Taxon resides in the hyporheic zone	0.00*	0.00	1	0
Lentic shores	E	Taxon resides in the lentic-littoral zone	0.20	0.28*	5	4
Lotic Margin	E	Taxon resides near the margins in lotic systems	0.05	0.14*	10	5
Riffles	E	Taxon resides in riffle areas	0.55*	0.38	13	8
Microhabitat	E					
Algae	E	Taxon resides in algae mats	0.02	0.07*	6	11
Coarse substrate	E	Taxon resides in/on coarse substrate	0.26*	0.18	3	11
Detritus	E	Taxon resides in detritus accumulations	0.07	0.08*	1	5
Gravel	E	Taxon resides in/on gravel	0.21	0.16	2	3
Large woody debris	E	Taxon resides in/on wood	0.15	0.12	2	4
Macrophytes	E	Taxon resides in/on macrophytes	0.14	0.16	8	7
Pelagic	E	Taxon resides in the pelagic zone	0.02	0.04	0	0
Sand	E	Taxon resides in/on Sand	0.06*	0.02	3	4
Silt	E	Taxon resides in/on silt	0.06	0.08	4	8
Substrate (system specific)	E					
Bedrock	E	Propensity toward bedrock subsrate	0.21	0.26*	2	1
Cobble	E	Propensity toward cobble substrate	0.58	0.56	3	0
Gravel (system	E	Propensity toward gravel substrate	0.62	0.58	5	2

Trait and Modality	Ecol./biol.	Explanation	Mean trait states		Associations	
			James River	Roanoke River	Ecol.	Biol.
specific)						
Substrate embeddedness (system specific)	E					
Embeddedness	E	Propensity toward areas of high substrate embeddedness	0.48	0.52	7	6
Vegetation (system specific)	E					
Vegetation	E	Propensity toward heavily vegetated environments	0.50	0.58*	7	2
Vertical habitat zone	E					
Benthic	E	Taxon resides in the benthic zone	0.66*	0.44	10	8
Hyporheic	E	Taxon resides in the hyporheic zone	0.14	0.10	0	4
Macrophytes	E	Taxon resides in/on macrophytes	0.11	0.25*	12	9
Pelagic	E	Taxon resides in the pelagic zone	0.04	0.06	5	7
Surface	E	Taxon resides on the water surface	0.05	0.15*	3	9
Case	B					
Case	B	Taxon carries a portable case	0.14	0.09	1	11
Feeding	B					
Filterer	B	Taxon filters organic matter from water column	0.23	0.25	8	7
Gatherer	B	Taxon collects deposited organic matter	0.17*	0.07	2	3
Parasite	B	Taxon parasitizes live animals	0.00	0.01*	1	2
Piercer-herbivore	B	Taxon pierces cells of live plants	0.00	0.01*	7	6
Predator	B	Taxon consumes live animals	0.09	0.06	4	14
Scraper	B	Taxon scrapes attached biofilm	0.42	0.52*	3	10
Shredder	B	Taxon shreds course organic matter	0.10	0.08	3	5
Hooks/claws	B					
Hooks/claws	B	Taxon employs hooks or claws	0.79*	0.27	9	16

Trait and Modality	Ecol./biol.	Explanation	Mean trait states		Associations	
			James River	Roanoke River	Ecol.	Biol.
Integument type	B					
Hard	B	Taxon has a hardened integument	0.16	0.35*	4	15
Soft	B	Taxon has a soft integument	0.04	0.35*	5	7
Maximum body size	B					
Large	B	Probability maximum body length is >1.6cm	0.29	0.39	4	7
Medium	B	Probability maximum body length is 0.9-1.6cm	0.21	0.24	2	3
Small	B	Probability maximum body length is <0.9cm	0.50*	0.37	4	5
Movement and substrate relation	B					
Burrower	B	Taxon moves primarily by burrowing in sediment	0.13	0.27*	11	7
Climber	B	Taxon moves primarily by climbing on substrate	0.03	0.02	5	9
Clinger	B	Taxon clings to substrate	0.72	0.61	20	6
Sprawler	B	Taxon sprawls on substrate surface	0.01	0.02*	8	4
Swimmer	B	Taxon moves primarily by swimming	0.10	0.08	9	3
Scleratization	B					
All scleratized	B	Taxon is completely covered by schlerites	0.29*	0.01	4	14
Partly scleratized	B	Taxon is partially covered by schlerites	0.55	0.62	5	10
Shape	B					
Flat	B	Body is flat	0.06	0.06	4	6
Round	B	Body is round	0.28	0.31	2	11
Streamlined	B	Body is streamlined	0.07	0.05	0	4
Tube	B	Body is tube-shaped	0.60	0.56	2	9
Silk	B					
Silk	B	Taxon employs silk	0.37	0.24	7	12
Suckers						
Suckers	B	Taxon employs suction discs for attachment	0.14	0.31*	4	13

Trait and Modality	Ecol./biol.	Explanation	Mean trait states James River	Mean trait states Roanoke River	Associations Ecol.	Associations Biol.
Voltinism						
Multivoltine	B	Probability populations produce more than one generation per year	0.24	0.62*	4	9
Semivoltine	B	Probability populations produce less than one generation per year	0.11*	0.04	6	3
Univoltine	B	Probability populations produce one generation per year	0.65*	0.33	1	5

Table 4.2: Mean abundance-weighted trait states and among-state associations for European traits. Shaded cells with asterisks indicate significant differences between hydropeaking and non-hydropeaking sites (permutation test, p<0.05).

Trait and Modality	Ecol./biol.	Explanation	Mean trait states		Associations	
			Upstream	Downstream	Ecological	Biological
Current	E					
Null current	E	Taxon resides in areas devoid of current	0.03	0.06	12	12
Slow current	E	Taxon resides in slow, moving current	0.21	0.26*	6	5
Fast current	E	Taxon resides in areas of fast current	0.70*	0.59	11	11
Food	E					
Coarse plant material	E	Taxon feeds on organic matter >1mm	0.09	0.12	1	3
Dead macro. animals	E	Taxon feeds on dead macroscopic animals	0.03	0.03	0	3
FPOM	E	Taxon feeds on fine particulate organic matter (<1mm)	0.21	0.20	5	11
Macroinvertebrates	E	Taxon feeds on macroinvertebrates	0.09	0.06	0	7
Macrophytes	E	Taxon feeds on macrophytes	0.11	0.10	0	5
Microinvertebrate	E	Taxon feeds on microinvertebrate animals	0.04	0.03	2	6
Microorganisms	E	Taxon feeds on microorganisms	0.01	0.01	7	8
Microphytes	E	Taxon feeds on microphytes	0.43	0.44	7	9
Substrate	E					
Flags/cobbles	E	Taxon occurs primarily on cobble or larger substrate	0.36*	0.29	11	10
Gravel	E	Taxon occurs primarily in or on gravel	0.14	0.14	2	3
Macrophytes	E	Taxon occurs primarily in or on macrophytes	0.19	0.21	1	4

Trait and Modality	Ecol./biol.	Explanation	Mean trait states Upstream	Mean trait states Downstream	Associations Ecological	Associations Biological
Microphytes	E	Taxon occurs primarily in or on microphytes (e.g. algae)	0.01	0.01	1	1
Mud	E	Taxon occurs primarily in or on mud	0.02	0.04*	11	11
Organics	E	Taxon occurs primarily in or on organic matter	0.08	0.08	6	3
Roots	E	Taxon occurs primarily in root mats	0.10	0.10	2	3
Sand	E	Taxon occurs primarily in or on sand	0.08	0.10*	1	3
Silt	E	Taxon occurs primarily in or on silt	0.02	0.03	7	8
Water body	E					
Banks and sidearms	E	Taxon resides in banks, connected side-arms	0.27	0.31*	4	2
Groundwater	E	Taxon resides in groundwaters	0.01	0.01	7	7
Lakes	E	Taxon resides in lakes	0.11	0.10	0	0
Marsh/peat	E	Taxon resides in marshes and peat bogs	0.02	0.03	6	10
Ponds/pools	E	Taxon resides in ponds, pools, disconnected side-arms	0.04	0.05	5	10
River channels	E	Taxon resides in the river channel	0.48	0.43	7	11
Temporary	E	Taxon resides in temporary waters	0.06	0.07	4	6
Case	B					
Case	B	Taxon carries a portable case	0.06	0.01	4	5
Feeding strategy	B					
Absorber	B	Taxon absorbs nutrients and organic matter through the body integument	0.00	0.00	6	6
Deposit	B	Taxon collects deposited organic matter	0.14	0.17	10	9

			Mean trait states		Associations	
Trait and Modality	Ecol./biol.	Explanation	Upstream	Downstream	Ecological	Biological
Filterer	B	Taxon filters organic matter from water column	0.09*	0.05	3	3
Parasite	B	Taxon parasitizes live animals	0.00	0.02*	1	1
Piercer	B	Taxon pierces cells of live organisms	0.01	0.01	2	0
Predator	B	Taxon engulfs live prey	0.08	0.06	7	3
Scraper	B	Taxon scrapes attached biofilm	0.52	0.53	13	7
Shredder	B	Taxon shreds course organic matter	0.16	0.16	4	8
Hooks/claws	B					
Hooks/Claws	B	Taxon employs hooks or claws	0.86*	0.69	11	13
Integument type	B					
Hard	B	Taxon has a hardened integument	0.00	0.00	1	2
Soft	B	Taxon has a soft integument	0.07	0.06	11	13
Maximum body size	B					
0.5-1cm	B	Probability taxon is within the length interval	0.46	0.49	4	2
1-2cm	B	Probability taxon is within the length interval	0.35	0.31	1	1
2-4cm	B	Probability taxon is within the length interval	0.03	0.02	3	6
4-8cm	B	Probability taxon is within the length interval	0.00	0.00	7	8
Movement and substrate relation	B					
Burrower	B	Taxon moves primarily by burrowing in sediment	0.04	0.06*	8	6
Clinger	B	Taxon clings to substrate	0.09*	0.05	6	6
Crawler	B	Taxon moves primarily by crawling on substrate	0.61	0.58	15	13
Flier	B	Taxon moves primarily by flying	0.02	0.02	1	2

Trait and Modality	Ecol./biol.	Explanation	Mean trait states		Associations	
			Upstream	Downstream	Ecological	Biological
Interstitial	B	Taxon moves within substrate interstices	0.12	0.13	10	8
Surface	B	Taxon moves primarily by skating on surface tension	0.00	0.00	3	1
Swimmer	B	Taxon moves primarily by swimming below the surface	0.13	0.17	2	2
Scleratization	B					
All scleratized	B	Taxon is completely covered by schlerites	0.11	0.11	1	3
Partially scleratized	B	Taxon is partially covered by schlerites	0.81	0.83	4	13
Shape	B					
Flat	B	Body is flat	0.24*	0.17	3	3
Streamlined	B	Body is streamlined	0.30	0.25	1	1
Tube	B	Body is tube-shaped	0.44	0.47	4	5
Silk	B					
Silk	B	Taxon employs silk	0.11*	0.05	7	9
Suckers	B					
Suckers	B	Taxon employs suction discs for attachment	0.02*	0.01	4	3
Voltinism	B					
Multivoltine	B	Probability populations produce more than one generation per year	0.26	0.31	8	7
Semivoltine	B	Probability populations produce less than one generation per year	0.10	0.08	6	6
Univoltine	B	Probability populations produce one generation per year	0.65	0.61	1	1

Table 4.3: Select North American traits used to for evaluation of hydropeaking effects. Cells with asterisks indicate significant differences between hydropeaking and non-hydropeaking sites (permutation test, $p<0.05$). Superscript letters indicate trait categories considered to be equivalent with European trait categories followed by the same superscript in Table 4. Cells with horizontal bars indicate trait states exhibiting consistent results with equivalent European states.

		Mean trait states		Associations (final traits)	
Trait and modality	Ecol./ Biol.	James River	Roanoke River	Ecol.	Biol.
Current (system specific)	E				
Velocity	E	0.66*	0.56	3	2
Substrate (system specific)	E				
Bedrock	E	0.21	0.26*	0	0
Cobble	E	0.58	0.56	1	1
Gravel (system specific)	E	0.62	0.58	3	1
Substrate embeddedness (system specific)	E				
Embeddedness	E	0.48	0.52	4	2
Current	E				
Quiet current[a]	E	0.11	0.14	4	1
Fast current[b]	E	0.63*	0.36	6	1
Slow current[c]	E	0.23	0.30*	3	0
Lateral habitat zone	E				
Lentic shores[d]	E	0.20	0.28*	1	1
Lotic Margin[d]	E	0.05	0.14*	5	1
Riffles[e]	E	0.55*	0.38	5	2
Microhabitat	E				
Coarse substrate[f]	E	0.26*	0.18	0	2
Gravel[g]	E	0.21	0.16	0	0
Sand[h]	E	0.06*	0.02	0	3
Silt[i]	E	0.06	0.08	2	1
Hooks/claws					
Hooks/claws[j]	B	0.79*	0.27	4	1
Movement and substrate relation	B				
Burrower[k]	B	0.13	0.27*	6	0
Clinger[l]	B	0.72	0.61	10	1
Scleratization	B				
All scleratized[m]	B	0.29*	0.01	2	0
Shape	B				
Flat[n]	B	0.06	0.06	1	0
Streamlined[o]	B	0.07	0.05	0	1
Silk	B				

Trait and modality	Ecol./ Biol.	Mean trait states James River	Roanoke River	Associations (final traits) Ecol.	Biol.
Silk[p]	B	0.37	0.24	2	2
Suckers	B				
Suckers[q]	B	0.14	0.31*	1	1

Table 4.4: Select European traits used to for evaluation of hydropeaking effects Cells with asterisks indicate significant differences between hydropeaking and non-hydropeaking sites (permutation test, $p<0.05$). Superscript letters indicate trait categories considered to be equivalent with North American trait categories followed by the same superscript in Table 3. Cells with horizontal bars indicate trait states exhibiting consistent results with equivalent North American states.

		Mean trait states		Associations (final traits)	
Trait and modality	Ecol/Biol	Upstream	Downstream	Ecol.	Biol.
Current					
Null current[a]	E	0.03	0.06	5	2
Fast current[b]	E	0.70*	0.59	5	3
Slow Current[c]	E	0.21	0.26*	4	2
Water body					
Banks/sidearms[d]	E	0.27	0.31*	4	0
River channels[e]	E	0.48	0.43	7	2
Substrate					
Flags/cobbles[f]	E	0.36*	0.29	7	2
Gravel[g]	E	0.14	0.14	0	0
Mud	E	0.02	0.04*	7	2
Sand[h]	E	0.08	0.10*	1	1
Silt[i]	E	0.02	0.03	5	2
Hooks/claws					
Hooks/Claws[j]	B	0.86*	0.69	4	3
Movement and substrate relation					
Burrower[k]	B	0.04	0.06*	5	3
Clinger[l]	B	0.09*	0.05	3	2
Scleratization					
All scleratized[m]	B	0.11	0.11	0	0
Shape					
Flat[n]	B	0.24*	0.17	2	1
Streamlined[o]	B	0.30	0.25	0	0
Silk					
Silk[p]	B	0.11*	0.05	5	1
Suckers					
Suckers[q]	B	0.02*	0.01	2	0

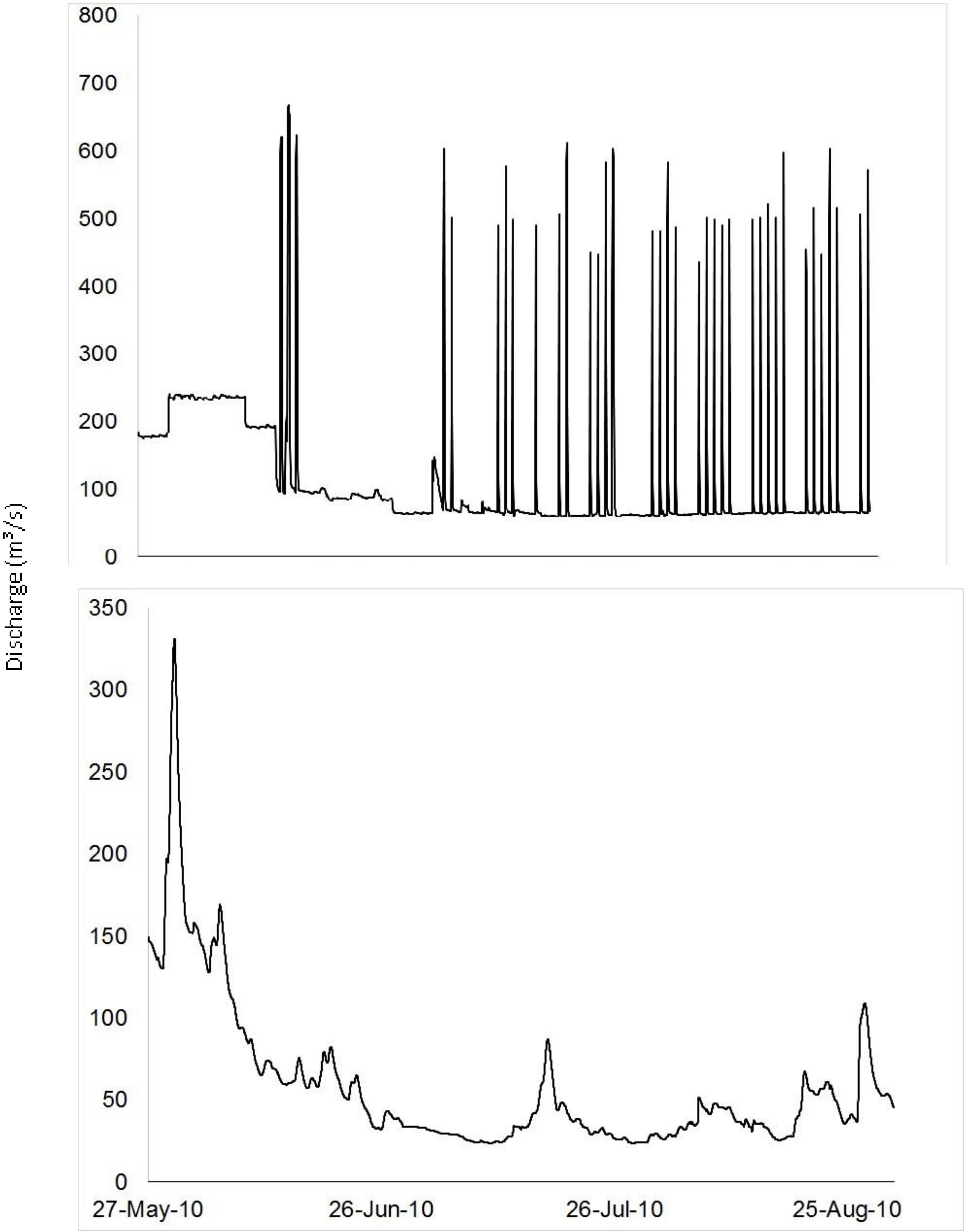

Figure 4.1: Discharge hydrographs for the Roanoke River (top panel) and James River (bottom panel) From 27 May to 31 August, 2010.

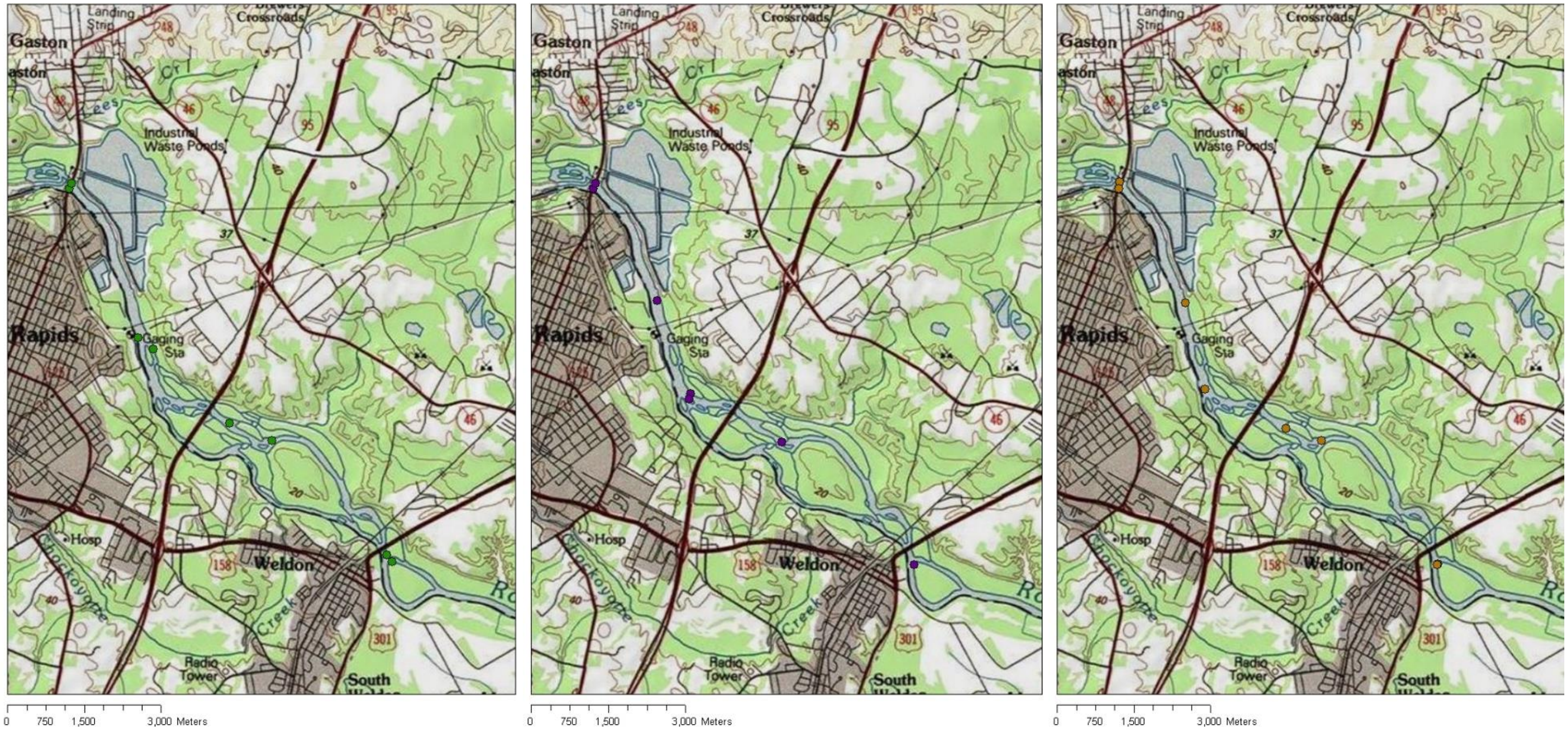

Figure 4.2: Benthic macroinvertebrate sampling locations on the Roanoke River. First panel: spring, second panel: early summer, third panel: late summer.

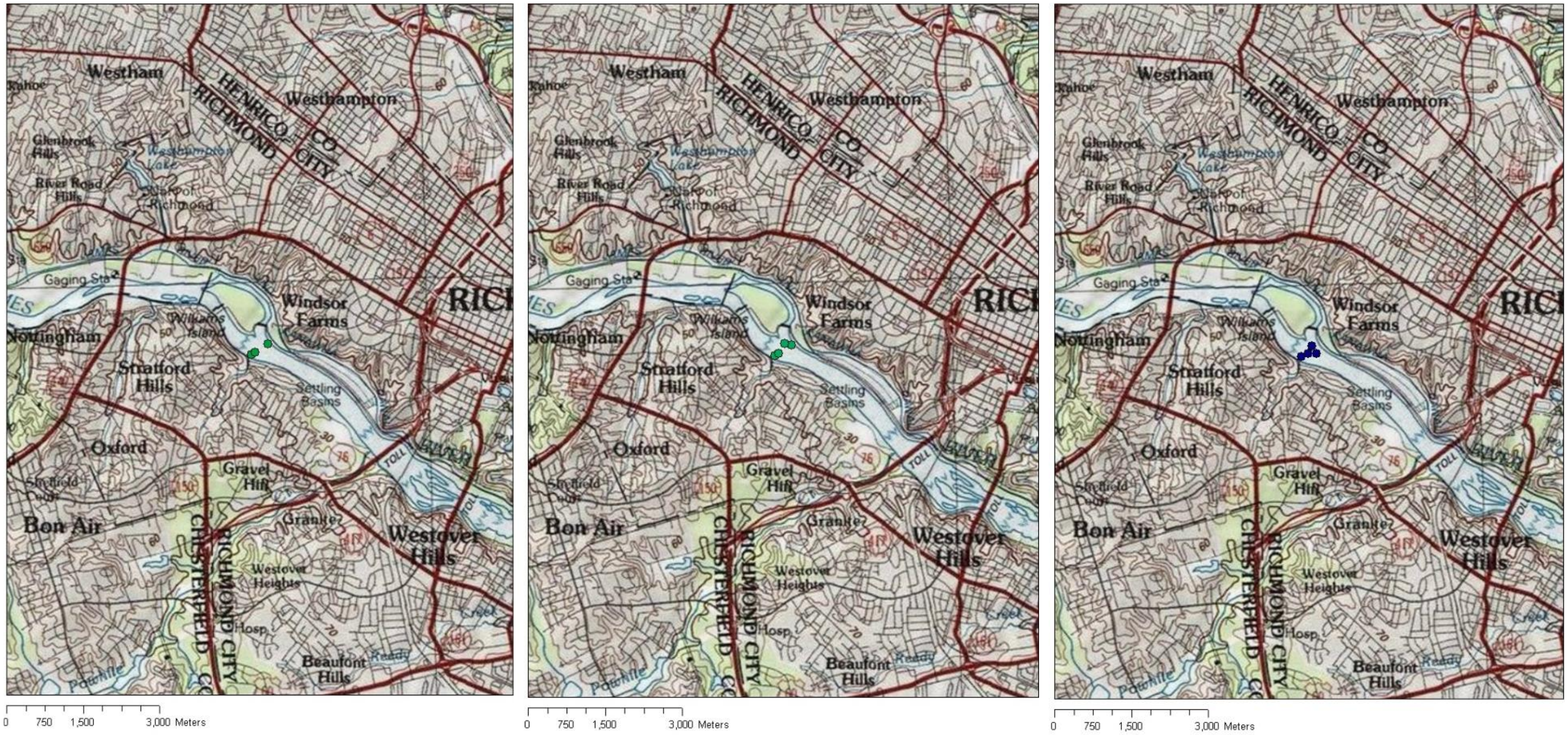

Figure 4.3: Benthic macroinvertebrate sampling locations on the James River. . First panel: spring, second panel: early summer, third panel: late summer.

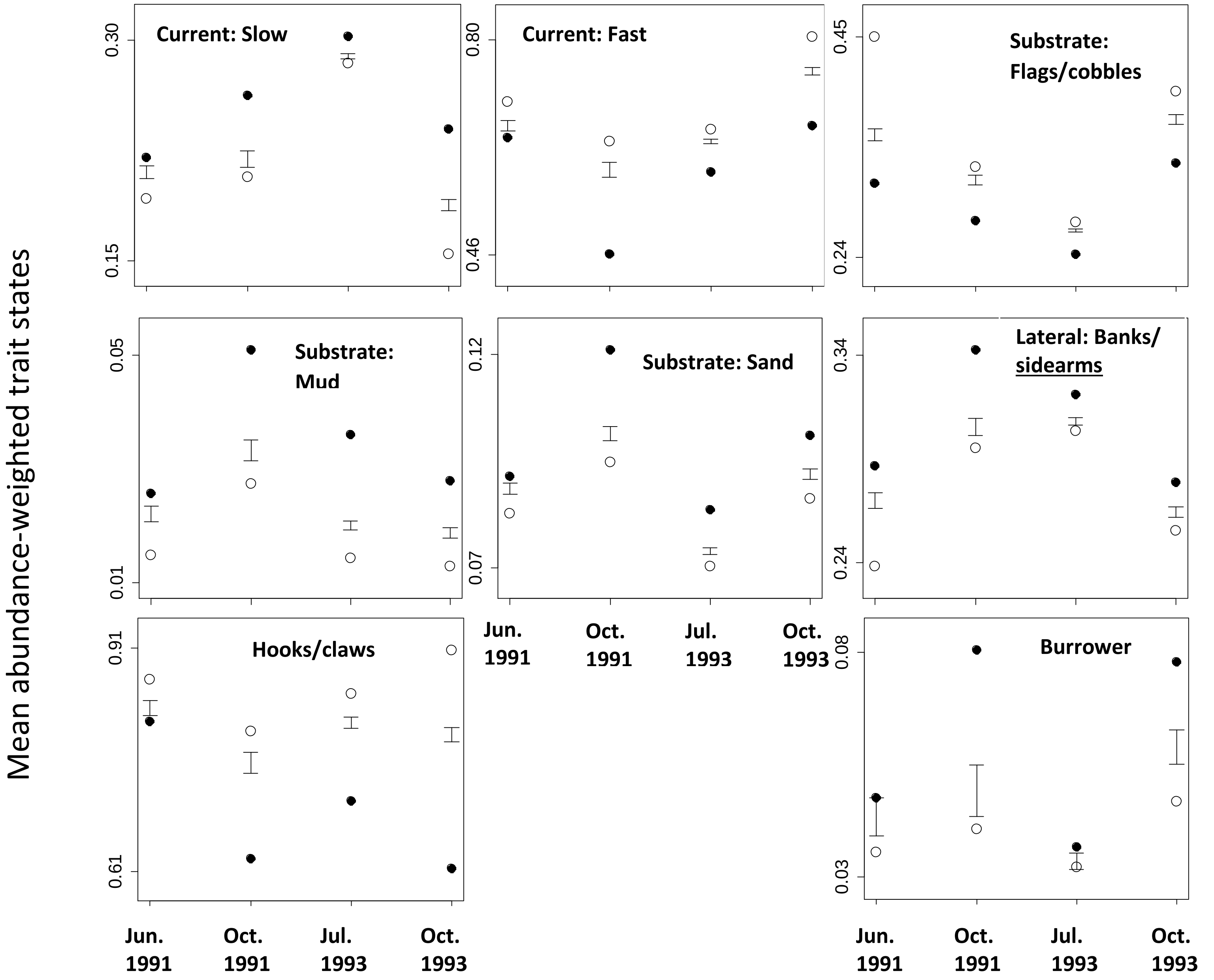

Figure 4.4: Abundance-weighted trait states for River Oriege sites. Closed circles: downstream site, Open circles: upstream site. Vertical bars: 95 % confidence interval for no effect of site on trait state. Note that y-axis scales differ, indicating variable ranges of trait states for each modality.

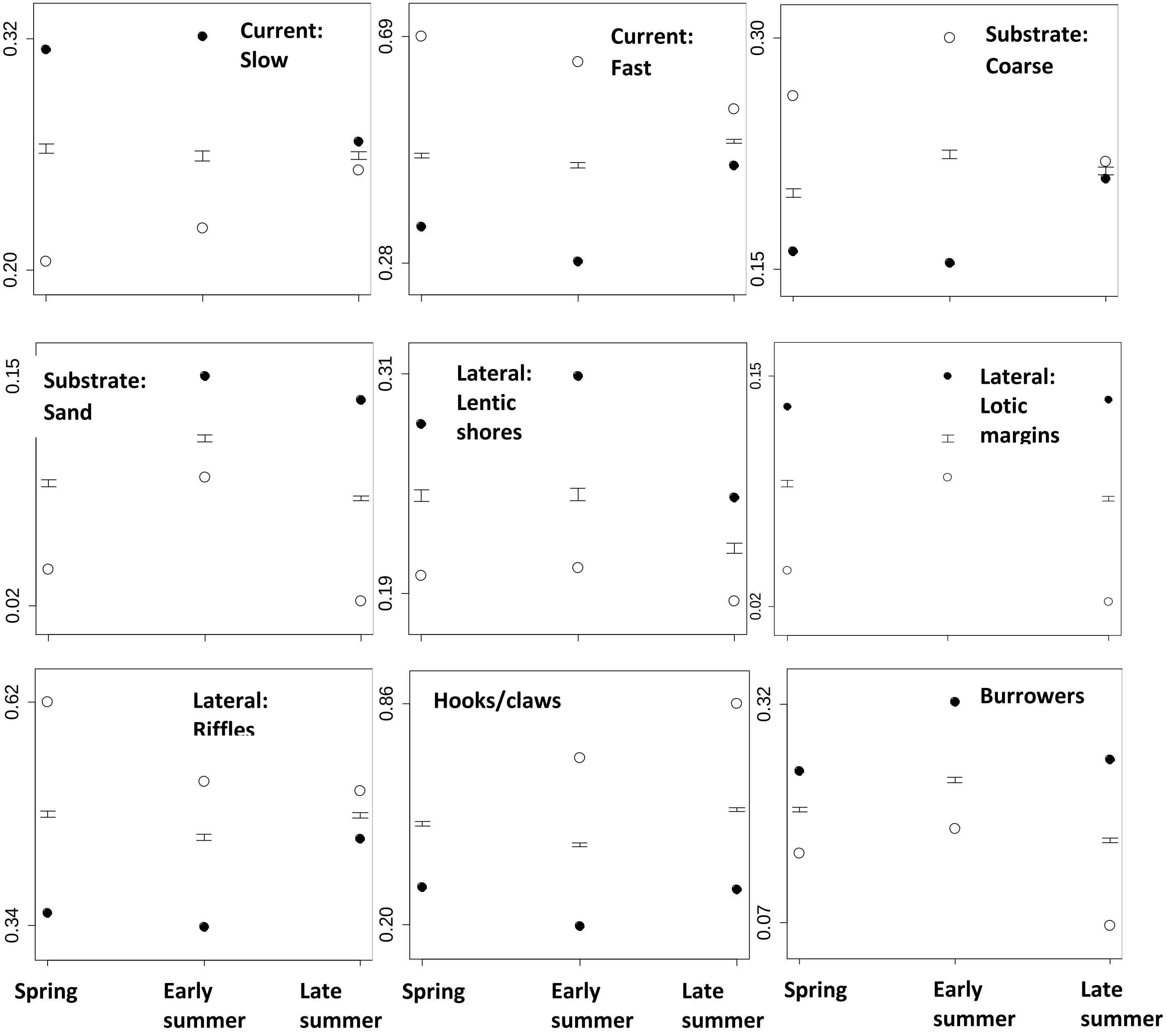

Figure 4.5: Abundance-weighted trait states for North American sites (Ecological traits). Closed circles: Roanoke River, Open circles: James River. Vertical bars: 95 % confidence interval for no effect of site on trait state. Note that y-axis scales differ, indicating variable ranges of trait states for each modality.

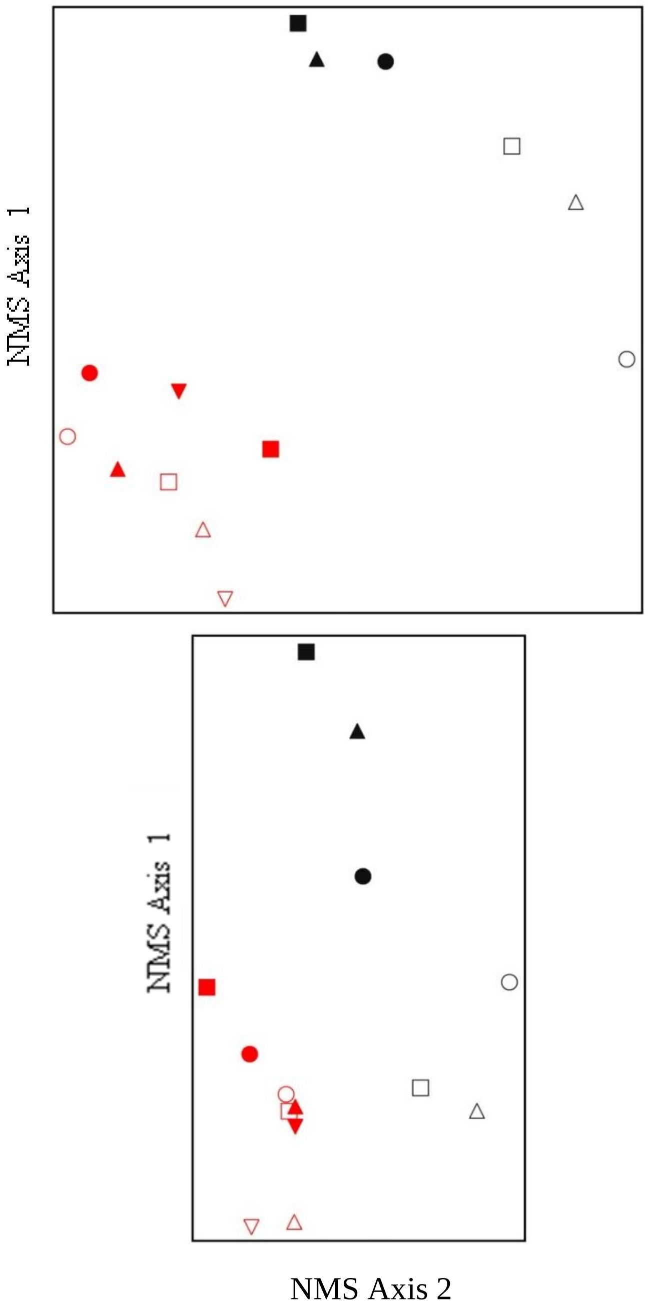

Figure 4.6: Non-metric multidimensional scaling plots of benthic macroinvertebrate assemblages at James River, Roanoke River (Black symbols) and River Oriege (Red symbols) study sites. Filled symbols indicate hydropeaking-impacted sites (Roanoke River and downstream River Oriege sites) and open symbols represent non-impacted sites (James River and upstream River Oriege). Shapes represent different sampling dates (River Oriege: up-pointing triangles: June 1991, squares: October 1991, circles: July 1993, down-pointing triangles: October 1993, James and Roanoke Rivers: triangles: spring, squares, early summer, circles: late summer).

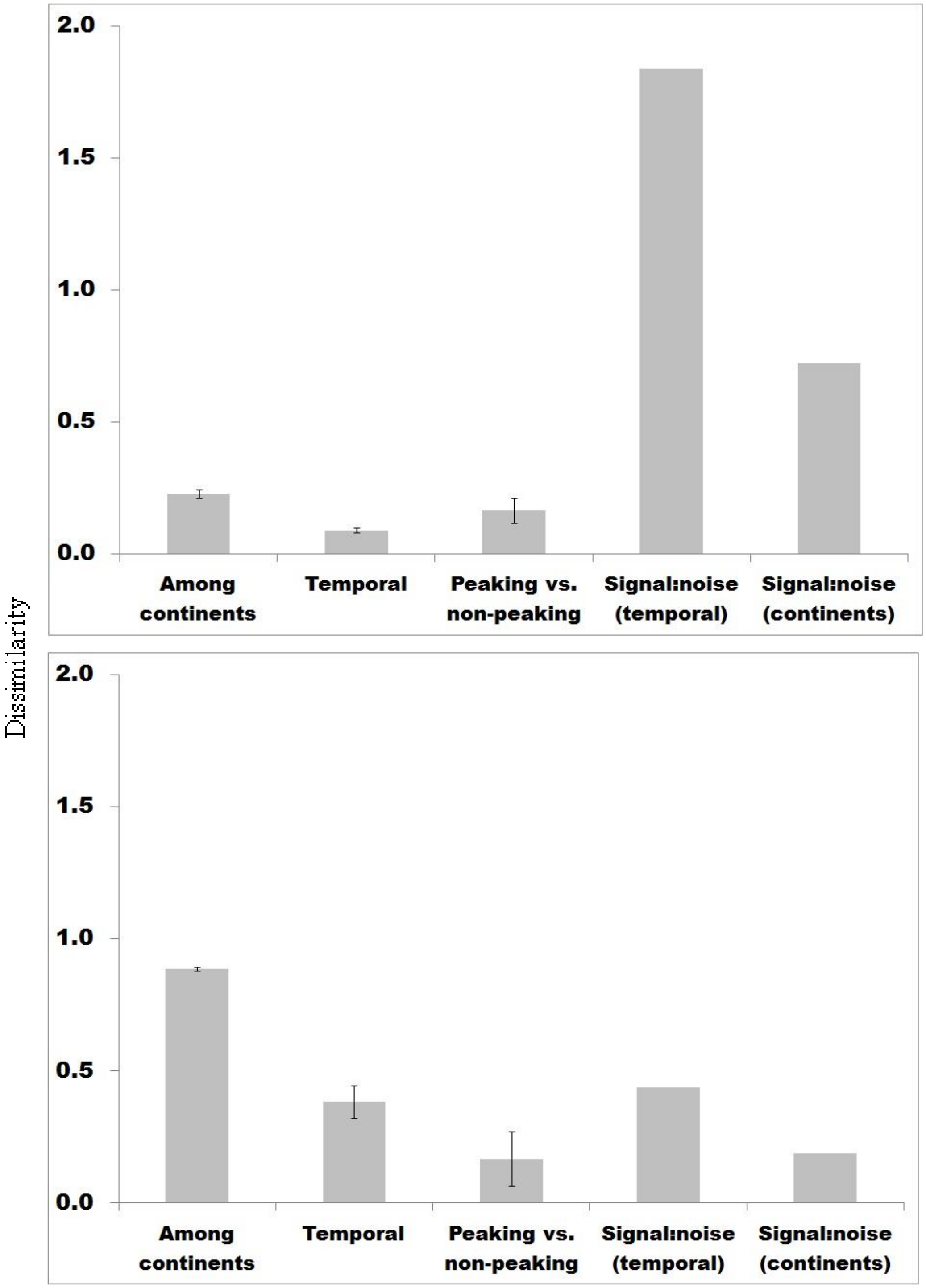

Figure 4.7: Mean Sorenson dissimilarity indices for study sites based on macroinvertebrate taxa (top panel) and ecological traits (bottom panel). Error bars represent one standard error. Signal: noise ratios indicate the ratio of mean pairwise dissimilarity based peaking status to dissimilarity based on temporal variability (Signal:noise [temporal]) and peaking dissimilarity based on peaking status to dissimilarity among North American and European sites (Signal:noise [continents]).

Chapter V

Conclusions and synthesis

Considered in combination, the major conclusions of Chapters 2-4 allow for a greater understanding of the likely consequences of flow modifications associated with hydropower generation. In Chapter 2, it was demonstrated that the primary factor affecting hydropeaking-induced drift of benthic macroinvertebrates was the maximum rate of discharge increase (i.e. the ramping rate) of a given event and, secondarily, that long time periods between pulses served to further increase drift densities. In contrast, the duration and magnitude of each discharge increase (proportional to base flow discharge) had little effect on drift. In Chapter 3, it was shown that taxa with affinities for unstable substrates and slow-water environments exhibited the highest abundances in the drift, in proportion to their abundances on the benthos. Therefore, pulse ramping rate is the most important hydrologic variable to consider for management strategies focused on controlling peaking-induced drift, and the effects of changing ramping rates are expected to have the greatest impacts on taxa inhabiting depositional environments.

Given the large number of works that indicate consistent patterns of elevated macroinvertebrate drift associated with hydropeaking pulses, it is surprising that stronger evidence of the consequences of this phenomenon on population survival are lacking. Chapter 4 of this work provides empirical evidence to this end. Here, it was shown that ecological traits associated with substrate composition, lateral habitat position and flow velocity, as well as biological traits associated with substrate interactions (specifically burrowing within, or clinging onto the substrate) were consistently associated with hydropeaking effects. Taxa with affinities toward depositional environments (slow current, marginal habitats, fine substrates and burrowing taxa) were more prevalent in hydropeaking-affected systems. In contrast, those associated with erosional environments (coarse substrate, main-channel habitats, fast current and clingers) were more prevalent at non-impacted sites. However, as indicated in Chapter 3, these same affinities toward erosional habitat characteristics appear to increase drift susceptibility. Collectively, these results suggest that increased pulse ramping rates, and the resulting increases in drift, may act as positive selective forces for the benthic macroinvertebrate populations adapted to life in the hydropeaking-impacted systems. Therefore, increased pulse ramping rates should be expected to increase the proportional abundances of taxa with high affinities for depositional habitats. This conclusion seems plausible given that macroinvertebrate populations persist in the affected systems despite the fact that hydropeaking operations have occurred over time scales much longer than the generation times of the populations, and because lotic macroinvertebrates typically exhibit rapid recoveries following physical disturbances (Matthaei *et al.*, 1996, Matthaei *et al.*, 1997).

The observational study results presented here would be strengthened by experimental manipulations of flow variables associated with hydropeaking pulses that allow for explicit quantifications of which factors are most important in affecting lotic assemblages. Some experiments have been attempted in artificial flume systems (Imbert and Perry, 2000, Mochizuki *et al.*, 2006, Bruno *et al.*, 2010, Carolli *et al.*, 2010), although none have included explicit statistical comparisons of flow variables and macroinvertebrate assemblage variations. Although in-situ experiments are likely to present considerable logistical challenges, ones that include manipulations of pulse magnitude, ramping rate and pulse duration, conducted repeatedly over varying time scales within natural river systems, would greatly improve our understanding of the effects of pulsed flow events.

Evaluations of the effects of flow modification are typically incomplete because data describing the systems of interest before modification began are lacking. This is the case here, as no studies concerning hydropeaking-impacted river systems were found that presented data that were collected in hydropeaking-impacted systems before construction of the hydropower facility. Given that hydropeaking for electricity generation is projected to increase in the coming decades (EIA, 2015), it is vital that future studies are conducted in systems projected to be modified for hydropeaking operations, before such operations are conducted. These data are essential for establishing true baseline conditions from which changes caused by hydropeaking operations can be measured.

The conclusions of this dissertation provide a foundation for future studies on the effects of anthropogenic flow modifications on aquatic assemblages. As illustrated in the seminal works of Poff *et al.* (1997) and Richter (2010), the impacts of anthropogenic flow modification depend on a suite of flow variables, including the magnitude of disturbance events, their frequency and duration, and the rate at which changes to the flow regime occur. Here, it was shown that, of these, the rate of change in discharge that occurs during a given hydropeaking pulse is most important for governing hydropeaking-induced drift of benthic macroinvertebrates. This conclusion could not have been reached, however, without a quantitative assessment of the effects of each factor, as was conducted in Chapter 2. In Chapters 3 and 4, it was demonstrated that the affinities of biota for different substrate compositions and flow regimes affect their susceptibilities to hydropeaking effects. Therefore, the effects of hydropeaking pulses should be expected to differ among habitat patches, based on differences in substrate composition and hydrology.

Additional studies, conducted across multiple river systems, are needed to improve our understanding of the effects of hydropeaking, and of the effects of flow modification in general. Such works should include explicit quantifications of not only river hydrology, but also of fine-scale variations in physical habitat composition, as well as interactions between hydrology and the substratum (e.g., turbulence effects of substrate and sheer stress imparted on the substrate by flow). Perhaps most importantly, data that describe the physicochemical, hydrologic and ecological conditions of river systems for which flow modifications are planned, collected before such modifications occur, are much-needed. Such data would allow for more comprehensive assessments of the effects of anthropogenic flow modifications than are currently possible.

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Appendix 3.1: Relative abundances, relative drift, and habitat affinities of each taxon on each sampling date. Only taxa observed on the benthos on both dates were used in the relative drift analysis. Light grey cells: propensities above the 90th percentile for all taxa, dark grey cells: propensities above the 95th percentile for all taxa. Rel. abund: relative abundance, embed: substrate embeddedness, veg: vegetation, Ag.1, Ag. 2: aggregate propensities 1 and 2.

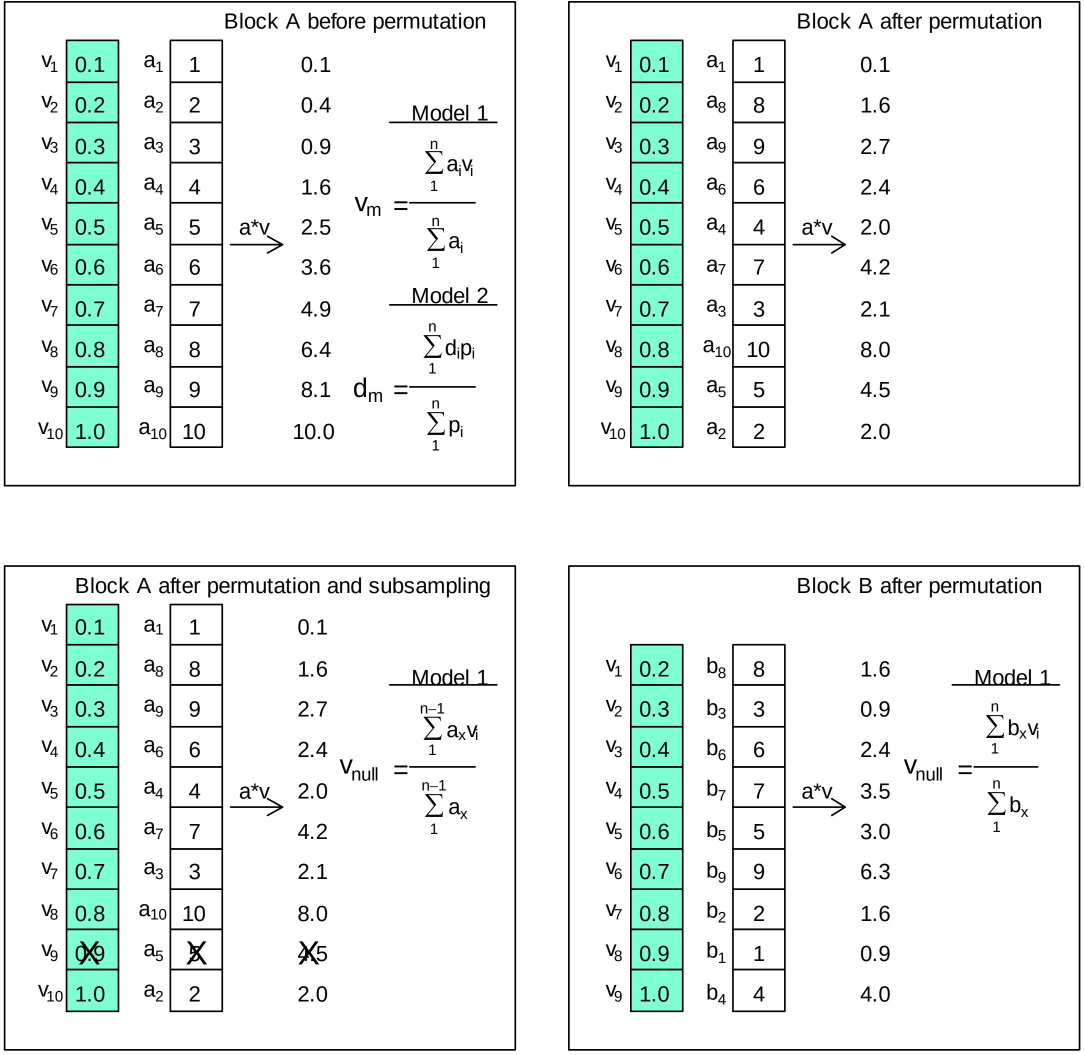
Taxon	Date observed	Rel. abund. benthos (E-02)	Rel. abund. drift (E-02)	Relative drift	Low embed.	Bedrock	Cobble	Gravel	High velocity	Low vegetation	Ag. 1	Ag. 2
Argia	Both	0.20 ; 0.01	0.01 ; 0.02	0.06 ; 2.36	0.27	0.00	0.24	0.97	0.15	0.00	0.00	0.18
Baetidae	Both	0.71 ; 2.16	0.99 ; 4.10	1.40 ; 1.90	0.35	0.58	0.11	0.87	0.60	0.00	0.00	0.19
Brachycentrus	Both	1.03 ; 0.43	0.30 ; 0.40	0.29 ; 0.95	0.45	0.18	0.88	0.21	0.97	0.23	0.46	0.92
Caenis	Both	0.09 ; 0.01	0.13 ; 0.40	1.41 ; 48.24	0.74	0.35	0.73	0.11	0.42	0.12	0.29	0.53
Cambaridae	Both	0.18 ; 0.09	0.00 ; 0.00	0.00 ; 0.00	0.10	0.07	0.45	0.86	0.30	0.48	0.23	0.36
Ceraclea	Both	1.33 ; 0.67	0.66 ; 3.00	0.49 ; 4.51	0.78	0.01	0.80	0.55	0.89	0.24	0.51	0.85
Cheumatopsyche	Both	10.78 ; 4.96	0.89 ; 1.22	0.08 ; 0.25	0.89	0.36	0.37	0.71	0.96	0.69	0.63	0.54
Chimarra	Both	0.06 ; 0.02	0.15 ; 0.76	2.67 ; 30.87	0.96	0.26	0.36	0.68	0.93	0.37	0.52	0.52
Chironomidae	Both	30.53 ; 37.53	54.63 ; 42.92	1.79 ; 1.14	0.48	0.43	0.49	0.70	0.70	0.53	0.53	0.57
Corbicula	Both	1.65 ; 6.36	3.74 ; 0.24	2.26 ; 0.04	0.60	0.04	0.25	0.94	0.18	0.62	0.31	0.21
Corduliidae	Both	0.01 ; 0.01	0.19 ; 1.27	27.17 ; 154.04	0.00	0.27	0.00	0.96	0.56	0.35	0.00	0.00
Crangonyx	Both	0.23 ; 0.30	0.10 ; 0.05	0.43 ; 0.17	0.86	0.00	0.96	0.09	0.64	0.05	0.15	0.77
Cura	Both	0.40 ;	0.20 ;	0.51 ; 0.01	0.76	0.37	0.05	0.97	0.89	0.30	0.16	0.10

Taxon	Date observed	Rel. abund. benthos (E-02)	Rel. abund. drift (E-02)	Relative drift	Low embed.	Bedrock	Cobble	Gravel	High velocity	Low vegetation	Ag. 1	Ag. 2
		1.19	0.01									
Dineutus	Both	0.14 ; 0.07	0.14 ; 0.00	0.97 ; 0.00	0.34	0.24	0.43	0.83	0.38	0.58	0.42	0.40
Elliptio	Both	0.01 ; 0.12	0.00 ; 0.00	0.00 ; 0.00	0.08	0.00	0.18	0.95	0.06	0.35	0.11	0.09
Elmidae	Both	0.17 ; 0.07	0.14 ; 0.11	0.83 ; 1.55	0.17	0.17	0.77	0.45	0.86	0.06	0.16	0.81
Enallagma	Both	0.01 ; 0.02	0.20 ; 1.56	28.01 ; 94.72	0.46	0.64	0.00	0.84	0.12	0.09	0.00	0.00
Hemerodromia	Both	0.06 ; 0.02	0.21 ; 1.80	3.67 ; 109.39	0.51	0.20	0.65	0.22	0.01	0.95	0.05	0.02
Heptageniidae	Both	1.08 ; 1.45	0.22 ; 0.25	0.20 ; 0.17	0.64	0.07	0.54	0.82	0.89	0.04	0.14	0.67
Hyalella	Both	0.62 ; 0.22	0.13 ; 0.42	0.22 ; 1.91	0.55	0.45	0.98	0.00	0.28	0.10	0.24	0.44
Hydracarina	Both	0.11 ; 0.34	2.15 ; 2.63	18.94 ; 7.83	0.11	0.09	0.26	0.94	0.04	0.11	0.08	0.07
Hydrobiidae	Both	13.23 ; 19.57	5.65 ; 1.49	0.43 ; 0.08	0.45	0.02	0.21	0.97	0.74	0.00	0.00	0.32
Hydropsyche	Both	4.65 ; 1.31	4.19 ; 1.70	0.90 ; 1.30	0.76	0.19	0.44	0.69	0.95	0.81	0.68	0.60
Hydroptila	Both	1.78 ; 1.28	5.76 ; 3.37	3.23 ; 2.63	0.70	0.04	0.16	0.99	0.49	0.91	0.37	0.24
Isonychia	Both	0.34 ; 0.06	0.00 ; 0.00	0.00 ; 0.00	0.59	0.20	0.91	0.24	0.81	0.11	0.31	0.86
Leptoxis	Both	18.04 ; 8.67	4.80 ; 0.05	0.27 ; 0.01	0.12	0.19	0.51	0.81	0.58	0.14	0.21	0.54
Lumbriculidae	Both	0.41 ; 0.24	0.15 ; 0.00	0.36 ; 0.00	0.02	0.00	0.35	0.99	0.27	0.20	0.05	0.30
Menetus	Both	0.14 ; 0.11	0.62 ; 0.67	4.38 ; 6.27	0.31	0.00	0.77	0.28	0.36	0.09	0.21	0.50
Naididae	Both	0.17 ;	3.17 ;	18.67 ;	0.51	0.37	0.15	0.91	0.64	0.39	0.31	0.24

Taxon	Date observed	Rel. abund. benthos (E-02)	Rel. abund. drift (E-02)	Relative drift	Low embed.	Bedrock	Cobble	Gravel	High velocity	Low vegetation	Ag. 1	Ag. 2
		0.44	0.42	0.95								
Nematoda	Both	0.03 ; 0.03	1.18 ; 0.38	41.82 ; 11.55	0.37	0.11	0.05	0.97	0.57	0.06	0.10	0.09
Oecetis	Both	0.20 ; 1.74	0.92 ; 1.61	4.66 ; 0.93	0.38	0.37	0.17	0.89	0.15	0.01	0.02	0.16
Orthotrichia	Both	0.03 ; 0.11	0.16 ; 0.46	5.57 ; 4.32	0.95	0.00	0.62	0.40	0.77	0.28	0.53	0.69
Palaemonetes	Both	0.06 ; 0.01	0.01 ; 0.05	0.12 ; 6.2	0.52	0.00	0.76	0.21	0.14	0.09	0.19	0.24
Physa	Both	0.21 ; 3.01	1.65 ; 2.63	8.04 ; 0.87	0.88	0.22	0.79	0.30	0.36	0.02	0.08	0.50
Pisidium	Both	0.08 ; 0.16	0.02 ; 0.05	0.19 ; 0.33	0.15	0.00	0.36	0.94	0.81	0.05	0.13	0.50
Placobdella	Both	0.01 ; 0.07	0.06 ; 0.03	8.23 ; 0.35	0.07	0.22	0.06	0.98	0.67	0.01	0.02	0.11
Pleuroceridae	Both	0.03 ; 0.11	1.02 ; 0.00	35.98 ; 0.00	0.65	0.00	0.74	0.15	0.31	0.09	0.23	0.44
Polycentropodidae	Both	1.08 ; 0.36	0.75 ; 3.65	0.70 ; 10.12	0.68	0.12	0.26	0.89	0.60	0.10	0.23	0.36
Simuliidae	Both	0.94 ; 0.34	2.68 ; 4.01	2.84 ; 11.90	0.93	0.84	0.03	0.90	0.98	0.52	0.12	0.06
Sphaerium	Both	0.09 ; 1.81	0.04 ; 0.01	0.42 ; 0.00	0.83	0.48	0.67	0.40	0.85	0.15	0.37	0.75
Tricorythodes	Both	8.98 ; 3.79	0.65 ; 1.73	0.07 ; 0.46	0.34	0.08	0.75	0.72	0.46	0.08	0.21	0.57
Trienodes	Both	0.02 ; 0.05	0.03 ; 0.38	1.46 ; 7.68	0.12	0.06	0.26	0.77	0.37	0.25	0.21	0.31
Atrichopogon	16-Jun	0.08	0.15	1.88	0.24	0.00	0.55	0.00	0.00	0.75	0.00	0.00
Corydalus	16-Jun	0.02	0.00	0.00	0.57	0.00	0.25	0.83	0.79	0.64	0.47	0.38
Basiaeschna	7-Jul	0.01	0.00	0.00	0.53	0.00	0.51	0.00	0.93	0.46	0.56	0.66
Boyeria	7-Jul	0.01	0.00	0.00	0.54	0.00	0.55	0.00	0.93	0.47	0.58	0.69

Taxon	Date observed	Rel. abund. benthos (E-02)	Rel. abund. drift (E-02)	Relative drift	Low embed.	Bedrock	Cobble	Gravel	High velocity	Low vegetation	Ag. 1	Ag. 2
Campeloma	7-Jul	0.01	0.00	0.00	0.53	0.71	0.00	0.24	0.78	0.37	0.00	0.00
Ferrissia	7-Jul	0.07	0.15	2.14	0.90	0.00	0.93	0.18	0.41	0.76	0.67	0.57
Gomphus	7-Jul	0.04	0.00	0.00	0.09	0.00	0.20	0.91	0.44	0.44	0.19	0.27
Macrostemum	7-Jul	0.31	0.93	3.00	0.46	0.00	0.00	0.96	0.86	0.56	0.00	0.00
Nectopsyche	7-Jul	0.10	0.56	5.60	0.05	0.57	0.02	0.96	0.06	0.06	0.04	0.03
Palpomyia	7-Jul	0.02	0.22	11.00	0.07	0.00	0.03	0.97	0.08	0.07	0.05	0.04
Tubificidae	7-Jul	0.11	0.00	0.00	0.05	0.43	0.04	0.98	0.50	0.20	0.08	0.08
				Median	0.48	0.11	0.36	0.82	0.57	0.20	0.19	0.36
				90th percentile	0.89	0.53	0.85	0.97	0.93	0.73	0.55	0.76
				95th percentile	0.94	0.66	0.94	0.98	0.96	0.84	0.64	0.85

Appendix 3.2: Explanation of permutation scheme developed for Chapter 3.



Block A before permutation

v_1	0.1	a_1	1	0.1
v_2	0.2	a_2	2	0.4
v_3	0.3	a_3	3	0.9
v_4	0.4	a_4	4	1.6
v_5	0.5	a_5	5	2.5
v_6	0.6	a_6	6	3.6
v_7	0.7	a_7	7	4.9
v_8	0.8	a_8	8	6.4
v_9	0.9	a_9	9	8.1
v_{10}	1.0	a_{10}	10	10.0

Model 1

$$v_m = \frac{\sum_1^n a_i v_i}{\sum_1^n a_i}$$

Model 2

$$d_m = \frac{\sum_1^n d_i p_i}{\sum_1^n p_i}$$

Block A after permutation

v_1	0.1	a_1	1	0.1
v_2	0.2	a_8	8	1.6
v_3	0.3	a_9	9	2.7
v_4	0.4	a_6	6	2.4
v_5	0.5	a_4	4	2.0
v_6	0.6	a_7	7	4.2
v_7	0.7	a_3	3	2.1
v_8	0.8	a_{10}	10	8.0
v_9	0.9	a_5	5	4.5
v_{10}	1.0	a_2	2	2.0

Block A after permutation and subsampling

v_1	0.1	a_1	1	0.1
v_2	0.2	a_8	8	1.6
v_3	0.3	a_9	9	2.7
v_4	0.4	a_6	6	2.4
v_5	0.5	a_4	4	2.0
v_6	0.6	a_7	7	4.2
v_7	0.7	a_3	3	2.1
v_8	0.8	a_{10}	10	8.0
v_9	~~0.9~~	a_5	~~5~~	~~4.5~~
v_{10}	1.0	a_2	2	2.0

Model 1

$$v_{null} = \frac{\sum_1^{n-1} a_x v_i}{\sum_1^{n-1} a_x}$$

Block B after permutation

v_1	0.2	b_8	8	1.6
v_2	0.3	b_3	3	0.9
v_3	0.4	b_6	6	2.4
v_4	0.5	b_7	7	3.5
v_5	0.6	b_5	5	3.0
v_6	0.7	b_9	9	6.3
v_7	0.8	b_2	2	1.6
v_8	0.9	b_1	1	0.9
v_9	1.0	b_4	4	4.0

Model 1

$$v_{null} = \frac{\sum_1^n b_x v_i}{\sum_1^n b_x}$$

Schematic of permutation models developed for determining habitat propensities (Model 1) and for evaluating associations between habitat propensities and relative drift (Model 2). For model 1, shaded cells represent measured flow velocities for each of ten hypothetical samples (m/s; v_1:v_{10}) and white cells represent corresponding abundances (a_1:a_{10}) of a hypothetical taxon in these samples. The mean abundance-weighted velocity inhabited by an individual in the population is calculated as in Model 1 (v_m: top left panel). The abundance vector is then permuted (top right panel), the weighted mean is re-calculated, and the process reapeated 1000 times to derive a null distribution of weighted-average velocities expected by chance (v_{null}; bottom panels). The propensity of the taxon for high-flow velocites is the proportion of v_{null} values that are less than v_m, which corresponds to the probability that the mean velocity inhabited by an individual in the population is higher than expected by chance. The bottom panels show the process of randomly eliminating one sample from Block A after each permutation to maintain a balanced study designed when a blocked analysis is employed. For model 2, shaded cells represent relative drift of each observed taxon, and white cells represent the corresponding trait propensities of the taxa for a given trait. The mean propensity-weighted relative drift is then calculated as in Model 2 (d_i: top left panel).

Appendix 4.1: Supplemental information on macroinvetebrate traits used in this investigation.

Trait state derivation

Quantitative macroinvertebrate trait states were developed from the European Traits Database of Tachet et al. (2000; complete database provided by P. Usseglio-Polatera) and the North American database of Vieira et al. (2006).

Records in the North-American database (NA database) represent individual publications. For most trait states, records from the NA database were converted into quantitative, continuous trait states by first selecting all relevant records for each taxon (discussed below) and then calculating the proportion of those records that addressed a given trait~~,~~ and indicated that the taxon occurred within each category. For example, a taxon indicated to occur in fast current by two studies, and in slow current by one study would be assigned continuous trait states of 0.66 and 0.33 for the *current* trait categories *fast current* and *slow current*. Biological trait states occurring in the NA database as binary data (i.e. present or absent) were assigned based on the majority of relevant records.

The NA database contains trait information aggregated at the genus level, as well as records for individual species within each genus. Records used in this analysis included all genus-level records for each taxon, species-level records from North Carolina and Virginia, all US states contiguous to North Carolina or Virginia, as well as Pennsylvania and Ohio.

The European database (EU database) consists of trait-state values ranging from 0-5 for each category, compiled primarily at the genus level. Increasing trait state values within a given category indicate increasing propensities toward that category. These rankings were based on a comprehensive review of over 6000 published records of macroinvertebrate traits (see Usseglio-Polatera et al. 2000 and Tachet et al. 2002 for further details). For continuous EU trait states, these values were converted to the same 0-1 scale as for the NA trait states by dividing each 0-5 value by the sum of the values for a given taxon across all categories. None of the morphology-associated trait categories (i.e. those for Shape, Integument type, Silk, Case and Hooks/Claws) were included in the European database, therefore, these were assigned based on knowledge of the morphology of each taxon.

Evaluation of peaking effects on selected traits

Ecological traits selected to assess hydropeaking effects were:

-The trait *current*, which included 3 categories indicating current preference for each dataset: *fast current*, *slow current*, and *null current* (EU database) or *quiet current* (NA database). Both databases originally contained four current categories, but the categories indicating the fastest current regimes; *fast turbulent* and *fast laminar* in the North American database and *medium* and *fast* in the European database were combined, because it was judged that taxa classified into these categories represented those generally disposed to rapid-flow, lotic environments.

-The *substrate* trait categories *cobble* and *boulder* of the NA database were combined to comprise the *coarse substrate* category, which was considered equivalent to the flags/cobbles category of the EU database. The categories *sand* and *silt* were listed in both databases and considered equivalent. The category *mud* in the EU database had no apparent equivalent in the NA database.

-The trait water body in the European database and the trait lateral habitat zone in the NA database were considered equivalent because both describe aquatic habitat types within the lateral continuum from flood plains to channel thalwegs in lotic watersheds. Within these traits, the categories *lotic margins* and *lentic shores* in the NA database were considered equivalent to the category *banks/sidearms* in the EU database, and the category *riffles* in the NA database was considered equivalent to the category *river channels* in the EU database.

Biological trait categories had (or were given) the same names in the two databases. Those considered equivalent among databases, and selected to assess hydropeaking effects, were:

Movement/substrate relation trait, categories: *clinger* and *burrower*, *scleritization* trait, category: *all scleratized*, *shape* trait, categories: *flat* and *streamlined*, and the single-category traits *hooks/claws*, *silk*, and *suckers*. The *clinger* category for the EU data was derived by summing the state values for the original categories *temporarily attached* and *permanently attached* in the EU database, as no such distinction was made in the NA database.

Vita

Andrew Louis Garey was born on April 4, 1976, in Richmond, Virginia, and is an American citizen. He graduated from Atlee High School in Hanover, Virginia in 1994. He received his Bachelor of Science in Environmental Science from Virginia Tech, Blacksburg, Virginia in 2000 and his Master of Science in Biology from Virginia Commonwealth University, Richmond, Virginia in 2008.