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ARTICLE

Freshwater Ecology

Movement behavior of a threatened native fish informs flow management in a modified floodplain river system

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Abstract

Movement is a key driver of the distribution of animals and the structure of populations, communities, and ecosystems. Habitat loss and fragmentation can compromise movement and contribute to population declines. However, there is often insufficient knowledge about when, why, and where animals move, particularly in highly modified environments. We present results from an 8-year study on the movement behavior of Murray cod *Maccullochella peelii*, an Australian freshwater fish species that has undergone major declines due in part to river flow regulations. We studied movement within and between different habitat types in a highly modified floodplain ecosystem in the lower Murray River to (1) identify the key environmental conditions associated with movement, (2) examine how a new regulating structure can be managed to influence movement behavior, and (3) explore movement mediated recovery following a hypoxic event. Movement within and between an anabranch and main river channel habitats increased during the core spawning period and during elevated discharge. The likelihood of Murray cod moving to an anabranch system from the Murray River declined substantially following construction of a new flow regulating structure (a weir and vertical slot fishway). Managed flows delivered through the anabranch after regulator construction in accordance with targeted recommendations (time-of-year and magnitude of discharge) increased the movement of adult fish within and between habitats. Finally, a hypoxic event caused not only high mortality but also resulted in a high proportion of fish migrating outside of the study reach, before returning to the system over several years. These results demonstrate how flow management can help a keystone species access habitats required to complete critical life history requirements including recovery from disturbance events. Importantly, the work provides an example of how timely and robust applied research has informed a major intervention program aimed at enhancing ecological outcomes.

KEYWORDS
conservation behavior, environmental flow, flow regulation, movement ecology, Murray cod

INTRODUCTION

Movement is a key driver of the spatial and temporal distribution of animals, affecting key processes and subsequently the structure and dynamics of populations, communities, and ecosystems (Nathan et al., 2008). Knowing how, when, and why animals move is fundamental ecological information, and there is increasing recognition that this knowledge can direct conservation and management efforts (e.g., Allen & Singh, 2016). Indeed, incorporation of movement ecology improves the likelihood that conservation and restoration actions promote population persistence in highly modified landscapes (Doherty et al., 2021; Doherty & Driscoll, 2018).

Stream fishes are ideal as model systems in which to explore the links between movement ecology and management for several reasons. First, movement is critical for many species (Crook et al., 2015), such as those that move between spawning, feeding, and overwintering habitats (Schlosser, 1991). Second, rapid technological advancements have dramatically increased our ability to study the movements of a range of species, both over relatively short periods (i.e., within individual life times) and intergenerational to evolutionary-time scales (Crook et al., 2015). Third, fish are restricted to relatively defined habitats (i.e., the stream network), which means studying their movements is more tractable than for species that inhabit more diffuse habitats (e.g., the ocean) where movement in any direction is theoretically possible. Finally, the global scale of human alteration to freshwater ecosystems (e.g., Döll et al., 2009; Vorosmarty et al., 2010), and the impacts on the ability of fish to move, highlights the importance of linking movement ecology to conservation. Understanding specific aspects about movement behavior of aquatic organisms in stream environments, particularly those which are highly modified, can therefore provide vital information to help guide management actions.

Reductions in many riverine native fish species are thought to be due in part to altered flow regimes (including widespread installation of weirs) that compromise movement pathways and fragment habitats critical for key population processes (Bice et al., 2014; Esguícero & Arcifa, 2010; Perkin et al., 2015; Sheer & Steel, 2006). Nevertheless, while shifts in ecosystem function and impacts of these river alterations relative to preinterventions are well established, migration pathways and habitat use by native species within these modified river systems is often less understood. Incorporating ecological data from modified river systems is critical to facilitate improved management, where competition between environmental and economic (e.g., irrigated agricultural crops) outcomes is high.

Here, we present the results of an 8-year study of the movement of Murray cod *Maccullochella peelii* in a highly modified floodplain ecosystem in southeastern Australia. Our study describes the movement behavior of adult Murray cod within and between different habitat types in the highly modified floodplain ecosystem in the lower Murray River; explores the key environmental conditions associated with this movement; and how a new regulating structure and its operation has and can be managed to influence movement behavior critical for key life-history processes governing Murray cod populations.

Many ecological projects are affected by unforeseen events, and this study was no exception. During field sampling, a hypoxic blackwater event occurred, dramatically lowering dissolved oxygen levels. While hypoxic blackwater events occur naturally in many streams—when flood waters inundate floodplains or dry river channels, and carbon leaches from organic matter—their frequency and severity has increased in some systems due to a combination of climatic effects and river regulation (e.g., Whitworth et al., 2012). The reductions in dissolved oxygen that subsequently occur can have lethal impacts for fish, including Murray cod (King et al., 2012; Leigh & Zampatti, 2013; Thiem et al., 2020). Consequently, we were also able to monitor fish mortality and movement in the context of understanding this disturbance and potential recovery.

Our hypotheses were that:

- Adult Murray cod would show seasonal movements during the spring spawning period (October–December), and that increased stream discharge will increase the likelihood of adult fish moving within and between anabranch and riverine habitats, based on studies from other areas (Koehn, 2009; Leigh & Zampatti, 2013; Stuart et al., 2019; Tonkin et al., 2020);
- The construction of an instream flow regulator will reduce the probability of movement by Murray cod between anabranch and main river channel habitats;
- Managed flows delivered through the anabranch in accordance with our recommendations (time-of-year and magnitude of discharge) after the construction of the regulator will enhance adult movement within and between habitats;
- Anoxic blackwater would detrimentally impact Murray cod populations, and movement would be a key process in avoidance and recovery (e.g., Thiem et al., 2020).

Collectively, we use our results to outline how the assembled movement information for Murray cod can be used to guide management in this highly modified system. More generally, we use this case study to discuss some ways in which insights from movement ecology can help inform conservation and management in highly modified aquatic ecosystems.

METHODS

Study species

Murray cod is a large (up to 1.5 m in total length and 40 kg in weight), long-lived (up to 48 years) freshwater fish, endemic to the Murray-Darling Basin (MDB) in southeastern Australia (Lintermans, 2007). The species has considerable recreational, cultural, and conservation value (Rowland, 1998), and like many large predatory freshwater fish across the globe, has undergone major declines in abundance across its range. The species occupies a broad range of flowing and standing waters (Koehn, 2009; Koehn & Nicol, 2014); however, it is considered a main river channel specialist, selecting channel habitats in the river, floodplain channels in high flood and also channels within lakes, for spawning (Koehn, 2009; Koehn & Nicol, 2014; Leigh & Zampatti, 2013).

Murray cod mature around 5 years of age and form breeding pairs (Rowland, 1998). Females lay adhesive eggs on hard substrata in austral spring (peak period October–November) when temperatures exceed 15°C (Humphries, 2005), with the eggs guarded by the male fish (Rowland, 1998). The movement of adult Murray cod within and between the main river channel and anabranches (Koehn et al., 2009; Leigh & Zampatti, 2013) appears to be largely associated with access to and quality of spawning habitat, and is cued by increasing temperature between August and November (Koehn, 2009). Increasing river discharge during this period also appears to enhance these migrations and spawning outcomes by providing cues for movement, enhancing the availability of flowing water and structural habitat for spawning and larval survival (e.g., Koehn, 2009; Stuart et al., 2019; Tonkin et al., 2020). Outside of this period, Murray cod typically exhibit high site fidelity (Koehn & Nicol, 2016).

In regulated lowland river reaches, and specific to this study, reductions of Murray cod are thought to be in part due to the installation of weirs that alter hydraulic conditions and compromise movement pathways critical for key population processes (Bice et al., 2014; Mallen-Cooper & Zampatti, 2018). This is the case in reaches such as those in the lower Murray River, which now consists of a series of weir pools (Mallen-Cooper & Zampatti, 2018). Reductions in reach-scale lotic conditions within the Murray River and conversely, creation of permanent lotic conditions in some anabranches have likely resulted in a high dependency by some riverine species on the latter. Adult Murray cod in particular, use some anabranches for spawning due to their (postregulation) unique lotic hydraulic characteristics and high density of instream woody habitat compared with weir pools in the Murray River (Henderson et al., 2013; Saddlier et al., 2007). As such, discharge and connectivity of many of these anabranches are now managed with the aim of enhancing key processes governing Murray cod populations, including adult movement (e.g., Stuart et al., 2019).

Study system

This study focuses on the Lindsay Island anabranch system of the lower Murray River in the southern MDB, Australia. The primary waterways investigated were the Mullaroo Creek, Lindsay River, Potterwalkagee Creek and Murray River between Lock 6 and Lock 8 (Figure 1). Adult Murray cod appear to rely on the upper Mullaroo Creek for spawning and recruitment due to its unique hydraulic permanent lotic characteristics (post regulation) and high density of instream woody habitat compared with sites within the lower Mullaroo Creek, Lindsay River, and Murray River (Henderson et al., 2013; Saddlier et al., 2007).

In addition to the aforementioned regulation and alteration to historic hydraulic conditions throughout the study site, there was a new regulator weir built in 2016 on Mullaroo Creek (Figure 1) to replace an old low-level rock weir/ford road crossing structure. This enabled additional control of discharge into the anabranch under varying weir pool levels in the Murray River at Lock 7. Despite also having: (1) a vertical slot fishway, (2) adjustable layflat overshot weir gates, and (3) a deep downstream plunge pool in its design, there is potential for this regulator (and future structures) to restrict fish movement (particularly downstream) and alter the hydrological and hydraulic characteristics of this reach (Saddlier et al., 2007). The influence of the new regulating structures on fish movement will be dependent on regulator and fishway operational procedures, movement dynamics, and key life-history requirements of individual fish species. Therefore, using ecological knowledge based on empirical data to guide operational procedures is an important component to facilitate future operation.

As data were collected during this research program, it became clear that movement rates of adult fish within and between anabranch habitats and the Murray River were strongly influenced by the time-of-year and discharge. As such, discharge recommendations for Mullaroo Creek were developed with the aim of enhancing movement into and within the anabranch for adult Murray cod. More specifically, the recommendations were to maintain elevated discharge within the creek at 1000–1200 Ml day^{-1} (near bank full) between September and early December (increasing from 600 Ml day^{-1} base flow).

Prior to construction of the new Mullaroo Creek regulator, the low-level rock weir/ford road crossing structure

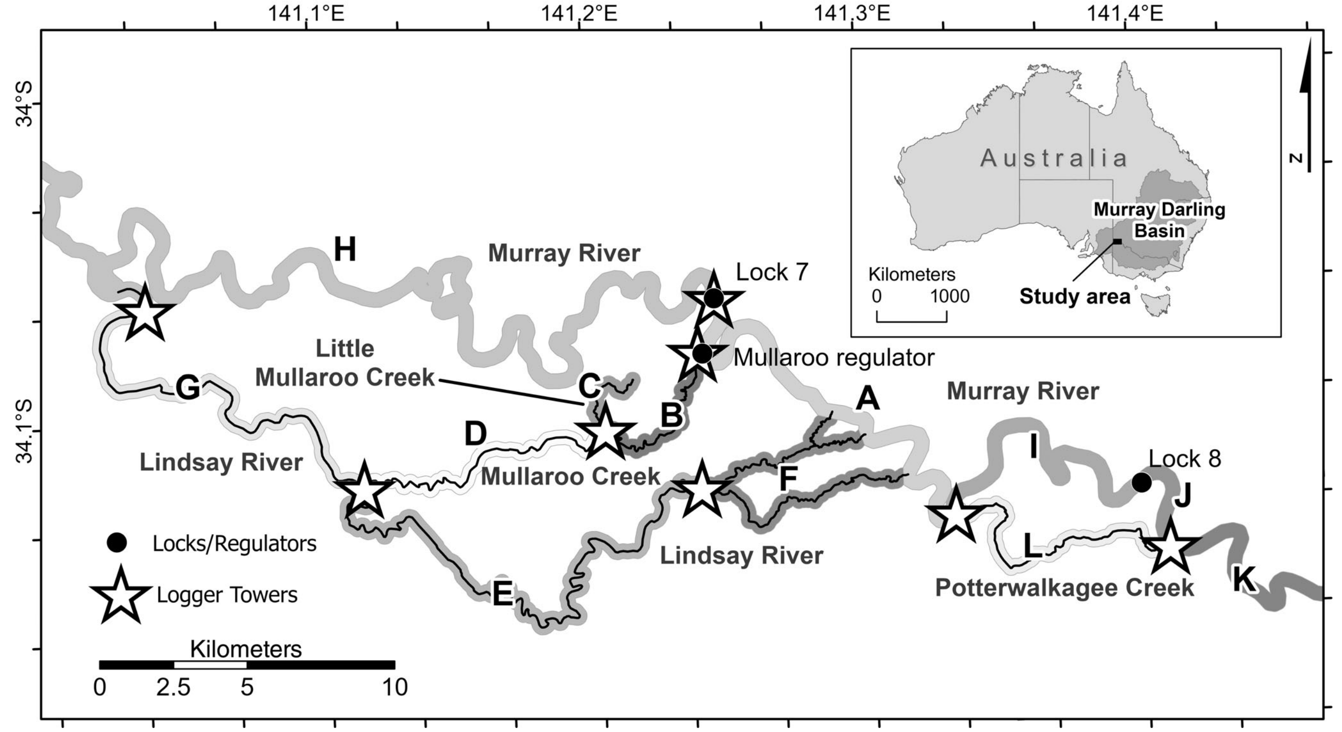

FIGURE 1 Map of the study site with letters representing fish tagging and movement zones, regulator and weir locations, and radio logging towers (stars)

passively regulated flow from the Murray River. As such, while the full width of the channel was engaged when discharge in the Murray River exceeded average irrigation demand (that generally occurred annually from September until April), there was no direct control on the flow entering the Mullaroo Creek. In recent years, there has been a shift in the management of Murray River weir pool water levels with greater emphasis on creating variability by raising and lowering pool levels. The objective is to recreate lotic habitats, improve primary productivity, and connect off-channel habitats (Mallen-Cooper & Zampatti, 2018). With the confluence of Mullaroo Creek <2 km upstream of Lock 7, weir pool variability, and particularly lowering would also change discharge into Mullaroo Creek. To regulate flows, the new Mullaroo Creek regulator weir construction, with adjustable layflat gates, allows independent control over flow at a range of Murray River weir pool heights during regulated conditions, weir pool manipulations, and natural high flows.

Flow conditions at the study site have varied considerably, ranging from stable low flow conditions for extended periods of up to 1 year, to extreme flood events (Figure 2). For example, in 2016, record rainfall in the upper catchment resulted in substantial flooding of the study area, with peak flows in the Murray River of over 80,000 Ml day^{-1} (exceeded <5% of the time historically) between 25 November and 4 December (Figure 2). This event inundated areas of the floodplain that had not been flooded for more than two decades and resulted in a widespread "hypoxic blackwater event" throughout large parts of the southern MDB (MDBA, 2016). At the study site, dissolved oxygen concentrations plummeted resulting in major fish kills in the area including large numbers of Murray cod as had been reported in other parts of the MDB (e.g., Thiem et al., 2020).

Telemetry array, fish capture, and tagging

The study region was separated into 12 zones (Figure 1) that encompassed a variety of both river and anabranch habitats and hydraulic conditions, including the moderate water velocities (>0.25 m s^{-1}) of the upper Mullaroo Creek (e.g., zone B), and semi-lotic weir pools of the Murray River (0.05–0.1 m s^{-1}; Mallee Catchment Management Authority, unpublished data). Eight data logging towers were installed along the Mullaroo Creek and Lindsay River. Each data logging tower was fitted with up to three directional antennas positioned in upstream and downstream directions on the river/creek, and a third antenna was posited toward any inflowing tributary and could receive radio signals from transmitters up to 300 m away (see O'Connor et al., 2005 for full description). Because signal strength and detection time were

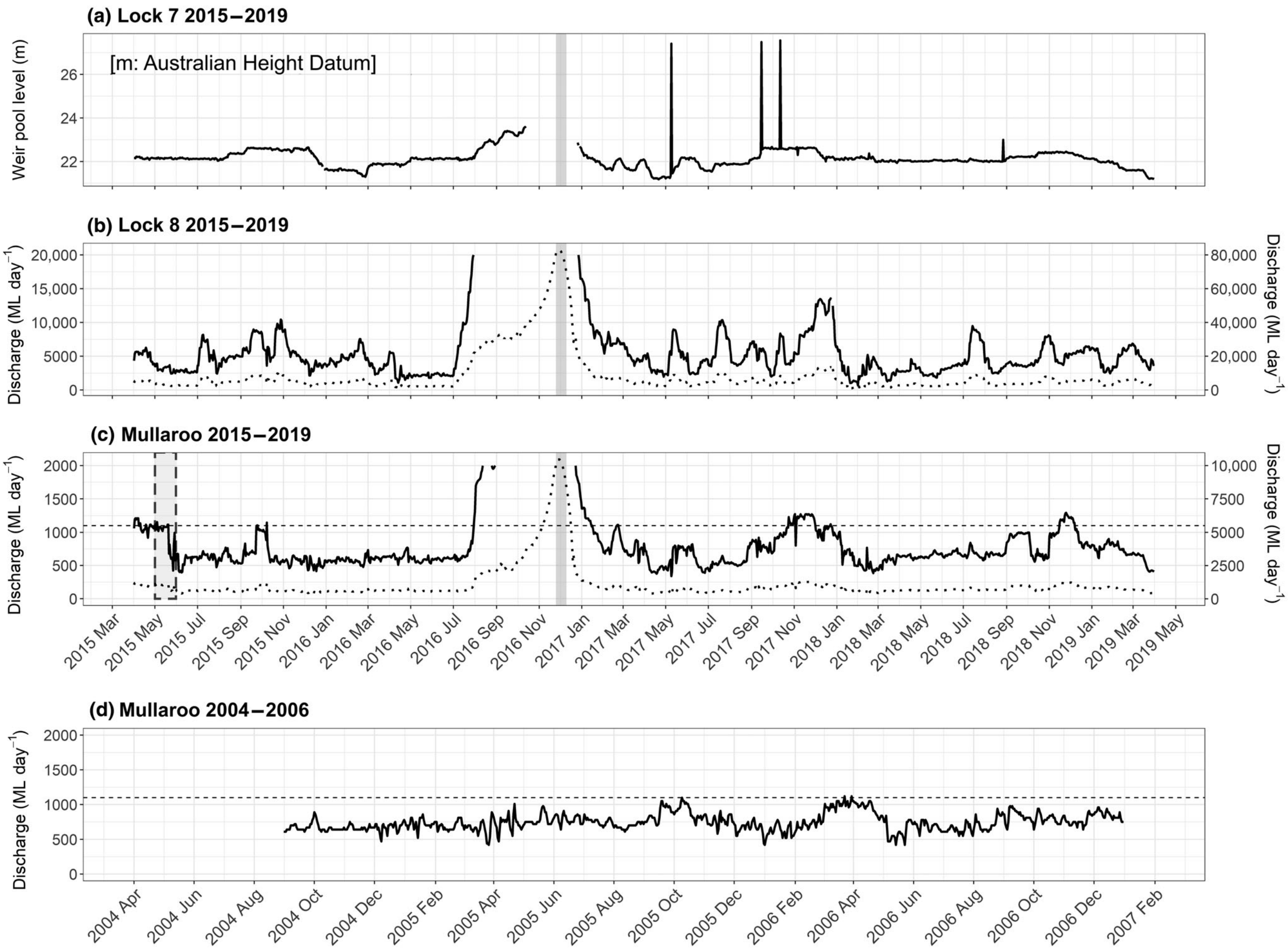

FIGURE 2 Lock 7 upstream weir pool height (m) is presented in (a). Average daily discharge (Ml day^{-1}; solid line) is shown for (b) the Murray River at Lock 8, (c) Mullaroo Creek from 2014 to 2020 and (d) Mullaroo Creek from 2004 to 2006. Full average daily discharge (dotted line) is shown in (b) and (c) on right-hand *y*-axis. Dashed horizontal line in (c) and (d) illustrates recommended minimum discharge in Mullaroo Creek to maximize fish transitions with the Murray River during spring. The vertical dark gray shaded bar represents the Blackwater event that occurred within the study area and the vertical gray dashed block indicates period of construction preceding operation of the Mullaroo Creek regulator (both periods excluded from the analysis)

recorded for each antenna, the position and direction of movement of each fish, and therefore, the exact zone a fish was occupying at any point in time could be determined. Murray cod were also manually tracked each year to verify position and to check if the transmitter was emitting a mortality signal (triggered if the fish had not moved for 168 h), therefore indicating if fish had either died (proving useful during the hypoxic event), rejected the transmitter or captured by an angler and the transmitter discarded.

Our study spanned 3 years initially (2004–2006) and then 5 years later (2014–2019). A total of 162 Murray cod were fitted with radio tags during the study, with 71 fish tagged in first period, and 91 fish tagged in the second (Appendix S1: Table S1). Most fish tagged were considered mature (>500 mm total length; Lintermans, 2007) and were captured using a Smith-Root 7.5 GPP boat-mounted electrofisher. Radiotransmitter size (14, 23, or 56 g) was determined as a proportion (<2%) of total fish body weight and operated on 150 MHz (manufactured by Advanced Telemetry Systems). Surgical procedures used to implant fish with radio transmitters broadly followed O'Connor et al. (2005). Briefly, fish were sedated by immersion in an anesthetic solution of Aqui-S at a concentration of 1.5 ml per 50 L of water. After fish were sedated, the underside of the fish was bathed with diluted (0.9% saline solution) Betadine solution to ensure the area was adequately sterile. A small incision (~2–3 cm long) was made through the body wall and a radio transmitter inserted into the body cavity of the fish, positioned so that the external aerial could be passed through the body wall approximately 3–7 cm posterior of the incision.

Once the transmitter was positioned, the incision was again bathed in Betadine solution before internal sutures were used to close the body wall. External sutures were used to close the outer incision and the entire area bathed with Betadine solution before the fish was returned to an aerated recovery tank containing a 10 g L^{-1} salt solution to limit the possibility of infection. Fish were also marked with an external identification tag (T-bar or Dart) adjacent to the dorsal fin and implanted with passive integrated transponder (PIT) tag. External tags display a telephone number for the reporting of fish capture data, which was incorporated into a fish database (Victorian fish tagging database). PIT tags have a unique individual code, which is read as fish pass PIT reading stations installed on nearby Murray River fishways (Baumgartner et al., 2010).

Statistical analysis

Murray cod transitions within and between the Murray River and anabranch habitats (Mullaroo Creek, Lindsay River, and Potterwalkagee Creek) were investigated using data generated from 82 Murray cod collated from 2014 to 2019 (detected fish from a total of 91 tagged) and 71 Murray cod from 2004 to 2006 (Saddlier et al., 2007). The first data collection period and the first year of the second period of data collection preceded the new Mullaroo regulator construction. Hydrology and water temperature data within the study area were obtained from gauges operated by WaterConnect South Australia and the MDBA (2020).

To assess the role of discharge, time-of-year, and the influence of the regulating structure on Murray cod movement, we fitted generalized additive models (GAMs) with a binomial distribution (with a logit link) to analyze the probability of fish movement between the Murray River and anabranches (between habitat movement) and among zones within each habitat (Murray River or anabranch). Specifically, Logistic Markov transition matrices incorporate the number of fish in each zone explicitly to examine relationships between the probabilities of fish moving between zones and several covariates aligned to our hypotheses. To account for the influence of time-of-year on movement (as has been previously demonstrated), we used Julian Day as a covariate, included as a smoothed term (Wood et al., 2016). Covariates used to assess the role of stream flows on movement were discharge (in megaliters per day) in the Mullaroo Creek and Murray River at Lock 7 and Lock 7 weir pool height (in meters). These were chosen because all transitions of fish outside of the major flood period (which was excluded in the analysis) encompassed the Murray River and either the upper Mullaroo Creek or lower Lindsay River. Both weir pool height and discharge (uncorrelated) were included in our assessment of fish movement within the Murray River due to recent management alterations in weir pool height aimed at modifying reach velocity (rather than discharge).

To assess the influence of the new regulating structure on movement between habitats (between the upper Mullaroo Creek or lower Lindsay River and the Murray River), we included the status of the Mullaroo regulator operation as a covariate, with three levels—preconstruction (2004–April 2015), postconstruction and operation (July 2015–March 2019; excluding flood period)—and the period during flood when gates were laid flat (August 2016–March 2017; period when the structure was not influencing the full channel width). All the analyses were conducted using the statistical program R version 3.4.4 (R Core Team, 2021). The GAMs were fitted using the package "mgcv" (Wood, 2011) with Akaike's information criterion, corrected for sample sizes (AIC_c) used to determine the model with the most evidence.

To test current recommendations of the elevated flows during spring in the Mullaroo Creek and lower Lindsay River (anabranch reaches occupied by fish outside of flood periods), we assessed the average number of movements between zones per Murray cod in the anabranches since the regulator was installed. This analysis only used data collected post-July 2015 but excluded the period where the regulator was inundated (June 2016–April 2017) due to floods. The monthly number of movements by tagged Murray cod was modeled using a negative binomial model in a Bayesian framework. Specifically, we tested if the expected number of movements was related to whether it was spring (September–November) or if the flow was greater than 800 Ml day^{-1}. While our analysis did not specifically test the 1000–1200 Ml day^{-1} recommendation for Mullaroo Creek, the 800 Ml day^{-1} was determined (using an assessment of discharge frequency) to be a suitable intermediate division between baseflows of around 600 Ml day^{-1}, and the recommended elevated discharge level. The number of movements was offset by the number of tagged Murray cod in the anabranches, to effectively give a movement rate per Murray cod per month. The effect of each variable was determined using their posterior distributions. A positive effect of a variable on the number of fish captured occurs when more of the posterior distribution is above zero, and a negative effect when more of the posterior distribution is below zero. Models were constructed in STAN (Carpenter et al., 2017) using the package brms (Bürkner, 2017). Model chains were run until the chains converged. Chains were considered converged using visual assessment and if all Gelman and Rubin's convergence diagnostic potential scale reduction factors were less than 1.05 (Gelman & Rubin, 1992).

RESULTS

Eighty-nine percent of tagged fish undertook movements outside the zone they were released (Appendix S1: Table S1). Many of the movements among zones encompassed transitions within and between anabranches and the Murray River main channel. Murray cod were detected occupying all reaches in the study area (including Potterwalkagee Creek during high flows) and displayed a high degree of spatio-temporal variability, both among and within years.

Movement between Murray River and anabranches, and impact of regulator construction

Transitions from the anabranches (lower Lindsay River or upper Mullaroo Creek) to the Murray River were influenced by day-of-year and discharge in the Mullaroo Creek (Appendix S1: Tables S2, S4, and S5). The probability of Murray cod in the anabranch staying in the anabranch was generally high (≥99% on any given day; Figure 3). However, there was a clear increase in movement rate to the Murray River during spring and early summer (September–December; ~2% per day; Figure 3a) and with increasing discharge in Mullaroo Creek (Figure 3b).

Murray cod movements from the Murray River to the anabranches (lower Lindsay River or upper Mullaroo Creek) were influenced by day-of-year and regulator status (Appendix S1: Tables S3–S5). Murray cod in the Murray River had an increased probability of movement to the anabranch in early spring and to a lesser extent in winter (Figure 4). In general, there was a greater likelihood of movement to the anabranch pre-Mullaroo Creek regulator and when the new regulator gates were fully open (during a flood event) compared with the regulator operation period (when gates were partially lowered). The likelihood of a Murray cod moving to the anabranch preregulator (which included the 2004–2006 data) was 16.9 (95% CI: 11.2–25.5) times greater than during the postregulator operation period (Figure 4). Murray cod were twice as likely (95% CI: 1.4–3.0) to move from the Murray River to the anabranch during the period of flooding (excluding the hypoxic period) when the

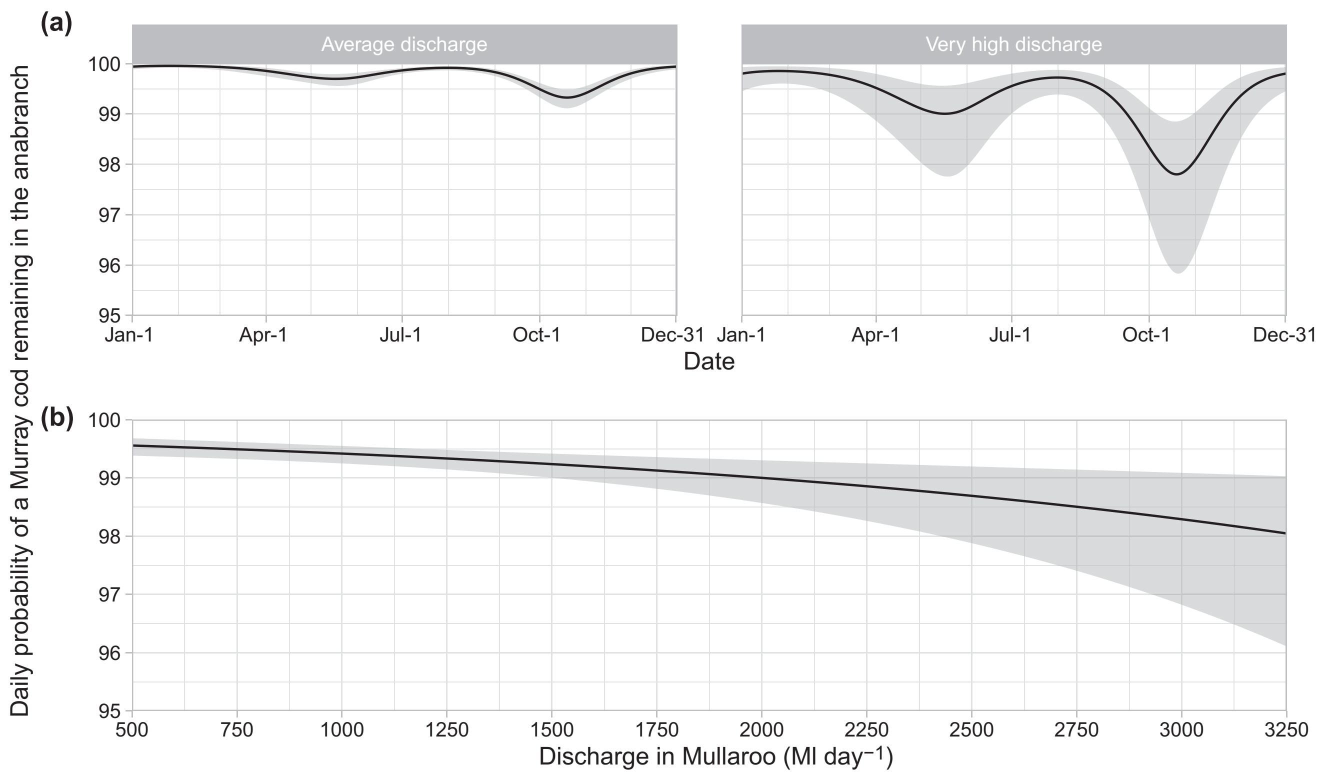

FIGURE 3 The probability that a Murray cod in the anabranch stays in the anabranch dependent on (a) day-of-year and discharge levels in the Mullaroo Creek (under average discharge <800 Ml day^{-1}; and high discharge ≥1500 Ml day^{-1}) and (b) discharge levels in the Mullaroo Creek (in mid-October)

regulator gates were laid flat compared with the nonflood periods during regulator operation when the gates were partially lowered (Figure 4).

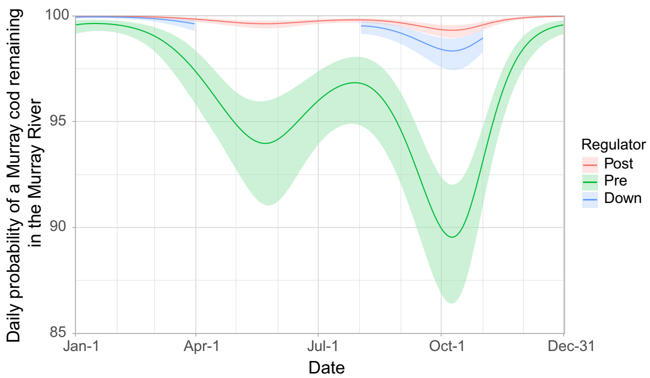

FIGURE 4 The probability that a Murray cod in the Murray River stays in the Murray River dependent on day-of-year and Mullaroo Creek regulator status (pre-, post- and when the gates were laid down during the flood event). Only dates where regulator gates were down (and therefore modeled) were included in the plot

Movement within habitats—Murray River

Our analysis of Murray cod movement in the Murray River was most influenced by day-of-year, weir pool height (i.e., gate settings on Lock 7), and discharge (not correlated with weir pool height; Appendix S1: Tables S6 and S7). Daily movement rates between zones within the Murray River were very low from November to May (<1% of fish moving between zones per day) but increased to ~2.5% from July to September (Figure 5a). At higher weir pool heights (>22.5 m), the probability of movement among zones within the Murray increased from ~1% to >5% on a mid-October day with average discharge (Figure 5b). While discharge is significant (Appendix S1: Table S7), its pattern is less clear, with movement responses varying as discharge changes.

Movement within habitat—Anabranch

Murray cod movements between zones within the anabranch (Mullaroo Creek and Lindsay River) were

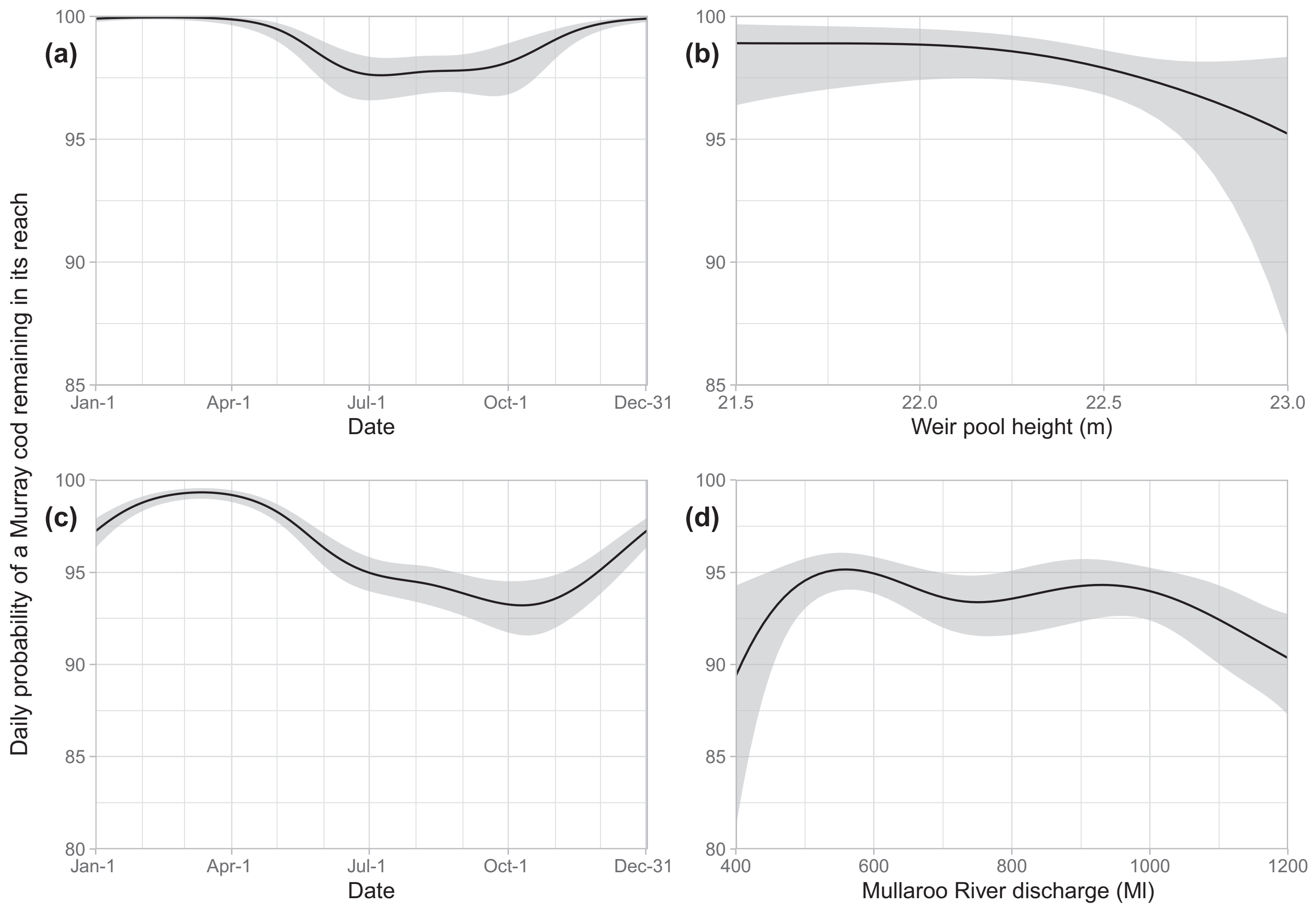

FIGURE 5 The probability that a Murray cod stays within its zone within the Murray River (top), dependent on (a) day-of-year (given average Lock 7 discharge and weir pool height) and (b) Lock 7 weir pool (given average discharge during mid-October); and stays within the Mullaroo Creek (bottom) dependent on day-of-year (given average discharge) and (b) average daily discharge in Mullaroo Creek (during mid-October)

influenced by day-of-year and the discharge in the Mullaroo Creek (Appendix S1: Tables S8–S10). Movements between zones were greatest in spring, with a peak of 7% of fish moving reaches on any given day in October (Figure 5c). At very low (<500 Ml day^{-1}) and high (>1000 Ml day^{-1}) discharge into Mullaroo Creek, the likelihood of a Murray cod moving within the reach also increased, with the greatest increase associated with high flows >1000 Ml day^{-1} (Figure 5d).

Movement responses by fish within the anabranch postregulator (since 2015, excluding the flood period) showed fish responded to the current flow recommendation of elevated discharge during spring (>800 Ml day^{-1}) aimed at enhancing movement within the anabranch and from the anabranch to the Murray River. In spring, the expected number of movements increased by a factor of 3.88 (95% CI: 1.5–11.57) compared with other times of the year (Figure 6). With elevated flows (monthly average flow over 800 Ml day^{-1}), the expected number of movements increase by a factor of 4.75 (95% CI: 1.81–13.96) compared with lower flows. There was some evidence for an interaction between discharge and time of year, with movement during elevated spring discharge reduced compared with each factor separately (zero only just included; Appendix S1: Table S10). This result does not indicate that elevated flow in spring has less of an effect than elevated flow or spring independently, but instead that there is uncertainty about whether fish movements are more strongly related to elevated discharge in spring (increase the rate by a factor of 6.25 [95% CI: 2.76–11.95]) than elevated discharge that occurred at any time (increase the rate by a factor of 5.48 [95% CI: 2.14–11.47]) or just by whether it is spring (increase the rate by a factor of 4.55 [95% CI: 1.71–9.48]). With few examples of lower flow in spring or high flow at other times of year, the standard error for the interaction term compared with the other parameters, reflected the high levels of uncertainty in those months (Figure 6; Appendix S1: Table S10).

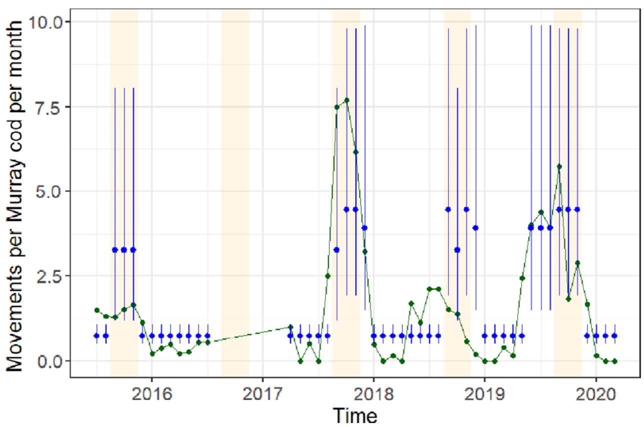

FIGURE 6 Average no. movements between zones in the anabranch system per adult fish in each month from 2015 to 2020 (period post regulator upgrade). Observed no. movements is in green. Modeled no. movements in blue. Vertical lines are the 95% credible interval for the model estimates. Months of spring are shaded in orange. Note 2016 spring blackwater period excluded

TABLE 1 The status and no. tagged Murray cod in the study area prior to and following the 2016 hypoxic blackwater event (numbers exclude Murray cod tagged after March 2016)

Tagged Murray cod status	Prior to November 2016	Post December 2017
Alive (detected in the study area)	63	21
Dead (mortality signal triggered)	6	24
Unknown (left the study area or not detected on loggers)	6	30

Movement in relation to the blackwater event

Prior to the 2016 hypoxic conditions where dissolved oxygen concentrations dropped below 1 mg L^{-1}, there were 63 tagged Murray cod in the study area (Table 1). Elevated levels of fish movement were detected from September to December 2016 in the lead up to and at the height of the flood. Monitoring of tagged fish during and following this event using a combination of mortality signals, detections and manual tracking revealed 21 tagged Murray cod (33% of fish), survived the hypoxic event. All 21 surviving fish moved out of the study area, most within days of each other, when dissolved oxygen levels first fell below 2 mg L^{-1}. Seventeen of these fish moved down the Murray River and Lindsay River anabranch, and out of the study area before eventually returning (two fish did not return until late 2017 and 2018). The remaining four surviving fish all remained in the Murray River within the study area. Seventy-eight percent of all surviving fish were 830–1190 mm in length.

Twenty-four tagged Murray cod (38%) that were alive prior to the blackwater event were confirmed dead, with the remains of most of these fish (or their transmitters) found on the floodplain. The location and status of 30 fish, 24 of which were present in the study area prior to the blackwater event (~39% of tagged fish) remain unknown (Table 1) with most moving downstream in the Murray River and out of the study reach.

DISCUSSION

Knowledge of the movement behavior of organisms in highly modified environments can provide vital information to help guide management actions (e.g., Allen & Singh, 2016; Doherty & Driscoll, 2018). Our long-term study of Murray cod movement throughout a regulated lowland river reach, where altered flow regimes, the installation of weirs and changes in hydraulic conditions have disrupted connectivity and ecohydraulic cues, has shown that (1) the patterns of Murray cod movement observed in the highly regulated system are broadly similar to previous work in reaches with higher water velocity; (2) the likelihood of Murray cod moving to the anabranch system from the Murray River has reduced substantially since construction of the new regulator, but the likelihood of fish moving in the other direction (i.e., to river) has remained unchanged; and (3) that flows delivered through the anabranch in accordance with our recommendations (time-of-year and magnitude of flows) increased the movement of adult fish within and between habitats. Finally, (4) Murray cod movement increased dramatically prior to and during a hypoxic blackwater event. The hypoxic event resulted in high mortality but an equal proportion of fish migrated downstream into the Murray River and returned to repopulate the system over an extended time period.

Factors governing Murray cod movement in a modified lowland river network

Murray cod movement, in terms of transitions between the anabranch and Murray River habitats, and also movements within these habitats peaked during the known spawning period for this species (September–December). This information on the timing of movement is consistent with previous work in the Murray River main channel, whereby Murray cod are often relatively sedentary for much of the year, with limited home ranges and high site fidelity, before undertaking movements that coincide with the period immediately prior to spawning (Koehn et al., 2009; Koehn & Nicol, 2016; Koster et al., 2020).

The probability of movement increased with increasing discharge within the anabranch and increasing water levels within the Murray River. For Murray cod, much like other riverine fish species, there was an increased proportion of fish moving and greater distances traveled, in association with increased river discharge. These movements are likely an adaptation to provide individuals with increased access to their preferred lotic and structural spawning habitats (Koehn et al., 2009; Leigh & Zampatti, 2013; Stuart et al., 2019; Tonkin et al., 2020).

Using movement to understand the impacts of disturbance and recovery

Most river networks globally are fragmentated by barriers (e.g., Belletti et al., 2020; Nilsson et al., 2005). Stream barriers have long been identified as detrimental to fish populations due to restricted connectivity between metapopulations and access to critical habitats for key life-history processes (Baras & Lucas, 2001). Unfortunately, barriers continue to be constructed in many streams. This is the case in the MDB, where these barriers present a considerable risk to native fish populations (Koehn et al., 2014). In our study region more specifically, a new anabranch weir regulator structure replaced an old ford road crossing structure (that did allow some fish movement) mid-way through our study. While there was no significant change in the probability of fish moving upstream from the anabranch to the Murray River, likely due to the vertical slot fishway, downstream movement of fish from the Murray to the Mullaroo Creek was reduced. Other studies have shown impacts of directional impacts on movement of fish species due to disturbances. For example, Perkin et al. (2015) describe how interactions between desiccation and fragmentation affect fish diversity in Great Plains rivers in North America, with pelagic species declining during drought that have their eggs drift downstream unimpeded but then latter life history stages cannot move back upstream to recolonize areas above stream barrier.

The pathway driving the changes in movement behavior we observed is unclear, but we propose two potential reasons. Fish now contend with a concrete barrier where there appears to be a behavioral inhibition to pass over the layflat weir gates unless they are fully open even though the headloss is low (i.e., <50 cm), therefore requiring the fish to find the 60 cm upstream opening of the fishway. Indeed, for most species (both in southern Australia and more broadly), downstream fish passage over weirs often results in passage avoidance and delay while passage through vertical slot fishways is less efficient in comparison to upstream movement (e.g., Baumgartner et al., 2010; Behrmann-Godel & Eckmann, 2003; O'Connor et al., 2006; Roscoe & Hinch, 2010) and is an area in need of further development. The second reason for a reduction in probability of fish moving into the anabranch system from the Murray following the Mullaroo regulator construction is through changes to the flow regime within the anabranch. Our data show movement within each habitat was positively associated with increased discharge or Lock 7 weir pool height. Previous studies have also shown Murray cod migrations to be enhanced by increased river discharge in other areas (e.g., Koehn, 2009). While current flow recommendations include elevating discharge in the Mullaroo Creek during the peak movement period as a whole, average daily discharge within the anabranch has reduced by 13% per day (110 Ml day^{-1}).

The increase of human-induced aquatic hypoxia is predicted to increase globally (Diaz, 2001; Thiem et al., 2020), and information about how fish may respond is important, given that dramatic and extensive fish kills can occur (Vertessy et al., 2019). While some species can be tolerant of harsh environmental conditions, including hypoxia (e.g., Labbe & Fausch, 2000), our data are consistent with other studies that have documented in situ mortality of fish, including Murray cod (King et al., 2012; Thiem et al., 2017, 2020). Nevertheless, our results also show that Murray cod left our study area immediately before, or during the early stages of the hypoxic event, and many returned to the study area over subsequent years. This highlights potential recovery pathways and resilience mechanisms to such disturbances (Reice et al., 1990). Indeed, an assessment of native fish recovery following a similar hypoxic event in the MDB indicated immigration of fish, rather than systematic stocking, was a fundamental recovery process (Thiem et al., 2017). Our results have added to this information, by highlighting the emigration and then return of fish back to these impacted areas as a major pathway to avoid impact and facilitate recover. More information about whether fish can either persist through blackwater events, or leave affected areas and recolonize later, will help understand and manage the effects of future blackwater events globally.

Using movement behavior to inform flow management to support Murray cod populations

A recent review of managing flows for native fish outcomes identified an urgent need by waterway and fisheries managers for timely advice, based on robust research and monitoring, to inform policy and recovery actions (Koehn et al., 2019). Our study provides an example of this and indicated that in response to managed flow events (elevated spring discharge) tagged Murray cod movements increased by a factor of 3.88 during spring compared with other times of the year; and increased by a factor of 4.75 when discharge was >800 Ml day^{-1} compared with <800 Ml day^{-1}. Enhanced fish movement and connectivity highlight the working relationship between scientists and management authorities in developing and delivering designed flow regimes.

Increasing weir pool height in the Murray River, rather than discharge, had the most support for increasing fish movement between zones in the Murray River. Waterway managers are currently trialing lowered weir pools (rather than increasing discharge), to recreate lotic habitats and cue native fish movement (Mallen-Cooper & Zampatti, 2018). The tagged adult Murray cod movements we observed do not support these actions. Instead, we found a strong positive association between adult fish movement and increasing Murray River weir pool height. What these results mean at a process and population level remain unclear. This result may be due to lower weir pool levels reducing structural habitat availability in the study reach or reducing fishway functionality between reaches in the lower Murray River. Conversely, habitat conditions may now be more favorable for processes such as reproduction within the Murray River during lower weir pool levels, and therefore fish are less likely to move out of these zones for these purposes—however, at this stage, there is no evidence that this is the case. It will be vital to assess these processes if weir pool levels continue to be manipulated. Continuing to monitor fish movement as well as reproduction and recruitment strength across the region will shed light on how these interventions are influencing fish populations.

CONCLUSION

Disturbance and habitat modification can alter movement behavior, leading to negative impacts on fitness, survival, and population viability (Doherty et al., 2021). Our study demonstrates that it is important to understand (1) movement behavior (i.e., when and why do fishes move, what cues trigger movement) and (2) how anthropogenic disturbances to streams effect movement behavior. We have used this approach to collect information to help Murray cod, a keystone species, access important habitats required to complete critical life history requirements including recovery following episodic disturbance events. However, stream fragmentation is a global threat to fishes, and similar knowledge is required elsewhere. More generally, addressing these steps can help mitigate the impacts of disturbances on movement in other aquatic and terrestrial ecosystems.

Our work provides an example of how timely and robust applied research has informed how flows and barriers are managed in a modified lowland river system to achieve ecological outcomes. It also provides a case for using animal behavior to help assess responses to management actions, which is often done based on population- and community-level indicators (Hale et al., 2019). This is likely to be especially important when the objectives of management interventions include processes such as connectivity and dispersal. In the past few decades, there has been a growing understanding of the role of animal behavior research in improving the outcomes of conservation and management programs, and we hope that further work in this field will help mitigate the effects of anthropogenic disturbances on ecosystems.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data is permanently archived in https://figshare.com/articles/dataset/Tonkin_etal_2021_lock_7_8_Mullaroo_discharge_and_levels_csv/16945771 (DOI: 10.6084/m9.figshare.16945771) and https://figshare.com/articles/dataset/Tonkin_etal_2021_fish_locations_csv/16945750 (DOI: 10.6084/m9.figshare.16945750). Note that specific data of fish size and location data are withheld to avoid access by recreational or illegal fishers, but this will not influence the repeatability of analysis.

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