

RESEARCH ARTICLE

Impacts of fishing, river flow and connectivity loss on the conservation of a migratory fish population

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Abstract

1. Migratory species depend on connected habitats and appropriate migratory cues to complete their life cycles. Diadromous fish exemplify species with migratory life cycles by moving between connected freshwater and saltwater habitats to reproduce. However, migration increases the exposure of fish to multiple threats and it is critical that managers integrate habitat connectivity into resource management and conservation.
2. The benefit of alternative management actions was assessed for a diadromous fish, the Australian bass *Percales novemaculeata*, using a spatio-temporal population model informed by individual-based movement data. The management actions comprise seasonal closures during the spawning season, and controlling fishing pressure by limiting catch or effort.
3. The benefits of implementing seasonal closures depend upon interactions among how fishing pressure is controlled, the response of anglers to fishery regulations and river flow regimes. The results indicated that seasonal closures are ineffective if fishing pressure is merely displaced to another location or time of year. In addition, shifting seasonal closures from spawning grounds to feeding grounds increased population abundances under low flow events when fishing effort was also controlled. However, when total annual catch is limited by a fishery closure, changing the location of seasonal closure schemes had little effect.
4. The findings in this study highlight the need for flexible management strategies that account for migratory movements and respond both to variations in connectivity (e.g. river flow regime) and direct pressures on survivorship (e.g. exploitation). As the implementation of one management action (e.g. fishing or water regulation) could affect the influence of another management action, this study emphasizes the importance of cooperation between resource managers in conserving migratory species.

KEYWORDS

acoustic telemetry, animal movement, conservation, diadromy, fishing regulation, human behaviour, water management

1 | INTRODUCTION

Migration is central to the life history of many species, but dependence on movement through a chain of intact habitats is expected to increase species vulnerability to multiple threats (McDowall, 1999). Migratory life cycles are exemplified by diadromous fish, which migrate between freshwater and saltwater habitats. These species are often both ecologically (Naiman, Bilby, Schindler, & Helfield, 2002) and socio-economically important (Kuroki, Righton, & Walker, 2014), but they

suffer from the interactive impacts of many threats (McCleave, 2001). For instance, overfishing, pollution, habitat loss and climatic change in the oceans and rivers have contributed to the decline of diadromous fish such as Chinook salmon *Oncorhynchus tshawytscha* (Hilborn, 2013) and European eel *Anguilla anguilla* (Kettle, Asbjørn Vøllestad, & Wibig, 2011). Diadromous fish are also susceptible to a loss of connectivity between habitats: dams block migration pathways (Rolls, 2011), and abstraction of water from rivers can alter migratory cues (Murchie et al., 2008), and reduce recruitment (Tanimoto, Robins,

O'Neill, Halliday, & Campbell, 2012). Furthermore, both barrier and flow modification may delay fish migration (Milner, Solomon, & Smith, 2012). Diadromous fish are therefore vulnerable to direct impacts on their populations and habitats, as well as impacts that threaten freshwater to saltwater connectivity.

A challenge for managing diadromous fish populations is to quantify increased likelihood of population persistence from actions that improve connectivity or reduce fishing pressure. The first steps are determining habitat use (McDowall, 1999) and quantifying species' movements between habitats (Pritt et al., 2013). However, changes in movement patterns do not directly translate to changes in population persistence. Quantifying the improvement of management actions to population persistence requires integrating information on how these actions facilitate connectivity and reduce direct impacts such as mortality.

Population modelling is a commonly used tool in fisheries management to model the direct impact of fishing on populations (Scheuerell et al., 2006). However, the effect of altering connectivity (Saunders et al., 2015) and the success of spawning migrations (Rideout & Tomkiewicz, 2011) are rarely integrated in population models. If spawning migrations are disrupted, fish might delay spawning (or have a failed spawning opportunity) until environmental conditions are suitable, which could influence the effectiveness of management. For example, reduced river flows cause the spawning migration of Australian bass *Percales novemaculeata* to cease (Harris, 1986) and delay the migration of Atlantic salmon *Salmo salar* (Solomon & Sambrook, 2004) during dry years. Furthermore, the response of fishers to fishing regulations might lead to unforeseen outcomes if fishing pressure increases at times and places where it is not prohibited, although this issue has received relatively little attention in models used for management plans (Fulton, Smith, Smith, & van Putten, 2011). To create more accurate population models for migratory fish species, it is therefore important to consider connectivity, delayed migration, failed spawning opportunity, and the response of both fishes and anglers to fishing regulations.

Here, a population model for migratory species that integrates parameters estimated from telemetry data with population traits was developed to simulate how different management strategies affect population persistence of a modelled migratory fish population. Specifically, the impacts of migration barriers, modified migratory cues, and fishing, on a migratory fish population were explored. The model helps address a key question for the conservation of migratory species of how stressors at one stage of the migratory cycle affect the overall population dynamics (O'Connor & Cooke, 2015). Australian bass, a species native to south-eastern Australia, was used to illustrate the application of this model.

2 | METHODS

2.1 | Case study for Australian bass

The Australian bass is catadromous, meaning individuals live in fresh water but spawn in salt water (Harris, 1987). Mature adults migrate from upstream freshwater areas to estuaries where they spawn during

autumn and winter. After 2–3 months in the estuary, juveniles migrate upstream the following summer to mature (Harris, 1986).

Peaks in freshwater flow have a primary role in controlling recruitment in Australian bass (Gowns & James, 2005) by affecting gonad maturation (Harris, 1986), migration initiation (Reinfelds, Walsh, van der Meulen, Gowns, & Gray, 2013) and larval survivorship (Harris, 1986). The abundance of Australian bass declined significantly after European settlement (Harris, 1983), and this species has suffered from multiple human interferences including water abstraction, artificial barriers, habitat destruction, pollution and introduced species (Jerry, 1997). Predicted changes in rainfall regimes through climate change might have additional impacts on the population by decreasing freshwater flow in estuaries (Gillanders et al., 2011).

Bass are only fished recreationally and different fishing regulations and water management plans are implemented across three of the Australian states that encompass the species' natural range. In the state of Victoria there are no closed seasons to bass fishing; in New South Wales bass fishing is prohibited during the spawning season in rivers below freshwater impoundments; in Queensland, bass fishing is prohibited during the spawning season and in tidal waters. To predict how regulations on fishing pressure, seasonal closures and river flow regimes affect fish abundance, a population model that accounted for shifts in angler behaviour was developed. While information on bass is at present insufficient for a quantitative stock assessment, the model provides guidance on interactions among fishing regulations and water management plans that may aid management agencies in setting priorities for their activities across these different issues.

2.2 | Population model with migration dynamics

The fish population model is based on a delay-difference model (Deriso, 1980) – a semi-age-structured model that simulates abundance over time based on survival and recruitment. A migration component was added to the model such that fish moved between the feeding and spawning grounds and there were two discrete stages of mortality in each location. The model tracked fish as they migrated from the feeding ground to the spawning ground and the return both of spawning adults and new recruits (Figure 1). This model took account of non-migrants such that fish could remain in feeding grounds or spawning grounds throughout seasons. The population in the feeding ground in year $t + 1$ was the sum of non-migrants, U_t , new recruits with a 4-year lag, R_{t-4} , and returning post-spawners, P_t :

$$N_{t+1} = U_t + R_{t-4} + P_t \quad (1)$$

The number of non-migrants, U_t , was.

$$U_t = N_t s_{f1} (1 - c_1) s_{f2} \quad (2)$$

where s_{f1} is the survivorship in the feeding season, s_{f2} is the survivorship of non-migrants in the spawning season and c_1 is the proportion of fish that migrated to spawn.

The abundance of spawning adults was.

$$S_t = (N_t s_{f1} c_1 s_m + P_{t-1} s_{s1}) s_{s2} \quad (3)$$

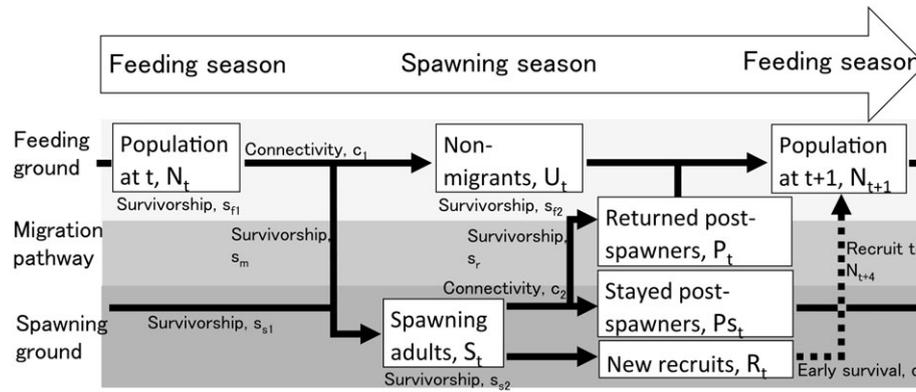


FIGURE 1 Population dynamics model for diadromous fish

where $P_{S_{t-1}}$ is the number of post-spawners that remained in the spawning grounds.

($P_{S_t} = S_t (1 - c_2)$), s_m is the survivorship during migration, s_{s2} is the survivorship of migrants in the spawning season, c_2 is the proportion of post-spawners that migrated back to feeding grounds after the spawning season and s_{s1} is the survivorship of remaining post-spawners during the feeding season.

New recruitment (R_t) was calculated using a Beverton–Holt recruitment function with parameters $a = E_0(1 - h)/4hR_0$ and $b = (5h - 1)/4hR_0$, in which E_0 is the abundance with no fishing, R_0 is the recruitment with no fishing and h is the steepness of the stock recruitment curve; defined as the proportion of R_0 produced by 20% of the E_0 (Mace & Doonan, 1988). The Beverton–Holt function was chosen because it has been successfully applied to barramundi, another Australian native fish species that shares some similarities in life history (i.e. catadromous, high fecundity, longevity >20 years and maturity at 5–6 years) (Tanimoto et al., 2012) and there is no reason to believe that recruitment rates would decline at very high spawning biomass. In addition, two parameters were incorporated to represent the early survivorship of new recruits, d , and the migration survivorship of post-spawners, s_r , when they move back to the feeding ground. The number of new recruits was.

$$R_t = d S_t / (a + b S_t) \quad (4)$$

and the number of post-spawners returning to the feeding ground was.

$$P_t = S_t s_r c_2 \quad (5)$$

A lag of 4 years was applied to allow recruits to join the adult population, because female bass are known to mature around age 5 (Harris, 1986).

Survivorship in feeding and spawning grounds (s_f and s_s) were calculated as $e^{-(F+M)}$. This was composed of an instantaneous fishing mortality rate, F , and an instantaneous annual natural mortality rate, M . The same natural mortality rates were applied on feeding and spawning grounds because no significant differences in mortality rate are observed between males and females collected from a variety of habitats (Harris, 1988). Natural mortality rates were assumed fixed across age classes as in previous studies (Harris, 1988; Morrongiello, Walsh, Gray, Stocks, & Crook, 2014). Fishing mortality was derived from Smith, Baumgartner, Suthers, Ives, and Taylor (2012) and Wilde and Sawynok (2005), and natural mortality was estimated as the mean of previous studies (Harris, 1988; Smith et al., 2012; Wilde & Sawynok, 2005). The spawning season is approximately 4 months (i.e. winter), therefore survivorships during the spawning season (s_{f2} and s_{s2}) were calculated as $e^{-(F+M)^{(1/4)}$, and during the feeding season (s_{f1} and s_{s1}) as $e^{-(F+M)^{(3/4)}$.

Life history traits and parameters were extracted from previous studies of the same or similar species (Table 1). Many parameters are

TABLE 1 Parameters used in simulation of Australian bass for figures. Numbers in parentheses indicate values tested in sensitivity analyses and the ranges of values. References: 1. Wilde and Sawynok (2005), 2. Harris (1988), 3. Smith et al. (2012), 4. Tanimoto et al. (2012), 5. Reinfelds et al. (2013)

Parameter	Values (range for testing)	Reference
Natural mortality rate, M	0.15 (0.02–0.3)	1, 2, 3
Fishing mortality rate, F	0.1 for lower; 0.2 for higher mortality (0.02–0.3)	1, 3
Steepness, h	0.7 (0.5–0.9)	4
Virgin population, E_0	10 000	Assumed, fixed
Virgin recruitment, R_0	40% of virgin population	2
Connectivity stochastic variation, v	0.05 (0–1)	Assumed, fixed
Catch amount	400 for lower; 800 for higher catch (300–1000)	Assumed, fixed, which produced comparable abundances to assumed mortality after 10 years simulation time
Proportion of post-spawners remaining in the spawning grounds	38% (without barriers); 86% (with barriers)	5; field data in this study

poorly known for bass, so the sensitivity of key findings was explored across ranges of plausible parameter settings. The survivorships during migration (s_m and s_r) were set to 1 because the migration distance for bass is relatively short and there was no observed migration mortality in field tagging studies. While we acknowledge that in general fishing mortality on bass may be low in many systems (Wilde & Sawynok, 2005), here a range of fishing mortality rates from the literature was applied to quantify the sensitivity of abundance to fishery management more generally.

Two parameters that are influenced by river flow were used in the model: c_1 was calculated as the proportion of individuals moving in response to increases in river flow extracted from fish tracking data (described below in the section 'Fish movement and connectivity'). A linear positive relationship was used to represent the relationship between river flow and early survivorship (d), where $d = 1$ under the maximum flow recorded. For Australian bass, positive relationships between early survivorship or the proportion of the total population as young-of-the-year (age-0) fish and river flows were observed (Growth & James, 2005; Harris, 1986).

The stochastic variation on both spawning migration (c_1) and recruit survivorship (d) was also modelled to represent the effect of annual flow variation. As no data were available on how bass abundance varied temporally, simulations with a range of standard deviations from normal distributions (v in Table 1) in c_1 and d were analysed.

2.3 | Fish movement and connectivity

To estimate the migration under different river flows, individual fish movement data were obtained from an acoustic telemetry study conducted on the Logan River in south-east Queensland (Figure 2). Bass ($n = 22$, mean fork length 338 mm, range 250–465 mm) were captured in the upstream feeding grounds using electrofishing, and an acoustic tag (V13-1X or V9-1X, VEMCO, Halifax, NS, Canada) was inserted surgically into the abdominal cavity following Walsh, Gray, West, and Williams (2011). The movements of tagged fish were then tracked using a network of omnidirectional underwater hydrophone receivers ($n = 32$) deployed between 42 km and 131 km from the river mouth and maintained by the Queensland Government's Department of Natural Resources and Mines. Further details on the acoustic telemetry study can be found in Harding et al. (2017).

How the proportion of downstream migration (c_1) varies with flow volumes and how this relationship differs between areas of high connectivity (without barriers) and areas of low connectivity (with barriers) were estimated from the tagging data. The release sites for tagged fish and the downstream spawning grounds were separated by two artificial barriers: Cedar Grove weir and South Maclean weir, positioned approximately 81 km and 71 km from the river mouth. The times when fish arrived at the receiver above the upstream Cedar Grove weir and below the downstream South Maclean weir were recorded and the corresponding river flow data (mean daily flow in cumecs, $m^3 s^{-1}$) were extracted to create curves relating the cumulative proportion of fish migrating with the flow. The river flow rate required to initiate the initial downstream movement was assumed to represent the spawning migration without interference by barriers. The river flow required for fish to pass two weirs, and move toward

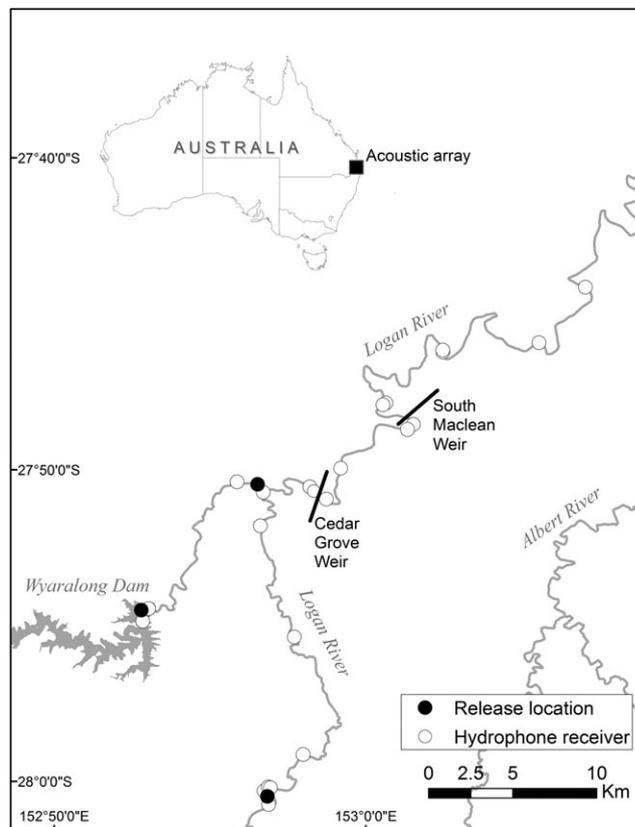


FIGURE 2 Fish movement survey sites

the estuary represented the flow required for migration with barriers. Data on downstream movements of tagged fish between hydrophones located in the upstream feeding grounds, and between hydrophones located immediately upstream of Cedar Grove weir and downstream of South Maclean weir were extracted using the V-Track software in R (Campbell, Watts, Dwyer, & Franklin, 2012). Flow data from the gauging station at Cedar Grove weir were recorded (unpublished data, Seqwater 2016) to parameterize the relationship of fish migration and river flow and examine the effect of migration barriers. A range of values based on the tracking data, and published estimates from a different river system (Table 1), were provided to represent the proportion of fish that returned to feeding grounds from spawning grounds (c_2).

2.4 | Scenarios for analysis

Simulations were run for two fishing regulation scenarios, crossed with four scenarios for seasonal closures and two alternative behavioural responses by anglers. For each of these scenarios the mean river flow was varied, with standard deviations described above, to simulate the theoretically possible full range of managed flow rates. The river flow variable represented the magnitude of river discharge pulse (as daily mean flow) during the spawning season. The abundance across scenarios was compared by running numerical simulations until the population reached equilibrium (i.e. steady state).

The fishing regulation scenarios included management with annual catch limitation (Experience sets 1 & 2 in Table 2) and management with fishing effort limitation (assigned fishing mortality of 0.1 and

TABLE 2 The assumptions underpinning the four experience sets analysed

Experience set	Fishing pressure regulation	Seasonal closure in spawning season	Anglers' behaviour	River flow regime
1	Catch limitation	Varied: None to all closed	No displacement	Varied: High to low
2	Catch limitation	None to all closed	Displacement	High to low
3	Effort limitation	None to all closed	No displacement	High to low
4	Effort limitation	None to all closed	Displacement	High to low

0.2, Experience sets 3 & 4 in Table 2). With effort limits, catch changes in proportion to population size. For each fishing regulation scenario, four seasonal closure scenarios were simulated to represent different management schemes applied across the natural range of Australian bass: (1) no closure, (2) spawning ground closure, (3) feeding ground closure and (4) all-habitats closure during the spawning season. The displacement of fishing pressure was also varied to represent the responses of anglers after seasonal closures were implemented (anglers' behaviour). In Experience set 2 and 4, total fishing pressure (catch or fishing effort) was fixed each year regardless of the seasonal closure scheme ('Displacement' in Table 2). After a seasonal closure begins, the fishing pressure (catch or effort) in that closed area will be evenly distributed over other non-closed seasons/fishing grounds so that the same overall annual catch or effort is maintained. In Experience sets 1 and 3, there was no displacement of fishing pressure, so the catch or effort in closed area(s) was set to zero while others remained ('No displacement' in Table 2). Different fishing pressures from feeding to spawning ground on every scenario were applied to compare the effect.

Four experience sets were developed to simulate how fishing regulations (catch or effort limitations, crossed with seasonal closures) and flow regime affects the whole population (included fish in feeding and spawning grounds) over a period of 10 years (Table 2). The mean of 1000 stochastic runs per scenario was calculated. Biological parameters such as mortality and the parameters in stock-recruitment relationships, and fishing regulation parameters were tested as part of a sensitivity analysis (percentage changes in population abundance when certain parameters changed 50%, ranges shown in Table 1). The influence of these parameters on population abundance, recruitment and vulnerability to disturbance were then compared. Vulnerability to disturbance represented the rate of population change through time under flow reduction when other parameters/disturbances were fixed. All scenarios and analyses were run in R programming language version 3.2.3 (R Core Team, 2015).

3 | RESULTS

3.1 | River flow and spawning migration

Of the 22 tagged bass (mean fork length 348.2 mm, range 278 to 465 mm) that exhibited a downstream migration, the majority (86%) initiated their migration under relatively low river flow ($< 20 \text{ m}^3 \text{ s}^{-1}$). This suggests that a small pulse of freshwater discharge can initiate spawning migrations in natural river systems with high connectivity (Figure 3). However, most tagged fish were unable to cross the two weir systems under medium and low flows ($< 50 \text{ m}^3 \text{ s}^{-1}$). Larger

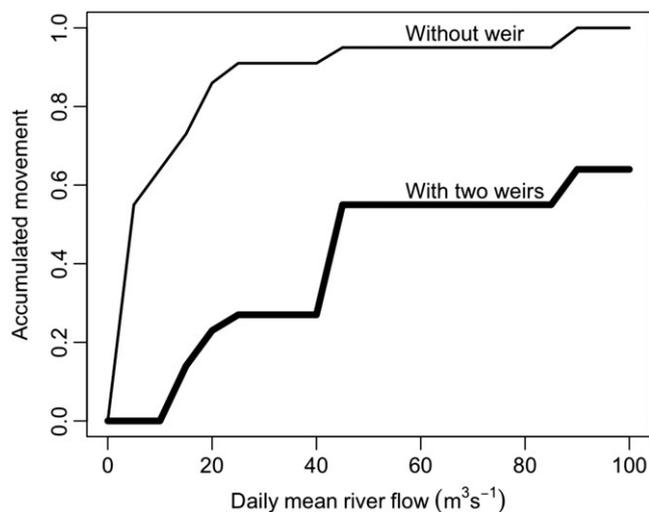


FIGURE 3 The empirical relationship between fish movement (0 means none of the fish move; 1 means all fish move) and river flow (daily mean river flow, $\text{m}^3 \text{ s}^{-1}$) in areas of river with high connectivity (without weirs; thin line) and areas of river with low connectivity (two weirs; thick line). This relationship was used as the variable c_1 in population modelling

discharges ($> 50 \text{ m}^3 \text{ s}^{-1}$) were required for around two-thirds of tagged fish to move across two artificial barriers. Around one-third (36%) of the fish were trapped in upstream habitats by barriers even under high river flow ($100 \text{ m}^3 \text{ s}^{-1}$).

3.2 | Fishing regulations and river flow regimes

Higher fishing pressure, reduced flow and reduced connectivity due to weirs, all reduced fish abundance (Figure 4, 5). However, the population outcome when fishing pressure was managed depended on how water flow and river connectivity were managed.

Under a catch limitation experience set, seasonal closures benefited the population when there was no displacement of fishing pressure (Figure 4a–d). Furthermore, seasonal closures could offset the negative effects of low connectivity or low flow. Closing all habitats maintained around 1700 more fish than no closures across all flow regimes. However, the effectiveness of closing the feeding or spawning grounds varied with local fishing pressures: closing the habitat with the higher fishing pressure maintained higher fish abundance. Feeding ground closures maintained higher abundances under low flow ($< 10 \text{ m}^3 \text{ s}^{-1}$) than spawning ground closures across most experience sets (Figure 4, 5) because more individuals stayed in feeding grounds instead of migrating downstream during the spawning season under low flows.

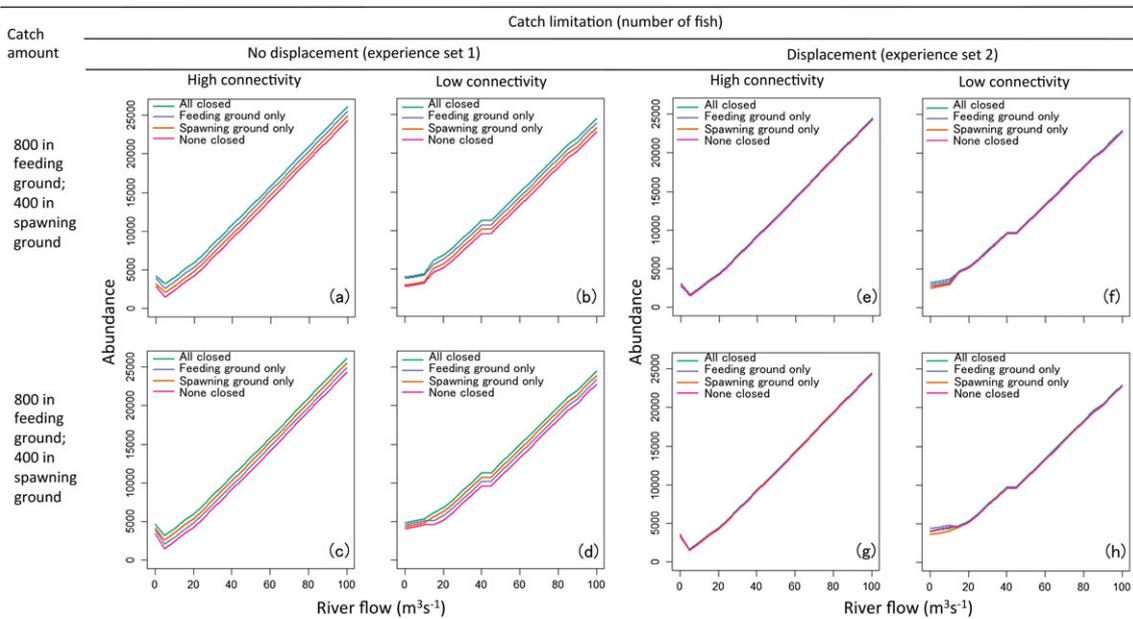


FIGURE 4 Mean population abundances under changing river flow with limits on catch. For example, (a) represents how population abundances change with river flow when no fishing displacement, high connectivity (no weirs) and catch amount is 800 in feeding ground and 400 in spawning ground

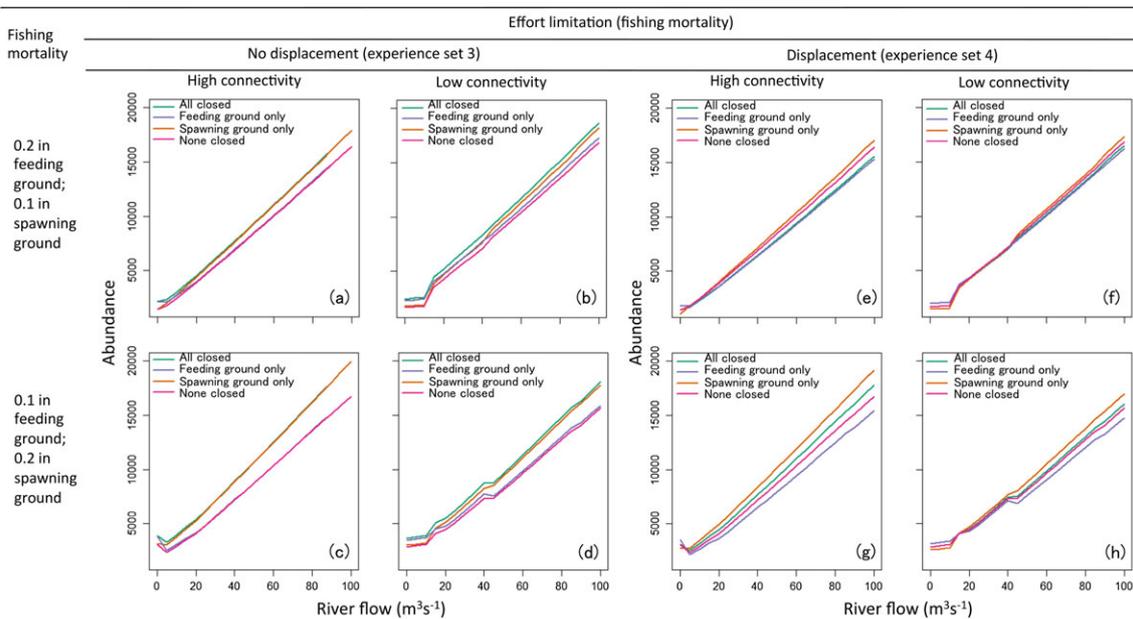


FIGURE 5 Mean population abundances under changing river flow with limits on effort (fishing mortality). For example, (a) represents how population abundances change with river flow when no fishing displacement, high connectivity (no weirs) and fishing mortality is 0.2 in feeding ground and 0.1 in spawning ground

With limits on fishing effort, seasonal closures increased abundance if there was no displacement of fishing pressure (Figure 5a–d). For example, while river flows $\sim 100 \text{ m}^3 \text{ s}^{-1}$ were required to maintain a population of $\sim 16\,000$ individuals in the absence of fishery closures, the closure of spawning grounds resulted in equivalent abundance estimates if flows were as low as $\sim 80 \text{ m}^3 \text{ s}^{-1}$ (Figure 5c). Closing the spawning grounds maintained a larger bass population size than closing the feeding grounds when river flows were medium to high.

The effectiveness of seasonal closures was reduced when fishing pressure was displaced (included both catch and effort limits, Figure 4e–h and Figure 5e–h). With displacement and catch limits all closure schemes became similar across all flow regimes (Figure 4e–h). Thus, seasonal closures could no longer offset the effects of low flow or weirs on abundance. The most effective way to increase abundance estimates with displacement was to increase flow or improve river connectivity when river flows were $>40 \text{ m}^3 \text{ s}^{-1}$. However, low connectivity (with weirs) maintained higher population

abundance if flows were low ($< 40 \text{ m}^3 \text{ s}^{-1}$) because weirs trapped more adult fish in habitats downstream of barriers that can contribute to following recruitment without the requirement of high river flows to overcome migration barriers.

When fishing effort was limited but displacement of effort occurred, the most effective season to close depended both on flow magnitude and the degree of river connectivity (weirs) (lines for seasonal closures cross in Figure 5e–h). Spawning ground closures were most effective when river connectivity and flow were both high. However, under an extreme low flow regime ($< 10 \text{ m}^3 \text{ s}^{-1}$, Figure 5e–g), feeding ground closures maintained higher bass abundance because most individuals stayed in the feeding grounds. In contrast to catch limitation (Figure 4a, b vs 4c, d), the differences between local fishing pressures influenced the relative effectiveness of closing all habitats and no seasonal closures (Figure 5a, b vs 5c, d). To summarize, the optimal scheme for fishery closures depended on the flow regime, because flow drove migration between fished and unfished habitats.

Sensitivity analysis showed that most biological and fishing-related model parameters influenced population abundance more strongly than recruitment (Table 3). In most cases, if a parameter decreased population abundance, then the vulnerability of a population to flow reduction increased. For example, increasing the natural mortality lowered simulated population abundance and raised the vulnerability to flow reduction. One exception was that while increased steepness (h) lowered population abundance, it also made the population less vulnerable to flow reduction. This was because a greater steepness makes recruitment depend less on population abundance, so that the compensatory response of a population to disturbance is stronger.

4 | DISCUSSION

A spatio-temporal population model and integrated fish movement data were used to simulate population dynamics of Australian bass under different management regimes. The results emphasize the importance of developing integrated management strategies that account for different river flow regimes, habitat connectivity and fishing pressure. For instance, closing all habitats to fishing during the spawning season could retain the greatest bass abundance if there were no displacement of fishing pressure. However if anglers shifted their efforts to other times of the year, spawning ground and feeding

ground closures conserved higher abundances under high and low flow, respectively. The population model highlights two important interactions in conserving and managing migratory species. The first is the beneficial effect of increasing habitat connectivity for populations over space and time. Second, uncertainties in how resource users respond to closures influence the impacts of disturbances on populations (Fulton et al., 2011).

This approach also demonstrates how tracking data can be combined within population models to predict the response of threatened species to multiple human impacts. Acoustic telemetry offers a solution for researchers studying aquatic organisms, because it provides high-resolution data (both in time and space), long-term monitoring (up to 10 years), remote measurement, and it is relatively cost-effective (Hussey et al., 2015). However, tracking studies alone do not show how human impacts on large-scale movements such as migration can affect population persistence. Here, individual fish movement data gathered using acoustic telemetry were incorporated into a population model. The findings in this study highlight some new research directions for animal movement studies. For example, telemetry techniques could be used to unveil latent threats (e.g. river flows or connectivity in this study), which may not be the direct cause of death but could influence a population's exposure to other threats, such as fishing. Once quantified, the emerging impacts and interactions of both direct and indirect disturbances can be simulated through population modelling. Because the number of studies using electronic devices, as well as accessibility to archival telemetry datasets has increased in recent years (Campbell et al., 2015; Dwyer et al., 2015), this modelling framework could be applied to optimize management for other migratory species.

4.1 | Connectivity change and consequences for management

Migratory species are susceptible to human activities that change their spatio-temporal distribution. The results indicated that the effectiveness of spawning ground and feeding ground closures varied according to river flow, migration barriers and local fishing pressures. Spawning ground closures maintained greater fish abundance than closing feeding grounds if river flows were able to trigger and facilitate spawning migration over barriers. Conversely, if river flow was low so that migration was not triggered or was blocked by barriers, the bass population was more vulnerable to fishing in the feeding grounds. Closures in the

TABLE 3 Sensitivity of mean population abundance, recruitment and vulnerability to key model parameters. Values indicate percentage change when associated parameter increases (\uparrow) 50%

Parameters (\uparrow)	Sensitivity		
	Population abundance	Recruitment	Vulnerability to flow reduction
Biological			
Mortality in baseline, M	-35%	-6%	7%
Steepness, h	-12%	-12%	-1%
Unfished population, E_0	-6%	-6%	1%
Unfished recruitment, R_0	56%	56%	-1%
Stochastic variation, v	-1%	-0.2%	1%
Fishing regulation			
Annual catch	-21%	-4%	14%
Fishing mortality	-19%	-5%	2%

habitat that had higher fishing pressure increased fish abundance. Therefore, understanding the spatio-temporal dynamics within a species' migration network and where humans have the greatest impact can reveal where management actions will have the greatest benefit for conserving a species (McDowall, 1999; Miles, Walsh, Butler, Ueda, & West, 2013).

Changes in human behaviour can influence the expected outcome of management actions in fisheries (Fulton et al., 2011) and land management (Meyfroidt, Rudel, & Lambin, 2010). The results here suggest that the effectiveness of seasonal closures can vary depending on whether (1) anglers reduce their overall effort or their effort is displaced to other times and places, and (2) fishing pressure is limited by catch or effort, which are comparable with previous studies (Horwood, Nichols, & Milligan, 1998; Metcalf, Moyle, & Gaughan, 2010). Policies that prevent displacement and mitigate overall exploitation rate are key to the success of resource management (Greenstreet, Fraser, & Piet, 2009; Meyfroidt et al., 2010).

River flow can be a dominant driver of fish abundance (Gillson, 2011) and this effect might be more prevalent in systems where fishing mortality is low, such as Australian bass in catch-and-release recreational fisheries (Wilde & Sawynok, 2005). Near linear declines were found in bass abundance with reductions in flow rate, suggesting that human impacts on river flow have had a greater effect on bass abundance in this system than fishing pressure. River flow is one of the main factors influencing the physiology, movement behaviour and habitat quality of many aquatic species (Milton, 2009; Murchie et al., 2008), and it also affects the productivity of fisheries (Gillson, 2011). As an example, reducing river flow might significantly decrease the fishery catch of barramundi (Tanimoto et al., 2012). Reducing river flow might amplify the effect of existing barriers (Milton, 2009) or create new barriers for migratory species (Gillanders et al., 2011; Jaeger, Olden, & Pelland, 2014). Although the spawning migration of Australian bass can be initiated by small flow pulses (Harding et al., 2017; Reinfelds et al., 2013), large river discharge events are required for fish to pass over barriers in this study area (Harding et al., 2017). Indeed, high river flows may facilitate fish migration over barriers (Nunn et al., 2017). Therefore, focusing on fishing pressure regulation without simultaneously maintaining river flow (or creating artificial flow pulses) and connectivity could fail to maintain population persistence of Australian bass or other diadromous fish species (McCleave, 2001; Parrish, Behnke, Gephard, McCormick, & Reeves, 1998).

4.2 | Model generalizations and assumptions

A simplified population model was used in this study to capture the migratory life history structure for diadromous fish that necessitated several assumptions. First, density dependence was incorporated only in the early survivorship component of the model, which is comparable with the original delay difference model and other models of diadromous fish (Piou & Prévost, 2013). Second, a linear relationship was used to represent changes in recruitment with river flow. While previous studies suggested a positive relationship between river flow and recruitment for Australian bass (Growth & James, 2005; Harris, 1986) and other species with similar reproductive behaviour such as estuary perch (Morrongiello et al., 2014) and barramundi (Tanimoto et al., 2012),

long-term studies are needed to explore the full range of flows (e.g. dome-shaped curve for black bream *Acanthopagrus butcheri* (Jenkins, Conron, & Morison, 2010)). Third, the empirical movement data from 22 fish were used to show how movement information can be used in population models. The modelling assumed that migratory variation is low in this system because all migrants showed strong consistency for moving at the same time under high flow events during the study period. While individual variations in movement have been observed in some cases (Reinfelds et al., 2013), exploring the relationship between fish movement and river flows from larger sample sizes in longer study periods by statistical methods (e.g. generalized linear mixed model in Harding et al., 2017) could be applied to this model.

The influence of river flow on migration and habitat connectivity was applied only to spawning migration and recruitment survivorship, but not to the migration of post-spawners and juveniles. At present there is a lack of long-term movement data of post-spawners and juveniles for many fish species (Milton, 2009; Morrongiello et al., 2011). Although river flow could facilitate post-spawning migration (Enders, Scruton, & Clarke, 2009), adult bass commonly make the return migration from spawning grounds under base-flow conditions (Reinfelds et al., 2013). As juveniles may be more vulnerable to barriers owing to small body size and weak swimming ability (Stuart, Zampatti, & Baumgartner, 2008), the recruitment to the upstream population in a system with multiple barriers could be lower than the results of the present study. How river flow interacts with barriers to influence the upstream movement of juveniles requires further study (Doehring, Young, & McIntosh, 2012). Although the results showed that barriers could maintain population abundance under low river flows by trapping fish in downstream habitats, the contribution of individuals in downstream habitats to recruitment might be overestimated. Differences in growth rate and body size among individuals in different feeding habitats have been observed in some migratory fish species such as Australian bass (Harris, 1987), salmonids (Phillis et al., 2016) and temperate eels (Cairns, Secor, Morrison, & Hallett, 2009). In the longer term, barriers may act as a type of artificial selection that influences the evolutionary process of migratory fishes (Junge, Museth, Hindar, Kraabøl, & Vøllestad, 2014; Phillis et al., 2016). Different mortality rates and stock-recruitment parameters will be required for these non-migrants when data are available.

4.3 | Future perspective and conclusions

This study suggests that conserving migratory fish requires coordinated management between different water managers and fishery managers. Previous studies indicate the importance of incorporating water management into conservation or fishery planning (Brown, Kimmerer, & Brown, 2009; Tanimoto et al., 2012). Because climate change and population growth are likely to increase competition for water resources between human society and other species (Gillanders et al., 2011; Vörösmarty, Green, Salisbury, & Lammers, 2000), it is critical to assess the dependence among different management approaches. This study provided a quantitative approach for evaluating possible cooperation opportunities between water and fishery managers. Further studies on location-specific fishing pressure (e.g. fishing mortality, catch-and-release rate, and post-release mortality), biological parameters (e.g. stock-recruitment relationship and natural

mortality), and long-term movement data (e.g. movement of juveniles and post-spawners with flows and barriers) could improve the accuracy of the model and allow it to be used to provide quantitative advice to management, in an analogous fashion to fishery stock assessments. While the response of species to barriers and flows varies with species' life history and dispersal patterns (Rolls, Ellison, Faggotter, & Roberts, 2013), this model may be applied to other species by using species-specific parameters. For example, increasing the natural mortality rate of post-spawners could be used to simulate semelparous species such as lampreys, freshwater eels, and some salmonids (Crespi & Teo, 2002).

In conclusion, this study introduces a population dynamics model that incorporates habitat connectivity and disturbance scenarios to understand the effectiveness of various fishing regulation strategies on population persistence in the Australian bass. The results suggest that while current strategies vary in their effectiveness, the response of anglers and indirect stressors such as water resource development must be taken into consideration to formulate more comprehensive and effective management and conservation plans.

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