Regional-scale extremes in river discharge and localised spawning stock abundance influence recruitment dynamics of a threatened freshwater fish

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Abstract

Highly variable recruitment is common for many riverine fish species, governed by a wide range of biotic and abiotic drivers that operate at local and regional scales. The dynamics and drivers of recruitment for many Australian freshwater fish species, particularly those that are rare and long-lived, are relatively undescribed. This study describes the recruitment dynamics of an endangered riverine fish, Macquarie perch *Macquaria australasica*, across five isolated populations from south-eastern Australia, and relates these dynamics to drivers that vary at local and regional scales. We hypothesised large flow events occurring during the core egg and larval period would be negatively associated with recruitment strength and that recruitment patterns across populations would fluctuate in synchrony in response to extremes in river discharge resulting from regional-scale climatic patterns.

Discharge during the core egg and larval period, which was highly correlated across the region; and a local scale variable, spawning stock abundance, were the covariates most important in explaining recruitment strength. We also observed synchronised patterns in recruitment across our populations, thus conforming to predictions of the Moran effect (environmental synchrony). The findings suggest most remnant populations of Macquarie perch, which are now predominantly isolated within small tributary systems characterised by highly variable flows, face a heightened risk of poor recruitment periods, particularly under climate change predictions. The synchronised patterns in recruitment suggests threatened freshwater fishes like Macquarie perch with highly fragmented isolated

populations, have an increased risk of the regional population becoming imperilled, thus, the need for a coordinated multijurisdictional conservation approach.

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Introduction

Environmental variability is a major driver of animal population dynamics (Ginzburg 1986).

For fish in riverine environments, large-scale disturbances such as floods and droughts, can have major influences on populations by altering their size- and age-structure and abundance (Labbe and Fausch 2000; Milner *et al.*, 2003; Arthington and Balcombe 2011).

Effective conservation and management of fish populations requires an understanding of how such environmental variability influences basic demographic processes such as

recruitment, mortality and migration. Recruitment, defined as the number of new fish entering a population, is often measured to a point in the life cycle, such as, to young-of-the-year, juvenile and adult (sexually mature) life-stages (Wootton 1998; King *et al.*, 2013).

Ultimately, the rate of successful recruitment to the mature population will determine long-term inter-generational population trends. Recruitment strength can be influenced by a range of biotic (e.g. competition, predation, disease) and abiotic (e.g. flow attributes, temperature, physical habitat) factors, with strong recruitment to the pool of reproductive individuals occurring only when combinations of such factors align (Nunn *et al.*, 2007).

Highly variable recruitment in space and time is a common characteristic of riverine fish populations, most likely due to the dynamic nature of the abiotic selective forces that act on lotic ecosystems (Biggs *et al.*, 2005). Whilst biotic interactions such as predation have been demonstrated to have localised influences on recruitment (e.g. Myers *et al.*, 1997), it is the abiotic environment that is most likely to have driven evolutionary development of specific ecological traits and associated life-history strategies (Lytle and Poff 2004; Biggs *et al.*,

2005). Stream flow, in particular, is a major driver of lotic ecosystems. Hydrological characteristics can influence life history processes governing recruitment both directly (e.g. spawning and movement cues) and indirectly through the alteration of physical habitat attributes linked to survival. Specific mechanisms driving the latter include the well documented “flood pulse advantage” (Bayley 1991), whereby appropriately timed high flow events provide food rich floodplain habitats (and therefore increased survival) for many fish species occupying floodplain rivers. Conversely, for species occupying lower order high-gradient streams, high flow events have been demonstrated to negatively affect survival, particularly of early life stages through mechanisms such as displacement or smothering of eggs (e.g. Lucas and Orth 1995; Smith *et al.*, 2005; Milner *et al.*, 2003) and decreased larval foraging success (e.g. Piccolo *et al.*, 2008).

Understanding the dynamics and drivers of recruitment for fish species, particularly those which are long-lived, requires data collected over, or representative of temporal scales which are commensurate with species specific life history stages as well as capturing the natural range of abiotic conditions. Additional challenges arise when the species of interest is threatened (and therefore often rare in samples), resulting in datasets with small numbers and often over limited time periods, which may be inadequate to detect trends.

One way to help overcome such limitations is to compile information gathered from multiple populations at a regional scale. Regional or landscape-level processes often strongly influence local populations (Labbe and Fausch 2000), with many animal populations fluctuating in synchrony as a result (Koenig 2002). Potential driving forces of spatial

synchrony include predation (Ims and Andreassen 2000), dispersal (Ranta *et al.*, 1995), and environmental synchrony, otherwise known as the Moran effect (Moran 1953, Koenig 2002). The natural environment is a spatially auto-correlated place (Legendre 1993) and both biotic (e.g. population density, or reproductive rate) and abiotic (e.g. rainfall, flows and temperature) variables may at times similarly co-vary (Rossi *et al.*, 1992; Liebhold *et al.*, 2004). Thus, if dispersal and predation mechanisms can be dismissed as strong drivers, synchronous fluctuations in population processes such as recruitment by localised populations can potentially provide a useful tool to identify the influence of climatic effects on population dynamics (Tedesco *et al.*, 2004; Nunn *et al.*, 2007).

Over the past decade, research investigating the role of abiotic drivers, in particular stream-flow, in governing fish recruitment has risen dramatically in Australia (King *et al.* 2013), likely due largely to the increasing application of environmental flows in river restoration. Much of this work has focussed on species occupying lowland floodplain river systems (e.g. Balcombe *et al.*, 2012; Zampatti and Leigh 2013; Beesley *et al.*, 2014; King *et al.*, 2015), with less work on species and populations inhabiting headwater streams. One example of the latter is the Macquarie perch *Macquaria australasica*, which is a medium-sized (up to 465 mm Total length; Lintermans 2007), long-lived (up to 26 years; Tonkin *et al.*, 2014) percichthyid fish, once widespread and abundant across the south-eastern reaches of the Murray–Darling Basin and several rivers of the eastern seaboard.

Macquarie perch has undergone major declines in distribution and abundance, and is now listed as nationally endangered under the *Environmental Protection and Biodiversity*

Conservation Act 1999 (Commonwealth) and as threatened in the south-eastern state of Victoria under the *Flora and Fauna Guarantee Act 1988* (Lintermans 2007; Tonkin *et al.*, 2015). Populations are highly fragmented and span multiple catchments within its native range, occurring in isolated reaches of tributaries that contain remnant high quality habitat (Ingram *et al.* 2000; Lintermans 2007; DELWP unpublished data) (within the Goulburn, Broken, Mitta Mitta, Ovens, and Campaspe catchments). An additional population, in the mid-reaches of the Yarra River south of the Great Dividing Range, resulted from translocations of fish from the Mitta Mitta and Goulburn catchments from 1910 – 1940 (Cadwallader 1981). Recent monitoring of some of these populations suggests poor recruitment is associated with years of large flow events during the core spawning period (late spring and early summer; King *et al.*, 2011; Kearns *et al.*, 2012; Tonkin *et al.*, 2014). Considering fertilised Macquarie perch eggs settle and develop in riffle areas (Cadwallader and Rogan 1977; Ingram *et al.*, 2000), it is likely that eggs and perhaps larvae are prone to disturbance which in turn, is reflected in recruitment strength. Nevertheless, this hypothesis has not been tested across multiple years or systems.

In this study, we describe recruitment dynamics of Macquarie perch across five isolated populations from south-eastern Australia and investigate these dynamics to drivers which fluctuate at local and regional scales. We hypothesise that large flow events during the breeding season (austral spring) disrupt the development of eggs and larvae, and hence reduce recruitment. Furthermore, because extremes in flow periods (e.g. droughts and wetter rainfall periods) tend to be associated with long-term, large-scale climate cycles (e.g.

la niña events; Verdon *et al.*, 2004), we hypothesise that if such events do suppress recruitment, then recruitment patterns should vary synchronously among the isolated populations. In testing this hypothesis, we explicitly account for the size of the spawning population when considering the expected magnitude of recruitment. We then explore how our results may explain the current distribution patterns and risks to the species, and inform future management options such as the delivery of environmental flows and translocation actions.

Methods

Study sites and fish surveys

We investigated the recruitment dynamics of Macquarie perch by using a collective assessment of multi-year surveys of five populations across Victoria (Figure 1; Table 1). The maximum linear distance between the furthestmost study regions, which lie within the south-eastern Australia, is approximately 245 km (Yarra River to Lake Dartmouth). The *Yarra River*, is a coastal stream approximately 240 km in length, draining a catchment of approximately 3,766 km² (DWR 1989). Boat- (Smith-Root® Model 5 GPP) and bank-(Smith-Root 7.5 Kva) mounted electrofishing surveys have been conducted at multiple sites between January –June during eight of the nine years from 2007 – 2015. Whilst surveys were conducted at more than 40 sites over this time, juvenile Macquarie perch (< 150 mm TL) were recorded only at 14 sites. Thus, for the purposes of this study (i.e. assessing recruitment), only these sites (8 – 14 sites per year) were used for our assessment. Electrofishing at each site was undertaken by using a standardised protocol developed for the Sustainable Rivers Audit (SRA; MDBC 2004). Briefly, at each site, 12 replicate (single-pass) 90 second electrofishing shots were conducted across all habitats within the river channel. Two of the fourteen sites were often sampled using Bank-mounted (Smith-Root 7.5 Kva) electrofishing using 10 x 150 second shots (SRA protocol) due to low flow periods. *Lake Dartmouth* impounds the Mitta Mitta River and is the largest freshwater impoundment in south-eastern Australia's Murray-Darling Basin. The Lake, primarily an irrigation storage,

has a surface area of 6380 ha and stores almost 4 000 000 ML of water at full capacity (Gray *et al.*, 2000). Whilst Macquarie perch are naturally a riverine fish, the species has maintained a population in this reservoir, likely due to them having access to suitable inflowing riverine habitat for spawning and rearing (Cadwallader 1981; Appleford *et al.*, 1998). Annual netting surveys of the Lake were undertaken over a five day period between February and May from 2010 to 2015. Between six to ten gill nets and four to six fyke nets were set for one overnight period across three sites in each of three regions of the Lake. Whilst numerous unregulated tributaries flow into Lake Dartmouth, the largest, the Mitta Mitta River (average annual discharge of approximately 800 ML day⁻¹ upstream of the Dam) is the primary spawning area used by Macquarie perch during their annual spring spawning migration out of the Lake (Douglas *et al.*, 2002; Tonkin *et al.*, 2010). Indeed, survey data have recorded early juvenile fish only in this region of the Lake, with fyke nets the primary method suited to the collection of juvenile fish (< 150 mm TL). Thus, as per the Yarra River, only data collected within this region (and method) of the Lake were used for our assessment of recruitment.

King Parrot Creek, Hughes Creek and Sevens Creek are all unregulated tributaries of the Goulburn River located in north-eastern Victoria. Each has an annual average discharge of 40 – 60 ML day⁻¹, draining a catchment of approximately 400 – 600 km². Despite historical connectivity, anthropogenic alterations to flow (regulation and extraction), connectivity (dams and weirs) and land use (sedimentation) have resulted in highly fragmented habitats and subsequent isolation of Macquarie perch among the waterways (as reflected in recent

genomic data; A. Pavlova, unpublished data). Annual surveys of King Parrot Creek were conducted between Feb – May from 2007 – 2015. Each year, between four and seven sites were sampled using a combination of 6 – 16 fyke nets and 1000 – 1200 seconds of backpack electrofishing (Smith-Root Model 12 or 20b). Backpack electrofishing surveys of Hughes Creek and Sevens Creek were conducted between January – May during six (Hughes; 5 – 12 sites) and five (Sevens; 12 – 24 sites) of the years between 2006 – 2015. Sampling of all sites in both Hughes Creek and Sevens Creek consisted of defined distances and / or electrofishing seconds fished (recorded at all sites).

For each of the populations, all sampling was conducted during periods of relatively stable low flow conditions to minimise detection bias. All fish captured were weighed (to the nearest gram) and measured for total length (TL; nearest millimetre) before release.

Analyses

Recruitment strength was investigated by using annual counts of young-of-year (YOY; fish less than 1 year of age). YOY fish were identified based on recently published length-age relationships for lacustrine (Dartmouth population) and riverine populations (all other populations; Tonkin *et al.*, 2014; see supplementary material 1). In brief, a standard non-linear regression model (Gompertz) of length L_x (mm) at age X (years) was constructed from known aged individuals to enable estimates of age from length data. Specifically:

Gompertz:
$$L_x = L_\infty e^{e^{-b(X-M)}}$$

Where L_x is the length at age X , L_∞ is the asymptotic length, b is the instantaneous growth rate, and M is the inflection point of the curve (years).

Although the outputs of the growth models were primarily to distinguish YOY fish as a measure of recruitment, a secondary output was the identification of adult (mature) fish, defined as > 4 years of age (Appleford *et al.*, 1998) to provide estimates of spawning stock abundance, which is also likely to influence recruitment strength (Nunn *et al.*, 2007).

For the purpose of examining annual fluctuations in recruitment among rivers, we pooled data from multiple sites within each river to create a time-series of abundance of YOY fish for each stream, standardised for survey effort (offset against the total number of nets or electrofishing seconds in a given year; see below). We then compiled complementary time-series of (primarily) environmental data considered as likely candidates to explain recruitment variability (Table 2). Of particular interest was our hypothesis of a negative association between Macquarie perch recruitment strength and flow magnitude and/or variability during the core period of egg and larval developmental (November – December; Tonkin *et al.*, 2015). River (used as a factor in the model to account for localised drivers); Pre- and post- spawning flows (named accordingly); spawning season water temperature (SP_TEMP); spawning stock abundance (standardised count of mature fish; PS_SSA) and river height (PS_RIV_HEIGHT) at the time of sampling (as a proxy for conditions which may influence sampling detection), were also variables considered in our suite of hypotheses (Table 2).

Whilst there are several mechanistic drivers which may govern our flow dependent hypotheses (e.g. turbidity and change depth), egg and larval disturbance is most likely to be related to water velocity (and its change; e.g. Smith *et al.*, 2005). Unfortunately, site-specific data on this metric was not readily available. Nevertheless, for lower order streams, there is a strong correlation between velocity and the most common metric of hydrological gauging, discharge. Thus, we generated flow and temperature variables using daily discharge and temperature (if available) values from permanent gauging stations in close proximity to each of the sample sites (Yarra River at Templestowe; Dartmouth = Mitta Mitta River at Hinnomunji Bridge; King Parrot Creek at Flowerdale; Hughes Creek at Tarcombe Rd; Sevens Creek at Polly McQuinn weir). Unfortunately, continuous records of daily water temperature were unavailable for the King Parrot Creek, Hughes Creek and Sevens Creek. We did, however, have temperature data collected during several spawning seasons using an in-situ temperature logger in the King Parrot Creek. Simple linear models have been used successfully to model water temperature using air temperature and /or other independent variables (see Benyahya *et al.* 2007). As such, we used minimum daily air temperature, average daily flow, month and day of month in combination with our water temperature data in a linear model to predict average daily water temperatures during the core spawning season for the King Parrot Creek, Hughes Creek and Sevens Creek (see supplementary material 2 for model parameters).

Generalised Linear Models (GLM's), using a negative binomial distribution due to the non-normal distribution of YOY count data (and to address over-dispersion associated with

Poisson distributed models) were used to analyse the data. The total count of YOY in a given year was standardised (offset) by the total effort applied in the surveys of that year (number of nets or electrofishing seconds standardised for each system). We then fitted a suite of additive models using combinations (of low correlation values; Pearson's correlation coefficient) of the aforementioned variables relating to our hypothesised drivers of Macquarie perch recruitment (Table 3). The relative support for each model was assessed by using Akaike's Information Criterion (AIC), corrected for small sample size (AICc) (Burnham and Anderson, 1998). AICc values were rescaled as differences between each model and the model with the lowest AICc value. The final model was checked for over-dispersion and goodness of fit by using a χ^2 -test based on residual deviance and degrees of freedom. All models were fitted using the R statistical programming environment (R Development Core Team 2013), with all GLM's constructed using the package MASS (Venables and Ripley, 2002).

Results

Environmental variables

All of the study waterways exhibited highly correlated patterns in seasonal discharge across years (Pearson's pairwise correlation coefficients of 0.704 – 0.998; Figure 2; Supplementary material 3). Specifically, the six year period from 2007 – 2012 was a period of highly variable annual discharges, with four years of extreme low and two years of very high flows

respectively. These extremes were most pronounced in the smaller waterways as compared to the Yarra and Mitta Mitta Rivers (Figure 2). The following three years consisted of relatively average to low flows (2013 – 2015). Whilst all discharge variables displayed strong correlations between waterways, there was a general trend of strongest correlations between the three smallest waterways (and closest proximity) in the Goulburn catchment (see supplementary material 3 for details).

Both temperature and flow variability during the spawning period exhibited more localised patterns, with higher variation between waterways. In 2011, mean daily water temperatures during the spawning period (Oct – Dec) were low across all waterways ($< 15^{\circ}\text{C}$). Other extremes in temperature during this period were most similar between the Goulburn systems and the Mitta Mitta River (Lake Dartmouth spawning tributary), with the Yarra River the most different (Figure 2a; Supplementary material 3f). Our flow variability metric during the peak egg and larval period (days of discharge change $> 100\%$) was similar between the Goulburn systems but not the other systems (Supplementary material 3e). All annual discharge values (excluding change in flow) within systems were strongly correlated (> 0.75 ; Supplementary material 4). As such, only one discharge variable could be included in each of the model structures (see below).

Recruitment dynamics

Counts of Macquarie perch YOY recorded across rivers from 2007–2015 were in general, higher in the 2010 and 2015 sample years (indicative of fish spawned the previous spring; Figure 3). Conversely, the 2011 and 2012 survey years (those of highest discharge and low temperatures during the preceding spring spawning period) were years of low recruitment for all surveyed populations. Our selection procedure, indicated that model 11 provided the best explanation of YOY abundance relative to other models (Table 3; Chi-Square goodness of fit test $P = 0.615$). The effects of discharge during November – December (SP_DIS_Nov-Dec); and spawning stock abundance (PS_SSA) were the covariates considered the most important in explaining variations in recruitment strength (Model 11). The parameter estimates and subsequent predictions of model 11 indicated a significant negative relationship between YOY abundance and SP_DIS_Nov-Dec (Figure 4; $p < 0.001$; GLM coefficient estimates of -1.525); and significant positive relationship between YOY abundance and spawning stock abundance (Figure 4; $p < 0.01$; GLM coefficient estimates of 0.7133).

There was also some support for the more complex models (12 and 15) which included the addition of our measure of flow variability during November – December (SP_DAYS>100) and average daily water temperature during October – December (SP_TEMP). The effects of these covariates on YOY abundance were negative and positive, respectively (GLM coefficient estimates of -0.017 and 0.243, respectively), but their effects were minor and not significant (both $p > 0.05$). None of the best supported models included the Factor *River*, indicating the response to flows was similar across systems and suggests the effects of more

local variables (not identified in the analyses) on recruitment dynamics were minor in comparison to discharge, which was highly correlated across the region.

Our predictions of YOY abundance for each of the study rivers from 2007 – 2015 provides some support for spatial synchrony in recruitment strength, with a general trend of decreasing recruitment strength from 2007 – 2012, followed by an increase in recruitment strength in the 2013 – 2015 sample years (spawned in the previous spring; Figure 5). Trends in recruitment dynamics were most similar for the three Goulburn populations (Figures 5b, d, and e, respectively). Unlike all other populations, the levels of recruitment in the Yarra population were somewhat dampened, having not yet approached (or exceeded) the levels predicted at the start of the sampling period in 2007 (Figure 5.).

Discussion

To our knowledge this study is the first to demonstrate a broad-scale correlation between regional-scale flow variability and localised recruitment dynamics of fish in south-eastern Australia. It also provides a greater understanding of the spatiotemporal recruitment dynamics of an endangered riverine fish, demonstrating the role of a local-scale biotic variable (spawning stock abundance), and an abiotic variable (discharge) which was highly correlated at a regional scale.

Our multi-population analyses demonstrated poorer recruitment in years of higher discharge during the core egg and larval period (November – December). This finding is not in itself surprising; recruitment of freshwater fishes is known to be affected dramatically by episodic adverse physical or chemical conditions (Houde 1989; King *et al.*, 2013). In particular, changes in water velocity and temperature have significant effects on the survival of eggs and larvae (Simonson and Swenson 1990; Mion *et al.*, 1998; Paul 2012; Suedel *et al.*, 2012). For fish species occupying lower order high-gradient streams, extreme high flows during critical reproductive periods has been demonstrated to negatively affect recruitment strength of numerous fish species (e.g. Freeman *et al.*, 2001; Nicola *et al.*, 2009). Specific mechanisms of how such flows reduce recruitment success could include nest or redd scour (e.g. Lucas and Orth 1995; Smith *et al.*, 2005), siltation of egg incubation substrate (Milner *et al.*, 2003), displacement of larvae (e.g. Simonson and Swenson 1990), loss of critical nursery habitat (Freeman *et al.*, 2001), and high turbidity and velocity which decreases larval foraging success (Piccolo *et al.*, 2008). Such mechanisms are theoretically relevant to the

early life- history characteristics of Macquarie perch where fertilised eggs settle into riffle areas to ensure maximum aeration and minimise the risk of smothering by sediments (Cadwallader and Rogan 1977; Ingram *et al.*, 2000).

Including the abundance of spawning stock into the model significantly improved the ability to predict recruitment strength. Specifically, years of high spawning stock abundance translated to years of high recruitment, particularly when coinciding with favourable flow conditions. Nunn *et al.*, (2007) pointed out that even if environmental conditions are ideal, recruitment strength will still be low if only a small number of adults are available for spawning. We suggest that drought conditions from 2007 to 2011 reduced adult population sizes in several of the smaller and more drought susceptible tributaries (especially Hughes and Sevens Creek systems), and that this translated into an overall decreasing trend in recruitment at those sites even though per capita recruitment rates may have been relatively high. This is an example of the clear relationship between biotic interactions, population dynamics and abiotic components (Power *et al.*, 1988; Jackson *et al.*, 2001). Whilst the status of a population's spawning stock is fundamental to understanding its dynamics (Wootton 1998), this factor is often overlooked in favour of considering only abiotic variables under the premise that they have the greatest effects on survival (e.g. Milner *et al.*, 2003). Our results reinforce this fundamental aspect of fisheries management, emphasising the need to account for this important biotic driver to gain a complete understanding of recruitment dynamics. This result also highlights the importance of conserving adult fish stocks, both through careful management of the recreational fishery

and safeguarding against extreme events (e.g. adult translocation from the King Parrot Creek following bushfire sedimentation events; Kearns *et al.*, 2012).

Stream landscapes are highly variable in space as well as time, with a general pattern of increasing stability of fish populations down a watershed gradient (Matthews 1986) attributed to increased stability of stream flow (Taylor and Warren 2001). Whilst species-specific responses to abiotic drivers are likely to be similar across populations, the relative importance of the driver is likely to vary among waterbodies. Nunn *et al.*, (2007) indicated that whilst temporal variation occurs because of inter-annual differences in river discharge relative to the timing of fish hatching (as per the findings of the current study), river discharge is likely to be of relatively greater importance in rivers which are prone to large and rapid fluctuations in flow.

The rivers used in this study have comparatively variable patterns in discharge, with the larger Yarra River and Dartmouth system (Mitta Mitta River) displaying lower variation compared to the smaller Goulburn tributaries. Interestingly, to some degree this pattern was also mirrored in patterns of recruitment strength. For example, average daily discharge variability in King Parrot Creek during November-December (using data from 1961 – 2015, inclusive) is more than twice that of the Mitta Mitta River (CV = 2.098 and 0.956, respectively). Smaller systems are also more likely to experience greater variability in adult fish abundance as a result of increased vulnerability to stochastic events such as extreme drought, flood and bushfire (Kearns *et al.*, 2011; Lintermans 2013a). It could therefore be expected that these remnant and now isolated populations of Macquarie perch exhibit less

stable recruitment patterns, and a reduced resilience to environmental extremes, particularly those which are likely to be exacerbated by climate change (as predicted by Balcombe *et al.*, 2011).

Our investigation of recruitment patterns across five isolated populations of Macquarie perch also revealed some evidence of spatial synchrony. One explanation for this covariance is through the process of dispersal (e.g. Ranta *et al.*, 1995), but this mechanism is highly unlikely given the isolation (resulting from human induced flow, passage and land use alterations) of our populations. We propose these observations are a result of the Moran effect (Moran 1953), whereby biotic (in this case recruitment strength) and abiotic (such as rainfall, flows and temperature) patterns co-vary across space (landscape and regional scales) and time (Rossi *et al.*, 1992; Liebhold *et al.*, 2004). Indeed, the recruitment dynamics of fish populations are often predictable along environmental gradients (Tedesco *et al.*, 2004; Nunn *et al.*, 2007). For example, the correlation scale for recruitment of marine species is typically 500 km whereas for freshwater species, it has been reported to range from 50 to 400 km (Myers *et al.*, 1997; 2015; Chevalier *et al.*, 2015). Whilst we performed no formal analyses of the spatial scales of such patterns, our observations are consistent with such patterns, with the linear distance between our furthestmost sites (Yarra River and Lake Dartmouth) being approximately 250 km. Our study has also demonstrated that when dispersal mechanisms can be dismissed (as was the case for the isolated populations used in this study), the Moran Effect is a useful theory to help identify the key regional scale drivers of population variation. Given the extreme fluctuations in recruitment strength for this

endangered species can be explained by large-scale factors (like regional scale fluctuations in flow), future management and conservation activities for the species will be made easier by integrating broad-scale climate forecasts particularly during extreme events such as extended droughts and flood.

Other variables are also likely to influence recruitment dynamics of riverine fish like Macquarie perch, particularly at local scales. For example, despite a relatively weak statistical effect, both temperature and our flow change parameter (both more localised effects), had some support for inclusion in our model selection process. Specifically, temperature during the spawning period had a positive association with Macquarie perch recruitment, conforming to patterns reported in spawning activity in both lacustrine (Cadwallader and Rogan 1977; Tonkin *et al.*, 2010) and riverine populations (Tonkin *et al.*, 2014). Secondly, there was a weak negative association between recruitment strength and flow change (equating to rapid changes in velocity) during the core egg and larval period. Other examples of localised drivers that influence Macquarie perch recruitment and / or populations include recreational harvest (e.g. Hunt *et al.*, 2011); and major habitat alterations that prevent access to key spawning habitat (Broadhurst *et al.*, 2013).

Our findings have implications for efforts to conserve this threatened species. A first step in threatened species recovery actions is to define critical habitat requirements for the species, thus informing habitat management and site selection for actions such as translocation (Foin *et al.*, 1998; Labbe and Fausch 2000). The results suggest conservation actions for Macquarie perch may be best targeted at maintaining or re-establishing

populations using hatchery reared fingerlings or translocations from wild populations (e.g. Todd and Lintermans 2015) into higher-order streams where hydraulic variation is lower, habitat characteristics are more stable and communities are able to persist for relatively longer periods of time (Jackson *et al.*, 2014). This differs from past stocking strategies for the species across Victoria, whereby fingerlings have been released into what were largely small low-order streams, with minimal success (Cadwallader 1981).

Managing river flows, including the use of environmental water, is another intervention increasingly being used to restore native fish populations, and is currently in use in the Yarra River (for Macquarie perch and other species; Tonkin *et al.*, 2015). Whilst the delivery of environmental flows during the reproductive period is used to stimulate the spawning of some native fish (e.g. King *et al.*, 2015), our results suggest that managing water delivery to avoid great increases in discharge during the spawning period will provide the best outcomes for Macquarie perch recruitment. We propose that if environmental water is to be used to sustain or enhance Macquarie perch, it should be targeted at other time periods to enhance other important population processes such as growth, survival and condition of juvenile and/or adult fish (the importance of the latter being emphasised in the current study). The maintenance of summer base flows during drought periods, or improving growth and condition of adults are logical choices based on our finding of the importance of adult stock abundance as a driver of recruitment strength (see also Lintermans 2013b; Tonkin *et al.*, 2014).

This study has improved the understanding of the role of both regional-scale variation in river flows and more localised abundance of spawning stock in governing recruitment dynamics of the endangered Macquarie perch. The synchronised patterns in recruitment observed across the isolated populations in this study suggest the importance of large-scale climatic patterns as a driver of annual variation in recruitment. This could also apply to other long-lived freshwater species with similar life histories to Macquarie perch. Importantly, regional-scale population synchrony highlights the vulnerability of these otherwise isolated populations to simultaneous declines, increasing the risk of regional populations becoming imperilled (e.g. Chevalier *et al.*, 2015). Thus, effective conservation of threatened freshwater fishes like Macquarie perch which have been reduced to small isolated populations will require a coordinated, multijurisdictional approach as is the case for many terrestrial species (Labbe and Fausch 2000).

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Table 1. Summary of the annual sampling protocol for each of the Macquarie perch population monitoring programs.

Population (system)	Date	Site No. year ⁻¹	Methods
Yarra River	2007, 2009 - 2015	8 - 14	Boat- and bank-mounted electrofishing; 12 x 90 sec shots site ⁻¹
Lake Dartmouth	2010 - 2015	3	Fyke netting; 3 – 12 nets per site
King Parrot Creek	2008 - 2015	4 - 7	Backpack electrofishing / Fyke net combination; Approx. 1000 sec. and 10 nets site ⁻¹
Hughes Creek	2007, 2011-2013, 2015	5 - 12	Backpack electrofishing; Approx. 1000 sec. site ⁻¹
Sevens Creek	2007-2009, 2011, 2015	12 - 24	Backpack electrofishing; Approx. 1000 sec. site ⁻¹ *

* Electrofishing seconds variable across sites and years.

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Table 2. Variables used to predict Macquarie perch recruitment strength using generalised linear models. Description and associated hypotheses of each also provided. Note: SP variables are those largely affecting the spawning period, PS are those largely affecting the post-spawning periods.

Variable	Description	Hypothesis
RIVER	Study River	Responses in recruitment strength will be dependent on the specific waterway
SP_DIS_Nov-Dec	Average daily discharge (November – December)	High discharge during core egg and larval development period will decrease survival and therefore recruitment strength
SP_TEMP	Average daily water temperature (October-December)	Higher water temperatures during core spawning and early development period will increase egg and larval survival and therefore recruitment strength
SP_DAYS>100	Number of days when discharge increases by more than 100% from the previous day (November - December)	Increased hydraulic variability during core egg and larval development period will decrease survival and therefore recruitment strength
SP_DIS_Sep-Oct	Average daily discharge (September – October)	High discharge in early spring will enhance migration and/or spawning substrate (riffle) condition and therefore recruitment strength.
PS_DIS_Dec-Mar	Average daily discharge (December – March)	Summer flows will influence habitat availability / survival of juveniles
PS_SSA	Spawning stock abundance calculated as the average annual abundance of mature fish (>4 years of age)	Higher numbers of mature adults in system will increase overall reproductive output and subsequent recruitment strength
PS_RIV_HEIGHT	River height at time of sampling	Higher river levels during sampling will decrease detection of juvenile fish

Table 3. Results of the model selection procedure for 24 additive models comparing the effects of river, discharge, temperature, spawning stock abundance (SSA) and sampling condition variables on Macquarie perch Young-of-year (YOY) abundance across five Victorian rivers between 2007 – 2015. AIC Akaike's Information Criterion (c, corrected for small sample size); $\Delta AICc$, difference in AICc between this model and the model with the lowest AICc.

Model no.	Model	AICc	d.AICc	Likelihood
1	YOY ~ River + SP_TEMP	237.564	20.083	0.000
2	YOY ~ River + SP_DIS_Nov-Dec	223.021	5.540	0.030
3	YOY ~ River + SP_DIS_Nov-Dec + SP_TEMP	226.081	8.600	0.006
4	YOY ~ SP_TEMP	234.676	17.195	0.000
5	YOY ~ SP_DIS_Nov-Dec	222.767	5.286	0.034
6	YOY ~ SP_DIS_Nov-Dec + SP_TEMP	225.201	7.720	0.010
7	YOY ~ PS_DIS_Dec-Mar	226.648	9.168	0.005
8	YOY ~ SP_DIS_Sep-Oct	234.632	17.151	0.000
9	YOY ~ SP_DAYS>100	236.930	19.450	0.000
10	YOY ~ SP_DIS_Nov-Dec+ SP_DAYS>100	223.891	6.410	0.019
11	YOY ~ SP_DIS_Nov-Dec + PS_SSA	217.481	0.000	0.473
12	YOY ~ SP_DIS_Nov-Dec + SP_DAYS>100 + PS_SSA	220.073	2.592	0.129
13	YOY ~ SP_DAYS>100 + PS_SSA+ PS_RIV_HEIGHT	234.039	16.559	0.000
14	YOY ~ SP_DAYS>100 + PS_SSA	231.597	14.116	0.000
15	YOY ~ SP_DIS_Nov-Dec + SP_TEMP + PS_SSA	218.437	0.957	0.293
16	YOY ~ River + PS_DIS_Dec-Mar	227.185	9.704	0.003
17	YOY ~ River + SP_DIS_Sep-Oct	234.288	16.807	0.000
18	YOY ~ River + SP_DAYS>100	240.477	22.997	0.000
19	YOY ~ River + SP_DIS_Nov-Dec+ SP_DAYS>100	224.864	7.384	0.011
20	YOY ~ River + SP_DIS_Nov-Dec + PS_SSA	222.965	5.485	0.028
21	YOY ~ River + SP_DIS_Nov-Dec + SP_DAYS>100 + PS_SSA	226.013	8.532	0.006
22	YOY ~ River + SP_DAYS>100 + PS_SSA+ PS_RIV_HEIGHT	242.138	24.657	0.000
23	YOY ~ River + SP_DAYS>100 + PS_SSA	238.835	21.354	0.000
24	YOY ~ River + SP_DIS_Nov-Dec + SP_TEMP + PS_SSA	225.560	8.079	0.007

Figure captions

Figure 1. Location of each of the five Macquarie perch populations used for the multi-population analyses.

Figure 2. Mean daily discharge during November and December (solid line) and water temperature during October - December (dotted line) in (a) Yarra River; (b) King Parrot Creek; (c) Mitta Mitta River (Lake Dartmouth spawning tributary); (d) Hughes Creek and; (e) Sevens Creek, preceding annual fish surveys from 2007 – 2015.

Figure 3. Standardised annual counts (fish 1000^{-1} electrofishing seconds or net fleet) of young-of-year (YOY) Macquarie perch captured across the five sample rivers during annual surveys from 2007 – 2015. Standardised spawning stock abundance (x; no. fish estimated as > 4 years of age per site) also included for reference. *ns* = not sampled.

Figure 4. The predicted young-of-year (YOY) abundance ($\pm$ SE) of Macquarie perch in response to different levels of standardised mean daily discharge during November-December (SP_DIS_Nov-Dec where 1 = average discharge; x-axis) and; Spawning stock abundance (PS_SSA; left to right) under minimum (below average), average and maximum (above average); values based on actual data range. Note differing scales of Y-axis.

Figure 5. The mean annual predicted ($\pm$ SE) count of young-of-year (YOY) Macquarie perch for the five study rivers over the sampling period (2007 – 2015). Annual predictions based on site specific annual discharge during November-December (SP_DIS_Nov-Dec) and

spawning stock abundance values (PS_SSA). For years lacking spawning stock abundance data, values were generated using the midpoint of the sample year prior to and following (generated over a three year period for Sevens); or the first year value for waterways missing prior data (King Parrot and Dartmouth).

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Supplementary material 1. Length-at-age growth curves for Macquarie perch displaying the relationship between total length (mm) and estimated age (years) predicted by the Gompertz growth model for a lacustrine population (Black) and riverine populations (red) populations.

$$\text{Length} \sim b1 * \exp(-b2 * \exp(b3 * \text{Age}))$$

Where $b1 = 406.024$; $b2 = 2.00532$; $b3 = -0.4244$ for lacustrine and; $b1 = 372.201$; $b2 = 1.83718$; $b3 = -0.37764$ for riverine.

Supplementary material 2. Linear regression model used to generate average daily water temperatures from October – December in the King Parrot Creek, Hughes Creek and Sevens Creek.

*lm(formula = Temp ~ Month * day2 + minT + log(Flow + 1) - 1, data = Flow.data)*

Where temp = average daily water temperature; Month = October, November or December; day2 = day of month; minT = minimum daily air temperature and; Flow1 = standardised daily discharge.

Model parameter and summary output below:

	Estimate	Std. Error	t value	Pr(> t)
MonthDecember	19.780	0.574	34.461	0.000
MonthNovember	14.517	0.508	28.604	0.000
MonthOctober	10.880	0.516	21.08	0.000
day2	-0.114	0.022	-5.073	0.000
minT	0.056	0.032	1.732	0.085
log(Flow1 + 1)	-3.881	0.174	-22.316	0.000
MonthNovember:day2	0.213	0.033	6.555	0.000
MonthOctober:day2	0.279	0.035	8.001	0.000

Residual standard error: 1.559 on 169 degrees of freedom

Multiple R-squared: 0.9929; Adjusted R-squared: 0.9925

F-statistic: 2947 on 8 and 169 DF, p-value: < 2.2e-16

Supplementary material 3. Pairwise correlation coefficients (Pearson's) between each study system calculated for all flow and temperature variables used in the recruitment modelling. Specifically (a) average daily discharge November – December; (b) average daily discharge September – October; (c) average daily discharge Dec – March; (d) No. days flow change > 100% Nov – Dec; (e) average daily water temperature Oct – Dec.

(a) Nov-Dec Discharge					
	Yarra	King Parrot	Dartmouth	Hughes	Sevens
Yarra	1				
King Parrot	0.940	1			
Dartmouth	0.737	0.892	1		
Hughes	0.704	0.869	0.870	1	
Sevens	0.777	0.917	0.899	0.993	1
(b) Sep-Oct Discharge					
	Yarra	King Parrot	Dartmouth	Hughes	Sevens
Yarra	1				
King Parrot	0.845	1			
Dartmouth	0.777	0.837	1		
Hughes	0.571	0.856	0.793	1	
Sevens	0.748	0.960	0.833	0.956	1
(c) Sum Discharge					
	Yarra	King Parrot	Dartmouth	Hughes	Sevens
Yarra	1				
King Parrot	0.984	1			
Dartmouth	0.909	0.887	1		
Hughes	0.976	0.994	0.870	1	
Sevens	0.990	0.998	0.893	0.995	1
(e) Nov-Dec flow change days					

	Yarra	King Parrot	Dartmouth	Hughes	Sevens
Yarra	1				
King Parrot	0.381	1			
Dartmouth	0.261	0.563	1		
Hughes	0.302	0.887	0.569	1	
Sevens	0.387	0.795	0.493	0.872	1
(f) Oct-Dec Temperature					
	Yarra	King Parrot	Dartmouth	Hughes	Sevens
Yarra	1				
King Parrot	-0.199	1			
Dartmouth	0.190	0.747	1		
Hughes	0.334	0.707	0.851	1	
Sevens	0.197	0.841	0.890	0.975	1

Supplementary material 4. Pairwise correlation coefficients (Pearson's) between standardised flow and temperature variables used in the recruitment modelling.

	<i>SO_flow</i>	SP_DIS_Nov-Dec	SP_TEMP	SP_DAYS>100	PS_DIS_Dec-Mar
SP_DIS_Sep-Oct	1				
SP_DIS_Nov-Dec	0.823	1			
SP_TEMP	-0.369	-0.399	1		
SP_DAYS>100	0.034	0.143	-0.160	1	
PS_DIS_Dec-Mar	0.753	0.920	-0.432	0.179	1

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