Larval fish sensitivity to a simulated cold-water pulse varies between species and age

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ABSTRACT

The release of cold-water from hypolimnetic zones of impoundments sharply reduces downstream riverine water temperature. This cold-water pollution (CWP) can extend for hundreds of kilometres, severely challenging the physiological ability of aquatic fauna, particularly ectotherms such as fish, to maintain essential processes such as metabolism, development and growth and survival. The impact of CWP on native fish, especially early life stages, is poorly known. We investigated the effect of a 24-hour exposure to a range of environmentally-related water temperatures (8, 10, 12, 14, 16, 18 and 20°C) on three age-classes (<24-hour-old, 7-day and 14-day-old larvae) of two Australian native fish species: Murray cod (*Maccullochella peelii*) and Macquarie perch (*Macquaria australasica*). Overall, larvae of *M. peelii* were more sensitive to lower water temperatures and hence CWP than *M. australasica*, indicated by higher rates of equilibrium loss. Larvae of *M. peelii* were most sensitive to exposure at seven days old whereas *M. australasica* larvae were most sensitive at <24-h-old. Using our results, we modelled pre- and post-impoundment temperature scenarios and estimated the downstream CWP footprint for both species in an Australian river reach. Larvae of *M. peelii* were predicted to be absent from the first 26 km of river downstream of the impoundment compared with no impact on the distribution of *M. australasica.* Managing riverine water temperature below impoundments is fundamental to promoting positive outcomes for endemic fish on not only a local, but global basis. This study emphasises the differential impact of CWP among the critical early life stages and fish species and highlights the urgent need to better manage hypolimnetic water releases to improve downstream river ecosystems.

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Key words: dams; rivers; Murray cod; Macquarie perch; cold water pollution.

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INTRODUCTION

Worldwide, anthropogenically driven demand for water has led to the construction of large (>15-m high) impoundments that have severely impacted riverine taxa and biodiversity (Vörösmarty *et al.*, 2010; Lehner *et al.*, 2011; Van Looy *et al.*, 2014). This is particularly so in arid and semi-arid landscapes with especially variable rainfall and run-off (Walker and Thoms, 1993; Maheshwari *et al.*,1 995; Arthington and Pusey, 2003). Impoundments affect riverine biota by modifying flow conditions (e.g., magnitude, frequency, and timing) which in turn disrupts the cycling of nutrients, sediment regimes (Poff *et al.*, 1997; Winton *et al.*, 2019), and productivity (Junk *et al.*, 1989; Benke *et al.*, 2000). Modified flows decouple river-floodplain hydraulic interactions (Kingsford and Thomas, 2004), and alter thermal and dissolved oxygen regimes of downstream reaches (Bolke, 1979; Pusey *et al.*, 1998; Olden and Naiman, 2010; Rolls *et al.*, 2013). In combination, outcomes for riverine taxa are disastrous, including declines in the abundance and distribution of native plants (World Commission on Dams, 2000), micro- and macro-invertebrate communities (Vinson, 2001; Collier, 2002) and fish (Abell *et al.*, 2008; Agostinho *et al.*, 2008). One of the most dramatic impacts of large impoundments is the downstream exposure of fish to water temperatures well below those occurring pre-regulation (Lugg and Copeland, 2014). Such exposure is referred to as cold water pollution (hereafter CWP) caused by cold water released from the hypolimnetic zone of stratified impounded waters (Hutchison and Maness, 1979; Agostinho *et al.*, 2008).

Temperature plays a key role in the structure, functioning and distribution of organisms across landscapes and underpins enzymatic-regulated metabolism, respiration, hormonal control, and skeletal development (Johnston and Dunn, 1987; Clarkson and Childs, 2000). In fish, these processes are critical to gamete maturation, embryogenesis, hatch rates, growth and survival rates of larvae (Olden and Naiman, 2010; Trip *et al.*, 2014; King *et al.*, 2015). Temperature is therefore considered an 'abiotic master factor', that is instrumental in defining temporal-spatial patterns of species diversity and abundance (Brett, 1971; Beitinger *et al.*, 2000; Preece and Jones, 2002; Buisson *et al.*, 2008; Comte and Olden, 2017). As early life-stages of fish are particularly sensitive to temperature (Mendiola *et al.*, 2007; VanDeHey *et al.*, 2013), the survival of larvae in reaches downstream of large impoundments is likely to be governed by riverine thermal profiles.

Most studies investigating the impacts of CWP on fish have been undertaken in the northern hemisphere, focusing on adult marine taxa (Kucharczyk *et al.*, 1997; Marshall *et al.*, 2006; Donaldson *et al.*, 2008). Few studies have investigated impacts of CWP on freshwater fishes (Gippel and Finlayson, 1993; Draštík *et al.*, 2008; Lugg and Copeland, 2014), with even less attention given to their highly sensitive early-life stages, particularly larvae (Sifa and Mathias, 1987; Reid and Holdway, 1995; Garrido *et al.*, 2015). Given the importance of this early-life stage to population persistence, this knowledge is critical to the management of not only Australian native freshwater fish, but fish species globally. Generally, riverine temperatures follow a gradient from cooler upland to warmer lowland water (Fig. 1). As ectotherms (cold-blooded animals), fish have evolved within temperature gradients that support their feeding, breeding, and survival (Comte and Olden, 2017; Kärcher *et al.*, 2019). Under altered conditions (e.g., the construction of a trans-channel dam), downstream water temperatures decline, challenging the adaptive capacity of fish, particularly early life stages (Song *et al.*, 2018; Michie *et al.*, 2020). In response, fish will either adapt, perish, or move further downstream to more favourable conditions (Carosi *et al.*, 2020). The decline in downstream water temperature may be rapid (within minutes) and of short duration (24-h) to accommodate specific operational requirements (e.g., water transfers, hydroelectricity).

The Murray-Darling Basin (MDB) in south-eastern Australia is one of the world's most regulated river systems (Maheshwari *et al.*, 1995). As a result, many large river reaches are affected by CWP (Lugg and Copeland, 2014) and this is considered to have adversely impacted the population structure and persistence of native fish assemblages (Humphries *et al.*, 1999; Kennard *et al.*, 2010; Morrongiello *et al.*, 2011). CWP reaches in the MDB are likely to be more suitable for species that can tolerate lower water temperatures than those species that would have historically been present and abundant (Koehn *et al.*, 1995; Todd *et al.*, 2005; Sherman *et al.*, 2007). The decline in naturally recruiting native fish populations in rivers below impoundments, have been attributed, in part, to reduced water temperatures (Koehn *et al.*, 1995; Todd *et al.*, 2005; Tonkin *et al.*, 2020).

Eildon Dam (3,334,000 ML capacity, 1,334,000 mean annual discharge), on the Goulburn River, south-eastern Australia (case study river, Fig. 1), was constructed to improve water security and to manage downstream flooding. The flow and temperature regime below the impoundment vary annually, seasonally and daily (Fig. 2; Supplementary Figs. S1-S3), with flow releases largely dependent on downstream irrigation (Feehan, 2014). Generally, winter/spring inflows are stored and released in late-spring/summer (Cottingham *et al.*, 2014). As Eildon Dam fills beyond 50% capacity, entrained waters begin to thermally stratify (Feehan, 2014), with warmer epilimnial water layered above cooler hypolimnial water. Release valves within the base of the dam promote the delivery of hypolimnial waters into the river below. The combination of operational procedures and structural constraints contributed to CWP extending >100 km downstream of the impoundment (Feehan, 2014), with modelled pre-impoundment temperatures estimated to be 7°C warmer than post-impoundment water (Gippel and Finlayson, 1993). Cold water releases from the impoundment coincide with early life-history stages (late austral spring/summer) of two Australian native freshwater fishes with distinct life history strategies (Murray cod *Maccullochella peelii* Mitchell and Macquarie perch *Macquarie australasica* Cuvier). The downstream distribution of larvae below the impoundment is likely to be dependent, in part, on thermal cues suitable for spawning and hatching in *M. peelii* (>15°C; Koehn *et al.*, 2020) and *M. australasica* (>16°C; Tonkin *et al.*, 2016).

Recent fish surveys report naturally recruiting riverine populations of *M. peelii* 190 km below Eildon Dam (Koster *et al.*, 2012) and sustainable *M. australasica* populations in warmer tributaries of the Goulburn River (60 km below the impoundment), and comparatively lower numbers of adults within the main river channel, predominantly at the mouth of tributaries (Kearns *et al.*, 2014). Wharton (1973) reported *M. australasica* to have been abundant in the mid-Goulburn River in the 1930s and absent by the 1960s, following the construction of Eildon Dam in 1955. Native fish survey data within the 50 km reach of the Goulburn River below the impoundment is depauperate (Feehan, 2014).

Here, we determined the relationship between Loss of Equilibrium (LOE, response variable and proxy of mortality) with lowered temperatures, then modelled downstream water temperatures pre- and post- impoundment construc-

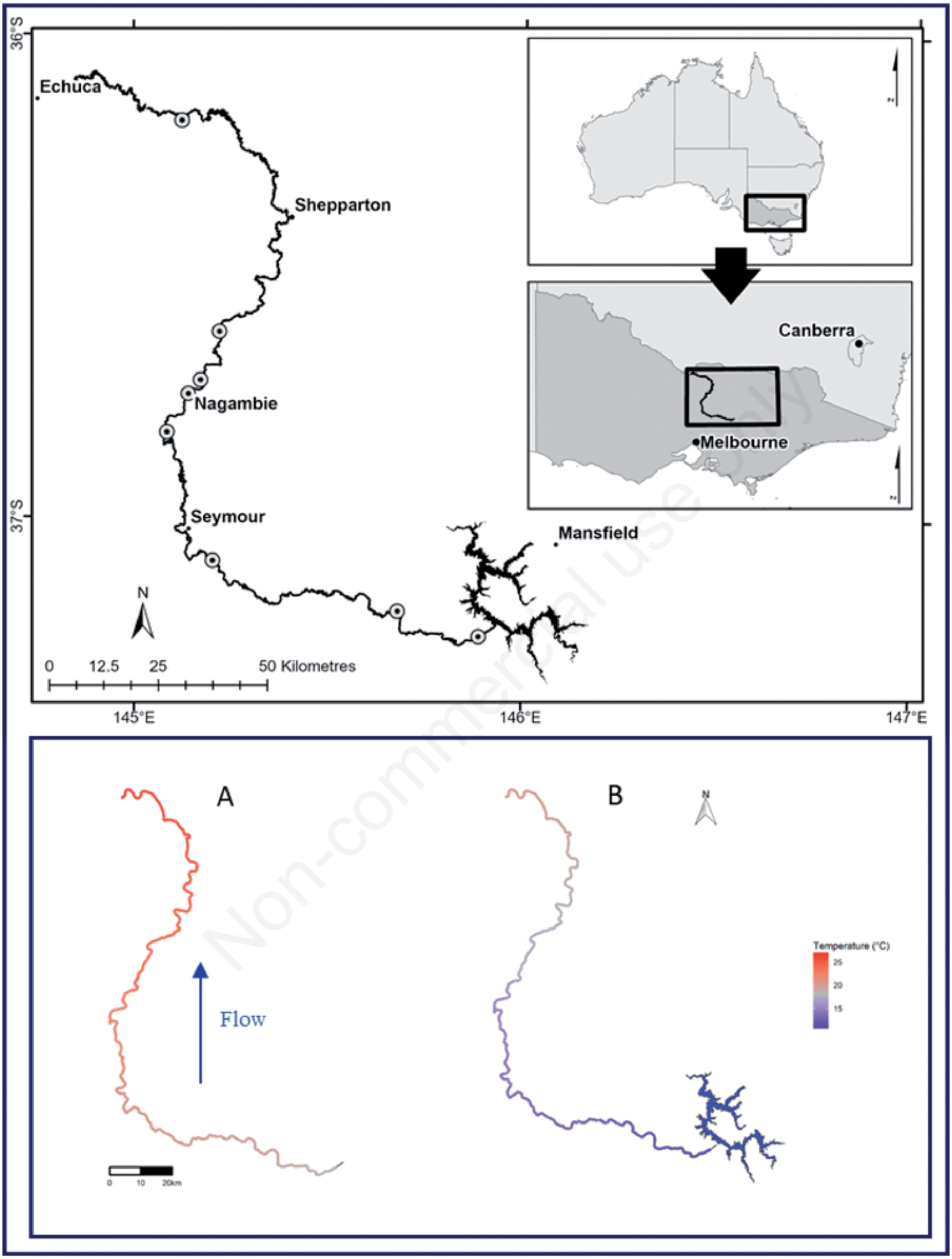

Fig. 1. Location of the conceptual case study reach, Goulburn River, Victoria, Australia and gauging stations (top). Comparative thermal profiles of the study reach, pre- (A) and post- (B) impoundment construction (bottom). Cold-water released from the impoundment warms as it flows further downstream. Colour transition from blue to red represents increasing distance and water temperature. Pre-impoundment temperatures are 7°C warmer than measured post-impoundment temperatures (Gippel and Finlayson 1993). The blue line represents the direction of water flow.

tion to estimate the spatial impact of cold-water releases on early life-stages of *M. peelii* and *M. australasic*a. Given the critical role of temperature in larval fish development and survival, the probability of larval fish losing equilibrium, riverine thermal gradients and distance downstream of a large impoundment (Fig. 1), and species ecology and biology, we hypothesised that i) sensitivity of larvae to cold-water would be size- and age-dependent (tolerance increasing with size and age), and ii) *M. australasica* larvae would be more tolerant to cold-water than *M. peelii* (*M. peelii* being a predominantly lowland species whereas *M. australasica* is a mid- to upland species). We compared thermal profiles pre- and post-impoundment construction to highlight the potentially adverse impacts CWP may have on the distribution of both species of fish in the Goulburn River, south-eastern Australia.

METHODS

We investigated the impact of CWP under laboratory conditions on larvae of *M. peelii* and *M. australasic*a, native to the MDB in south-eastern Australia (Lintermans, 2007) and thought to have been impacted by CWP (Koehn *et al.*, 1995; Gehrke *et al.*, 2002; Lintermans *et al.*, 2008; Cottingham *et al.*, 2014). Results of laboratory trials were used to model the likely impact of CWP on these species in a representative river reach downstream of a large impoundment.

Fish species

Maccullochella peelii is Australia's largest exclusively freshwater fish, weighing up to 113 kg and attaining lengths of 1.8 m (Lintermans, 2007). Formerly widespread and abundant in the lower and mid-altitudinal reaches of the MDB, commercial fisheries data convey dramatic declines in the species' abundance (Cadwallader and Gooley, 1984; Rowland, 1989). *Maccullochella peelii* are now listed as Vulnerable under Federal (Environmental Protection and Biodiversity Conservation Act, 1999) and state (Victorian Flora and Fauna Guarantee Act, 2013) threatened species legislation, respectively (Koehn *et al.*, 2020).

Adults mature at 4-6 years of age (500–600 mm TL, ≈2 kg) (Cadwallader and Gooley, 1984; Rowland 1988) and undertake spawning migrations up to 120 km (Koehn *et al.*, 2009, 2020), which are cued by increasing temperature (Koehn, 2006). Paired adult *M. peelii* spawn and fertilize eggs that adhere to hard substrate (e.g., hollow logs, clay banks) in low velocities (<0.1 m s^{-1}) with eggs guarded by the parental male until hatch (Cadwallader, 1979; Koehn *et al.*, 2020). Spawning occurs from mid-October to mid-December in response to increasing water temperatures of 15-23.5°C (Gooley *et al.*, 1995; Humphries, 2005; Koehn and Harrington, 2006), with larvae hatching 5-13 days later (Humphries *et al.*, 2002; Koehn and Harrington, 2005). Following hatching, larvae are dependent on large yolk-sacs for up to a week as they drift and disperse downstream for 5-7 days (Humphries, 2005; Koehn and Harrington, 2006) and commence feeding prior to the completion of yolk-sac absorption, 7-10 days post-hatch (Cadwallader and Gooley, 1985; Humphries, 2005).

Eggs and juveniles of *M. peelii* are adversely affected by exposure to CWP (Ryan *et al.*, 2003; Whiterod, 2013; Forbes *et al.*, 2015), indicating that larval growth and survivorship may also be impacted by water temperature.

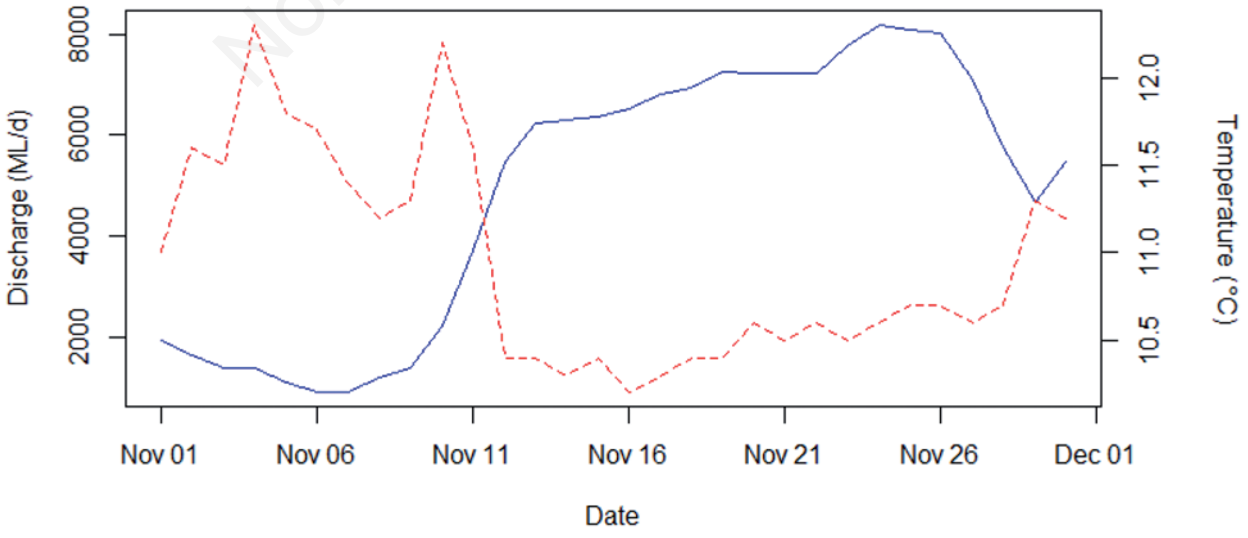

Fig. 2. Goulburn River (case study river) daily discharge (solid blue line) and water temperature (dashed red line) recorded below Eildon Dam, Australia, November, 2012. Data (https://data.water.vic.gov.au/) was collected from gauge station #405203.

Modelled impacts of CWP and the absence of naturally recruiting *M. peelii* populations in the Mitta Mitta River below Dartmouth Dam (3,856,232 ML capacity) was attributed, in part, to reduced water temperatures (Koehn *et al.*, 1995; Todd *et al.*, 2005; Tonkin *et al.*, 2020). Bio-energetic models showed that suppressed water temperatures were linked with reduced growth in juvenile *M. peelii*, yellow perch *Perca flavescens* and Walleye *Stizostedion vitreum*, compromising species fitness (Kitchell *et al.*, 1977; Whiterod *et al.*, 2018).

Macquarie australasica are a medium-sized fish, growing to a maximum length of 550 mm and weighing up to 3.5 kg (Lintermans, 2007). The species is endemic to the south-eastern reaches of the MDB and southern coastal drainages of New South Wales. Once widespread in mid- and upland reaches of the MDB (Cadwallader, 1981; Trueman, 2012), the species has undergone major declines in range and abundance and is now listed nationally as Endangered, while under state legislation it is listed as Threatened in New South Wales, Victoria and Australian Capital Territory and is considered extinct in South Australia (Lintermans, 2007; Hammer *et al.*, 2009; Tonkin *et al.*, 2014).

*Macquarie australasic*a are aggregate spawners, demersal eggs are settled within riffles with flows of 0.3-0.6 m s^{-1}, with no parental care. Larvae are swept into downstream pools and begin active feeding 3-5 days post-hatch (Cadwallader and Rogan, 1977; Ingram *et al.*, 2000; Lintermans, 2007). Spawning occurs from October to late December (Cadwallader and Rogan, 1977; Ingram *et al.*, 2000; Tonkin *et al.*, 2009). While spawning has been documented to occur once water temperatures reach 16°C, peak egg abundances occur when mean daily water temperatures exceed 18°C (Tonkin *et al.*, 2016). Eggs hatch 5-11 days post-fertilisation at 18-20°C (Ingram *et al.*, 2000). Newly hatched larvae (4.4-6.5 mm) have been found in high numbers in the water column within pools downstream of spawning sites (Broadhurst *et al.*, 2012). Larvae begin feeding on zooplankton 3-5 days post-hatch (Ingram *et al.*, 2000).

Cold-water releases from impoundments are thought to have impacted *M. australasica* (Lintermans, 2007) with recent localised extinctions below impoundments probably driven by spawning and recruitment failure following construction (Koehn *et al.*, 1995). Within the MDB, there are no populations of *M. australasica* in large, regulated river reaches below impoundments. Small, fragmented, geographically isolated populations persist in tributaries or rivers upstream and downstream of impoundments (Ingram *et al.*, 1990; Pavlova *et al.*, 2017).

Larval experiments and data analysis

To test the impact of CWP, larvae were exposed to cold water for 24-h to imitate short-term cold-water releases from impoundments. Larval ages (<24-hour-old, 7-day-old and 14-day-old larvae) were chosen to reflect critical physiological processes occurring at the time (Ryan *et al.* 2001; Raymond, 2007). To replicate temperature regimes reported in the chosen river reach during the period that larvae are likely to occur (November–December, Koehn and O'Connor 1990), larvae were exposed to seven water temperatures ranging from 8 to 20°C for 24-h, covering temperatures reported to occur in the reach (Gippel and Finlayson, 1993).

Loss of equilibrium (response variable, LOE) was used as a surrogate for fish mortality (Beitinger *et al.*, 2000; Anweiler *et al.*, 2014) to determine the impact of short-term (24-h) exposure to CWP. Equilibrium was recorded as lost if a larva was unable to maintain its dorso-ventral positioning in the water column. LOE_{50} values (where 50% of larvae lost equilibrium) are commonly used to represent significant response to stimuli (Reid and Holdway, 1995; Sokal and Rohlf, 1995; Raymond, 2007). LOE is a valuable tool in assessing immediate mortality impacts of cold water in fish, particularly for early life-history stages (Martinez-Porchas and Hernandez-Rodriguez, 2010; Ryal, 2017). The adverse impacts of cold water on cellular, tissue and organ functioning almost certainly result in death through direct systemic failure and indirectly through predation, starvation, and fungal infection (Brett, 1971; Anweiler *et al.*, 2014). Other sub-lethal metrics such as changes in behaviour (e.g., predator avoidance), prey catch rates, reproductive output, respiration rates and a range of physiological (e.g., growth, movement) parameters likely provide additional insight into the impacts of CWP (Lyon *et al.*, 2008; Martinez-Porchas and Hernandez-Rodriguez, 2010; Michie *et al.*, 2020).

Maccullochella peelii and *M. australasica* eggs were sourced from Snobs Creek Hatchery (Victorian Fisheries Authority), where they were incubated at water temperatures of 18°C to mimic those occurring naturally over the spawning period (Ingram *et al.*, 2000). *Maccullochella peelii* broodstock are permanently housed and spawned in earthen ponds at Snobs Creek Hatchery while broodstock of *M. australasica* were collected from the wild one month prior to being hormonally induced to spawn. Eggs were transported, acclimated and hatched at the Arthur Rylah Institute aquarium (Victorian Department of Environment, Land, Water and Planning). Newly hatched (<24-h old) *M. peelii* and *M. australasica* larvae were held in separate 500-L hatching tanks which were aerated and filled with 50-L of aged water, connected to a flow-through system to simulate riverine flows. Exogenous feeding *M. peelii* (8 to 14-day-old) and *M. australasica* (3 to 5-day-old) larvae were fed a diet of *Artemia* nauplii, nematodes (*Panagrellus redivivus*) and grindal worms (*Enchytraeus buchholzi*) while in holding tanks. Larvae were not fed during the 24-h exposure to cold-water. The effects of short-term exposure to CWP (24-h LOE$_{50}$) were determined for *M. peelii* larvae aged <24-hour-old-old, 7-day-old, and 14-day-old and for *M. australasica* larvae aged <24-hour-old and 7-day-old. LOE effects were recorded at the conclusion of the 24-h exposure.

For testing cold-water impacts on larval equilibrium, ten larvae were randomly assigned to 21 floating cups (210 larvae in total, ten larvae per cup) within a holding tank set at 18°C, duplicating breeding temperature. A set of three floating cups (three x 10 larvae) was assigned to each treatment temperature (8, 10, 12, 14, 16, 18 and 20°C). Each cup was then randomly assigned to one of 21 re-circulating aquarium systems (22-L total volume). Re-circulating aquaria were distributed across two benches within the laboratory. Species were tested independently (*M. australasica* in October 2016 and *M. peelii* in December 2016) and larvae were replaced for each age assessment. Water temperature in treatment aquaria was maintained using submersible 50-W heaters (Worx®) and chillers (Teco TR20). Treatment temperatures were reached within an hour.

Modelling and analysis

Data analyses were performed using R (R Core Development Team, 2013). To assess the relationship between measured water temperature and LOE, we ran a generalised additive mixed model (GAMM) using the GAMM4 function in the 'mgcv' package (Wood and Scheipl, 2016). Separate models for each species were run with an assumed binomial distribution for the response variable (number of larvae exhibiting LOE). We included water temperature as a penalised thin-plate spline (Wood, 2003). To control for potential nuisance effects, we included laboratory bench (two levels) as a fixed factor and tank as a random effect.

To determine the effect of age on sensitivity to cold-water exposure, we compared three models (Supplementary Tab. S1) using the Akaike information criterion *(*AIC) based on maximum likelihood (ML): Model 1 had no age effect; Model 2 included age as a fixed effect, testing for an overall difference of age on LOE; and Model 3 included age as a fixed effect as well as fitting separate splines for each age, and thus allowing to test for age-specific temperature relationships. Models with ΔAIC > 2 were considered poorer models (Zuur *et al.*, 2010). The best model (*M. peelii* [Model 3] and *M. australasica* [Model 2]) was then re-fitted using a restricted maximum likelihood (REML) mixed model, and we explored the model's Pearson residuals for evidence of any remaining overdispersion and misfit with the data.

Extrapolating laboratory findings to a CWP-impacted river

Thermal profiles of the Goulburn River downstream of Lake Eildon (impoundment) were constructed from gauge data (Fig. 1) collected (post-impoundment) in 2012 and pre-impoundment values modelled (plus 7°C) using this gauge data (Gippel and Finlayson, 1993; Feehan 2014) over the spawning season of *M. peelii* and *M. australasica* (mid-October to mid-December) (Ingram *et al.*, 2000; Humphries, 2005). Hourly temperature measurements covering the core spawning period (November) of *M. peelii* and *M. australasica* (Tonkin *et al.*, 2009; Koehn *et al.*, 2020) are available from 2003 onwards, with 2012 containing the most complete water temperature dataset for the Goulburn River below the impoundment. The addition of 7°C to pre-impoundment thermal profiles account for differences in water temperature post- to pre-impoundment construction (Gippel and Finlayson, 1993). Daily gauge temperatures from 16-23 November 2012 were linearly interpolated to model water temperature for the Goulburn River below Lake Eildon. Interpolation was calculated using a linear relationship between water temperature and distance between gauge station, with a base temperature reported from the gauge immediately below the impoundment on November 16, coinciding with the coldest hourly water temperature for each day. Water temperatures from successive downstream gauge stations (Supplementary Fig. S3), on consecutive days, tracked daily water temperature, providing a method to generate the thermal profile for the study reach and to account for temperature impacts from tributaries. Using estimated Goulburn River water temperature profiles, we used the best GAMM to predict LOE, conditioned on age (7-day-old) and marginalised over the nuisance parameters (laboratory bench and tank). Goulburn River water temperatures and corresponding LOE$_{50}$ values for 7-day-old *M. peelii* and 7-day-old *M. australasica* were used to estimate the locations where larvae were presumed to be absent downstream of Lake Eildon, pre- and post-impoundment construction. We compared 7-day-old larvae for two reasons, 1) to present the theoretical relationship between interpolated thermal profiles, LOE values and distribution of larvae, and 2) the high variability (large CI's, Fig. 3) of <24-h-old *M. australasica* larvae excluded this age class from further analysis.

Predicting cold-water impacts in a regulated river reach

Hypothetical maps of the Goulburn River show the predicted downstream distribution of 7-day-old larval *M. peelii* pre- and post-construction of Lake Eildon (Fig. 4). LOE$_{50}$ values of 7-day-old larvae were chosen to reflect an age where *M. peelii* larvae were most sensitive to exposure to cold water. This species and age-class provide an example of how cold water may impact the downstream distribution of fish populations below an impoundment. Based on LOE$_{50}$ values, 7-day-old *M. peelii* larvae were estimated to be absent from the Goulburn River for

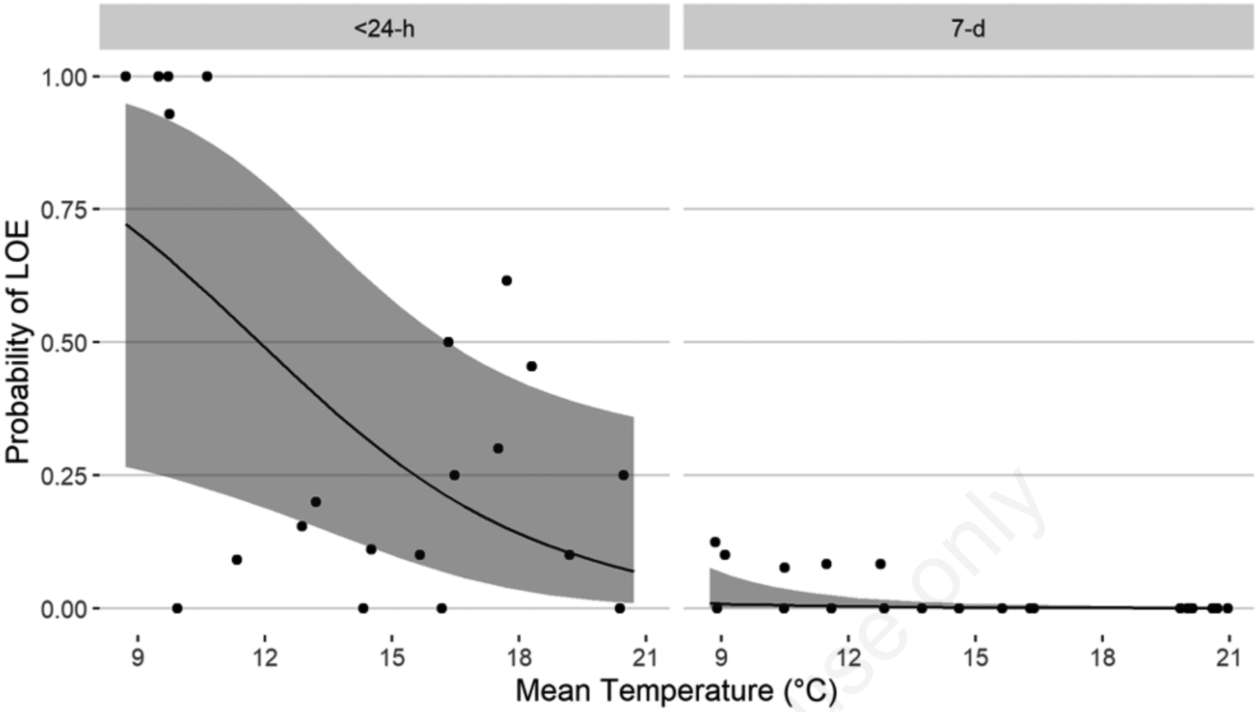

Fig. 3. The impact of mean temperature on the probability of larvae exhibiting LOE in *M. australasica* at two ages, following exposure to cold-water for 24-h. The black line represents the model fit with 95% CI (shaded grey). Black dots are the observed proportion of larvae exhibiting LOE for each treatment replicate.

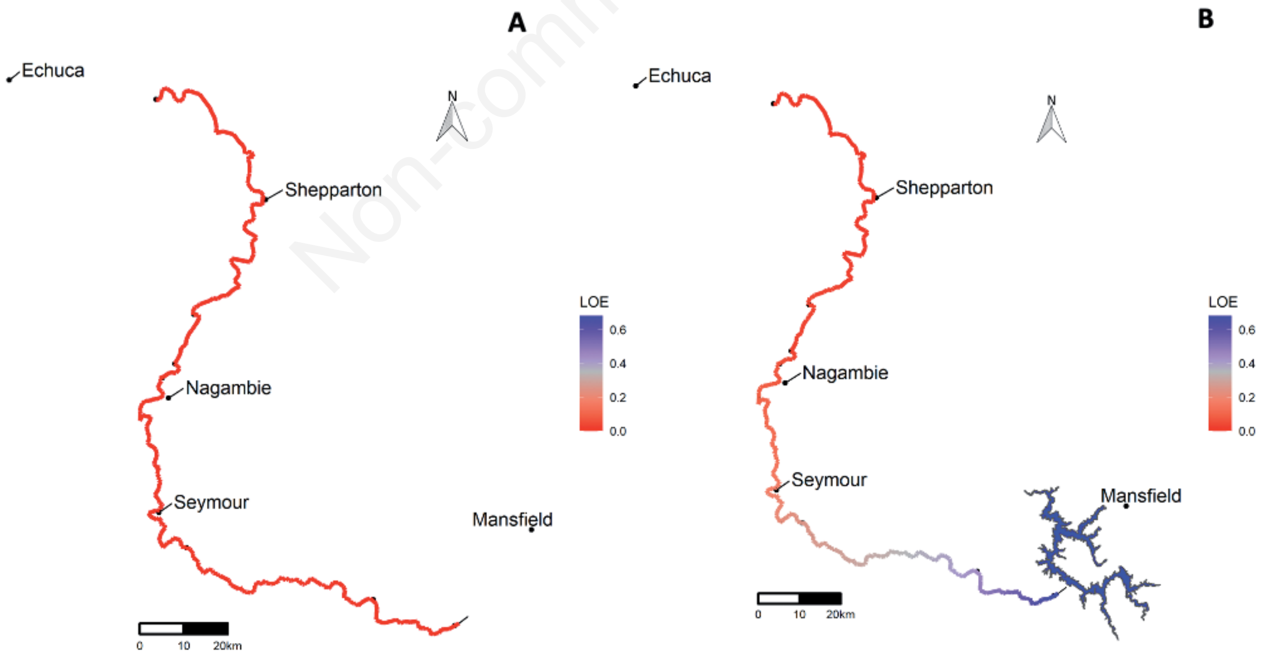

Fig. 4. The conceptual distribution of 7-day-old *M. peelii* larvae downstream of Lake Eildon, pre- (A) and post- (B) Eildon impoundment construction, based on the relationship between interpolated river thermal profiles and loss of equilibrium (impact; purple = high impact/low survival, red = low impact/high survival). Seven-day-old *M. peelii* larvae are estimated to be distributed further downstream post- impoundment construction compared with pre-construction.

up to 26 km downstream of Lake Eildon (post-construction) compared with no impact detected on the downstream distribution of 7-day-old *M. australasica* pre-impoundment construction (Fig. 4). Impacts on larval *M. peelii* declined with distance downstream of Eildon impoundment, with a likelihood of <0.1 LOE at Nagambie, 175 km downstream of the impoundment (Fig. 4).

RESULTS

Laboratory studies

Maccullochella peelii

The probability of larva exhibiting LOE at a water temperature varied by age (Fig. 5 and Tab. 1). The model

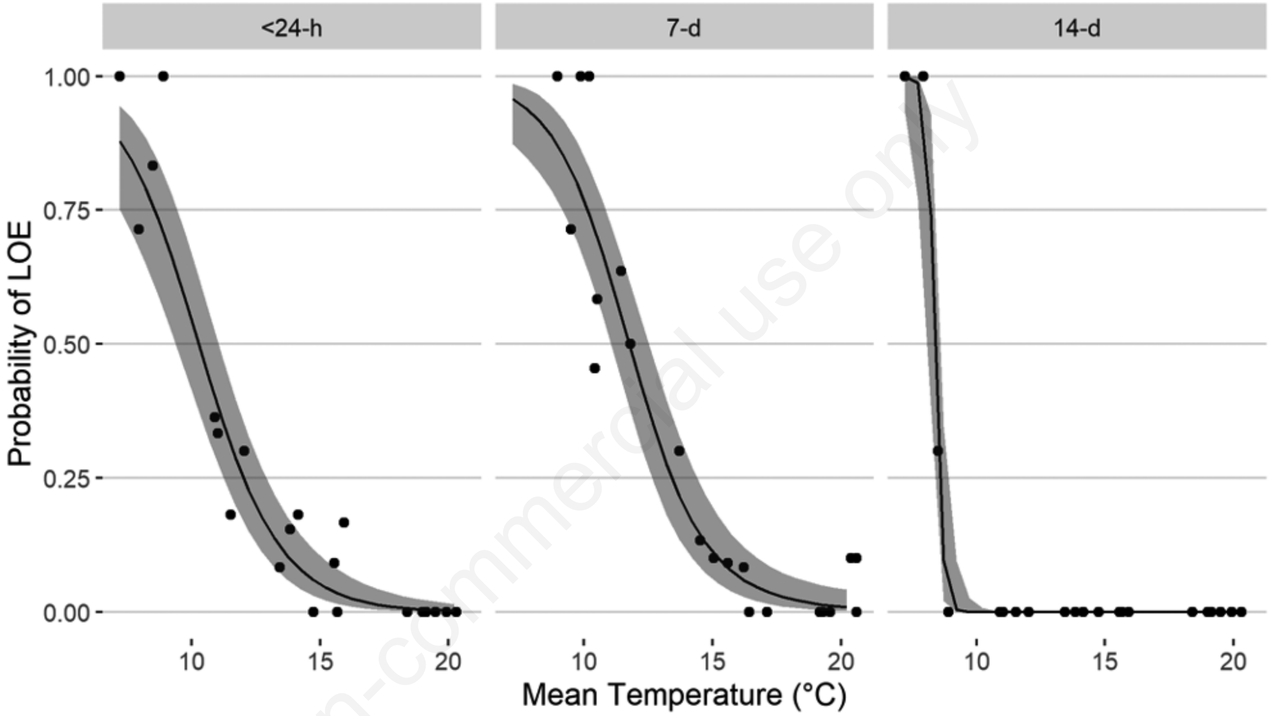

Fig. 5. Model predictions for the relationship between 24-hour exposure to various temperatures and the probability of *M. peelii* larvae exhibiting LOE for three ages (<24-hours-old, 7-days-old and 14-days-old). The black line represents the model fit with 95% CI (shaded grey). Black dots are the observed proportion of larvae entering LOE for each treatment replicate.

Tab. 1. Summary statistics for *M. peelii* following a 24-h exposure to cold-water. Determined using the GAMM4 function (REML method) in the package 'mgcv' and 'lme4'.

Parametric coefficients	Estimated St. Dev.	Error	Z value	p value
Intercept	-2.9649	0.5407	-5.483	<0.001
7-d-old	1.0281	0.4464	2.303	0.02
14-d-old	-36.6896	12.8907	-2.846	0.004
Bench	0.4638	0.3086	1.503	0.132
Significance of smoothed terms	**Estimated degrees of freedom**	**Degrees of freedom**	**Chi^2**	**p value**
<24-h-old	1.1780	9	58.84	<0.001
7-d-old	1.3418	9	71.03	<0.001
14-d-old	0.8977	9	11.09	<0.001
R^2(adj)= 0.935				

fitted the data well, with an adjusted R^2 = 0.94. A water temperature of 8°C resulted in >80% of larvae experiencing LOE regardless of age. Increasing water temperature decreased the probability of LOE to nearly zero at the highest temperatures. Seven-day-old *M. peelii* larvae were most sensitive to a 24-h cold-water exposure, followed by <24-h-old larvae, then 14-day-old larvae. Seven-day-old and <24-h-old had similar response curves with water temperature (Fig. 5) though 7-day-old had an overall higher sensitivity as reflected by the significantly higher intercept (Tab. 1). In contrast, 14-day-old had a completely different response curve as reflected clearly in a much lower LOE$_{50}$ (Fig. 5 and Tab. 2).

Macquarie australasica

Water temperature affected the probability of *M. australasica* exhibiting LOE for each age, though the relationship varied (Fig. 3 and Tab. 3). The model had an adjusted coefficient of determination (R^2 = 0.51) indicating that model fitted the data; however, the large confidence intervals encompassing the relationship between temperature and mean LOE (<24-h-old) are indicative of significant uncertainty and a poor model fit.

For <24-h-old larvae, a 24-h exposure to water temperatures of 8°C caused >90% of *M. australasica* larvae to experience LOE. As for *M. peelii*, increasing water temperature decreased the probability of LOE to near 0 at the highest temperature. In contrast, <20% of 7-day-old *M. australasica* larvae experienced LOE during the 24-h cold-water exposure. Fourteen-day-old larval *M. australasica* were not tested due to the insignificant response of 7-day-old larvae to the coldest test temperature and to minimise further testing on this threatened species.

DISCUSSION

Our results indicate that larval fish responses to cold-water were species- and age-specific. Both *M. peelii* and *M. australasica* larvae are sensitive to 24-h exposure to cold-water. Seven-day-old *M. peelii* larvae and <24-h-old *M. australasica* larvae were most sensitive to cold-water exposure compared with other ages investigated. The simulated impact of CWP downstream of a large impoundment showed that 7-day-old *M. peelii* have a high probability (>80%) of LOE, suggesting that acute effects from reduced temperatures may adversely influence the survival of this species for 26 km downstream of the impoundment. The combination of laboratory data and thermal profiles of a river below a large impoundment were

Tab. 2. Summary of key Loss of equilibrium (LOE) values for *M. peelii* and *M. australasica* larvae, following exposure (24-hour) to cold-water. LOE values were determined using best fit Generalised Additive Mixed Models. Downstream distances were calculated using the relationship between LOE and the interpolated Goulburn River thermal profile post-impoundment construction. Interpolation was calculated using a linear relationship between water temperature and distance between gauge stations, with a base temperature collected from the Eildon gauge (# 405203) on November 16, 2012.

	M. peelii						***M. australasica***			
	<24-hour-old		**7-day-old**		**14-day-old**		**<24-hour-old**		**7-day-old**	
LOE values	**Temperature (°C)**	**Distance (km)**	**Temperature (°C)**	**Distance (km)**	**Temperature (°C)**	**Distance (km)**	**Temperature (°C)**	**Distance (km)**	**Temperature (°C)**	**Distance (km)**
LOE$_{10}$	13.87°C	127.3km	15.42°C	172.4km	8.72°C	-	19.2°C	311.3km	-	-
LOE$_{25}$	12.03°C	32.0km	13.42°C	113.2km	-	-	15.42°C	180.1km	-	-
LOE$_{50}$	10.49°C	-	11.74°C	26.3km	-	-	11.87°C	28.2km	-	-
LOE$_{75}$	8.72°C	-	10.22°C	-	8.22°C	-	8.72°C	-	-	-
LOE$_{90}$	7.22°C	-	8.72°C	-	-	-	-	-	-	-

Tab. 3. Summary statistics for *M. australasica* following a 24-h exposure to cold-water. Determined using the GAMM4 function (REML method) in the package 'mgcv' and 'lme4'.

Parametric coefficients	**Estimated St. Dev.**	**Error**	**Z value**	**p value**
Intercept	-0.9198	1.5175	-0.606	0.544
7-d-old	-5.5643	0.7303	-7.620	<0.001
Bench	0.1103	1.0776	0.102	0.918
Significance of smoothed terms	**Estimated degrees of freedom**	**Degrees of freedom**	**Chi^2**	**p value**
s(mean temperature)	0.8784	9	5.384	<0.0122
R^2(adj)= 0.513				

useful to identify the degree of vulnerability of species and age classes to CWP, providing valuable information to understand the impacts of thermal regime alteration due to impoundment construction.

Species and age- specific exposure to a cold-water pulse

As hypothesised, our results revealed larval responses, measured as LOE, to a 24-h exposure to cold-water that were species- and age-specific. The greater sensitivity of *M. peelii* larvae to cold-water when compared with *M. australasica* may be due to species-specific physiology and evolutionary based thermal habitat preferences. *M. peelii* are more likely to occupy warmer lowland habitats (Cadwallader and Gooley, 1984; Koehn, 1993; Rowland, 2005) compared with *M. australasica* that show a preference for cooler mid- to upland reaches (Lintermans, 2007). The absence of *M. australasica* from lowland rivers where they were once abundant may reflect their comparative intolerance to regulated river conditions (e.g., higher turbidity, seasonal flow reversal, barriers, proliferation of exotic species), leading to a contraction in their range into mid- and upper- river reaches (Cadwallader, 1981; Trueman, 2012). While we might expect divergence across fish genera in responses to temperature, responses in fish are highly variable, even among closely related species and populations (Carlisle *et al.*, 2008; Laurel and Blood, 2011). Differences in physiology and biochemical pathways, developmental processes and size at hatch have been used to explain species-specific responses in fish to temperature (Beitinger *et al.*, 2000; Whiterod, 2013; Ryall, 2017), with the temporal loss or suppression of pathways and processes likely contributing to variability between and within species.

The extent of impact of cold-water exposure on larvae of *M. australasica* was determined to be age-based, thereby supporting our hypothesis that sensitivity to CWP is age-dependent, with increasing tolerance correlated with increasing age. We expected newly hatched larvae to be most sensitive to cold-water exposure due to them going through very early stages of development (e.g., organ development) and consequently more likely to be subject to the detrimental impacts associated with delayed, suppressed or inhibited development (Garrido *et al.*, 2016). This reasoning is consistent with the relatively greater impact of toxicants on very early life stages of Murray-Darling rainbowfish *Melanotaenia fluviatilis* Castelnau, where increased sensitivity of 3-day-old larvae of *M. fluviatilis* (compared with 7-day-old larvae) was attributed to differences in the development of the digestive tract (Reid and Holdway, 1995). Further, the larger size of 7-day-old *M. australasica* larvae may afford physiological advantages over younger larvae through improved thermodynamic capacity (e.g., decreasing surface area to volume), reducing temperature-related impacts noted in smaller individuals (Brill, 1994; Whiterod *et al.*, 2018).

The impact of cold-water exposure on larvae of *M. peelii* was also age-based, once again supporting our hypothesis that larval sensitivity to CWP is age-dependent. However, in contrast with *M. australasica*, sensitivity of larvae of *M. peelii* exposed to CWP for 24-h was higher in 7-day-old larvae than <24-h-old larvae, contradicting our age-based hypothesis for *M peelii*. Intra-species sensitivity to cold-water may be influenced by the transition between developmental stages, specifically the transition from endogenous to exogenous feeding, regarded as a critical point in larval survival (Mischke *et al.*, 2001; Somarakis and Nikolioudakis, 2010; Garrido *et al.*, 2015). *Maccullochella peelii* are reported to commence exogenous feeding 7–10 days post-hatch (Humphries, 2005), encapsulating our 7-day-old test larvae. Further, heat loss through exposure of the digestive tract to cold water may also contribute to the disproportionate impact (hypersensitivity) of 7-day-old *M. peelii* larvae to CWP as survival past the endogenous feeding stage requires larvae to meet minimum bioenergetic demands (Schulte, 2015). This potential stage-based impact from exposure to CWP was consistent with the observations of Humphries (2005), yet conflicts with the age-dependent sensitivity of *M. australasica*, perhaps as the transition from endogenous to exogenous feeding in *M. australasica* occurs at 3–5 days post-hatch (Ingram *et al.*, 2000).

We do recognise that there was some uncertainty in test results which may have been due to minor differences in ages of test subjects, with larvae used in the experiment having hatched throughout the night prior. Given the age classes used, however, these are not expected to have significantly influenced results. Further, broodstock of *M. australasica*, collected from the wild one month prior, were hormonally induced to spawn, possibly resulting in oocytes being extracted that were at various stages of maturation. Oocytes may also have been damaged during extraction, influencing larval quality. In contrast, *M. peelii* broodstock were permanently housed at the hatchery and spawned without hormonal intervention. Differences in sensitivity to temperature may also vary between hatchery-reared fish and those collected from the wild, with captive broodstock (and consequently their early life-stages) adapted to more stable conditions compared with wild-caught fish. Testing of more age classes and greater replication should be considered in further studies.

Predicting the impacts of CWP on fish downstream of a large impoundment

Populating a hypothetical response model using our laboratory-derived results and modelled river temperature data, we were able to predict the impact of short-term exposure to CWP on the downstream distribution of *M. peelii* and *M. australascia* larvae. The riverine thermal profiles and CWP impacts on test species show that *M. peelii* larvae would have survived through the entire reach prior to impoundment construction, but post-construction, there is likely detrimental impacts of CWP. Exposure of 7-day-old *M. peelii* larvae to a simulated cold-water pulse challenged their survival (as LOE_{50}) for 26 km of river downstream of the impoundment (post-impoundment temperatures). These predictions for *M. peelii* larvae agree with other research on cold-water impacts driven by hypolimnetic impoundment releases (Ryan *et al.*, 2003; Sherman *et al.*, 2007; Whiterod *et al.*, 2018) and support the notion that temperature is an important factor in defining fish distribution (Hari *et al.*, 2006; Hundt *et al.*, 2015). While temperature plays a fundamental role in determining spatio-temporal patterns in freshwater fish (Almodóvar *et al.*, 2012; Kärcher *et al.*, 2019), flows (Horwitz, 1978; Bunn and Arthington, 2002), channel morphology (Poff *et al.*, 1997; Ward, 1998; Torgersen *et al.*, 2006), species composition (Gehrke and Harris, 2000; Taylor and Warren, 2001) and density-dependence (Einum *et al.*, 2006) also influence spatial-temporal patterns across life-history stages of fishes.

In contrast with our predictions for *M. peelii*, we anticipated no change in survivorship and distribution of 7-day-old *M. australasica* larvae below Eildon impoundment. The absence of early life stages of *M. australasica* from the Goulburn River reach immediately below the impoundment was not adequately explained by our LOE predictor, suggesting that CWP was not the main driver responsible for the observation or that there is an effect that was undetected through pathways in the 24-h exposure and related LOE values. An alternate explanation is that alterations in the flow regime and associated changes in hydraulics below the impoundment are responsible for the absence of *M. australasica* larvae from the mainstem of the river. Breeding and/or spawning of adult fish may be adversely impacted by unfavourable temperatures, unsuitable spawning and rearing habitats in impounded waters and the prevention of reproductive migrations to upstream river reaches.

We have shown that short-term (24-h) exposure to a cold-water pulse adversely impact early life stages of two native fish species. However, longer-term (months to years) exposure to cold-water can have chronic impacts on growth, behaviour, reproduction, recruitment, and movement of fishes (Todd *et al.*, 2005; Whiterod, 2013) as well as acute impacts (Todd *et al.*, 2005). The reduction of fitness, measured as sub-lethal impacts of CWP on larval *M. peelii* and *M. australasica* likely impairs natural recruitment, with follow-on impacts on population dynamics, distribution patterns and species persistence.

The predicted downstream contraction of *M. peelii* larvae (based on LOE_{50}) is likely an underestimate given the likelihood that *M. peelii* larvae drift for 5-7 days (Humphries, 2005), potentially covering distances of up to 300 km depending on flow rates (Koehn, 2011). This may provide increased exposure to predation, starvation, and physical damage (McCarthy, 1999) perpetuated by additional sub-lethal impacts including impaired swimming performance (Lyon *et al.*, 2008; Whiterod, 2013) during exposure to cold-water.

CONCLUSIONS

Previous studies on the impacts of CWP on native fish have largely focused on juvenile energetics and spawning and movement ecology of adults, with a shortage of data on early life-history stages. Sensitivity of two Australian native larval fish exposed (24-h) to a cold-water pulse showed that impacts were both species- and age-specific. This disparity in sensitivity was used to predict the downstream distribution of larvae in a CWP impacted river. Managing flow releases from impoundments to avoid CWP during early life-stages of native fish may be facilitated through the provision of suitable (warmer) flows using structural modifications as well as more suitable timing of water parcels to provide positive ecological outcomes for critical early life-history stages in native fish, requiring implementation across international and regional river health plans.

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