
http://researchrepository.murdoch.edu.au/22186/

Copyright: © 2013 John Wiley & Sons Ltd.

It is posted here for your personal use. No further distribution is permitted.
Implications of climate change for potamodromous fishes

STEPHEN J. BEATTY*, DAVID L. MORGAN and ALAN J. LYMBERY
Freshwater Fish Group & Fish Health Unit, School of Veterinary and Life Sciences, Murdoch University, South St Murdoch, Western Australia

*Correspondence: Stephen J. Beatty, tel. +618 9360 2813, fax +618 9360 7512, e-mail: s.beatty@murdoch.edu.au

Keywords: freshwater fishes, Mediterranean climate, surface flow decline, groundwater reduction, secondary salinisation, south-western Australia, aquatic refuge

Primary Research Article

Abstract

There is little understanding of how climate change will impact potamodromous freshwater fishes. Since the mid-1970’s, a decline in annual rainfall in south-western Australia (a globally recognised biodiversity hotspot) has resulted in the rivers of the region undergoing severe reductions in surface flows (~50%). There is universal agreement amongst Global Climate Models that rainfall will continue to decline in this region. Limited data are
available on the movement patterns of the endemic freshwater fishes of south-western Australia or on the relationship between their life-histories and hydrology. We used this region as a model to determine how dramatic hydrological change may impact potamodromous freshwater fishes. Migration patterns of fishes in the largest river in south-western Australia were quantified over a four year period and were related to a number of key environmental variables including discharge, temperature, pH, conductivity and dissolved oxygen. Most of the endemic freshwater fishes were potamodromous, displaying lateral seasonal spawning migrations from the main channel into tributaries, and there were significant temporal differences in movement patterns between species. Using a model averaging approach, amount of discharge was clearly the best predictor of upstream and downstream movement for most species. Given past and projected reductions in surface flow and groundwater, the findings have major implications for future recruitment rates and population viabilities of potamodromous fishes. Freshwater ecosystems in drying climatic regions can only be managed effectively if such hydro-ecological relationships are considered. Proactive management and addressing existing anthropogenic stressors on aquatic ecosystems associated with the development of surface and groundwater resources and land use is required to increase the resistance and resilience of potamodromous fishes to ongoing flow reductions.

Introduction

Freshwater ecosystems are in crisis throughout the world. Aquatic habitats associated with 65% of global river flow are moderately or highly threatened, principally by water resource development and pollution (Dudgeon et al., 2006; Vörösmarty et al., 2010). Freshwater fishes are one of the most threatened faunal groups and are expected to be among the most severely impacted by climate change, due to it adding to a wide range of current and future
anthropogenic stressors (Ficke et al., 2007; Palmer et al., 2008; Olden et al., 2010; Comte et al., 2013). Freshwater fishes in Mediterranean climatic regions are particularly imperilled and while flow reduction due to water extraction and climate change is recognised as a major threat (Hermoso & Clavero, 2011; Maceda-Veiga, 2013), its impacts are difficult to quantify due to the complexity of abiotic and biotic interactions (Clavero et al., 2010).

The challenge of conserving critical habitat for freshwater species is exacerbated by life-cycles that often involve movement between habitats for different life-history stages (Magoullick & Kobza, 2003) and the linear nature of rivers, whereby upstream activities influence downstream habitat quality and availability (e.g. Gorman & Karr, 1978; Allan et al., 1997). Seasonal migrations in potamodromous fishes are critical for completing life-cycles; particularly in accessing spawning and nursery habitats and refugia (Reynolds, 1983; O’Connor et al., 2005; Munz & Higgins, 2013). Understanding refuge use and species mobility is important for enhancing conservation efforts; particularly under drought or flow reduction scenarios (Magoullick & Kobza, 2003; Morán-López et al., 2012; Chessman, 2013).

In comparison to the amount of research on diadromous fishes (e.g. Crozier et al., 2008; Lassalle & Rochard, 2009; Finstad & Hein, 2012; Piou & Prévost, 2013), there is little information on how flow reductions due to climate change will impact potamodromous species (but see Buisson et al., 2008; Clews et al., 2010). The vast majority of research examining the impacts of climate change on freshwater fishes has focussed on salmonids and other cold water species, those with commercial or recreational value, and those in the Northern Hemisphere (e.g. Comte et al., 2013). Broadening our understanding of these impacts to other regions and to non-diadromous fishes with little commercial or recreational value is needed for a more complete understanding of the vulnerability of freshwater ecosystems to climate change. As predicted globally (e.g. Thieme et al., 2010), climate change is expected to exacerbate the current anthropogenic stressors on Australian freshwater...
fishes (Morrongiello et al., 2011a, b) and cause major range contractions of several species (Balcombe et al. 2011; Bond et al. 2011).

South-western Australia, a global biodiversity hotspot (Myers et al., 2000), has a Mediterranean climate that is isolated from high rainfall temperate and tropical regions by extensive arid zones. Although the region has only 11 native freshwater fish species, nine are regionally endemic (Morgan et al., 1998; Allen et al., 2002). These species are highly imperilled, principally due to the synergistic impacts of a number of stressors such as secondary salinisation (Morgan et al., 2003; Beatty et al., 2011), instream barriers (Morgan & Beatty, 2006; Beatty et al., 2007), and the impacts of introduced species (Morgan et al., 2004; Marr et al., 2010; Beatty & Morgan, 2013).

Since the mid-1970’s, a considerable climatic shift has occurred in south-western Australia, resulting in a reduction of ~16% in annual rainfall corresponding to an ~50% reduction in the annual volume of stream flow (Suppiah et al., 2007; Petrone et al., 2010; Silberstein et al., 2012). There is an unusually uniform consensus across global climatic models (GCMs) for this region as they all project this drying trend to continue, with median reductions of an additional ~8% in annual rainfall and ~25% (range of 10-42%) in annual stream flow expected by 2030 (Suppiah et al., 2007; Silberstein et al., 2012). Furthermore, reductions in fresh groundwater levels of >10m are predicted in many areas in the region by 2030 (Barron et al., 2012). Quantifying the potential impacts of this dramatic hydrological change on freshwater fishes of the region is currently hampered by a lack of ecological data on these species (Beatty et al., 2010, Morrongiello et al., 2011a).

The two non-endemic native freshwater fishes in south-western Australia are the galaxiids Galaxias maculatus and Galaxias truttaceus that may have diadromous (marine larval phase) or land-locked populations; the latter utilising coastal lacustrine environments for larval development (Morgan 2003; Chapman et al., 2006). While almost nothing is
known on the migration patterns of the nine endemic freshwater fishes, they are not
diadromous and are known to breed during the major rainfall and surface flow periods (Pen
& Potter, 1991; Morgan et al., 1998). Given the timing of their breeding period, they may be
highly reliant on seasonal surface discharge and could be potamodromous in order to breed
within intermittent lotic systems that are common to the region.

Secondary salinisation is a major global threat that is expected to be amplified by climate
change (Cañedo-Argüelles et al., 2013). This process is severe in south-western Australia,
with most of the major rivers salinised due to the mobilisation of saline groundwater from
large scale land-clearing in their upper catchments (Mayer et al., 2005). While rising saline
groundwater is a major cause of secondary salinisation (Cañedo-Argüelles et al., 2013), fresh
groundwater aquifers can have a dilution effect in salinised rivers. The fresh south-west
Yarragadee Aquifer (SWYA) underlies a considerable area of south-western Australia and
can contribute to between 30-100% of the baseflow riverine discharge of the Blackwood
River (the largest of the region) during the prolonged dry-season (Strategen, 2006). This
contribution significantly dilutes the main channel during baseflow, when most tributaries fail
to flow or dry completely (Del Borrello, 2008; Beatty et al., 2010).

Freshwater fishes of the region are stenohaline and have undergone major downstream
range contractions away from the most salinised inland habitats towards those regions
underlain by fresh aquifers (Morgan et al., 2003; Beatty et al., 2011). Fresh groundwater
discharge maintains habitat connectivity for at least one species (Beatty et al., 2010) and is
likely to play a key role in maintaining fresh baseflow refuge for other species. As the
groundwater level and surface discharge during the annual dry season are positively related to
the previous year’s rainfall in the Blackwood River (Golder & Associates, 2008), both will be
affected by projected rainfall reductions (Barron et al., 2012; Silberstein et al., 2012).
Understanding the movement patterns and habitat utilisation of freshwater fishes and their relationships to hydrology and physicochemical variables will be vital in understanding how hydrological change will affect future population viabilities. The current study aimed to elucidate the spatial and temporal movement patterns of freshwater fishes, their life-histories, and their relationships with environmental variables in a drying climatic region, using the Blackwood River as a model system. The study hypothesised that: 1) south-western Australian freshwater fishes are potamodromous, based on existing information on their reproductive biology; 2) both fresh surface water and groundwater discharge are important in maintaining remnant populations; and 3) ongoing reductions in rainfall and discharge due to climate change will negatively impact potamodromous fishes.

**Materials and methods**

*Sampling regime*

Spatial and temporal patterns in the movement and demographics of native freshwater fishes were determined in the Blackwood River main channel and four of its tributaries between October 2005 and December 2009 (Fig. 1). Three main channel sites included one downstream of the major zone of groundwater discharge from the SWYA (Denny Rd), one at the upstream margin of the SWYA discharge zone (Milyeannup Pool) and one upstream of the SWYA discharge zone (Jalbarragup) (Fig. 1). The tributary sites included one perennially flowing system (Milyeannup Brook) that is maintained by groundwater from the SWYA, and three seasonally intermittent systems (Layman Brook, Rosa Brook and McAtee Brook) (Fig. 1).

The seven sites were sampled on a regular basis between October 2005 and December 2009. In each sampling event (n = 30 within the 50 month period), all sites that had flowing water at the time were sampled. All seven sites were sampled during the major flow period
between August and December (i.e. late winter through to early summer). However, as three of the four tributaries naturally dry during late summer through autumn (i.e. February to May), sampling did not occur in those systems during that period due to a lack of flow. For each sampling event, two fyke nets (each net having a width of 11.2 m, including two 5 m wings and a 1.2 m wide mouth, depth of 0.8 m, length of 5 m with two funnels all comprised of 2 mm woven mesh) were simultaneously set for three consecutive 24 hour periods. One net faced upstream, to determine downstream movements of fishes, and the other faced downstream, to determine upstream movements of fishes (following Beatty et al., 2010). As it was not always possible to set the nets across the entire wetted channel, the proportion of the total stream cross-section that was covered by each fyke was determined in order to standardise captures (see statistical analysis). All fish captured were identified to species, enumerated, measured to the nearest 1-mm total length (TL) and released either upstream or downstream of the capture point, depending on their original movement direction.

Environmental variables

One of the most important steps in modelling species distributions is careful variable selection, particularly when using predictors when there is a degree of *a priori* expectation of ecological relevance (Elith & Leathwick, 2009; Burnham & Anderson, 2010). Many physical, geographical and ecological characteristics of the study streams were very similar. The catchments were all effectively completely forested by natural vegetation and the streamlines had qualitatively similar, near-pristine riparian zones (CENRM, 2005; Strategen, 2006). Furthermore, all streams were highly consistent in terms of overall channel morphology, slope, altitude, dissection and soil type (CENRM, 2005; Strategen, 2006). Finally, all four study sites were situated within 14 km of each other and each was located at a similar distance from the main channel of the Blackwood River with no artificial instream
barriers existing in the streams (Figure 1). Therefore, given the considerable spatial and temporal sampling effort undertaken, we focussed on other environmental variables that are commonly associated with freshwater fish distributions and movement. These were temperature, conductivity, pH, dissolved oxygen, and discharge (Matthews, 1998). In order to determine the spatial and temporal patterns in water temperature and their relationship to air temperature, data loggers (Tinytag™ Gemini Data Loggers, Chichester, West Sussex, UK) were placed in situ in all the tributary sites and two main channel sites and were programmed to log water temperature every three hours. Temperature loggers were downloaded periodically and the water temperature regimes of the various sites were graphically compared to maximum daily air temperature obtained from the nearest Australian Bureau of Meteorology weather station (Bridgetown). On each sampling event at each site, instantaneous temperature, conductivity, pH, and dissolved oxygen were measured using a handheld water quality meter (Oakton PCD650) in the middle of the water column at three locations and a mean (± 1 SE) determined.

Flow velocity was measured using a hand held flow meter (Global F101) and instantaneous discharge measurements were determined in all tributary sites during each sampling event by undertaking cross-sectional depth-flow profiles (measured every 0.5m) and applying the formula: $D_{\text{inst}} = V \times D \times W$ where $D_{\text{inst}}$ = instantaneous discharge $m^3$.sec$^{-1}$, $V$ = mean water velocity (m.sec$^{-1}$) over the cross-section, $D$ = mean depth (m) over the cross-section, $W$ = width (m) of the cross-section.

Statistical analysis

In order to determine the spatial and temporal patterns of movements and demographics of the five most commonly captured native freshwater fishes in the tributary sites, i.e. the western minnow *Galaxias occidentalis*, western mud minnow *Galaxiella munda*, western
pygmy perch *Nannoperca vittata*, Balston’s pygmy perch *Nannatherina balstoni*, and nightfish *Bostockia porosa* (see Results), the mean (±1 SE) numbers of each species captured moving upstream and downstream over the three 24 hour periods (numbers were standardised from the proportion of cross-section of the stream covered by each fyke to assume 100% coverage) in each sampling event at each site were determined. To elucidate population structure of each species and best illustrate movement patterns in relation to life-history stage, the monthly length-frequency distribution (separated on movement direction) of the above freshwater fishes throughout the study were plotted separately for Milyeannup Brook (*G. occidentalis, N. balstoni, N. vittata*, and *G. munda*), Rosa Brook (*G. occidentalis, N. vittata*, and *B. porosa*) and Layman Brook (*B. porosa*).

To test the effects of each species captured and the sampling month on fish captures, we used general linear models (GLMs) with a repeated measures design. The log_{10}(x+1) transformed number of fish captured in the fykes moving in either an upstream or downstream direction at each sampling event was used as a response variable, with species as a between-subject fixed effect, months as a within-subject fixed effect and tributary nested within species as a random effect.

The relationships between the upstream and downstream movement of the five native species in tributaries and the prevailing environmental variables in those systems were explored by first determining the mean of each environmental variable and the overall mean upstream and downstream movements of each species in each system over the major flow period in each year (i.e. the period that all four tributaries were flowing between August to December). As excessive flooding of the tributary sampling sites occurred in August 2009, they were excluded from the above analysis.

Bivariate correlations (using Pearson’s correlation coefficient) were calculated for each pair of environmental variables (all except pH log_{10} transformed) to examine possible inter-
relationships. Mean velocity was consistently highly correlated with discharge and was therefore excluded from subsequent analyses; no other variable pairs showed correlations > 0.6 (Table S1). To determine which environmental variables explained most of the variation in upstream and downstream migrations of each fish species during the major flow period, we used GLMs, with a multimodel inference approach (Burnham & Anderson, 2010). For each fish species and for each movement direction, a global model of number of fish captured ($\log_{10}(x+1)$ transformed) against all environmental predictor variables was fitted using the R program (R Development Core Team, 2013). The global model was then used to generate a set of models containing all combinations of predictor variables, using the R package MuMIn (Bartoñ, 2013). Models were ranked by the Akaike Information Criterion, corrected for small sample size ($AIC_c$) and model averaging performed across those models that were within four $AIC_c$ values of the best model (Burnham & Anderson, 2010), using MuMIn. The relative importance of each environmental predictor variable was determined by summing the Akaike likelihood weights across all models within the top-ranked set; this gives the selection probability that a given variable will appear in the AIC-best model (Burnham & Anderson, 2010). For each fish species and each movement direction, we report the relative importance of all of the environmental predictor variables, along with the model-averaged parameter estimates and their standard errors.

As estimates of parameters and variable importance from model averaging can be adversely affected by collinearity among predictors (Murray & Conner, 2009; Freckleton, 2011), we attempted to account for this in three ways. First, only predictor variables with bivariate correlations $\leq 0.6$ with all other predictors were used in the analysis (see Table S1). Second, for each predictor we calculated the variance inflation factor (VIF), which represents the overall correlation with all other predictors, using the R package HH (Heiberger, 2013). As a general rule of thumb, VIF’s $> 10$ are thought to indicate excessive collinearity (Myers,
1990; although see O’Brien, 2007 for a contrary view). Finally, we also used a hierarchical partitioning approach to determine variable importance, as this has been shown in some simulations to outperform model averaging when predictor variables are correlated (Murray & Conner, 2009; although see Smith et al., 2009). $R^2$ values were hierarchically partitioned to determine the proportion of variance explained independently and jointly by each variable (Chevan & Sutherland, 1991; Mac Nally, 2002), and the independent effect of each predictor was calculated as the percentage of total independent contributions, using the R package hier.part (Walsh & Mac Nally, 2013). The significance of independent effects was assessed with $Z$ scores from a comparison of observed effects with those obtained after 500 randomisations of the data, using hier.part.

**Results**

**Environmental variables**

Water and air temperatures were highly associated at all sites (Fig. 2). Temperatures in the main channel sites were much higher than tributary sites during summer and autumn, with the greatest differences occurring between main channel sites and the perennial (groundwater maintained) Milyeannup Brook, which experienced a less variable temperature regime than other tributaries. For example, between late December and March (i.e. summer to early autumn) in 2006 and 2008, Milyeannup Brook was generally $>$1°C cooler than the non-perennial Rosa Brook and McAtee Brook, and $>$6°C cooler than the main channel sites. Between May and August (i.e. late autumn to late winter) 2006, Milyeannup Brook was $\sim$2°C warmer than the non-perennial systems and was similar in temperature to the main channel sites (Fig. 2).

Mean conductivity in the main channel sites increased in an upstream direction, ranging from 3564 to 4955 µS.cm$^{-1}$ at the Denny Rd and Jalbarragup sites, respectively (Table S2).
In contrast, the tributary sites were always fresher with mean values that did not exceed 500 µS.cm\(^{-1}\) (Table S2). Mean dissolved oxygen at all sites was >6.00 mg.l\(^{-1}\) and pH in the tributary sites was slightly acidic (means from 6.04-6.67), whereas pH was near neutral in the main channel sites (means from 7.18-7.33) (Table S2).

Species captures and spatial distributions

Six of the nine endemic freshwater fishes of south-western Australia, along with four estuarine fishes, three introduced fishes and one native anadromous agnathan were captured during the study. The six endemic freshwater fish species were the galaxiids *G. occidentalis* and *G. munda*, the percichthyids *N. vittata*, *N. balstoni* and *B. porosa* and the plotosid *Tandanus bostocki* (Table S3).

*Galaxias occidentalis* was the most commonly recorded species, present in 92.2% of all sites sampled in all months, with *N. vittata*, *B. porosa*, and *T. bostocki* recorded at similar frequencies (~66-67%), *N. balstoni* at 38.5%, and *G. munda* (16.5%) being the least encountered (Table S3). Stark contrasts existed in captures of the various species between main channel and tributary sites, with five of the six endemic freshwater species more commonly encountered in the tributary sites (Table S3). The most difference in habitat usage was recorded for *G. munda* (32.4 cf 2.7% in tributary and main channel samples, respectively) (Table S3). *Galaxiella munda* was recorded in tributary sites that were cooler, fresher, and had lower mean discharge than habitats occupied by all other species (Table S3). *Galaxias occidentalis* was recorded in similar frequency between the two habitat types (i.e. 95.2 and 90.3%, in tributary and main channel sites, respectively) whereas *T. bostocki* was much more frequently recorded in main channel (99.0%) compared with tributary (30.5%) sites (Table S3).
Patterns of species movements

There were clear spatial and temporal patterns of movements of the five endemic freshwater fish species that were most commonly encountered in the tributaries (i.e. *G. occidentalis*, *G. munda*, *N. balstoni*, *N. vittata* and *B. porosa*). Upstream fish movements were significantly affected by species ($F = 8.25, P = 0.0003$) and month of sampling ($F = 6.14, P < 0.0001$), with a significant interaction between species and month ($F = 2.51, P < 0.0001$). Downstream movement did not quite differ significantly among species ($F = 2.79, P = 0.05$), but was significantly affected by the month of sampling ($F = 8.63, P < 0.0001$), with a significant interaction between species and month ($F = 3.27, P < 0.0001$).

Details of the habitat utilisation, spatial and temporal movements and population structure of the five fish species in each sampling month at each site are shown in the supporting information (Table S3, Figs S1-S13). Schematic diagrams of the movement patterns of adults and juveniles of the two species of galaxiids and three species of percichthyids (Figs 3 and 4) are based on the data presented in the Supporting Information. While interspecific variation existed in migration patterns (spatially and temporally), all but *G. munda* moved laterally between the main channel of the Blackwood River and its tributaries (Figs 3 and 4).

Downstream movements of *G. occidentalis* occurred predominately within tributary sites between August and December (i.e. late winter to early summer), with an upstream directional movement occurring in main channel sites between June and August (i.e. winter) (Figs 3 and S1). Downstream movement of juveniles (<40 mm TL) generally occurred annually between October to December, with a notable one to two month earlier movement occurring in the perennial Milyeannup Brook compared to Rosa Brook (Figs 3, S2 and S3). Larger individuals (>120 mm TL) were also much more prevalent in Milyeannup Brook compared with the seasonally flowing systems. Unlike all other species, there were no strong
movement patterns associated with *G. munda* within the tributaries (Figs 3 and S4). However, downstream movement of juveniles (>35 mm TL) were recorded during late spring (October and November) in most years in Milyeannup Brook (Fig. S5). Notably, *G. munda* was the only species found to be effectively absent from the main channel (Fig. 3 and Table S3).

*Nannatherina balstoni* only utilised Milyeannup Brook as a breeding and nursery area and was recorded very infrequently in all other tributaries (Figs 4 and S6). A clear annual downstream movement of juveniles (<50 mm TL) occurred in that system between November and December (i.e. late spring to early summer) (Fig. S7). Although this species was not abundant in the main channel sites (Fig. 4 and Table S3), it was recorded occasionally at the Denny Rd and Milyeannup Pool sites; both located downstream of the confluence of Milyeannup Brook (Figs 1 and S6). *Nannoperca vittata* migrated within all tributaries (aside from Layman Brook), with both upstream and downstream directional movements of the species occurring between August and December (Figs 4 and S8). The species was also recorded to lesser degree moving within the main channel sites, with the vast majority moving in a downstream direction (Fig. S8). Juvenile (<30 mm TL) *N. vittata* were recorded moving downstream within tributaries and the timing of that movement varied between systems. For example, it occurred mostly in March (with some November and December movement of <20 mm TL fish) in the perennial Milyeannup Brook, compared with August to November in the ephemerally flowing Rosa Brook (Figs S9 and S10). Large downstream movements of juvenile (<30 mm TL) *B. porosa* occurred in a number of tributaries between November and December (Figs 4 and S11) and were most prevalent in Milyeannup, Rosa and Layman Brooks, where it was recorded in all years aside from 2009 in Layman Brook (Figs S11, S12, S13).
The influence of environmental variables on the average upstream and downstream movements of the five fish species over the major flow periods in the four tributaries between 2005 and 2009 are shown in Tables 1 and 2. Variance inflation factors were relatively low for all variables (temperature 3.11; conductivity 3.31; pH 1.95; dissolved oxygen 3.29; discharge 1.83) and both model averaging and hierarchical partitioning analyses gave very similar indications of variable importance (Tables 1 and 2). This suggests that these measures were not biased by collinearity among predictors. Discharge ranked as the most important predictor variable in four of the five species for both upstream and downstream movement, being included in between 43-100% of the best fitting models (Tables 1 and 2). In particular, discharge explained a substantial proportion of the upstream movements of the three most widespread and abundant species, *N. vittata*, *B. porosa* and *G. occidentalis* (Table 1). With the exception of one case (i.e., downstream movement in *B. porosa*), more fish were captured with greater discharge levels. Temperature also figured prominently as an important predictor variable, particularly for *N. vittata*, with more fish captured at lower temperatures. Of the other variables, pH was positively associated with upstream movements, and dissolved oxygen was negatively associated with downstream movements of *B. porosa*.

**Discussion**

There has been limited research on potamodromous fishes that migrate laterally between main channel and low order streams, compared to those that undertake longitudinal migrations within the main streams of large river networks (e.g. O’Connor *et al.* 2005; Dugan *et al.*, 2010) or between lentic and lotic systems (e.g. Barthel *et al.*, 2008; Conallin *et al.*, 2011). The new recruits of five of the six endemic freshwater fishes found within the study area were recorded almost exclusively within tributaries, and their downstream movement
into main channel habitats occurred for four of the five species during periods of declining surface flows (i.e., late spring and early summer). As with other climatic regions with pronounced dry seasons, most lower order tributaries in south-western Australia either dry completely or consist of separated, often isolated refuge pools during summer and autumn. Therefore, our findings strongly suggest that most species are potamodromous and undergo lateral spawning migrations into lower order tributaries during the seasonal flow period. Discharge was clearly the most important environmental variable related to the upstream and downstream movement of most species and therefore our findings have considerable implications in understanding how life-cycles of potamodromous fishes in drying temperate regions may be impacted by climate change.

Influence of hydrology on life-histories

Hydrologic regime has been shown to significantly influence the life-history strategies of freshwater fishes in lotic systems over broad biogeographic scales (Mims & Olden, 2012; Chessman, 2013; Sternberg & Kennard, 2013). Due to the highly seasonal and predictable flow regimes of aquatic systems in south-western Australia, its freshwater fishes would be expected to have periodic life history strategies (Mims & Olden, 2012). Consistent with this expectation is that most species have annual spawning periods that coincide with peak flow in winter and spring (e.g. Pen & Potter, 1991; Morgan et al., 1998; this study). Periodic species are also characterised by having large body size, late maturation, and high fecundity. Most of the freshwater fishes of south-western Australia, however, have many traits that would classify them as opportunistic (r strategists), such as small body sizes (<190 mm TL) and early maturation (most in the first or second year of life) (Morgan et al., 1998). This may be due to these species having evolved in relatively small, seasonally intermittent, naturally unproductive aquatic systems typical of this region (Bunn & Davies, 1990), which would
limit their maximum sizes and reproductive investment. Despite having several opportunistic life-history traits, the movements of most species were undoubtedly associated with spawning and recruitment and they would be therefore vulnerable to reductions in amount of surface discharge.

Rivers that are free-flowing in relatively undeveloped basins are predicted to be resilient to climate change compared with those that are more highly regulated (Palmer et al., 2008). Artificial instream barriers can have profound, wide-ranging impacts on aquatic ecosystems, particularly on migratory fishes (Bunn & Arthington, 2002; Katopodis & Aadland, 2006). Most other studies relating to anthropogenic impacts on the migrations of potamodromous fishes have focused on the impacts of barriers and river connectivity (e.g. Baumgartner & Harris, 2007; Mallen-Cooper & Brand, 2007; Branco et al., 2012). While our study systems are free from artificial barriers, our findings suggest that the numerous natural instream barriers that exist elsewhere throughout the region may also be disrupting the life-cycles of these potamodromous fishes by restricting access to upstream spawning habitats exacerbating the impacts of past and projected declines in surface discharge.

Several species in the current study are known to also occupy natural and artificial lentic systems (Morgan et al., 1998; Beatty et al. 2013) and this suggests they have a degree of habitat flexibility. This could help at least some populations survive the expected ongoing reductions in flow period and surface discharge due to climate change by utilising main channel lotic habitats or artificial lentic habitats for spawning and recruitment. Nonetheless, these projected hydrological changes will undoubtedly reduce recruitment to some degree through reductions or loss of spawning habitats in lower order streams.

Galaxiids are generally known to migrate for spawning purposes (McDowall & Frankenberg, 1981; Baker & Montgomery, 2001; Baker & Hicks, 2003; Morgan, 2003) and *G. occidentalis* in the current study showed the strongest movement patterns; migrating
laterally into all tributaries to spawn, with this movement positively associated with amount of stream discharge during the annual flow period. As opposed to galaxiids, pygmy perches are generally not known to be strong migrators (e.g. Hammer et al., 2009), although movement between water bodies has been linked to flooding events (Morgan et al., 1995; Hughes et al., 1999; Knight & Arthington, 2008). We demonstrated that the two pygmy perches were also potamodromous and that the upstream spawning movements of N. vittata and the other percichthyid, B. porosa, were positively associated with amount of surface discharge. Furthermore, hydrological seasonality would explain why N. balstoni, the most threatened species in the study, only breeds within the groundwater maintained perennial Milyeannup Brook, despite other tributaries appearing to provide equally suitable habitat when they are flowing. The onset of breeding by N. balstoni is earlier than others in this study (i.e. from early winter cf late winter and spring (Morgan et al., 1995, 1998)), requiring its spawning habitat to be available at a time when seasonal tributaries are yet to flow. Ongoing changes in both the amount and timing of discharge may therefore have serious implications for this and other potamodromous species.

*Declines in refuge habitats due to climate change*

Understanding refuge habitat requirements is crucial in assessing impacts of climate change on freshwater fishes in seasonal systems (Hodges & Magoulick, 2011; Morán-López et al., 2012; Davis et al., 2013). System size and the volume and periodicity of discharge, along with a number of other abiotic characteristics, such as anthropogenic pollution, have been demonstrated to influence refuge availability and use by freshwater fishes (e.g. Magoulick & Kobza, 2003; Hodges & Magoulick, 2011; Morán-López et al., 2012). Groundwater maintained aquatic refuges can be thought of as ‘evolutionary refugia’ and are extremely important in maintaining endemic aquatic species (Davis et al., 2013). Our study identified

This article is protected by copyright. All rights reserved.
that the key refuge habitats for freshwater fishes during the dry season in the Blackwood River were the secondarily salinised main channel and a fresh perennial tributary; both reliant on fresh groundwater.

Pollution caused by human activities is one of the major global stressors on riverine ecosystems (Vörösmarty et al., 2010). Secondary salinisation of rivers is a major threat to aquatic ecosystem health and climate change is expected to amplify the problem, particularly in climates that experience prolonged periods of drought (Cañedo-Argüelles et al., 2013). Salinisation in south-western Australia has caused fundamental ecosystem change, including widespread range contractions of many stenohaline freshwater fishes and concomitant colonisation by estuarine euryhaline species (Morgan et al., 2003; Mayer et al., 2005; Beatty et al., 2011). Reduced rainfall is projected to cause severe reductions in surface flow and fresh groundwater levels in many catchments (Barron et al., 2012; Silberstein et al., 2012), which may cause remnant fresh perennial tributaries to be lost and further increase the salinity in main channel refuges to levels that may exceed the tolerances of several species (Beatty et al., 2011). In order to model future distributions and identify viable refuges in this region and elsewhere, robust analyses of physicochemical thresholds of freshwater fishes are required (e.g. Segurado et al., 2011).

The effect of interactions between pollution and other stressors on aquatic ecosystems can be complex and difficult to predict (Cañedo-Argüelles et al., 2013). For example, although reductions in rainfall and fresh surface flow may reduce the dilution capacity of rivers in south-western Australia, this may be partially offset by concomitant reductions in saline groundwater levels (Mayer et al., 2005). Specifically, the disconnection of saline groundwater with low order streams due to rainfall decline results in a disproportionally greater reduction in streamflow and also a reduction in the stream salinity (Kinal & Stoneman, 2012). Given the vital importance of dry-season refuge in the life-cycles of
potamodromous fishes in temperate environments, the impact of climate change on its availability and quality warrants much greater research attention.

**Impacts of climate change on migrations**

Globally, reductions in the discharge from rivers due to water extraction and climate change is predicted to cause a loss of up to 75% of freshwater fish diversity by 2070 (Xenopoulos *et al.*, 2005; Xenopoulos & Lodge, 2006). However, the threat of climate change to freshwater ecosystems on the Australian continent, particularly freshwater fishes, has only recently begun to be investigated (Koehn, 2011; Morrongiello *et al.*, 2011a,b; Chessman, 2013). There is universal agreement amongst GCMs that rainfall will continue to decline in south-western Australia (Suppiah *et al.*, 2007; Silberstein *et al.*, 2012). The dramatic past and projected climatic shift that has occurred in this region renders it a ‘living experiment’ in assessing the ecological impacts of climate change in temperate regions.

We found that spawning migrations of potamodromous fishes in the current study were almost always positively related to discharge. Our study streams were remarkably similar in most geophysical and many ecological variables and we therefore examined only a modest number of potential predictors of migrations. A study with a wider geographical range may reveal other environmental variables that also influence migrations in these potamodromous fishes. Nevertheless, the projected reductions in annual surface water discharge and stream flow periods of the region (Silberstein *et al.*, 2012) will reduce spawning habitat availability and connectivity for freshwater fishes on both a temporal and spatial scale. The amount of river discharge has previously been shown to be positively associated with migration, reproduction and recruitment of fishes elsewhere (e.g. Reynolds, 1983; O’Connor *et al.*, 2005; Beatty *et al.*, 2010; Crook *et al.*, 2010; Walsh *et al.*, 2012; Munz & Higgins, 2013). Our findings suggest that potamodromous fishes may be particularly impacted by flow...
reductions via reduced levels of recruitment and increased resource competition, with potentially serious implications for population dynamics and viabilities (e.g. Morán-López et al., 2012).

Along with causing flow reductions, climate change is projected to increase mean air temperatures and the number of extreme hot days (>35°C) in south-western Australia (Suppiah et al., 2007). As expected, water temperatures in the current study were closely linked to air temperatures. As temperature affects the aerobic scope of fishes, which dictates their swimming performance (Farrell et al., 2008), these increases may further restrict the migratory capacity and population viability of potamodromous species in this region. Hague et al. (2011) modelled the effects of climate change on sockeye salmon populations and concluded that increasing temperatures would result in most being forced to migrate at sub-optimal aerobic scopes. The geographical location of south-western Australia (i.e. the southern edge of the Australian continent) means that aquatic species including freshwater fishes cannot migrate southward in response to increasing temperatures and this greatly increases their vulnerability to climate change (Davies, 2010).

In a recent assessment of how 39 species of south-eastern Australian fishes fared under a ‘Millennium’ drought, the most impacted species had a small maximum size, were invertivorous (cf omnivorous), had a low age at maturity, spawned in low temperatures, had a prolonged spawning period, low fecundity, demersal eggs and a low upper thermal limit (Chessman, 2013). The species in the current study have almost all of these vulnerable traits (Morgan et al. 1998). There is a paucity of research into how Australian freshwater fishes affect aquatic food webs (Stoffels, 2013). The lack of any comprehensive food-web studies that have incorporated freshwater fishes in south-western Australia precludes predicting what impact their decline will have on the prevailing aquatic ecosystems. However, the loss of...
such highly abundant top-order consumers (Morgan et al., 1998) may cause considerable ecological change through shifts in prey populations and trophic cascades.

Protecting freshwater biodiversity, particularly migrating fauna, is extremely challenging as freshwater ecosystems are impacted by activities that occur on terrestrial and aquatic landscapes and there is a fundamental ‘thirst’ by humans for fresh water (Dudgeon et al. 2006). Altered flow regimes caused by climatically induced reductions in runoff and water abstraction coupled with pollution, particularly salinisation, are acting synergistically in south-western Australia. Setting thresholds of declines in discharge in order to guide management intervention has been undertaken globally but can also be undertaken on a more local scale to increase sensitivity (Palmer et al., 2008). Our study suggests that spawning migrations of potamodromous fishes will inevitably decline, leading to reduced recruitment and threatening the viability of populations and species. Such hydro-ecological research is urgently required elsewhere to better understand the resistance and resilience of potamodromous fishes to climate change (see Moilanen et al., 2008; Williams et al., 2011).

Given the recent climatic shift and consensus among GCMs of continued severe drying in south-western Australia, there is little excuse not to undertake proactive management strategies and adapt our responses to buffer the impacts on aquatic ecosystems (see Palmer et al., 2009). Remediation strategies to re-connect aquatic habitats may help mitigate the impact of flow declines (Palmer et al., 2008, 2009; Beatty et al., 2013). Addressing existing stressors on freshwater ecosystems in drying climatic regions at their source, such as undertaking more sustainable land use practices and approaches to both surface water and groundwater resource development (Xenopoulos et al., 2005; Xenopoulos & Lodge, 2006; Palmer et al., 2008, 2009; Vörösmarty et al., 2010; Davis et al., 2013) must also be a priority if the current and projected impacts of climate change are to be reduced.
Acknowledgements

This project was jointly funded by the Department of Water Government, of Western Australia and the Australian Government under its Water for the Future Plan. Special thanks to Adrian Goodreid, Natasha Del Borrello and Rob Donohue (Department of Water, Government of Western Australia) for project management. Many thanks also to the Department of Water Bunbury staff including Ash Ramsay, Richard Pickett and Andrew Bland for hydrological data. We are grateful for the field assistance that was provided by Fiona and Andrew Rowland, Travis Fazeldean, Simon Visser, Mark Allen, David John, Joshua Johnston and Trine Beatty. Thanks also to Adrian Gleiss for reviewing earlier drafts of the manuscript, and to three anonymous referees and Rhea Kressman, who made many constructive suggestions which substantially improved the manuscript. The study complied with permits provided by the Murdoch University Animal Ethics Committee, the Department of Environment and Conservation and the Department of Fisheries, Government of Western Australia.

References


Bartoñ K (2013) MuMIn: multi-model inference. Version 1.9.5. Available at: <cran.r-project.org/web/packages/MuMIn/>


This article is protected by copyright. All rights reserved.


This article is protected by copyright. All rights reserved.


This article is protected by copyright. All rights reserved.


Heiberger RM (2013) HH: statistical analysis and data display. Version 2.3-37. Available at: <cran.r-project.org/web/packages/HH/>


This article is protected by copyright. All rights reserved.


This article is protected by copyright. All rights reserved.


This article is protected by copyright. All rights reserved.


**SUPPORTING INFORMATION**

**Table S1** Matrix of Pearson product-moment correlations among environmental predictor variables (all except pH log10 transformed).
Table S2 Water quality at sites sampled in the Blackwood River.

Table S3 Prevalence of species and the water quality at their capture sites in the Blackwood River.

Fig. S1 Mean number of *Galaxias occidentalis* moving in the tributary and main channel sites of the Blackwood River. NF indicates that the system was not flowing and therefore was not sampled.

Fig. S2 Length-frequency distributions of *Galaxias occidentalis* in Milyeannup Brook.

Fig. S3 Length-frequency distributions of *Galaxias occidentalis* in Rosa Brook.

Fig. S4 Mean number of *Galaxiella munda* moving in the tributary sites of the Blackwood River. NF indicates that the system was not flowing and therefore was not sampled.

Fig. S5 Length-frequency distributions of *Galaxiella munda* in Milyeannup Brook.

Fig. S6 Mean number of *Nannatherina balstoni* moving in the tributary and main channel sites of the Blackwood River. NF indicates that the system was not flowing and therefore was not sampled.

Fig. S7 Length-frequency distributions of *Nannatherina balstoni* in Milyeannup Brook.

Fig. S8 Mean number of *Nannoperca vittata* moving in the tributary and main channel sites of the Blackwood River. NF indicates that the system was not flowing and therefore was not sampled.

Fig. S9 Length-frequency distributions of *Nannoperca vittata* in Milyeannup Brook.

Fig. S10 Length-frequency distributions of *Nannoperca vittata* in Rosa Brook.

This article is protected by copyright. All rights reserved.
**Fig. S11** Mean number of *Bostockia porosa* moving in the tributary and main channel sites of the Blackwood River. NF indicates that the system was not flowing and therefore was not sampled.

**Fig. S12** Length-frequency distributions of *Bostockia porosa* in Rosa Brook.

**Fig. S13** Length-frequency distributions of *Bostockia porosa* in Layman Brook.

**Table 1** Association between environmental variables and number of fish moving upstream for five freshwater fish species over the major flow period in four tributaries of the Blackwood River. All variables except pH were log$_{10}$ transformed. Variables are ranked by relative importance, with coefficient estimates and standard errors from model averaging. The percentage independent contribution of each environmental variable to total explained variance was determined by hierarchical partitioning of $R^2$ values. Significant predictors ($P < 0.05$) from model averaging are shown in bold and from hierarchical partitioning with an asterix.

<table>
<thead>
<tr>
<th>Response</th>
<th>Environmental variable</th>
<th>Importance</th>
<th>Estimate</th>
<th>SE</th>
<th>Independent effect (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>N. balstoni</em></td>
<td>Discharge</td>
<td>0.44</td>
<td>0.44</td>
<td>0.29</td>
<td>38.3</td>
</tr>
<tr>
<td></td>
<td>Conductivity</td>
<td>0.39</td>
<td>-2.49</td>
<td>1.70</td>
<td>35.2</td>
</tr>
<tr>
<td></td>
<td>pH</td>
<td>0.19</td>
<td>-0.27</td>
<td>0.42</td>
<td>11.7</td>
</tr>
<tr>
<td></td>
<td>Dissolved oxygen</td>
<td>0.16</td>
<td>-0.93</td>
<td>2.52</td>
<td>9.1</td>
</tr>
<tr>
<td></td>
<td>Temperature</td>
<td>0.15</td>
<td>-1.97</td>
<td>5.10</td>
<td>5.7</td>
</tr>
<tr>
<td><em>N. vittata</em></td>
<td>Discharge</td>
<td>0.98</td>
<td>1.00</td>
<td>0.27</td>
<td>49.8</td>
</tr>
<tr>
<td></td>
<td>Temperature</td>
<td>0.81</td>
<td>-12.02</td>
<td>4.48</td>
<td>25.3</td>
</tr>
<tr>
<td></td>
<td>Conductivity</td>
<td>0.20</td>
<td>1.90</td>
<td>1.71</td>
<td>14.0</td>
</tr>
<tr>
<td></td>
<td>Dissolved oxygen</td>
<td>0.15</td>
<td>-2.19</td>
<td>3.05</td>
<td>5.5</td>
</tr>
<tr>
<td></td>
<td>pH</td>
<td>0.10</td>
<td>0.14</td>
<td>0.41</td>
<td>5.4</td>
</tr>
<tr>
<td><em>B porosa</em></td>
<td>Discharge</td>
<td>0.99</td>
<td>0.46</td>
<td>0.12</td>
<td>63.0*</td>
</tr>
<tr>
<td></td>
<td>pH</td>
<td>0.57</td>
<td>0.29</td>
<td>0.13</td>
<td>23.9</td>
</tr>
<tr>
<td></td>
<td>Conductivity</td>
<td>0.34</td>
<td>-1.13</td>
<td>0.68</td>
<td>4.6</td>
</tr>
<tr>
<td></td>
<td>Temperature</td>
<td>0.13</td>
<td>-1.40</td>
<td>1.99</td>
<td>2.2</td>
</tr>
<tr>
<td></td>
<td>Dissolved oxygen</td>
<td>0.10</td>
<td>0.02</td>
<td>1.01</td>
<td>6.3</td>
</tr>
<tr>
<td><em>G. occidentalis</em></td>
<td>Discharge</td>
<td>0.86</td>
<td>0.69</td>
<td>0.26</td>
<td>61.8</td>
</tr>
</tbody>
</table>

This article is protected by copyright. All rights reserved.
### Table 2

Association between environmental variables and number of fish moving upstream for five freshwater fish species over the major flow period in four tributaries of the Blackwood River. All variables except pH were log_{10} transformed. Variables are ranked by relative importance, with coefficient estimates and standard errors from model averaging. The percentage independent contribution of each environmental variable to total explained variance was determined by hierarchical partitioning of $R^2$ values. Significant predictors ($P < 0.05$) from model averaging are shown in bold and from hierarchical partitioning with an asterix.

<table>
<thead>
<tr>
<th>Response</th>
<th>Environmental variable</th>
<th>Importance</th>
<th>Estimate</th>
<th>SE</th>
<th>Independent effect (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>N. balstoni</strong></td>
<td>Discharge</td>
<td>0.63</td>
<td>0.52</td>
<td>0.55</td>
<td>26.3</td>
</tr>
<tr>
<td></td>
<td>Conductivity</td>
<td>0.33</td>
<td>-4.60</td>
<td>3.32</td>
<td>37.9</td>
</tr>
<tr>
<td></td>
<td>pH</td>
<td>0.22</td>
<td>-0.77</td>
<td>0.78</td>
<td>20.7</td>
</tr>
<tr>
<td></td>
<td>Temperature</td>
<td>0.16</td>
<td>-6.10</td>
<td>9.69</td>
<td>6.3</td>
</tr>
<tr>
<td></td>
<td>Dissolved oxygen</td>
<td>0.14</td>
<td>-1.93</td>
<td>4.63</td>
<td>8.8</td>
</tr>
<tr>
<td><strong>N. vittata</strong></td>
<td><strong>Discharge</strong></td>
<td><strong>1.00</strong></td>
<td><strong>1.15</strong></td>
<td><strong>0.22</strong></td>
<td><strong>51.1</strong>*</td>
</tr>
<tr>
<td></td>
<td>Temperature</td>
<td>0.98</td>
<td><strong>-14.84</strong></td>
<td>3.81</td>
<td>31.7***</td>
</tr>
<tr>
<td></td>
<td>Conductivity</td>
<td>0.15</td>
<td>1.33</td>
<td>1.39</td>
<td>8.8</td>
</tr>
<tr>
<td></td>
<td>Dissolved oxygen</td>
<td>0.09</td>
<td>0.62</td>
<td>2.59</td>
<td>5.9</td>
</tr>
<tr>
<td></td>
<td>pH</td>
<td>0.08</td>
<td>0.00</td>
<td>0.30</td>
<td>2.6</td>
</tr>
<tr>
<td><strong>B porosa</strong></td>
<td><strong>Dissolved oxygen</strong></td>
<td><strong>0.89</strong></td>
<td><strong>3.87</strong></td>
<td><strong>1.31</strong></td>
<td><strong>62.7</strong>*</td>
</tr>
<tr>
<td></td>
<td>Discharge</td>
<td>0.84</td>
<td>-0.19</td>
<td>0.17</td>
<td>21.2</td>
</tr>
<tr>
<td></td>
<td>Temperature</td>
<td>0.11</td>
<td>-0.02</td>
<td>4.21</td>
<td>9.9</td>
</tr>
<tr>
<td></td>
<td>Conductivity</td>
<td>0.10</td>
<td>0.26</td>
<td>1.15</td>
<td>4.5</td>
</tr>
<tr>
<td></td>
<td>pH</td>
<td>Discharge</td>
<td>Conductivity</td>
<td>pH</td>
<td>Dissolved oxygen</td>
</tr>
<tr>
<td>----------</td>
<td>--------</td>
<td>-----------</td>
<td>--------------</td>
<td>--------</td>
<td>------------------</td>
</tr>
<tr>
<td><strong>G. occidentalis</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>pH</td>
<td>0.09</td>
<td>0.55</td>
<td>0.43</td>
<td>0.41</td>
<td>0.16</td>
</tr>
<tr>
<td>Conductivity</td>
<td>0.02</td>
<td>0.59</td>
<td>-3.35</td>
<td>-0.69</td>
<td>1.91</td>
</tr>
<tr>
<td>pH</td>
<td>0.23</td>
<td>0.32</td>
<td>2.03</td>
<td>0.43</td>
<td>2.67</td>
</tr>
<tr>
<td>Discharged</td>
<td>1.7</td>
<td>38.6*</td>
<td>22.3</td>
<td>23.5</td>
<td>8.8</td>
</tr>
<tr>
<td><strong>G. munda</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>pH</td>
<td>0.41</td>
<td>0.99</td>
<td>0.42</td>
<td>0.33</td>
<td>0.16</td>
</tr>
<tr>
<td>Conductivity</td>
<td>-0.69</td>
<td>0.13</td>
<td>-1.01</td>
<td>-0.20</td>
<td>1.91</td>
</tr>
<tr>
<td>pH</td>
<td>0.43</td>
<td>0.10</td>
<td>0.58</td>
<td>0.13</td>
<td>2.67</td>
</tr>
<tr>
<td>Discharged</td>
<td>1.7</td>
<td>38.8</td>
<td>33.9</td>
<td>18.7</td>
<td>8.8</td>
</tr>
</tbody>
</table>

FIGURE LEGENDS

**Fig. 1** Sites sampled in the Blackwood River and its tributaries to determine the movement patterns of south-western Australian freshwater fishes.

**Fig. 2** Water temperatures at the sites sampled in the Blackwood River and its tributaries. Note the close association between the water temperatures in all sites and the maximum daily air temperature.

**Fig. 3** Schematic diagram of the temporal and spatial movement patterns of two species of Galaxiidae in the main channel of the Blackwood River and in a seasonal and a perennial tributary, south-western Australia. Direction of movement (upstream or downstream) is indicated by the orientation of fish. New recruits are indicated by smaller sized fish.

**Fig. 4** Schematic diagram of the temporal and spatial movement patterns of three species of Percichthyidae in the main channel of the Blackwood River and in a seasonal and a perennial tributary, south-western Australia. Direction of movement (upstream or downstream) is indicated by the orientation of fish. New recruits are indicated by smaller sized fish.