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Ecological responses to altered flow regimes: a literature review to inform the science and management of environmental flows

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SUMMARY

1. In an effort to develop quantitative relationships between various kinds of flow alteration and ecological responses, we reviewed 165 papers published over the last four decades, with a focus on more recent papers. Our aim was to determine if general relationships could be drawn from disparate case studies in the literature that might inform environmental flows science and management.
2. For all 165 papers we characterised flow alteration in terms of magnitude, frequency, duration, timing and rate of change as reported by the individual studies. Ecological responses were characterised according to taxonomic identity (macroinvertebrates, fish, riparian vegetation) and type of response (abundance, diversity, demographic parameters). A 'qualitative' or narrative summary of the reported results strongly corroborated previous, less comprehensive, reviews by documenting strong and variable ecological responses to all types of flow alteration. Of the 165 papers, 152 (92%) reported decreased values for recorded ecological metrics in response to a variety of types of flow alteration, whereas 21 papers (13%) reported increased values.
3. Fifty-five papers had information suitable for quantitative analysis of ecological response to flow alteration. Seventy per cent of these papers reported on alteration in flow magnitude, yielding a total of 65 data points suitable for analysis. The quantitative analysis provided some insight into the relative sensitivities of different ecological groups to alteration in flow magnitudes, but robust statistical relationships were not supported. Macroinvertebrates showed mixed responses to changes in flow magnitude, with abundance and diversity both increasing and decreasing in response to elevated flows and to reduced flows. Fish abundance, diversity and demographic rates consistently declined in response to both elevated and reduced flow magnitude. Riparian vegetation metrics both increased and decreased in response to reduced peak flows, with increases reflecting mostly enhanced non-woody vegetative cover or encroachment into the stream channel.
4. Our analyses do not support the use of the existing global literature to develop general, transferable quantitative relationships between flow alteration and ecological response; however, they do support the inference that flow alteration is associated with ecological change and that the risk of ecological change increases with increasing magnitude of flow alteration.
5. New sampling programs and analyses that target sites across well-defined gradients of flow alteration are needed to quantify ecological response and develop robust and

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general flow alteration–ecological response relationships. Similarly, the collection of pre- and post-alteration data for new water development programs would significantly add to our basic understanding of ecological responses to flow alteration.

Keywords: ecological response, fish, flow alteration, macroinvertebrates, riparian, streams and rivers

Introduction

The importance of a river's flow regime for sustaining biodiversity and ecological integrity is well established (Poff *et al.*, 1997; Hart & Finelli, 1999; Bunn & Arthington, 2002). Streamflow is viewed as a 'maestro' (Walker, Sheldon & Puckridge, 1995) or 'master variable' (Power *et al.*, 1995) that shapes many fundamental ecological characteristics of riverine ecosystems. From a basic ecological perspective, extreme events such as high flows and low flows exert selective pressure on populations to dictate the relative success of different species, and patterns of variation in 'sub-lethal' flows can influence the relative success of different species and regulate ecosystem process rates (Resh *et al.*, 1988; Hart & Finelli, 1999). The range and variation of flows over recent historical time, referred to as the natural flow regime (Richter *et al.*, 1996; Poff *et al.*, 1997), sets a template for contemporary ecological processes (Resh *et al.*, 1988; Doyle *et al.*, 2005), evolutionary adaptations (Lytle & Poff, 2004) and native biodiversity maintenance (Bunn & Arthington, 2002).

Flow regime varies geographically in response to climate (precipitation and temperature) and catchment controls on runoff (topography, geology, land cover, position in network). All flow regimes may be considered unique in some measure of their details; however, many authors have stressed the need to characterise the similarity among flow regimes to provide typologies that can support *a priori* predictions (e.g. ecological and evolutionary convergence under geographically disjunct selection regimes) and development of general principles for flow regime management (Arthington *et al.*, 2006; see Poff *et al.*, 2006 for a brief review).

Numerous case studies (and expert knowledge) provide the foundation of our scientific understanding that many types of flow alteration (e.g. magnitude, frequency, and timing) induce a variety of ecological responses (Bunn & Arthington, 2002). This, combined with the recognition that ubiquitous flow alteration threatens the biodiversity and ecosystem functions of rivers on a global scale (Postel & Richter, 2003; Nilsson *et al.*, 2005; Dudgeon *et al.*, 2006; Poff *et al.*, 2007) has led to an accelerating interest in developing a general, quantitative understanding of aquatic ecosystem response to various types and degrees of flow alteration. Such understanding is needed to help support scientifically defensible guidelines for developing flow standards that could be applied to all streams and rivers, even those lacking baseline data (Arthington *et al.*, 2006; see Poff *et al.*, 2010).

A comprehensive synthesis of case studies has the potential to reveal generalised, possibly quantitative, relationships between ecological responses and specific types of flow alteration. Such a synthesis can advance general understanding in the science of environmental flows (Poff *et al.*, 2003) and can help set priorities in the next phases of hydro-ecological research to support development and implementation of regional environmental flow standards (Poff *et al.*, 2010). Reviews to date have been incomplete or inconclusive. For example, Poff *et al.* (1997) and Bunn & Arthington (2002) selectively reviewed the literature and clearly illustrated general ecological principles of flow regime alteration. In the most complete effort to date, Lloyd *et al.* (2003) examined 70 studies for relationships between hydrologic change and ecological or geomorphological change and reported that 87% of the studies documented changes in either or both of these variables in response to reduced flow volumes. However, a more focused quantitative analysis of only 14 studies found no evidence to reject the null hypothesis that ecological change was independent of hydrological change, nor was there any simple linear or threshold relationship between the size of ecological change and the size of the hydrological change.

Lloyd *et al.* (2003) identified several constraints that limit attempts to derive quantitative relationships from a literature review, including lack of control or reference sites for 'unaltered' conditions, other environmental changes (e.g. sediment flux, temperature) occurring at the impacted sites and inadequate historical information. Given that alteration of flow regimes is typically confounded with other environmental factors, we would not necessarily expect unambiguous relationships between single measures of flow alteration and ecological response (see Konrad, Brasher & May, 2008; Poff *et al*., 2010). However, any general relationships that did emerge would presumably indicate strong responses to flow alteration and thus be of both scientific and management interest. Lloyd *et al*. (2003) also suggested that a larger dataset that spanned a broader range of response types and hydrologic alterations might be able to detect more robust relationships.

With these considerations in mind, we had three major goals for the present paper. First, we aimed to conduct a more comprehensive review of the literature on ecological responses to alteration of natural flow regimes, focusing primarily on publications in the last 10 years, i.e. since the publication of Poff *et al*. (1997) who reviewed much of the older literature. Second, where possible, we wanted to assemble quantitative relationships published in these disparate studies to determine if any statistically supported patterns could be extracted between defined types of flow alteration and ecological response metrics. In particular we were interested in detecting any potential 'threshold' relationships that would be especially useful in a management context (see Arthington *et al*., 2006). Third, we wished to identify 'gaps' in information presented in the published papers that represent research needs and priorities to advance the development of robust flow alteration–ecological response relationships that can support development of science-based, regional flow guidelines, as proposed in the new framework called ELOHA – Ecological Limits of Hydrological Alteration (Poff *et al*., 2010).

Methods

Literature review and qualitative relationships

We extensively reviewed the literature and compiled a list of 165 papers that reported on either aquatic (in-channel) or riparian responses to flow regime alteration. Most of the studies were conducted in North America (89), with good representation from Europe (44) and Oceania (25), but with only a few from South America (4) and Africa (3). We logged responses as ecosystem, community, or population-level responses. Most papers (145) reported responses in terms of population or community change, and we partitioned them into six taxonomic categories: macroinvertebrates, fishes, riparian vegetation, aquatic primary producers, birds, and amphibians (Fig. 1).

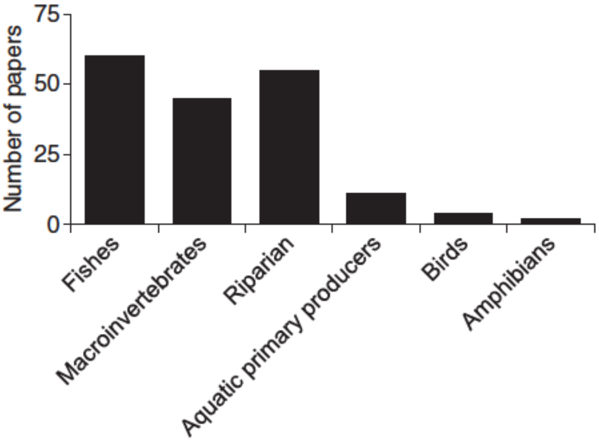

Fig. 1 The number of papers (out of a total of 145 papers) that measured population or community responses to flow alteration, by organism category. Some papers reported on multiple categories of organisms; thus the number of papers across categories adds up to more than 145.

Flow alteration often involves simultaneous modification of several components of the natural flow regime (magnitude, frequency, duration, timing and rate-of-change; Poff *et al.*, 1997). Many papers reported on more than one altered flow component; however, for the purposes of our analysis we focused on the primary flow component reported for each study, i.e. the one that was given the most emphasis by the authors, either in terms of alteration or study design. Most papers (99) reported flow alteration primarily in terms of some metric of magnitude. Changes in duration (25), timing (16), frequency (16) and rate of change (5) were also reported, and four papers did not specify a flow component. Of the total number of studies that we reviewed, 70% focused only on flow modification. A subset of the 165 papers also mentioned alterations in other environmental drivers, including sediment (14%), temperature (11%), or sediment plus temperature (5%).

Most of the flow alterations reported in the reviewed studies were primarily the result of dams and impoundments (88 papers). Other flow alterations resulted from water diversions (17), groundwater abstraction (6) and levees (7). A few studies reported flow alterations from weirs, road construction or channelisation, but many did not report a source (32) or reported unspecified multiple sources of factors affecting the flow regime.

For all 165 papers we summarised the reported results 'qualitatively', i.e. we categorised the reported change in ecological metrics that were associated with the different kinds of flow alteration. This general analysis was conducted to provide a broad synopsis of the reviewed literature.

Quantitative relationships

A specific goal of this study was to determine if the published literature could be used to quantify relationships between flow alteration and ecological change. To do this, we identified papers that reported both flow alteration and ecological response in quantitative units that could be represented as percent change. Pre-impact (reference) and post-impact (altered) data had to be reported for both for streamflow conditions and for ecological response variables. Some papers reported pre-impact and/or post-impact flow or ecological data as a range; in those cases, we recorded percent change as the midpoint of the range. To increase sample size, we included papers that used an upstream reference site (e.g. river reach above a dam) for the pre-impact data.

Of the 165 papers in the total qualitative analysis, only 34 met our criteria to support a quantitative analysis. However, we contacted the authors of several papers reporting some quantitative data to determine if more extensive quantitative data were available through field notes or other unpublished data sources. We obtained quantitative data from an additional 21 papers using the author surveys, giving a total of 55 studies suitable for our quantitative analysis. Because 20 of these 55 papers reported on more than one ecological response variable, there were a total of 89 data points relating ecological response to flow alteration. A few papers reported on other factors, such as changes in temperature or sediment that were related to flow alteration and may have therefore also affected an ecological response. Because these factors were neither uniformly reported nor generally quantified relative to the pre-alteration state, we excluded them from our analysis. Therefore, we attempted only to identify direct relationships between reported flow alteration and ecological change.

For each of the 55 studies we identified the major type of flow alteration as noted by the authors or the flow component with the largest percent change, as described above. Most studies reported alteration in flow magnitude, frequency, and/or duration. Many studies reported changes to multiple components of the flow regime; however, we chose to examine only changes in the primary type of flow alteration because we did not have a large enough sample size to examine ecological response to all reported combinations of altered flow variables. Of the 89 total data points (from 55 studies), 65 were related primarily to magnitude, 15 to frequency, and the remaining nine were spilt among duration, timing and rate of change. Therefore, we restricted our quantitative analysis to the 65 data points relating ecological response to alteration in flow magnitude.

The metric of alteration of flow magnitude that could be extracted from the 55 studies fell into one of four categories: peak flow (reported as alterations in flood, peak, or high flow), average discharge (reported as alteration in total flow or mean flow), base flow (reported as alteration in base flow, low flow or drought conditions) and short-term variation (reported as a change in magnitude that occurred over a period of hours, or less than 1 day). Small sample sizes limited our ability to examine multiple ecological responses to each of these metrics of flow magnitude alteration; therefore, we expressed flow alteration as the degree of alteration of flow magnitude for any of these four categories. Values ranged from −100% (i.e. a 100% decrease in flow magnitude or complete loss of all flow) to +800% (i.e. nine times the flow compared with pre-impact conditions). Because of this wide range in values, we scaled the response to fall within the range of −100% to +100% by truncating all values greater than 100% (i.e. all alterations in magnitude greater than 100% were assigned the value of 100%).

Ecological data were organised in terms of taxonomic group (macroinvertebrates, fish and riparian species) and in terms of the type of ecological response (changes in species or population abundance, demographic rates or community diversity, which included both taxonomic richness and abundance-weighted community diversity). Few data were available for aquatic primary producers, birds or amphibians (Fig. 1) so these taxonomic groups were not included in the quantitative analysis. Virtually no information was reported on ecological process rates (e.g. metabolism, production) and thus ecosystem functional responses were not represented in our analyses. As with our calculations of change in flow metrics, we calculated the percent change for ecological response variables by comparing the pre-impact (reference or upstream condition) and post-impact (altered or downstream condition) data. Ecological response metrics could either increase or decrease in value relative to the pre-impact condition. We plotted the percent change in each ecological response against the percent change in flow magnitude to visualise relationships and to assess potential statistical associations.

A bibliography of all reviewed papers is available as an online appendix (cite URL for *Freshwater Biology* supplementary material website). In this appendix, we have also indicated the 55 papers used in the quantitative analysis.

Results

Qualitative analysis

A summary of the data used for the qualitative analysis, in terms of flow components affected and taxa studied, is presented in Table 1. The majority of ecological changes were reported as responses to altered flow magnitude, most commonly as high flow stabilisation. Ecological responses to altered magnitude were largely reported as decreases, although some increases in value of an ecological response variable occurred, more so for riparian than instream taxa.

Alterations in flow frequency were reported primarily as decreases in frequency of floods or peak flows. All papers focusing on aquatic macroinvertebrates and fishes indicated negative ecological responses, but one also reported an increased response. Riparian responses to flow frequency alteration were consistently reported to decline; however, half of the papers also indicated some increase in response.

Alterations in flow duration, mostly in the form of changes in the duration of floodplain inundation, were primarily associated with decreases in both instream and riparian ecological variables. Similarly, changes in the timing of flows due to loss of seasonal flow peaks reduced both aquatic and riparian variables. Only a few studies reported ecological responses to alterations in the rate of change of flows and results were mixed.

Quantitative analysis

Quantitative estimates of macroinvertebrate response to flow magnitude alteration were available for 25 data points. Macroinvertebrate abundance and diversity both generally declined in response to alteration in flow magnitude, whether an increase or a decline (Fig. 2). Most measurements of flow magnitude represented large changes of near −100% or +100%, with few intermediate values. This lack of data points throughout the entire gradient of alteration makes it difficult to detect any threshold or nonlinear responses to changes in flow magnitude. Flow alteration was measured as either a change in total discharge or a change in base flow (i.e. low flow or drought conditions). There was no consistent difference in direction or magnitude of macroinvertebrate response in terms of source of flow magnitude alteration.

Fishes showed consistent negative responses to alteration in flow magnitude, whether measured by changes in abundance, population demographic parameters or diversity of assemblages (Fig. 3). As with macroinvertebrates, response of fishes tended to be measured in relation to higher values of flow alteration (−50% to −100% and +75% to +100%). The lack of data points in the more moderate ranges of flow alteration precluded estimation of any potential threshold response and limited inference on lower levels of alteration that may not have negative impacts on fish species and assemblages. The two specific types of flow alteration reported for these papers were changes in average discharge and short-term variation, for which both increases and declines in flow magnitude were reported.

Riparian responses did not demonstrate any consistent trends with respect to alteration in flow magnitude (Fig. 4). The studies we reviewed examined reductions in peak discharge (15 papers) and average flow (five papers); no increases in discharge magnitudes were reported. All of the riparian studies recorded changes in peak flows, so riparian responses in Fig. 4 can be associated with decreases in flood peaks, leading to reduction or elimination of overbank

Table 1 The total number of studies that reported on each flow component, the number of studies that showed decreases or increases in ecological responses to flow alteration, the primary flow alterations reported for each flow component, number of papers reporting each type of alteration as the primary alteration, and most common ecological responses reported from a literature review of 165 papers We only present the most common types of flow alteration reported for aquatic (in-channel) and riparian organisms (reported by ≥4 papers for all flow components except rate of change)

Flow component	Organism(s) studied	Total no papers	No papers reporting decreased ecological responses	No papers reporting increased ecological responses	Primary flow alteration	No papers	Common ecological responses
Magnitude	Aquatic	71	66	5	Stabilisation (loss of extreme high and/or low flows)	31	Loss of sensitive species Reduced diversity Altered assemblages and dominant taxa Reduced abundance Increase in non-natives
					Greater magnitude of extreme high and/or low flows	23	Life cycle disruption Reduced species richness Altered assemblages and relative abundance of taxa Loss of sensitive species
	Riparian	28	24	7	Stabilisation (loss of peak flows)	18	Altered recruitment; failure of seedling establishment Terrestrialisation of flora Increased success of nonnatives Lower species richness Vegetation encroachment into channels Increased riparian cover Altered assemblages
Frequency	Aquatic	12	12	1	Decreased frequency of peak flows	8	Aseasonal reproduction Reduced reproduction Decreased abundance or extirpation of native fishes Decreased richness of endemic and sensitive species Reduced habitat for young fishes
	Riparian	4	4	2	Decreased frequency of peak flows	4	Shift in community composition Reductions in species richness Increase in wood production

Table 1 (*Continued*)

Flow component	Organism(s) studied	Total no papers	No papers reporting decreased ecological responses	No papers reporting increased ecological responses	Primary flow alteration	No papers	Common ecological responses
Duration	Aquatic	7	7	1	Decreased duration of floodplain inundation	4	Decreased abundance of young fish Change in juvenile fish assemblage Loss of floodplain specialists in mollusk assemblage
	Riparian	18	17	1	Decreased duration of floodplain inundation	13	Reduced growth rate or mortality Altered assemblages Terrestrialisation or desertification of species composition Reduced area of riparian plant or forest cover Increase in abundance of nonnatives
Timing	Aquatic	12	12	0	Shifts in seasonality of peak flows	12	Disruption of spawning cues Decreased reproduction and recruitment Change in assemblage structure
					Increased predictability	5	Change in diversity and assemblages structure Disruption of spawning cues Decreased reproduction and recruitment
	Riparian	4	4	0	Loss of seasonal flow peaks	4	Reduced riparian plant recruitment Invasion of exotic riparian plant species Reduced plant growth and increased mortality Reduction in species richness and plant cover
Rate of change	Aquatic	3	2	2	Reduced variability	2	Increase in crayfish abundance Increase in schistosomiasis
	Riparian	2	2	0	Increased variability	2	Decreased germination survival and growth of plants Decreased abundance and change in species assemblage of waterbirds
Not specified	Aquatic	4	2	2	River regulation; type unspecified	4	Decrease in species richness Increased abundance of some macroinvertebrate taxa No change

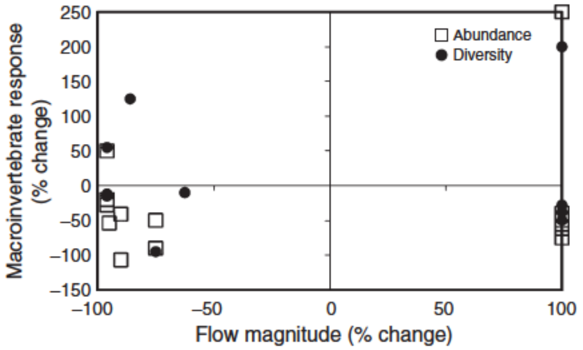

Fig. 2 Percent change in macroinvertebrate abundance and species diversity (and/or richness) with respect to percent alteration of flow magnitude. Percent change for both macroinvertebrates and flow magnitude represents alteration relative to a pre impact or 'reference' condition. Alteration in flow magnitude includes changes in peak flow, total or mean discharge, baseflow, or hourly flow. [Note: one extreme value for a change in abundance (+3000%) is plotted at +250% for presentation purposes.] [Correction added after online publication 23 September 2009: Figure 2 graph was replaced].

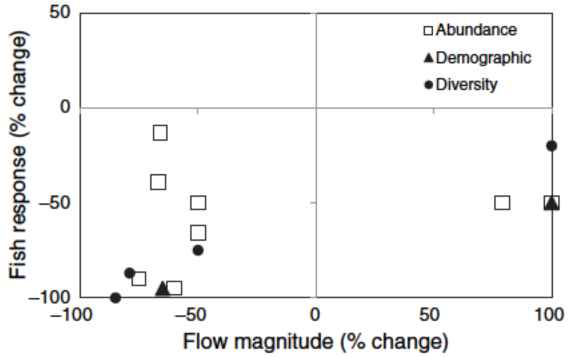

Fig. 3 Percent change in fish abundance, demographic parameters and species diversity (and/or richness) with respect to percent alteration of flow magnitude. Percent change for both fishes and flow magnitude represents alteration relative to a pre impact or 'reference' condition. Alteration in flow magnitude includes changes in peak flow, total or mean discharge, baseflow or hourly flow.

flooding. Two studies reported demographic responses that were both negative, but the small sample size precludes any general inference. Five of the studies reported increased values of riparian response metrics to flow reductions. These were mostly associated with riparian encroachment into the channel, increased species via terrestrialisation of the riparian community and an increase in herbaceous cover in the riparian understory.

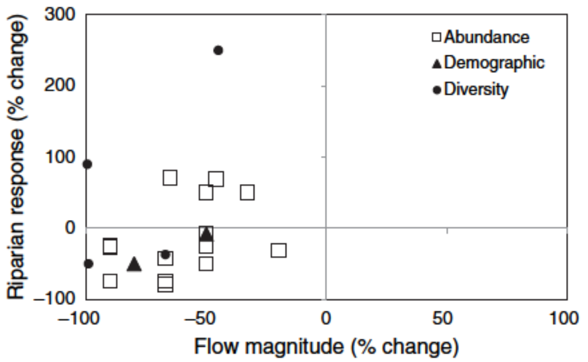

Fig. 4 Percent change in riparian abundance, demographic parameters and species diversity (and/or richness) with respect to percent alteration of flow magnitude. Percent change for riparian species and communities and flow magnitude represents alteration relative to a pre impact or 'reference' condition. Alteration in flow magnitude represents changes in peak flow only.

Discussion

Our goal was to extract information from published papers and search for any consistent patterns in ecological response to flow regime change. We hoped that a careful examination of the literature would reveal quantitative relationships that could advance our general understanding of flow alteration–ecological response relationships and thus inform environmental flow management.

As expected, our qualitative analyses clearly demonstrated the many ecological consequences of flow alteration. Of the 165 papers reviewed, 152 (92%) of them reported negative ecological changes in response to a variety of types of flow alteration. Only 21 papers (13%) reported an increased value for ecological response metrics, and these often reflected shifts in ecological organisation such as increase in non-native species or non-woody plant cover on dewatered floodplains. Thus our findings broadly corroborate earlier summaries of ecological responses to flow regime alterations (Poff *et al.*, 1997; Bunn & Arthington, 2002), and particularly those of Lloyd *et al.* (2003), who found that 56 of 65 (86%) studies examining ecological responses to flow modification documented ecological changes. Moreover, our findings suggest that larger changes in flow alteration are associated with greater risk of ecological change from pre-management conditions (Figs 2–4). Interestingly, no studies reported on primarily ecosystem functional responses (e.g. riparian production, nutrient retention), even though many ecological processes are clearly flow-dependent (Hart & Finelli, 1999; Doyle *et al.*, 2005). This absence points to an obvious research gap in the environmental flows literature, one that perhaps reflects the often short-term, 'snapshot' nature of biological sampling done to document ecological change in flow-altered systems.

Most of the studies included in our review (60%) examined flow alteration in terms of changes to some measure of flow magnitude (99 of 165 papers). This bias toward alteration in flow magnitude is similar to previous surveys. Lloyd *et al.* (2003) found 45 of 70 publications (64%) to report flow alteration in terms of abstraction or water withdrawals for irrigation. In the present paper we were able to extend the analysis of flow alteration to other important components of the natural flow regime, including frequency (16 papers), duration (25), timing (16) and rate-of-change (5). Previous review papers have not thoroughly documented the ecological responses to altered flow frequency and timing of peak flows, and the information in Table 1 (see also the online appendix) advances our general knowledge base for these kinds of flow alterations.

We were able to extract quantitative relationships between flow alteration and ecological responses of macroinvertebrates, fishes, and riparian vegetation from 55 papers. This represents a substantial improvement in sample size compared to Lloyd *et al.*'s (2003) effort, which yielded only 14 papers suitable for quantitative analysis. However, similar to their effort, we found almost 75% of the ecological data available to be reported as responses to alteration in some measure of flow magnitude. We were not able to extract any robust statistical relationships between the size of the flow alteration and the ecological responses, which varied among the different taxonomic groups. This probably reflects, at least in part, the paucity of data points in the low to middle range of flow alteration (0–50%), particularly for macroinvertebrates and fish.

Fish were the only taxonomic group to consistently respond negatively to changes in flow magnitude irrespective of whether the flows increased or decreased. Under reduced flows all 10 fish responses were negative and eight of these exceeded 50% (Fig. 3). Diversity showed a consistently large decline, especially where flow magnitudes exceeded 50% change. Together, these observations suggest that fish are sensitive indicators of flow alteration, at least as measured and reported by these studies. In contrast, no clear patterns emerged for responses of macroinvertebrates or riparian species to changes in flow magnitude. For riparian species, responses were recorded only for decreases in magnitude (measured as decreases in peak flows) and responses showed both increases and decreases; however, the increased riparian responses mostly reflected more non-woody vegetation cover on the floodplain or an increase in upland species.

One potential reason for the different responses among taxonomic groups may be the types of taxa that were examined and differences in species-specific responses to alterations in flow magnitude. Consistent patterns in responses of fish to altered flow magnitude may arise because the studies we reviewed primarily examined responses of native, sensitive and/or specialist taxa. Studies of other taxonomic groups, such as macroinvertebrates and riparian vegetation, included taxa that may be hypothesised to have conflicting responses to changes in flows, such as non-native, tolerant or generalist taxa, in addition to native, sensitive, and specialist organisms. We were not able to refine our analysis based on such differences among taxonomic groups or other fine details of species-specific responses. For example, riparian responses to reductions in peak flows may depend on organism physiology for tolerance to reduced soil moisture or to changes in soil chemistry (see Merritt *et al.*, 2010). Knowledge of the autecology of the particular species reported in the studies could have allowed us to examine whether ecological responses were dominated by particular types of species, such as tolerant, specialist or non-native species. For example, it is well documented that riparian cottonwood tress (*Populus* species) suffer greatly diminished success following peak flow reductions compared to invasive saltcedar (*Tamarix*) in flow-altered rivers of the American West (e.g. Stromberg *et al.*, 2007; Merritt & Poff, in press), a result not captured in our global-scale statistical analysis.

In general, while our analysis does provide some insight into the possible relative sensitivity of different ecological endpoints to alteration in flow magnitude, it does not yield unambiguous, transferable empirical relationships for developing quantitative guidelines to support regional environmental flow standards. This finding is similar to that reported by Lloyd *et al.*

(2003), who with a smaller dataset found little quantitative support for either simple linear relationships or threshold relationships between ecological responses and flow magnitude alteration. Several possible reasons can be invoked to explain this.

First, as with all surveys of a broad literature, the individual studies composing the analysis were not designed specifically to address our hypothesis, i.e. that degree of ecological alteration is associated with degree of hydrological alteration. Despite the fact that we assembled a reasonably large set of papers in this review, a wide variety of ecological metrics and types of flow alteration was reported. Measures of flow modification were not consistently reported, and criteria for establishing reference conditions were variable. For example, some studies calculated a site-specific percent change in flow relative to a historical period, whereas others reported flow alteration relative to a spatial reference (such as a site upstream of a dam).

Another constraint in our analysis was the inability to place flow alteration in each study into a more specific environmental context. Aquatic and riparian species will respond to multiple hydrologic drivers, and these are often confounded. For example, a change in magnitude of high flows is often accompanied by a change in frequency, and either or both of these may be influencing biological response. We were unable to evaluate such multiple drivers in any consistent manner across all studies; indeed, these factors were generally unreported in the original publications. Likewise, other environmental characteristics, such as temperature regime or sediment-habitat factors (including hydraulic structure and dynamics) were not reported and could not be assessed in our retrospective analysis. Flow alteration is only one environmental factor to which riverine species respond (Poff *et al.*, 1997; Bunn & Arthington, 2002) and incorporation of other environmental factors is important to advancing environmental flows science (Lloyd *et al.*, 2003; Konrad *et al.*, 2008; Olden & Naiman, 2010; Poff *et al.*, 2009; Stewart-Koster *et al.*, 2009), even when those factors cannot be rigorously accounted for statistically. For example, Konrad *et al.* (2008) used quantile regression to develop statistical relationships between macroinvertebrate metrics and flow characteristics across more than 100 sites that differed in terms of non-flow environmental features. Unfortunately, the shortage of data points in the low alteration range in our dataset prevented us from effectively using quantile regression to develop meaningful relationships between flow alteration and ecological responses.

A potentially significant limitation in our analysis was the inability to account for hydroclimatic and other regional differences among the study sites. Given the relatively small sample size, we did not stratify the studies according to natural flow regime type or geomorphic setting, although these factors are expected to influence ecological responses to hydrologic alteration (Poff & Ward, 1989; Arthington *et al.*, 2006) and potentially offer a basis for transferring flow alteration–ecological response relationships geographically (see Poff *et al.*, 2010 for an extended discussion). Thus, we would argue that our inability to find statistical relationships in a limited set of studies at the global scale does not necessarily imply such relationships would not be found by reviewing studies conducted over a smaller geographic extent or within particular stream types where environmental conditions (e.g. temperature, geomorphology) are more similar.

One conclusion from our analysis is that to develop quantitative relationships useful for supporting regional environmental flow efforts like ELOHA (Poff *et al.*, 2010), synthesising existing literature at the global scale will not be sufficient. Indeed, several data gaps have been clarified by constraints inherent in our analysis. These include design of the original studies, variation in the reporting of mode and magnitude of flow alteration, inability to examine species-specific responses, lack of data points for the entire range of flow alteration and inability to distinguish among types of alteration within a flow component. These limitations point to the need for prescribed monitoring programs (e.g. following water development projects) in which data could be collected in a before-after-control-impact design (Underwood, 1994) to support statistical inference of ecological responses to flow alteration. Likewise, incorporating knowledge from ecosystem-scale experiments and monitoring associated with environmental flow releases could advance our understanding of ecological responses to flow alteration. Such experimental flow releases offer exceptional opportunities to learn about the interactions of flow alteration and other environmental drivers (King *et al.*, 2010; Shafroth *et al.*, 2010).

However, new efforts and approaches are also needed to gather information on flow alteration–

ecological response relationships. One promising approach would be to design sampling programs that target existing flow-altered sites across gradients of flow alteration to allow general relationships between flow alteration and ecological response to be inferred (Arthington *et al.*, 2006; Poff *et al.*, 2010). Often, biological sampling is concentrated in smaller streams and areas that represent reference or good biological condition, and fewer sampling sites are available across a range of stream sizes and condition types. Similarly, monitoring of sites that have experienced flow alteration is generally not done and so learning opportunities are missed (Souchon *et al.*, 2008; Webb *et al.*, 2010). New data collection efforts directed at sampling a range of undisturbed to highly flow-altered sites would be useful in testing specific hypotheses that could inform environmental flow science and management. In addition, existing data could also be marshaled to test such hypotheses. For example, large biological datasets exist in several countries (and state or provincial jurisdictions within countries), including the United States Environmental Protection Agency's Environmental Monitoring and Assessment Program (EMAP), United States Geological Survey's National Water Quality Assessment (NAWQA), Europe's Euro-limpacs program, Europe's River Invertebrate Prediction and Classification System (RIVPACS), and the Australian River Assessment System (AusRivAS). These large databases, if analysed with an eye toward degree of flow alteration, carefully selected ecological response metrics, stream typology, and multiple environmental drivers, hold the potential to reveal important relationships and key information gaps needed to guide research and application in environmental flows science.

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References

Arthington A.H., Bunn S.E., Poff N.L. & Naiman R.J. (2006) The challenge of providing environmental flow rules to sustain river ecosystems. *Ecological Applications*, **16**, 1311 1318.

Bunn S.E. & Arthington A.H. (2002) Basic principles and ecological consequences of altered flow regimes for aquatic biodiversity. *Environmental Management*, **30**, 492 507.

DeGasperi C., Berge H., Whiting K., Burkey J., Cassin J. & Fuerstenberg R. (2008) Relationships among hydrologic metrics, B-IBI, and land cover: Implications for protecting stream ecosystems. *Journal of the American Water Resources Association*, **45**, 512 533.

Doyle M.W., Stanley E.H., Strayer D.L., Jacobson R.B. & Schmidt J.C. (2005) Effective discharge analysis of ecological processes in streams. *Water Resources Research*, **41**, W11411, doi:10.1029/2005WR004222.

Dudgeon D., Arthington A.H., Gessner M.O. *et al.* (2006) Freshwater biodiversity: importance, threats, status and conservation challenges. *Biological Review*, **81**, 163 182.

Hart D.D. & Finelli C.M. (1999) Physical-biological coupling in streams: the pervasive effects of flow on benthic organisms. *Annual Review of Ecology and Systematics*, **30**, 363 395.

King A.J., Ward K.A., O'Connor P., Green D., Tonkin Z. & Mahoney J. (2010) Adaptive management of an environmental watering event to enhance native fish spawning and recruitment. *Freshwater Biology*, **55**, 17 31.

Konrad C.P., Brasher A.M.D. & May J.T. (2008) Assessing streamflow characteristics as limiting factors on benthic invertebrate assemblages in streams across the western United States. *Freshwater Biology*, **53**, 1983 1998.

Lloyd N., Quinn G., Thoms M., Arthington A., Gawne B., Humphries P. & Walker K. (2003). *Does Flow Modification Cause Geomorphological and Ecological Response in Rivers? A Literature Review From an Australian Perspective*. Technical Report 1/2004, CRC for Freshwater Ecology. ISBN 0-9751642-02

Lytle D.A. & Poff N.L. (2004) Adaptation to natural flow regimes. *Trends in Ecology & Evolution*, **19**, 94 100.

Merritt D.M. & Poff N.L. (In Press) Shifting dominance of riparian *Populus* and *Tamarix* along gradients of flow alteration in western US rivers. *Ecological Applications*.

Merritt D.M., Scott M.L., Poff N.L., Auble G.T. & Lytle D.A. (2010) Theory, methods and tools for determining environmental flows for riparian vegetation: riparian vegetation-flow response guilds. *Freshwater Biology*, **55**, 206 225.

Nilsson C., Reidy C.A., Dynesius M. & Revenga C. (2005) Regulation of the world's large river systems. *Science*, **308**, 405 408.

Olden J.D. & Naiman R.J. (2010) Incorporating thermal regimes into environmental flows assessments:

modifying dam operations to restore freshwater ecosystem integrity. *Freshwater Biology*, **55**, 86–107.

Poff N.L. & Ward J.V. (1989) Implications of streamflow variability and predictability for lotic community structure: a regional analysis of streamflow patterns. *Canadian Journal of Fisheries and Aquatic Sciences*, **46**, 1805–1818.

Poff N.L., Allan J.D., Bain M.B., Karr J.R., Prestegaard K.L., Richter B.D., Sparks R.E. & Stromberg J.C. (1997) The natural flow regime: a paradigm for river conservation and restoration. *Bioscience*, **47**, 769–784.

Poff N.L., Allan J.D., Palmer M.A., Hart D.D., Richter B.D., Arthington A.H., Rogers K.H., Meyer J.L. & Stanford J.A. (2003) River flows and water wars: emerging science for environmental decision making. *Frontiers in Ecology and the Environment*, **1**, 298–306.

Poff N.L., Olden J.D., Pepin D.M. & Bledsloe B.D. (2006) Placing global stream flow variability in geographic and geomorphic contexts. *River Research and Applications*, **22**, 149–166.

Poff N.L., Olden J.D., Merritt D.M. & Pepin D.M. (2007) Homogenization of regional river dynamics by dams and global biodiversity implications. *Proceedings of the National Academy of Sciences of the United States of America*, **104**, 5732–5737.

Poff N.L., Richter B.D., Arthington A.H. *et al.* (2010) The ecological limits of hydrologic alteration (ELOHA): a new framework for developing regional environmental flow standards. *Freshwater Biology*, **55**, 147–170.

Postel S. & Richter B. (2003) *Rivers for Life: Managing Water for People and Nature*. Island Press, Washington, DC.

Power M.E., Sun A., Parker G., Dietrich W.E. & Wootton J.T. (1995) Hydraulic food-chain models. *BioScience*, **45**, 159–167.

Resh V.H., Brown A.V., Covich A.P., Gurtz M.E., Li H.W., Minshall G.W., Reice S.R., Sheldon A.L., Wallace J.B. & Wissmar R. (1988) The role of disturbance in stream ecology. *Journal of the North American Benthological Society*, **7**, 433–455.

Richter B., Baumgartner J.V., Powell J. & Braun D.P. (1996) A method for assessing hydrologic alteration within ecosystems. *Conservation Biology*, **10**, 1163–1174.

Shafroth P.B., Wilcox A.C., Lytle D.A., Hickey J.T., Andersen D.C., Beauchamp V.B., Hautzinger A., McMullen L.E. & Warner A. (2010) Ecosystem effects of environmental flows: modelling and experimental floods in a dryland river. *Freshwater Biology*, **55**, 68–85.

Souchon Y., Sabaton C., Deibel R. *et al.* (2008) Detecting biological responses to flow management: missed opportunities; future directions. *River Research & Applications*, **24**, 1–13.

Stewart-Koster B., Bunn S.E., Mackay S.J., Poff N.L., Naiman R.J. & Lake P.S. (2010) The use of Bayesian networks to guide investments in flow and catchment restoration for impaired river ecosystems. *Freshwater Biology*, **55**, 243–260.

Stromberg J.C., Lite S.J., Marler R., Paradzick C., Shafroth P.B., Shorrock D., White J.M. & White M.S. (2007) Altered stream-flow regimes and invasive plant species: the *Tamarix* case. *Global Ecology and Biogeography*, **16**, 381–393.

Underwood A.J. (1994) On beyond BACI: sampling designs that might reliably detect environmental disturbances. *Ecological Applications*, **4**, 3–15.

Walker K.F., Sheldon F. & Puckridge J.T. (1995) A perspective on dryland river ecosystems. *Regulated Rivers: Research & Management*, **11**, 85–104.

Webb J.A., Stewardson M.J. & Koster W.M. (2010) Detecting ecological responses to flow variation using Bayesian hierarchical models. *Freshwater Biology*, **55**, 108–126.

Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Studies used in literature review of relationships between hydrologic alteration and ecological response. All papers were included in qualitative analyses; papers included in quantitative analyses are noted.

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