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Tracking the resource pulse: movement responses of fish to dynamic floodplain habitat in a tropical river

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Abstract

1. Natural river floodplains are among Earth's most biologically diverse and productive ecosystems but face a range of critical threats due to human disturbance. Understanding the ecological processes that support biodiversity and productivity in floodplain rivers is essential for their future protection and rehabilitation.
2. Fish assemblage structure on tropical river floodplains is widely considered to be driven by dispersal limitation during the wet season and by environmental filtering and inter-specific interactions during the dry season. However, the individual-level movement behaviours (e.g., site attachment, nomadism, homing) that regulate dispersal of fish on floodplains are poorly understood.
3. We combined radio-telemetry and remote sensing to examine the movement behaviour of two large-bodied fishes (barramundi *Lates calcarifer*, forktail catfish *Neoarius leptaspis*) over the flood cycle in a tropical river-floodplain system in northern Australia to: 1) quantify movement responses in relation to dynamic habitat resources at a

landscape scale; and 2) determine the extent of spatial ‘reshuffling’ of individual fish following the wet season.

4. Both species altered their behaviour rapidly in response to changes in the availability and distribution of aquatic habitat, with most individuals undertaking extensive movements (up to ~27 km from the tagging location) on the inundated floodplain during the wet season. Although there was considerable individual variation in movement patterns, overall barramundi distributions closely tracked the extent of floodplain primary productivity, whereas catfish distributions were most closely associated with the extent of flooded area. Most individuals of both species exhibited homing back to previously occupied dry season refugia during the wet-to-dry transition, even though other potential refugia were available in closer proximity to wet season activity areas.
5. We postulate that homing behaviour modulates temporal variation in fish assemblage composition and abundance and limits the transfer of aquatic-derived energy and nutrients into terrestrial food webs by reducing fish mortality on drying floodplains. Our study demonstrates the importance of quantifying individual-level behaviour across the three stages of dispersal (emigration, inter-patch movement, immigration) for our understanding of how animal movement influences energetic subsidies and other large-scale ecosystem processes.

Key words: migration; homing; movement behaviour; metacommunity structure; food web subsidies; refugia; barramundi; catfish.

Introduction

Natural river floodplains are among Earth’s most biologically diverse and productive ecosystems but face critical threats due to a range of human disturbances (Whited et al., 2007). In the US and Europe, >90% of river floodplain ecosystems are now functionally extinct (Tockner & Stanford, 2002) and floodplain habitats continue to be lost at an alarming rate globally (Tockner, Pusch, Borchardt & Lorang, 2010; Ziv, Baran, Nam, Rodríguez-Iturbe & Levin, 2012). Developing a detailed understanding of the processes that support the biodiversity and productivity of natural floodplain ecosystems is essential for their protection and for the rehabilitation of degraded floodplains into the future (Schiemer, Baumgartner, & Tockner, 1999; Tockner et al., 2010).

Episodic inundation of low-lying land during periods of high river flow is a defining feature of natural river floodplains (Tockner et al., 2010), providing pulsed resources for fish and other biota (the “flood pulse” *sensu* Junk, Bayley & Sparks, 1989) and acting as a conduit for material subsidies between terrestrial and riverine environments (Polis, Anderson & Holt, 1997; Pettit et al., 2017). Floodplain inundation greatly increases the area of available aquatic habitat and can provide access to abundant terrestrial and aquatic prey and other food sources, such as fruit and epiphytic algae (Winemiller & Jepsen, 1998; Douglas, Bunn & Davies, 2005; Correa, Costa-Pereira, Fleming, Goulding, & Anderson, 2015). The dynamism of habitat and food availability across the flood cycle strongly influences food web structure and ecosystem productivity on floodplains (Winemiller, 1996; Warfe et al., 2011; Bayley, Castello, Batista & Fabré 2018) and creates complex spatial patterns of species distribution and primary productivity (Tonolla, Wolter, Ruhtz & Tockner, 2012; Pettit et al., 2017). The periodicity of floodplain inundation may also vary greatly among climatic regions, ranging from highly predictable, seasonal floods to unpredictable, arrhythmic events driven by stochastic climatic factors (Jardine et al., 2015). This hydrologic diversity and the resulting differences in pulsed resource availability lead to variable biotic responses and ecosystem processes among regions (e.g., patterns of resource-consumer coupling; Jardine et al., 2012a).

In tropical floodplain rivers, many species of fish move from dry season refugia onto inundated floodplains during the wet season (Winemiller & Jepsen, 1998; Fernandes, Henriques-Silva, Penha, Zuanon, & Peres-Neto, 2014), and it has been suggested that dispersal limitation may be a strong driver of fish assemblage structure during the wet season (i.e., community assembly via random dispersal from colonist sources) (Arrington, Winemiller, & Layman, 2005; Fernandes et al., 2014). Movement of fish on inundated floodplains during the wet season has been observed over long distances (e.g., up to ~6 km by individual *Colossoma macropomum*, Anderson, Nuttle, Saldaña Rojas, Pendergast, & Flecker, 2011) and plays important roles in large-scale ecological processes, including seed dispersal for tropical forest vegetation (Anderson et al., 2011; Correa et al., 2015) and the transport of assimilated nutrients and energy across ecotone boundaries (Jardine et al., 2012b). During the wet-to-dry season transition, refugia are recolonised by fishes and habitat characteristics and inter-specific interactions appear to exert increasingly important influences on species composition and abundance as the refugia become hydrologically isolated (Rodríguez & Lewis, 1994, 1997; Willis, Winemiller & Lopez-Fernandez, 2005; Arantes, Castello, Cetra, & Schilling, 2013; Fernandes et al., 2014).

Although dispersal during the wet season has been widely invoked as a key driver of fish
115 assemblage structure in tropical floodplain habitats, to date there has been little empirical
study of the individual-level movement behaviour (e.g., site attachment, nomadism, homing)
that regulates dispersal and assemblage stability, nor the effects of intra-specific variation in
movement behaviour (see Chapman, Brönmark, Nilsson & Hansson, 2011) on energetic
120 subsidies and other large-scale ecosystem processes in floodplain rivers. Information on how
individual behaviour influences the colonisation of habitat patches over the flood cycle
provides a potential means of resolving the relative importance of stochastic processes (e.g.,
random dispersal and spatial ‘reshuffling’ [Hoeinghaus, Layman, Arrington, & Winemiller,
2003]) versus deterministic processes (e.g., homing, species niche) in shaping fish
assemblages in these systems.

125 The current study combines radio-telemetry and remote sensing to examine the movement
behaviour of two large-bodied fishes, barramundi *Lates calcarifer* and forktail catfish
Neoarius leptaspis, in a lowland river in the wet-dry tropics of northern Australia.
Movements of individual fish are tracked at the landscape scale over a full wet season and
related to spatial and temporal variation in inundated floodplain habitat, emergent vegetation,
130 algal productivity, habitat depth and water temperature over the flood cycle. The study tests
two key hypotheses regarding the movement behaviour and dispersal of these fishes: 1) that
movement behaviour predictably tracks the large-scale spatial distribution of dynamic habitat
resources over the flood cycle; 2) that fish disperse widely during the wet season, before
colonising nearby patches of permanent aquatic habitat as the floodwaters recede, resulting in
135 a spatial reshuffling of the individuals residing in habitat patches after the wet season. The
results of the study are discussed with regards to the role of individual-level behaviour as a
driver of fish assemblage structure and associated ecosystem processes in floodplain rivers.

Methods

Study site

140 The study was conducted in the South Alligator River, a relatively undisturbed river-wetland
system whose catchment is fully contained within Kakadu National Park in the wet-dry
tropical region of the Northern Territory, Australia (Fig. 1). The global significance of the
floodplain wetlands of the region is recognised by its inclusion on the World Heritage
Register and the Ramsar Convention on Wetlands. The hydrology of the South Alligator
145 River is intermittent, ceasing to flow during the dry season (typically May-October) and

forming a series of main channel pools (hereafter referred to by the Australian term ‘billabong’). During the wet season (typically November-March), main channel billabongs in the South Alligator system become hydrologically connected to form a contiguous main channel that flows from the escarpment of the upper catchment into the estuary. Extensive floodplain wetlands become inundated during the monsoonal wet season, creating vast areas of highly productive, temporary aquatic habitat for several months each year (Ward et al., 2014; 2016).

Fish tagging and tracking

Fish for tagging with radio-transmitters were collected by angling and boat electrofishing (MBS Series, ETS, Madison, WI, USA) from three connected billabongs on the main river channel ~120 km upstream of the estuary mouth: Yellow Water Billabong (~7 km in length), Home Billabong (~2km length), Mardugal Billabong (~ 3 km length) (Fig. 1). Coded radio-transmitters fitted with encapsulated coil antennas and mortality sensors (Model F1215, length 64 mm, diameter 12 mm, weight 13 g; Advanced Telemetry Systems, Isanti, MN, USA) were surgically implanted into the peritoneal cavities of 25 barramundi *Lates calcarifer* (410-720 mm SL) and 29 forktail catfish *Neoarius leptaspis* (360-490 mm SL) between 5 October and 4 November 2013. A further 15 barramundi (390-610 mm SL) were tagged on 16 January 2014 (Model F1210, encapsulated coil antenna, length 57 mm, diameter 12 mm, weight 11 g; Advanced Telemetry Systems, Isanti, USA). The radio-transmitters were surgically implanted using the method described by Crook et al., (2017).

The locations of tagged fish were estimated at approximately two-week intervals from 8 October 2013 to 14 May 2014. Prior to the onset of the first major wet season rain event in November 2013, fish were tracked within the three billabongs from a boat using a hand-held, three-element Yagi antenna attached to a receiver/data logger fitted with an in-built GPS (R4500C, Advanced Telemetry Systems, Isanti, MN, USA). Subsequent tracking surveys were conducted from a Robinson R44 helicopter using the same receiver and a fixed, four-element antenna. Upon locating a transmitter, the helicopter was flown repeatedly over the area and the strongest signal recorded was matched to its corresponding GPS location to derive the location estimate. Median location accuracy based on 17 fixes of stationary transmitters within the study area during the regular helicopter surveys was 79 m (95% CI = 34-201 m). Although this location accuracy is coarse compared with smaller scale telemetry studies, location error was low relative to the spatial scale of the study area (approx. 800 km²) and the generally large distances moved by fish between surveys (see below).

180 Five habitat variables were considered in the analyses: 1) Surface water area (ha) was measured to represent variation in the total area of available aquatic habitat over the flood cycle; 2) The area of emergent vegetation (ha) was measured because it was hypothesised that the expansion of extremely dense vertical grasses (see Ward et al., 2016) as the wet season progressed might impede fish movement on the inundated floodplain; 3) The area of
185 deep water habitat (ha) was measured to represent variation in the amount of suitable habitat for barramundi and catfish over the flood cycle. A threshold depth of >0.25 m was used as an approximate minimum for deep water based on extensive field observations of fish behaviour by the authors; 4) The area of 'warm' temperature was measured to represent variation in the availability of optimal water temperatures over the flood cycle. A threshold of $>25^{\circ}\text{C}$ was
190 used because previous studies of barramundi suggest that temperatures above this value are necessary for maximum growth and feeding (Katersky & Carter, 2007); 5) The % of the study area with periphyton density $>10\text{ g m}^{-1}$ was measured to represent changes in the spatial distributions of primary production across the study area over the flood cycle. This threshold value was chosen based on the criteria used by Ward et al. (2016) to define
195 "hotspots" of primary productivity on the South Alligator floodplain.

Classification and regression tree modelling were applied to combine microwave and optical satellite data with extensive field-sampling across the study area. A multi-sensor fusion of microwave L-band, HH polarization SAR data and Landsat TM optical/infrared based metrics, combined with Lidar survey data and field-based measurements of floodplain
200 inundation extent, water depth, water temperature, vegetation cover and primary productivity, was used to produce maps of the distribution of the five habitat variables at the time of satellite image capture (for full details of the methodology, see Ward et al., 2014; 2016). Nine maps of the habitat variables were produced over the study period using the available Landsat images.

205 The available Landsat derived habitat maps did not align with our fish survey dates. We therefore used generalised additive models (GAMs) to describe the temporal pattern in each habitat variable across the study period, and then used these modelled relationships (see Results) to predict environmental conditions on other days. The GAMs explained a substantial amount of temporal variation in habitat data (deviance explained: floodplain area:
210 82.2%; emergent vegetation area: 77.4%; floodplain depth >0.25 = 88.5%; percent temp >25 degrees = 90.6%; percentage productive 83.6%).

Analysis of fish distribution data

ArcGIS was used to derive three variables for statistical analysis based on the individual location data and remotely sensed habitat characteristics for each survey. We excluded fish location data from day 0 and day 100 of the study as these corresponded to tagging days and thus the fish's location at release. "Distance from home" was calculated as the straight-line distance (km) between each fish location estimate and the initial release location. This variable provides an indication of movement extent throughout the study period. "Distance from permanent water" was calculated as the straight-line distance (km) between each fish location estimate and the nearest permanent water. To account for the spatial resolution of the available Landsat imagery, a 30-m buffer was placed around the areas of permanent water (i.e. those which persisted all year) and locations within these buffer zones were classified as being associated with permanent water and given a value of 0 km. This variable provides a measure of how far fish ventured onto the temporarily inundated floodplain. "Floodplain use" was a binary variable and indicated whether an individual was on the floodplain or in permanent water at each survey time. A 30-m buffer was again placed around the areas of permanent water and locations outside of the buffer zones were classified as being associated with inundated floodplain habitat.

Generalised additive mixed effects models (GAMMs) were used to analyse patterns in the three movement metrics for each species. All models included a random intercept for each fish to account for the repeated measures nature of the data. "Distance from home" and "distance from permanent water" are continuous and strictly positive and were therefore modelled with a gamma distribution and log-link function. "Floodplain use" was a binary variable and modelled with a binomial distribution. We initially explored temporal patterns in movement across the study period, then the effects of each floodplain habitat variable, by fitting a smoother to predictors with a maximum basis dimension $k=4$ (Wood, 2017). We compared seven competing models for each movement metric (temporal habitat variables included in different models due to collinearity) using rescaled Akaike's Information Criterion corrected for small sample sizes ($\Delta AICc$) (Burnham & Anderson, 2002). Analyses and model selection were conducted using R 3.5.0 (R Development Core Team, 2018) with the `gamm4` and `bbmle` packages. Model predictions were back-transformed to the observed scale using the appropriate link function to aid the interpretation of results.

Results

Wet season habitat dynamics

The first rainfall of the wet season consisted of a series of isolated events in early-mid November (Fig. 2) that did not increase the area of surface water on the South Alligator River floodplain (Fig. 3a, b). At this time, habitat depth, emergent vegetation cover and periphyton productivity remained at low, dry season levels and 100% of the surface water in the study area was $>25^{\circ}\text{C}$ (Fig. 4). The first monsoonal rain event of the wet season occurred from late November to early December (Fig. 2). This event connected the main channel billabongs and caused extensive inundation of the low-lying floodplain surrounding Yellow Water Billabong (Fig. 3c, Fig. 4a). Coincident with the increase in flooded area, the area of emergent vegetation, deep habitat and high periphyton biomass increased, while the area of warm water temperature declined (Fig. 4). These patterns continued to strengthen as further monsoonal events increased the extent of flooding, peaking in mid-February 2014. The frequency of intense rainfall declined after mid-February and flooded area, emergent vegetation, deep habitat and periphyton biomass all began to gradually decline until the end of the study period. The spatial extent of warm water declined to a minimum in February/ March and then increased towards the end of the study.

Fish movement

Prior to the first significant rain event in late November and early December, radio-tagged barramundi and catfish were restricted to the billabongs in which they were collected and exhibited only small-scale movements (generally less than 1 km) (Fig. 3a, b; Fig. 5a, c). The movement behaviour changed immediately following the first monsoonal rain event of the wet season, with a large proportion of both species moving rapidly onto the newly inundated floodplains (Fig. 3c; Fig. 5a, c). In early December 2013, ~50% and 60% of barramundi and catfish respectively were utilising the newly inundated floodplain habitat (Fig. 5e, g); the modelled distance from the tagging location was ~3 km for barramundi and ~1.5 km for catfish; and the distance from permanent water was ~600 m for barramundi and ~250 m for catfish (Fig. 5i, k). Barramundi moved greater distances onto the floodplain in the early stages of the wet season than catfish (~750m for barramundi versus ~500 m for catfish) but tended to begin moving closer to permanent water earlier than catfish (mid January for barramundi versus mid-February for catfish) (Fig. 5i, k).

The mean distance from the tagging location peaked at ~5 km in early-mid January for barramundi and at ~3.8 km in early February for catfish (Fig. 5a, c). The maximum distance

an individual was located from the tagging location was 26.7 km for barramundi and 16.7 km for catfish in early February. Fish which had moved long distances away from their tagging site during the wet season did not colonise nearby permanent water as the floodwaters receded, even though extensive areas of permanent water (including the main river channel and several large billabongs that support populations of barramundi and catfish) were available closer to the maximum displacement location than the tagging site (see Fig. 3a). Instead, most individuals of both species exhibited directed homing behaviour, with the distance from the tagging site declining to ~1 km for both species by the end of the study (Fig. 5a, c). All eight barramundi and 13 out of 17 catfish that were located in the last survey (14 May) were detected within the same billabong they had inhabited prior to the wet season. The four remaining catfish were detected in other areas of permanent water 3-9 km from the original tagging location (Fig. 3 i).

Over the 7-month study period, the transmitters of 11 barramundi and three catfish emitted mortality signals. Detections had ceased by the final survey on 14 May for a further 21 barramundi and 9 catfish. The high abundance of high-order predators in the South Alligator River, including estuarine crocodiles *Crocodylus porosus* and bull sharks *Carcharhinus leucus*, likely accounts for some of the observed mortality. Barramundi are also a popular recreational target in the study region and it is likely that mortality and failure to locate some of the tagged barramundi is due to fishing effects. One of the transmitters implanted in a barramundi was returned by an angler in early April 2014 and it is possible that other radio-tagged fish were captured but not noticed or reported by anglers.

Of the 21 barramundi and 9 catfish that were no longer being detected by the last survey on 14 May 2014, 14 and four respectively were last detected in April or later. Expiration of the transmitter batteries likely accounts for the failure to detect at least some of these fish; the estimated date of battery expiry based on the manufacturer's specifications was 13 May - 12 June 2014 for the 54 transmitters deployed from October to November 2013, and 13 April 2014 for the 15 transmitters deployed in January 2014. It also is possible that some fish undertook migrations into saline estuarine waters where the radio signals could not be detected. A concurrent acoustic tracking of barramundi and catfish in the South Alligator River showed that two of 25 barramundi but none of 25 catfish moved into the saline reaches of the estuary during the 2013/14 wet season (Crook et al., 2017; authors unpubl. data).

Habitat associations

Modelling of the relationships between fish distributions and dynamic habitat variables over the study period suggested different responses for each species (Table 1, Figure 6). For barramundi, the area of high periphyton productivity was positively related to how far individuals dispersed from 'home' (Figure 5b) and how far onto the floodplain they ventured (Figure 5j). The probability of barramundi being located on the floodplain generally declined as more of the area exceeded 25°C, although a slight increase was detected around 60% of floodplain warmer than this threshold (Figure 5f). All three catfish movement metrics increased as more of the floodplain became inundated with water (Figure 5d, h, l).

Individual variation in movement behaviour

Although there were clear general patterns in the movements of both species in response to dynamic habitat resources (e.g., rapid utilisation of inundated floodplain habitat, homing to previous locations), considerable variation in movement behaviour among individuals was also evident: *maximum distance from home* (median, range), barramundi 6.3, 1.0-26.7 km, catfish 7.7, 0.9-16.7 km; *maximum distance from permanent water*, barramundi 1.0, 0.1-2.3 km, catfish 0.9, 0.1-2.6 km; *proportion of wet season floodplain use*, barramundi 0.4, 0-0.9, catfish 0.6, 0.3-1.0 (Fig. 6). Neither species showed evidence of a dichotomy between sedentary and mobile contingents. However, there was evidence of correlation between movement behaviours for barramundi, with "maximum distance from permanent water" positively correlated with both "maximum distance from home" and probability of "floodplain use" (Table 2). There were no statistically significant correlations among the three movement behaviour variables for catfish.

Discussion

Movement responses to dynamic habitat

Our results demonstrate that individuals of both species altered their movement behaviour rapidly in response to changes in the availability and distribution of aquatic habitat across the monsoonal wet season. After a period of small-scale movement within billabong habitats prior to the first monsoonal rainfall event, individuals of both species undertook extensive lateral movements onto the floodplain as it became inundated by floodwaters and then retreated to dry season refugia as the floodwaters receded. The movement of barramundi and catfish onto inundated floodplains during the wet season is comparable to the findings of Anderson et al., (2011), who radio-tracked the large-bodied characid *C. macropomum* on inundated floodplains of the Amazon Basin during the wet season and reported movements of

up to 5.9 km over periods of up to 29.5 days. However, Anderson et al., (2011) did not track individual fish over the full flood cycle and their study does not provide information on the spatial distributions of individuals prior to and after the wet season. Our results are also compatible with previous studies that used fish survey data to make inferences regarding fish dispersal in other tropical regions. For example, in a study of fish assemblages in 20 floodplain lakes in the Orinoco Basin, Venezuela, Rodriguez & Lewis (1994) reported much higher densities of fish during dry periods than when lakes were connected by floodwaters to the surrounding floodplain. Although unable to make direct inferences regarding the movements of individual fish over the flood cycle, these authors attributed the decline in fish density in the lakes to movements of fish onto surrounding floodplain habitats. Similar evidence of rapid dispersal by fish onto inundated floodplains has been reported in other tropical river systems (e.g., Amazon Basin; Fernandes, 1997; Castello, 2008; Parana River, Brazil; Petry, Agostinho & Gomes, 2003; Niger River, Mali; Bénech & Peñáz 1995), as well temperate regions (Kankakee River, USA; Kwak, 1988; Murray River, Australia; Lyon, Stuart, Ramsey, & O'Mahony, 2010; Stoffels, Rehwinkel, Price, & Fagan 2016).

While there was a clear general pattern of extensive movement during the wet season and homing behaviour during the wet-to-dry transition, considerable intra-specific variation in movement behaviour was observed for both species. Unlike many studies of temperate riverine fish, we did not observe a clear dichotomy of movement behaviours among individuals (e.g., movers versus stayers; Petty & Grossman, 2004; Radinger & Wolter, 2014). Instead, a spectrum of movement behaviours was exhibited, ranging from individuals that stayed near their dry season refuges (within ~2 km) throughout the study, to individuals that moved large distances (>20 km) away from their refuges and between consecutive surveys. High levels of intra-specific variation in the movement behaviours of riverine fish have now been observed repeatedly across a wide range of geographic regions and river types (e.g., Fraser, Gilliam, Daley, Le & Skalski, 2001; Harrison et al., 2017) and appear to confer resilience at the species level due to the stabilising effects of alternate migratory phenotypes whose fitness is variably favoured under different environmental conditions (the portfolio effect; see Schindler, Armstrong & Reed, 2015). The implications of intra-specific variation in migratory behaviour have, to date, received most attention in relation to the sustainability of salmonid fisheries in temperate regions. Our study suggests that portfolio effects may also be important considerations for the management of tropical river fish populations and the fisheries they support.

Significance of directed homing behaviour

Based on previous observations that movement by fish on tropical river floodplains during the wet season is extensive (see Winemiller, 1996; Anderson et al., 2011), our *a priori* expectation was that barramundi and catfish would disperse widely during the wet season, before colonising nearby patches of permanent aquatic habitat as the floodwaters recede. Such a scenario would result in a high proportion of individual fish colonising habitat patches different to those occupied in the previous dry season. In contrast to this expectation, the radio-tracking results revealed high levels of directed homing behaviour by both species (Fig. 5a, c). All of the barramundi and most of the catfish located in the final survey in May had returned to the same billabong they had inhabited prior to the wet season, despite undertaking extensive movements away from their home billabongs during the wet season which allowed them to encounter other potential dry season refugia. Whilst homing behaviour over large spatial scales has been previously reported for riverine fishes (e.g., Pellett, Van Dyck, & Adams, 1998; Stancill, Jordan & Paukert, 2002; Koehn et al., 2009), to our knowledge this is the first time that such behaviour has been observed by fish utilising inundated floodplain habitats.

The directed homing behaviour exhibited by barramundi and catfish during the wet-to-dry transition has potentially important implications for our understanding of the spatiotemporal dynamics of species distributions in tropical river ecosystems. If we consider the study system through the lens of island biogeography (Macarthur & Wilson, 1967; Brown & Kodric-Brown, 1977), refugia that retain water over the dry season can be considered “islands” of aquatic habitat in a predominantly terrestrial landscape: these island habitats are colonised at the end of each wet season by aquatic animals seeking dry season refuge (Fig. 7). The tenets of island biogeography in this situation would predict that, in addition to refuge size, the rates of immigration into refugia are strongly influenced by their distances from sources of potential colonists (under the neutral assumption of random dispersal; see Hubbell, 2001). In tropical floodplain rivers, sources of colonists might include specific locations where fish move to feed or reproduce during the wet season, such as hotspots of primary productivity on the floodplain (Ward et al., 2016) or patches of floodplain forest with dense stands of fruiting trees.

Directed homing behaviour has the potential to strongly influence the colonisation of billabongs and other refugia in river-floodplain systems (e.g., ‘ria’ lakes, Carvalho et al., 2017) by weakening the relationship between colonisation rates and the distance of refuges

from colonist sources. Accurate homing to specific refuge billabongs during the wet-to-dry transition by barramundi and catfish suggests that they have the cognitive capabilities to seek out and re-colonise specific habitat patches with desirable attributes as dry season refugia (e.g., depth, position; Hoeinghaus et al., 2003), as opposed to colonising the first potentially suitable habitat patch they encounter. Presumably, such cognitive abilities would also allow these fish to repeatedly return to specific feeding or reproductive areas during the wet season. Although our results are limited to barramundi and catfish on the South Alligator River, it is possible that other fishes in tropical rivers also exhibit directed homing behaviour. Similar to our findings, Arantes et al., (2013) found that the large-bodied arapaima (*Arapaima* spp.) undertakes extensive movements onto inundated floodplains in the wet season before moving back to large, deep floodplain lakes as the floodwaters recede. However, their study did not determine whether individual fish returned to the same dry season refugia each year.

In the context of species-specific dispersal characteristics as a driver of metacommunity structure on floodplains (Fernandes et al., 2014; Stoffels et al., 2016), our results suggest that dispersal limitation in large, long-lived fishes might function as a threshold process whose spatial scale is determined by the homing abilities of fish, rather than the commonly assumed probabilistic relationship between immigration rate and habitat patch isolation (see Bowler & Benton, 2005). For barramundi and catfish, these spatial scales would appear to be large: accurate homing to refugia was commonly exhibited from distances of >10 km in the current study and has been reported for barramundi at distances of >80 km (Crook et al., 2017). Homing behaviour by other large-bodied, riverine fishes has similarly been recorded at scales of 10s to 100s of kms (Pellett et al., 1998; Stancill et al., 2002; Koehn et al., 2009).

The immigration of individuals to previously occupied habitat patches during the wet-to-dry transition - as observed for a single flood cycle here and over multiple flood cycles by Crook et al. (2017) - could potentially also act as a rescue effect (*sensu* Brown & Kodric-Brown, 1977) at the metacommunity level by dampening species turn-over rates and inter-annual variation in species abundance, compared to random dispersal (see Fig. 7). We note, however, that homing behaviour is not exhibited by all fish species and expression of this behaviour can vary across ontogeny and among individuals within a species (Bélanger & Rodriguez, 2001; Crook, 2004; Shima, McNaughtan, Geange, & Wilkinson 2012). The spatial scales over which fish move also varies among taxa, with a general tendency for large-bodied fishes to exhibit higher levels of vagility than small-bodied fishes (Minns, 1995; Griffiths, 2006). Thus, the modulating effects of homing behaviour on the amplitude of

temporal variation in species assemblages within habitat patches would likely vary according
440 to the composition of taxa and life stages present (which may, in turn, be affected by
deterministic processes such as environmental filtering during the dry season; Winemiller,
1996; Fernandes et al., 2014).

Another potentially important implication of directed homing behaviour is its effect on the
transfer of energy and nutrients from aquatic to terrestrial food webs on the floodplain (i.e.,
445 the aquatic/terrestrial transition zone (ATTZ), *sensu* Junk et al., 1989). It has long been
recognised that terrestrial ecosystems provide a pulsed subsidy of allochthonous material to
aquatic food webs during floodplain inundation events via incorporation of dissolved and
particulate carbon and nutrients, and terrestrial food items such as invertebrates and fruit
(e.g., Junk et al., 1989; Pettit et al., 2017). The importance of material transferred from
450 aquatic to terrestrial food webs via the mortality of fish stranded on drying floodplains is
much less known, although it has been widely observed that many fish perish in floodplain
pools that dry completely (Lowe-McConnell, 1987; Winemiller & Jepsen, 1988; Fernandes et
al., 2014).

Our results for barramundi and catfish suggest that, while these fish may move large
455 distances to access food or other resources on the inundated floodplain, they are able to
recognise the onset of the wet-to-dry transition and reduce the resultant mortality risk by
returning to patches of aquatic habitat that have sustained them over the previous dry
season(s). By reducing the biomass of fish that would otherwise suffer mortality on drying
floodplains, directed homing behaviour might limit the transfer of aquatic energy and
460 nutrients to terrestrial food webs in the ATTZ (see Fig. 7). Nonetheless, at least 28% and
12% of tagged barramundi and catfish, respectively, suffered mortality during the wet season
(i.e. their transmitters emitted mortality signals), suggesting that even species which exhibit
accurate homing potentially contribute energy and nutrients to terrestrial food webs via
mortality on inundated floodplains (Fig. 7). Quantification of the magnitude and direction of
465 material subsidies in the ATTZ of floodplain rivers, and how these subsidies are affected by
the behaviour of animals, remains an important area for future research. An important step
towards achieving this goal is to determine the generality of directed homing behaviour by
fish on inundated floodplains both across species and among geographic regions.

Conclusions

470 Whilst studies of spatial and temporal variation in species composition and abundance have provided crucial evidence regarding the processes that structure river-floodplain fish assemblages, a limitation of these studies is that they do not allow for inference regarding the behaviour and fates of individual fish. Our study demonstrates the value of individual-level information for understanding large-scale ecological processes, such as dispersal limitation
475 and food web subsidies, in floodplain rivers. For instance, the movement paths associated with the conceptualised behaviours explored in Fig. 7 (random dispersal, retreat to nearest refuge, directed homing) appear essentially identical and a snapshot ‘sample’ of fish distributions during the wet season would not identify clear differences among these behaviours. It is only by tracking the locations of individual fish over the full flood cycle that
480 we can discern important aspects of behaviour that may interact with environmental factors (e.g., environmental filtering) to regulate fish species assemblage structure and food web subsidies. Based on these considerations, we conclude that integration of information on individual-level movement behaviour across the three stages of dispersal (emigration, inter-patch movement, immigration; Bowler & Benton, 2005) is an essential step towards
485 improved conceptual and quantitative understanding of large-scale ecosystem processes in spatially complex and dynamic environments.

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Authors’ contributions

DC, MD, TS and DB conceived the ideas and designed methodology; DC, DB, MD, QA and WB collected the data; DC and JM analysed the data; DC led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

Data accessibility

Data and R code associated with this paper are deposited in the Charles Darwin University Research Webportal: <http://dx.doi.org/10.25913/5db7c250a2437> (Crook et al., 2019).

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Tables

Table 1: Model selection table for different predictor variables using GAMMs. $\Delta AICc$ values
675 should be compared down each column (best fitting model: $\Delta AICc = 0$ and highlighted in bold). edf refers to each smoother's effective degrees and indicates the degree of nonlinearity

in the term, with edf=1 being a straight line. Intercept only (null) models do not include any smoothers.

Variable	Barramundi						Catfish					
	Distance from home		Probability of floodplain use		Distance from permanent water		Distance from home		Probability of floodplain use		Distance from permanent water	
	ΔAIC	edf	$\Delta AICc$	edf	$\Delta AICc$	edf	$\Delta AICc$	edf	$\Delta AICc$	edf	$\Delta AICc$	edf
Intercept only	119.2	-	69.6	-	20.3	-	126.1	-	139.9	-	28.2	-
Time	18.1	2.91	10.1	2.83	6.1	2.59	4.6	2.88	3.4	2.90	0.4	2.62
Floodplain inundation	47.1	2.83	9.8	1.00	16.9	2.01	0	1.00	0	2.85	0	1.66
Emergent vegetation	63	2.80	15.1	1.00	21.4	1.00	13.5	1.00	8.9	2.86	6.6	1.59
Depth >0.25m	56.5	2.78	10.3	1.00	19.2	1.88	6.7	1.00	5.1	2.82	2.6	1.89
% area temp <25°C	49.9	2.90	0	2.85	18.9	1.92	6.2	2.79	8.8	2.86	2.7	1.84
% area periphyton >10g/m ²	0	1.00	10.8	2.32	0	1.82	14.1	2.64	8.9	2.48	15.9	1.98

Table 2: Correlation matrix for the three movement variables for barramundi and catfish. Values are Pearson's correlation coefficients with Bonferroni adjusted probabilities (* = $P < 0.05$, ** = $P < 0.001$). Catfish values are presented in italics.

	Max. distance from home	Max. distance permanent water	Probability of Floodplain use
Max. distance from home	-	<i>0.414</i>	<i>-0.013</i>
Max. distance onto floodplain	0.510*	-	<i>0.102</i>
Probability of floodplain use	0.380	0.677**	-

Figure legends

690 **Figure 1:** Map of the study area showing locations of the three billabongs in which fish were tagged.

Figure 2: Daily rainfall over the study period recorded at Jabiru, ~33 km from the study area (source: Bureau of Meteorology, <http://www.bom.gov.au/climate/data/index.shtml?bookmark=136>).

695 **Figure 3:** Distribution of remotely sensed surface water and radio-tracked fish distributions for nine of the 17 surveys (barramundi: yellow dots, catfish: orange dots). The dates shown are the radio-tracking survey dates and the surface water distributions were derived using the closest date with available Landsat imagery (see Methods).

700 **Figure 4:** Predicted temporal patterns ($\pm$ 95% confidence intervals) in habitat variables in the study region over the flood cycle. Observed values from satellite imagery analysis are shown as black dots.

Figure 5: Predicted temporal patterns ($\pm$ 95% confidence intervals) in the movement response variables and predicted relationships between environmental drivers and movement response variables ($\pm$ 95% confidence intervals) for barramundi (left) and catfish (right).
705 Temporal patterns: (a, c) distance from home; (e, g) probability of floodplain use; (i, k) distance from permanent water. Environmental drivers: (b, d) distance from home; (f, h) probability of floodplain use; (j, l) distance from permanent water. Note that the distance onto floodplain models start on 24 November 2013 because all fish were confined to permanent water prior to this date.

710 **Figure 6:** Three-dimensional plots showing individual variation in the three movement variables for (a) barramundi and (b) catfish. This figure shows the maximum distance from home and the maximum distance from permanent water for each fish over the entire study. “Proportion floodplain” was calculated as the proportion of detections identified as being positioned on the floodplain for each fish after the first floodplain inundation event (i.e.,
715 including and after the 2 December 2013 tracking survey).

Figure 7: Conceptualisation of the influence of movement behaviour on post-wet season fish distributions. The left-hand panel shows the distributions of fish (open circles) in dry season refuges (ovals) prior to the onset of the wet season. The oval with the broken line represents a refuge that contains water at the end of the wet season but is unable to sustain fish survival
720 over the entire dry season (e.g., due to desiccation or deteriorating water quality). The central

panel shows the movement paths of fish over the wet season and their locations post-wet season (open circles = survivors, closed circles = mortalities). The right-hand panel shows the final locations with movement paths removed. The grey background represents the floodplain. Note that this conceptualisation presents all refuge billabongs as equal in size.

In scenario 1 (random dispersal), most individuals do not settle in a suitable dry season refuge and suffer mortality on the floodplain. In scenario 2 (retreat to nearest refuge), most individuals settle in suitable refuges, but a minority settle in unsuitable refuges or suffer mortality on the floodplain (those unable to locate the nearest refuge). In scenario 3 (directed homing), most individuals settle into the same suitable refuge they inhabited the previous dry season, but a minority suffer mortality on the floodplain or in unsuitable refuges (those unable to locate their home refuge). Note that the post-wet season compositions of each refuge (colour-coded circles) in scenario 3 are more similar to the pre-wet season compositions than in the other scenarios.

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