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Complete List of Authors:	Kopf, R.; Charles Sturt University, Institute for Land Water and Society Humphries, Paul; Charles Sturt University, Institute for Land, Water and Society Bond, Nick; LaTrobe University Sims, Neil; CSIRO Watts, Robyn; Charles Sturt University Thompson, Ross; University of Canberra Hladysz, Sally; Monash University Koehn, John; Arthur Rylah Institute for Environmental Research King, Alison; Charles Darwin University, McCasker, Nicole; Charles Sturt University, Institute of Land, Water and Society McDonald, Simon; Charles Sturt University
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**Macroecology of fish community biomass-size structure:
effects of invasive species and river regulation**

R. Keller Kopf ^{1, 8}, Paul Humphries ¹, Nick R. Bond ², Neil C. Sims ³, Robyn J. Watts ¹, Ross
M. Thompson ⁴, Sally Hladyz ⁵, John D. Koehn ⁶, Alison J. King ⁷, Nicole McCasker ¹,
Simon McDonald ¹

¹ *Institute for Land Water & Society, Charles Sturt University, Albury, New South Wales
2640, Australia*

² *School of Life Sciences, La Trobe University, Wodonga, Victoria, 3690, Australia*

³ *CSIRO, Land and Water, Melbourne, Victoria 3169, Australia*

⁴ *Institute for Applied Ecology, University of Canberra, Canberra, Australian Capital
Territory, 2601, Australia*

⁵ *School of Biological Sciences, Monash University, Melbourne, Victoria 3800, Australia*

⁶ *Arthur Rylah Institute for Environmental Research, Department of Environment, Land,
Water and Planning, Heidelberg, Victoria 3084, Australia*

⁷ *Research Institute for the Environment and Livelihoods, Charles Darwin University,
Darwin, Northern Territory 0909, Australia*

⁸ Corresponding author: rkopf@csu.edu; +61 2 6051 9294

Abstract:

The biomass of organisms of different sizes is increasingly being used to explore macro-scale variation in food-web and community structure. Here we examine how invasive species and river flow regulation affect native fish biomass and fish community $\log_{10}$ biomass-body mass scaling relationships in Australia's largest river system, the Murray-Darling. The $\log_{10}$ biomass-body mass scaling exponent (*scaling B*) of invasive fishes (95% CI; -0.14 to -0.18) was less negative than for native fishes (95% CI; -0.20 to -0.25), meaning that invasive species attained a higher biomass in larger size-classes compared to native species. Flow alteration and invasive common carp (*Cyprinus carpio*) biomass were correlated with severe reductions in native fish biomass ranging from -47% to -68% (95% CI). Our study provides novel evidence suggesting that invasive and native communities have different biomass-body mass scaling patterns, which likely depend on differences in their trophic ecology and body size distributions. Our results suggest that restoration efforts using environmental flows and common carp control has potential to boost native fish biomass to more than double the current level.

Keywords: body size; ecosystem energetics, environmental flows; restoration; food web; alien species; common carp; size spectra

Introduction

Ecological communities are size-structured (Hildrew et al. 2007) whereby large-bodied predators generally consume smaller prey and there are disproportionately more smaller organisms, with a higher total biomass, than large ones (Elton 1927; Kerr 1974; Hatton et al. 2015). Consistent macroecological patterns of abundance and biomass scaling with body size in a diverse range of taxa and environments has stimulated size spectrum theory (Sprules and Barth 2016) and is predicted by the metabolic theory of ecology (Brown et al. 2004; Sibly et al. 2012). Sized-based models are gaining popularity in applied environmental and fisheries science owing to their low parameter requirements, the relative ease and low cost of collecting body size data and their sensitivity to ecological changes (Petchey and Belgrano 2010; Andersen et al. 2016a-b; Blanchard et al. 2017; Yen et al. 2017).

Biomass size spectrum theory (Sprules and Barth 2016) and the metabolic theory of ecology (Brown et al. 2004; Sibly et al. 2012) predict that within a community at a steady-state, normalized biomass should scale log-linearly and negatively with a scaling exponent of ~ -1.0 . The negative log-linearity of the community size structure is thought to emerge because of physical and physiological constraints associated with: 1) the inefficient transfer of energy across trophic levels (Lindeman 1942); 2) predators being larger than their prey (Kerr 1974; Hatton et al. 2015); and 3) the scaling of metabolic rate with body mass (Brown et al. 2004), all of which appear to be roughly consistent across diverse taxa and environments.

Although community biomass size structure is known to be largely determined by energetics, metabolism and predatory-prey dynamics, it can also be influenced by factors such as fishing, variation in primary productivity or population demographics (Banse and Mosher 1980; Andersen et al. 2016a). Fishing, for example, often has top-down effects because the selective removal of larger individuals results in trophic cascades that generate

72 steeper (more negative) size spectra scaling exponents (Jennings and Blanchard 2004,
73 Petchey and Belgrano 2010). In contrast, global climate change may have bottom-up
74 ecosystem energetic effects that alter the size-structure of plankton communities, with
75 negative consequences for the production of higher trophic level consumers (Yvon-Durocher
76 et al. 2011; Woodworth-Jefcoats et al. 2013). However, there is a dearth of empirical
77 evidence and no theory available to explain how or if other globally-important anthropogenic
78 pressures influence community biomass-size structure.

79 Invasive species (Strayer 2010) and river flow alteration via dams (Bunn and
80 Arthington 2002; Nilsson et al. 2005) represent two of the major drivers of biodiversity
81 change in aquatic ecosystems world-wide. These anthropogenic pressures can adversely
82 affect the biomass and abundance of native species (Gehrke et al. 1995; Propst et al. 2008),
83 thereby altering species and community size-structure at varying spatial scales (Blanchet et
84 al. 2010; Jellyman et al. 2014; Fritschie and Olden 2016). However, no studies have
85 examined whether these anthropogenic pressures affect community biomass-body size
86 scaling relationships.

87 Here we examine how fish community biomass scales with body mass in Australia's
88 largest river system, the Murray-Darling. We evaluate how $\log_{10}$ biomass-body mass scaling
89 patterns and native fish biomass vary among sub-catchments with different proportions of
90 invasive species and varying types of river flow alteration. The objectives of this study were
91 to: 1) estimate the $\log_{10}$ biomass-body mass scaling exponent of native and invasive fishes
92 and to evaluate whether river flow alteration or other environmental factors were correlated
93 with variation in the scaling exponent; and 2) estimate whether native fish biomass was
94 correlated with river flow alteration, invasive species biomass or other environmental factors.
95 Lastly, given the negative effects of invasive common carp (*Cyprinus carpio*; Linnaeus 1758)
96 and river flow alteration on native fish biomass identified in objective 2, we used our model

to estimate the potential biomass of native fish that may be possible under future restoration scenarios.

Methods

Study area and fish community data

The Murray-Darling Basin (MDB) extends over 1 million km², across 14% of the continent of Australia (Fig. 1). The MDB fish fauna is naturally depauperate, comprising 38 native freshwater species (Unmack 2013). Our analysis of the MDB fish community focuses on lowland river systems which have been extensively surveyed as part of a basin-wide fish monitoring program. Invasive fishes, particularly common carp, goldfish *Carassius auratus* (Linnaeus 1758), European perch *Perca fluviatilis* (Linnaeus 1758) and eastern gambusia *Gambusia holbrooki* (Girard 1859), now make up a large proportion of the fish community in the MDB (Davies et al. 2010). All of these species, and other less pervasive alien fishes, are considered in the current analysis.

We draw on fish monitoring data collected as part of the Sustainable Rivers Audit (SRA) program (Davies et al. 2010). The SRA was a multi-year river-basin scale ecological condition survey of rivers and streams across the MDB. Our analysis used results from in-channel boat electro-fishing from 251 sites (Fig. 1) within 17 of the 23 sub-catchments of the MDB sampled on two occasions from 2004-2009. Sampling included: 1) randomized, fixed and roving site design; 2) standardized and consistently implemented field protocols; and 3) coordinated quality-assurance and data management programmes (Davies et al. 2010). All sites (5-18 sites) within each sub-catchment were aggregated to estimate biomass and biomass-size scaling exponents for fish communities in the Murray-Darling Basin (Fig. 1). Sampling at each site was undertaken using a SmithRoot[®] model 7.5 GPP boat-mounted electrofisher following the standard SRA protocol of 12 replicate 90 s units of 'power on'

time with settings of 1000V, 60 Hz and 40% duty cycle pulsed DC current. Sampling was conducted in an upstream direction fishing all accessible habitats with one team member on the boat netting all stunned fish (Murray-Darling Basin Commission 2004). All fish greater than 15 mm were identified, enumerated and had total length (mm; TL) measured in the field. Up to 50 individuals of each species were weighed (± 0.01 g) on each sampling occasion, and species-specific length-mass regressions were used to convert TL into mass.

Boat electro-fishing detection rates vary with environmental conditions (e.g. depth, turbidity, salinity), among habitat types and species (Bayley and Austen 2002; Lyon et al. 2014). It is generally size-biased, and can underestimate the abundance of fishes smaller than approximately 100 g (Zalewski 1985; Dolan and Miranda 2003). In deep rivers larger individuals may also be under-represented (Lyon et al. 2014). Although different species have different boat electro-fishing detection probabilities we assumed that, within the river channel habitats sampled, capture efficiency was primarily a function of body size (Dolan and Miranda 2003) and river depth (Bayley and Austen 2002). To correct for the size and depth-bias of boat electro-fishing, we calculated capture efficiency using two correction models (Model 1 and 2; Table 1). Correction models used body size of individual fish and depth of the electrofishing pass to estimate detection probabilities which were then used to calculate the number of individual fish of a given size that were not detected.

Correction 1 (Model 1; Table 1) was developed by Bayley and Austen (2002), and the numerical values used were based on capture efficiency estimates for common carp (Bayley and Austen 2002) because this species had the highest biomass of all fishes in our sample. Model 1 was dome-shaped, similar to correction functions developed for several fishes in Australia (Lyon et al. 2014), and was used here because it was the most conservative model,

145 peaking at a low estimated capture efficiency of approximately 9% in fishes between 200 and
146 300 mm TL (Bayley and Austen 2002).

147 Correction 2 (Model 2; Table 1) assumed a higher capture efficiency and was
148 therefore less conservative and assumed a different shaped function, based on a simple $\log_{10}$ -
149 linear relationship developed for stream and large river fish communities (Zalewski 1983,
150 1985). Model 2 assumed that capture efficiency was mass-based regardless of species and
151 that efficiency was higher and constantly increasing $\log_{10}$ -linearly from approximately 20%
152 at 4 g to 95% at over 20,000 g. No depth-correction coefficient was available for this model.
153 It should be noted that detection rates are usually ignored in the analysis of such sampling
154 data (e.g. Davies et al. 2010) but are an integral component for providing community biomass
155 estimates. In light of limited detailed information on detection rates under all conditions and
156 species, the two correction models used here in combination with the raw data provided an
157 opportunity to explore the sensitivity of our results to some of the potential biases of boat-
158 electrofishing.

159 To evaluate the sensitivity of our results to the aforementioned biases of boat-
160 electrofishing and to different methods of correction, scaling exponents and biomass were
161 calculated using: raw uncorrected mass (raw data); Model 1 corrected mass (Model 1
162 corrected); and Model 2 corrected mass (Model 2 corrected). In order to minimize other
163 potential biases which can affect sampling efficiency, including river discharge variability,
164 differences among habitat types and differences among sampling gears, analyses were
165 restricted to in-channel boat electro-fishing in large perennial lowland rivers (stream order $\geq$
166 5) that were sampled during low-flow conditions during the same season each year. Sampling
167 for the SRA program examined here occurred during a 10 year drought (see Bond et al.

2008), which resulted in low but consistent flows and sampling conditions within the perennial systems.

Biomass-body size scaling

We used maximum likelihood (MLE) to estimate the scaling exponent (b) of the $\log_{10}$ abundance-mass relationships for fish communities in each of 17 sub-catchments of the MDB. We fitted the mass of individual fish within each sub-catchment to the log-likelihood of a bounded power law distribution using a probability density function (Model 3; Table 1) based on *R* code adapted from Edwards et al. (2017). The exponent b estimated from Model 3 (Table 1) represented the $\log_{10}$ abundance-mass scaling relationship, and therefore the scaling exponent for the $\log_{10}$ biomass-body mass (*scaling B*) relationship was calculated as $b + 1$ (Edwards et al. 2017). Body size scaling relationships in aquatic communities have traditionally been estimated by summing the number of individuals within $\log_2$ scale body size bins (e.g. Jennings and Blanchard 2004) and fitting ordinary least squares regression. More recent methodological comparisons have revealed that bin-based regression approaches can yield biased estimates of scaling exponents (White et al. 2008) and therefore we used maximum likelihood here.

The $\log_{10}$ biomass-size scaling exponents (*scaling B*) were estimated separately using raw data, Model 1 corrected data and Model 2 corrected data for each sub-catchment and each of three fish community groupings: 1) the entire fish community comprising all species; 2) native species only; 3) invasive species only. First, each fish sampled was classified as native or invasive (Table S1). *Scaling B* was then estimated for native species, invasive species and for the entire community (native and invasive species) for each sub-catchment using the adapted MLE *R* code (Edwards et al. 2017) described previously. The MLE

function was fitted to the mass distribution of native species, invasive species and the entire community (native and invasive species) separately for each sub-catchment. The median *scaling B* of 1000 Monte Carlo simulations (see below) for each sub-catchment served as replicates in statistical analyses for each respective community grouping (native; invasive; entire fish community).

Prior to estimating scaling exponents using maximum likelihood, we used a Monte Carlo resampling procedure modified from Robinson et al. (2017) in order to reduce the potential bias owing to geographic differences in the number of fish sampled across sub-catchments. This process started by randomly sampling 400 individual fish based on raw uncorrected data, 10,000 randomly sampled fish using Model 1 corrected data, and 10,000 randomly sampled fish using Model 2 corrected data for each respective sub-catchment. The scaling exponents for each respective sub-catchment, correction dataset, and fish community group (invasive; native; whole community) were then estimated from 1000 repeated simulations of randomly sampling fish and the median exponent of the simulations for each sub-catchment were used as the response variables in statistical analyses.

The respective sample sizes of fish were chosen following sensitivity analyses (Table S2) which evaluated variation in scaling exponents with increasing sample sizes. The advantages of using the largest sample sizes of fish were offset by the decreasing number of sub-catchments (replicates) which could then be used in statistical analyses. Each sub-catchment used in statistical analyses had greater than 400 raw individual mass measurements, while three sub-catchments (Avoca; Loddon; Castlereagh) had insufficient sample sizes and three sub-catchments were excluded because they were not considered to be lowland systems across the sites sampled (Mitta Mitta; Upper Murray; Kiewa). These six

river systems were excluded from further analyses, which resulted in 17 suitable sub-catchments out of the 23 in the MDB.

Biomass of native fish and ecological pyramids

To evaluate factors contributing to variation in native fish biomass we assigned individual native fish to one of fifteen $\log_2$ -scale body mass bins ranging from 2-32,768 g and the bins were $\log_{10}$ transformed for statistical analyses (Jennings and Blanchard 2004). This bin-based approach is the traditional method used in aquatic size spectra analyses (Kerr and Dickie 2001) and, although we use it here to examine variation in native fish biomass, all scaling exponents were estimated using MLE as previously described. After classifying individual fish as native or invasive, the biomass of native fish was calculated as the sum of individual native species mass for each $\log_2$ body mass class and each respective sub-catchment. Biomass was standardized per 100 electrofishing shots which represented the approximate mean sampling effort per sub-catchment. Lastly, biomass was normalized for linear bin-width (White et al. 2008) by dividing the sum native species biomass by the linear width of each respective $\log_2$ body mass class. The resulting biomass of native fish within each $\log_2$ body mass class for each sub-catchment was the response variable used in statistical analyses. Ecological pyramids of native fish biomass were constructed following Trebilco et al. (2013) whereby biomass was calculated separately for each $\log_2$ body mass class and the mean ($\pm$ 95% CI) was calculated across sub-catchments.

Environmental attributes and anthropogenic pressures

We examined whether four environmental attributes and seven indicators of anthropogenic pressure (Table S3), correlated with changes in fish community scaling exponents (*scaling B*) and native fish biomass. Environmental attributes were sourced from the MDB Aquatic Assets database version 2.0 (Ward et al. 2012) which included mapped rivers, lakes, wetlands and floodplains on a 9" digital elevation model of Australia (Version 3). The extent of floodplains was mapped over a 10 year period between 1984 and 1993. Environmental attributes included (Table S3): annual sub-catchment mean air temperature (T ; °C), sub-catchment terrestrial net primary production (NPP ; tC ha⁻¹), sub-catchment floodplain area (FPA ; km²) and stream order (SO). Stream order, T and NPP were calculated as the median, and FPA as the sum, calculated across each sub-catchment. Terrestrial NPP was used as a surrogate for aquatic primary production since these estimates are unavailable.

Anthropogenic pressure indicators included two that focused on invasive species and five metrics of river flow alteration. The relative biomass (g) of carp (*carp biomass*) within each sub-catchment and the biomass of all other invasive fishes (*other invasive*) standardized per 100 electrofishing shots were used as explanatory variables in statistical analyses. Five metrics of river flow alteration previously developed by Sims et al. (2012) were evaluated as potential predictors of native fish biomass and *scaling B* in statistical analyses.

Flow alteration metrics represented the differences between current regulated flows and modelled 'natural' estimates of flow without river regulation between 1895 and 2006 across the MDB. We used an aggregate metric of river flow alteration (*Flow alt.*) which was a composite of nine metrics relating to historical changes in the frequency, duration and volume of floods, and seasonality of the highest and lowest flow periods (Sims et al. 2012). We also examined the effects of four more specific measures of flow regime alteration including the: mean change in duration of above bank-full flooding (*Flood dur. av.*); mean change in number of above bank-full floods per year (*Flood freq. av.*); mean change in Julian

day within the year of the annual minimum flow (*Min. flow av.*); and the coefficient of variation in Julian day within the year of the annual minimum flow (*Min. flow cv.*). These metrics were used because they explain the majority of historical changes to flows in MDB river-floodplain ecosystems (Sims et al. 2012), have previously been associated with changes in fish communities and river ecosystem function (Junk et al. 1989; Humphries et al. 1999) and were uncorrelated with one other, and therefore could be used together in statistical analyses.

Statistical analyses

Generalized Linear Mixed Effects Models (GLMMs) were used to examine whether environmental attributes or anthropogenic pressures influenced $\log_{10}$ biomass-body mass scaling exponents (*scaling B*; Table 1; Models 4 and 5) or native fish biomass (Table 1; Models 6 and 7) modelled at the sub-catchment level. Prior to analyses, all continuous predictor variables were centred by subtracting the mean across sub-catchments ($n = 17$) and standardized by dividing each by the standard deviation. After excluding fixed effects and interactions with variance inflation factor (VIF) scores of ≥ 4 , we fitted the full Models 4-7 (Table 1) to evaluate whether any environmental attributes, or anthropogenic pressures were correlated with variation in *scaling B* or native fish biomass in comparison to null models. Models with and without interactions were ranked according to the lowest Akaike Information Criterion (AIC) value and pseudo r^2 values were calculated as a measure of goodness of fit (Nakagawa and Schielzeth 2013). A difference of 2 or more between AIC values was used to distinguish important differences among models. Fixed-effects and interactions were evaluated by plotting variable coefficients and their 95% confidence intervals estimated from the full Models 4-7 (Table 1). Since all predictors were standardized

and centred, we assumed that all coefficients not overlapping zero (null model) were important predictors of *scaling B* or native fish biomass.

Region was specified as a random effect (1/region) in all GLMMs (Table 1; Models 4-7) in order to avoid spatial auto-correlation among sub-catchments. The *scaling B* was normally distributed and therefore we fitted a GLMM (Table 1; Model 4) to the raw data, Model 1 corrected and Model 2 corrected datasets, where the intercept was denoted β_0 ; βx_{1-3} were categorical classifications representing invasive species, native species or all fishes in the community; *Flow alt.* was the aggregate river flow alteration metric (Sims et al. 2012); *T* was river temperature (°C), *NPP* was terrestrial net primary production (tC ha⁻¹), *FPA* was sub-catchment floodplain area (km²) and *SO* was stream order. We tested Model 4 with and without an interaction between *Flow alt.* (βx_4) and different fish community groupings (βx_{1-3}) and selected the best model using the lowest AIC. Since the aggregate flow alteration metric (*Flow Alt.*) was calculated in part using *Flood dur. av.*, *Flood freq. av.*, *Min. flow av.* and *Min. flow cv.* (Sims et al. 2012), the last four metrics of flow alteration were examined in a separate Model (5).

To evaluate whether more detailed measures of invasive species or river flow alteration influenced *Scaling B*, we fitted GLMMs (Table 1; Model 5) to the raw data, Model 1 corrected and Model 2 corrected datasets where the intercept was denoted β_0 ; βx_{1-2} were categorical classifications representing native species and all fishes in the community; *carp biomass* was the relative biomass of common carp within each sub-catchment standardized per 100 electrofishing shots; *other invasive* was the standardized relative biomass of all invasive fishes excluding common carp; *Flood dur. av.* was the mean change in duration of above bank-full floods per year; *Flood freq. av.* was the mean change in number of above bank-full floods per year; *Min. flow av.* was the mean change in Julian day within the year of the annual minimum flow and *Min. flow cv.* was the coefficient of variation in Julian day

within the year of the annual minimum flow (Sims et al. 2012). We tested Model 5 with and without interactions between *carp biomass* (β_{x_3}) and each of the four flow alteration metrics ($\beta_{x_{5-8}}$) separately and selected the best model using the lowest AIC.

The biomass of native fish was not normally distributed and we applied a $\log_{10}$ transformation and fitted the GLMMs using Model 6 and Model 7 (Table 1), where *body mass class* represented the $\log_2$ body mass class ($\log_{10}$ transformed) and all other variables were the same as defined previously. We tested Model 7 with and without interactions between *carp biomass* (β_{x_2}) and each of the four flow alteration metrics ($\beta_{x_{4-7}}$) and selected the best model using the lowest AIC value.

We evaluated the sensitivity of results to each of the three methods of boat electrofishing correction including: raw uncorrected; Model 1 corrected; and Model 2 corrected. For each of the full Models 4-7 we considered coefficients important predictors if their 95% confidence intervals did not overlap zero (null model), and reliable if their response was consistently significant in the same direction (positive or negative) across the three methods of correction. To evaluate how the important and reliable predictors influenced biomass, we plotted the model fitted estimates against the range of centred and standardized values with all other variables held constant (Robinson et al. 2017) and constructed ecological pyramids of biomass (Trebilco et al. 2013). Ecological pyramids were constructed using the raw data by plotting the mean ($\pm$ 95% CI) biomass of native species across sub-catchments using model fitted estimates.

Native fish biomass restoration scenarios

We estimated native fish biomass in response to theoretical restoration scenarios by fitting GLMM (Model 7) to dummy datasets that were pre-assigned to different combinations of restored river flows and invasive common carp control. The scenarios were set based on the

important predictors determined in statistical analyses and included: 1) restoration of the seasonal timing of minimum flows (*Min. flow av.*); 2) control of common carp down to 30% of the total fish community biomass; and 3) restoration of all four flow regime metrics together with control of common carp down to 30% of the total fish community biomass. The flow metric values used in the dummy datasets were set based on their estimated unregulated values, while 30% was selected because it was the lowest percentage of invasive common carp biomass observed in sub-catchments (Table S3).

Model 7 parameters were fitted to the raw data and to each of the restoration scenario datasets in order to estimate potential changes in native fish biomass. This model did not account for the impacts of other significant anthropogenic pressures (e.g. habitat alteration, climate change, fishing pressure) since these data were not available. Instead, the model provides a quantitative measure of how native fish biomass may be expected to respond if components of the natural river flow regime were restored and invasive common carp were effectively controlled. Size-specific differences in native fish biomass between current conditions and each of the scenarios were illustrated using ecological pyramids as described previously. The current sum biomass of native fish was divided by the estimated biomass under each restoration scenario, minus one in order to calculate a percent change in native fish biomass for each sub-catchment.

Results

The fish community analysed in the SRA database included 30,097 individuals, comprising 22 native and 9 invasive species, and spanned 6 orders of magnitude in body mass (0.01-24,064 g) (Table S1). Invasive common carp made up the highest biomass of all species and ranged from 29% to 76% of the total biomass of fish communities sampled across 17 sub-catchments. Bony herring *Nematalosa erebi* was the most abundant native species sampled,

while Murray cod *Maccullochella peelii*, Australia's largest freshwater fish, comprised the greatest biomass of the native fishes (Table S1).

Biomass-body size scaling

The $\log_{10}$ biomass-body mass scaling exponents (*scaling B*; Table 2) of native species, invasive species and the whole community were significantly different in the raw data ($DF = 2, 41$; $F\text{-value} = 207$; $P < 0.001$), Model 1 ($DF = 2, 41$; $F\text{-value} = 204$; $P < 0.001$) and Model 2 ($DF = 2, 41$; $F\text{-value} = 131$; $P < 0.05$) corrected datasets. The method of sampling bias correction (raw data, Model 1, or 2 corrected) resulted in significantly different estimates of *scaling B*, but native and invasive species were consistently important predictors using all three datasets (Fig. 2 a-c). Invasive species generally had shallower (less negative) estimates of *scaling B* (Table 2) when compared to native species, but Model 2 corrected data was an exception. No other environmental or anthropogenic pressure variables examined (Fig. 2) using Models 4 or 5 were consistently important predictors of *scaling B* across the different methods of correction, but increasing floodplain area resulted in significantly steeper exponents in the raw data and Model 1 corrected data (Fig 2. a, b). Net primary production was excluded from Model 4 since it had variance inflation factor (VIF) scores ≥ 4 in all three datasets (Table S4).

After considering VIF scores (Table S4) and AIC values, the GLMMs fitted to Models 4 and 5 (Table 1) with no interactions were used in all analyses (Fig. 2 a-f). All GLMMs fitted to Model 4 that incorporated interaction terms between flow alteration and community group (native; invasive; whole community) had VIF scores of ≥ 4 . Therefore, the base model fitted to Model 4 with no interactions was considered the best model for raw data (AIC = -121; pseudo $R^2 = 0.55$), Model 1 (AIC = -83; pseudo $R^2 = 0.41$) and Model 2 corrected data (AIC = -30; pseudo $R^2 = 0.36$). GLMMs fitted to Model 5 that incorporated

interaction terms between *carp biomass* and each of the flow metrics also had VIF scores of ≥ 4 , or their respective AIC values were greater than the base models fitted with no interactions using the raw data (AIC = -56; pseudo $R^2 = 0.27$), Model 1 (AIC = -41; pseudo $R^2 = 0.25$) and Model 2 corrected data (AIC = -8; pseudo $R^2 = 0.27$).

Native fish biomass

The $\log_{10}$ biomass of native fishes fitted to GLMM Model 6 (Table 1) declined significantly with increasing $\log_{10}$ body mass class and river flow alteration (*Flow Alt.*), but increased with stream order (Fig. 3 a-c; Table 3) for all three methods of correction, including raw data (AIC = 353; pseudo $R^2 = 0.53$), Model 1 (AIC = 392; pseudo $R^2 = 0.61$) and Model 2 corrected datasets (AIC = 358; pseudo $R^2 = 0.74$). The coefficients describing the negative effects of river flow alteration and positive effects of stream order (Table 2) on $\log_{10}$ native fish biomass varied little depending on the method of correction and therefore the significant positive or negative trends were illustrated using raw data (Fig. 4 a-b). Temperature and net primary production were excluded from all GLMMs fitted to Model 6 because they had VIF scores of ≥ 4 (Table S4).

The GLMM (Table 1; Model 7), which examined the effects of specific components of flow regime alteration and invasive species (Fig. 3 d-f; Table 4), provided an equal or more parsimonious fit to $\log_{10}$ native fish biomass for raw data (AIC = 343; pseudo $R^2 = 0.58$), Model 1 (AIC = 392; pseudo $R^2 = 0.63$) and Model 2 corrected data (AIC = 357; pseudo $R^2 = 0.76$) when compared to their respective AIC values in Model 6. Decreasing $\log_{10}$ native fish biomass with increasing, $\log_{10}$ body mass class, carp biomass and alteration of the mean timing of low-flow conditions (*Min. flow av.*) were the only significant predictors across all three correction methods (Fig. 3 d-f; Table 4). $\log_{10}$ native fish biomass declined significantly with increasing biomass of carp and low-flow alteration (Fig. 4 c-d). The only

significant difference among methods of correction was an estimated increase in $\log_{10}$ native fish biomass in response to altered flood duration (*Flood dur. av.*) based on the raw data only. Variations of GLMM Model 7 which explored the potential effects of interactions between invasive carp biomass and flow metrics all had VIF scores of ≥ 4 and were therefore excluded.

The pattern of declining native fish biomass with increasing $\log_{10}$ body mass was significant in all models (Table 3; 4) and this negative $\log_{10}$ biomass-body mass relationship resulted in an Eltonian-shaped ecological pyramid structure (Fig. 5a). Alteration of the mean timing of low-flow conditions was correlated with a mean change in native fish biomass of $-22\% \pm 5$ (SE) with a 95% CI ranging from -11% to -32% across sub-catchments (Fig. 6). Carp biomass was correlated with mean change in native fish biomass of $-53\% \pm 4$ across sub-catchments with a 95% CI ranging from -44% to -63%. River flow alteration and carp biomass together predicted a $-58\% \pm 5$ change in native fish biomass with a 95% CI ranging from -47% to -68% (Fig. 6). Relative to current conditions (Fig 5a), ecological pyramids of native fish biomass increased by a factor of 1.23, 2.16 and 2.33 respectively under scenarios of low-flow restoration (Fig. 5b), control of common carp (Fig. 5c) and the combined restoration of all flow regime metrics and common carp control (Fig. 5d).

Discussion

Our study provides quantitative estimates of how invasive fishes and flow regime alteration affect fish community biomass and its size structure in regulated river systems. Our results suggest that invasive species have the potential to disrupt biomass-body mass allometric scaling patterns and therefore understanding the causal food web mechanisms warrants further investigation, including studies on different aquatic and terrestrial ecosystems. These alterations are important from an applied fisheries and biodiversity conservation perspective,

because invasive common carp biomass and river flow alteration were associated with declines in native fish biomass of 47% to 68% across the inland river systems of south-east Australia.

Biomass-body mass scaling

Negative allometric scaling of native fish biomass, spanning six orders of magnitude in body mass and encompassing an entire large river basin was remarkably consistent, regardless of the method of sampling bias correction. Energy availability and related metabolic constraints associated with increasing body mass and trophic level are widely accepted mechanisms explaining this general pattern (Brown et al. 2004; Sibly et al. 2012). The consistent negative allometric scaling of native fish community biomass is broadly consistent with an emerging energetic paradigm (*sensu* Isaac et al. 2012) suggesting that energy and its transfer are fundamental constraints affecting community structure. This is an important consideration for river ecology and management because it suggests that energy plays a key role in shaping the structure of fish communities, and therefore builds on mounting evidence emphasizing the importance of biotic interactions and food web dynamics on river ecosystem functioning (Thorp and Casper 2003; Naiman et al. 2012).

The whole-of-assemblage fish community biomass-size scaling exponents estimated here, ranging from -0.19 to -0.42, must be compared carefully with other studies owing to methodological differences in sampling, but were within the range of values estimated from fish communities in the North Sea (-0.20; Jennings and Mackinson 2003) and coral reefs in the Pacific (-0.13 to -0.95; Robinson et al. 2017), but were less negative than the St. Lawrence river in North America (-0.43 to -0.86; Murry and Farrell 2014). The shallower (less negative) scaling exponents observed in the present study compared to the St. Lawrence

river may be attributed to the higher relative abundance of invasive common carp in Australian waterways.

A major obstacle for making valid comparisons of scaling exponents among studies sampling fish and other vertebrates and testing community-based theoretical scaling predictions is that sampling methods rarely provide estimates of density, usually have unquantified size and species detection probabilities, and do not sample all taxa within the size-spectrum in a consistent manner. Given that the method of correcting for fish body size detection probability, including no correction, influenced our estimates of scaling exponents future studies should carefully consider the size-bias of sampling methods. In some cases it may be necessary to sample all taxa within the food web or invest in further research (e.g. Zalewski 1983, 1985; Bayley and Austen 2002; Lyon et al. 2014) to quantify community (e.g. zooplankton, invertebrates, fish, water-birds) size detection probabilities with the aim of making generalizable correction-factors. If the purpose of the study is to compare scaling exponents to theoretical predictions then correction models, or absolute estimates of density are essential. However, if the purpose of the study is to examine the effects of environmental or anthropogenic factors on the distribution of community biomass then our results suggest that correction factors may not be necessary. Although the method of correction influenced the scaling exponent, the significant predictor variables were generally similar for all methods of correction (Fig. 2). However, correction Model 2 deviated from the pattern of invasive species having a shallower scaling exponent than native species in the raw data and Model 1 corrected data. This result was likely attributed to the higher assumed capture efficiency of fish larger than approximately 100-200 g by Model 2. In our sample where large-bodied invasive common carp had the highest biomass, the higher assumed capture efficiency of Model 2 may have caused the steeper scaling exponent for invasive species.

The scaling exponents estimated here were calculated according to a normalized biomass size spectrum and theory based on complete food webs predicts that this exponent should be approximately -1.0 (Brown et al. 2004; Sprules and Barth 2016). Our estimates did not encompass all taxa (e.g. zooplankton, macroinvertebrates, waterbirds) within the river food webs and the method of sampling bias correction influenced our estimates of scaling exponents. Therefore, the scaling exponents estimated here should not be compared directly to theoretical predictions based on macroecology, or size spectrum theories which rely on comprehensive sampling of entire food webs (Brown et al. 2004; Sprules and Barth 2016).

Within the consumer size range of 1 - 24,000 g and the river channel environments sampled here, our analyses and correction methods provided a reasonable approximation of the potential range of consumer biomass. River-floodplain food webs generally comprise a relatively small number of trophic pathways and consumer species, whereby the standing biomass is typically dominated by detritivorous, herbivorous or omnivorous fishes (Winemiller 2004). The MDB appears to match this general pattern, but the species with the highest standing biomass documented here was a large-bodied invasive omnivore, common carp, and the most abundant species was bony herring, a native detritivore (Stoffels et al. 2013). Although the scaling exponents estimated here should not be compared directly to theoretical scaling predictions, the effects of invasive species on the scaling of biomass or abundance-size relationships warrants further investigation, both in terms of theoretical and applied size-based research (Reuman et al. 2014; Andersen et al. 2016b; Sprules and Barth 2016; Blanchard et al. 2017; Yen et al. 2017).

Macroecology of invasion

We hypothesize that shallower biomass-body mass scaling exponents may be expected in invaded systems, such as those in Australia and rivers in North America (Chick and Pegg 2001; Kulhanek et al. 2011), where large-bodied but low trophic-level invasive cyprinids

have proliferated (Fig. 7). Common carp (Koehn 2004) and other large-bodied cyprinid fishes (Chick and Pegg 2001; Ou et al. 2017) often feed at low trophic-levels on micro-crustaceans and macroinvertebrates, or plankton which are several orders of magnitude smaller than themselves. Food web theory predicts that the introduction of consumers feeding on prey much smaller than themselves can result in more top heavy biomass pyramids, equivalent to less negative size spectra (Fig. 7), and these changes can destabilize community structure (Law et al. 2009; Rip and McCann 2011).

Mechanisms affecting change in fish communities cannot be deduced from our analyses but we hypothesize that the low trophic level feeding strategy, coupled with the large body-size (up to 650 cm) and long life-span (up to 28 years) of common carp (Koehn 2004), means that more energy (Fig. 7) is available for potential biomass production in large body size-classes than similar-sized native fishes which are mostly piscivores (Stoffels et al. 2013). The low trophic level feeding strategy of invasive cyprinids grants early, largely competition-free access to the most abundant and productive basal energy resources and, due to the loss of energy with increasing trophic level, it maximizes the amount of energy available for conversion into biomass (Fig. 7), or reproduction. Furthermore, energy may be retained for long periods of time, since common carp are known to have a life-span of up to 28 years in the MDB and few predators have the capacity to consume mature carp.

Our estimate of the biomass scaling exponent for the native fish community here may be different from ecosystems without invasive species (e.g. Fig. 7), since all rivers in the present study were inhabited by common carp. Future studies evaluating the effects of invasive species on scaling exponents would benefit from replicated field-experimental comparisons of independent systems with and without invasive species, or before-after comparisons. This was not possible in the present study since common carp were present in all sub-catchments of the MDB and no standardized pre-carp invasion data exist.

We hypothesize that food webs invaded by large-bodied invasive cyprinids will have (Fig. 7): 1) shallower biomass-size scaling exponents; 2) higher energy transfer efficiency; 3) higher predator-prey mass ratios (PPMR) and 4) a lower standing biomass of native species when compared to systems without these invasive species. Invasive cyprinids are known to alter a range of ecological functions (Kulhanek et al. 2011), but their effect on native species via food web and ecosystem energetics remains poorly understood. Large-bodied species, including invasive cyprinids (Crook 2004), have the ability to forage over large geographic areas and, due to their size and longevity, have an enhanced capacity to store energy over long periods, thus buffering their susceptibility to spatio-temporal variation in food availability (Barnes et al. 2010).

Given that the median body size of riverine alien fishes is larger than native fishes world-wide (Blanchet et al. 2010), invasive fishes are likely to have altered the biomass size-structure of fish communities elsewhere, possibly toward a more top-heavy biomass pyramid structure, equivalent to shallower biomass-size scaling exponents. Different types of changes to community biomass-body mass scaling exponents and trophic structure may be expected in systems where the most prolific invasive species are large-bodied piscivores (e.g. salmonidae), or where the most prolific invasive species are small-bodied and feed at low trophic levels (e.g. *Gambusia* spp.). For example, Fritschie and Olden (2016) found that individual size distributions non-native species were generally smaller than native fishes in dryland rivers of Arizona but their dominance did not influence community trophic structure. Conversely, non-native salmonids have had profound impacts on food webs and have caused trophic cascades affecting native species (Crowl et al. 1992; Jellyman et al. 2017), most likely with alterations to the community biomass-size structure, trophic energy transfer efficiency and predator-prey mass ratios.

Restoring native fish biomass

Extensive restoration and conservation efforts world-wide (Bernhardt et al. 2005; Arthington et al. 2006; Koehn et al. 2014a) are attempting to halt and potentially reverse the severe degradation that has occurred in river ecosystems owing to invasive species and flow alteration. In order to assess the effectiveness of these efforts, it is essential to have baselines from which change can be assessed. The size-based approach applied here in combination with new methods of analysing disturbance gradients (Yen et al. 2017) may be useful to help set baselines or targets for restoration efforts.

Historical fisheries records from northern hemisphere rivers indicate declines in large-bodied fish abundance and biomass which often exceed 85% to 90% (Gresh et al. 2000; Pikitch et al. 2005; Limburg and Waldman 2009). Despite the presence of early-settlement commercial fisheries, quantitative estimates of historic fish biomass are largely unavailable for the MDB (Humphries and Winemiller 2009). The estimated 58% mean decline in native fish biomass here represents the first quantitative estimate for the MDB. To help inform native fish restoration targets, an expert panel previously guesstimated that native fish abundance may have declined by ~ 90% from pre-European abundances (Koehn et al. 2014a). Our estimated decline is less than 90% but it is important to clarify that our models are based on the effects of invasive common carp and natural flow regime disturbance alone. Our estimates do not incorporate the effects of other important changes to river systems, such as habitat alteration, land clearing, over-fishing, or barriers, and therefore should be considered conservative.

River basins world-wide have been severely impacted by invasive species (Crowl et al. 1992; Strayer 2010; Gallardo et al. 2016) and river flow regime alteration (Bunn and Arthington 2002; Nilsson et al. 2005; Poff and Zimmerman 2010; McManamay and Frimpong 2015). Our results provide empirical evidence demonstrating that these

anthropogenic pressures are strongly correlated with large spatial scale reductions in native fish biomass. Native fish biomass in the MDB was strongly and negatively associated with increasing carp biomass, but not other invasive fishes. This indicates that the extremely high biomass attained by common carp may be adversely affecting the native fishes via resource competition, or indirect effects. The mechanistic effects of common carp on water quality, nutrient dynamics, macrophytes, phytoplankton and on benthic invertebrates in ponds and lakes is well-established (Kulhanek et al. 2011; Vilizzi et al. 2015), yet the bottom-up consequences of these changes for communities in rivers is poorly understood. Based on the evidence from ponds and lakes, it is presumed that native fish in rivers may be adversely affected most by feeding competition associated with reduced benthic biofilm or invertebrate abundance, or the effects of macrophyte loss on food production, recruitment or habitat.

Our models suggest that native fish would benefit from effective control of common carp. Native fish biomass could be expected to increase by 216% across the MDB if common carp populations were reduced to 30% of the total fish community. In other words, for every 1 g of native fish biomass sampled under current conditions, one could expect 2.16 g of native fish following the control of common carp. Effective control of invasive common carp populations in Australia is not currently feasible but the proposed release of a herpes virus biocontrol is regarded by some as a potential solution (McColl et al. 2017). Population modelling suggests that if the herpes virus causes mortality rates of 90% or higher in 20% of years, then common carp biomass could be reduced to 10% of its current level (Brown and Gilligan 2014). Despite laboratory analyses reporting 90-100% mortality of common carp exposed to the herpes virus (McColl et al. 2017), the ecological risks and benefits of releasing the virus (Kopf et al. 2017) have yet to be subjected to peer-review and the realized mortality rate, frequency of outbreak and long-term efficacy of the disease in Australian waterways may be much lower than desired (Marshall et al 2018).

River flow alteration and specifically the effects of altered timing of low-flow conditions were significantly and negatively correlated with native fish biomass. This result is consistent with literature suggesting that the seasonal reversal of low and high-flow periods in regulated river systems is severely detrimental to biodiversity (Bunn and Arthington 2002; Rolls et al. 2012; McGarvey and Terra 2016). The detrimental effects of low-flow alteration may be especially true for fish communities in temperate or dry-land regions with unpredictable flooding, where many species have adapted to spawn and recruit under low spring and summer flows (Humphries et al. 1999; Humphries et al. 2002). Restoration of natural flow regime components is a key rehabilitation measure for the MDB under ‘the Basin Plan’ (Koehn et al. 2014b) and our results suggest that native fish populations would benefit substantially from restoration of low-flow periods.

The relative importance of flow regime alteration, in comparison to invasive common carp, may have been underestimated in our study, owing to sampling the fish community during a 10 year drought. River regulation in irrigated regions typically reduces the frequency and duration of flooding, thereby reducing a key source of energy available to support fish production (see Junk et al. 1989; Winemiller 2004). Therefore, the difference between native fish biomass production in flow-altered and free-flowing rivers may have been higher if sampling was undertaken following over-bank flood periods. Under drought conditions some of the most highly regulated rivers downstream of large dams and barrages, such as the Darling, Central Murray and Lower Murray river systems, which are used to transport water for irrigation, may have acted as refuges for native fish and carp (Bice et al. 2014). Consistent with this drought refuge explanation, we detected a significant increase in native fish biomass with increasing stream order.

This study provides novel evidence suggesting that invasive species have the potential to modify biomass-body mass scaling patterns. We hypothesize (Fig. 7) that the changes in

fish community biomass-size structure observed here may be attributed to underlying food web and energetic changes affected by the proliferation of large-bodied but low trophic level common carp and river flow alteration. Our analysis suggests that environmental flows and specifically restoration of low-flow periods, in combination with effective long-term control of common carp could more than double the biomass of native fishes, with likely effects for the broader environment and ecosystems services provided by native fish.

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Table 1. Equations used in statistical analyses examining variation in $\log_{10}$ native fish biomass and biomass-body mass scaling exponents of the Murray-Darling Basin fish community.

Model number	Equation ^a
1	$q = 1 + \exp[-(-2.179 - 0.593 \times 1 + 0.146 \times L_j - 0.00250 \times L_j^2 - 0.490 \times d_j)]^{-2}$
2	$q = 7.201 + 20.461 \times \log_{10} \text{bodymass}_j$
3	$f(x) = \frac{(b+1) \text{bodymass}_j^b}{\text{bodymass}_j^{b+1 \text{ max}} - \text{bodymass}_j^{b+1 \text{ min}}}$
4	$\text{Scaling } B \sim \beta_0 + \beta x_{1-3 \text{ invasive; native; all species}} + \beta x_{4 \text{ FlowAlt}} + \beta x_{5 \text{ T}} + \beta x_{6 \text{ NPP}} + \beta x_{7 \text{ FPA}} + \beta x_{8 \text{ SO}}$
5	$\text{Scaling } B \sim \beta_0 + \beta x_{1-2 \text{ native; all species}} + \beta x_{3 \text{ carpbiomass}} + \beta x_{4 \text{ otherinvasive}} + \beta x_{5 \text{ FloodDurAv}} + \beta x_{6 \text{ FloodFreqAv}} + \beta x_{7 \text{ MinFlowAv}} + \beta x_{8 \text{ MinFlowCv}}$

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$$\text{Log}_{10} \text{ Native biomass} \sim \beta_0 + \beta x_{1\text{bodymassclass}} + \beta x_{2\text{FlowAlt}} + \beta x_{3T} + \beta x_{4\text{NPP}} + \beta x_{5\text{FPA}} + \beta x_{6\text{SO}}$$

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$$\text{Log}_{10} \text{ Native biomass} \sim \beta_0 + \beta x_{1\text{bodymassclass}} + \beta x_{2\text{carpbio mass}} + \beta x_{3\text{otherinvasive}} + \beta x_{4\text{FloodDurAv}} + \beta x_{5\text{FloodFreqAv}} + \beta x_{6\text{MinFlowAv}} + \beta x_{7\text{MinFlowCv}}$$

a parameter definitions in alphabetical order: *b* = abundance-body mass scaling exponent; β_0 = y-axis intercept; *invasive, native, all species* = categorical fish community group; *body mass_j* = individual fish *j* body mass (g); *bodymassclass* = log₁₀ body mass (g) class; *carp biomass* = relative biomass (g) of common carp standardized per 100 electrofishing shots; *d_j* = average depth (m); *Flood Dur Av* = the mean change in duration of above bank-full floods per year; *Flood Freq Av* = the mean change in number of above bank-full floods per year; *FlowAlt* = aggregate river flow alteration metric; *FPA* = sub-catchment floodplain area (km²); *L_j* = individual fish *j* total length (cm); *max.* = maximum mass (g) of individual fish sampled within sub-catchment; *min.* = minimum mass (g) of individual fish sampled within sub-catchment; *Min Flow Av* = the mean change in Julian day within the year of the annual minimum flow; *Min Flow Cv* = the coefficient of variation in Julian day within the year of the annual minimum flow; *Native biomass* = normalized biomass of native fish (g) per 100 electrofishing shots; *NPP* = sub-catchment terrestrial net primary production (tC ha⁻¹); *other invasive* = relative biomass (g) of all invasive species other than common carp standardized per 100 electrofishing shots; *q* = the estimated detection probability of a fish of a given body size and depth sampled in an electrofishing pass out of actual number present; *Scaling B* = biomass-body mass scaling exponent; *SO* = stream order; *T* = annual sub-catchment mean air temperature (°C).

Table 2. Log₁₀ biomass-body mass scaling exponents (*scaling B*) of the Murray-Darling Basin fish community estimated from maximum likelihood estimated values from (*n* =17) sub-catchments and comparing different methods of correcting for sampling bias.

Correction method	Fish community grouping	Scaling <i>B</i>	(<i>SE</i>)	95% min.	95% max.
Raw uncorrected	Invasive only	-0.17	0.01	-0.18	-0.14

Model 1 corrected	Native only	-0.22	0.01	-0.24	-0.20
	All species	-0.19	0.01	-0.21	-0.18
	Invasive only	-0.25	0.02	-0.28	-0.22
Model 2 corrected	Native only	-0.29	0.02	-0.32	-0.26
	All species	-0.26	0.02	-0.30	-0.23
	Invasive only	-0.52	0.03	-0.58	-0.46
	Native only	-0.43	0.03	-0.50	-0.37
	All species	-0.42	0.03	-0.48	-0.36

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707 Table 3. Generalized linear mixed effects Model 6 results explaining variation in $\log_{10}$ native
 708 fish biomass using three methods of sampling bias correction. Asterisks denote significant
 709 predictors.

Correction method	Variables	Coefficient	<i>SE</i>	<i>t</i>	P-value
Raw data	Body mass	-0.40	0.03	-13.02	<0.0001*
	Flow alteration	-0.10	0.04	-2.25	0.03*
	Temperature ^a				
	Net primary production ^a				
	Floodplain area	-0.08	0.04	-1.93	0.06
	Stream order	0.14	0.05	3.39	<0.001*

Model 1 corrected	Body mass	-0.54	0.03	-15.72	<0.0001*
	Flow alteration	-0.12	0.05	-2.67	0.01*
	Temperature ^a				
	Net primary production ^a				
	Floodplain area	-0.09	0.05	-1.97	0.06
	Stream order	0.18	0.05	3.86	<0.001*
Model 2 corrected	Body mass	-0.70	0.03	-22.18	<0.0001*
	Flow alteration	-0.11	0.04	-2.57	0.01
	Temperature ^a				
	Net primary production ^a				
	Floodplain area	-0.09	0.04	-1.93	0.06
	Stream order	0.16	0.05	3.39	<0.001*

^a Variables with variance inflation factor (VIF) scores ≥ 4 were excluded from analyses.

Table 4. Generalized linear mixed effects Model 7 results explaining variation in log₁₀ native fish biomass using three methods of sampling bias correction. Asterisks denote significant predictors.

Correction method	Fixed effects	Coefficient	SE	t	P-value
Raw data	Body mass	-0.41	0.03	-14.40	<0.0001*
	Carp biomass	-0.17	0.04	-3.86	<0.0001*
	Other invasive	-0.02	0.04	-0.50	0.62
	Min. flow av.	-0.18	0.04	-3.99	<0.0001*
	Min. flow cv.	0.02	0.05	0.39	0.70
	Flood dur. av.	0.15	0.05	3.07	<0.001*
	Flood freq. av.	-0.07	0.07	-1.06	0.29

Model 1 corrected	Body mass	-0.54	0.03	-16.78	<0.0001*
	Carp biomass	-0.11	0.05	-2.19	0.03*
	Other invasive	0.03	0.05	0.55	0.59
	Min. flow av.	-0.23	0.05	-4.56	<0.0001*
	Min. flow cv.	0.02	0.06	0.35	0.72
	Flood dur. av.	0.09	0.06	1.69	0.09
	Flood freq. av.	-0.05	0.08	-0.65	0.52
Model 2 corrected	Body mass	-0.70	0.03	-23.80	<0.0001*
	Carp biomass	-0.11	0.04	-2.50	0.01*
	Other invasive	-0.02	0.05	-0.49	0.63
	Min. flow av.	-0.23	0.04	-5.20	<0.0001*
	Min. flow cv.	0.04	0.06	0.64	0.52
	Flood dur. av.	0.09	0.05	1.86	0.06
	Flood freq. av.	-0.05	0.07	-0.73	0.46

FIGURE CAPTIONS

Fig. 1. Australia's Murray-Darling Basin showing river sub-catchments stratified into northern, southern and central west regions and sampling sites (open circles) used to examine variation in fish community biomass and scaling exponents. Map created by Charles Sturt University, Spatial Data Analysis Network using the Murray-Darling Basin Aquatic Assets Geodatabase (Ward et al. 2012).

Fig. 2. Environmental and anthropogenic pressure coefficients ($\pm$ 95% CI) explaining variation in $\log_{10}$ biomass-body mass scaling exponents (*scaling B*) of the Murray-Darling

Basin fish community. Generalized Linear Mixed Effects Models (GLMMs) were fitted to raw data, Model 1 corrected and Model 2 (Table 1) corrected data respectively using Model 4 (a-c) and Model 5 (d-f). Significant variables not over-lapping zero (null model) are filled black and non-significant variables are filled white. Variables with variance inflation factor (VIF) scores ≥ 4 were excluded (see Table S4).

Fig. 3. Environmental and anthropogenic pressure coefficients ($\pm 95\%$ CI) explaining variation in the $\log_{10}$ native fish biomass in the Murray-Darling Basin. Generalized Linear Mixed Effects Models (GLMMs) were fitted to raw data, Model 1 corrected and Model 2 corrected (Table 1) data respectively using Model 6 (a-c) and Model 7 (d-f). Significant variables not over-lapping zero (null model) are filled black and non-significant variables are filled white. Variables with variance inflation factor (VIF) scores ≥ 4 were excluded (see Table S4).

Fig. 4. $\log_{10}$ native fish biomass in response to: (a) aggregate river flow alteration (*FlowAlt*) and (b) Stream order (*SO*) fitted using Generalized Linear Mixed Effects Model (GLMM) Model 6 (Table 1) and $\log_{10}$ native fish biomass in response to: (c) the biomass of invasive common carp (*carp biomass*) and (d) the mean change in day within the year of the annual minimum flow (*Min. flow av.*) using Model 7 (Table 1). The units of predictor variables represent centred and standardized values used in statistical analyses and $\log_{10}$ native fish biomass calculated per 100 units of electrofishing effort normalized for linear bin-width.

Fig. 5. Ecological pyramids illustrating the mean estimated biomass ($\pm 95\%$ CI) of native fish under restoration scenarios including: (a) current conditions; (b) no alteration of the seasonal timing of low-flows (*Min. flow av.*); (c) control of invasive common carp down to 30% of the total fish community; and (d) control of invasive common carp combined with restoring all river flow regime components including the: mean duration of above bank-full flooding

(*Flood dur. av.*); mean number of above bank-full floods per year (*Flood freq. av.*) and the mean and coefficient of variation (*Min. flow av.*; *Min flow cv.*) in day within the year of the annual minimum flow.

Fig. 6. Percent change in native fish biomass in sub-catchments of the Murray-Darling Basin correlated with invasive common carp biomass and river flow alteration including the seasonal timing of low-flows (*Min. flow av.*) and flow regime alteration combining the: mean duration of above bank-full flooding (*Flood dur. av.*); mean number of above bank-full floods per year (*Flood freq. av.*) and the mean and coefficient of variation (*Min. flow av.*; *Min. flow cv.*) in day within the year of the annual minimum flow.

Fig. 7. Hypothesized $\log_{10}$ biomass-body mass scaling relationship of a river-floodplain ecosystem without invasive species (black line) compared to a system following the introduction and proliferation of large-bodied invasive cyprinids (grey line). The thick black-grey arrow represents how invasive cyprinids efficiently convert food/energy at low trophic levels, previously available to native fishes, into biomass in large body-size classes.

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Fig. 1. Australia's Murray-Darling Basin showing river sub-catchments stratified into northern, southern and central west regions and sampling sites (open circles) used to examine variation in fish community biomass and scaling exponents. Map created by Charles Sturt University, Spatial Data Analysis Network using the Murray-Darling Basin Aquatic Assets Geodatabase (Ward et al. 2012).

Fig. 2. Environmental and anthropogenic pressure coefficients ($\pm$ 95% CI) explaining variation in log10 biomass-body mass scaling exponents (scaling B) of the Murray-Darling Basin fish community. Generalized Linear Mixed Effects Models (GLMMs) were fitted to raw data, Model 1 corrected and Model 2 (Table 1) corrected data respectively using Model 4 (a-c) and Model 5 (d-f). Significant variables not over-lapping zero (null model) are filled black and non-significant variables are filled white. Variables with variance inflation factor (VIF) scores > 4 were excluded (see Table S4).

208x255mm (300 x 300 DPI)

Fig. 3. Environmental and anthropogenic pressure coefficients ($\pm$ 95% CI) explaining variation in the log₁₀ native fish biomass in the Murray-Darling Basin. Generalized Linear Mixed Effects Models (GLMMs) were fitted to raw data, Model 1 corrected and Model 2 corrected (Table 1) data respectively using Model 6 (a-c) and Model 7 (d-f). Significant variables not over-lapping zero (null model) are filled black and non-significant variables are filled white. Variables with variance inflation factor (VIF) scores > 4 were excluded (see Table S4).

200x224mm (300 x 300 DPI)

Fig. 4. Log₁₀ native fish biomass in response to: (a) aggregate river flow alteration (FlowAlt) and (b) Stream order (SO) fitted using Generalized Linear Mixed Effects Model (GLMM) Model 6 (Table 1) and log₁₀ native fish biomass in response to: (c) the biomass of invasive common carp (carp biomass) and (d) the mean change in day within the year of the annual minimum flow (Min. flow av.) using Model 7 (Table 1). The units of predictor variables represent centred and standardized values used in statistical analyses and log₁₀ native fish biomass calculated per 100 units of electrofishing effort normalized for linear bin-width.

147x147mm (300 x 300 DPI)

Fig. 5. Ecological pyramids illustrating the mean estimated biomass ($\pm$ 95% CI) of native fish under restoration scenarios including: (a) current conditions; (b) no alteration of the seasonal timing of low-flows (Min. flow av.); (c) control of invasive common carp down to 30% of the total fish community; and (d) control of invasive common carp combined with restoring all river flow regime components including the: mean duration of above bank-full flooding (Flood dur. av.); mean number of above bank-full floods per year (Flood freq. av.) and the mean and coefficient of variation (Min. flow av; Min flow cv.) in day within the year of the annual minimum flow.

123x85mm (300 x 300 DPI)

Fig. 6. Percent change in native fish biomass in sub-catchments of the Murray-Darling Basin correlated with invasive common carp biomass and river flow alteration including the seasonal timing of low-flows (Min. flow av.) and flow regime alteration combining the: mean duration of above bank-full flooding (Flood dur. av.); mean number of above bank-full floods per year (Flood freq. av.) and the mean and coefficient of variation (Min. flow av.; Min. flow cv.) in day within the year of the annual minimum flow.

120x82mm (300 x 300 DPI)

179x176mm (150 x 150 DPI)