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Fish assemblages in sub-tropical rivers: low-flow hydrology dominates hydro-ecological relationships

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ABSTRACT

Effective environmental flow management depends on identification of ecologically-relevant flow attributes to maintain or restore in the context of other natural and human influences on stream ecosystems. This study in sub-tropical eastern Australia identified associations of fish with climatic and flow gradients, catchment topography, reach geology, habitat structure and land-use across 20 catchments. Land-use patterns and associated stressors accounted for very little variation in fish assemblage structure. Of the 35 fish species analysed, 24 were strongly associated with gradients in mean daily flows and their variability, baseflow, number of zero flow days and high flow pulses, magnitude of the 1-year ARI flood and the constancy and predictability of monthly flows. The finding that 22 species (benthic and pelagic) were associated with gradients of antecedent low-flow hydrology indicates that these species (or functional trait groups) should be the focus of further analysis to explore hydro-ecological relationships in systems with regulated flow regimes.

Key words Fish assemblages, flow variability gradients, hydro-ecological relationships, catchment land-use, environmental flows

1 INTRODUCTION

River discharge patterns (flow regimes) influence biotic community structure, life history strategies, productivity and the ecological functioning of riverine ecosystems (Poff *et al*. 1997, Bunn and Arthington 2002, Naiman *et al*. 2008, Mims and Olden 2012). The ecological roles of flow have received particular attention in countries seeking to improve the ecological condition of rivers by providing environmental flows – "*the quantity, timing and quality of water flows required to sustain freshwater and estuarine ecosystems and the human livelihoods and well-being that depend upon these ecosystems*" (Brisbane Declaration: http://www.eflownet.org/). Numerous environmental flow methods and frameworks have been devised to relate flow variables and ecological responses in streams and wetlands (Tharme 2003, Acreman and Dunbar 2004, Arthington *et al*. 2010). The measurement of ecological associations with gradients of natural and altered flow variability is central to many approaches, for example the framework ELOHA (Ecological Limits of Hydrologic Alteration) designed to set acceptable limits to hydrologic alterations in the streams and rivers of user-defined biogeographic regions or jurisdictions (Arthington *et al*. 2006, Poff *et al*. 2010, Kendy *et al*. 2012, Belmar *et al*. 2013). Hydro-ecological relationships for systems of measured hydrological character underpin applications of the ELOHA framework. Knowing the broad environmental context (climate, catchment topography, reach geology) within which river flow signatures and hydro-ecological relationships are generated is important because it helps us to understand the limits of generalisation of such relationships (Poff *et al*. 2010).

This paper presents fish assemblage data gathered during a field trial of ELOHA in south-east Queensland, Australia (Arthington *et al*. 2012). The overall objective of the paper is to demonstrate how multivariate analyses can be used to identify gradients of flow magnitude and variability in the context of regional patterns of natural environmental variation and catchment land-use, and to extract associations of fish assemblages and species with patterns of flow variability. Such analyses can guide the development of flow-ecology relationships and environmental flow recommendations for ecosystem protection/restoration in streams and rivers of a defined region (Poff *et al*. 2010). The possible influence of other stressors (e.g. intensive catchment land-use) has tended to be neglected in many environmental flow studies (e.g. Stewart-Koster *et al*. 2010 and references therein). Accordingly, this study quantified catchment land-use patterns as part of the environmental matrix within which flow patterns may influence fish assemblages and species.

The aims of this contribution are to: (1) identify gradients of flow magnitude and variability, natural regional environmental variation and catchment land-use across multiple river catchments of south-east Queensland; (2) quantify associations of fish assemblages and species with these environmental gradients; (3) identify the most important flow variables associated with patterns in fish assemblages and species; and (4) outline implications for the development of hydro-ecological relationships.

2 STUDY AREA AND METHODS

2.1 Study area

The ELOHA study was conducted in the South Coast, Logan-Albert, Brisbane, Pine-Caboolture, Maroochy, Noosa and Mary River catchments of coastal south-east Queensland, Australia (Arthington *et al.* 2012). The region has complex geology, soils and topography; coastal plains and river floodplains characterise the east, and foothills and mountains with plateaux over 300m above sea level lie to the west, north and south (Whitaker and Green 1980). The climate is sub-tropical, dominated by summer rainfall with warm summers and mild winters but temperate zone influences can generate erratic rainfall patterns. The region exhibits a strong gradient of rainfall decreasing in a westerly (inland) direction (Bridges *et al.* 1990).

The flow regimes of many rivers have been altered by the construction and operation of dams and weirs, water extraction, inter- and intra-basin water transfers and land-use changes. Twenty-four dams with wall height >15 m store approximately 38% of the total natural mean annual runoff in south-east Queensland.

2.2 Study design

The broader ELOHA trial involved comparisons of riparian vegetation, aquatic vegetation and fish assemblages at sites that represented stream reaches regulated by dams and comparable non-regulated reference sites spread across the east-west rainfall gradient. This design captured regional gradients in flow magnitude and daily, monthly and inter-annual flow variability across 40 sites suitable for sampling fish in riffles, runs and pools. Sites were located close to a stream flow gauge to minimise differences between flow measured (or modelled) at the gauge and flow at each field site. Wherever possible field sites were minimally disturbed by land use and management practices close to stream channels, however influences of broader catchment land-use (forestry, grazing, agriculture, residential and industrial use) could not be eliminated entirely by site selection because this was focused on flow and accessibility criteria. Land-use patterns were therefore assessed and analysed.

2.3 Environmental characteristics

Environmental variables incorporated in multivariate analyses of fish assemblage patterns included climatic factors, catchment topography, reach geology, habitat structure, hydrology and catchment land-use. Reach mean annual temperature and reach hottest and coldest month mean temperatures were acquired from Stein *et al.* (2009). Mean annual rainfall was supplied by the Bureau for Meteorology (http://www.bom.gov.au/climate). Catchment boundaries for each site were delineated in a GIS using stream networks based on 1:25 000 and 1:100 000 scale maps and a 30m DEM (digital elevation model) (NASA DTED2, http://gcmd.nasa.gov/records/GCMD_Canada_DND_DTED2.html). Catchments topographic characteristics (area above each site, drainage basin shape and elongation ratio, distance of sampling site to river source and mouth, elevation) were computed using geometry functions of GIS software. Valley slope and relief ratio were acquired from Stein *et al.* (2009). Geological characteristics of reach-scale substrates were derived from the south-east Queensland Region Geoscience data set and geology maps for the region. Geological groupings were based on broad composition characteristics (% mafic, % felsic, % sedimentary, % mixed sedimentary and igneous, % unconsolidated rocks) following Stein *et al.* (2009).

Catchment land use was assessed using the Queensland Land Use Mapping Program (QLUMP) and dataset. .Percentages of land use upstream from each site were recorded as conservation and natural environments (e.g. national park), production from relatively natural environments (forestry, grazing natural vegetation), dryland agriculture and plantations, irrigated agriculture and intensive uses (residential and industrial). These data were treated as consistent throughout the 1-year study.

Daily flow records from stream gauges were analysed to characterise the antecedent flow regime of each study site (i.e. flow patterns leading up to each of three sampling times). Antecedent flows were calculated for two time periods that reflected differences in the mean longevity of fish species in south-east Queensland (Pusey *et al.* 2004). The fauna was grouped as small-bodied and short-lived (≤~4 years, e.g. Australian smelt, *Retropinna semoni*) and large-bodied longer-lived (≤~15 years, e.g. Australian bass, *Macquaria novemaculeata*). Flow metrics (28) were selected to reflect gradients in the magnitude, timing, frequency, duration, rate of change, variability and predictability of stream/river flows based on global and regional analyses of ecologically-relevant variables (Olden and Poff 2003; Kennard *et al.* 2007). Metrics were calculated using the River Analysis Package (Marsh *et al.* 2003) and the Indicators of Hydrologic Alteration (Nature Conservancy 2009).

2.4 Fish sampling

Fish were sampled three times at 40 sites during July-August 2009 (winter), October-November 2009 (spring) and March-April 2010 (late summer). No sampling was undertaken during the hot and wet summer period (December-February/March) as higher river flows prevented effective electrofishing. Fish sampling sites were delineated by block seine netting and sampled using multiple pass backpack electrofishing with a Smith-Root LR-24 backpack electrofisher (Pusey *et al.* 2004). Seine nets captured pelagic species that could be under-represented by backpack electrofishing. Native species were identified and returned to the water alive. Alien species were euthanased according to animal ethics permits. Fish sample records were standardised to 450 m^2 reach surface area to permit comparisons among study sites.

2.5 Habitat structure

In-stream habitat variables were recorded from 10 random points in each site and averaged to represent habitat conditions on each sampling occasion. Reach width (m), depth (m), flow velocity (m s^{-1}), substrate composition (percentage of mud, sand, fine gravel, coarse gravel, cobble and bedrock) and the presence of leaf litter, overhanging, submerged and emergent vegetation, root masses, undercut banks, large and small woody debris (>15 cm and <15 cm diameter, respectively)) and filamentous algae were recorded (following Pusey *et al.* 2004).

2.6 Data analysis

Environmental data sets were subjected to separate Principal Components Analysis (PCA) to derive a reduced set of independent, composite variables that summarise the major patterns of environmental variation in the study area. All variables were normalised to produce a common variance, then transformed using log (X + 1). Input environmental variables with the highest loadings on each PC axis (eigenvalues >1) were identified and retained in multivariate analyses. Flow and in-stream habitat variables differed significantly over the three sampling occasions (1-way PERMANOVA, $P<0.05$) and were subjected to separate PCAs to permit interpretation of their time-varying influence on temporal fish assemblage patterns. The PCAs identified 15 composite explanatory variables (two catchment land-use, two climate, two capturing catchment topography and reach geology/topography, three time-variable in-stream habitat descriptors, three time-variable 4-year and three time-variable 15-year flow variables, Table 1).

To assess the strength of relationships between environmental gradients (composite PC axes) and patterns of fish assemblages, distance-based linear modelling (DISTLM) was used in Primer V6 with the PERMANOVA+ add-on package (Anderson *et al.* 2008). DISTLM is a multiple multivariate regression analysis that uses permutation to test for the strength and significance of relationships between predictor (i.e. environmental) and ecological variables. DISTLM analysis was undertaken using an AICc (Akaikes Information Criterion adjusted for small sample size) selection procedure run with the standard 9999 permutations (Anderson *et al.* 2008). The BEST selection procedure was employed to model all possible combinations of variables. Patterns in presence-absence fish patterns were compared using the Sørensen similarity measure to indicate how the distributions of individual taxa were associated with environmental predictor variables. Patterns in the composition of fish assemblages (based on relative abundance) were compared using the modified Gower (log base 2) similarity measure (Anderson *et al*. 2006). Fish assemblages across all sites differed significantly among the three sample times (PERMANOVA F=1.710, P=0.0213) hence their relationships with environmental variables were analysed separately for each sampling period.

3 RESULTS

3.1 Fish fauna of south-east Queensland

Totals of 14,261 individuals and 35 species in 17 families were recorded across the three sampling periods. Long-finned eel (*Anguilla reinhardtii)*, Duboulays rainbowfish (*Melanotaenia duboulayi*) and Australian smelt (*Retropinna semoni*) were collected in >75% of all samples, freshwater catfish (*Tandanus tandanus)*, western carp gudgeon (*Hypseleotris klunzingeri)* and firetailed gudgeon (*Hypseleotris galii)* occurred in >50% of all samples, and Pacific blue-eye (*Pseudomugil signifer)*, gambusia (*Gambusia holbrooki*), Midgley's carp gudgeon (*Hypseleotris* sp.*)* and striped gudgeon (*Gobiomorphus australis*) in >25% of all samples. These species comprised 85% of total fish in electrofishing samples. The remaining 25 species were infrequently sampled (<25% of all samples). Five alien species contributed 3.7% of all fish collected: common carp (*Cyprinus carpio)*, gambusia (*G. holbrooki)*, tilapia (*Oreochromis mossambicus)*, swordtail (*Xiphophorus helleri)* and platy (*Xiphophorus maculatus)*.

3.2 Catchment and reach characteristics

Results from the PCAs revealed several major environmental gradients in the region (Table 1). Catchment PC1 and PC2 accounted for 55.9% of variation in catchment land use, describing gradients of change from conservation and natural environments to increasingly intensive agricultural and residential/industrial land use upstream of sampling sites. Two climatic gradients (PC1 52.3%, PC 2 44.7%) represent prominent temperature and rainfall patterns across the study area. Catchment topography PC1 (20.7% of variation) represents a gradient of increasing catchment area and distance to source (i.e. upland to lowland catchments) and associated topographic features (valley slope and relief ratio). Reach geology PC2 (15.6%) describes a geologic gradient from rocky upland reaches to sites with increasing sedimentary and unconsolidated rock substrates.

3.3 Flow gradients

The PCAs based on 4-year and 15-year antecedent daily flows each distinguished three independent flow gradients and these were consistent in the percentage of antecedent flow variation explained in relation to each sampling date (Table 1), as might be expected given temporal overlaps in the flow sequences analysed. For example, 4-year PC1 accounted for 65-66% of antecedent variation in mean daily flow, mean daily baseflow and the magnitude of the 90th percentile exceedance flow, that is, a gradient of increase in these low flow variables across drier to wetter catchments. PC2 (4-year) explained much less variation (17-18%) in relation to a gradient of increasing baseflow accompanied by increasing daily flow stability (decreasing CV). The third 4-year flow component, PC3 (5.5-7.0% of variation), combines a gradient of increasing lack of flow (number of zero flow days per year), decreasing minimum daily flow and decreasing number of floods of greater volume than the median daily flow (Table 1). PCAs of 15-year daily flows represent a gradient of increasing mean daily flow accompanied by increasing magnitude of the 1-year ARI flood (15-yr PC1, 62% of variation), the longer time period of analysis allowing data on flood sequences to be included. The second component (15-year PC2, 17.7-18.5% of variation) duplicates the daily baseflow magnitude/variability gradient represented by 4-year PC2, while 15-year PC3 (7.3-8.6% of variation) represents a gradient of increasing constancy and predictability of mean monthly flows, that is, high to low inter-annual variation in mean monthly flows based on Colwell's 1974 index P (predictability = constancy + contingency).

3.4 Habitat characteristics

Habitat PCs 1-3 summarise spatial variations in habitat structure reflected in substrate characteristics (fine to coarse particles), and the occurrence of cover elements including submerged vegetation, filamentous algae, leaf litter, root masses and undercut banks (Table 1). Temporal shifts in the particular habitat variables associated with habitat PCs 1-3 reflect seasonal trends in site depth, wetted width and flow velocity as stream flows transitioned from winter (July-August 2009) low flows, to rising/variable flows in spring (October-December 2009) and post wet-season flood conditions (April-May 2010) across the study year.

3.5 Relationships between gradients of environmental variables and fish assemblage structure

Across the three sampling periods, distance-based multivariate linear regression models (DISTLM) determined that 52.9-57.4% of spatial variation in fish presence-absence patterns was associated with six to eight environmental gradients, based on paired combinations of composite variables extracted by PCAs, whereas variation in assemblage composition (based on relative abundances of component species) were associated with 3-4 environmental gradients and these explained less variation in fish assemblage composition (25.7-38%) (Table 2).

Most variation in fish presence-absence (27%, dbRDA axis 1, November-December 2009) was positively associated with climate PC1 (increasing temperature and rainfall) and reach geology PC2 (increasing igneous rock and distance to river mouth), with geology the stronger correlate with fish assemblage patterns. Gradients in 4-year flow PCs were associated with fish assemblage (presence-absence patterns) during all sampling periods in association with gradients in reach geology (e.g. July-August 2009, dbRDA axis 1, 24.6% of variation in fish assemblages explained), climate (July-August 2009, dbRDA axis 3, 7.9%; November-December 2009, dbRDA axis 2, 11.4%), and habitat structure (March-April 2010, dbRDA axis 4, 4.6%). In March-April 2010, 15-year flow PC2 forming a gradient with reach geology (dbRDA axis 2, 14.8%), but flow was the weaker association (0.37) with fish assemblage presence-absence patterns (Table 2)

Gradients exclusively reflecting flow variability were associated with variation in fish presence-absence patterns in all three sampling periods but had most effect in the winter (July-August 2009) period when 4-year flow PC1 and 15-year flow PC3 formed a gradient explaining 13.3% of spatial variation in assemblage patterns (dbRDA axis 2) associated with low daily flows and fewer floods greater than the median daily flow.

Patterns in fish assemblage abundance composition were associated with 11 composite gradients of climate (temperature and rainfall), reach geology, catchment disturbance, habitat structure and flow across the three sampling periods (Table 2). Most variation in fish assemblage composition (19%, dbRDA axis 2, November-December 2009) was negatively associated with a gradient of reach geology (PC2, increasing igneous rock and distance to river mouth) and positively associated with 4-year flow PC1, however geology had a stronger association with assemblage patterns (-0.9) than flow (0.17). In winter (July-August 2009) 4-year flow PC1 and reach geology explained 14.4% of variation in fish assemblage composition (dbRDA axis 1), while 4-year flow PC1 and 15-year flow PC3 (increasing constancy and predictability of mean monthly flows, and decreasing number of floods) were associated with fish assemblage structure (dbRDA axis 2, 7%). Flow PCs were not associated with fish assemblage composition in late summer (March-April 2010) when climatic factors and habitat structure had more influence (dbRDA axes 1-3).

3.6 Species associations with flow gradients

Twenty-four of the 35 species in fish samples showed strong correlations with distance-based redundancy analysis (dbRDA) axes that reflected associations of fish assemblages (presence-absence and percentage abundance composition) with time-varying hydrologic and other environmental gradients (Table 3).

Presence-absence patterns of five species in July-August 2009 were strongly negatively correlated with dbRDA axis 2 reflecting 15-year flow PC3 (increasing constancy and predictability of mean monthly flow and decreasing number of floods greater than the median daily flow). Pearson correlations ranged from -0.37 (platy, *X. maculatus*) to 0.64 (purple-spotted gudgeon, *M. adspersa*). Presence-absence of two species of eels, three species of gudgeons, Duboulays rainbowfish (*M. duboulayi*), Australian smelt (*R. semoni*), Australian bass (*Macquaria novemaculeata*), *Arrhamphus sclerolepis* and carp (*C. carpio*) were associated with dbRDA axes reflecting gradients of 4-year flow PC1 in one or more sampling periods (Table 3). For eels, smelt and bass these correlations were positive whereas for the remaining species they were negative. Fish associations with dbRDA axes reflecting 4-year flow PC3 (increasing number of zero flow days, decreasing minimum daily flow and decreasing number of floods greater than the median daily flow) only occurred in the spring and late summer sampling periods and most correlations were positive (*A. australis* 0.38, *H. galii* 0.34, *Philypnodon grandiceps* 0.3, *X. helleri* 0.3, carp -0.34). In the late summer sampling period four species (*A. australis*, *N. erebi*, *P. grandiceps* and *P. signifer*) showed negative correlations with dbRDA axes reflecting 15-year flow PC2 (increasing baseflow index and decreasing CV of mean daily flow).

Abundances of 15 species were significantly correlated with dbRDA axes that reflected 4-year flow PC1 and 15-year PC3 (Table 3). The 4-year flow PC1 was important for four species of gudgeons, two rainbowfishes, eels (*A. reinhardtii*) and the catfish, *T. tandanus*. Relative abundance patterns of glassfish, *A. agassizii* (-0.6), Midgley's carp gudgeon, *Hypseleotris* sp. (-0.56) and purple-spotted gudgeon, *M. adspersa* (0.64) were strongly positively correlated with 15-year flow PC3. Mouth almighty (*Glossamia aprion*), cod (*Maccullochella peelii mariensis*), mullet (*Mugil cephalus*), ornate rainbowfish (*Rhadinocentrus ornatus*) and freshwater catfish (*T. tandanus*) were the only species associated with flow PCs in terms of abundance patterns but not presence–absence patterns.

4 DISCUSSION

Environmental gradients across 20 catchments in south-east Queensland comprised climatic factors (temperature, rainfall), catchment topography and land-use, reach geology, in-stream habitat structure and flow characteristics. Gradients of flow magnitude and variability were associated with the pronounced rainfall gradient increasing in an easterly (coastal) direction (Bridges *et al.* 1990) and a south-north gradient of increasing mean annual runoff per unit catchment area (Arthington *et al.* 2012).

In this region between 52.9 and 57.4% of spatial variation in fish presence-absence patterns and 25.7 to 38% of variations in fish relative abundance patterns were correlated with gradients of flow, climatic factors, catchment topography and land-use, reach geology, in-stream habitat structure and flow characteristics, consistent with many stream fish studies (Esselman and Allan 2010, Grossman and Sabo 2010, Stewart-Koster *et al.* 2010). The position of sampling sites along river profiles (i.e. distance to source and river mouth) and reach-scale geologic correlates (coarse versus fine substrates) in association with climate variations (temperature and rainfall) and marked flow gradients had the strongest associations with fish assemblage patterns across south-east Queensland. Species' temperature tolerances, reproductive strategies, dispersal capabilities relative to riverscape connectivity, and preference for particular substrate, cover and flow conditions provide mechanistic explanations for strong correlations of fish assemblage structure with climatic factors, longitudinal physical gradients and flow conditions in lotic systems (e.g. Johnson *et al.* 2007, Kennard *et al.* 2007, Mims and Olden 2012).

Fish assemblage patterns and the relative abundance of species were associated with antecedent flow gradients leading up to all sampling periods except late summer (March-April 2010) when climatic variables and habitat structure were more important. These late-summer fish assemblages were likely to be adjusting to the flood-induced habitat disturbances of the previous summer (Pusey *et al.* 1993, 2004). Variations in fish assemblage structure were strongly associated with 4-year and 15-year antecedent flows (mean daily flows and their variability, baseflow, number of zero flow days and high flow pulses, magnitude of the 1-year annual return interval flood and the constancy and predictability of monthly flows). Of the 35 species analysed, 24 showed strong associations with 4-year and/or 15-year antecedent flow history. In particular, 22 benthic and pelagic species were associated with low flows and their variability and/or spells of zero flows, suggesting that antecedent low flow characteristics and associated habitat availability/quality were particularly important in structuring fish assemblages in this sub-tropical region characterised by low-flow variability and intermittency (Pusey *et al.* 2004, Kennard *et al.* 2010). High flow events revealed by the 15-year antecedent flow analysis were also important. For example, gambusia (*G. holbrooki*) was more abundant at sites that experienced decreasing number of floods over the preceding 15 years; this small alien species is susceptible to flood displacement (Ho *et al.* 2013). A trait-based approach (e.g. Mims and Olden 2012, 2013) could deepen understanding of the species or trait groups associated with particular antecedent patterns of flow magnitude and variability, and inform predictions of likely responses to flow regime alterations.

Catchment land-use accounted for a small proportion of variation in species presence-absence and relative abundance patterns of fish assemblages. This result reflects the relatively natural condition of large areas (84%) of catchment upstream from study sites. Ecological impacts associated with forestry, grazing, horticulture and irrigated agriculture typically involve incursion of sediments, nutrients and toxicants (herbicides and pesticides) to streams (Allan 2004, Esselman and Allan 2010). Such impacts have been documented in the more developed rural and urban catchments of south-east Queensland (Sheldon *et al.* 2012).

5 CONCLUSIONS

Multivariate analyses can be used to identify gradients of climatic factors, catchment topography, reach geology, habitat structure, hydrology and land-use at regional scale, and to extract associations between patterns of fish assemblage structure and antecedent flow history. Within the matrix of natural environmental factors that characterise the study region, catchment land-use had minor associations with patterns of fish assemblage structure. This finding will facilitate the development of hydro-ecological relationships that are unlikely to be confounded by stress factors typically associated with agricultural land-use. The fact that 22 of 35 species comprising this fish assemblage were associated with gradients of antecedent low-flow hydrology indicates that these species (or functional trait groups) should be the focus of further analysis to explore response patterns in regulated systems. Knowing the broad environmental context (climate, catchment topography, reach geology) within which river flow signatures and hydro-ecological relationships are generated is important because it helps us to understand the limits of generalisation of such relationships.

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Table 1. Principal Components (PCs) from the PCA of catchment land-use, climate, catchment topography, reach geology, in-stream habitat and flow variables, showing percentage of variation explained and the variables most highly correlated with each component. Percentages of variation explained by flow and habitat PCs varied temporally in relation to the three sampling times. Note that temporally variable antecedent flow PCs are presented as the range of variation explained across the three sampling dates.

Principal components	*Variation explained*	*Increasing*	*Decreasing*
1. Catchment land-use PC1	33.3%	Production from natural environments	Intensive land use
2. Catchment land-use PC2	22.6%	Natural land	Dryland agriculture
3. Climate PC1	52.3%	Hottest month mean temp.	Mean annual rainfall
4. Climate PC2	44.7%	Mean annual temp, coldest month mean temp.	
5. Catchment topography PC1	20.7%	Catchment area, distance to source	Valley slope and relief ratio
6. Reach geology PC2	15.6%	Igneous rock, distance to mouth	Sedimentary and unconsolidated rock
Temporally variable PCs (range of variation explained across 3 sampling dates)			
7. 4yr flow PC1	65-66.3%	Mean daily flow, mean daily baseflow, magnitude of 90th percentile exceedance flow	
8. 4yr flow PC2	17-18%	Baseflow index	CV mean daily flow
9. 4yr flow PC3	5.5-7%	Number of zero flow days	Minimum daily flow, number of floods greater than median daily flow
10. 15yr flow PC1	62.0-62.1%	Mean daily flow, magnitude of 1yr ARI	
11. 15yr flow PC2	17.7-18.5%	Baseflow index	CV mean daily flow
12. 15yr flow PC3	7.3-8.6%	Constancy, predictability of mean monthly flow	Number of floods greater than median daily flow
Temporally variable PCs (% variation explained per sampling date)			
July-August 2009			
1. Habitat PC1	25.20%	Sand, large woody debris	Coarse gravel, cobble
2. Habitat PC2	14%	Fine gravel, stream width	Submerged vegetation, Rock substrate
3. Habitat PC3	10.80%	Filamentous algae, macrophyte cover	Root mass, undercut bank
November-December 2009			

1. Habitat PC1	23%	Sand, large woody debris	Overhanging vegetation, cobble
2. Habitat PC2	15.90%	Leaf litter, filamentous algae	Site depth, submerged vegetation
3. Habitat PC3	14.40%	Rock, mud	Fine and coarse gravel
March-April 2010			
1. Habitat PC1	26.60%	Sand, small and large woody debris	Submerged vegetation
2. Habitat PC2	14.80%	Fine gravel, flow velocity	Rock
3. Habitat PC3	10.00%	Stream width	Mud, filamentous algae

Table 2. Results of distance-based multivariate linear model (DISTLM) analysis based on fish presence-absence and assemblage composition during 2009-2010, showing individual and cumulative variation explained (%) by each predictor couplet included in the model, followed by the composite (PCA) environmental gradients most strongly negatively and positively associated (multiple partial correlations) with each dbRDA axis.

	Fish assemblage composition (presence-absence)						Fish assemblage composition (percentage abundance)						
July-August 2009													
Axis	Individual (%)	Cumulative (%)	Negative		Positive		Axis	Individual (%)	Cumulative (%)	Negative		Positive	
1	24.59	24.59	Geol_PC2	0.83	Flow4yr_PC1	0.02	1	14.43	14.43	Flow4yr_PC1	0.55	Geol_PC2	0.59
2	13.32	37.91	Flow4yr_PC1	0.44	Flow15yr_PC3	0.71	2	7.01	21.45	Flow15yr_PC3	0.99	Flow4yr_PC1	0.13
3	7.93	45.84	Flow4yr_PC1	0.61	Climate_PC1	0.43	3	6.21	27.66	Flow4yr_PC1	0.82	-	-
4	4.35	50.19	Climate_PC2	0.67	CatchLu_PC1	0.40	4	2.88	30.53	Climate_PC1	0.75	Geol_PC2	0.64
5	2.37	52.57	Climate_PC2	0.36	Climate_PC1	0.64							
6	0.35	52.92	Geol_PC2	0.48	CatchLu_PC1	0.66							
November-December 2009													
Axis	Individual	Cumulative					Axis	Individual	Cumulative	Negative		Positive	
1	27.11	27.11	Climate_PC1	0.54	Geol_PC2	0.77	1	19.06	19.06	Geol_PC2	0.92	Flow4yr_PC1	0.17
2	11.44	38.55	Flow4yr_PC1	0.55	Climate_PC1	0.34	2	11.05	30.11	Climate_PC2	0.85	CatchLu_PC1	0.39
3	8.46	47.01	Climate_PC2	0.71	CatchLu_PC1	0.11	3	4.57	34.68	CatchLu_PC1	0.33	Flow4yr_PC1	0.89
4	3.89	50.9	Climate_PC2	0.35	Climate_PC1	0.67	4	3.42	38.1	Geol_PC2	0.30	CatchLu_PC1	0.81
5	2.3	53.2	CatchLu_PC1	0.73	Geol_PC2	0.35							
6	0.88	54.08	Flow4yr_PC3	0.55	Flow4yr_PC1	0.50							
March-April 2010													
Axis	Individual	Cumulative					Axis	Individual	Cumulative				
1	22.31	22.31	Geol_PC1	0.23	Climate_PC1	0.67	1	13.86	13.86	Climate_PC2	0.45	Climate_PC1	0.81
2	14.78	37.09	Geol_PC1	0.57	Flow15yr_PC2	0.37	2	7.31	21.17	Habit_PC1	0.92	Climate_PC2	0.14
3	8.62	45.71	Habit_PC1	0.73	CatchLu_Pc2	0.58	3	4.58	25.75	Habit_PC1	0.05	Climate_PC2	0.88
4	4.61	50.32	Habit_PC1	0.10	Flow4yr_PC1	0.72							
5	3.5	53.82	Flow4yr_PC3	0.37	Geol_PC1	0.73							
6	2.05	55.87	CatchLu_Pc2	0.62	Flow15yr_PC2	0.48							
7	0.87	56.74	Flow15yr_PC2	0.46	Flow4yr_PC1	0.58							
8	0.71	57.45	Geol_PC2	0.60	Climate_PC1	0.61							

Table 3. Pearson correlations of fish species to dbRDA axes that strongly reflect hydrologic gradients associated with structuring fish assemblage presence-absence and percentage abundance composition (see Table 2). Correlations greater than ρ = ±0.3 are identified in bold, indicating strong associations between species and hydrologic gradients. Alien species are marked with an asterisk (*). Time 1 = July-August 2009, Time 2= November-December 2009, Time 3 = March-April 2010.

	Fish assemblage composition (presence-absence)							Fish assemblage composition (percentage abundance)		
	Time 1		Time 2		Time 3			Time 1		Time 2
Species	15yr PC3	4yr PC1	4yr PC1	4yr PC3	4yr PC1	4yr PC3	15 yr PC2	4yr PC1	15 yr PC3	4yr PC1
Ambassis agassizii	**-0.59**	0.12	0.05	0.28	0.20	-0.01	0.19	-0.19	**0.60**	0.10
Anguilla australis	0.10	**0.34**	0.14	**0.38**	-0.12	-0.10	**-0.32**	0.23	-0.01	0.24
Anguilla reinhardtii	0.03	**0.37**	**0.38**	0.27	0.03	0.23	-0.14	**0.40**	0.04	0.13
Arrhamphus sclerolepis	0.00	0.00	0.00	0.00	**-0.47**	-0.17	-0.08	0.00	0.00	0.00
*Cyprinus carpio**	0.15	0.03	**-0.49**	0.06	0.17	**-0.34**	0.04	-0.01	0.02	0.30
*Gambusia holbrooki**	**-0.67**	0.14	0.02	-0.15	-0.05	0.00	-0.16	-0.02	**0.62**	-0.04
Glossamia aprion	0.00	0.00	0.17	-0.09	0.14	0.07	0.11	0.00	0.00	**-0.36**
Gobiomorphus australis	-0.03	-0.15	**-0.35**	-0.05	0.15	-0.10	0.24	**0.37**	-0.20	0.04
Hypseleotris compressa	-0.21	-0.12	**-0.35**	-0.03	0.12	-0.12	0.20	**0.45**	0.02	0.01
Hypseleotris galii	0.05	**-0.33**	-0.10	**0.34**	0.24	-0.13	0.07	**-0.32**	-0.08	**0.31**
Hypseleotris Sp1	**-0.56**	0.12	0.02	-0.11	0.21	0.00	0.04	-0.07	**0.52**	-0.11
Maccullochella peelii mariensis	0.00	0.00	0.22	-0.10	0.00	0.00	0.00	0.00	0.00	**-0.31**
Macquaria novemaculeata	0.10	**0.34**	-0.08	0.12	0.04	-0.11	0.19	0.23	-0.01	0.11
Melanotaenia duboulayi	0.04	**-0.43**	-0.28	-0.03	0.27	-0.07	-0.01	**-0.55**	-0.08	0.21
Mogurnda adspersa	**-0.64**	0.15	-0.07	0.09	0.29	-0.17	0.10	-0.06	**0.60**	0.18
Mugil cephalus	0.00	0.00	0.11	-0.02	0.21	-0.29	-0.01	0.00	0.00	**-0.33**
Nematalosa erebi	0.00	0.00	0.12	-0.14	-0.03	-0.09	**-0.31**	0.00	0.00	-0.21
Philypnodon grandiceps	0.01	-0.22	-0.07	0.08	0.23	**0.30**	**-0.35**	**-0.32**	-0.18	0.16
Pseudomugil signifer	0.03	-0.14	-0.13	-0.04	0.25	0.19	**-0.32**	-0.22	-0.17	0.15

Retropinna semoni	0.05	0.02	**0.43**	0.08	0.01	0.24	-0.26	-0.27	-0.01	-0.25
Rhadinocentrus ornatus	-0.16	-0.13	-0.24	0.02	0.07	0.03	0.14	**0.53**	-0.07	0.03
Tandanus tandanus	0.03	-0.19	0.07	-0.03	0.11	0.18	-0.14	**-0.39**	0.02	-0.12
*Xiphophorus helleri**	0.00	0.00	0.00	0.00	-0.06	**0.31**	-0.12	0.00	0.00	0.00
*Xiphophorus maculatus**	**-0.37**	-0.02	-0.28	0.04	0.06	0.07	0.10	0.27	0.23	0.11