

# Predicting the Influence of Streamflow on Migration and Spawning of a Threatened Diadromous Fish, the Australian Grayling *Prototroctes Maraena*

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**Abstract** The development of effective strategies to restore the biological functioning of aquatic ecosystems with altered flow regimes requires a detailed understanding of flow-ecology requirements, which is unfortunately lacking in many cases. By understanding the flow conditions required to initiate critical life history events such as migration and spawning, it is possible to mitigate the threats posed by regulated river flow by providing targeted environmental flow releases from impoundments. In this study, we examined the influence of hydrological variables (e.g., flow magnitude), temporal variables (e.g., day of year) and spatial variables (e.g., longitudinal position of fish) on two key life history events (migration to spawning grounds and spawning activity) for a threatened diadromous fish (Australian grayling *Prototroctes maraena*) using data collected from 2008 to 2015 in the Bunyip–Tarago river system in Victoria. Our analyses revealed that flow changes act as a cue to downstream migration, but movement responses

differed spatially: fish in the upper catchment showed a more specific requirement for rising discharge to initiate migration than fish in the lower catchment. Egg concentrations peaked in May when weekly flows increased relative to the median flow during a given spawning period. This information has recently been incorporated into the development of targeted environmental flows to facilitate migration and spawning by Australian grayling in the Bunyip–Tarago river system and other coastal systems in Victoria.

**Keywords** Environmental flow · Reproductive behaviour · Acoustic telemetry

## Introduction

Many of the world's freshwater ecosystems have been severely affected by human activity, especially where water resources are in great demand. Natural flow regimes have often been greatly altered by water storage, extraction and even seasonal inversion, causing major changes to the ecology and functioning of riverine ecosystems (Bunn and Arthington 2002). The strong life history dependence of riverine fish on the natural flow regime has resulted in widespread declines in abundance and species diversity in flow-impacted systems (Murchie et al. 2008; Poff and Zimmerman 2010). For example, increases in river flow that are an important cue for movement to spawning grounds in many freshwater fishes have often been disrupted or completely stopped (e.g., O'Connor and Mahoney 2004). In response, strategies are being developed and implemented in regulated riverine environments such as the provision of

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flows to conserve or restore important ecological processes and functions (Arthington 2012). However, the development of effective strategies requires a detailed understanding of flow-ecology relationships, which are unfortunately lacking for many species in impacted systems.

Although a growing body of scientific literature exists in relation to fish–flow relationships (e.g., Taylor and Cooke 2012; Stewart-Koster et al. 2013; Koster et al. 2016), studies have often focused on single events with few examples of long-term monitoring (>3 years), which limits the temporal applicability and robustness of findings (e.g., Grown and James 2005; King et al. 2015a), or involve biological metrics (e.g., adult abundance) that make it difficult to establish, which flow components are directly responsible for observed changes (Poff and Zimmerman 2010). Many studies also lack clear hypotheses concerning specific flow impacts on key life history stages that are then explicitly tested with targeted data collection (King et al. 2015b). Such an ad-hoc approach to exploring fish–flow relationships severely limits the development of targeted and effective flow management strategies for fish conservation (Koehn et al. 2014) because there is no underlying conceptual model that allows meaningful predictions of ecological outcomes from flow scenarios to be made (Morrongiello et al. 2011).

In this study, we examined the influence of flow on key aspects of the life history (migration and spawning) of a threatened fish Australian grayling (*Prototroctes maraena*), in the Bunyip–Tarago river system in Victoria, Australia, using acoustic telemetry and drift sampling of eggs. The Australian grayling is a diadromous species that undertakes downstream migrations to lower fresh water reaches of rivers to spawn in autumn in response to increased flows, and the eggs and larvae drift downstream to the sea, from where juveniles migrate back into fresh water in spring–summer (Berra 1982; Crook et al. 2006; Koster et al. 2013). Promoting migration to spawning grounds and increasing the occurrence of successful spawning events by providing flow cues is a key management action to support the reproductive requirements of this species and assist the recovery of its populations (Backhouse et al. 2008; SKM 2012). Indeed, environmental flows aimed specifically at initiating migration and spawning in Australian grayling have been introduced into the management of the Bunyip–Tarago river system and other coastal systems in Victoria in recent years by the Victorian Environmental Water Holder with planning and delivery in partnership with Catchment Management Authorities and Melbourne Water.

Early environmental flow recommendations for the Australian grayling focused on delivering short-lived (e.g., 1-day) flows to trigger spawning (e.g., SKM 2005; Earth

Tech 2006). This was based on research suggesting that adults spawn in upriver reaches and do not migrate to spawn (Berra 1982). However, following the identification of a long-distance downstream migration to spawning grounds just upstream of the estuary in response to increased flow (Koster et al. 2013), it was evident that environmental flow recommendations for the Australian grayling needed to include flows that allowed adult migration to spawning areas. This has recently been achieved through reviews of the environmental flow recommendations for the Australian grayling in the Bunyip–Tarago river system and other coastal systems in Victoria (SKM 2013; Alluvium 2015; Jacobs 2015).

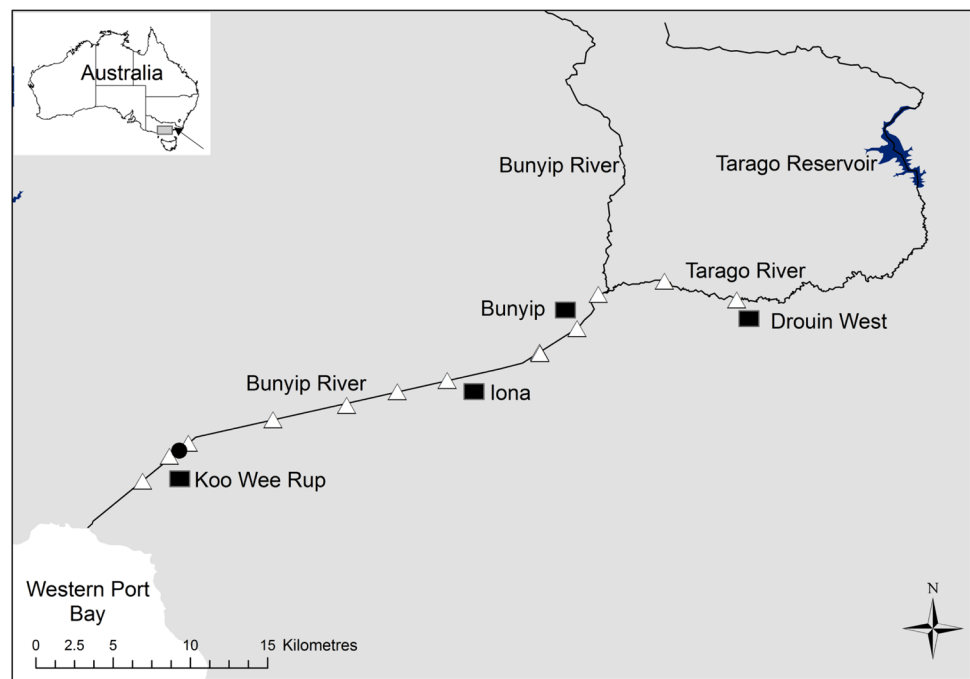
While recent research has resulted in significant new information on the spawning and migration of Australian grayling and their links to flows, evaluations of the flow requirements of this species have been based on short-term studies (e.g., 2 years) and constrained by factors such as small sample sizes (Koster et al. 2013; Amtstaetter et al. 2015; Koster et al. 2017). In this study, we integrated all of the available movement and spawning data collected between 2008 and 2015 on Australian grayling in the Bunyip–Tarago river system, and examined the influence of *a priori* determined hydrological, temporal and spatial variables on Australian grayling migration to spawning grounds and spawning activity. The study uses data previously analysed by Koster et al. (2013, 2017), but builds on this previous work by incorporating more data and using more sophisticated statistical methods. For migration, we predicted that short-term flow changes act as a cue for movement, although we also tested for absolute flow magnitude effects. For spawning, we predicted that fish respond to changes in flow relative to prevailing conditions, rather than the absolute level of river discharge. This information is needed to improve the understanding about how components of the flow regime such as timing, duration, and magnitude affect migration and spawning in order to develop and refine environmental flow delivery strategies.

## Methods

### Study Area

The study was conducted in the Bunyip–Tarago river system in Victoria, south-eastern Australia (Fig. 1). The Tarago river is the main tributary of the Bunyip river and is regulated by the Tarago reservoir. The upper reaches of the Bunyip–Tarago catchment are forested, while the mid to lower reaches consist predominantly of cleared agricultural land and small urban areas. Average annual discharge in the Bunyip River is about 153,000 ML.

**Fig. 1** The location of the study site in the Bunyip–Tarago river system in Victoria, Australia. *Black circle* represents the drift sampling site and *white triangles* the acoustic listening stations



## Fish Movement

A total of 81 Australian grayling were collected by electrofishing in 2009, 2010 and 2015 from the Bunyip and Tarago rivers, and acoustic transmitters were surgically implanted in each fish (see Koster et al. 2013 for details). The lengths of fish ranged from 150 to 240 mm, with a mean of 203 mm ( $\pm$ SE = 1.9 mm). Different fish were tagged in each year. Vemco V7 transmitters (22 × 7 mm, frequency 69 kHz, mass 1.8 g in air, estimated battery life 150–170 days; Vemco, Nova Scotia, Canada) were used in 2009 ( $n=21$ ) and 2010 ( $n=34$ ). In 2015, 26 fish were tagged with newly available Vemco V4 transmitters (11 × 5.7 mm, frequency 180-kHz, mass 0.4 g in air, estimated battery life 50–60 days). An array of Vemco VR2W acoustic listening stations was deployed in the Bunyip River between Bunyip and Koo Wee Rup, and in the Tarago River between Drouin West and the Bunyip River junction (Fig. 1). Each listening station was deployed using a length of plastic-coated steel cable attached to a star picket as an anchor point. Data were downloaded from the listening stations at approximately monthly intervals throughout the study.

## Fish Spawning

Fish eggs were collected at one site on the lower reaches of the Bunyip River near Koo Wee Rup using two drift nets (Fig. 1). Previous sampling at other sites had shown that the vast majority of eggs occurred in the lower reaches (Koster

et al. 2013; Koster et al. 2017). Sampling was conducted once or twice per week from March to June in each year from 2008 to 2015, except 2012. Drift nets were of 500- $\mu$ m mesh, 150 cm long with a 50 cm mouth diameter, and had flow meters (General Oceanics, Florida, USA) fitted to the mouth of the net to measure the volume of water filtered. Nets were set in late afternoon (1500–1700 h) and retrieved the following morning (08:00–10:00 h). Drift-net samples were immersed into an anaesthetic solution of 4 mL Alfaxan (Jurox, Rutherford, Australia) per litre water for 10 min to euthanase any fish, and then preserved in 70% ethanol. These samples were sorted in the laboratory under a dissecting microscope.

## Data Analysis

We modelled the probability of an individual Australian grayling undertaking a downstream movement on a given day (binary response variable: 0 or 1) during the spawning season or spawning activity (counts of eggs) as a function of hydrological, temporal and spatial predictor variables (Table 1) using generalised linear mixed effects models (GLMMs). The analysis for spawning activity included counts only of eggs, not larvae, as larvae comprised only about 10% of the total catch. Hydrological variables were defined *a priori* based on our understanding of how Australian grayling are likely to respond to changes in their environment (Koster et al. 2013; Koster et al. 2017). GLMMs were fitted using a binomial distribution in the lme4 package in R 3.2.2 (R Development Core Team 2015).

**Table 1** Description of predictor variables used in the analysis of Australian grayling movement to spawning grounds and spawning activity

Predictor	Description
<b>Movement</b>	
Fixed effects	
Lag-1	Dummy variable characterising the movement state of a fish on the previous day; accounts for a potential Markov process whereby future movement states are dependent on preceding state and also any temporal auto-correlation in movement observations
Flow change	Mean daily flow on day fish was detected and 1 day prior, divided by mean daily flow 2 and 3 days prior; describes any change in flow conditions recently experienced by a fish ( $\Delta$ -108 to +219 ML)
FlowMagCurrent	Flow magnitude relative to current conditions: Mean daily flow divided by median flow during the spawning season (Mar–May) for that year; puts current flow conditions into its spawning season context (51.6 to 1039% of current spawning season flow)
FlowMagNat	Flow magnitude relative to historical conditions: Mean daily flow divided by historical median flow in the spawning season; puts current flow conditions into a historical context (18 to 405% of historical spawning season flow)
DOY	Day-of-year to describe any seasonal change in spawning migrations (56 to 212)
Year	Categorical variable to account for potential differences in migration probability among years (2009, 2010, 2015)
Distance	Distance in kilometres from the estuary of a fish's daily location (3.5 to 46.5 km)
Random effect	
Fish ID	Random intercept for each individual to account for repeated measurements made for each fish (33 fish)
<b>Spawning</b>	
Fixed effects	
PerFlowChange	% flow change: Maximum minus minimum flow, compared to average flow, in the week before each collection date
HighFlowDur	High flow duration: Number of days daily flow increased in the week before each collection date
PerFlowMag	% flow magnitude: Average flow in the week before each collection date compared to median flow during the peak spawning period (Mar–May) for that year
DOY	As above
Watertemp	Water temperature (°C)
Random effect	
Year	7 years over which data were collected seen as a random draw of all possible years

*Note:* Movement data was analysed using a GLMM (hence fixed and random effects)

### *Movement model*

As there were multiple daily observations of an individual's movement status, a GLMM was fitted with a random intercept for individual fish (Fish ID) (Bestley et al. 2010; Koster et al. 2013). The random intercept induces a correlation among observations within a fish and accounts for the repeated measures nature of the data.

We compared a series of increasingly complex models fitted to the movement data that explored potential spatially and temporally dependent flow responses (flow\*DOY (day of year); flow\*distance), and year-to-year variation in seasonal migration patterns (Year\*DOY). We also allowed for curvilinear flow responses by fitting a quadratic term. All models included Lag-1 to account for a potential Markov process in which future movement states depend on preceding state and temporal autocorrelation in the data (Bestley et al. 2010). Continuous predictors were first scaled  $[(x-\text{mean})/SD]$  to

ensure model convergence. In the case of FlowMagCurrent and FlowMagNat, data were then  $\log_{10}$ -transformed to ensure linearity between the predictor and the link function. Because of colinearity among hydrological variables, flow change, FlowMagCurrent and FlowMagNat were fitted in separate models. Competing models were compared using rescaled Akaike's Information Criterion corrected for small sample sizes ( $\Delta AICc$ ) (Burnham and Anderson 2002). Parameter estimates and 95% credible intervals were derived from the posterior distribution of the fixed effects in the best model using 1000 model simulations generated by the arm R package.

### *Spawning model*

The response variable in the spawning model (number of eggs) is a count with values that ranged from 0 to 3974. As these counts were dependent on the volume of water filtered by each net, we fitted an offset term for filtered flow volume

that adjusted counts for sampling effort and still allowed us to predict values on the original, count scale. We used GLMMs that included Year as a random effect (seven levels) as we were not interested in these seven years *per se*, but rather treated them as a random draw of all possible years. We initially fitted a Poisson GLMM, but these models were significantly over-dispersed and, therefore, a negative binomial GLMM was used.

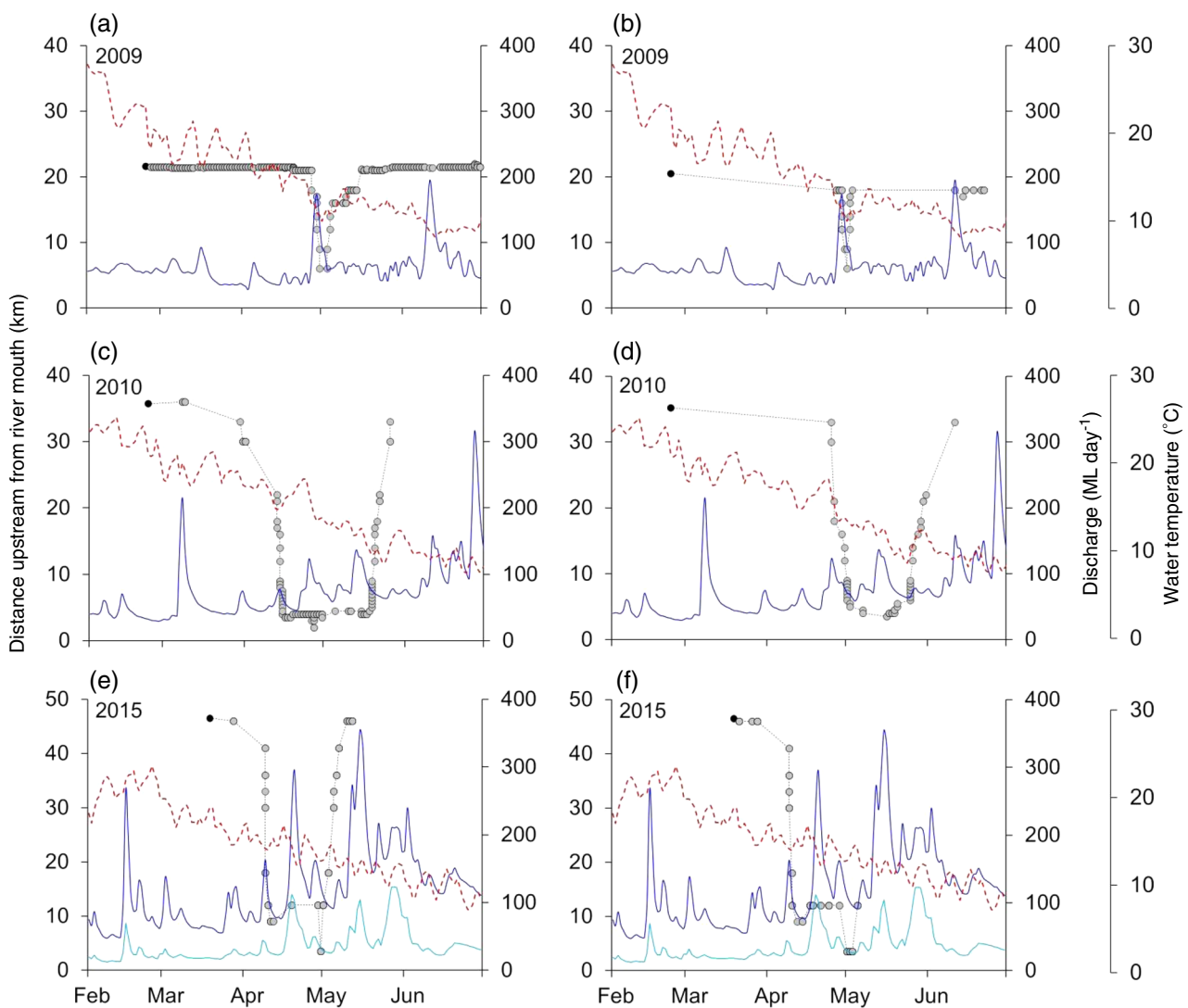
Because of strong colinearity ( $r=0.94$ ), we fitted DOY and water temperature models separately. We included quadratic terms for each variable to allow for curvilinear relationships with spawning magnitude and also tested for interactions between DOY or water temperature and each flow variable. Continuous predictors were scaled, competing models were

compared using  $\Delta AICc$  and parameter estimates and 95% credible intervals were generated using 1000 model simulations derived from the arm R package.

## Results

### Fish Movement

Tagged adult Australian grayling in the Bunyip–Tarago system undertook rapid downstream migrations over distances of up to 45 km to the lower reaches of the Bunyip River near Koo Wee Rup from late March to late April during increases in flow (Fig. 2). The percentage of tagged



**Fig. 2** Examples of movement patterns of individual Australian grayling tagged in 2009, 2010 and 2015 in the Bunyip and Tarago rivers. *Black circles* show the date and location of tagging and *grey circles* show detections of tagged fish on the listening stations. *Dark blue line* denotes mean daily discharge in Bunyip River at Iona. *Light*

*blue line* denotes mean daily discharge in Tarago River at Drouin West. *Dashed red line* denotes mean daily water temperature in the Bunyip River at Iona (2009, 2010) and Tarago River at Drouin West (2015). Figure 2a–d reproduced from Koster et al. (2013)

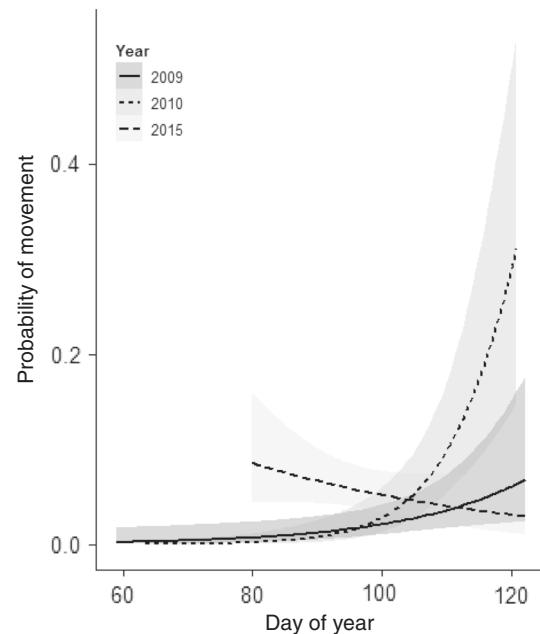


fish detected migrating to the lower reaches varied between years: 33% in 2009, 18% in 2010, and 85% in 2015. The much greater percentage of fish detected migrating in 2015 compared with 2009 and 2010 likely reflects a higher rate of transmitter retention in 2015, attributable to refinement of the tagging procedure. Movements to the lower reaches during the spawning season in response to increased flows were partially synchronised: some fish moved together for part of their journey, and although not all moved on the same flow event, all fish migrated at the same time of year.

The best movement model included the terms Lag-1 and the interactions Year\*DOY and flow change\*distance (Table 2). Models including FlowMagCurrent and FlowMagNat received little support given the data ( $\Delta AICc$  values > 21). Fish that moved at time  $t-1$  (yesterday) were 2.78 times more likely to move at time  $t$  (today), indicating that migrations occurred over subsequent days. There was considerable among-year variation in the timing of spawning migrations (Fig. 3). In both 2009 and 2010, the probability of fish moving increased with time (peak spawning on average occurred around day 140; see spawning results), whereas in 2015 fish had a greater probability of moving earlier in the season.

Fish were more likely to move downstream when higher in the river system, but this relationship was flow-change dependent (Fig. 4). Fish located higher in the catchment (more than 20 km above the estuary) moved only on the

rising limb of flows (positive flow change) and had a higher probability of moving on larger flow changes. Once fish had moved farther down in the system, the probability of moving as a function of flow change was lower, and fish were just as likely to move on negative and positive flow changes (Fig. 4). The downstream migrations corresponded to the timing of spawning (Figs 2 and 5).

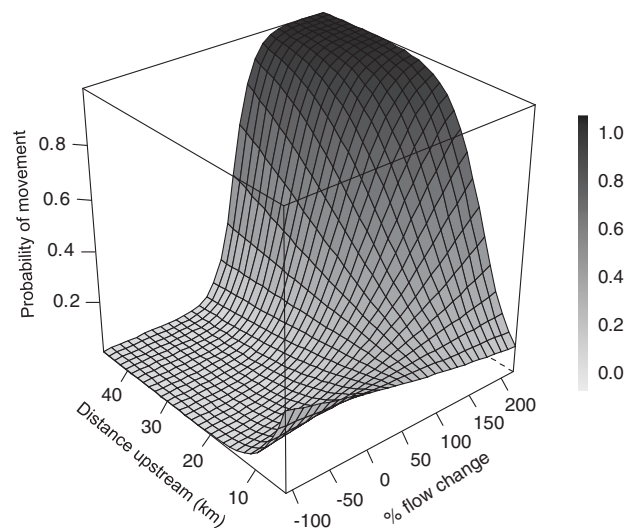


**Fig. 3** Predicted probability of fish migrating as a function of year and day-of-year (+/– 95% CI). Peak spawning occurred around day 140 (see spawning results). All other covariates held at their mean values

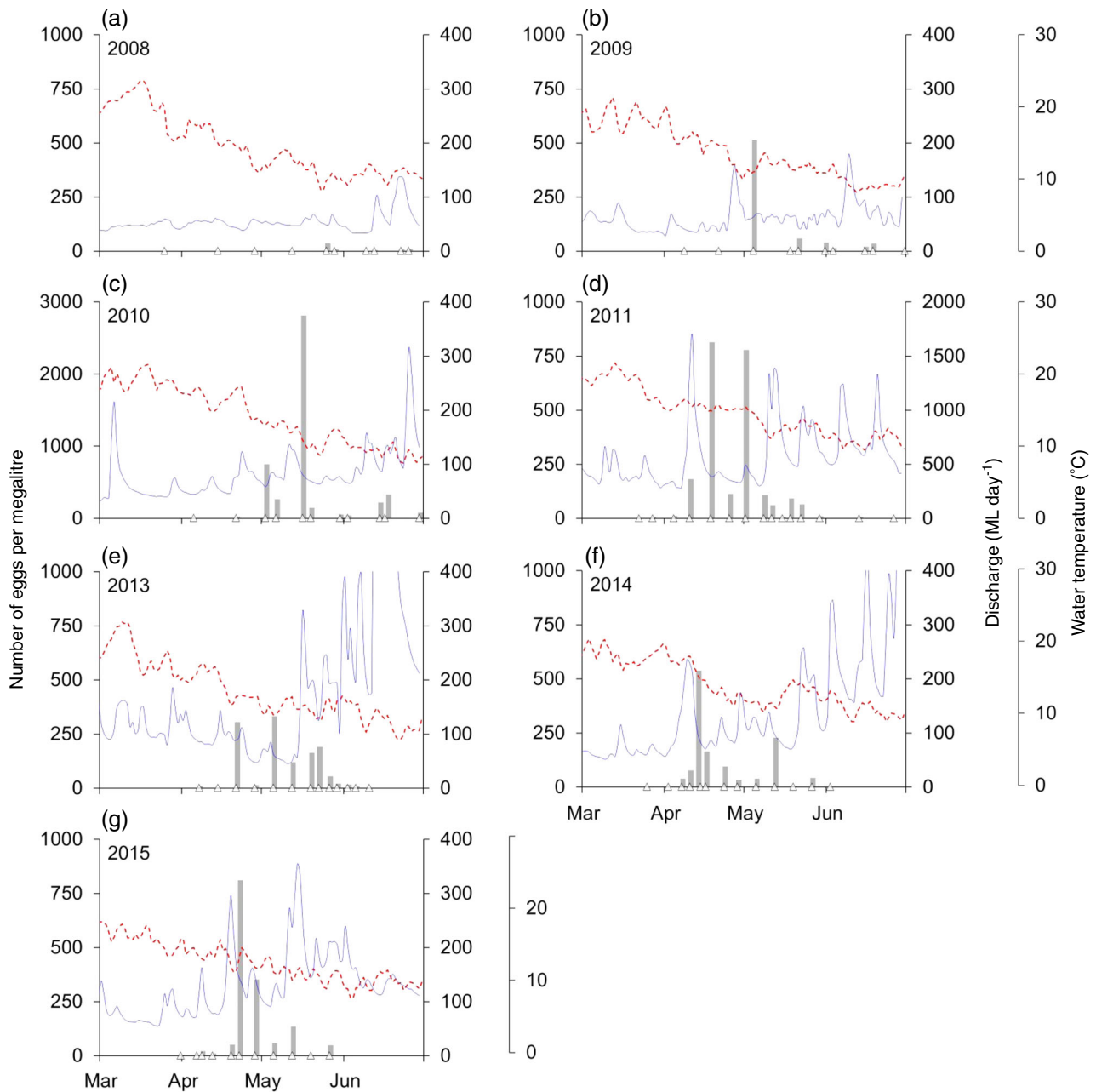
**Table 2** Fixed effect parameter estimates and 95% credible intervals (derived from posterior distribution of 1000 model simulations) for the best movement and spawning magnitude models selected using AICc

Parameter	Estimate (95% credible intervals)
<i>Movement</i>	
Intercept	–4.33 (–5.26, –3.55)
Lag-1 (1)	1.02 (0.51, 1.59)
DOY	0.79 (0.22, 1.44)
Year (2010)	–0.36 (–1.57, 1.27)
Year (2015)	1.60 (0.76, 2.71)
Flow change	1.19 (0.87, 1.51)
Distance	–1.03 (–1.37, –0.72)
Year*DOY (2010)	1.12 (–0.13, 2.01)
Year*DOY (2015)	–1.16 (–1.93, –0.41)
Flow change*Distance	0.61 (0.41, 0.82)
<i>Spawning</i>	
Intercept	–1.58 (–2.16, –1.00)
PerFlowMag	0.81 (0.34, 1.26)
PerFlowMag <sup>2</sup>	–0.37 (–0.65, –0.09)
DOY	–0.68 (–1.13, –0.25)
DOY <sup>2</sup>	–0.88 (–1.18, –0.55)
PerFlowMag*DOY	–0.01 (–0.49, 0.46)

See Table 1 for description of parameters



**Fig. 4** Predicted probability of fish moving downstream as a function of distance upstream from the spawning area and % flow change (positive values indicate rising limb, negative values falling limb of hydrograph). Grey scale colour bar denotes probability of movement. All other covariates held at their mean values



**Fig. 5** Adjusted total density of Australian grayling eggs per megalitre collected in drift nets in the Bunyip River. *Dark blue line* denotes mean daily discharge in Bunyip River at Iona. *Dashed red line* denotes mean daily water temperature in the Bunyip River at Iona (2008–2013)

and Tarago River at Drouin West (2014–15). Clear *triangles* on x-axis indicate sampling event. Figure 5a–e reproduced from Koster et al. (2013) and Fig. 5f reproduced from Koster et al. (2017)

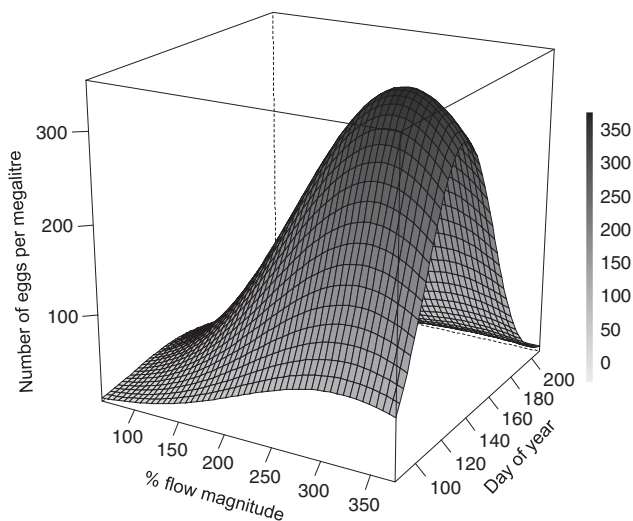
**Fish Spawning**

In total, 11,711 Australian grayling eggs were collected in the drift sampling (Table 3). Eggs were collected from April to June, with peak egg abundances collected between mid April and mid May, coinciding with autumn within-channel flow pulses (Fig. 5). Australian grayling larvae were much less abundant in the samples ( $n = 1310$ ).

The best spawning model included an interaction between PerFlowMag and DOY, and their quadratic terms (Table 2). Collections of eggs peaked around day 140 (mid to late May) when flows in the week prior to sampling were about 300% higher than the median flow during the spawning period (March–May) (Fig. 6). Collections steadily declined at lower and higher flows, and also earlier and later in the year.

**Table 3** Number and density (number per megalitre) of Australian grayling eggs and larvae collected in drift samples from the Bunyip River at Koo Wee Rup between 2008 and 2015

		2008	2009	2010	2011	2013	2014	2015
Number	Egg	91	788	6336	1575	823	651	1447
	Larvae	81	164	89	124	124	58	670
Density	Egg	6.3	96	429	99.8	69.4	80.5	115.6
	Larvae	5.6	19.9	6	7.9	10.5	7.2	53.5



**Fig. 6** Predicted spawning activity (number of eggs per megalitre) as a function of % flow magnitude and day of year. Grey scale colour bar denotes magnitude of spawning

Eggs were collected over a broad range of water temperatures (as high as 18 °C), with peak abundances at 13–14 °C (Supplementary Fig. 1), but this model (which also included percentage flow magnitude) received little support from the data ( $\Delta\text{AICc} > 25$ ). This suggests that spawning is triggered by day length rather than just temperature.

## Discussion

Our study analysed data collected over 8 years (2008–2015) for two key life history events associated with reproduction in a threatened diadromous fish. Previous studies of this species (i.e., Koster et al. 2013; Amtstaetter et al. 2015; Koster et al. 2017) were each based on 2–4 years of data only. Combining these data sets and incorporating new data provided temporal replication that allowed us to investigate potentially complex relationships between Australian grayling behaviour and flow variability, and generate a robust synthesis of how flow alteration and restoration affects this species. We confirm the importance of a rise in river flow for downstream migration and spawning of Australian grayling (Koster et al. 2013; Amtstaetter et al.

2015; Koster et al. 2017). More specifically, our analyses show that adult fish undertake partially synchronised downstream spawning migrations to freshwater reaches immediately upstream of the estuary predominantly during periods of increased streamflow. The statistical modelling also demonstrated that the rising limb of the hydrograph is a critical cue for initiating downstream spawning migration. Downstream migrations over long distances to spawn at times of increasing flow occur in many fish species for which transport of eggs or larvae to the sea is an obligatory part of the life cycle (Boubée et al. 2001; Durif and Elie 2008; Crook et al. 2010). For these fishes, movement on the rising hydrograph limb of a flow likely represents an evolutionary adaptation that allows individuals to take maximum advantage of a flow pulse for travelling to spawning grounds (i.e., reduced energy expenditure, improved connectivity) and to assist the subsequent transport of eggs or larvae to the sea (Northcote 1984).

The clear behavioural response of the Australian grayling to increases in river discharge highlights the threats posed by artificially altered flow regimes (i.e., altered frequency, magnitude and duration of flow events) because it shows that spawning and subsequent recruitment are unlikely to occur in the absence of specific flow cues during the autumn spawning period (see also O'Connor and Mahoney 2004). Damping of variations in streamflow caused by the capture of small to moderate rises in river discharge and the development of stable base flows is recognised as one of the most significant ecological effects of river regulation (e.g., McMahon and Finlayson 2003). Our study provides further evidence of how reduced flow variability can deleteriously impact the sustainability of riverine fish populations (Freeman et al. 2001). Our results also provide important insights into the influence of hydrology and its timing on spawning of Australian grayling. It has been suggested that spawning takes place from February to July (Bishop and Bell 1978; Berra 1982; Hall and Harrington 1989; Koehn and O'Connor 1990), but we have shown that the highest concentrations of eggs typically occurred in May when flows in the week prior to sampling are higher than the median flow during the spawning period for that year. Our analyses also identified an upper bound of flow beyond which spawning declines (i.e., when weekly flows greater than 300% of the seasonal median). Together, these results suggest fish respond to increases in flow relative to the prevailing seasonal



conditions rather than the absolute level of river discharge, and that larger flows do not necessarily result in more spawning.

By understanding the flow conditions required to initiate migration and spawning, it is possible to mitigate the threats posed by regulated river flow by providing targeted environmental flow releases from impoundments. For example, a flow release designed to maximise the duration of the rising limb of the flow would likely increase movement activity and spawning by Australian grayling, and different flow magnitudes could be delivered in different rainfall years to match the prevailing seasonal conditions (as opposed to providing a single flow magnitude across all years). Consideration of flow duration and timing is now a key component of seasonal watering plans for the Bunyip–Tarago recently developed by the Victorian Environmental Water Holder and Melbourne Water (VEWH 2016), based on the supporting evidence from this study, and the responses of fish are currently being monitored. More broadly, our study demonstrates the importance of quantifying flow-ecology relationships for multiple life history events through targeted research to develop appropriate flow regimes for aquatic biota in regulated rivers (King et al. 2010; Koster et al. 2017). While our study found clear responses to flow, the specific mechanisms for how flow affects movement and spawning behaviours need to be explored further. For example, the roles of hydrodynamic characteristics that constitute flow such as velocity, depth and turbulence are unknown, despite the fact that fish are likely to respond to these rather than flow *per se* (Silva et al. 2011; Piper et al. 2015).

Another key finding of this study relates to the synchronised movement by Australian grayling to the lower reaches during the spawning season. Some fish moved together for part of their journey, and although not all fish moved on the same flow event, all migrated at the same time of year. Furthermore, once an individual commenced migrating, it was more likely to keep moving. Similar synchronised patterns have been observed for other flow-dependent spawning species, such as Colorado pikeminnow (*Ptychocheilus lucius*) in White River, Colorado (Irving and Modde 2000), and surubim (*Pseudoplatystoma corruscans*) in the São Francisco River, Brazil (Godinho et al. 2007). Synchronised behaviour in species with reproductive strategies strongly linked to flow (and, therefore, somewhat opportunistic) may allow individuals to maximise their ability to successfully exploit favourable environmental conditions when they occur, thereby enhancing reproductive success (Lytle and Poff 2004). For species such as the Australian grayling that undertake synchronised movements, the predictability of movement has important implications for conservation management, such as allowing for specific management actions to maintain or protect populations during critical periods (Nemeth et al. 2006).

Our analyses also revealed different responses to flow by Australian grayling in different parts of the river system; fish in the upper reaches showed a more specific requirement for rising discharge to initiate migration than fish in the lower catchment. This is likely because fish in the lower catchment had already initiated downstream movement (fish were more likely to move on subsequent days if they have already begun moving), so flow change appears to become less important as a cue as fish move downstream. Indeed, fish in the lower reaches of the system were just as likely to move in response to negative flow changes as they were to positive flow changes. These findings suggest that environmental flow releases intended to initiate downstream migration to specific spawning areas may need to consider longitudinal variation in the migratory behaviour and requirements of resident fish. Consideration of spatial variation in behaviour may be particularly important for developing environmental flow recommendations in systems whose discharge can be regulated at several locations along the length of a river system. Although intraspecific variation in movement behaviour of fishes is an increasingly recognised phenomenon (e.g., Brodersen et al. 2008; Chapman et al. 2011), there has been little attempt to incorporate information on intra-specific variation into flow management of rivers. This is an important area for future research.

In conclusion, the empirical research and statistical modelling undertaken during this study enabled the prediction of the occurrence of fish spawning behaviour in relation to river discharge in a regulated river system. In particular, the study highlights how specific components of flows (in this case, the rising limb) and timing of flows can affect migration and spawning of fish. It also highlights the importance of considering spatial and temporal aspects of fish distributions and behaviour, and flow effects when implementing and adaptively managing environment flows. Applying this type of information to the development of targeted environmental flows to facilitate migration and spawning by diadromous fish could greatly improve the long-term viability of their populations and related fisheries.

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**Conflict of Interest** The authors declare that they have no competing interests.

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