Stewart-Koster, B., Olden, J.D., Kennard, M.J., Pusey, B.J., Boone, E.L., Douglas, M. & Jackson, S. (2011). Fish response to the temporal hierarchy of the natural flow regime in the Daly River, northern Australia. *Journal of Fish Biology*. 79: 1525–1544.
doi:10.1111/j.1095-8649.2011.03072.x.

Published version on Journal website available at:

<http://onlinelibrary.wiley.com/doi/10.1111/j.1095-8649.2011.03072.x/abstract>

**Fish response to the temporal hierarchy of the natural flow regime in the Daly
River, northern Australia**

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Running headline: Hierarchical fish-flow relationships

In this study, relationships between flow variation across multiple temporal scales and the distribution and abundance of three fish species, western rainbowfish *Melanotaenia australis*, sooty grunter *Hephaestus fuliginosus* and barramundi *Lates calcarifer* were examined at eight sampling reaches in the Daly River, Northern Territory, Australia. Discharge was highly seasonal during the study period of 2006-2010 with a distinct wet-dry discharge pattern. Significant catchment wide correlations were identified between species abundance and hydrologic variables across several scales describing the magnitude and variability of flow. A Bayesian hierarchical model which accounted for > 80% of variation in abundances for all species and age classes (*i.e.* juvenile and adult), identified the extent to which the influence of short term flow variation was dependent upon the historical flow regime. There were distinct ontogenetic differences in these relationships for *H. fuliginosus*, with variability of recent flows having a negative effect on juveniles which was stronger at locations with higher historical mean daily flow. *Lates calcarifer* also displayed ontogenetic differences in relationships to flow variation with adults showing a positive association with increases in recent flows and juveniles showing a negative one. The effect of increased magnitude of wet season flows on *M. australis* was negative in locations with lower historical mean daily flow but positive in locations with higher historical mean daily flow. The results highlighted how interactions between multiple scales of flow variability influence the abundance of fish species according to their life history requirements.

Key words: Bayesian hierarchical model; ecohydrology; flow; ontogeny; temporal variation.

INTRODUCTION

Natural flow variability is critical for sustaining the structure and function of fish assemblages at local to regional scales, and at time intervals ranging from days to millennia (Schlosser, 1985; Bain *et al.*, 1988; Angermeier & Winston, 1998; Humphries *et al.*, 1999). In the absence of human activities, floods and droughts interact with channel geology to shape the river's biophysical template upon which fish assemblages are formed and maintained (Poff *et al.*, 1997; Bunn & Arthington, 2002; Lytle & Poff, 2004). From an evolutionary perspective, floods and droughts that are predictable over time can exert primary selective pressures that favour certain fish life histories synchronized to avoid or exploit extreme flow events (*e.g.* Meffe, 1984; Olden *et al.*, 2006a). By contrast, at ecological time scales, extreme flows that are less frequent and unpredictable in timing, but large in magnitude have low selection strength for life-history timing, even though they might inflict high mortality on fish populations (*e.g.* Matthews, 1986; Labbe & Fausch, 2000; Lake, 2003). Such extreme disturbance events occur within the context of the long term flow regime which is itself a hierarchical system (Poff & Ward, 1990; Poff, 1997).

The temporal hierarchy of the natural flow regime implies that the ecological effects of recent (*i.e.* short-term) flow events on instream biota will depend on the historical (*i.e.* longer-term) flow regime (Biggs *et al.*, 2005). Extreme floods can have a major influence on resident fish species by flushing downstream those unable to hold position or find refuge or by providing new habitats for feeding and spawning of

other species (Junk *et al.*, 1989; Tockner *et al.*, 2000; Balcombe *et al.*, 2007). Such flow events are likely to trigger a successional sequence *via* recruitment and mortality that may last several years (Humphries *et al.*, 1999; Tockner *et al.*, 2000). Similarly, prolonged periods of low flow may allow species to colonise areas previously unavailable due to isolation by high velocity habitats (Detenbeck *et al.*, 1992; Grossman *et al.*, 2010). Understanding how these scales of flow variation interact to influence the distribution and abundance of fish species is important to advance our ecological understanding of freshwater ecosystems and to inform environmental flow management.

In addition to riverine fish species' ecological dependencies on the flow regime, human societies modify natural flow regimes to provide dependable ecological services, including water supply, hydropower generation, flood control, recreation and navigation (Baron *et al.*, 2002). In recent decades, scientists have sought to inform flow management schemes through improved understanding of how riverine fishes respond to natural, altered and restored flow regimes (*e.g.* Sedell *et al.*, 1990; Kinsolving & Bain, 1993; Bednarek & Hart, 2005; Kennard *et al.*, 2007; King *et al.*, 2009). Concepts such as the landscape approach to river ecology (*e.g.* Schlosser, 1991; Wiens, 2002) have facilitated a deeper understanding of the impact of multiscale abiotic variation, including hydrology, on abundance of fish species (Fausch *et al.*, 2002). Such information is critical for supporting the conservation of large, unregulated river systems, which are increasingly rare in the world (Nilsson *et al.*, 2005).

The Daly River in tropical northern Australia is one such river; this system is currently free-flowing and unlike many rivers globally and in the region, it has perennial flow (Kennard *et al.*, 2010), making it an attractive option for further water development (Chan *et al.*, 2011). With the expected changes to the flow regime following such development in the catchment, it is particularly important to understand how aspects of the natural flow regime influence the distribution and abundance of aquatic biota to better predict the ecological consequences of altered hydrology and inform decision-making in future water planning. Emerging statistical approaches now provide an exciting opportunity to elucidate fish-flow relationships across multiple temporal dimensions of the riverine flow regime.

The hierarchical nature of temporal flow variability complicates analyses of the relationships between the natural flow regime and the abundance of fish species necessitating specific quantitative methods. Hierarchical regression models are applicable when multiscale data are collected resulting in explanatory variables that vary at different hierarchical levels (Raudenbush & Bryk, 2002; Gelman *et al.*, 2004) which is common in studies of riverine environments (Fausch *et al.*, 2002). Increasingly, such models are analysed within a Bayesian framework because of the flexibility to develop statistical models with mathematical structures that more accurately reflect the hierarchical understanding of ecological systems such as riverine environments (Clark, 2005; Cressie *et al.*, 2009; Webb *et al.*, 2010). Bayesian methods also provide a framework for quantifying uncertainty around the biological relationships under analysis (Hoeting *et al.*, 1999; Cressie *et al.*, 2009).

In the present paper relationships between multiple scales of flow variation and the distribution and abundance of fish are quantified for three species; sooty grunter *Hephaestus fuliginosus* (Macleay 1883), western rainbowfish *Melanotaenia australis* (Castelnau 1875) and barramundi *Lates calcarifer* (Bloch 1790), in the Daly River Basin, Australia. It was hypothesised that changes in species abundances due to short-term hydrologic events would be dependent on spatial variation in the characteristics of the long-term flow regime. Furthermore, it was hypothesised that the flow determinants of juvenile and adult abundances would differ both within and between species. These questions were addressed with a Bayesian hierarchical model which accounted for multiple scales of variation in hydrologic predictors.

MATERIALS AND METHODS

STUDY AREA

The Daly River (Fig. 1) is an unregulated, large river (catchment area = 53 000 km²), with minimal water withdrawals for agriculture, stock and domestic and urban water supply (Chan *et al.*, 2011). Annual rainfall in the catchment averages ca. 1000 mm, with 90% falling during the wet season months between November and May. As a result, river discharge is highly seasonal, with monsoonal and cyclonic weather producing wet season flows of up to 2000 m³ s⁻¹ at Mt Nancar, 100 km upstream of

the river's mouth (Fig. 1). Rainfall is negligible during the dry season, with flow in the Daly River and its major tributaries supplied predominately from groundwater. Many of the smaller tributaries cease to flow entirely during the dry season.

Sampling of fish assemblages at eight study sites was undertaken biannually (early and late dry seasons) over a 5 year period from 2006 to 2010 resulting in a total of 80 observations. Sampling sites were selected according to a stratified random sampling design (i.e. randomly stratified by river size and flow regime type) but was constrained by available access points to the river. Five sites were located along the perennial mainstem of the Daly River, two sites were located on the perennial Katherine River and one site was located on the intermittent Fergusson River (Fig. 1). Variation in river flows over the period leading up to and including the field data collection period (2004 – 2010; Fig. 2) were characterised by a wide range of hydrologic conditions when compared to the long-term record. Two large flood events occurred in the wet seasons of 2006 and 2008 (9 year and 8 year average recurrence interval maximum instantaneous flows, respectively). These large flows contributed to significant recharge of the groundwater aquifer resulting in elevated baseflows during the following dry seasons (Fig. 2).

FISH SAMPLING

Within each sampling site (500–1000 m reach length), fish assemblages were sampled at multiple discrete locations (hereafter termed electrofishing „shots“) using a boat-mounted, generator-powered electrofishing unit (Engineering Technical Services Model MBS-2DHP-SRC; <http://www.etsselectrofishing.com/>) or a backpack-mounted, battery-powered electrofisher (SmithRoot Model 12B; <http://www.smith-root.com/>). Water conductivities varied widely among study sites ($50 - 600 \mu\text{S cm}^{-1}$) so electrofisher output settings were adjusted to maximise efficiency at each site but with the minimum power required to stun fish (pulsed DC current, <250 pulses per second, <500 volts, <25% duty cycle, maximum 35 amps). Each electrofishing shot was fixed to five minutes duration (elapsed time) and averaged 65m stream length. At least 15 electrofishing shots were usually undertaken at each site, with the intent of sampling the full range of habitat types present (e.g. riffles, runs, pools, macrophyte beds, stretches of mid-channel open water, undercut banks, woody debris piles, etc). This was determined by visual inspection of the study reach prior to sampling and electrofishing shot locations were then stratified to ensure that each habitat type was sampled at least once and the remaining sampling effort occurred in the most common habitat types. At the completion of each electrofishing shot, fish were identified to species level, measured (standard length; L_S) and returned alive to the approximate point of capture. Fish catches were standardized to catch per-unit-effort in the statistical modelling process (CPUE: total number of individuals per electrofishing shot).

Of the three species that were selected for this analysis, *H. fuliginosus* and *L. calcarifer* abundances were divided into two age classes (cutoff lengths = 150 mm L_S

and 300 mm L_S for *H. fuliginosus* and *L. calcarifer*, respectively), while *M. australis* abundances consisted of adults and juveniles. All three species have important ecological, cultural and economic values (Pusey *et al.*, 2004; Jackson *et al.*, 2011). *Hephaestus fuliginosus* and *M. australis* both complete their life-cycles entirely in freshwater, with spawning occurring during the wet season and larvae recruiting to the juvenile phase by the following dry season (Pusey *et al.*, 2004; Chan *et al.*, 2011). Adult male *L. calcarifer* migrate from the freshwater reaches of the river into the estuary and nearshore marine environment to spawn, where the eggs hatch and go through larval stages to become juveniles in their first year. Juveniles then migrate back into the freshwater reaches of the river system, maturing from sub-adults to adults within the third year, by which time they are reproductively mature (Pusey *et al.*, 2004; Balston, 2009).

ENVIRONMENTAL AND HYDROLOGIC DATA

A set of ecologically-relevant variables quantifying hydrologic and hydraulic variation across multiple temporal scales was chosen from a larger number of candidate variables for use as predictors of variation in abundance of fish species (Table I). At the finest temporal scale, one variable was selected to describe instantaneous hydraulic characteristics of the study sites at each sampling occasion (mean velocity/depth ratio). This was calculated based on five replicate measures of water depth and average water velocity taken at each electrofishing shot at each site and sampling occasion. At the next temporal scale, two hydrologic descriptors (mean

and coefficient of variation of daily discharge) were derived to describe the nature of the recent flow regime over three different antecedent time periods: recent flows (one month prior) and seasonal flows (prior wet or dry) and interannual flows (wet season flows two seasons prior). Short-term hydrologic conditions indicate the presence of potential disturbance events prior to sampling as well as the extent to which conditions at the time of sampling differ greatly from those in the preceding sample. The group of flow attributes that characterised conditions for spawning and recruitment were defined as the dry season (1 June to 31 October) prior to each sample and the wet season (1 November to 31 May) one and two seasons prior to each sample. In addition to the metrics that describe short term hydrologic fluctuations, the historical mean daily flow at each site was included to describe the long term flow history, thereby summarising conditions relating to overall habitat availability and connectivity at each site. This variable, which varies in space but not in time, may be a surrogate for other covarying and ecologically important environmental factors such as proximity to estuarine spawning areas (for *L. calcarifer*), hydraulic habitat complexity or the presence of large predators in downstream reaches. This selection of hydraulic and hydrologic variables describes the instantaneous hydraulics at the point and time of sampling, the recent flows that govern the hydraulics, the previous seasonal hydrologic variation that may influence spawning and recruitment success and the long term flow history in which these other variables are nested. All hydrologic predictor variables were scaled and standardised for statistical modelling to ease parameter estimation. An ordinal measure of time, *TIME*, being the number of each sampling occasion (*i.e.* sampling trips 1 to 10) was also used to quantify any long-term temporal trends in abundances.

249

250 All flow variables for each study site were derived using 25 years (1975–
251 2010) of simulated daily discharge data obtained from a finite-element model for
252 subsurface flow and transport, including ground water–surface water interactions
253 (FEFLOW - Trefry & Muffels, 2007). The data were provided by the Land and Water
254 Division of the Northern Territory Department of Natural Resources, Environment,
255 the Arts and Sport (NRETAS) and further description is available in Chan *et al.*,
256 (2011).

257

258

259 STATISTICAL MODELLING

260

261

262 Initial investigation of potential relationships between the abundance of
263 species and flow variation at multiple scales was conducted with catchment-wide
264 correlation analyses and plotting of spatial and temporal variation of species
265 abundances. Subsequently, a two-level Bayesian hierarchical model structure was
266 developed to quantify the relationship between abundance and spatial and temporal
267 flow variation at different scales. The hierarchical structure of this model quantifies
268 the extent to which relationships between the abundance of species and short-term
269 flow variation are dependent on long-term flow history. This model structure was
270 applied to a univariate, single species response for *M. australis* and a bivariate
271 response for the two age classes of each of *L. calcarifer* and *H. fuliginosus*. For the
272 univariate response (*M. australis* abundance) the observed species count at the j th site
273 on the k th sampling trip, y_{jk} , is assumed to have a Poisson distribution with mean λ_{jk} ,

which is derived from the catch per unit effort, CPUE: μ_{jk} (*sensu* Wyatt, 2002). Effort is defined as total number of electrofishing shots (TES) so, $CPUE = \text{total catch} \times TES^{-1}$. The natural logarithm of CPUE is then related to descriptors of hydraulics, recent and seasonal flows for each site and sampling occasion, X_{jkl} :

$$y_{ij} \sim \text{Poisson}(\lambda_{ij})$$

$$\lambda_{jk} = \mu_{jk} \times TES_{jk}$$

$$\log(\mu_{jk}) = \beta_{j0} + \beta_{j1}X_{jk1} + \beta_{j2}X_{jk2} \dots \beta_{jl}X_{jkl}$$

This model was modified for the bivariate response where the observed count for the i th age class at the j th site on the k th sampling trip, y_{ijk} , is assumed to have a Poisson distribution with mean λ_{ijk} (*sensu* Gotelli *et al.*, 2010). Here again, λ_{ijk} is a function of the CPUE, μ_{ijk} of the sampling site j on trip k , $area_{jk}$ (*sensu* Wyatt, 2002) which is related to descriptors of hydraulics, recent and seasonal flows for each site and sampling occasion, X_{jkl} :

$$\begin{pmatrix} y_{1jk} \\ y_{2jk} \end{pmatrix} \sim \begin{pmatrix} \text{Poisson}(\lambda_{1jk}) \\ \text{Poisson}(\lambda_{2jk}) \end{pmatrix}$$

$$\begin{pmatrix} \lambda_{1jk} \\ \lambda_{2jk} \end{pmatrix} = TES_{jk} \times \begin{pmatrix} \mu_{1jk} \\ \mu_{2jk} \end{pmatrix}$$

$$\begin{pmatrix} \log(\mu_{1jk}) \\ \log(\mu_{2jk}) \end{pmatrix} = \begin{pmatrix} \beta_{1j0} & \beta_{1j1} & \dots & \beta_{1jl} \\ \beta_{2j0} & \beta_{2j1} & \dots & \beta_{2jl} \end{pmatrix} \begin{pmatrix} 1 \\ X_{jk1} \\ \vdots \\ X_{jkl} \end{pmatrix}$$

293

294 The terms β_{jl} and β_{ijl} in each of the univariate and bivariate response models,
295 quantify the relationship between species or age class abundance (on the log scale)
296 and the l th predictor variable at the j th site, one of the seasonal flows, recent flows,
297 hydraulics and *TIME* (Table I). These terms are assumed *a priori* to be normally
298 distributed with the mean ϕ_{jl} or ϕ_{ijl} and precision τ_l^2 or τ_{il}^2 for the univariate and
299 bivariate response variables, respectively. Uninformative gamma prior distributions
300 were used for the precision terms: $\tau_l^2 \sim \Gamma(2, 0.5)$. The subscript j on each of the β
301 parameters indicates that the estimated fish-flow relationships are estimated separately
302 for each sampling site. At the next level of the hierarchy, the model quantifies how
303 relationships between antecedent flow and fish abundances vary among sampling sites
304 according to the long-term hydrologic context, or flow history: $\phi_{jl} = \gamma_{jl0} + \gamma_{jl1}Z_{j1}$ for
305 the univariate response and $\phi_{ijl} = \gamma_{ijl0} + \gamma_{ijl1}Z_{j1}$ for the bivariate response.

306

307

308 Here the γ_{jl1} and γ_{ijl1} parameters quantify the effect of historical mean daily
309 flow, Z_{j1} , on the relationship between the abundance of species and the short-term
310 flow variables X_{jkl} . Where there is no such relationship, the intercept term γ_{jl0} and
311 γ_{ijl0} , quantifies the relationship between the l th site-scale variable and species
312 abundance, averaged across the catchment. Uninformative multivariate normal prior
313 distributions were used for the regression relationships at this level of the model:
314 $\gamma_{jlm} \sim MVN(\mathbf{0}, 100\mathbf{I})$. In summary, this model quantifies the relationships between
315 the abundance of species and short term hydrologic variation with the β_{jl} and β_{ijl}

regression coefficients and also how these relationships depend on the long term flow regime with the γ_{jl1} and γ_{ijl1} regression coefficients.

Bayesian model averaging (BMA) was used to account for model uncertainty when estimating the parameters in the hierarchical models and to identify the statistical importance of each predictor variable (Hoeting *et al.*, 1999). The rationale behind BMA is to combine the predictions and parameter estimates from several competing models using a weighted average with weights determined by the posterior probability of each of model (Raftery *et al.*, 1997; Hoeting *et al.*, 1999). The posterior probability of a hierarchical model is very difficult to estimate analytically; therefore the Deviance Information Criterion (DIC, Spiegelhalter *et al.*, 2002) was used as an approximation. The probability that any predictor variable is related to the response variable in the model is known as the inclusion probability, $P(\beta \neq 0|D)$, and is the sum of the posterior probabilities of each model in which the variable occurs. Thus, these values are different from frequentist P values in that high inclusion probabilities suggest that a variable is important (Hoeting *et al.*, 1999).

To avoid overfitting of the statistical models the number of variables in the lower level of the model was restricted to five. However, the temporal variable, TIME, was included in all models to quantify the long-term effect of the large flood in the year before sampling began, leaving four possible additional variables from the nine temporal flow variables (seasonal and recent flows and hydraulics) as possible sets of predictors. The resulting model space consisted of all 126 possible four-variable

combinations that could be formed from these nine predictor variables. Each of the models was run as candidate models for model selection.

The initial stage of analysis involved identifying the best fitting 5% of all possible variable combinations, according to the DIC. At this stage of model selection, two chains of 20 000 iterations were run for each model with 10 000 iterations discarded for burn-in. Once the subset of the best 5% of models was obtained, two chains of 100 000 samples after burn-in were run with every 10th sample retained for parameter estimation and model averaging. At each stage, convergence was achieved as assessed by Brooks, Gelman and Rubin's measure of convergence, $\hat{R}$ (Brooks & Gelman, 1998) and with visual inspection of trace plots. After the completion of parameter estimation through model averaging, plots of residuals against time were inspected and showed little or no evidence of residual temporal autocorrelation.

To evaluate the predictive performance of the averaged models, ten-fold cross-validation was undertaken (Wilks, 2006). The accuracy and bias of the predicted values were quantified with a cross-validated predictive R^2 and the unscaled mean error, ME (Walther & Moore, 2005). All correlation analyses and exploratory plotting were conducted in R, Version 2.10.1 (R Development Core Team, 2009). The hierarchical modelling (including DIC estimation and cross validation) was implemented in WinBUGS Version 1.4.3 (Lunn *et al.*, 2000), called from the R statistical environment, Version 2.10.1 (R Development Core Team, 2009) using the R2WinBUGS library (Sturtz *et al.*, 2005).

RESULTS

SPECIES-HYDROLOGIC CORRELATIONS

For all species and age classes, there were significant catchment-wide correlations between abundance and flow variation at multiple temporal scales (Table II; Fig. 3). There were predominantly negative relationships between the abundance of small-bodied fishes (*M. australis* and juvenile *H. fuliginosus*) and temporal flow variables describing the magnitude of antecedent flows (M_{w2} , M_{w1} , M_d and M_{1m} ; Table II). By contrast, large-bodied fishes (*L. calcarifer* and adult *H. fuliginosus*) typically displayed positive correlations to antecedent flow magnitude. Measures of antecedent flow variability (CV_{w1} , CV_{w2} , CV_d , CV_{1m}) were positively related to the abundance of *M. australis* and juvenile *H. fuliginosus* and *L. calcarifer*, whereas adult *H. fuliginosus* and *L. calcarifer* displayed negative correlations to these variables (with one notable exception: Table II). Correlations between mean abundance at each site and the long-term mean daily flow (M_{LT}) were high ($r > 0.5$) for the majority of species and age classes but only statistically significant for *M. australis* and juvenile *H. fuliginosus*. The catchment-wide correlations between fish abundances and time were not significant for any comparisons; however, there were strong temporal trends in abundance at particular sites for some species and/or age classes. For example, the abundance of juvenile *H. fuliginosus* showed a distinct long-term increasing trend

over the study period at site 5 whereas adults showed no obvious trend [Fig. 3(a,b)]. Both juvenile and adult *L. calcarifer* increased in abundance over the study period at Site 4 [Fig. 3(c,d)] and *M. australis* decreased in abundances at sites 3 and 4 [Fig. 3(e,f)]. At a finer temporal scale, there are also clear fluctuations within this trend at specific sampling reaches that occur at seasonal to annual time scales [Fig. 3(a-f)].

BAYESIAN HIERARCHICAL MODELLING

The model selection process identified a single model for *M. australis* and three different plausible models for *H. fuliginosus* and *L. calcarifer* to combine with BMA (Table III). The subsequent averaged models produced very accurate fitted values with R^2 values >0.8 (Fig. 4). Inclusion probabilities, $P(\beta \neq 0|D)$, which define the statistical importance of each predictor variable to the regression, differed substantially across species with more variables being included in the average model for *H. fuliginosus* than the other two species (Table III). Variables describing flow magnitude and variability at various antecedent time periods prior to sampling (one month, wet season prior, two wet seasons prior) had very high inclusion probabilities for both *H. fuliginosus* and *L. calcarifer*. This is despite these variables showing little or no catchment-wide correlation with *L. calcarifer* species (Table II). By contrast, primarily measures of flow variability rather than magnitude were included in the model for *M. australis*.

416 Cross-validation of the BMA models indicated reasonable predictive
417 performance for all models. Average predictive R^2 values across all test datasets were
418 0.27 for *L. calcarifer* (adults = 0.19, juveniles = 0.39), 0.39 for *H. fuliginosus* (adults
419 = 0.37, juveniles = 0.41) and 0.37 for *M. australis*. The ME, which is a measure of
420 predictive bias and is on the scale of the response variable, indicated low bias in the
421 predictive performance with 0.35 for *L. calcarifer* (adults = 2.19, juveniles = -1.7),
422 0.67 for *H. fuliginosus* (adults = 0.10, juveniles = 1.24) and 6.6 for *M. australis*.
423 Comparing the values of the ME with mean abundances from Table I shows that these
424 values are all well below the mean abundance for each species and are relatively close
425 to zero which would indicate little or no bias in predictive performance.

426

427

428 The hierarchical modelling revealed strong evidence of interactions between
429 the long-term flow regime (measured as mean daily flow) and short-term flow
430 variation affecting the abundances of each species. For both *H. fuliginosus* and *L.*
431 *calcarifer* there were distinct ontogenetic differences in the nature of these
432 interactions (Table III). Juvenile *H. fuliginosus* generally displayed negative
433 hierarchical relationships to increasing variability of flows (negative slope terms for
434 CV_{1m} and CV_{w2}) whereas adults displayed positive hierarchical relationships to these
435 variables. Coupled with the negative intercept terms (Table III), this suggests that as
436 historical mean daily flow increases in lower reaches of the catchment the relationship
437 between juvenile *H. fuliginosus* abundance and flow variability becomes increasingly
438 negative. By contrast, the positive slope terms for adults suggest that as historical
439 mean daily flow increases the strength of relationships between variability of flows
440 and adult *H. fuliginosus* increases. Both adult and juvenile *H. fuliginosus* displayed

negative hierarchical relationships to descriptors of mean daily flows with low inclusion probabilities (M_{w1} and M_{w2}). The results were not so consistent for *L. calcarifer* with variables showing high inclusion probabilities being hierarchically related to either juveniles or adults but not both. For example, adults displayed positive relationships to mean daily flow one month prior to sampling (M_{1m}), which was dampened as historical mean daily flow increased. The positive intercept for juveniles and M_{1m} coupled with a highly uncertain slope term near zero, indicates that this relationship, on average does not change according to the long-term flow regime. Despite time being included in all models to account for long-term temporal trend in abundance, only adult *H. fuliginosus* displayed a positive temporal trend, and only at sites with higher long-term mean daily flow (Table III).

The most probable model for *M. australis* identified several relationships to temporal flow variation and site-scale hydraulics, some of which were constrained by the long-term flow regime (Table III). This species showed a negative response to increased flow variability across two scales (CV_{1m} and CV_{w2}) which was not mediated by historical mean daily flow, indicated by the strong negative intercept terms coupled with highly uncertain slope terms that were close to zero. However, the relationships to mean daily flow in the wet season two years prior to sampling and the ratio of velocity to depth were both dependent on the long-term flow regime. There was considerable uncertainty surrounding the temporal trend in abundance over the period of sampling, however, there was evidence of a negative trend across the entire catchment which tended to become more strongly negative as historical mean daily flow increased (slope and intercept terms, Table III).

DISCUSSION

The results of this study illustrate the importance of flow variation operating across multiple temporal scales in shaping fish abundances in the Daly River. There were significant catchment wide correlations between abundance of species and short-term hydrologic variables across scales. However, the hierarchical nature of riverine systems (Frissell *et al.*, 1986; Fausch *et al.*, 2002) suggests that species' relationships to flow variation at fine scales may depend on flow variation at larger scales (Biggs *et al.*, 2005). The Bayesian hierarchical models developed in this study revealed where these hierarchical flow-fish relationships exist for the three species under study.

SPECIES-SPECIFIC RELATIONSHIPS TO THE TEMPORAL FLOW HIERARCHY

Overall, there were important relationships between the abundance of both age classes of *H. fuliginosus* and hydrologic variation in the wet seasons and immediately prior to sampling (Tables II and III). Previous studies in the Burdekin River have found that higher wet season flow enhances *H. fuliginosus* recruitment through increased food availability for juveniles which results in a positive association between wet season discharge and *H. fuliginosus* abundance (Pusey *et al.*, 2004). In

the present study, there were negative relationships between the magnitude of flows and juvenile abundance across the catchment (Table II). However, the results of the Bayesian hierarchical model (Table III) indicate that the variability of flows may be more important to *H. fuliginosus* abundance in the Daly River, rather than the magnitude, and that these relationships may depend on the long-term flow regime or the position in the catchment. Juveniles were negatively related to increased flow variability two wet seasons prior to sampling, particularly in downstream sites with higher historical mean daily flow (Table III). This may be due to poor spawning and recruitment success during periods of highly variable wet season flows. *Hephaestus fuliginosus* move into shallow, fast flowing riffle habitats to spawn during the wet season and juveniles use this habitat for refuge and feeding before occupying deeper pools as adults (as indicated by the significant positive correlation between juvenile abundance and velocity:depth ratio - Table II; see also Pusey *et al.*, 2004; Chan *et al.*, 2011). Highly variable flows during the wet season may reduce the quality of riffle spawning habitat by increasing turbulence and rapidly altering water levels which may desiccate eggs deposited in shallow marginal areas. Consequent decreases in egg survivorship and larval recruitment may explain the low juvenile abundance observed during dry seasons that follow highly variable wet seasons. These results suggest that the magnitude and variability of flows and their interactions with site-scale hydraulics are likely to be important determinants of spatial and temporal variation in the abundance of *H. fuliginosus*.

Interpretation of the results for *L. calcarifer* is complicated by the life-history of this species. *Lates calcarifer* undertake extensive movements in both upstream and

downstream directions (Pusey *et al.*, 2004; Milton & Chenery, 2005; Walther *et al.*, 2011). Adults migrate from freshwaters downstream to estuarine habitats to spawn and juvenile fish move upstream to freshwaters at age 1 or 2 (Davis, 1985; Pusey *et al.*, 2004). Upstream juvenile movements are likely to be triggered by the coincidence of elevated flows and large spring tides (Davis, 1985). Previous studies relating fish catch to hydrologic variation have found positive correlations with high wet season flows one or two years prior to sampling (Staunton-Smith *et al.*, 2004; Balston, 2009). The results of the catchment-wide correlations are consistent with these earlier findings with positive relationships to the magnitude of wet season flows for both one and two seasons prior to sampling (Table II). This may be related to elevated flows improving juvenile survival (Balston, 2009) by providing access to more productive and predator free habitat (Davis, 1985). However, looking beyond these relatively strong catchment-wide relationships between flow variation and *L. calcarifer* abundance, the results of the hierarchical model suggest more complex relationships to flow variation at multiple scales. For example, adult *L. calcarifer* displayed a stronger positive relationship to the magnitude of flows one month prior to sampling at upstream sites than in downstream sites where historical mean daily flow was higher (Table III). The positive relationship to increased magnitude of flow is likely due to increased flows stimulating movement of individuals from estuarine to freshwater habitats (Walther *et al.*, 2011). However, the weaker nature of this relationship in downstream sites with high historical mean daily flow may be related to the greater availability of off-channel floodplain habitats adjacent to downstream river reaches in comparison to further upstream where *L. calcarifer* are restricted to the main channel.

541

542 The results in entirety for *M. australis* showed that the catchment-wide
543 correlations between abundance and hydrologic variables, which indicated a negative
544 relationship to the magnitude of flows and positive relationships to variability (Table
545 II), were not the complete story. The Bayesian hierarchical model identified
546 contrasting results with a generally negative relationship to short-term flow variability
547 and a positive relationship to the magnitude of wet season flows, both of which were
548 dependent on the historical mean daily flow (Table III). Many species of
549 *Melanotaenia* in northeastern Australia spawn year round but are most active
550 reproductively during the dry season to ensure juveniles have relatively stable
551 conditions for growth (Pusey *et al.*, 2001). However, populations of lowland
552 *Melanotaenia* species in northern Australia have been found to spawn most actively at
553 the onset of the wet season (Bishop *et al.*, 2001) presumably to take advantage of
554 floodplain habitats and backwaters made available with elevated flows (Beumer,
555 1979). This contrasting lowland wet season/upland dry season spawning strategy may
556 explain the negative relationship to the magnitude of wet season flow in the
557 headwaters, where such flows may have a flushing effect, and the positive
558 relationship in the lower reaches where elevated wet season flows would provide
559 access to floodplain and backwater habitats (M_{w2}, Table III). Further research into the
560 potential for differential spawning strategies within the Daly River catchment could
561 provide a clearer understanding of this relationship and contribute toward future
562 management of water resources in the region.

563

564

565 BAYESIAN HIERARCHICAL MODELLING

566

567

568 The ability to quantify species-environment relationships across multiple spatial
569 and temporal scales in a statistical model is an important goal in ecological research
570 (Austin, 2002; Olden *et al.*, 2006b). However, identifying key environmental
571 determinants of in-stream distribution and abundance of species is complicated by the
572 hierarchical nature of river systems (Parsons *et al.*, 2004). The “riverscape” concept
573 (Fausch *et al.*, 2002) was developed in part to achieve this goal and specifically examines
574 riverine ecosystems as part of broader landscape in which they are nested. This approach
575 to fish ecology involves examining environmental determinants of fish distribution and
576 abundance at multiple scales (Schlosser, 1991; Wiens, 2002). Recent technological
577 advances, including data collection and modelling (*e.g.* Carbonneau *et al.*, 2011) have
578 provided an opportunity to test this concept and understand ecological relationships
579 across the riverine hierarchy.

580

581

582 A hierarchical approach to regression modelling, such as the present study, is
583 ideally suited to applying the riverscape approach to quantify relationships between
584 fish abundances and multiscale hydrologic variation. The flexibility of Bayesian
585 approaches (Clark, 2005; Cressie *et al.*, 2009) which enabled the development of the
586 hierarchical bivariate response model for *H. fuliginosus* and *L. calcarifer*, suggests
587 that there may be considerable advantage to applying these methods under the
588 riverscape approach. The hierarchical structure of the models identified interactions
589 between multiple scales of flow variation that influenced the abundance of species
590 that a more traditional, non-hierarchical, regression model could not (Latimer *et al.*,
591 2006). However, the relatively poor predictive performance of the models in the

present study indicates these particular models should not be relied upon for prediction. Predictive performance could be improved with additional data collection. This dataset consists of a relatively small number of sites (eight in total), selected to represent a large catchment, sampled on ten occasions. Increased spatial coverage, which would encompass more of the gradient of variation in the long term flow regime along with longer term sampling which would encompass more than a single generation of most species, should improve predictive performance. The relatively small sample size also limited the number of candidate predictor variables in the models and the use of additional ecologically-relevant predictor variables (e.g. measures of aquatic and riparian habitat composition) or different metrics of flow variation may improve model fit and predictive performance. Overall, however, the Bayesian hierarchical statistical approach provides the capacity to develop statistical models that more closely reflect the hierarchical nature of the riverine environment to quantitatively apply the riverscape approach and make efficient use of available data.

IMPLICATIONS FOR WATER RESOURCE DEVELOPMENT

The findings of the Bayesian hierarchical models are particularly important given the possible water resource development and subsequent regulation of the Daly River catchment. Presently, there is a paucity of quantitative information on the flow requirements of aquatic species for many northern Australian rivers (Chan *et al.*, 2011). However, it is clear from the results of this study that the hierarchical nature of temporal variation in the flow regime is an important aspect of species' flow

requirements. Fish species" responses to short-term fluctuations in discharge depend on the long-term hydrologic regime in which they are nested. Information such as this should be incorporated into environmental flow programs and/or the quantitative models that underpin them to improve the ecological outcomes of future river management (*e.g.* Chan *et al.*, 2011). It should be noted that the results of the predictive performance suggest that these models should not be used to forecast ecological change under water resource development. However, the ecological relationships the models described could still be used in water resource planning, given the strong descriptive capacity of the models. Decisions regarding the flow of the Daly River that ignore the temporal hierarchy of the flow regime may not achieve the desired ecological outcome; the landscape and hydrologic context of environmental flows and water abstractions must also be considered.

ACKNOWLEDGEMENTS

We thank two anonymous reviewers for their comments that improved the final manuscript. Financial support for this project was provided by the Tropical Rivers and Coastal Knowledge (TRaCK) research program. TRaCK receives major funding for its research through the Australian Government's Commonwealth Environment Research Facilities initiative; the Australian Government's Raising National Water Standards Program; Land and Water Australia; the Fisheries Research and Development Corporation; the National Environmental Research Program and the Queensland Government's Smart State Innovation Fund. For assistance in the field we

thank Q. Allsop, I. Dixon, V. Hermoso, P. Kurnoth, P. Kyne, D. Warfe and D. Wilson. Members of the Wagiman, Wardaman and Jawoyn traditional owner groups provided access to their land, local knowledge and assistance in the field. This research project was approved by the Griffith University Ethics Committee for Experimentation on Animals (approval number AES/0406/AEC) and the Charles Darwin University Animal Experimentation and Ethics Committee (permit number AO6004) and the applied research protocols used were conducted in accordance with the requirements of these committees.

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831

832

832 Table I. Summary statistics of abundances of each species as well as hydrologic and hydraulic
833 predictor variables used in the analysis. The units for species abundance are total number of
834 individuals at the sampling reach. The units of all hydrologic predictors are in m³s⁻¹.

Species data	Common name	Age class	Mean	S.D.	Min	Max
<i>Hephaestus fuliginosus</i>	Sooty grunter	Adults Juveniles	2.56 13.61	4.71 10.56	0 0	38 46
<i>Lates calcarifer</i>	Barramundi	Adults	5.34	6.16	0	32
		Juveniles	9.16	10.47	0	53
<i>Melanotaenia australis</i>	Rainbowfish	NA	67.05	69.79	0	337

Predictor variables	Code	Mean	S.D.	Min	Max
Flow history					
Long term mean daily flow	M _{LT}	144.67	92.98	17.68	281.52
Seasonal flow					
Mean daily flow previous wet season	M _{W1}	325.84	272.29	23.14	897.10
CV daily flow previous wet season	CV _{W1}	1.77	0.42	1.14	2.75
Mean daily flow two wet seasons prior	M _{W2}	334.04	269.33	10.84	897.10
CV daily flow two wet seasons prior	CV _{W2}	1.73	0.40	1.14	2.73
Mean daily flow previous dry season	M _D	12.57	11.72	0	41.79
CV daily flow previous dry season	CV _D	0.23	0.48	0	2.52

Recent flows

Mean daily flow 1 month prior	M_{1M}	14.11	14.34	0	71.75
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CV daily flow 1 month prior	CV_{1M}	0.09	0.14	0	0.71
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Hydraulics

	$V:D$	0.21	0.12	0	0.58
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Velocity to depth ratio					
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836 Table II. Correlation between abundance (CPUE) and hydrologic, hydraulic and temporal
837 predictor variables across multiple scales. Significant correlations, ($P<0.05$) are indicated by an
838 asterisk (*). See Table I for explanations of variables codes.

	<i>H. fuliginosus</i>		<i>L. calcarifer</i>		<i>M. australis</i>
	Adult	Juvenile	Adult	Juvenile	
Flow history[§]					
M _{LT}	0.15	-0.76*	0.67	0.54	-0.73*
Seasonal flow					
M _{W1}	0.18	-0.46*	0.25*	0.32*	-0.38*
CV _{W1}	-0.29*	0.19	-0.17	-0.16	0.41*
M _{W2}	0.05	-0.23*	0.40*	0.10	-0.43*
CV _{W2}	-0.02	0.13	-0.30*	-0.07	0.42*
M _D	0.06	-0.39*	0.43*	0.21	-0.46*
CV _D	-0.10	0.10	-0.21	-0.15	0.27*
Recent flows					
M _{1M}	0.02	-0.39*	0.47*	0.57*	-0.43*
CV _{1M}	-0.14	0.22	0.00	0.08	-0.06
Hydraulics					
V:D	-0.14	0.40*	-0.16	-0.11	-0.34*
Trend					
TIME	0.08	0.02	0.14	-0.03	-0.02

839 [§] correlations performed on mean abundance for each site

840 Table III. Hierarchical regression slope parameters, γ_{ijl} , from the upper level of the model $\hat{\beta}_{ijl} = \gamma_{ijl0} + \gamma_{ijl1}Z_{j1}$ for variables included in the
841 averaged model for each species, indicating how relationships to temporal flow variation are constrained by the long term flow regime, defined
842 by the historic mean daily flow at each location. Estimates shown are the mean of the posterior distribution of each model averaged regression
843 parameter (95% credible interval in brackets). The slope parameters describe the relationship between the local-scale regression coefficients and
844 the historic mean daily flow. For example, the mean of the parameter estimate for *H. fuliginosus* juveniles and CV1month, -0.24, indicates that
845 for every increase of 1 standard deviation of MDF the relationship between *H. fuliginosus* and CV1month decreased by $e^{-0.24} = 0.78$. Inclusion
846 probability, $P(\beta_{ijl} \neq 0 | D)$, of each variable is the sum of the posterior probabilities of the models in which it occurs from the Bayesian model
847 averaging. See Table I for explanations of variable codes.
848

Species	Variable	$P(\beta \neq 0 D)$	Intercept (γ_{ijl0})		Slope (γ_{ijl1})	
			Adults	Juveniles	Adults	Juveniles
<i>H. fuliginosus</i>	Intercept		-2.05 (-3.2, -0.98)	-0.3 (-1.1, 0.9)	-1.36 (-3.5, 0.33)	-1.55 (-2.9, -0.57)
	M _{w1}	0.16	0.35 (0, 2.72)	0.19 (0, 1.49)	-0.19 (-1.8, 0)	-0.12 (-1.04, 0)

	CV _{W1}	0.84	-0.52 (-1.12, 0)	-0.20 (-0.58, 0.12)	0.07 (-0.51, 0.66)	0.08 (-0.28, 0.47)
	M _{W2}	0.2	0.05 (-0.32, 0.83)	0.16 (0, 1.14)	-0.11 (-1.27, 0.13)	-0.10 (-0.9, 0)
	CV _{W2}	0.80	-0.05 (-0.8, 0.54)	-0.54 (-1.16, 0)	0.31 (-0.69, 1.25)	-0.25 (-0.86, 0.15)
	M _{1M}	1	-0.18 (-1.46, 1.18)	0.02 (-0.74, 0.82)	-0.11 (-0.74, 0.82)	0.15 (-0.98, 1.1)
	CV _{1M}	0.80	-0.12 (-0.71, 0.37)	-0.03 (-0.36, 0.27)	0.23 (-0.29, 0.91)	-0.24 (-0.65, 0.05)
	V:D	0.2	-0.16 (-1.19, 0)	0.02 (-0.11, 0.35)	-0.04 (-0.59, 0.2)	-0.02 (-0.35, 0.14)
	TIME*		0.00 (-0.29, 0.29)	-0.06 (-0.33, 0.19)	0.15 (-0.16, 0.48)	0.02 (-0.27, 0.3)
<i>L. calcarifer</i>	Intercept		-1.53 (-2.41, -0.61)	-0.19 (-1.44, 1.1)	0.22 (-0.91, 1.29)	-0.64 (-2.09, 0.96)
	M _{W1}	0.39	-0.2 (-1.41, 0.32)	0.24 (-0.44, 1.56)	0.18 (-0.46, 1.46)	-0.31 (-1.84, 0.37)
	CV _{W1}	1	0.29 (-0.22, 0.76)	0.06 (-0.47, 0.54)	0.08 (-0.42, 0.59)	-0.04 (-0.58, 0.54)
	M _{W2}	0.11	-0.05 (-0.75, 0)	-0.11 (-1.27, 0)	0.07 (0, 1.05)	0.13 (0, 1.49)

	CV _{W2}	0.5	0.05 (-0.3, 0.49)	0.00 (-0.46, 0.44)	-0.12 (-0.69, 0.21)	-0.12 (-0.72, 0.3)
	M _{1M}	1	0.7 (-0.27, 1.65)	1.1 (-0.04, 2.25)	-0.19 (-1.23, 0.9)	-0.04 (-1.31, 1.28)
	CV _{1M}	1	-0.08 (-0.52, 0.33)	0.45 (-0.08, 0.96)	0.06 (-0.39, 0.53)	0.22 (-0.3, 0.84)
	TIME*		0.02 (-0.31, 0.27)	0.2 (-0.54, 0.11)	0.08 (-0.22, 0.4)	0.08 (-0.26, 0.47)
<i>M. australis</i>	Intercept		0.44 (-0.67, 1.52)		0.08 (-1.12, 1.29)	
	M _{W2}	1	-1.23 (-2.45, -0.11)		1.02 (-0.23, 2.33)	
	CV _{W2}	1	-0.47 (-1.17, 0.19)		-0.08 (-0.89, 0.65)	
	CV _{1M}	1	-0.33 (-0.71, 0.05)		-0.10 (-0.51, 0.34)	
	V:D	1	-0.36 (-0.78, 0.06)		-0.55 (-1.02, -0.08)	
	TIME*		-0.11 (-0.41, 0.18)		-0.09 (-0.42, 0.24)	

849 * TIME was included in every model making its inclusion probability subjectively predetermined as 1

Figure Captions

Fig. 1. Location of fish sampling reaches in the Daly River catchment with intermittent reaches indicated by thinner drainage lines. Numbers next to the sites indicate each site ID used in later figures. The inset shows the location of the study area in northern Australia.

Fig. 2. Daily discharge at in the perennial Daly River main channel (site 1, solid line) and intermittent Fergusson River tributary (site 8, dashed line) for the period leading up to and including the study period. The timing of each sampling trip at the beginning and end of each dry season is indicated by open and closed arrows, respectively.

Fig. 3. Temporal variation in catch per unit effort (CPUE: total number of individuals per electrofishing shot) for each species/age class at selected sampling reaches. Dashed lines indicate the long term trend in CPUE over time (line of best fit). X-axis labels indicate the year and season of sampling, for example, early dry season 2006 = ED06 and late dry 2006 = LD06.

Fig. 4. Plots of Observed abundance against fitted values for each model. For *L. calcarifer* and *H. fuliginosus*, juveniles are adults are indicated by closed circles (◐) and plus symbols (+) respectively. Pseudo- R^2 values for each are *M. australis* = 0.83, *H. fuliginosus* = 0.85, *L. calcarifer* = 0.81.

Figure 1

Figure 2

Figure 3

Figure 4