DOES FLOW DETERMINE FRESHWATER FISH SPAWNING IN THE MURRAY RIVER, AUSTRALIA? IMPLICATIONS FOR ENVIRONMENTAL FLOW MANAGEMENT

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Species-specific, flow-biotic relationships are increasingly being used to determine environmental flow needs in flow-degraded river systems. However, describing these relationships can be challenging, as other environmental variables may also influence biotic outcomes from environmental flows. This study evaluated the relationships between a range of environmental covariates and spawning intensity of an assemblage of fish using a ten-year dataset in the mid-Murray River, Australia. Our hierarchical multi-species model, that incorporated factors accounting for imperfect sampling detection, demonstrated that temperature was an important predictor of spawning intensity for all seven species studied, while both concurrent and antecedent flow conditions were important for a number of species. This suggests that both temperature and flow influence the timing and strength of spawning for many species. We also compared the relative spawning outcomes across species using realistic alternative management scenarios; with the aim of optimising spawning outcomes for native fish, whilst reducing outcomes for non-native fish. This study highlights the benefits of long-term datasets for determining flow-biotic relationships, and demonstrates the importance of considering flow and non-flow factors in managing environmental flows.

1 BACKGROUND

In flow degraded rivers, environmental flows aim to maintain or restore ecological function by reinstating components of natural flow regimes using controlled water allocations specifically for environmental purposes. Native fish are a common target species for environmental flow restoration due to their high social, cultural and conservation value; and also as flow is also thought to influence key aspects of riverine fishes life cycles. Indeed, a number of studies have highlighted the potential for environmental flows to enhance fish spawning and recruitment (see e.g. [1,2,3]).

A common approach to designing environmental flows uses target species' life history requirements to determine the flow components to be restored [4]. This relies on a sound understanding of species-specific flow-biota relationships. Whilst there have been an increasing number of studies investigating flow and fish reproduction relationships, it still remains difficult to describe and apply these relationships to develop suitable environmental flows [5]. While some of the difficulty is undoubtedly due to the complexity of ecological systems, in many instances it is a due to limitations in research design and analytical approach e.g. short-time frames that limit inference, failure to assess influence of other abiotic factors other than flow, failure to account for sampling efficiency and not linking statistical outcomes to management options.

This study investigated the importance of multiple abiotic factors on the spawning of seven fish species in the Murray River, Australia, and used the aforementioned relationships to inform a range of environmental flow delivery strategies for fish conservation. We analysed a long-term data set (10 years) of egg and larval fish collections using a novel, multi-species hierarchical model that accounted for incomplete detection. We applied our model to predict the outcomes of hypothetical flow management strategies aimed at manipulating the spawning intensity of different fish species, allowing managers to determine the benefits and tradeoffs that can be achieved by varying when and how much environmental water is allocated.

2 METHODS

2.1 Study area

This study was conducted at three sites at the Barmah-Millewa Forest in the Murray River, south-eastern Australia. The natural flow regime of the Forest and River in this region has been highly modified, and environmental flow management is one of the main restoration tools being applied. Environmental flows in this region are typically released in small volumes during regulated irrigation flows or in larger volumes to increase the duration and magnitude of natural floods.

This study was conducted from 2003 to 2013 during highly variable hydrological conditions; ranging from regulated bank-full conditions (2003/04, 2004/05), floods (2005/06, late 2010, 2012, 2013) and severe drought (2006 – 2010) (Figure 1). In late 2010, flooding resulted in an extensive hypoxic blackwater and subsequent fish kill event in the Murray River [6]. The blackwater event undoubtedly affected spawning intensity, and since this was an abnormal event, all 2010 data were excluded from our analysis.

2.2 Sample collection

We collected the eggs and/or larvae of six native species (golden perch *Macquaria ambigua*, silver perch *Bidyanus bidyanus*, Murray cod *Maccullochella peelii peelii*, trout cod *Maccullochella macquariensis*, Australian smelt *Retropinna semoni*, and flathead gudgeon *Philypnodon grandiceps*) and one non-native species (common carp *Cyprinus carpio*). Flow has been linked to aspects of the early life history of these species, and all are known to exhibit drifting behaviour as eggs and/or larvae; and therefore we used the abundance of eggs and/or larvae in the water column to index spawning intensity. Eggs and/or larvae were collected every two weeks throughout the spawning season with replicate passive drift nets set overnight at three sites in the Murray River. More details on sampling collection can be found in King et al. [7].

2.3 Analysis and Flow Management Scenarios

A multi-species abundance model (similar to Beesley *et al.* [8]), was used to evaluate the relationship between environmental covariates and spawning intensity, while accounting for the imperfect ability to detect eggs/larvae with our sampling methods. The model was constructed in a Bayesian hierarchical framework, where species-specific parameters were random effects drawn from a community distribution. We hypothesized that spawning intensity could be influenced by various parameters that were included as covariates in the model: water temperature (*temp*, $temp^2$), weekly change in water temperature (*Chwtemp*), discharge (*flow*, $flow^2$), weekly change in discharge (*Chwflow*) and flooding history (*Flood90d*). Further details on the modelling approach can be found in King et al. [7].

3 RESULTS AND DISCUSSION

Temperature-related and flow-related variables were found to be important determinants of spawning intensity for nearly all species (Figure 1). Temperature was the primary variable, with our analysis demonstrating that maximum spawning output for many species occurs within discrete lower and upper thresholds. This confirms temperature as an important determinant of freshwater fish spawning in temperate regions [9]. Although apparent upper temperature thresholds (i.e. when spawning ceases) are rarely reported in relation to spawning activity, they have equally important management implications in this context, as they aid in narrowing the time period when spawning would occur.

Flow was an important determinant of spawning intensity for Murray cod, silver perch, golden perch and common carp, with increased spawning intensity occurring at flooding levels (>10,000 ML day^{-1}) (Figure 1). However, the relationship differed among species and its influence was dependent on suitable water temperatures. For example, golden and silver perch spawned without floods or flow pulses if water temperature was suitable, but spawning intensity significantly increased with greater flows, particularly above flood levels. This may explain why these species have been described as both requiring, and not requiring, floods to spawn (see references in Koehn et al. [10].These findings reinforce the need to consider multiple environmental factors when determining flow-biota relationships.

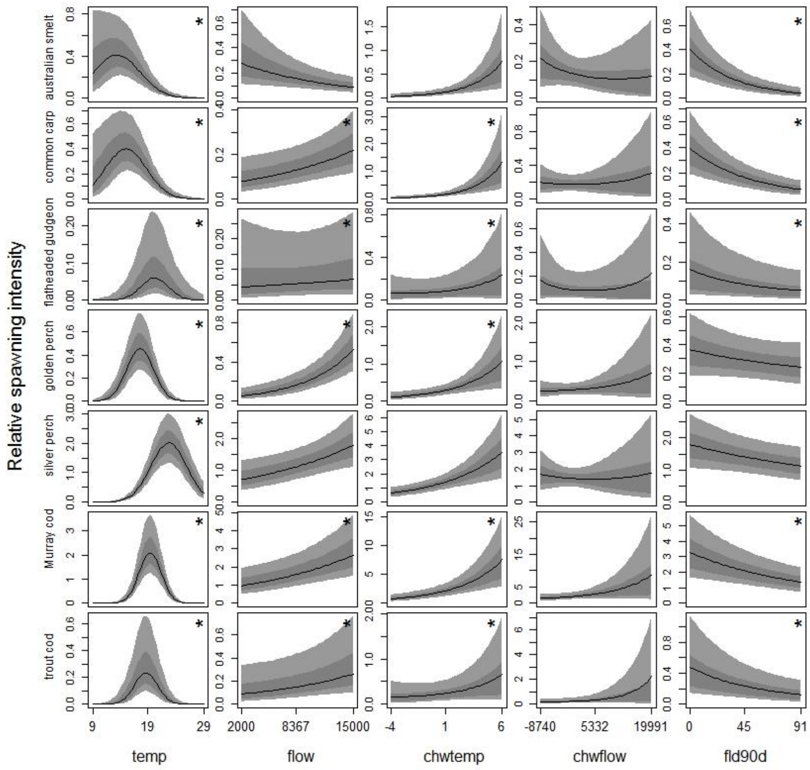

Figure 1. Predicted response of spawning intensity of each species (rows) to model covariates. Shading represents 60% and 90% credible intervals of predictions, * indicates statistically significant relationships. temp = water temperature in ⁰C; flow = river discharge (ML day^{-1}); chwtemp = change in water temperature over the week prior to sampling; chwflow = change in discharge over the week prior to sampling; fld90d = number of flood days three months prior to sampling.

This study demonstrated that spawning intensity of five out of seven species was related to antecedent flood conditions. We expected that an increase in antecedent flood days would positively affect spawning output via direct benefits to adult condition and gamete production [11], but our analysis revealed negative relationships for Murray cod, trout cod, silver perch, common carp and Australian smelt. This could suggest that flooding may provide unpredictable, minimal and/or short-lived reproductive benefits to fish in this system, and further research is required to investigate the importance of flow-energy production on spawning.

Further analysis using three realistic environmental flow scenarios, demonstrated that spawning can be influenced by manipulating different flow and temperature components of environmental water delivery. The analysis predicted that a 5000 ML day^{-1} water delivery will provide the greatest benefit to natives, while minimizing benefits to carp when water is delivered: on top of a smaller magnitude flood (25,000 ML day^{-1}), following lower antecedent flow conditions, and at water temps of 18–20˚C (Figure 2).

Our analysis highlights the importance of understanding the influence of interrelated factors (especially non-flow related factors) when designing environmental flows. Furthermore, applying our model to evaluate outcomes of competing management strategies facilitated the application of our findings for environmental flow decision making. As scrutiny of environmental water rises, managers are increasingly faced with trade-offs between ecological benefits and monetary cost. Our analysis demonstrates an approach to describing flow-biotic relationships and linking them to water management alternatives to more effectively inform environmental flow management.

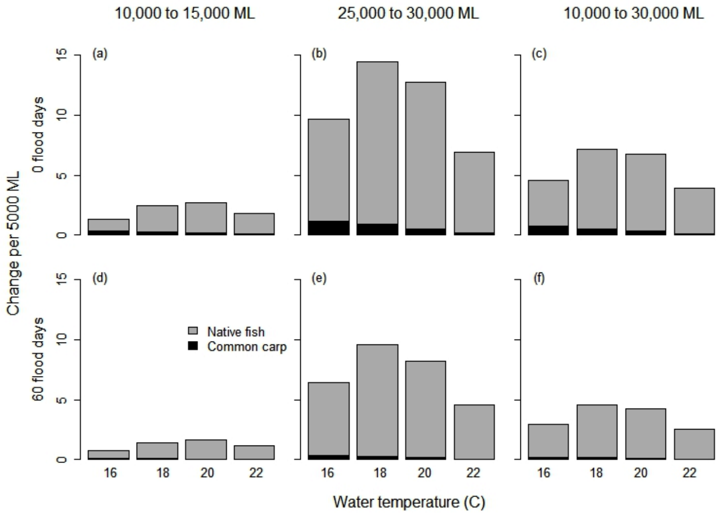

Figure 2. Change in the predicted increase in relative abundance of eggs and larvae for statistically significant species grouped as all native fish or common carp, per 5000 ML for multiple water temperatures and two flow histories. (a & d) flow increase from 10,000 to 15,000 ML day^{-1}; (b & e) flow increase from 25,000 to 30,000 ML day^{-1}; (c & f) flow increase from 10,000 to 30,000 ML day^{-1}. Flood histories represent the lower 25 percentile (upper panels, four flood days) and upper 75 percentile of *Flood90d* (lower panels 70 flood days).

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