Fish assemblages respond to altered flow regimes via ecological filtering of life history strategies

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SUMMARY
1. In riverine ecosystems, streamflow determines the physical template upon which the life history strategies of biota are forged. Human freshwater needs and activities have resulted in widespread alteration of the variability, predictability and timing of streamflow, and anticipating the biotic consequences of anthropogenic streamflow alteration is critical for successful environmental flow management. In this study, we examined relationships between dam characteristics, metrics of flow alteration and fish functional community composition according to life history strategies by coupling stream flow records and fish survey data in paired flow-regulated and free-flowing rivers across the conterminous United States.
2. Dam operations have generally reduced flow variability and increased flow constancy based on a comparison of pre- and post-dam flow records (respective mean record lengths 26.2 and 43.1 years). In agreement with ecological theory, fish assemblages downstream of dams were characterised by a lower proportion of opportunistic species (a strategy favoured in environmental settings dominated by unpredictable environmental change) and a higher proportion of equilibrium species (a strategy favoured in more stable, predictable environments) compared to free-flowing, neighbouring locations.
3. Multiple linear regression models provided modest support for links between alteration of specific flow attributes and differential life history representation below dams, and they provided strong support for life history associations with dam attributes (age and release type). We also found support for a relationship of both reduced flow variability and dam age with higher representation of non-native species below dams.
4. Our study demonstrated that river regulation by large dams has significant hydrological and biological consequences across the United States. We showed that on ecological time scales (i.e. the order of years to decades), dams are effectively changing the functional composition of communities that have established over millennia. Furthermore, the changes are directional and indicate a filtering by dams for some life histories (equilibrium strategists) and against other life histories (opportunists). Finally, our study highlights that dependence upon long-term flow records and availability of biotic surveys extracted from national survey efforts limit our ability to guide environmental flow standards particularly in data-poor regions.

Keywords: dams, flow regulation, freshwater fishes, life histories, United States

Introduction
Streamflow defines the physical template of riverine ecosystems (Poff et al., 1997), provides longitudinal and lateral access to foraging, spawning and recruitment habitat (Junk, Bayley & Sparks, 1989), and acts as an evolutionary selective force and an ecological filter of various survival strategies employed by aquatic and riparian organisms (Townsend & Hildrew, 1994; Lytle & Poff, 2004). At the same time, human society requires water for life. Over the millennia, humans have altered streamflow in riverine systems for a myriad of reasons, including harnessing water for drinking, irrigation and recreation and providing flood control and hydropower (Gleick, 2003). The human freshwater footprint encircles the globe with nearly half of major river systems affected by dams (Vörösmarty et al.,...
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Future construction of dams, particularly in economically developing nations, is an inevitable consequence of human population growth and the increasing freshwater and electricity needs in a changing climate (Palmer et al., 2008). Despite providing many societal benefits, river regulation by dams has also caused considerable ecological damage and the loss of important ecosystem services valued by society. Dams fragment rivers creating strings of artificial lakes punctuated by often impassable barriers (Reidy Liermann et al., 2012), and they alter physical riverine habitat (Vörösmarty et al., 2003) and water quality in both up- and downstream directions (Olden & Naiman, 2010). In particular, dams have been shown to be the primary driver of altered streamflows throughout the United States (Carlisle, Wolock & Meador, 2011), resulting in reduced flow seasonality and variability (Poff et al., 2007) and generally increasing short-term minimum flows while decreasing short-term maximum flows (Magilligan & Nislow, 2005). These changes alter the historical disturbance regime, rendering some biotic adaptations to these regimes obsolete while potentially favouring others. For example, reduced flow variability by dams has been associated with significant losses of native fish species (Meador & Carlisle, in press) while concurrently creating new niche opportunities that are often occupied by non-native species with life histories novel to the system or basin (Bunn & Arthington, 2002; Olden, Poff & Bestgen, 2006).

Social, political and scientific pressure to ‘legitimise’ rivers as water users has resulted in a move to find compromises in dam management to meet both human and ecosystem water needs (Arthington et al., 2010) through the provisioning of ‘environmental flows’ (Arthington et al., 2006) and large-scale flood events (Konrad et al., 2011). However, despite the growing recognition of ecologically sustainable water management, natural resource agencies cite a lack of scientific information required to support the application of this approach. Poff & Zimmerman (2010) conducted an extensive review of ecological responses to flow regulation and reported that the biotic integrity of fish assemblages generally decreased with increased flow alteration. Dam-induced changes to the flow regime can vary by region and modes of dam operation (Magilligan & Nislow, 2005; McManamay, Orth & Dolloff, 2012); however, due to overall sample size and disparate reporting practices across studies, Poff & Zimmerman (2010) were unable to distinguish the impacts of different components of the flow regime and were limited to reporting the effects of altered flow magnitudes.

Broader applicability of realised relationships between flow alteration and biotic responses is important for understanding the ecological impacts of dams and for guiding environmental flow practices for ecologically sustainable river management (Poff et al., 2010; Konrad et al., 2011). General frameworks for prediction of biotic responses to flow regulation, such as vegetation-flow response guilds built upon traits rather than taxonomy (Merritt et al., 2010), are more widely applicable than river or reach-specific models that often do not translate beyond their intended locality. Increasingly, freshwater ecologists have turned to the use of species traits as a universal currency for studying flow:ecology relationships across diverse taxonomies and geographies (reviewed in Poff et al., 2006; Frimpong & Angermeier, 2010). Life history traits of freshwater fishes are well studied and well suited as a platform to test general relationships between the flow regime and biological communities; they also have direct implications for ecosystem functioning (Winemiller, 2005). Winemiller & Rose (1992) identified three life history strategies in both freshwater and marine fishes that represent the essential trade-offs among the basic demographic parameters of survival, fecundity and onset and duration of reproduction. Opportunistic strategists are small-bodied species with early maturation and low juvenile survivorship and are predicted to be associated with habitats defined by frequent and intense disturbance. Periodic strategists are characterised by large body size, late maturation, high fecundity and low juvenile survivorship and are likely to be favoured in highly periodic (seasonal) environments. Equilibrium strategists are typically small to medium in body size with intermediate times to maturity, low fecundity per spawning event and high juvenile survivorship largely due to high parental care and small clutch size. Equilibrium strategists are predicted to be favoured in more stable habitats with low environmental variation.

The three life history strategies of the continuum are hypothesised to be adaptive with respect to variability, predictability and seasonality of environmental regimes (Winemiller, 2005). Convergence of trait composition along hydrologic gradients has been demonstrated for freshwater fishes (e.g. Lamouroux, Poff & Angermeier, 2002; Logez, Pont & Ferreira, 2010), and empirical investigations that test predictions from life history theory support these relationships (e.g. Tedesco et al., 2008; Olden & Kennard, 2010; Carlisle et al., 2011). Recently, we reported that life history composition of fish assemblages in free-flowing rivers of the United States are associated with critical flow dimensions of variability, predictability and seasonality and that these associations
are largely predicted by Winemiller and Rose’s trilateral continuum model (Mims & Olden, 2012). Taken together, a traits-based approach to establishing flow–ecology relationships provides a promising yet largely untested framework to evaluate and generalise the ecological effects of flow regulation by dams.

In this study, we quantified the relationships between major facets of the flow regime and life history composition of fish assemblages downstream from large dams across the United States and tested whether these associations are predicted by life history theory. We posited and tested three main hypotheses. (i) We expected dams to reduce variability and increase predictability of flows, and we also expected to see changes in timing and duration of seasonal flows. (ii) We predicted fish assemblages at flow-regulated sites to show proportionally lower number of species exhibiting opportunistic and periodic life histories and higher richness of equilibrium life history strategies relative to fish assemblages at free-flowing sites. (iii) We predicted that observed changes in three primary components of the flow regime (variability, predictability and seasonality) caused by dam operations will predictably shape native and non-native fish assemblage structure via the ecological filtering of life history strategies.

Methods

Study sites

Study sites consisted of ‘triplet’ sets of a dam, flow gauge and fish survey that met strict search criteria to ensure that the hydrologic conditions measured at the gauge station reflect the conditions where fish assemblages were surveyed (following Larned et al., 2010). Dams were identified through the Army Corps National Inventory of Dams (NID: U.S. Army Corps of Engineers, 2000), a data set of c. 79 000 large dams (>2 m) throughout the United States. Pre- and post-impoundment daily flow records were obtained from the U.S. Geological Survey’s (USGS) gauge records, reflecting over 25 000 gauging stations. Fish occurrence data for sites were synthesised from a number of regional and national survey efforts, including the Environmental Protection Agency’s (EPA) Environmental Monitoring and Assessment Program (EMAP) and the regional counterpart (Regional EMAP or REMAP) (Hughes, Paulsen & Stoddard, 2000), the USGS National Water Quality Assessment Program (NAWQA) (Gilliom, Alley & Gurtz, 1995) and from various state agencies. This resulted in a national database of 5951 unique sampling sites (data collected between 1989 and 2002) with 530 native and non-native fishes in North America represented (Herlihy, Hughes & Sifneos, 2006). Because the data available to us represented one-time surveys spanning a 14-year period from potentially disparate (but effective and efficient) survey techniques, we examined species presence/absence rather than abundance.

Identification of candidate study sites was performed by overlaying (in a Geographic Information System) locations of dams, gauges and fish surveys onto a national hydrography of streams and rivers (NHD Plus: Simley & Carswell, 2009). Dams with both a fish survey and a gauge within a radius of 20 km were identified. Candidate triplets were then manually evaluated to ensure (i) the gauge and survey were downstream of the dam; (ii) the components of the triplets were within 20 river km of each other and (iii) maximum difference in mean annual flow (modelled by NHD Plus) between the components of the triplets was <20% in order to ensure that tributary input did not disproportionately influence flow conditions at the fish survey location. Additionally, we screened for any upstream dams (within 50 river km on the mainstem or any major tributaries with >10% of mean annual flow at the dam) built prior to the pre-impoundment flow record.

Once candidate sites were identified, gauge records were evaluated for completeness. We required at least 15 years of data (<10 days of missing data per year) prior to the fish survey to ensure accurate and precise estimates of hydrologic metrics following Kennard et al. (2010). Our only exception to this rule was the Ridgeway Dam study site for which only 12 years of flow data are available post-impoundment and pre-fish survey due to the relatively recent construction of the dam. The McCloud and Trenton Dam study sites required a second gauge to provide complete pre-impoundment flow records. In both these cases, the total maximum distance of the triplet was minimally relaxed to incorporate the second gauge. The maximum difference in mean annual flow for these additional gauges adhered to our search criteria (13.3% for McCloud and 6.1% for Trenton).

Finally, each study site was assigned a reference fish survey from a nearby free-flowing stream because pre-impoundment fish surveys were not available. Search criteria were designed to identify the best available reference survey and were as follows: (i) candidate surveys were geographically close (within a 200-km search radius) and located in the same major river drainage; (ii) reference site had no dams within 50-km upstream along the mainstem or any major (>10%) tributaries and (iii) if multiple candidate sites were identified, the reference site selected was that most similar

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in cumulative drainage area to triplet fish survey (mean % difference in cumulative drainage area = 33.8, SD = 26.0).

Species life history strategies

Fish life history strategies were evaluated according to the model of Winemiller & Rose (1992) that positions species along three primary life history axes defining the opportunistic, periodic and equilibrium endpoints. The three axes of the model are (i) ln(sexuality) defined as the number of eggs or offspring per female per spawning season; (ii) ln(length at maturation) defined as mean female total length at maturation (mm) and (iii) ln(parental care + 1) (termed juvenile investment), defined as the mean diameter of mature, fully yolked ovarian oocytes (mm) and an index of parental care following Winemiller (1989). Fish life history traits were obtained from a comprehensive database for freshwater fishes of the United States and Canada synthesised from various literature, agency and expert accounts (reported in Mims et al., 2010). Because many species occupy intermediate positions in life history space, we followed Olden & Kennard (2010) by conducting a ‘soft’ classification according to a species’ relative affinity with each strategy. This was accomplished by calculating the Euclidean distance in trivariate life history space between the species’ position and the strategy endpoints, normalising the distances between 0 and 1, and then computing the inverse of these values to provide a ‘strategy weight’ for each species. This resulted in each fish species having a proportional weight or affinity to the opportunistic, periodic or equilibrium strategies. For each site, we summed the strategy weights of species present and computed the proportional value for each strategy to represent relative life history composition.

Hydrologic metrics

We examined six key hydrologic metrics: annual coefficient of variation (AnnCV), high pulse count (HPC), base flow index (BFI), flow predictability (FPred), flow constancy (Const) and high pulse duration (HPD). These metrics were chosen because they address fundamental dimensions of the flow regime (variability, predictability and seasonality) that drive patterns of fish occurrence via the selection of life history strategies (Bunn & Arthington, 2002; Lytle & Poff, 2004; Mims & Olden, 2012) and represent the broader suite of hydrologic metrics that are available from the literature (Olden & Poff, 2003). The metrics were calculated for pre- and post-impoundment records using the software Indi-

We also calculated an overall flow alteration index by performing a principal component analysis (PCA) of six hydrologic metrics for each pre- and post-alteration record to extract synthetic axes representing the dominant gradients of variability in flow conditions. All hydrologic metrics were first ln(x + 1) transformed to help achieve normality, and we performed a PCA by computing a singular value decomposition of a correlation matrix to account for data measurement along disparate scales. The index of flow alteration was then computed for each site as Euclidean distance between the pre- and post-alteration scores from the first three PCs (all statistically significant according to a Monte Carlo randomisation test of the eigenvalues). All statistical analyses were performed in R version 2.14.1 (R Development Core Team, 2011) using the vegan 2.0-3 package (Oksanen et al., 2012).

Statistical analyses

A paired Student’s \( t \)-test was used to evaluate directional differences in flow metrics (variability, predictability and seasonality) and proportional life histories (opportunistic, periodic and equilibrium) between flow-regulated and free-flowing river sites. A Wilcoxon signed rank test was performed for those comparisons where the assumption of normality was not met.

Next, we examined whether dam-induced changes in flow variability, predictability and seasonality were related to differences in proportional life history composition at flow-regulated versus free-flowing sites. This involved modelling a series of response variables as a function of the hydrologic metrics and dam attributes using multiple linear regression. Comparisons of fish assemblages in flow-regulated versus free-flowing rivers resulted in four response variables representing per cent change in proportional life history composition of the opportunistic, periodic and equilibrium strategies and proportional species composition of fishes non-native to the particular locality at the scale of the 6-digit hydrologic unit code (HUC) as described by Lawrence et al. (2011). A total of 11 predictor variables was examined: the % difference of the six previously described hydrologic metrics, number of years since dam construction referenced to the year of fish survey (YearsAlt), location of water release from dam (hypolimnetic or surface) and the overall index of flow alteration. We also considered % difference in cumulative drainage area (%ACDA) and linear distance between the flow-regulated versus free-flowing sites to account for the possible effects of
reference river selection. Similarly, we also tested for relationships between the response variables and the straight-line distance between surveys to check for spatial autocorrelation that may confound analyses.

An iterative but strategic approach was used to evaluate candidate models. Each response variable was modelled independently as a function of both dam descriptors and hydrologic alteration. Hydrologic alteration was measured either by the Flow Alteration Index or by a subset of the six major hydrologic variables. Rather than modelling all six major hydrologic variables, we modelled a maximum of three hydrologic metrics at one time. This was done both to avoid over-parameterisation of the model (given our limited sample size) and to minimise correlation between hydrologic metrics. The six major hydrologic variables were divided into two groups of three variables each (first group: HPC, HPD and BFI; second group: AnnCV, constancy/predictability and flow predictability). The fundamental characteristics of the flow regime (variability, predictability and seasonality) were represented in each set. We then evaluated models using backward stepwise model selection. Goodness of fit of models was evaluated by the Akaike information criterion, corrected for low sample size (AICc) (Burnham & Anderson, 2002). ΔAICc, likelihood and the evidence ratios were calculated for the top four candidate models for each response variable.

Results

We identified 12 sites that met our strict criteria for inclusion (Table 1, Fig. 1). The length of pre-impoundment discharge records in our study ranged from 15 to 52 years (mean = 26.2 years), and the length of post-impoundment discharge records ranged from 12 to 95 years (mean = 43.1 years). Distance between flow-regulated and free-flowing surveys was not correlated with any measure of per cent difference in fish assemblages, and although free-flowing sites were generally located higher in watersheds than flow-regulated surveys, per cent difference in cumulative drainage was not correlated with any observed difference in fish assemblages.

Dams significantly reduced downstream flow variability with lower AnnCV (Wilcoxon signed rank test, n = 12, z = −2.12, P = 0.034) and fewer high flow pulses (HPC, Wilcoxon signed rank test, n = 12, z = −2.11, P = 0.037) (Fig. 2a). Dam operations also increased flow constancy/predictability ratios (ConstPred, paired t-test, t11 = 2.26, P = 0.045) but decreased flow predictability (FlowP, paired t-test, t11 = 2.39, P = 0.036) (Fig. 2a). Dams did not cause a significant overall reduction or increase BFI or HPD (Fig. 2a). Fish assemblages downstream of dams had proportionally lower representation of the opportunistic life history strategy than their free-flowing counterparts (paired t-test, t11 = 3.43, P = 0.006), proportionally higher representation of the equilibrium life history strategy (paired t-test, t11 = −3.575, P = 0.004), and no significant difference in the proportion of species displaying periodic strategies (Fig. 2b).

We identified a consistent assemblage shift towards dominance by equilibrium strategists and away from opportunistic strategists downstream of dams (Fig. 3a). The direction of change in strategy composition was largely independent of primary dam purpose. We also identified via PCA two major axes characterising 74% of the overall variation observed among the six major hydrologic metrics (Fig. 3b). The first principal component (PC1) explained 55% of the variation along a gradient from more variable flows (positive scores associated with higher Annual CV) to more steady flows (negative scores associated with higher BFI). Sites generally shifted towards steadier, less variable flows post-impoundment with 10 of 12 sites having a lower score along PC1 for post-impoundment flow records than pre-impoundment records; this pattern was largely independent of dam purpose. PC2 explained 19% of the total variation and represented a gradient from more seasonal flows (negative values associated with an increase in HPD) to less seasonal flows (positive values associated with an increase in HPC). In contrast to PC1 (x-axis), trends were less clear, with movement following no general uniform direction along PC2 (y-axis).

Multiple linear regression analysis identified some potential mechanisms for observed differences in life history composition between flow-regulated and free-flowing river sites (Table 2). Proportional change in opportunistic strategist composition was positively related to BFI; this model was more than twice as likely given the data than the next most competitive model that included the constancy/predictability ratio. The most supportive model for proportion of periodic strategists included a positive relationship with dam age (YearsAlt), with younger dams being associated with reduced representation of the periodic life history at flow-regulated sites. Proportional change of equilibrium strategists was associated with the positive effect of flow predictability (FlowP) alone, with this model having 1.7 times more support than hypolimnetic release alone (HypoReIs) and 2.9 times more support than both flow predictability and hypolimnetic release (HypoReIs) together. Finally, the most supportive model for proportion of non-native
species included a negative association with annual variability (AnnCV) and dam age (YrsAltered); both drivers together had 2.9 times the support of annual variability alone.

Overall flow alteration (Flow Alteration Index) was not identified as a significant predictor of any response variables. This may be due to more nuanced relationships that vary by dam operation or flow regime. Our sample size prohibits explicit statistical testing of relationships by dam operation purpose; however, we plotted Flow Alteration Index versus proportional life history and % non-native changes to explore possible associations (Fig. 4). Perhaps the most suggestive pattern is that flow alteration downstream of hydropower dams appears to have a negative relationship with periodic life history (Fig. 4b) (the opposite being true for flood control dams) and a positive relationship with equilibrium life history (Fig. 4c); no trends are readily apparent for the opportunistic life history (Fig. 4a) or the % non-native species (Fig. 4d).

**Discussion**

Our study demonstrates that river regulation by large dams has significant hydrological and biological consequences for riverine ecosystems across the United States. Despite varying release schedules due to different dam purposes, changes in flow variability and representative fish life history composition were in most cases consistent in direction across study sites and largely agreed with our

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**Table 1** Study site attributes, including dam type that indicates primary dam purpose and includes hydropower (Hydro), flood control (FloodC) and locks. Fish survey year’ refers to the year the flow-regulated survey was conducted; ‘Triplet distance’ refers to the maximum distance between any two components (gauge(s), fish survey and dam) of a given triplet; ‘Δ MAF’ indicates absolute value of maximum % difference (estimated using NHD+) between any two components of a given triplet; ‘Δ Drainage area’ refers to % difference between drainage area at flow-regulated and free-flowing fish survey pairs (calculated as [(reference dam) - flow-regulated dam] × 100) and ‘Survey distance’ is the straight-line distance between flow-regulated and free-flowing fish survey pairs.

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predictions. Dams reduced flow variability across sites and altered seasonality and predictability of flows (as evidenced by reduced flow predictability and increased flow constancy). Consistent with this pattern, fish assemblages downstream of dams generally had lower representation of opportunistic strategists and higher
representation of equilibrium strategists than their free-flowing counterparts. Life history theory (Winemiller & Rose, 1992; Winemiller, 2005) and empirical evidence (stream reaches: Mims & Olden, 2012; catchments: Tedesco et al., 2008) from free-flowing rivers suggest that reduced flow variability and increased flow constancy will favour equilibrium strategists that are well suited to environments characterised by low disturbance.

Although the correlation between flow alteration and life history representation below dams was predicted robustly by life history theory, isolating and identifying mechanistic relationships between individual flow metrics and individual life histories proved more difficult. The positive relationship between equilibrium strategists and flow predictability is in agreement with life history theory; however, because flow predictability is largely reduced by dams in our data set, increased flow predictability is not a likely driver for elevated representation of equilibrium strategists below dams. Life history theory predicts that increased variability and reduced predictability/constancy should favour opportunistic species; instead, we found a positive relationship between opportunistic strategists and flow predictability (BFI) and constancy (ConstPred). Our inability to identify mechanistic relationships predicted by life history theory might be resolved with a larger data set allowing for analysis within regions or by dam operation type, or may point to alternative drivers of lower opportunistic and higher equilibrium representation below dams.

The negative correlation between streamflow variability (AnnCV) and % non-native species is consistent with increased invasion success of non-native species as streamflow variability is reduced. By changing the disturbance regime in rivers, dams can select against native species well adapted to a historical regime but poorly equipped for a new one (Bunn & Arthington, 2002). Meador & Carlisle (in press) report an association between decreased streamflow variability and a loss of native species, particularly fluvial specialists, at roughly half of 97 locations in the eastern United States. Similar declines in fluvial specialist species have been reported for the Guadalupe and San Marcos Rivers in Texas (Perkin & Bonner, 2011) and for the White River in Arkansas (Quinn & Kwak, 2003) following impoundment. A new flow regime creates new niche opportunities, and although natural flow variability can result in a range of life history strategies represented among native taxa (Freeman et al., 2001), not all life history niche space is occupied in all assemblages (Olden et al., 2006). Phylogenetic constraints operating at regional scales and ecological ‘filters’ acting at local scales restrict available life histories in a given assemblage (Southwood, 1977; Jackson, Peres-Neto & Olden, 2001). Dominant life history strategies of North American freshwater fishes indeed vary regionally and are associated with historical large-scale climatic selection pressures (Mims et al., 2010). Dams can create different thermal and flow regimes that suddenly provide ecological niches to which few native species are adapted. Non-native species equipped for new flow and thermal regimes are particularly well poised to establish downstream of dams. In one example, species tending towards the equilibrium life history endpoint strategy are notably rare from native fish assemblages of the Colorado River Basin (U.S.A.), historically characterised by flashy, highly variable flows. However, as flow

\[ \text{Flow regime} \]

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Variability | Predictability | Seasonality

\[ \text{Life histories} \]

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Fig. 2 Box plots of per cent difference between free-flowing reference sites and flow-regulated rivers of (a) six flow metrics and (b) three major life history strategies. Open circles indicate outliers; values of large outliers are noted in parentheses (a). Variables for which paired \( t \)-test results were significantly different from 0 \((P < 0.05)\) are marked with an asterisk (*)

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alteration has led to more predictable, less variable flows, many established non-native fishes such as rainbow trout (*Oncorhynchus mykiss*) and channel catfish (*Ictalurus punctatus*) represent historically absent equilibrium life history strategists (Olden *et al.*, 2006).

Although flow regime alteration is often credited as the primary factor leading to changes in downstream fish assemblages (Carlisle *et al.*, 2011), other factors may play a role in the selection of certain life histories by dams. For example, our results identify hypolimnetic release, predominantly from hydroelectric facilities releasing cold water, as a likely driver of increased equilibrium strategists downstream of dams. Like flow, water temperature plays a critical role in metabolic rates, physiology and life history traits of freshwater species and helps determine rates of important ecological processes such as nutrient cycling and...
productivity (Caissie, 2006). Fluctuations in cold water resulting from hydropeaking operations are often associated with reductions in river productivity (reviewed in Cushman, 1985), and our study supports predictions that equilibrium life history strategies of optimising juvenile survivorship by investing resources into fewer offspring are favoured in resource-limited environments (McCann, 1998). In some cases, flow and thermal events are so tightly coupled that only a synergistic change in both is sufficient to illicit fish responses such as spawning, migration and foraging (reviewed by Olden & Naiman, 2010). Cooler temperatures below dams are often desirable for establishment of coldwater (often non-native) salmonid and trout fisheries popular with recreational fishermen, but these cooler temperatures are detrimental to native species that require warmer temperatures to survive and/or reproduce (Olden & Naiman, 2010). With conditions favouring non-native species and potentially disadvantaging native species, it is not surprising that increases in equilibrium strategists were positively correlated to sites with hypolimnetic releases.

We identified dam age as another non-flow driver of life history differences between free-flowing and flow-regulated rivers. Dam age was positively associated with the proportional representation of periodic strategists in flow-regulated regimes. This at first seems counterintuitive given that dams (i) fragment river ecosystems and often block movement of periodic strategists (Reidy Liermann et al., 2012) and (ii) dampen predictable, seasonal fluctuations in flow that are important in the survival and success of many periodic strategists that often migrate at times of large flow events (Bunn & Arthington, 2002). However, we identified three reasons why we may see this pattern. First, we show that, although dams do generally dampen variability and increase constancy of flows, seasonal changes vary between sites and do not show a clear pattern of alteration. It is possible that these changes act upon periodic strategists in different ways and thus illicit varying responses across sites. Second, the ecological effects of dams vary with time since construction. For example, water chemistry downstream of dams will change as organic matter collects and decomposes in the reservoir, and geomorphological changes to the stream channel also manifest slowly over time (Ligon, Dietrich & Trush, 1995). The biotic response to dams may also fall along a temporal gradient depending on attributes such as species generation time. Quinn & Kwak (2003) found that fish assemblages sampled immediately post-impoundment on the White River, Arkansas, showed only limited change and retained many of the native species observed prior to impoundment. However, sampling 30-year post-impoundment revealed that many fluvial specialists adapted to fast-flowing water were absent and that communities downstream of the dam were dominated by non-native salmonid species and only a few native species. Our observation of a positive relationship between dam age and long-lived periodic strategists may simply be a proportional response to the decrease in short-lived opportunistic species. Periodic strategists...
may show longer persistence simply due to differential longevity. Re-analysing species presence/absence data from Quinn & Kwak’s (2003) study and using life history data (described in this study), we found that equilibrium strategists proportionally increased over time ($R^2 = 0.97$), opportunistic strategists decreased ($R^2 = 0.72$) and periodic strategists showed no strong trend (decreasing immediately post-impoundment and then increasing 30 years post-impoundment) ($R^2 = 0.33$). This lends support to this mechanism.

The third possible explanation for the positive relationship between dam age and periodic strategists is that this relationship is not mechanistic but instead is explained by regional biogeography. The oldest dams in our data set are generally located in the eastern or midwestern United States, and the younger dams are in the western United States. The presence of the periodic life history in native fish assemblages increases from east to west across the United States (Mims et al., 2010), such that fish assemblages in the western United States simply have greater potential for change than assemblages in the eastern United States. Lastly, dam age was also identified as a significant predictor of % non-native species with higher % non-native species downstream of dams associated with younger dams. This may also be a spurious regional association as non-native fish species constitute a greater proportion of fish assemblages in western United States (Rahel, 2000).

Relationships between flow and life history strategies do appear to transcend regions (Mims & Olden, 2012); however, characterisation of biotic responses by region may provide greater utility to dam managers attempting to set ecological flow standards (Poff et al., 2010). Our sample size prevents a rigorous examination of biotic impacts of dams within-region and within-operation types, and this may prevent us from detecting biotic relationships that are indeed present (Magilligan & Nislow, 2005). Despite the wide availability of dam, gauge and fish survey data, we were only able to identify 12 sites throughout the United States that met our strict criteria. Close to 100 candidate triplets were identified throughout the country, but closer inspection of flow records from these gauges revealed many years or even decades of missing flow data. Magilligan & Nislow (2005) reported similar problems when conducting an analysis of hydrologic changes by dams throughout the United States, and this issue highlights the need for continued efforts at hydrologic classification of flow regimes for data-poor streams (Olden, Kennard & Pusey, 2012) and predicting altered flow conditions at ungaged rivers (Eng et al., in press). Furthermore, the continuation and creation of regional and national biomonitoring programmes in data-poor regions as well as the development of information systems that increase access to local, state and federal databases are recommended. Surveys and monitoring programmes specifically designed to understand the roles of flow regime and flow alteration will help avoid potential biases of monitoring data not designed for that purpose.

Our findings demonstrate that life history composition of freshwater fish assemblages that are built over millennia upon particular habitat templates are significantly altered downstream of dams in the order of a few decades. That we detected this result using a conservative presence/absence approach applied to a relatively small sample size holds promise for the utility of a life history, traits-based approach to understanding how dams alter downstream fish communities. Further elucidation of mechanistic links may require modelling of flow regimes and biotic communities to inform environmental flow standards.

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References


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