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Go with the flow: the movement behaviour of fish from isolated waterhole refugia during connecting flow events in an intermittent dryland river

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Summary

1. In many intermittent, dryland rivers, fishes are confined to isolated waterholes for much of the year. It is only during brief flow events, which typify the hydrology of these systems, that fish are able to move between waterholes and explore surrounding habitat. Because most of the river channel will dry afterwards, there is a strong advantage for selection of persistent waterholes.

2. Two-hundred and fifteen individual fish of three common large-bodied species were tagged in two isolated waterholes in the Moonie River (Queensland, Australia) over 3 years. Their movements were monitored to identify the flow events that trigger fish movement between waterholes, differences in response among species and size classes and refuge selection preferences.

3. Some individuals of all species moved during flow events and others remained within the same waterhole. There was no clear upstream or downstream preference, and most individuals used a reach of up to 20 km, although some individuals ranged over more than 70 km in only several days. Above a threshold flow of 2 m above commence-to-flow level, timing of flow was more important than magnitude, with most movement occurring in response to the first post-winter flow event, independent of its magnitude and duration. Many of the fish that moved displayed philopatry, and subsequently returned to their starting waterhole either by the end of a flow event, or on subsequent events, suggesting ability to navigate, and a preference for more permanent refuge pools. Maximising survival in a highly variable environment provides a plausible mechanism for maintaining these behaviours.

4. Modifications to both flow regime and hydrological connectivity may reduce movement opportunities for fishes in intermittent rivers. Our findings show that fish in intermittent systems use networks of waterholes and that management and conservation strategies should aim to maintain movement opportunities at large spatial scales to preserve population resilience.

Introduction

Arid climates dominate the continents, with large areas of Australia (78%), Africa (57%), Europe (36%), Asia (24%) and the Americas (15%) classified as desert and steppe (Peel, Finlayson & McMahon, 2007). Most rivers in arid regions have intermittent flow, with the magnitude, duration

and timing of flow highly unpredictable through time and linked in many cases to highly irregular rainfall events (Acuna *et al.*, 2014). Long periods without flow are a form of disturbance to riverine aquatic ecosystems, constricting available habitat and disrupting ecological connectivity (Lake, 2011). As water levels recede during dry periods, habitat and food can become limiting, environmental conditions can exceed species tolerances and concentrations of toxic substances can increase to lethal levels (Sheldon *et al.*, 2010). The intensity of biotic interactions may also increase as species are forced together with predators and competitors within shrinking habitats (Closs & Lake, 1996). Biotic assemblages therefore vary considerably across the network of drying pools, with physicochemistry, pool morphology and species-specific responses all important determinants of assemblage composition (Pires *et al.*, 2010; Hodges & Magoulick, 2011; Pires, Beja & Magalhães, 2014). Sites that remain wet or damp during dry periods, such as remnant pools within river channels (waterholes), the hyporheic zone, crayfish burrows, accumulations of coarse woody debris, and litter and stones in the streambed, serve as important refugia for aquatic organisms (Stanley *et al.*, 1994, Arthington *et al.*, 2010; Stubbington & Datry, 2013; Datry *et al.*, 2015; Whitney *et al.*, 2015). Although a few riverine fishes can aestivate underground when surface water disappears, remnant waterholes along the river channel act as critical drought refugia for most fish species in intermittent streams and rivers (Perry & Bond, 2009).

The ways that fish use waterhole refugia over time and space to either re-establish populations following dry periods (resilience) or maintain populations during dry periods (resistance) are key determinants of population persistence in intermittent rivers (Bond *et al.*, 2015). Although there is little empirical information on the movements of fish in relation to the spatial distribution of waterholes in intermittent rivers, observations of changed distributions following floods and the colonisation of previously dry habitat patches (Kerezszy *et al.*, 2013) indicate long-distance movement. The characteristics of the physical environment probably interact strongly with the movement capacities of fish to determine population persistence (Perry & Bond, 2009). For example, past experience of dry periods and previous use of local refugia may increase the probability of individual behaviour that results in survival (Chapman & Kramer, 1991). It is also likely that serendipity strongly influences individual survival, and thus population persistence may be highly stochastic (Chapman & Kramer, 1991).

Patterns in the landscape-scale spatial and temporal distribution of waterhole persistence and quality within a river provide a relatively easily defined template within which the movement of fishes generates population structure at local and regional scales and over both contemporary and evolutionary time-frames (Huey *et al.*, 2011; Bond *et al.*, 2015). Thus the characteristics of the

landscape and the resident biota make networks of waterhole refugia in intermittent rivers ideal systems for developing understanding of how local extinction events, connectivity and species movement behaviour interact to structure populations. Understanding developed for these systems may then be transferred to other patchy, but less well defined habitats within riverine landscapes.

To advance this understanding we investigated the macro-scale movement behaviour of large-bodied native fishes in an intermittent, dryland river. The study was undertaken over 3 years using acoustic tagging of individual fish in two isolated waterholes during no-flow periods with telemetric tracking of subsequent movements during wet periods using a network of receiver stations, both upstream and downstream of the tagging locations. This information was interpreted in relation to hydrology and the morphology of refuge waterholes to determine the behaviour of fishes during short-lived episodes of connectivity. We expected that the patterns in waterhole habitat distribution would influence fish behavioural responses to connectivity, because of the strong adaptive benefits of making good decisions about when to move among waterhole refugia versus the potentially lethal outcomes of bad decisions.

Methods

Study area

This study was undertaken in the mid-reaches of the Moonie River (Fig. 1) in southwest Queensland, Australia; a tributary of the Barwon River in the Murray-Darling Basin. The study reach was 113 km of the main channel of the river between Kurmala and Hollymount Road, over which distance bed elevation dropped from 241.5 m to 206.2 m (Australian Height Datum), resulting in an average bed slope of 0.0312%.

The Moonie catchment has a relatively simple dendritic structure, with persistent waterholes largely limited to the main channel and surface water in the sparse tributary network being highly ephemeral. Draining an area of c. 14 870 km², the Moonie catchment is a dryland, intermittent system in a semi-arid climate with low and variable annual rainfall (mean 560 mm yr⁻¹ at Verena; Fig. 1) and high evaporation rates (mean 2070 mm yr⁻¹ at Verena), with mean daily maximum and minimum temperature 27°C and 13°C, respectively (SILO Data Drill, 2015). Hydrology is rainfall-runoff dominated, with very little base-flow contribution (Sternberg *et al.*, 2008). There is very little water resource development in the catchment and the hydrology of the study reach is near-natural, although river flow is somewhat affected by abstraction further downstream (Queensland Government, 2006; 2014a). Due to the shallow gradient of the river channel, flow velocities during flow events are low and the river's moderately expansive floodplains of cracking clay throughout the

mid and low reaches are inundated for several days to c.2-3 weeks at a time, with an average flood event frequency of 1.5 to 2 years (Queensland Government, unpublished data). During periods without flow, which are common and can last up to 700 days (Queensland Government, unpublished data), a series of isolated waterholes along the main river channel provide refugia for aquatic biota including fishes. Waterholes connect only during flow events which tend to be brief and associated with large rainfall events, typically during the Austral summer. Small instream structures (weirs and crossings) increase the depth and permanence of some waterholes, but may also further limit longitudinal movement between waterholes.

Habitat mapping

We surveyed the river channel to generate a longitudinal depth profile and identify waterholes. A kayak-mounted sonar system (Altimeter – Trittech Int Ltd, Model PA500/6-S) attached to a data recorder (Rugged Brookhouse NMEA 0813) and GPS (Garmin GPSMAP 60Cx) navigation system, was used to collect paired depth-location measurements, with a minimum depth 0.5 m, at 2-second intervals along the thalweg of the channel, at a time when flow conditions were slightly above cease-to-flow. Resulting data were simplified by reducing the sample intensity to one average value for each 10 m segment and then smoothing the depths as a 20-point moving average. This smoothing was necessary to remove noise from instrument error, particularly at shallow depths. From this survey data the locations, length and maximum depth of likely waterhole refugia were identified as segments with water depth greater than 2 m which, based on mean annual evaporation rates of c. 2 m (SILO Data Drill, 2015) and observations that seepage loss is minimal (Queensland Government, unpublished data), were expected to retain surface water for c.1 year or longer.

A satellite image analysis to identify persistent waterholes was also undertaken to validate the results of the habitat survey. The longest no-flow period within the Landsat image era (1988 to present) was identified from the record of the Flinton stream gauge (417205A , Fig. 1). The Landsat scene from the date closest to and just before the end of this no-flow period was selected to cover the study reach. Surface water on the image was identified using the Landsat-based Water Index (Danaher & Collett, 2006). It was necessary to modify the Water Index standard threshold value from 68 to 80 to optimise water identification in local in-stream waterholes in the Moonie River. Pixels on this image were classified as 'water' or 'non-water' and the scene was clipped to a 1 km buffer of the river network (Australian Hydrological Geospatial Fabric (Geofabric) Version 2.1 drainage lines – Major rivers class) to ensure only in-stream waterholes were identified. This identified all pixels in the river channel that were wet at the driest time in the past 27 years. Clusters of four or more adjacent water pixels defined the locations of all waterholes that persisted at this

time. Results were compared with the location of waterhole refugia identified by the habitat survey by overlaying them in a GIS system.

Hydrology

Water level and water temperature were recorded hourly at the Flinton stream gauge (Queensland Government, 2014b). The cease-to-flow height for this gauge is 1.0 m meaning that its recorded water level values are 1.0 m greater than actual water levels during flow events (Queensland Government, 2014b). Records from this gauge indicate that December until March is the wet season and April to November the dry season, although over the period of record flow has occurred in every month of the year, as have months without any flow (Queensland Government, 2014b). Gauge data were augmented by a barometric pressure-compensated *in situ* depth and temperature logger at Altonvale Weir (Fig. 1) (Van Essen Instruments, TD Divers paired with TD Baros).

Water level data from the period commencing 2 months before initial fish tagging (i.e. from August 2007) up until completion of the study (March 2010) were analysed to identify discrete flow events which could connect waterholes and thus provide opportunity for fish movement between waterholes. Flow events were defined to have commenced on the day and hour when water level rose by more than 0.05 m hour^{-1} , commencing at levels between the cease-to-flow level at the gauge and 1 m above this level. Events were defined to finish when water level fell to 0.5 m above the gauge cease-to-flow level. Events defined in this way encompassed all occasions where tagged fish were recorded to move between waterholes. Individual events were further characterised by water temperature on the day events commenced (from the gauge and depth-logger time series), event duration, time since the last event, time and magnitude of the initial peak of the event, the rate of rise of an event (the increase in level between its commencement and its initial peak divided by the time over which this rise occurred), the time and magnitude of the maximum peak in an event, and its rate of fall (the loss of level from the maximum peak to the end of the event divided by the time elapsed). Individual events were classified as first post-winter flow (FPWF) events if they were the first of the spring-summer period, small flow events if gauged maximum peaks were $<2 \text{ m}$, large flow events if they were $2\text{--}6 \text{ m}$, and very large events if they were $>6 \text{ m}$. Small events were considered as primer events if they immediately preceded larger events. Finally the relationships between rate of rise and both initial peak and event duration were investigated by linear regression to identify if this rate had potential to convey information to fish on eventual flow attributes as potential movement cues.

Fish Tagging and monitoring

Each year for 3 years (2007/8–2009/10) fish were caught and tagged in two isolated waterholes (Verena and Kooroon Waterholes) (Fig. 1) at the end of the dry season (September/ October) using fyke nets (Sternberg *et al.*, 2008), for a total of 215 fishes from three species (see Appendix S1 in Supporting Information). After a short holding period in aerated plastic tubs filled with river water, individual fish were measured (standard length- SL), electrically anaesthetised by electro-narcosis (Balazik *et al.*, 2013) and tagged using surgically implanted acoustic tags (V7-4L-69KHz, Vemco Corporation; cylindrical 7 mm diameter, 22.5 mm maximum length, 1.8 g air weight, 136 dB output, battery life 220 days; Vemco, 2015). As soon as they regained equilibrium in similar holding tubs, tagged fish were released back into the waterhole from which they were caught.

Movements of tagged fish were recorded using a network of $n=12$ (2007/08) up to $n=18$ (2009/10) acoustic receiver stations (VR2W, Vemco Corporation) located within, upstream and downstream of the tagging waterholes over a reach of c.113 km. The tagging waterholes both contained two nearby stations (0.5 km apart at Verena and 1.3 km at Kooroon) to detect within-waterhole movement of tagged fish and thus provide evidence of individuals surviving the tagging procedure. The remaining remote stations were positioned to record movement beyond the confines of the tagging waterholes during flow events. These stations were generally located within other waterholes but some were placed in shallower sections of stream channel that quickly dried without flow (see Appendix S2 in Supporting Information). The locations of stations varied slightly from year to year (Fig. 1).

The spread of 12 acoustic receiver station locations in the first year was based on assumptions about movement behaviour informed by similar species in other regions. Initial movement results from the first year allowed some spatial refinement of the receiver network in the second year. After reviewing detections from the first year of the study, the farthest upstream stations, which had received no fish detections, were removed and placed in waterholes in the middle of the network, plus two new stations were added to shorten the distances between stations. In the final year, four additional stations were added to further shorten the gaps within the monitoring network. Creating a shorter, denser network of stations increased the likelihood of detecting fish when they moved over short distances. To investigate if this evolving spatial design biased our results, we tested if recorded movement distances for golden perch (*Macquaria ambigua*) were different between the first year (when the network was sparsest) and the third year (when the network was densest). A t -test detected no such bias in the data with equivalent mean distances moved in the first and third years of 23 km and 24 km respectively ($t = 2.2$, $P = 0.88$). We therefore pooled results from the 3 years to provide more power.

Data analysis

Tagged fish that were not recorded on both stations within their tagging waterhole over the study were classified as 'no data' and were excluded from analyses. Such fish may have died or remained within the tagging waterhole, or the transmitters may have failed or been rejected. Fishes that were confirmed to have been successfully tagged were classed as either vagile (recorded by at least one receiver station outside the tagging waterhole) or sedentary (remained within the tagging waterhole, i.e. detected by both receivers of that waterhole).

A preliminary test confirmed that fish moving up- or downstream were in most cases recorded at each receiver which they passed: 10 vagile individuals selected at random were recorded by each receiver along their journey in 91% of cases. Despite this, remaining data deficits had to be addressed by a logical process of gap-filling. The basis of this was that fish could not move between waterholes during times with no flow as there was no connectivity to permit it; therefore some data points defining beginning and end points of movements had to be assumed based on earlier or later location records generated during periods without flow.

Of those that moved, individuals were classed as initially moving either up- or downstream based on the location of the receiver station outside the tagging waterhole at which they were first recorded. The maximum distance fish moved from their tagging waterhole (either up- or downstream) was recorded as the distance to the most remote receiver station at which they were detected. Movements were noted where vagile individuals travelled either up- or downstream beyond the nearest-neighbour waterhole refugium from the starting location, identified based on the habitat survey results. Maximum observed movement velocity was also calculated as the minimum time, given by latest recording at origin, and first recording at destination, taken to move between receiver stations over known river distances, for both up- and downstream movements. Finally, the proportion of up- and downstream philopatry (vagile individuals which returned to their tagging waterhole by the end of the tagging season) was calculated for individuals returning home either over the course of single events, or over multiple events within a season. We used simple linear regression to determine if there was a relationship between fish length and maximum distance moved (up- and downstream), and a one-way ANOVA to determine if there was a difference in the mean length of sedentary, vagile and philopatric individuals.

Individual location records of tagged fish were interpreted in relation to species-specific hydrological cues for movement. Individual flow events that provided potential movement opportunities over the three wet seasons of the study were characterised in terms of attributes that could act as cues

for fish to move from tagging waterholes. These attributes were month, water temperature, rate of rise and fall of the flow event, initial and peak event height and event duration. The timing of movements was then compared to event attributes to identify likely movement cues and event-scale behavioural responses. This included assessment of when all participating fish were recorded to first commence to move (date and time) during individual events in relation to event hydrology. Any differences in these aspects for fish moving up- or downstream as their first direction of movement were also noted.

Associations between movement behavioural responses and potential environmental drivers were further analysed by linear regression. Separate analyses were conducted for each species for four behavioural responses: the proportion of successfully tagged individuals that moved on each flow event (movement participation), the total distance (km) moved per individual per event (distance moved), the number of waterhole refugia individuals passed through while moving per event (waterholes passed), and the probability of individual waterhole refugia (i.e. > 2 m deep) being selected by individuals moving during an event (waterhole selection). Explanatory variables included waterhole size, flow event properties (magnitude, timing, duration and rate of change, and the occurrence of preceding flow events) and water temperature. The number of explanatory variables in the models was first reduced by undertaking correlation analysis and selecting a single variable with the most plausible association with the response to represent any sets that were collinear with $r > 0.6$ (see Appendix S3 in Supporting Information). Best resulting models for each response variable and species were selected based on strength of model fit (adjusted R^2) and model parsimony (fewer explanatory variables and minimum AIC).

Results

Habitat mapping and hydrology

Fifteen persistent waterholes >2 m deep were identified within the study reach, including both tagging waterholes. These ranged in maximum depth from 2.1 – 4.3 m with a mean of 2.9 m, and were between 0.3 – 5.1 km long with a mean length of 1.5 km (Fig. 1; see Table S2). Three small weirs (0.8 – 2.6 m high) and seven road crossings (0.6 – 1.9 m high) were identified within the study reach.

The longest no-flow spell within the Landsat era was 299 days (1 June 2013 to 26 March 2014) and the Landsat image closest to the end of this spell for the study region was taken on 11 March 2014 (284 day spell). Based on the waterhole evaporative loss rate for the region (SILO Data Drill, 2015; Queensland Government, unpublished data), waterholes deeper than 1.6 m at cease-to-flow were

estimated to retain surface water after a spell of this duration. Thus, all of the waterhole refugia found by the habitat survey (> 2 m deep, persisting for at least 1 year) were expected to retain water at this time and analysis of the Landsat image confirmed this to be the case. This provides additional confidence in the veracity of the habitat survey results.

Seventeen flow events occurred in the Moonie River in the period during and shortly preceding the 3 years of tagging. These events were variable across the attributes considered, including timing (September – May), antecedence (2 – 235 days), magnitude (1.4 – 7.5 m), rates of change (0.2 – 10.8 m day⁻¹) and duration (1 – 32 days) (Table 1). It is notable that the rates of rise of events were often an order of magnitude greater than their rates of fall. Relationships between rate of rise and both initial peak and event duration were weak and not significant (in both cases $R^2 < 0.20$, $P > 0.05$). Thus, at this temporal scale rates of rise did not seem to have potential to convey information to fish on eventual event attributes as potential movement cues.

Fish movement

Data were obtained for 88% and 94% respectively of tagged golden perch and eel-tailed catfish, but for only 29% of tagged bony bream (Table 2). The majority of bony bream that survived with functioning tags remained in the waterholes in which they were tagged, whereas the majority of surviving individuals of the other two species moved (Table 2). Philopatry amongst vagile individuals was high in all three species with half or more returning to the waterhole from which they were tagged (Table 2), either over the course of a single flow event, or over subsequent events within the same wet season.

Because of the high proportion of individuals generating no data and high proportion of the remainder that were sedentary (Table 2), there were insufficient cases of bony bream movement recorded to fully characterise their movement behaviour

Of the vagile individuals, initial event-based movements of golden perch (n=140) were 60% in an upstream direction, with a mean distance moved of 27.8 km (range 9.4 – 55.8 km), and 40% downstream, with a mean of 12.4 km (range 6.3 – 26.8 km) (Figs. 2, 3). For vagile eel-tailed catfish (n=20) 55% of initial event-based movements were upstream, with a mean distance moved of 25.4 km (range 6.3 – 74.8 km), and 45% downstream with a mean of 12.6 km (range 2.4 – 67.3 km) (Figs. 2, 3). Of the two bony bream recorded moving, one moved upstream 26.9 km and the other downstream 28.7 km.

Vagile golden perch and eel-tailed catfish commonly moved through nearest-neighbour waterhole refugia. For golden perch, 82.3% passed through the nearest waterhole and on average they moved

through the nearest two, but up to the nearest six waterholes. For eel-tailed catfish the proportion passing through the nearest neighbour waterhole was very similar at 82.4%, with vagile individuals passing on average three and up to nine waterholes when moving. Both vagile bony bream also bypassed waterhole refugia. The maximum and mean observed movement velocities of golden perch and eel-tailed catfish were higher when moving downstream than upstream, and the sparse data for bony bream were similar (Table 3).

There was no significant difference between the mean lengths of eel-tailed catfish that were static, vagile or philopatric ($F=0.75$, $P=0.52$), but there were small but significant differences for golden perch ($F=5.8$, $P<0.001$). Fish that were sedentary (mean 212 mm) were slightly smaller on average than those that were vagile (mean 242 mm); there was no significant difference in length between vagile individuals that were philopatric and non-philopatric, and philopatric individuals returning home on a single event (mean 230 mm) were on average smaller than those doing so over multiple events (mean 246 mm). There was no significant relationship between the size of individual fish and the maximum distance they moved away from their home waterhole for either golden perch or eel-tailed catfish, either overall or in the upstream or downstream direction (all $R^2<0.04$, all $P>0.05$).

Responses to cues

Movement out of waterholes by vagile individuals of both golden perch and eel-tailed catfish commenced during flow events with water temperatures of 15 – 28°C, and between November and May (Figs. 4, 5). For both species, more of these movement events were initiated early in flow events when the water level was increasing, but considerable numbers also commenced moving when the water level was stable or falling (Figs. 4, 5).

Movement responses of tagged individuals to individual flow events were variable for both golden perch and eel-tailed catfish (see Appendix S4 in Supporting Information). Small flow events (A5, B1, B2, C1 and C2 for both species and also B6 for eel-tailed catfish; see Table 1 for event codes) failed to elicit any detectable movement from waterholes, regardless of time of year or rate of rise. All flow events with maximum peaks >3 m and durations of >5 days elicited fish movement (with the exception of B6 for eel-tailed catfish as outlined above). In every year, the first post winter flow (FPWF) event >3 m elicited the greatest movement response, irrespective of the month in which it occurred, or its magnitude or duration (Table S4). In all years the FPWF was preceded by a smaller 'primer' event (< 3 m) which did not trigger movement of tagged fish. The proportion of individuals moving downstream also varied for both species; ranging between all vagile individuals for some

flow events and no individuals on others, as did the mean distance moved for individual events (Table S4).

Significant regression models were developed for all four behavioural responses for both golden perch and eel-tailed catfish (Table 4; see Table S3). Models representing golden perch movement participation and distance moved had low explanatory power (adjusted R^2 values ≤ 0.15), but all other models had higher explanatory power, accounting for 30-70% of variability. For eel-tailed catfish, movement participation, distance moved and waterholes passed increased as a function of event size. They were also likely to move further the shallower the waterhole they were in at the commencement of a flow event. The distance moved by golden perch showed the same associations with hydrology and waterhole morphology. For both species the number of waterholes passed when moving was a function of flow event size rather than waterhole attributes, with larger events resulting in more waterholes being passed. Golden perch were less likely to move when their starting waterhole was large (and when flow level was falling more rapidly), and conversely, when they were moving they were more likely to stop in a waterhole if it was large and the flow level was falling more rapidly. When eel-tail catfish were moving they were more likely to stop in waterholes based on time of year and hydrology, (earlier in the flow season and when there had been preceding flow events), rather than waterhole attributes (Table 4).

Discussion

Patterns of movement

We found high levels of vagility by fish during the infrequent periods of high flow in the Moonie River, with golden perch and eel-tailed catfish frequently moving >10 km from their tagging location within a few days during high flows. Of the fish that moved away from their tagging waterholes during high flows, more than half returned to their previous positions as flows subsided or during subsequent flow events within a wet season. Previous understanding of the movement of fishes in intermittent rivers has largely come from indirect observations of the outcomes of movement such as the colonisation of previously dry habitat patches (e.g. Kerezy *et al.*, 2013; Pires *et al.*, 2014; Whitney *et al.*, 2015), changes in fish assemblages in waterhole refugia following floods (e.g. Balcombe *et al.*, 2007; Magalhães *et al.*, 2007) or inferences from molecular studies of population genetics (e.g. Huey *et al.*, 2011). Our study complements this previous work by providing direct observational evidence of the spatial and temporal patterns of fish movement, participation rates, cues, distances, direction and velocities of movement.

Although our study was conducted in an intermittent river with highly unpredictable hydrology, the movement behaviour exhibited by golden perch is broadly consistent with previous studies of the species in more predictable, perennial systems. Golden perch in perennial rivers of the Murray-Darling Basin (MDB) occupy restricted home ranges (usually <1 km) and exhibit strong site fidelity during periods of low flow. These extended periods of sedentary behaviour are interspersed by periods during which many individuals undertake large-scale (often >10 km and up to nearly 80 km) movements in both up- and downstream directions in response to high flows (Crook 2004a,b; O'Connor, O'Mahony & O'Mahony, 2003; Koster *et al.*, 2014). Our finding of large-scale movement by some eel-tailed catfish differs considerably from previous studies of the species. A conventional tagging study in the lower Murray River in the southern MDB suggested that most catfish individuals are relatively sedentary, with 35 out of 36 (97%) recaptured fish moving <10 km over extended periods that included a major flood (Reynolds, 1983). A more recent radio-telemetry study (Koster *et al.*, 2014) conducted in a floodplain wetland in the southern MDB found that most fish occupied restricted areas (median linear range of movement 0.6 km) over the 6-month study period, although a few fish moved up to 5.2 km. Where large-scale movements have been recorded in eel-tailed catfish, these have been in both directions with a tendency for movement to be upstream (Battaglene & Talbot, 1990; Stuart & Berghuis, 2002). There have been no previous telemetry studies of bony bream, possibly because of their sensitivity to handling stress (see Blessing, Marshall & Balcombe, 2010), which may have led to the low data return from this species in our study. Despite this limitation, bony bream is often considered a vagile species, capable of dispersing over large distances (Stuart, 1977; Hughes and Hillyer, 2006; Kerezszy *et al.*, 2013). Our limited results suggest low movement participation rates, but the few vagile individuals recorded confirmed that at least some bony bream undertake large-scale movements in response to flow events of up to nearly 30 km.

Large-scale movement appeared to be associated with specific environmental cues. For example, we observed golden perch and eel-tailed catfish moving during all flow events that peaked at ≥ 2 m above cease-to-flow levels during the 3 years of our study, and during none that peaked below this level. Two metres thus appears to represent a threshold for flow peaks that cue movement in the Moonie River. Similar studies in other rivers will be needed to determine if this rise in water level is the actual cue, or if it represents a threshold in the Moonie River because it relates to some aspect of the river cross-section and geomorphology that provide other hydraulic, chemical or habitat-based cues to fish. If the latter is the case, we would expect different thresholds for the same species in other rivers.

Golden perch swimming capacity is reduced at water temperatures below 16°C making movement less likely (Lyon, Ryan & Scroggie, 2008). This is very close to the minimum temperature of 15°C we observed for an event that triggered movement of both this species and eel-tailed catfish, suggesting this temperature as another possible threshold for movement. The first post-winter flow event (FPWF) is an important cue for golden perch spawning in the north of their range (Cocayne *et al.*, 2013). These events had the highest movement participation rates for both golden perch and eel-tailed catfish in our study, suggesting that this movement in the Moonie River was associated with spawning. Small 'primer' flows prior to the first FPWF do not trigger movement, but improve golden perch spawning and recruitment success (Cocayne *et al.*, 2013). A small event which did not trigger movement preceded the FPWF in each year of our study, so we could not test whether such primers are required as movement cues.

Individual variation in movement

Variation within populations of river fishes, whereby some individuals are sedentary and others vagile over a given timeframe, appears to be a consistent pattern amongst fish species that do not have obligate and synchronised reproductive migrations (Chapman *et al.* 2011; Kendall *et al.* 2014). The three species studied here conform to this generalisation, with some individuals moving out of waterholes during connecting flow events, while the remainder stayed confined to their resident waterhole. A recent meta-analysis of quantitative studies of river fish movement (Radinger & Wolter, 2014) found that the vagile component of the populations studied (62 species from 12 families) ranged from 2% to 87% of individuals with a median of 33%, and that the movement distance of the vagile component ranged from 2 m to 166 km with a median of 361 m. The definition of sedentary versus vagile components of fish populations depends on the spatial scale considered and the duration of the study (i.e. more movement is detected as the duration of the study increases, Radinger & Wolter 2014). Nonetheless, golden perch and eel-tailed catfish in the Moonie River fell well above the global medians for vagility, even though our study was relatively brief.

Of the 83 studies considered by Walter & Radinger (2014), only 4 were conducted in intermittent streams. Rates of vagility in those systems ranged from 5 - 53% (Table 6, see Appendix S5 in Supporting Information). Additionally, all of the quantitative intermittent stream fish movement studies considered were from small, first or second order streams (Table 6, see Table S5), whereas the Moonie River is a lowland river with stream order 5 to 6 in the study area. This paucity of information precludes any generalisations about rates of vagility in intermittent versus perennial streams. However, in perennial systems environmental factors such as river flow and water

temperature can strongly influence rates of vagility (Kendall *et al.*, 2014). Given the prevalence of intermittent, lowland rivers and streams in arid regions across the world, fish movement behaviour and its influence on ecological processes clearly warrant further investigation.

Habitat connectivity and risks associated with movement

Most rivers are highly variable environments in which flow affects connectivity, habitat availability, environmental harshness and food availability (Resh *et al.*, 1988, Lancaster & Hildrew, 1993; Puckeridge *et al.*, 1998; Matthews & Marsh-Matthews, 2003; Lake, 2011). In intermittent, dryland rivers such as the Moonie, this variability is extreme (Walker, Sheldon & Puckridge, 1995; Datry *et al.*, 2015), and local environmental conditions within waterholes become increasingly harsh and local resources scarce during long periods without flow (Arthington *et al.*, 2010; Sheldon *et al.*, 2010), forcing resident fishes to switch to low quality food (Sternberg *et al.*, 2008), increasing rates of mortality and reducing the health and fitness of survivors (Balcombe *et al.*, 2012; Balcombe, Arthington & Sternberg, 2014). In such circumstances, there is a strong imperative for individuals to move to seek more profitable and benign habitat patches, or to reproduce (Bond *et al.*, 2015). However, such opportunity is a double-edged sword; while the benefits of moving can be great, so can the risks.

As is the case with most intermittent systems, the Moonie River offers limited, patchy refugia for fish during spells with no flow (Magoulick & Kobza, 2003; Bunn *et al.*, 2006). If individual fish move out of refugia and then fail to find suitable habitat, they are likely to die as a consequence (e.g. Albanese, Angermeier & Dorai-Raj, 2004). Thus, there is strong selective pressure against intermittent river fish moving at random out of refugia (Whitney *et al.*, 2015). In support of this concept, we found that fish movement was strongly influenced by both the morphology of waterhole refugia and flow event hydrology. Both golden perch and eel-tailed catfish preferred to select and stay in large waterholes, those most likely to persist through subsequent spells without flow. They also tended not to move when flows were receding rapidly. Another study of fish in an intermittent river also found the probability of movement out of refugia was inversely related to pool size, a surrogate for water persistence during dry spells (Walker & Adams, 2014). This spatial risk in intermittent rivers is in addition to the 'normal' costs of moving, such as a high energy cost and elevated exposure to predation (Brodersen *et al.*, 2008). However, in intermittent rivers like the Moonie, some years are wet and some are dry, favouring vagile fish in some years, and sedentary fish in other years. As proposed for birds (Chan, 2001), natural selection may favour sedentary individuals on some occasions and vagile individuals on others, thus maintaining the coexistence of

both behaviours as adaptive responses to environmental and resource variability (Wolf & Weissing, 2012).

Philopatry

The high levels of philopatry (homing) amongst golden perch and eel-tailed catfish in the Moonie River may allow individuals to avoid the costs of settling and perishing in a doomed habitat patch, yet gain benefits from temporarily occupying ephemeral habitats or shifting home locations. The capacity of fish to undertake homing movements in rivers may be conferred via an ability to develop cognitive maps of the surroundings which can be used to navigate home following displacement (Odling-Smee & Braithwaite, 2003; Braithwaite & De Perera, 2006). By means of this capacity to return to a waterhole that has provided suitable habitat during at least one prior dry season (Chapman & Kramer, 1991), they can explore the river, in this case over distances of tens of kilometres, gain whatever benefits this proffers, and return to their 'safe haven' before the following dry season. This behaviour is consistent with the model proposed by Crook (2004b), in which homing abilities allow fish to assess the profitability of potentially available habitats without the risk of losing their original home range should they fail to find a more profitable location. Following this model, vagile individuals that did not return home may have located and elected to remain in a more favourable habitat, which in this case must be a different persistent waterhole.

Because intermittent rivers around the world are under increasing threats from climate change, exploitation and lack of regulatory protection (Steward *et al.*, 2012; Acuna *et al.*, 2014; Datry, Larned & Tockner, 2014), our study highlights the importance of understanding the intricate relationships between flow variability, biota and ecological processes if native fish populations are to remain viable. We found flow event magnitude, duration and rate of change to be the most important hydrological drivers of fish movement and it is significant that these aspects are amongst those most susceptible to being altered by water resource development. Our study provides parameters to inform spatially explicit population dynamics models, which are very useful tools for flow management (Radinger & Wolter, 2014; Bond *et al.*, 2015; Datry *et al.*, 2015), especially when it aims to maintain or expand the current distributions of target fish populations (e.g. MDBA, 2014). Our results also demonstrate that management of fish populations in intermittent rivers cannot rely merely on efforts to conserve or restore individual sites, such as individual wetlands or waterholes (e.g. Aquatic Ecosystems Task Group, 2012; Keppel *et al.*, 2012). These populations require both catchment-scale networks of functioning waterhole refugia and appropriate flows to provide cues and opportunities for successful movement among habitat patches.

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Supporting Information Titles

Table S1. Details of the species, length, tag codes and movement behaviour of all tagged fish.

Table S2. Morphological characteristics of waterhole refugia (> 2 m deep) and other receiver station locations within the 113 km study reach

Table S3 Description of variables and correlations between variables considered for linear regression analyses.

Table S4. Movement responses of tagged fish to individual flow events, (as characterised in Table 1). Figures for % vagile relate to the proportion of the living population of tagged fish that moved and those for % downstream relate to the proportion of the vagile element of the population that moved initially in a downstream direction. Mean distances are the average maximum distance individuals moved from their point of departure on the event.

Table S5. Classification of the flow regime of published quantitative studies of fish movement to identify those conducted in intermittent rivers.

Tables

Table 1. Characteristics of all flow events recorded at the Moonie River at Flinton stream gauge during and shortly preceding the study.

event code	event start time	time since last event (days)	event start temperature (°C)	rate of rise (m/day)	initial peak (m)	initial peak time	maximum peak (m)	maximum peak time	rate of fall (m/day)	duration (days)	event class
A1	26/08/2007 4:00	45	15.5	4.4	-	26/08/2007 18:00	3.57	29/08/2007 14:00	0.2	16	small event, primer (prior to tagging)
A2	11/10/2007 6:00	45	18.6	1.9	-	-	1.37	11/10/2007 5:00	0.9	1	small event, primer (prior to tagging)
A3	1/11/2007 17:00	9	21.4	2.3	3.52	2/11/2007 19:00	3.85	3/11/2007 18:00	0.4	9	FPWF, large event
A4	1/12/2007 4:00	28	21	5.7	3.83	1/12/2007 16:00	5.48	12/12/2007 8:00	0.3	28	large event
A5	19/01/2008 18:00	49	26.5	1.2	-	-	1.53	20/01/2008 5:00	0.1	5	small event
A6	4/02/2008 2:00	15	26	2.6	-	-	7.04	6/02/2008 9:00	0.2	32	very large event
B1	5/09/2008 7:00	212	15.3	10.8	-	-	1.43	5/09/2008 8:00	1.0	1	small event, primer
B2	22/09/2008 21:00	15	24.5	2.2	-	-	2.47	23/09/2008 13:00	0.6	3	small event, primer
B3	21/11/2008 7:00	59	22.1	7.8	3.26	21/11/2008 14:00	3.67	26/11/2008 2:00	0.3	13	FPWF, large event
B4	8/12/2008 10:00	17	25.8	2.1	3.58	9/12/2008 16:00	3.67	11/12/2008 22:00	0.3	13	large event
B5	28/12/2008 12:00	19	26.7	2.8	-	-	5.04	29/12/2008 23:00	0.6	8	large event
B6	25/01/2009 13:00	27	25.9	5.4	2.56	25/01/2009 20:00	3.26	27/01/2009 8:00	0.8	5	small event
B7	13/02/2009 15:00	19	24.9	0.3	1.98	16/02/2009 22:00	4.31	19/02/2009 5:00	0.4	14	large event
B8	19/05/2009 17:00	92	14.2	3.0	-	-	6.89	21/05/2009 17:00	0.3	25	large event
C1	11/01/2010 14:00	235	28.1	1.1	-	-	1.39	11/01/2010 23:00	0.4	1	small event, primer
C2	16/01/2010 4:00	4	29	2.9	-	-	1.94	16/01/2010 12:00	1.0	1	small event
C3	11/02/2010 14:00	26	25.9	2.2	3.94	12/02/2010 23:00	7.52	3/03/2010 4:00	0.2	51	FPWF (late), very large event

Table 2. Summary of fish tagged, individuals with no movement data collected, movement types for fish with data and rates of philopatry (i.e., homing) for vagile individuals over the 3 years of the study. Single event is the percentage of all philopatric individuals that returned home during the same event on which they left, as opposed to over multiple events within the season.

	number tagged	no data (%)	sedentary (%)	vagile (%)	philopatric (%)	single event (%)
golden perch	124	12.1	37.6	62.4	64.7	34.0
eel-tailed catfish	53	5.7	58.0	42.0	52.4	38.6
bony bream	38	71.1	81.8	18.2	50	100

Table 3. Maximum and mean observed velocities of each species recorded moving up- and downstream between successive receiver stations, and sample size (n). Bony bream results are for single movement events so no mean values are presented.

		golden perch (km/h)	eel-tailed catfish (km/h)	bony bream (km/h)
upstream	maximum	1.1	0.6	0.1
	mean	0.5	0.3	-
	n	38	7	1
downstream	maximum	1.8	2.2	0.8
	mean	0.8	0.8	-
	n	41	13	1

Table 4. Linear regression models for golden perch and eel-tail catfish movement behaviour in relation to waterhole and flow event characteristics (* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$; see Table S3 for variable descriptions and correlations).

species	movement response	linear regression model	adjusted R^2	P
golden perch	movement	$y = 0.76007 - 0.09948 * \text{waterhole length} - 0.42036 * \text{event rate of fall}$	0.15	**

participation				
	distance moved	$y = 28.48341 - 5.12342 * \text{waterhole depth} + 0.47433 * \text{event duration}$	0.13	*
	waterholes passed	$y = 4.6002 * \text{event peak level}$	0.63	***
	waterhole selection	$y = 0.00052 * \text{waterhole length} + 0.00028 * \text{event rate of fall}$	0.68	***
eel-tailed catfish	movement participation	$y = 0.008811 * \text{event duration}$	0.62	***
	distance moved	$y = -4.01672 * \text{waterhole depth} + 1.94194 * \text{event duration}$	0.67	***
	waterholes passed	$y = 0.1941 * \text{event duration}$	0.69	***
	waterhole selection	$y = 0.889 - 0.149 * \text{month increment} + 0.321 * \text{number preceding events}$	0.38	***

Table 5. Movement characteristics of populations of river fishes included in a recent meta-analysis that were from intermittent waterways (after Radinger & Wolter 2014). See Table S5 for further information.

Family	Species	Stream Order	vagile (%)	Movement distance (m)	Waterbody	Country	Reference
Centrarchidae	<i>Lepomis cyanellus/megalotis</i>	2	5	376	Little Glazypeau Creek	USA	Smithson & Johnston (1999)
Cyprinidae	<i>Barbus haasi</i> ¹	1	39	82	Vallvidrera Creek	Spain	Aparicio & Sostoa (1999)
Cyprinidae	<i>Ptychocheilus grandis</i>	2	50	361	Pine Creek	USA	Grant & Maslin (1999)
	<i>Semotilus atromaculatus</i> ^{1,2}	2	53	388	North Sylamore Creek	USA	Walker & Adams (2014)
Salmonidae	<i>Onchorynchus gilae</i>	1	40	414	South Diamond	USA	Rinne (1982)

¹ mean of multiple data sets

² not included in Radinger & Wolter (2014)

Figure Legends

Fig. 1. Map of the study reach indicating the named locations of receiver stations for each of the 3 years of the study in relation to persistent waterholes (represented here as circles at the centre of each to indicate position but not length) plus the locations of Flinton stream gauge and the Verena and Kooroon Waterholes where fish were tagged. Insets show the location of the study reach in Australia and an example longitudinal profile of water depth derived from a sonar habitat survey.

Fig. 2. Histogram, with 10 km bins, of initial movement direction and distances of vagile a) golden perch and b) eel-tailed catfish over the 3 years of the study. Black bars indicate upstream distances and white bars downstream distances from the locations at which movement commenced.

Fig. 3. Examples of the recorded movements of selected golden perch (GP) and eel-tailed catfish (TAN) over the 3 years of the study to illustrate the range of responses observed. Numbers in the figure legends are the tag identification codes of individual fish (see Table S1). Distances are positive upstream and negative downstream of the release waterhole of each individual. Flow levels are from the Flinton stream gauge.

Fig. 4. Commencement of movement of individual golden perch (black bars) in relation to water level (solid line) and water temperature (dashed line) in each of the 3 years of the study. Vertical black arrows indicate the dates of fish tagging.

Fig. 5. Commencement of movement of individual eel-tailed catfish (black bars) in relation to water level (solid line) and water temperature (dashed line) in each of the 3 years of the study. Vertical black arrows indicate the dates of fish tagging.

Illustrations

Figure 1

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Figure 2.

Figure 3.

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Figure 4.

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Figure 5

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