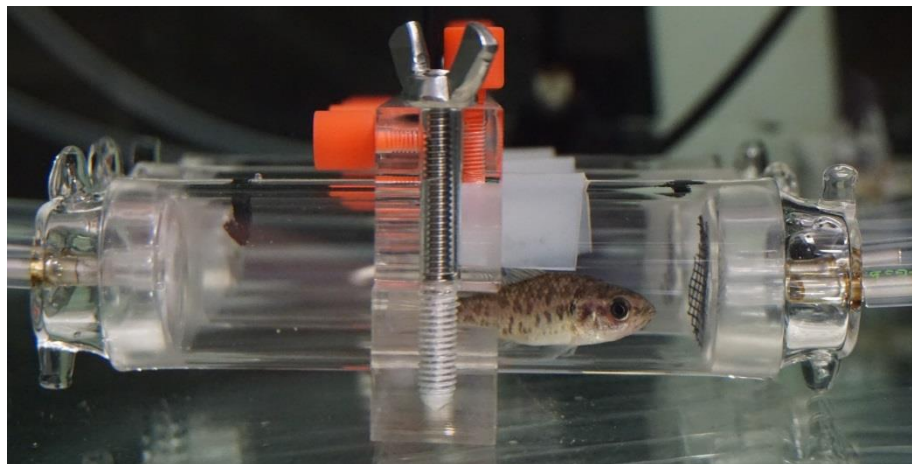


Will heat and hypoxia in floodplain wetlands give alien mosquitofish (*Gambusia holbrooki*) the edge over endemic pygmy perch (*Nannoperca australis*)?

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Final report

MDFRC Publication 94

Winter 2015



Will heat and hypoxia in floodplain wetlands give alien mosquitofish (*Gambusia holbrooki*) the edge over endemic pygmy perch (*Nannoperca australis*)?

Final Report prepared for the Goulburn-Broken Catchment Management Authority by The Murray-Darling Freshwater Research Centre.

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This report was prepared by The Murray-Darling Freshwater Research Centre (MDFRC). The aim of the MDFRC is to provide the scientific knowledge necessary for the management and sustained utilisation of the Murray-Darling Basin water resources. The MDFRC is a joint venture between La Trobe University and CSIRO.



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Report Citation: Stoffels RJ, Weatherman KA (2015) Will heat and hypoxia in floodplain wetlands give alien mosquitofish (*Gambusia holbrooki*) the edge over endemic pygmy perch (*Nannoperca australis*)? Final Report prepared for the Goulburn-Broken Catchment Management Authority by The Murray-Darling Freshwater Research Centre, MDFRC Publication 94/2015, August, 22pp.

Cover Images: Pygmy perch and mosquitofish in static respiration chambers

Photographer: Kyle Weatherman

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**Document history and status**

Version	Date Issued	Reviewed by	Approved by	Revision type
Draft	August 2015	Keith Ward, MDBA	Rick Stoffels	External

Distribution of copies

Version	Quantity	Issued to
Draft	1 x PDF	Keith Ward - GBCMA and the MDBA
Final	1 x PDF	Keith Ward - GBCMA

Filename and path: SHE – Life Sciences – MDFRC > Projects > GBCMA > 639 Pygmy Perch Vs Mosquitofish

Author(s): Rick Stoffels and Kyle Weatherman

Author affiliation(s): CSIRO and MDFRC

Project Manager: Rick Stoffels

Client: GBCMA

Project Title: Will heat and hypoxia in floodplain wetlands give alien mosquitofish (*Gambusia holbrooki*) the edge over endemic pygmy perch (*Nannoperca australis*)?

Document Version: Final

Project Number: M/BUS/639

Purchase Order: PPU22943-2

Finalised December 2015

Acknowledgements:

This work was funded by the Goulburn Broken Catchment Management Authority (GBCMA) from funding supplied by MDBA under The Living Murray Initiative, and funding by the Yorta Yorta Nations Aboriginal Corporation, with in-kind contributions from MDFRC. The Living Murray is a joint initiative funded by the New South Wales, Victorian, South Australian, Australian Capital Territory and Commonwealth governments, coordinated by the Murray–Darling Basin Authority.

We thank Keith Ward (GBCMA), Neil Morris (Yorta Yorta), Mick Caldwell (Parks Victoria) and Zeb Tonkin (Arthur Rylah Institute) for their help with site selection at Barmah Forest. In particular, we thank Mick Caldwell for his time spent showing us potential sites within the Forest. We also thank Simon Mom and the Yorta Yorta people for their assistance with the completion of fieldwork.

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Executive summary

The **objectives** of the present work were:

- Determine the comparative resistance of pygmy perch (*Nannoperca australis*) and mosquitofish (*Gambusia holbrooki*) to heat waves (the combined effects of heat and hypoxia).
- Determine the relative swimming capacity of pygmy perch and five other native small-bodied fishes of the Murray-Darling Basin. Swimming capacity is a component of a species' resilience to localised disturbance; it's capacity to 'bounce back' after localised reductions in abundance.
- Undertake a field survey of Barmah Forest wetlands to determine whether pygmy perch are present within Barmah, following strong reductions in population size during the Millennium Drought.

Resistance: responses to heat and hypoxia:

- Mosquitofish exhibited significantly greater resistance to environmental hypoxia at 25 °C than pygmy perch. Indeed, resistance indices indicated that mosquitofish are 2-3 times more resistant to hypoxia at 25 °C than mosquitofish.
- A 4 °C increase in temperature has minimal impact on the high resistance of mosquitofish to hypoxia, but significantly and strongly erodes the resistance of pygmy perch to low dissolved oxygen.
- Any environmental change that results in water temperatures exceeding ~29 °C and/or environmental hypoxia (low dissolved oxygen) will result in a less desirable fish assemblage; one where pygmy perch may be driven locally extinct, but where the invasive mosquitofish persist, and possibly thrive.

Resilience: capacity for endurance swimming:

- While adult pygmy perch showed intermediate capacity to swim at high water velocities, they proved to have very low swimming efficiency. Indeed, of the six species tested, pygmy perch exhibited the least efficient swimming at their optimal cruising speed, and their optimal cruising speed was the second slowest of all species studied (only flathead gudgeon were slower).
- These experiments add to other lines of evidence supporting the idea that pygmy perch are relatively poor dispersers. Inasmuch as their resilience is shaped by adult dispersal, they are a species with poor resilience to localised declines.

Field survey:

- No pygmy perch were detected in wetlands of the Barmah Forest during Winter 2015. This does not necessarily mean that pygmy perch were not present in Barmah wetlands; they may be present in low numbers, but our sampling effort was not sufficiently intensive to detect them.
- Carp-gudgeon dominated the fish assemblage.

Implications for management of floodplain habitat:

Water quality on floodplains

- This work adds strong scientific support to the need to frequently water floodplains to maintain high water quality in wetlands.

- Floodplains need to be flooded frequently to minimise the likelihood of environmental hypoxia and heat at all scales. At broad scales the impact of flood frequency on hypoxic blackwater flows are relatively well understood and appreciated. At smaller scales (e.g. individual wetlands), the impacts of watering frequency—hence depth and volume—on temperature and dissolved oxygen dynamics are less well understood.
 - *Knowledge need:* There is a need to better understand how watering strategies affect temperature and dissolved oxygen dynamics in managed wetlands. There is surprisingly little scientific literature on this matter.
- We speculate that one of the key benefits submerged and emergent macrophytes provide to pygmy perch (and perhaps other native fish) is to lower water temperatures in wetlands through shading. A literature search on this topic—the effect of aquatic plants on thermal dynamics in wetlands—yielded essentially no scientific papers.
 - *Knowledge need:* We need an improved understanding of how aquatic plants affect thermal dynamics in wetlands. This understanding may open an avenue for managing threatened species, through regulating the effects of heat waves.

Manage localities within the context of a regional, whole-of-catchment strategy

- To build regional resilience of populations, individual localities like Barmah should not be managed in isolation, but within the context of a regional, whole-of-catchment strategy, such that a greater diversity and area of river-floodplain habitat is protected and restored.
- An approach towards building regional resilience of pygmy perch might include:
 1. Identify likely source populations throughout the Goulburn-Broken catchments.
 - *Knowledge need:* This would involve an extensive scientific survey, specifically targeting pygmy perch throughout the catchment.
 2. Link regional distribution (from (1)) with GIS layers and coarse habitat maps to infer land-use and habitat characters that might promote local source populations.
 - *Knowledge need:* Overlapping habitat mapping with survey in (1) and couple with species-distribution modelling to infer land-use and habitat drivers of regional distribution.
 3. Once drivers of local source populations have been identified (from (1) and (2)) protect and restore those drivers in stream and river segments most likely to yield outcomes for pygmy perch.
 - This is exclusively a management activity, but its success hinges on a scientific understanding of the population at the catchment scale.
 - A further scientific contribution to this management activity could be optimisation of restoration resources to maximise outcomes for any given level of financial investment.
 4. Identify in-channel features that facilitate the dispersal of pygmy perch throughout the catchment.
 - *Knowledge need:* What in-stream habitat features facilitate the dispersal of pygmy perch (and other threatened fauna) among key source populations? (Elements of this question may be answered by (2) above.)
 5. Protect and restore in-stream habitat that promotes movement of pygmy perch throughout catchment.

6. Monitor outcomes as part of adaptive management of small-bodied fish diversity within the Goulburn-Broken Catchment.

Active management of species with low resilience.

- Given the current high levels of fragmentation of fish habitat, populations of pygmy perch on floodplains might need very active management towards securing their local persistence.
- Active localised management of fishes in Barmah with low resilience will require:
 - A solid understanding of their habitat requirements and key threats (e.g. mosquitofish abundance);
 - Knowledge about the status of their population, habitat and threats each year;
 - The resources to actively maintain requirements on an annual basis (e.g. pumping infrastructure) while reducing threats (e.g. carp screens).

1 Introduction

'Resistance' and 'resilience' have proved to be very useful ecological concepts in the study of how environmental change affects the long-term persistence of a species within a region. Both concepts are specific to a species and an environmental variable (Carpenter et al. 2001, West and Salm 2003, Allison 2004). The *resistance* of, say, Species A to temperature, is a measure of how warm the temperature of a locality needs to get before Species A is driven locally extinct. The *resilience* of that species to temperature is a measure of how quickly that species rebuilds a viable population in that locality, after the localised extinction (Stoffels 2015).

The recent Millennium Drought has focused the attention of ecologists and managers on fish resistance-resilience to drought (Bond et al. 2008). Numerous indigenous species have suffered substantial declines. The southern pygmy perch, *Nannoperca australis*, is one such species. Recent observations of floodplain pygmy perch populations in NE Victoria have raised at least two questions concerning their resistance-resilience ecology.

1. What is the resistance of the threatened pygmy perch to heat-waves and how does their resistance compare to that of the mosquitofish? In a survey of wetlands of the Killawarra Forest (Ovens floodplain) in 2014, pygmy perch were only detected in one wetland. Pygmy perch were moderately abundant in this wetland at the beginning of summer, but at the end of summer, following repeated heat-waves, we could no longer detect them. By contrast, the invasive mosquitofish, *Gambusia holbrooki*, persisted in this wetland through the heat-wave. Logged temperature and dissolved oxygen (DO) data showed that, during the peak of one heat wave, surface temperatures exceeded 30 degrees, but bottom DO levels fell below 1.7 mg L⁻¹, potentially creating a strong vertical compression of productive habitat. Perhaps pygmy perch are more vulnerable than mosquitofish to poor water quality on floodplains.

The question posed at the beginning of the previous paragraph has relevance to management of environmental water allocations (EWAs) since frequency of floodplain inundation has a strong influence on water quality (Hladyz et al. 2011, Whitworth et al. 2012). Understanding the comparative resistance of endemic and invasive species may improve our ability to predict the effects of changes in water quality on the relative abundance of desirable and undesirable species (Stachowicz et al. 2002, Sorte et al. 2010, Zerebecki and Sorte 2011, Fey and Cottingham 2012). In turn, this predictive understanding may help us prioritise management objectives (Kolar and Lodge 2001).

2. If driven locally extinct within a floodplain reserve (e.g. Barmah-Millewa), what is the capacity of pygmy perch to disperse from other localities towards recolonising the reserve and re-establishing a local population there? Pygmy perch have suffered substantial declines on floodplains in south-eastern Australia, and despite the fact that the drought broke in 2010, we have not observed significant population recovery on floodplains (Stoffels and Weatherman 2014). Does this mean that pygmy perch have low resilience to local perturbation? How does their dispersal capacity (part of resilience) compare with that of other small-bodied fishes?

An improved understanding of dispersal capacity is required when making decisions concerning resource allocations in a river-floodplain landscape. Species with poor dispersal capacity are likely to be more susceptible to fragmentation of floodplain habitats than those with higher dispersal capacity. If these poor dispersers are also particularly dependent on floodplain habitats, then their habitat requirements should feature heavily in decisions concerning EWAs, as they may not be easy to recover if driven locally extinct.

The objectives of the present project were as follows:

1. **Determine the comparative resistance of pygmy perch and mosquitofish to heat waves.**

Specifically, we sought answers to the following questions:

- a. What are the critical oxygen tensions (P_{crit}) of pygmy perch and mosquitofish? P_{crit} has been espoused as an indicator of the relative resistance of fishes to environmental hypoxia (low dissolved oxygen) (Farrell and Richards 2009, Mandic et al. 2009); the lower a species' P_{crit} , the more resistant that species is to environmental hypoxia (but see Stoffels 2015). Increased water temperature holds less dissolved oxygen and also increases the oxygen demand of the biota, so the ability to resist environmental hypoxia is a key component of a species resistance to heat waves.
- b. How does the pygmy perch's capacity for metabolic depression during hypoxia compare with that of the mosquitofish? Fish that are particularly resistant to hypoxia may exhibit the capacity to reduce their metabolic rate—hence oxygen requirements—as hypoxia ensues (Nilsson and Renshaw 2004, Bickler and Buck 2007, Stoffels 2015).
- c. How does temperature affect the comparative resistance of pygmy perch and mosquitofish to hypoxia (as measured through P_{crit} and metabolic depression)? Certain studies have demonstrated that pygmy perch are moderately resistant to hypoxia (low DO) at cool water temperatures (McMaster and Bond 2008), but how does heat interact with their physiology to affect resistance to hypoxia? Basic principles of physiology indicate that warmer water temperature should greatly reduce fish resistance to hypoxia, but by how much in pygmy perch? Is our perception of acceptable water quality biased by experiments that do not incorporate interactive effects of multiple stressors (e.g. heat AND DO) (Claireaux and Lagardere 1999, Claireaux et al. 2000)?

2. **Determine the endurance swimming capacity of pygmy perch relative to other small-bodied fish species of the Murray-Darling Basin.** We sought answers to the following questions:

- a. How does the cost of transport (COT)—hence swimming efficiency—of pygmy perch compare with that of rainbowfish (*Melanotaenia fluviatilis*), carp-gudgeon (*Hypseleotris* sp.), purple-spotted gudgeon (*Mogurnda adspersa*), unspotted hardyhead (*Craterocephalus stercusmuscarum fulvus*) and flathead gudgeon (*Philypnodon grandiceps*)? Given pygmy perch is a benthopelagic species we propose it will have an intermediate COT comparable with that of a species like carp-gudgeon.

3. **With the assistance of Yorta Yorta, undertake a survey of Barmah Forest wetlands to**

determine whether pygmy perch are present on the floodplain. Intensive field surveys during 2014 showed that pygmy perch were very rare or absent from Barmah Forest wetlands. We hypothesise that pygmy perch have low resilience to localised disturbance and, therefore, that pygmy perch will not be detected during 2015.

2 Materials and Methods

2.1 Resistance: metabolic response to heat and hypoxia

Computerised, intermittent-flow respirometry was used to estimate metabolic rates of fishes (Steffensen 1989). Each respirometer consists of a glass respiration chamber connected to an oxygen sensor, a flush circuit and a recirculation circuit. Fibre-optic oxygen sensing was used (PreSens, Regensburg, Germany), and a housing unit ensured fibre cables (bare tip) were held alongside sensor spots within the respiration chambers (Loligo Systems, Tjele, Denmark). Each respirometer was immersed within an ‘ambient tank’ containing water whose temperature and dissolved oxygen (DO) concentrations were monitored and controlled by computers (Loligo Systems, Tjele, Denmark). The measurement circuit of the respirometer enabled recirculation of water during intermittent measurement loops, while the flush circuit enabled flushing of respiration chambers with water from the ambient tank in between measurement loops. Masterflex peristaltic pumps were used for circulation of water through both these circuits, and Masterflex Tygon CHEM tubing was used for its extremely low oxygen permeability (Masterflex, John-Morris Scientific, Chatswood, NSW, Australia). Each measurement loop consisted of three ‘phases’: a ‘flush’, ‘wait’ and ‘measurement’ phase. The flush and measurement phases are self-explanatory; the wait phase enabled stabilisation of the slope of the line describing change of DO within the chamber. The flush, wait and measurement phases for all three species were 180 s / 120 s / 240 s. Blanks were run to control for any background respiration. The entire respirometry apparatus was situated behind a screen to minimise disturbance from observers.

For estimation of P_{crit} and metabolic depression variables, oxygen consumption rates (\dot{M}_{O_2} , mg O₂ kg⁻¹ h⁻¹), were measured over a normoxic, hypoxic and EPHOC period (Excess Post-Hypoxic Oxygen Consumption, following Svendsen et al. 2012). Fish were placed within chambers at 12:00 on day 1, after which \dot{M}_{O_2} was recorded in water with a DO concentration corresponding to 100% air-saturation (20 kPa) over a night-day-night sequence. \dot{M}_{O_2} measurements from the first 12 h were excluded as effects of fish stress might have biased estimates of RMR (see below). Following this 12 h acclimation period, \dot{M}_{O_2} was collected over a ~ 28 h period to calculate the SMR and RMR of individual i (SMR_i and RMR_i ; A minimum of 250 \dot{M}_{O_2} measurements were made during the normoxic period). SMR_i and RMR_i were calculated as the mean of the lowest 10%, and the mean (respectively) of the \dot{M}_{O_2} values from the ~ 28 h normoxic period. Given RMR was calculated over ~ 28 h—hence a day-night sequence—it is unlikely any interspecific differences in diurnal activity patterns biased inferences pertaining to RMR among species. At approximately 09:00 on day 3, hypoxia was induced by bubbling N₂ gas into an O₂ stripping column connected to the ambient tank. Oxygen tension was decreased at a rate of 1 kPa every 18 min until 1.5 kPa, after which ambient oxygen tension was maintained at 1.5 kPa (+/- 0.25 kPa) until a fish lost equilibrium or 2h elapsed. A minimum of 40 \dot{M}_{O_2} measurements were made during gradual hypoxia. Thus the hypoxic period ended between 14:00 and 17:00 on day 3 of each trial, after which time EPHOC began. As soon as a fish lost equilibrium or 2h elapsed ambient oxygen tension was rapidly restored to 6 kPa, then steadily increased at a rate of ~3.6 kPa h⁻¹. A minimum of 100 \dot{M}_{O_2} measurements were made during EPHOC. Five replicate trials were conducted for each species at each of two temperatures: 25 and 29 °C.

2.2 Resilience: capacity for endurance swimming

A Blazka-type, 1.5 L mini-flume was used for swimming energetics experiments (Beamish 1978). Details of the design can be obtained from www.loligosystems.com (Loligo Systems, Tjele, Denmark). Black plastic was wrapped around the upper 3rd of the swimming section, which encouraged fish to swim against the current. Water velocity was calibrated against voltage of the motor using dye and a high-speed camera (Optronis, Kehl, Germany). Plastic honeycomb was inserted into both ends of the inner flume to promote micro-turbulent flow. The flume was immersed in a bath whose water was air-saturated, filtered and maintained at 25 °C ± a range of 0.2 °C. DO tension was measured using a fibre optic dipping probe inserted into the end of the flume (PreSens, Regensburg, Germany). The entire swim flume was situated behind a screen to avoid disturbance from observers. Fish behaviour was monitored using a camera mounted above the flume (uEye, Imaging Development Systems, Germany).

Intermittent-flow respirometry was used to determine \dot{M}_{O_2} as a function of water velocity. Individuals used for static respirometry were not reused for swimming respirometry. Fish were placed in the swim flume on the afternoon before each swim trial, and allowed to acclimate for 2 h before a practice swim, after which fish were then allowed to further acclimate to the flume overnight at a velocity of 0.5 body lengths per second (BL s⁻¹). During the swim trial, each measurement loop was 8 min in duration (including flush, wait and measurement phases; see Static Respirometry) for all species. Velocity was increased at a rate of 0.5 BL s⁻¹ every 16 min, thus enabling two 8 min measurement loops per velocity. Velocity continued to increase at this rate until the fish became exhausted and rested against the downstream honeycomb baffle for longer than 5 s.

Table 1. Description of floodplain sites and number of small-mesh fyke nets at Barmah National Park. Site coordinates recorded using GDA map datum in UTM UPS position format. Australian National Aquatic Ecosystem (ANAE) classification is a broad-scale and nationally consistent scheme used for classifying aquatic ecosystems, and was determined in ESRI ArcMap 10.2 using the 'Victorian Wetland Environments and Extent – up to 2013' spatial data file, which was sourced from the Victorian Government Data Directory website (<http://www.data.vic.gov.au>).

Site	Site name	Coordinates	ANAE classification	Number of small-mesh fyke nets set		
				Summer 2014	Autumn 2014	Winter 2015
1	Cucumber Gully at Sand Ridge Track	55 H 319561 E 6021599 N	2. Freshwater meadow	7	6	7
2	Paddy Farrel Lagoon	55 H 323333 E 6029974 N	4. Deep freshwater marsh	7	6	7
3	Keyes Point (West) #1	55 H 324860 E 6026700 N	3. Shallow freshwater marsh	6	7	0 (dry)
4	Keyes Point (East)	55 H 326172 E 6027661 N	3. Shallow freshwater marsh	7	6	7
5	Gulf Creek (South) at Four Mile Track	55 H 328442 E 6028913 N	3. Shallow freshwater marsh	7	6	7
6	Unnamed near Sandy Crossing at Four Mile Track	55 H 329654 E 6028507 N	2. Freshwater meadow	6	7	0 (dry)
7	Unnamed at Hughes Track	55 H 330354 E 6026265 N	2. Freshwater meadow/3. Shallow freshwater marsh	6	1 (nearly dry)	0 (dry)
8	Pigsty Lagoon at Long Plain Track	55 H 331369 E 6031681 N	2. Freshwater meadow/3. Shallow freshwater marsh	7	6	2 (nearly dry)
9	Tullah Creek at Nicks Crossing at Gulf Track	55 H 330250 E 6024200N	2. Freshwater meadow/3. Shallow freshwater marsh	0	0	7
10	Gulf Creek (North) at Four Mile Track	55 H 328650 E 6029150 N	3. Shallow freshwater marsh	0	0	7

11	Keyes Point (West) #2	55 H 325080 E 6026493 N	2. Freshwater meadow	0	0	3 (nearly dry)
12	Tullah Creek Trib. near Tarma Crossing at Gowers Track	55 H 323065 E 6024677 N	2. Freshwater meadow	0	0	7
13	Little Budgee Creek at Sand Ridge Track	55 H 319865 E 6026255 N	2. Freshwater meadow	0	0	10

2.3 Field survey: small-bodied fish

The small-bodied fish communities of the Murray River floodplain at Barmah National Park were sampled across 13 sites during 3 occasions between summer 2014 and winter 2015 (Table 1; Figure 1). This included the sampling of 8 sites during summer 2014 and autumn 2014, and the sampling of 10 sites during winter 2015. Additional sites were sampled in winter 2015 since 3 sites that were sampled in 2014 were dry.

Sites were chosen to represent the diversity of wetland types present at Barmah Forest, comprising a gradient in size, shape and macrophyte cover. Small-bodied fish were sampled using double-winged small-mesh fyke nets (<2 mm stretched mesh, each wing 2.00 x 1.00 m; first supporting hoop $\varnothing = 0.40$ m). Small-mesh fyke nets were set randomly at each site between 0700 – 1600 hours, usually for 3 hours. Six or seven small-mesh fyke nets were set per site. All fish captured were identified and enumerated, before being released back into the water.

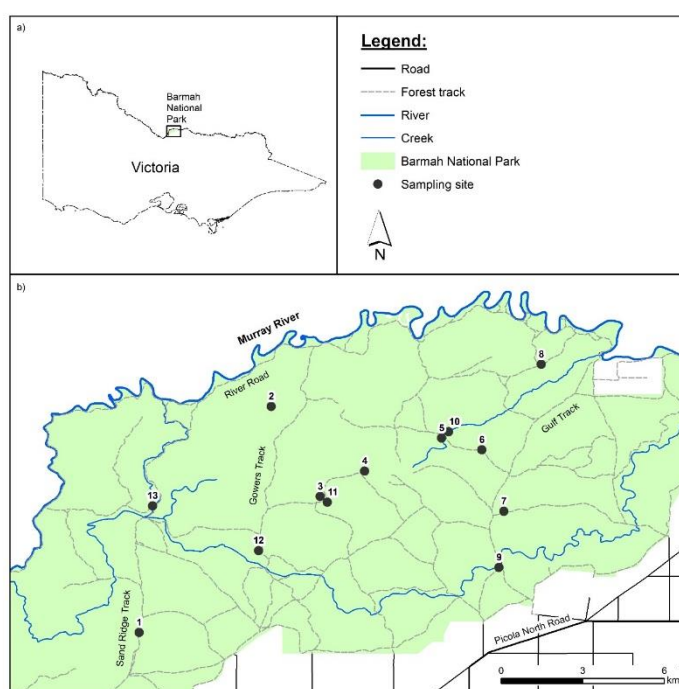


Figure 1. Map (a) Victoria showing the location of Barmah National Park; and (b) floodplain sites at Barmah National Park. Map created using ESRI ArcMap 10.2. Spatial data sourced from Victorian Government Data Directory website (<http://www.data.vic.gov.au/>).

2.4 Data analysis

Oxygen consumption rate, \dot{M}_{O_2} (mg O₂ kg⁻¹ h⁻¹), was calculated using:

$$\dot{M}_{O_2} = -(\Delta O_f - \Delta O_b) V_{resp} \alpha B^{-1} \quad (1)$$

where ΔO_f is the rate of change in oxygen tension (kPa h⁻¹) due to fish respiration, ΔO_b is the rate of change in oxygen tension due to background (microbial) respiration (S1 protocol), V_{resp} is the volume of the respirometer (L; minus the volume of the fish, measured by displacement in a measuring cylinder), α is the solubility of oxygen in the water at a known temperature and salinity (mg O₂ L⁻¹ kPa⁻¹) and B is the mass of the individual (kg). The following equation was used to standardise metabolic rates to a common mass (S2 protocol):

$$\dot{M}_{O_2,i,t} = \dot{M}_{O_2,i,o} (B_t / B_i)^\beta \quad (2)$$

where $\dot{M}_{O_2,i,o}$ and $\dot{M}_{O_2,i,t}$ are the observed and standardised mass-specific metabolic rates of individual i , respectively, B_i and B_t are the observed and standardised masses (= 3 g here; the mean mass of all individuals used in static respirometry, calculated across species, to the nearest gram), while β is the mass-specific allometric scaling exponent (Dwyer et al. 2014). We assumed $\beta = -0.247$ for all species based on the work of Downs et al. (2008).

P_{crit} values were determined using the algorithm of Yeager and Ultsch (1989; henceforth YU algorithm), which permits an objective, mathematically-explicit, standardised method for determining P_{crit} . Two estimates of P_{crit} were calculated for each individual: (1) $P_{crit,YU}$, the P_{crit} of Yeager and Ultsch (Yeager and Ultsch 1989); (2) $P_{crit,SMR}$, determined by the point of intersection between the steep oxyconformation zone and the straight line defined by the SMR of that individual. For both $P_{crit,YU}$ and $P_{crit,SMR}$ the parameters of the line defining the oxyconformation zone were estimated using the approach described in Yeager and Ultsch (Yeager and Ultsch 1989), hence no subjective 'eyeballing' of the data was required.

Individual i 's magnitude of metabolic reduction during hypoxia, RM_i , was calculated as $[(SMR_i - M_{O_2,min,i}) \times SMR_i^{-1}] \times 100$, where $M_{O_2,min,i}$ is the mean of the three lowest \dot{M}_{O_2} values obtained during the hypoxic period (invariably at the end of that period, during maximum reduction). Reduction capacity of individual i , RC_i , was measured as the logarithm of the ratio of two areas:

$$RC_i = \ln \left(\frac{A_{r,i}}{A_{e,i}} \right) \quad (3)$$

where $A_{r,i}$ is the area between the depressed metabolic rate curve and either the SMR (RC_{SMR}) or RMR (RC_{RMR}) of that individual during gradual hypoxia, and $A_{e,i}$ is EPHOC of that individual following hypoxia (Stoffels 2015). When estimating the areas for individual i , the first step was to fit a spline smoother, S_i , to its \dot{M}_{O_2} time series. The smoothing statistic was fixed at 0.9 for all individuals.

We tested for interspecific differences in SMR, RMR, MMR, AS, $P_{crit,YU}$, $P_{crit,SMR}$, RM, RC_{SMR} and RC_{RMR} using one-way ANOVA.

Corrected swimming speeds, U_F , were obtained using:

$$U_F = U_T(1 + \varepsilon_S) \quad (6)$$

(Bell and Terhune 1970), where U_T is the velocity in the flume without fish and ε_S is the fractional error due to solid-blocking (all velocities, U , are in units of BL s^{-1}). The solid-blocking error is found using:

$$\varepsilon_S = \tau\gamma(A_O \times A_T^{-1})^{3/2} \quad (7)$$

where τ is a dimensionless factor depending on flume cross-section shape, and γ is a shape factor for the fish. Here, $\tau = 0.8$ for any sectional shape and $\gamma = 0.5$ (body length / body thickness) (Bell and Terhune 1970). Body thickness was calculated as the average of fish depth and width (Korsmeyer et al. 2002). A_O is the maximal cross sectional area of the fish (assumed to be an ellipse), and A_T is the cross sectional area of the flume.

The critical swimming velocity, U_{crit} , was calculated as

$$U_{crit} = U_{end-1} + \frac{t_{end}}{t_U} U_{end} \quad (8)$$

where U_{end} is the velocity at which the fish becomes exhausted, t_{end} is the time swum at U_{end} prior to exhaustion, t_U is the standard time exposed to a velocity increment (16 min in our case), and U_{end-1} is the velocity immediately prior to the one at which exhaustion occurred (Brett 1964).

Gross COT (Joules km^{-1}) was modelled using (Videler and Nolet 1990):

$$COT_{gross} = aU^{-1} + bU^{c-1} \quad (9)$$

where a , b and c are parameters. Oxygen consumption rates were converted to Joules by, first, converting to calories using the oxycaloric average of 3.22 cal / mg O_2 then, second, converting calories to Joules assuming 1 cal = 4.184 J. Some calculus on Eqn 9 yields optimum swimming velocity:

$$U_{opt} = \left(\frac{a}{b(c-1)} \right)^{1/c} \quad (10)$$

which, when substituted back into Eqn 9 gives the cost of transport at U_{opt} , COT_{opt} (Joules km^{-1}).

Non-linear mixed-effects regression was used to model COT_{gross} as a function of U ; a method appropriate for the repeated measures nature of swim flume experiments (Lindstrom and Bates 1990). In using this approach each parameter in Eqn 9 can be decomposed into a fixed population effect—assumed to be the same each time the population is sampled—and a random effect of the individual fish—sample-dependent random variables. Although the population parameters were of primary interest for modelling COT_{gross} , the individual-specific parameter estimates for Eqn 9 were used to solve for individual-specific values of U_{opt} and COT_{opt} which, in turn, could be analysed using one-way ANOVA. All regression was carried out using MATLAB's Statistics Toolbox.

Field survey data is presented as catch-per-unit-effort (CPUE; individuals per net per hour) and presented as tables.

3 Results

3.1 Resistance: metabolic response to heat and hypoxia

Mosquitofish exhibited significantly greater resistance to heat and hypoxia than pygmy perch. Mosquitofish were generally more resistant to environmental hypoxia at 25 °C, then as temperature increased to 29 °C, pygmy perch suffered a significantly greater reduction in resistance to hypoxia than mosquitofish. As temperature increased from 25 to 29 °C mosquitofish exhibited no significant difference in P_{crit} , while that of pygmy perch increased significantly and strongly (Two-way ANOVA; Figure 2A). Similarly, while pygmy perch lost equilibrium at a mean oxygen tension of 1.28 kPa at 25 °C, at 29 °C they lost equilibrium at 2.08 kPa on average, further indicating that an increase in 4 °C from 25 °C significantly erodes resistance of pygmy perch to hypoxia (One-tailed t-test; Figure 2B). Mosquitofish did not lose equilibrium in any treatment, again confirming their superior resistance to heat waves (Figure 2B).

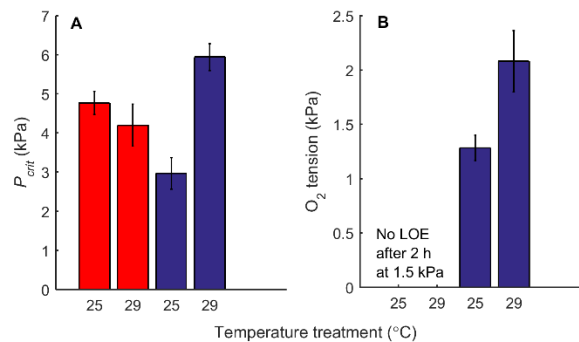


Figure 2. The mean (\pm SE) critical oxygen tension (P_{crit}) of mosquitofish (*G. holbrooki*; red) and pygmy perch (*N. australis*; blue), and the mean (\pm SE) oxygen tension at which loss of equilibrium (LOE) was observed in pygmy perch, at 25 and 29 °C. Note that mosquitofish did not lose equilibrium after 2 h at 1.5 kPa. Certain researchers have suggested that a high P_{crit} indicates low resistance to hypoxia. The lower the oxygen tension at which a fish loses equilibrium, the greater the resistance to hypoxia.

Mosquitofish exhibited significantly greater magnitude of, and capacity for, metabolic reduction than pygmy perch, indicating greater resistance to hypoxia at both 25 and 29 °C (Two-way ANOVA main effect of species; Figure 3). Although there was a trend for increasing water temperature to erode the capacity for metabolic reduction—hence resistance to heat waves—in both mosquitofish and pygmy perch (Figure 3C and D), we had insufficient power to demonstrate a significant impact of temperature on metabolic reduction; further replicates are required. The impact of temperature on reduction magnitude was species-specific. There was evidence that a 4 °C increase in temperature is associated with increased magnitude of metabolic reduction in mosquitofish, but not pygmy perch (significant interaction term, two-way ANOVA; Figure 3B). Overall, the metabolic reduction indices indicate mosquitofish have greater resistance against hypoxia than pygmy perch.

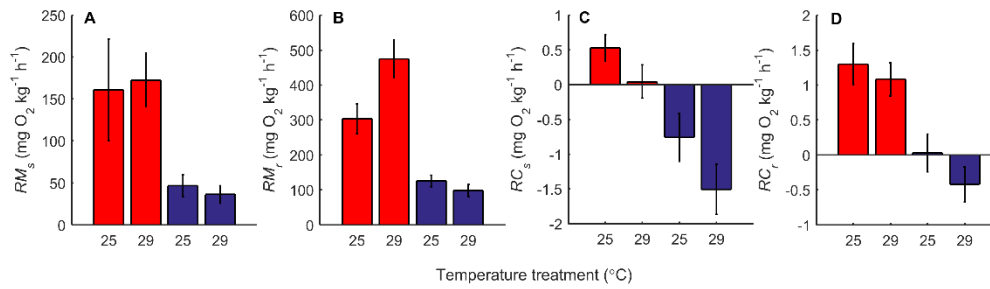


Figure 3. Metabolic reduction (another index of resistance) of mosquitofish (*G. holbrooki*; red) and pygmy perch (*N. australis*; blue) to hypoxia at 25 and 29 °C. Resistance indices presented are mean (+/- SE) magnitude of reduction below standard (RM_s ; A) and routine (RM_r ; B) metabolic rates; and capacity for reduction below standard (RC_s ; C) and routine (RC_r ; D) metabolic rates. For plots A – D the higher the value the greater the resistance to hypoxia.

3.2 Resilience: capacity for endurance swimming

There were strong and significant ($P < 0.001$; ANOVA) differences among species in all swimming performance metrics (Figure 4). Only the notable aspects of pygmy perch swimming performance relative to other species will be covered here.

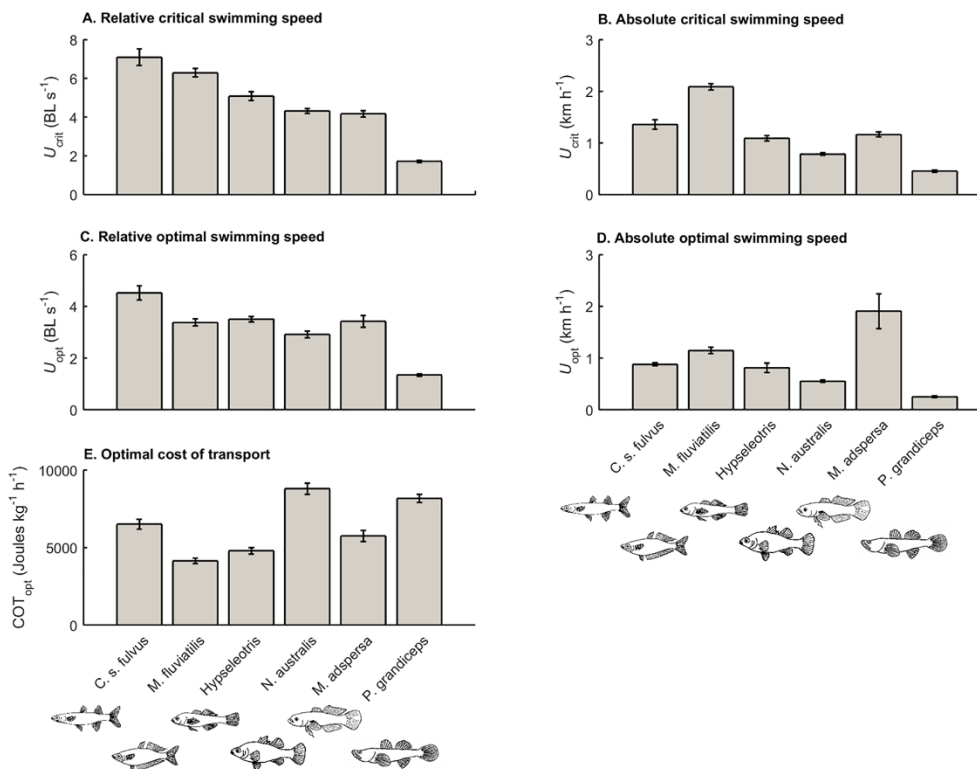


Figure 4. Mean endurance swimming performance of six species of native small-bodied fish. Means (+/- SE) are presented for relative critical swimming speed (A); absolute critical swimming speed (B); relative optimal swimming speed (C); absolute optimal swimming speed (D) and the optimal cost of transport (E). Of note: *pygmy perch* have a very low optimal absolute swimming speed, and they exhibited the greatest cost of transport (least efficient swimmers, of the six species tested). Species: hardyhead (*Craterocephalus*

stercusmuscarum fulvus), rainbowfish (*Melanotaenia fluviatilis*), carp-gudgeon (*Hypseleotris* sp.), pygmy perch (*Nannoperca australis*), purple-spotted gudgeon (*Mogurnda adspersa*) and flathead gudgeon (*Philypnodon grandiceps*).

With respect to relative critical and optimal swimming speed—where speed is measured in units of body-lengths per unit time—pygmy perch exhibited intermediate performance as expected (Figure 4A and B). In terms of absolute speed/distance, however, pygmy perch exhibited comparatively low critical and optimal swimming speeds. Most importantly, pygmy perch were the least efficient swimmer of the six species tested. That is, pygmy perch use significantly greater quantities of energy when swimming than the other five species (Figure 5).

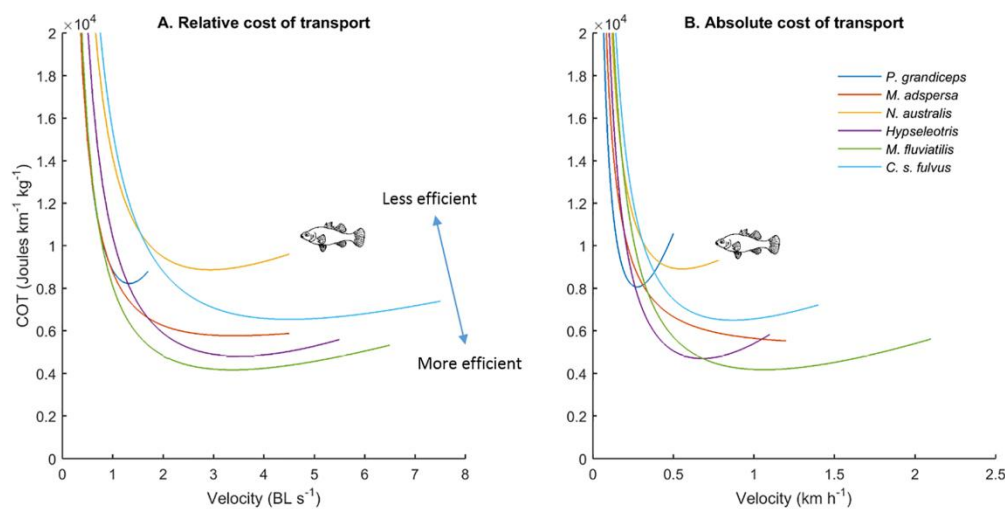


Figure 5. Relative (A) and absolute (B) cost-of-transport (COT) functions for six species of small-bodied fish of the Murray-Darling Basin. The functions indicate how much energy, on average, each species expends swimming at a certain velocity at 25 °C. The pygmy perch COT function is highlighted, showing they are among the least efficient swimmers.

3.3 Field survey: small-bodied fish

The small-bodied fish community of the floodplain sites at Barmah National Park comprised of three native species (carp-gudgeon, flathead gudgeon and smelt) and four alien species across the three sampling periods (goldfish, carp, mosquitofish and weatherloach; Table 3 & 4). However, flathead gudgeon were detected during summer 2014 only, and carp were not detected during winter 2015. Southern pygmy perch were not detected at any of the sites during any of the sampling periods. Data for the small-bodied fish communities by site and sampling period are presented in Appendix 1.

Table 2. Mean CPUE (individuals net⁻¹ h⁻¹) calculated across all floodplain sites at Barmah National Park. * Alien species.

Species name	Common name	Mean CPUE across all sites (individuals net ⁻¹ h ⁻¹)		
		Summer 2014 Sites 1 - 8 (n = 8)	Autumn 2014 Sites 1 - 8 (n = 8)	Winter 2015 Sites 1, 2, 4, 5, & 8 - 13 (n = 10)
<i>Hypseleotris</i> spp.	Carp-gudgeon	15.748	15.755	7.601
<i>Philypnodon grandiceps</i>	Flathead gudgeon	0.007	0.000	0.000
<i>Retropinna semoni</i>	Smelt	1.081	0.376	0.470
<i>Carassius auratus</i> *	Goldfish*	2.805	1.015	0.046
<i>Cyprinus carpio</i> *	Carp*	2.086	1.745	0.000
<i>Gambusia holbrooki</i> *	Mosquitofish*	47.934	101.175	1.006
<i>Misgurnus anguillicaudatus</i> *	Weatherloach*	0.314	0.664	0.022

4 Discussion

The implications of this work for management of floodplain wetlands can be summarised under two statements: (1) Pygmy perch are less resistant to low water quality than mosquitofish; (2) Adult pygmy perch have poor dispersal capacity.

4.1 Pygmy perch are less resistant to low water quality than mosquitofish

The experiments conducted here indicate that mosquitofish are much more resistant to low water quality than pygmy perch. Specifically, mosquitofish show significantly greater resistance to heat and hypoxia than the threatened pygmy perch. We present evidence demonstrating that a 4 °C increase in temperature has minimal impact on the high resistance of mosquitofish to hypoxia, but significantly and strongly erodes the resistance of pygmy perch to low dissolved oxygen.

Clearly, any environmental change that results in water temperatures exceeding ~29 °C and/or environmental hypoxia (low dissolved oxygen) will result in a less desirable fish assemblage; one where pygmy perch may be driven locally extinct, but where the invasive mosquitofish persist, and possibly thrive. With respect to management of floodplain wetlands, the following suggestions can be offered:

1. Floodplains need to be flooded frequently to minimise the likelihood of environmental hypoxia and heat at all scales. This suggestion is not novel, but the work conducted here adds further scientific evidence of the detrimental consequences of failing to manage flows to sustain high water quality on floodplains. At broad scales the impact of flood frequency on hypoxic blackwater flows are relatively well understood and appreciated (Whitworth et al. 2012), so we offer no further commentary here. At smaller scales (e.g. individual wetlands), the impacts of watering frequency—hence depth and volume—on temperature and dissolved oxygen dynamics are less well understood.

- **Knowledge need:** There is a need to better understand how watering strategies affect temperature and dissolved oxygen dynamics in managed wetlands. There is surprisingly little scientific literature on this matter.
- 2. We speculate that one of the key benefits submerged and emergent macrophytes provide to pygmy perch (and perhaps other native fish) is to lower water temperatures in wetlands through shading. A literature search on this topic—the effect of aquatic plants on thermal dynamics in wetlands—yielded essentially no scientific papers.
 - **Knowledge need:** We need an improved understanding of how aquatic plants affect thermal dynamics in wetlands. This understanding may open an avenue for managing threatened species, through regulating the effects of heat waves.

4.2 Adult pygmy perch have poor dispersal capacity

Efficiency of swimming makes a significant contribution to the capacity for adult fishes to disperse (Nathan et al. 2008). At the beginning of this project we expected the benthopelagic pygmy perch to have intermediate dispersal capacity, somewhere between ‘fast’ species like the pelagic hardyhead and rainbowfish, and ‘slow’ species like the benthic purple-spotted and flathead gudgeons (Dwyer et al. 2014, Stoffels 2015). Contrary to this expectation, pygmy perch exhibited the least efficient swimming, in that they utilised the greatest amount of energy per unit distance travelled, even when travelling at their most efficient speed. The data presented here accord well with other recent studies inferring pygmy perch have low dispersal capacity (Cook et al. 2007, Dexter et al. 2014). This low swimming efficiency will erode their resilience to localised disturbances on floodplains.

If pygmy perch have low resilience, then how should floodplains be managed to build the resilience of pygmy perch to environmental change? First, individual localities like Barmah should be managed not in isolation but within the context of a regional, whole-of-catchment strategy, such that a greater diversity and area of river-floodplain habitat is protected and restored. Second, given the current high levels of fragmentation of fish habitat, populations of pygmy perch on floodplains might need very active management towards securing their local persistence.

4.2.1 *Manage localities within the context of a regional, whole-of-catchment strategy*

Currently river-floodplain management—flow management in particular—hinges on the validity of the ‘string of beads’ approach, whereby small, discrete parcels of floodplain are set aside for restoration and/or preservation (Bond et al. 2014, Stoffels et al. 2014, Humphries et al. 2015). This approach is particularly risky when it comes to preservation of rare species with a high dependence on floodplain habitat for their persistence. If a particular locality, like Barmah, suffers a disturbance like a hypoxic event, then large proportions of the regional population can be eliminated in single events. Without the neighbouring network of sub-populations to supply colonists, the regional population then incurs extremely low resilience to environmental change.

The alternative to the string of beads approach does not require abandoning use of reserves, but complementing reserve management with a ‘whole-of-catchment’ management mentality; an approach that acknowledges the interconnectedness of populations and the importance of this interconnectedness to regional resilience. Pygmy perch, for example, would likely benefit from such an approach. Although pygmy perch appear to benefit immensely from floodplain habitats, they can also reach high abundances in smaller tributaries of the large lowland rivers (e.g. Sevens Creek

network within the Goulburn-Broken region, and certain small tributaries of the King and Ovens in the NE region). Other segments of floodplain not specifically set aside as iconic reserves might also provide source populations of pygmy perch (Stoffels and Weatherman 2014). There are numerous ways by which a broader, regional network of pygmy perch sub-populations could be maintained, thereby building the resilience of localised populations—like that of Barmah—to environmental change. Once sub-populations have been identified throughout catchments surrounding Barmah, practices like limiting stock access and in-stream habitat restoration/protection might bolster the persistence of those sub-populations, hence resilience of the regional population. An approach towards building regional resilience of pygmy perch might include:

1. Identify likely source populations throughout the Goulburn-Broken catchments.
 - **Knowledge need:** This would involve an extensive scientific survey, specifically targeting pygmy perch throughout the catchment.
2. Link regional distribution (from (1)) with GIS layers and coarse habitat maps to infer land-use and habitat characters that might promote local source populations.
 - **Knowledge need:** Overlapping habitat mapping with survey in (1) and couple with species-distribution modelling to infer land-use and habitat drivers of regional distribution.
3. Once drivers of local source populations have been identified (from (1) and (2)) protect and restore those drivers in stream and river segments most likely to yield outcomes for pygmy perch.
 - This is exclusively a management activity, but its success hinges on a scientific understanding of the population at the catchment scale.
 - A further scientific contribution to this management activity could be optimisation of restoration resources to maximise outcomes for any given level of financial investment.
4. Identify in-channel features that facilitate the dispersal of pygmy perch throughout the catchment.
 - **Knowledge need:** What in-stream habitat features facilitate the dispersal of pygmy perch (and other threatened fauna) among key source populations? (Elements of this question may be answered by (2) above.)
5. Protect and restore in-stream habitat that promotes movement of pygmy perch throughout catchment.
6. Monitor outcomes as part of adaptive management of small-bodied fish diversity within the Goulburn-Broken Catchment.

4.2.2 Active management of species with low resilience

As suggested herein, pygmy perch likely have very low resilience to localised disturbance, given the extensive fragmentation of their habitat. It follows that, if pygmy perch are a management priority within localities like Barmah, then they may require active management to avoid localised extinction. That is, we may need to be very conscious of their requirements and status within each year and manage resources (environmental water, primarily) in an *ad hoc* way with the aim of maintaining a local viable population. For example, during drought periods certain refuge wetlands may need to have their water levels and quality maintained to ensure local persistence; if those refuges dry we may be faced with translocation in order to restore the local population.

As touched above, active management of fishes with low resilience will require:

- A solid understanding of their habitat requirements and key threats (e.g. mosquitofish abundance);
- Knowledge about the status of their population, habitat and threats each year;
- The resources to actively maintain requirements on an annual basis (e.g. pumping infrastructure) while reducing threats (e.g. carp screens).

5 References

- Allison, G. 2004. The influence of species diversity and stress intensity on community resistance and resilience. *Ecological Monographs* **74**:117-134.
- Beamish, F. W. H. 1978. Swimming capacity. Pages 101-187 in W. S. Hoar and D. J. Randall, editors. *Fish Physiology: Locomotion*, Volume 7. Academic Press, Inc., New York.
- Bell, W. H., and L. D. B. Terhune. 1970. Water tunnel design for fisheries research. Fisheries Research Board of Canada Technical Report **195**:1-69.
- Bickler, P. E., and L. T. Buck. 2007. Hypoxia tolerance in reptiles, amphibians, and fishes: Life with variable oxygen availability. *Annual Review of Physiology* **69**:145-170.
- Bond, N., J. Costelloe, A. King, D. Warfe, P. Reich, and S. Balcombe. 2014. Ecological risks and opportunities from engineered artificial flooding as a means of achieving environmental flow objectives. *Frontiers in Ecology and the Environment* **12**:386–394.
- Bond, N. R., P. S. Lake, and A. H. Arthington. 2008. The impacts of drought on freshwater ecosystems: an Australian perspective. *Hydrobiologia* **600**:3-16.
- Brett, J. R. 1964. The respiratory metabolism and swimming performance of young sockeye salmon. *Journal of the Fisheries Research Board of Canada* **21**:1183-1226.
- Carpenter, S., B. Walker, J. M. Anderies, and N. Abel. 2001. From metaphor to measurement: Resilience of what to what? *Ecosystems* **4**:765-781.
- Claireaux, G., and J. P. Lagardere. 1999. Influence of temperature, oxygen and salinity on the metabolism of the European sea bass. *Journal of Sea Research* **42**:157-168.
- Claireaux, G., D. M. Webber, J. P. Lagardere, and S. R. Kerr. 2000. Influence of water temperature and oxygenation on the aerobic metabolic scope of Atlantic cod (*Gadus morhua*). *Journal of Sea Research* **44**:257-265.
- Cook, B. D., S. E. Bunn, and J. M. Hughes. 2007. Molecular genetic and stable isotope signatures reveal complementary patterns of population connectivity in the regionally vulnerable southern pygmy perch (*Nannoperca australis*). *Biological Conservation* **138**:60-72.
- Dexter, T., N. Bond, R. Hale, and P. Reich. 2014. Dispersal and recruitment of fish in an intermittent stream network. *Austral Ecology* **39**:225-235.
- Downs, C. J., J. P. Hayes, and C. R. Tracy. 2008. Scaling metabolic rate with body mass and inverse body temperature: a test of the Arrhenius fractal supply model. *Functional Ecology* **22**:239-244.
- Dwyer, G. K., R. J. Stoffels, and P. A. Pridmore. 2014. Morphology, metabolism and behaviour: responses of three fishes with different lifestyles to acute hypoxia. *Freshwater Biology* **59**:819-831.
- Farrell, A. P., and J. G. Richards. 2009. Defining hypoxia: An integrative synthesis of the responses of fish to hypoxia. Pages 487-503 in J. G. Richards, A. P. Farrell, and C. J. Brauner, editors. *Fish Physiology: Hypoxia*, Volume 27. Elsevier Inc.
- Fey, S. B., and K. L. Cottingham. 2012. Thermal sensitivity predicts the establishment success of nonnative species in a mesocosm warming experiment. *Ecology* **93**:2313-2320.
- Hladyz, S., S. C. Watkins, K. L. Whitworth, and D. S. Baldwin. 2011. Flows and hypoxic blackwater events in managed ephemeral river channels. *Journal of Hydrology* **401**:117-125.
- Humphries, P., S. Kumar, and P. S. Lake. 2015. Engineered artificial flooding: more questions than answers. *Frontiers in Ecology and the Environment* **13**:242-243.
- Kolar, C. S., and D. M. Lodge. 2001. Progress in invasion biology: predicting invaders. *Trends in Ecology & Evolution* **16**:199-204.
- Korsmeyer, K. E., J. F. Steffensen, and J. Herskin. 2002. Energetics of median and paired fin swimming, body and caudal fin swimming, and gait transition in parrotfish (*Scarus schlegeli*) and triggerfish (*Rhinecanthus aculeatus*). *Journal of Experimental Biology* **205**:1253-1263.

- Lindstrom, M. J., and D. M. Bates. 1990. Nonlinear mixed-effects models for repeated measures data. *Biometrics* **46**:673-687.
- Mandic, M., A. E. Todgham, and J. G. Richards. 2009. Mechanisms and evolution of hypoxia tolerance in fish. *Proceedings of the Royal Society B-Biological Sciences* **276**:735-744.
- McMaster, D., and N. Bond. 2008. A field and experimental study on the tolerances of fish to *Eucalyptus camaldulensis* leachate and low dissolved oxygen concentrations. *Marine and Freshwater Research* **59**:177-185.
- Nathan, R., W. M. Getz, E. Revilla, M. Holyoak, R. Kadmon, D. Saltz, and P. E. Smouse. 2008. A movement ecology paradigm for unifying organismal movement research. *Proceedings of the National Academy of Sciences of the United States of America* **105**:19052-19059.
- Nilsson, G. E., and G. M. C. Renshaw. 2004. Hypoxic survival strategies in two fishes: extreme anoxia tolerance in the North European crucian carp and natural hypoxic preconditioning in a coral-reef shark. *Journal of Experimental Biology* **207**:3131-3139.
- Sorte, C. J. B., S. L. Williams, and R. A. Zerebecki. 2010. Ocean warming increases threat of invasive species in a marine fouling community. *Ecology* **91**:2198-2204.
- Stachowicz, J. J., J. R. Terwin, R. B. Whitlatch, and R. W. Osman. 2002. Linking climate change and biological invasions: Ocean warming facilitates nonindigenous species invasions. *Proceedings of the National Academy of Sciences of the United States of America* **99**:15497-15500.
- Steffensen, J. F. 1989. Some errors in respirometry of aquatic breathers: How to avoid and correct for them. *Fish Physiology and Biochemistry* **6**:49-59.
- Stoffels, R., and K. Weatherman. 2014. Floodplain fish communities of the Barmah and Killawarra Forests: pygmy perch status; knowledge needs; management suggestions. Final Report prepared for the Goulburn-Broken Catchment Management Authority by The Murray-Darling Freshwater Research Centre.
- Stoffels, R. J. 2015. Physiological trade-offs along a fast-slow lifestyle continuum in fishes: What do they tell us about resistance and resilience to hypoxia? *Plos One* **10**:e0130303.
- Stoffels, R. J., K. R. Clarke, R. A. Rehwinkel, and B. J. McCarthy. 2014. Response of a floodplain fish community to river-floodplain connectivity: natural versus managed reconnection. *Canadian Journal of Fisheries and Aquatic Sciences* **71**:236-245.
- Svendsen, J. C., J. F. Steffensen, K. Aarestrup, M. Frisk, A. Etzerodt, and M. Jyde. 2012. Excess posthypoxic oxygen consumption in rainbow trout (*Oncorhynchus mykiss*): recovery in normoxia and hypoxia. *Canadian Journal of Zoology-Revue Canadienne De Zoologie* **90**:1-11.
- Videler, J. J., and B. A. Nolet. 1990. Costs of swimming measured at optimum speed: Scale effects, differences between swimming styles, taxonomic groups and submerged and surface swimming. *Comparative Biochemistry and Physiology a-Physiology* **97**:91-99.
- West, J. M., and R. V. Salm. 2003. Resistance and resilience to coral bleaching: Implications for coral reef conservation and management. *Conservation Biology* **17**:956-967.
- Whitworth, K. L., D. S. Baldwin, and J. L. Kerr. 2012. Drought, floods and water quality: Drivers of a severe hypoxic blackwater event in a major river system (the southern Murray-Darling Basin, Australia). *Journal of Hydrology* **450**:190-198.
- Yeager, D. P., and G. R. Ultsch. 1989. Physiological regulation and conformation: A BASIC program for the determination of critical points. *Physiological Zoology* **62**:888-907.
- Zerebecki, R. A., and C. J. B. Sorte. 2011. Temperature Tolerance and Stress Proteins as Mechanisms of Invasive Species Success. *Plos One* **6**:7.

6 Appendix 1

Mean CPUE (individuals net⁻¹ h⁻¹) calculated across all fyke nets set at each floodplain site at Barmah National Park. * Alien species.

Site	Species name	Common name	Mean CPUE across all sites (individuals net ⁻¹ h ⁻¹)		
			Summer 2014 Sites 1 - 8 (n = 8)	Autumn 2014 Sites 1 - 8 (n = 8)	Winter 2015 Sites 1, 2, 4, 5, & 8 - 13 (n = 10)
1	Hypseleotris spp.	Carp-gudgeon	41.401	42.328	66.567
1	Philypnodon grandiceps	Flathead gudgeon	0.000	0.000	0.000
1	Retropinna semoni	Smelt	2.639	2.128	0.000
1	Carassius auratus*	Goldfish	3.180	0.000	0.000
1	Cyprinus carpio*	Carp	5.023	0.673	0.000
1	Gambusia holbrooki*	Mosquitofish	53.155	62.478	3.973
1	Misgurnus anguillicaudatus*	Weatherloach	0.000	0.000	0.000
2	Hypseleotris spp.	Carp-gudgeon	6.533	2.005	0.571
2	Philypnodon grandiceps	Flathead gudgeon	0.000	0.000	0.000
2	Retropinna semoni	Smelt	0.000	0.000	0.000
2	Carassius auratus*	Goldfish	1.929	1.631	0.000
2	Cyprinus carpio*	Carp	6.702	1.122	0.000
2	Gambusia holbrooki*	Mosquitofish	28.565	33.649	0.224
2	Misgurnus anguillicaudatus*	Weatherloach	0.739	0.157	0.000
3	Hypseleotris spp.	Carp-gudgeon	3.003	0.426	Dry
3	Philypnodon grandiceps	Flathead gudgeon	0.000	0.000	Dry
3	Retropinna semoni	Smelt	1.764	0.344	Dry
3	Carassius auratus*	Goldfish	0.651	0.182	Dry
3	Cyprinus carpio*	Carp	0.994	5.250	Dry
3	Gambusia holbrooki*	Mosquitofish	18.118	117.435	Dry
3	Misgurnus anguillicaudatus*	Weatherloach	0.426	4.410	Dry
4	Hypseleotris spp.	Carp-gudgeon	1.515	0.319	2.132
4	Philypnodon grandiceps	Flathead gudgeon	0.000	0.000	0.000
4	Retropinna semoni	Smelt	0.191	0.079	0.000
4	Carassius auratus*	Goldfish	1.517	0.227	0.000
4	Cyprinus carpio*	Carp	1.533	0.356	0.000
4	Gambusia holbrooki*	Mosquitofish	12.125	61.981	0.104
4	Misgurnus anguillicaudatus*	Weatherloach	0.125	0.090	0.000
5	Hypseleotris spp.	Carp-gudgeon	4.229	1.657	1.388
5	Philypnodon grandiceps	Flathead gudgeon	0.000	0.000	0.000
5	Retropinna semoni	Smelt	0.000	0.051	0.107
5	Carassius auratus*	Goldfish	0.182	0.000	0.044
5	Cyprinus carpio*	Carp	0.070	0.099	0.000
5	Gambusia holbrooki*	Mosquitofish	6.416	13.037	0.000
5	Misgurnus anguillicaudatus*	Weatherloach	0.000	0.123	0.000

6	Hypseleotris spp.	Carp-gudgeon	7.040	0.810	Dry
6	Philypnodon grandiceps	Flathead gudgeon	0.059	0.000	Dry
6	Retropinna semoni	Smelt	0.000	0.000	Dry
6	Carassius auratus*	Goldfish	1.741	1.460	Dry
6	Cyprinus carpio*	Carp	1.838	0.379	Dry
6	Gambusia holbrooki*	Mosquitofish	146.989	27.933	Dry
6	Misgurnus anguillicaudatus*	Weatherloach	1.223	0.054	Dry
7	Hypseleotris spp.	Carp-gudgeon	33.230	37.551	Dry
7	Philypnodon grandiceps	Flathead gudgeon	0.000	0.000	Dry
7	Retropinna semoni	Smelt	3.983	0.408	Dry
7	Carassius auratus*	Goldfish	13.202	4.490	Dry
7	Cyprinus carpio*	Carp	0.000	5.306	Dry
7	Gambusia holbrooki*	Mosquitofish	69.889	297.143	Dry
7	Misgurnus anguillicaudatus*	Weatherloach	0.000	0.408	Dry
8	Hypseleotris spp.	Carp-gudgeon	29.030	40.946	3.515
8	Philypnodon grandiceps	Flathead gudgeon	0.000	0.000	0.000
8	Retropinna semoni	Smelt	0.070	0.000	0.000
8	Carassius auratus*	Goldfish	0.035	0.133	0.224
8	Cyprinus carpio*	Carp	0.528	0.780	0.000
8	Gambusia holbrooki*	Mosquitofish	48.217	195.744	3.943
8	Misgurnus anguillicaudatus*	Weatherloach	0.000	0.067	0.224
9	Hypseleotris spp.	Carp-gudgeon	Not sampled	Not sampled	0.000
9	Philypnodon grandiceps	Flathead gudgeon	Not sampled	Not sampled	0.000
9	Retropinna semoni	Smelt	Not sampled	Not sampled	0.000
9	Carassius auratus*	Goldfish	Not sampled	Not sampled	0.188
9	Cyprinus carpio*	Carp	Not sampled	Not sampled	0.000
9	Gambusia holbrooki*	Mosquitofish	Not sampled	Not sampled	0.063
9	Misgurnus anguillicaudatus*	Weatherloach	Not sampled	Not sampled	0.000
10	Hypseleotris spp.	Carp-gudgeon	Not sampled	Not sampled	0.147
10	Philypnodon grandiceps	Flathead gudgeon	Not sampled	Not sampled	0.000
10	Retropinna semoni	Smelt	Not sampled	Not sampled	1.177
10	Carassius auratus*	Goldfish	Not sampled	Not sampled	0.000
10	Cyprinus carpio*	Carp	Not sampled	Not sampled	0.000
10	Gambusia holbrooki*	Mosquitofish	Not sampled	Not sampled	0.038
10	Misgurnus anguillicaudatus*	Weatherloach	Not sampled	Not sampled	0.000
11	Hypseleotris spp.	Carp-gudgeon	Not sampled	Not sampled	0.000
11	Philypnodon grandiceps	Flathead gudgeon	Not sampled	Not sampled	0.000
11	Retropinna semoni	Smelt	Not sampled	Not sampled	0.000
11	Carassius auratus*	Goldfish	Not sampled	Not sampled	0.000
11	Cyprinus carpio*	Carp	Not sampled	Not sampled	0.000
11	Gambusia holbrooki*	Mosquitofish	Not sampled	Not sampled	0.000
11	Misgurnus anguillicaudatus*	Weatherloach	Not sampled	Not sampled	0.000
12	Hypseleotris spp.	Carp-gudgeon	Not sampled	Not sampled	1.687
12	Philypnodon grandiceps	Flathead gudgeon	Not sampled	Not sampled	0.000
12	Retropinna semoni	Smelt	Not sampled	Not sampled	0.041
12	Carassius auratus*	Goldfish	Not sampled	Not sampled	0.000

12	<i>Cyprinus carpio</i> *	Carp	Not sampled	Not sampled	0.000
12	<i>Gambusia holbrooki</i> *	Mosquitofish	Not sampled	Not sampled	1.712
12	<i>Misgurnus anguillicaudatus</i> *	Weatherloach	Not sampled	Not sampled	0.000
13	<i>Hypseleotris</i> spp.	Carp-gudgeon	Not sampled	Not sampled	0.000
13	<i>Philypnodon grandiceps</i>	Flathead gudgeon	Not sampled	Not sampled	0.000
13	<i>Retropinna semoni</i>	Smelt	Not sampled	Not sampled	3.375
13	<i>Carassius auratus</i> *	Goldfish	Not sampled	Not sampled	0.000
13	<i>Cyprinus carpio</i> *	Carp	Not sampled	Not sampled	0.000
13	<i>Gambusia holbrooki</i> *	Mosquitofish	Not sampled	Not sampled	0.000
13	<i>Misgurnus anguillicaudatus</i> *	Weatherloach	Not sampled	Not sampled	0.000