Comparative movements of four large fish species in a lowland river

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A multi-year radio-telemetry data set was used to comparatively examine the concurrent movements of the adults of three large-bodied Australian native freshwater fishes (Murray cod *Maccullochella peelii*, trout cod *Maccullochella macquariensis* and golden perch *Macquaria ambigua*) and the introduced carp *Cyprinus carpio*. The study was conducted over a reach scale in the regulated Murray River in south-eastern Australia. Differences were identified in the movements among these species. The predominant behaviour was the use of small movements (<1 km) for all species, and although larger-scale movements (>1 km) did occur, the frequency varied considerably among species. Large-scale movements were least evident for *M. macquariensis* and more common for *M. ambigua* and *C. carpio* with these two species also having a greater propensity to change locations. *Macquaria ambigua* displayed the largest movements and more *M. ambigua* moved on a 'continual' basis. Although a degree of site fidelity was evident for all species, the highest levels were exhibited by *M. macquariensis* and *M. peelii*. Homing was also evident to some degree in all species, but was greatest for *M. peelii*.

INTRODUCTION

Movement patterns of fishes vary in relation to life stage, habit, life-history strategy and environmental conditions and considerably differ among species (Hutchings & Morris, 1985; Lucas & Baras, 2001). Connectivity with essential resources and life cycle needs (Albanese *et al.*, 2004) is critical for the long-term survival of fish populations (Smithson & Johnston, 1999; Jungwirth *et al.*, 2000). The benefits of movement include optimization of feeding, avoidance of unfavourable conditions, exploitation of refugia, gene flow, colonization or recolonization of unoccupied habitats and optimization of reproductive success (Northcote, 1978; Albanese *et al.*, 2004). World-wide fish movement pathways are now often blocked by man-made structures such as dams and weirs (Liermann *et al.*, 2012) and this has been widely considered to have contributed to

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declines of fish populations (Cadwallader, 1978; Cowx & Welcomme, 1998; Lundqvist *et al.*, 2008).

Semi-arid lowland rivers are widely degraded throughout the world and their rehabilitation is now receiving some attention (Gore & Shields, 1995; Murray-Darling Basin Commission, 2004). This includes the provision of fish passage, which is now recognized as a key rehabilitation measure (Cowx & Welcomme, 1998; Cooke *et al.*, 2012). Understanding the movement patterns of stream fishes is essential to effectively manage populations (Gowan *et al.*, 1994), to provide support for restorative actions such as the provision of fish passage (Cowx & Welcomme, 1998; Mallen-Cooper, 1999; Barrett & Mallen-Cooper, 2006) and providing biological information for the effective design of fishways (Mallen-Cooper & Brand, 2007; Williams *et al.*, 2011). Limited understanding of migrations, the specific requirements of individual species and the level of connectivity needed to sustain populations is a key factor hindering the conservation and restoration of river fish populations (Cooke *et al.*, 2012).

The Murray-Darling Basin (MDB) is a large catchment, covering more than 1 million km^2, in the semi-arid inland of south eastern Australia (Murray-Darling Basin Commission, 2004). The native fish populations of the MDB, comprising 46 species, have undergone significant reductions in distribution and abundance (Lintermans, 2007). Overall, population levels are now estimated to be at about 10% of those prior to European settlement (*c.* 1800s) (Koehn & Lintermans, 2012). There are many reasons offered for the decline of Australian native fishes (Cadwallader, 1978) but loss of habitat connectivity through restricting fish movements has been identified as a major contributing factor (Murray-Darling Basin Commission, 2004). Indeed, the MDB rates amongst the most highly affected river basins in the world with only 40–50% of its water course length remaining free-flowing (Liermann *et al.*, 2012). It is suggested that >10 000 barriers have been constructed on MDB rivers and floodplain channels that pose barriers to fish passage (Baumgartner *et al.*, 2014).

Rehabilitation of this unique fish community is now the focus of a multi-state government initiative (Murray-Darling Basin Commission, 2004; Koehn & Lintermans, 2012). Actions include a major fish passage restoration programme ('the Sea to Lake Hume') that includes the construction of 14 fishways to improve fish passage along 2225 km of the Murray River (Barrett & Mallen-Cooper, 2006). This programme is aimed at providing benefits to multiple, rather than single fish species (Stuart *et al.*, 2008), and includes the trapping and removal of carp *Cyprinus carpio* L. 1758 at these fishways (Stuart *et al.*, 2006). Alien species invasion has also been identified as a major factor in the decline of MDB native fishes (Cadwallader, 1978), and understanding the movements of alien species, especially *C. carpio*, is needed so that management actions can be undertaken to reduce their effects and limit population expansion (Koehn *et al.*, 2000).

The three native species studied here, Murray cod *Maccullochella peelii* (Mitchell 1838), trout cod *Maccullochella macquariensis* (Cuvier 1829) and golden perch *Macquaria ambigua* (Richardson 1845) are all potadromous species that co-occur in the lowland rivers of the MDB (Lintermans, 2007). Their populations have suffered substantial declines. *Maccullochella peelii* and *M. macquariensis* are now listed as nationally threatened species (www.environment.gov.au/biodiversity/threatened). Taking of *M. macquariensis* by anglers is prohibited and *M. peelii* is managed for both conservation and recreational fishing (Koehn & Todd, 2012). The fourth species studied, *C. carpio*, is an introduced species that has invaded the MDB and now dominates most

fish communities in south-eastern Australia, and is being managed as a pest species (Koehn *et al.*, 2000).

Whilst the three native species are all large-bodied carnivores, *M. peelii* and *M. macquariensis* have large mouth gapes and may be described as 'sit and wait predators' (Lintermans, 2007). Both are highly associated with structural woody habitats (Nicol *et al.*, 2007; Koehn, 2009*a*; Koehn & Nicol, 2014) with *M. peelii* being largely demersal (Koehn, 2009*b*). By comparison, *Macquaria ambigua* have a smaller mouth and are a mid-water species that may school (Lintermans, 2007). *Cyprinus carpio* are also a mid-water schooling species but are a benthivorous omnivore with many other characteristics that differ markedly from most MDB native fishes, including those in this study (Koehn, 2004). *Cyprinus carpio*, especially smaller individuals, may also become prey of each of the native species, but especially *M. peelii*, with its larger mouth gape. While there are some general similarities in habitat use between these four species (especially wood habitats), *C. carpio* prefer slower waters closer to the river banks, and are most similar to *M. ambigua* (Koehn & Nicol, 2014). *Maccullochella peelii* and *M. macquariensis* also differ from *M. ambigua* and *C. carpio* in their breeding strategy, being site-specific spawners and exhibiting parental care, compared with the pelagic, communal spawning of the other two species (Lintermans, 2007). A combination of these characteristics may infer that *M. ambigua* and *C. carpio* may move more widely than *M. peelii* and *M. macquariensis*, but this has never truly been tested.

Fish movements occur across a range of spatial and temporal scales but many studies focus on single species with fewer longer-term, multispecies studies that allow comparison between species (Lucas & Baras, 2001). Although knowledge of the movement ecology of Australian potamodromous fishes has advanced in the last decade (Koehn & Crook, 2013), the differing methods, spatial and temporal scales and environmental conditions of these separate studies make direct comparison between species difficult. This study uses a multi-year data set collected using radio-tagged fishes over a reach-scale to concurrently determine the comparative movements of four large-bodied potamodromous fishes in a semi-arid lowland river, the Murray River, in south-eastern Australia. It uses quantitative methods to assess movement patterns, highlights differences between species and provides a ranking of mobility according to their movements.

MATERIALS AND METHODS

STUDY AREA

The study was conducted in a 250 km reach of the Murray River, downstream of Lake Mulwala (36° 00′ S; 146° 00′ E) (Fig. 1) from 1994 to 1997. The Murray River in this region is a larger, low flowing lowland river that is characterized by meandering bends (Mackay, 1990; Rutherfurd, 1990). Flows in the study reach are largely regulated by upstream storages that has led to a pattern of seasonal flow reversal [*i.e.* high summer irrigation flows (December to February) and low winter (June to August) flows due to dam capture of water; Close, 1990; Thoms *et al.*, 2000]. The average river width is 108 m, with an average depth of 2 m at low flows and a maximum depth of *c.* 11 m under average conditions (Koehn, 2009*a*).

STUDY METHODS

Fishes were captured by a boat-mounted electro fisher (7.5 GPP Smith Root Inc.; www.smith-root.com) and implanted with radio-tags during the austral autumn and winter
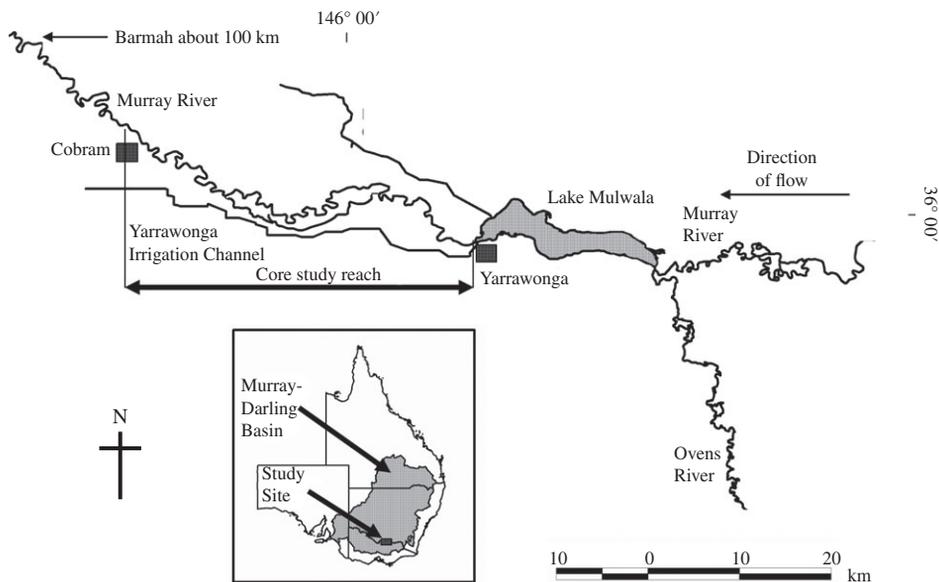
FIG. 1. Map of study area on the Murray River in south-east Australia. Murray-Darling Basin indicated (▪) in the inset map.

(March through to August), which was prior to major gonad development. Surgery and tracking procedures have previously been described in detail (Koehn, 2009a; Koehn *et al.*, 2009). Briefly, fishes of suitable size were anaesthetized using a 5 mg l^{-1} Maranil solution and had a 48–49 MHz radiotransmitter (Advanced Telemetry Systems; www.atsionline.com) surgically implanted into their abdominal cavity. Transmitter mass never exceeded 2% of the body mass of the fish (Knights & Lasee, 1996) in air or 1·25% of the mass in water (Winter, 1983). Attempts to determine the sex of the fish by inspection of the gonads during surgery was often inconclusive as capture and surgery were generally undertaken when gonads were less developed. A range of fish sizes, fish sex, tagging and tracking details were collected (Table I). Immediately after surgery, fishes were revived and released at the point of capture. The transmitters contained a 'mercury motion sensor' to indicate mortality (had the fish died or expelled the transmitter). Manual tracking was undertaken by boat on a monthly basis, during daylight hours and delayed for >1 month after implantation to avoid any non-representative behaviour from handling (Guy *et al.*, 1994). Fishes could be tracked with an accuracy of 0·19 ± 0·13 m (mean ± S.E.) (Koehn *et al.*, 2012) and river locations were established by measurements made from river markers placed every 200 m along the bank. If fishes could not be located when tracked by boat, additional tracking by aircraft was undertaken for a river length of 250 km from the upstream end of the study site. The accuracy of locations determined by aircraft tracking was estimated to be ±0·5 km and these locations were only used for calculations of large-scale movements. Fishes were captured from a 20 km river section and tagged between March 1994 and October 1996 and locations determined from April 1994 to December 1997. Flow and temperature data were collected from the gauges immediately downstream of the weir wall at Yarrawonga (Fig. 1).

ANALYSIS OF MOVEMENTS

Previous information on adult mobility documents a mix of movement classes ranging from small (*e.g.* site fidelity to particular areas; Koehn *et al.*, 2008) to large (*e.g.* seasonality; Stuart & Jones, 2006a). Mobility may include small movements within an area followed by a large movement to another area (Crook, 2004) and in the case of *M. peelii* another large movement returning the individual back to its initial area (*i.e.* homing; Koehn *et al.*, 2009). The data were

TABLE I. Summary details for each fish species fitted with radiotransmitters and the number of individuals tracked in each year of the study (1994–1997)

Species	Number of fish tagged	Length*(mm)		Mass (g)		Sex		Number of individuals tracked each year			
		Median	Range	Median	Range	Male	Female	1994	1995	1996	1997
Macullochella macquariensis	21	485	420–600	1458	950–3150	6	4	13	14	6	2
Macullochella peelii	13	715	470–1200	6000	1350–27 100	3	7	9	8	7	3
Macquaria ambigua	34	480	400–580	2100	1090–3550	8	15	10	17	15	8
Cyprinus carpio	33	520	252–690	2600	862–5550	6	11	10	14	15	8

*Total length for *M. peelii* and *M. macquariensis* and fork length for *M. ambigua* and *C. carpio*.

analysed to test for site fidelity, seasonality and homing in movements. To categorize movement data into small or large, kernel densities were initially computed of the linear distances moved for each individual, for each species, in each month to determine if the distribution of movement was unimodal or multi-model for each species. The distributions for each species were multi-modal, with modes evident for movements with a linear length <1, between 1 and 5 and >5 km for *M. peelii*, *M. ambigua* and *C. carpio*. *Macullochella macquariensis* was unimodal with the mode <1 km. This was consistent with previous observations that small movements for these species are generally <1 km and large movements are >1 km (Crook, 2004; O'Connor *et al.*, 2005; Stuart & Jones, 2006*a*; Koehn *et al.*, 2008, 2009; Ebner & Thiem, 2009; Ebner *et al.*, 2009) in this region. Based on these distributions, if the detected movement of the individual during a month was <1 km, the fish was classified as undertaking a 'small movement'. If movements >1 km were detected, the fish was classified as undertaking a 'large movement'. Probabilities of transition between these two states could then be calculated.

An individual was defined as exhibiting site fidelity when three consecutive small movements for an individual were observed. The mean, quartiles and range for these small movements for each species were calculated. To calculate homing, the number of fishes showing location shifts where returns after large movements and continuous large movements were observed was calculated. To examine species differences and seasonality in large movements, mixed-effects binomial regression models were used to estimate probabilities of movement. All explanatory variables were categorical and included season, year and species as fixed effects and individual as a random effect. The model was implemented in R (R Core Team, 2014; www.r-project.org) using the GAMLSS package (Rigby & Stasinopoulos, 2005). A stepwise AIC (Akaike, 1973) based procedure was used to select terms to model mean movement probability, μ, using the GAMLSS function stepGAIC.VR with forwards and backwards selection applied. The fit of the selected model was visually assessed by examining normal Q–Q, density v. residual and fitted v. residual plots of the randomized quantile residuals.

The full model was: $M_{ijkl} = \beta_0 + b_{0l} + \beta_1 S_i + \beta_2 Y_j + \beta_3 Se_k + \beta_4 S_i Y_j + \beta_5 S_i Se_k + \beta_6 Y_j Se_k + \varepsilon_{ijkl}$, where M is movement, S is species, Se is season, Y is year, l is individual, $\{b_l\}$ are independent normal $(0, \sigma_b^2)$, errors $\{\varepsilon_{ijkl}\}$ are independent normal $(0, \sigma_b^2)$ and $\{b_i\}$ are independent of the errors $\{\varepsilon_{ijkl}\}$. Mean movement probabilities were estimated for species and season using the predict function in the GAMLSS library. Graphing was undertaken using the ggplot2 library (Wickham, 2009).

Site fidelity was defined when three consecutive monthly records for an individual were registered within 1 km of each other. Using this definition, the proportion of fishes exhibiting site fidelity was determined for each species for each month. To examine seasonality in movements, the proportion of individuals undertaking movements >1 km in each month was calculated. As

the number of individuals per species was typically <10 in any month for both site fidelity and seasonality, data were pooled across years. Weighted logistic regressions were fitted to the proportion of fishes moving >1 km in each month for each species using the R statistical package. Month was categorized into season and was fitted as the predictor. The main effect and null (intercept only mode) were fitted and the most parsimonious of these models was selected to describe the effect of season on movement.

The movements >1 km were also categorized into one of the four outcomes for all fishes with records >3 months: a shift to a new site with fidelity was demonstrated; a return to the original location (homing); continuous movements to new sites but where no site fidelity was shown; or no large movement was observed. The proportion of movements >5 km were also calculated to be consistent with O'Connor *et al.* (2005).

RESULTS

A total of 21 *M. macquariensis*, 13 *M. peelii*, 34 *M. ambigua* and 33 *C. carpio* were radio-tagged for this study. As fishes sometimes could not be located, despite the additional tracking by aircraft, different numbers of fishes provided data in each year (Table I).

Maccullochella macquariensis were shown to undertake the least movements >1 km with 75% moving <25 m over the study period (Table II). *Maccullochella peelii* undertook greater movements with 75% moving <577·7 m. *Cyprinus carpio* showed a greater median movement (226 m), compared with *M. ambigua* (112 m) but *M. ambigua* showed greater variation in movement and hence, greater maximum distance (633 km compared with 120 km) (Table II). The largest monthly movements were in a downstream direction with three *M. ambigua* (150 km) and two *C. carpio* (120 km) moving from the study area to a large wetland (Barmah Forest). *Maccullochella macquariensis* and *M. peelii* were observed to move a maximum monthly distance of *c.* 8 and 12 km, respectively. *Maccullochella macquariensis* were found to have the highest level of site fidelity with most individuals of both *M. macquariensis* and *M. peelii* demonstrating site fidelity on multiple occasions (Table II). *Macquaria ambigua* and *C. carpio* also demonstrated site fidelity; however, fewer individuals demonstrated this fidelity on multiple occasions (Table III). Small movements were ≤100 m for all species (Table III).

While examination of movement distances showed that the proportion of movements undertaken >1 km were similar for *M. ambigua* and *C. carpio* (28·4 and 25·4%, respectively), *M. ambigua* undertook a greater proportion of movements >5 km (14·7 compared with 3·8% for *C. carpio*, $\chi^2 = 58·6$, d.f. = 1, $P < 0·001$) (Table IV). These movements occurred from June to February for *M. ambigua* and August to December for *C. carpio*. Both *M. peelii* and *M. macquariensis* had >50% of individuals that showed no movements. *Macquaria ambigua* and *C. carpio* had higher levels of location shifts (37·5 and 40·7%), with none exhibited by *M. peelii* as all movements resulted in homing (to within 200 m) to their original location. Three of these *M. peelii* exhibited the same return behaviour in consecutive years. In some cases, there were multiple returns to locations, even after periods of site fidelity elsewhere. *Macquaria ambigua* had 17·9% of individuals return to a previous location, while this was 35·9% for *C. carpio*. 'Continuous' movements (where individuals moved to a new location each month) were only exhibited by *M. ambigua* (14%).

All species were observed to use the floodplain and floodplain channels during the study (Table IV). Three *M. peelii* and three *M. macquariensis* used the nearby

TABLE II. Quartile distances and range (m) for all movements for all species in the study

Species	Q25%	Median	Q75%	Range
Maccullochella macquariensis	0	0	25	0–8012
Maccullochella peelii	6	77	578	0–11 810
Macquaria ambigua	0	112	1861	0–633 760
Cyprinus carpio	19	226	1014	0–119 692

floodplain (<100 m from the main river channel), while four *M. ambigua* and seven *C. carpio* were definitively recorded on the floodplain proper (up to *c.* 2 km from the main river channel) during this study. Access onto the floodplain for radio-tracking was limited on many occasions (especially the Barmah-Millewa floodplain forest), necessitating reliance on tracking by air only. Hence, determining exact locations between floodplain and floodplain channels was often difficult, probably leading to an underestimate of floodplain use by these two species. Both *C. carpio* and *M. ambigua* were recorded as becoming trapped in these off stream waters when flows receded.

There was support for models of species differences and seasonality in large move-ment movements that included the fixed effects of year, season and species and the interaction terms species × year, season × year and species × season (Table V). The evi-dence for the inclusion of the fixed effects was strong as these were included in the top four models with a combined model weight of 0·87. The evidence for inclusion of species and season as fixed effects was stronger than the evidence for the inclusion of year (Table V). The difference in AIC was 1·31 with the removal of the year effect. The evidence for the inclusion of the species × year interaction term was stronger than the evidence for the inclusion of season × year and species × season (Table V). Three of the four top models included the species × year interaction. The mean probability of large movements for *M. macquariensis* was near zero (1·005e-06; Fig. 2). There was support for large movements for *M. peelii*, *M. ambigua* and *C. carpio* (Fig. 2). The mean prob-ability of large movements was low in the austral autumn, winter and summer (<0·1; Fig. 3). Movement was greater in the austral spring (September, October and Novem-ber) when the mean probability of individuals undertaking large movements was 0·36 (Fig. 2). Large movements of both *C. carpio* and *M. ambigua* may have been under-estimated as many individuals of both species went 'missing' coinciding with higher flows in the austral winter of 1995. Median flows during the study period were similar to those of the long-term monthly medians, except for the months of July and August where higher flows were observed in July 1995 and August 1996 (Fig. 4). Temperatures

TABLE III. Mean ± S.E., quartile distances and range (m) for site fidelity for all species in the study

Species	Mean ± S.E.	Q25%	Median	Q75%	Range
Maccullochella macquariensis	90·4 ± 7·9	89	100·0	100	9–100
Maccullochella peelii	81·2 ± 6·7	72	89	100	36–100
Macquaria ambigua	45·9 ± 5·7	0	47	94	0–100
Cyprinus carpio	48·1 ± 7·9	0	50	75	0–100

TABLE IV. Movement type, total numbers of fishes or fish movements (given in parenthesis) for all species in the study

	Species			
Movement type	*Maccullochella macquariensis*	*Maccullochella peelii*	*Macquaria ambigua*	*Cyprinus carpio*
Number of movements >1 km	6 (177)	32 (187)	62 (218)	47 (185)
Number of movements >5 km	1 (177)	5 (187)	32 (218)	7 (185)
Number of fish showing no movement	10(19)	7(14)	9(28)	9(27)
Number of fish showing return movements	3 (19)	7 (14)	5 (28)	7 (27)
Number of fish showing location shifts	1 (19)	0 (14)	10 (28)	11 (27)
Number of fish showing continuous movements	0 (19)	0 (14)	4 (28)	0 (27)
Number of fish located in floodplain channels	6	5	12	25
Number of fish located on the floodplain	3	3	4	7

followed a pattern of higher austral summer temperatures, decreasing temperatures in austral autumn, coolest temperatures in austral winter and rising temperatures in austral spring (Fig. 4). There were some intermittent months where the temperature gauge failed to record data. In these months, the data were replaced by *ad hoc* data collected as part of other research being undertaken in the study area at that time (Koehn, 2009*a*). At the scale of this study (monthly aggregated data), these environmental variables are confounded with season (Fig. 3). The monthly interval between data records prevents more 'environmental event' based analyses.

DISCUSSION

There are many variables that may influence fish movements (*e.g.* turbidity, season and light intensity; Horký *et al.*, 2008; Kuliskova *et al.*, 2009) which, along with the time span of the study, can confound the calculation of movement distances (*i.e.* the longer the study, the greater the likelihood of larger movement distances; Lucas & Baras, 2001) and subsequent metrics such as home range size. The examination of a multispecies, multi-year, large spatial scale data set allowed for a comparative consideration of fish movements over the same time interval with similar conditions. Results showed a gradient of movements and allowed a relative 'mobility ranking' for the four species: *M. macquariensis* (least mobile), *M. peelii*, *C. carpio* and *M. ambigua* (most mobile). The study also identified similarities and differences among the species. This information provides a step forward in multispecies management, especially as it identified the movement needs of the least mobile species (in this case, *M. macquariensis*). The variability in behaviours identified within and between species demonstrated the necessity for the use of large spatial and temporal scales when determining the

TABLE V. AIC and ΔAIC values and model weight from the model selection process

Model	AIC	ΔAIC	weight
Move ~ Species + season + year + random (ind) + species:year + season:year	616·7182	0	0·25
Move ~ Species + season + year + random (ind) + species:year	616·9706	0·252408	0·23
Move ~ Species + season + year + random (ind) + season:year	617·2109	0·492721	0·20
Move ~ Species + season + year + random (ind) + species:season + species:year	617·3184	0·60023	0·19
Move ~ Species + season + year + random (ind) + species:season + species:year + season:year	619·7555	3·037336	0·06
Move ~ Species + season + year + random (ind)	620·5879	3·869711	0·04
Move ~ Species + season + random (ind)	621·902	5·183829	0·02
Move ~ Species + season + year + random (ind) + species:season + season:year	622·4525	5·734274	0·01
Move ~ Species + season + year + species:year + season:year	641·407	24·68878	0
Move ~ species + year + random (ind)	643·1984	26·48024	0
Move ~ Species + season + year + species:season + species:year + season:year	647·7647	31·04645	0
Move ~ Species + season + year + random (ind) + species:season:year + species:season + species:year + season:year	650·5563	33·83809	0
Move ~ Species + random (ind)	653·2252	36·50699	0
Move ~ Species + season + year + species:season: year + species:season + species:year + season:year	680·1544	63·43616	0
Move ~ 1	731·5102	114·792	0

movements of potamodromous fishes and the need to consider updated and expanded conceptual models of movement to assist management.

Movement data collected from individual animals (such as by telemetry) are intrinsically variable (Patterson *et al.*, 2008) and pose many difficulties for standard analyses (White & Garrott, 1990). A comparison of models offers a more quantifiable assessment of fish movements which can be supplemented by descriptive statistics to elucidate species' movement patterns. Such state-space models are being used to provide a robust method of analysis for terrestrial animal movements (Patterson *et al.*, 2008) and could be utilized more widely in fish studies.

The predominant behaviour was the use of small movements (<1 km) for all species, although larger-scale movements (>1, >5 and up to 150 km) did occur; the frequency of which varied considerably among species. Large-scale movements were least evident for *M. macquariensis* and more common for *M. ambigua* and *C. carpio*. *Macquaria ambigua* displayed the largest movements and had more individuals that moved on a 'continual' basis. The more mobile species also had a greater propensity to shift location. The larger-scale movements for this species call for increased connectivity along the whole river system. A degree of site fidelity was evident for all species with the highest levels exhibited by *M. macquariensis* and *M. peelii* and
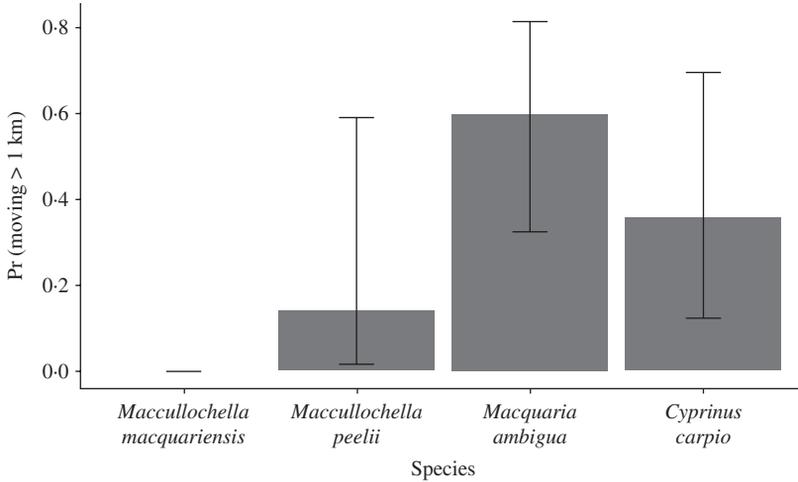
FIG. 2. Probability of large movements (>1 km) (±95% C.I.) for each species as estimated by the mixed-effects binomial regression.

homing (return to previous sites) was also evident for all species, but greatest for *M. peelii*.

Movements of fishes can contain central areas where the majority of normal activities occur (*e.g.* foraging and resting), intermediate areas where normal activities are undertaken less frequently and outer areas where infrequent exploratory behaviour occurs (Crook, 2004). It is recognized that the coarse measurement of movements in this study (monthly) may not necessarily accommodate some of the finer-scale movements of these species. For example, many species that are nocturnal or affected by light
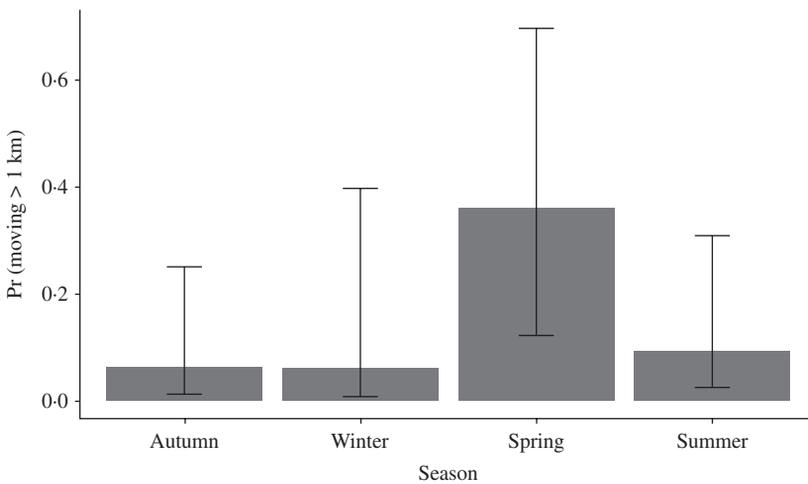

FIG. 3. Probability of large movements (>1 km) (±95% C.I.) during each season as estimated by the mixed-effects binomial regression.
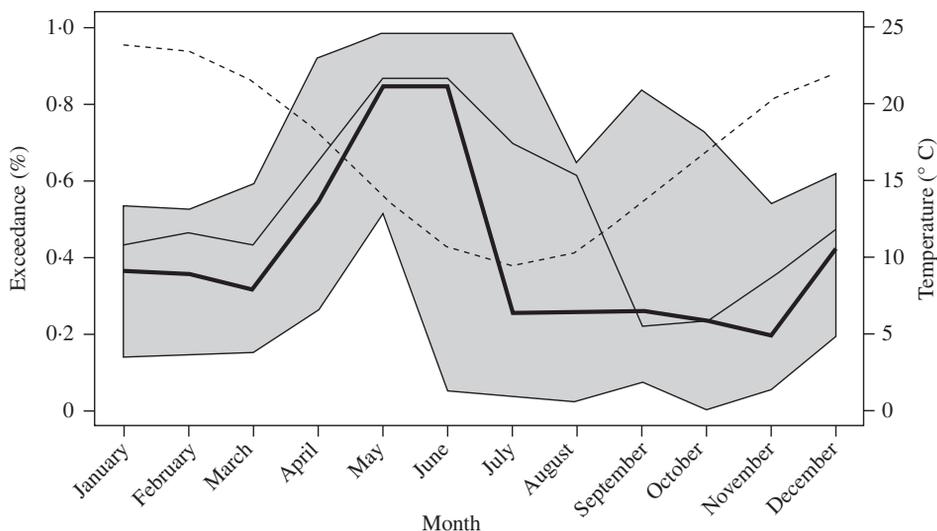
Fig. 4. Flow exceedance during the study period (——, the median exceedance between 1994 and 1997; ▢, the 2·5–97·5 quartiles between 1994 and 1997; ▬, the median exceedance between 1961 and 2006; - - - -, median monthly temperature).

intensity show short-term temporal variations in movement distances (Horký *et al.*, 2008; Kuliskova *et al.*, 2009). Results from this study suggest that for *M. macquariensis*, the movements for core activities are <1 km, supporting the descriptive statistics previously presented for this species (Koehn *et al.*, 2008). This aligns with other studies for this species where home ranges have been more accurately defined. Koehn *et al.* (2008) suggested a linear home range of mean ± s.e. = 61 ± 41 m, and Thiem *et al.* (2008) calculated a diel range of mean ± s.e. = 83 ± 30 m, with activity peaking in periods of low light and linear movement range being correlated with fish size. Ebner & Thiem (2009) clearly set out and calculated a home range size of mean ± s.e. = 78 ± 13 m which they then used as the basis for quantifying home range shifts of up to 36 km.

Transitions from small to large (<1 to >5 km) movements were the smallest for *M. macquariensis* of the four species examined indicating that larger movements were rare. This was further supported by the high rates of transition from large to small movements with all *M. macquariensis* observed to undertake a large movement than observed to be in the small movement state on the next sampling occasion. Furthermore, estimates of the proportion of *M. macquariensis* undertaking large movements in any month were low, with zero detected movement being plausible for most months. Dispersal of this species over larger distances has, however, been reported in upstream and downstream directions up to 100 km for juvenile *M. macquariensis* (Ebner *et al.*, 2007; Koehn *et al.*, 2008).

Movement analyses in this study were affected for the two most mobile species (*M. ambigua* and *C. carpio*) by the 'loss' of individuals from the study area. It is plausible that some of these 'missing' fishes may have undertaken true 'home range' shifts (Crook *et al.*, 2001) but data are not available to truly test this hypothesis. Such large movements, either up or down the river, or onto inaccessible floodplain areas, would be

consistent with results from other studies (Crook *et al.*, 2001; O'Connor *et al.*, 2005; Stuart & Jones, 2006*a*, *b*) and could have resulted in underestimates of movements.

Seasonal migrations, often for spawning or feeding, are common for river fishes (Koed *et al.*, 2000; Winter & Fredrich, 2003). No seasonality of movements was detected for *M*. *macquariensis* and homing was only observed for three individuals. This may have been due to the spatial scales used in this study as homing behaviour has been noted by Koehn *et al.* (2008) where the spatial criteria used for classifying larger movements was less than the 1 km used in the current analysis. Koehn *et al.* (2008) also reported some seasonality in movements with a small number of individuals moving large distances in association with spring over-bank river flooding. Shifts in core locations have been reported in a stocked population of *M*. *macquariensis*, occurring up to 2·4 km away from previous core area locations (Ebner & Thiem, 2009). Results in this study were consistent with these observations with one individual observed to shift its core area 3 km downstream. Such shifts, however, appear rare for *M*. *macquariensis* in comparison to *M*. *ambigua* and *C*. *carpio*. Habitat use by *M*. *macquariensis* is closely associated with structural woody habitats (Nicol *et al.*, 2007), more so than for *M*. *ambigua* and *C*. *carpio* (Crook *et al.*, 2001; Koehn & Nicol, 2014) and so changes to habitat location may be less likely.

The core habitat areas used by *M*. *peelii*, *M*. *ambigua* and *C*. *carpio* appear larger than those observed for *M*. *macquariensis*. The probabilities of transition from small to large movements were higher and the probabilities from large to small movements were lower, indicating a greater propensity to undertake larger movements. *Maccullochella peelii* showed a seasonal (austral spring) increase in the proportion of individuals undertaking larger movements from August to December (late winter to early summer), a pattern consistent with that shown in the nearby unregulated Ovens River (Koehn *et al.*, 2009) and sites in the lower Murray River (Saddlier *et al.*, 2008; Leigh & Zampatti, 2013). Koehn *et al.* (2009) proposed that this seasonal movement for *M*. *peelii* may be associated with spawning and the timing of their movements in this study was consistent with known spawning times in this river reach (Koehn & Harrington, 2006). The Ovens River observations involved a proportion of adults migrating upstream and establishing a new core area in association with the spawning period and then returning to their previous core habitat area (Koehn *et al.*, 2009). Whilst an increased proportion of *M*. *peelii* undertaking larger movements was observed during their spawning period, any establishment of new habitat areas that were consistent with a 'home range shift' was not observed and homing to original locations occurred on all occasions.

The movements observed for *M*. *ambigua* and *C*. *carpio* were consistent with the 'home range shift hypothesis' that proposes that extended periods of home range occupation can be interspersed by relatively short periods of mobility associated with a shift in the location (Crook, 2004). This hypothesis was developed with fine-scale radio-telemetry data on the movement of *M*. *ambigua* and *C*. *carpio* in a small, unregulated tributary of the Murray River (Crook, 2004) over a limited 3 month period. Consistent shifts were observed over the multiple years in this study and the high proportion of individuals (35% *M*. *ambigua* and 40% *C*. *carpio*) undertaking at least one shift provides further evidence that this is a common movement behaviour for these species. Such behaviour may be more likely for these mid-water, more mobile, wider ranging species (Reynolds, 1983; Crook, 2004) that appear less closely associated with structural habitats compared with *M*. *peelii* and *M*. *macquariensis* (Crook

et al., 2001; Nicol *et al.*, 2007; Koehn, 2009*a*; Koehn & Nicol, 2014). This is consistent with the greater short-term movements of *C. carpio* compared with *M. peelii* for juveniles (Jones & Stuart, 2007). Greater propensity to move may also be related to their foraging feeding behaviour, compared with the suggested 'sit and wait predation' method of *M. peelii* and *M. macquariensis*.

Fish habitats occur in patches within the 'riverscape' (Wiens, 2002; Winemiller *et al.*, 2010) and these should be managed at scales that are relevant to the fish, rather than those imposed arbitrarily by humans (Crook *et al.*, 2001). All four species in this study show some preference for structural woody habitats (Koehn & Nicol, 2014) and the reinstatement of such habitats is seen as a key action for the rehabilitation of native fish populations (Murray-Darling Basin Commission, 2004; Nicol *et al.*, 2004). For effective colonization of such newly created habitat patches by native species, the distance from existing population sites, and the spacing between patches should be appropriate for the least mobile species; in this case, *M. macquariensis*.

The seasonality of movements detected in this study, being higher in the austral spring detected for *M. peelii*, *M. ambigua* and *C. carpio*, complements results from other studies. O'Connor *et al.* (2005) observed *M. ambigua* undertaking movements between 11 and 290 km and noted increased movement distances in spring, coinciding with increasing water temperatures and river discharge. In particular, *M. ambigua* were not detected to move distances >5 km during winter months (O'Connor *et al.*, 2005). Seasonality in the movements of *M. ambigua* and *C. carpio* through fishways has also been reported (Mallen-Cooper, 1999), with peaks occurring over October to February (spring to summer). *Cyprinus carpio* moving into wetlands have been reported as being less active in June and July when day lengths and temperatures were declining (Conallin *et al.*, 2012). Other studies have also suggested large movements for *C. carpio* (Crook, 2004; Stuart & Jones, 2006*a*) with Stuart & Jones (2006*a*) reporting that most *C. carpio* made localized movements but others were capable of migrating large distances. They reported that 80% moved <5 km, with 7% moving >100 km, including distances of up to 890 km over a time span of up to 1898 days. The large-distance movements of *C. carpio* downstream to the Barmah Forest [an important spawning area for *C. carpio* (Stuart & Jones, 2006*b*)] observed in this study was confirmed by Stuart & Jones (2006*a*). The longer seasonal movements exhibited by *C. carpio* in this study indicates their ability to disperse over most of the year and this is important in directing an extended seasonality of management actions, especially the harvesting of this pest species in traps located at fishways and wetland entrances (Stuart *et al.*, 2006; Thwaites *et al.*, 2010) and the use of exclusion screens (Hillyard *et al.*, 2010).

Floodplain habitats provide critical habitats for many large river fishes, but generally such use is not well documented (Burgess *et al.*, 2013) especially for large Australian native fishes (Humphries *et al.*, 1999). An exception is for *C. carpio*, where lateral movements onto the floodplain, particularly to spawn, have been widely recorded (Stuart & Jones, 2006*a*, *b*; Jones & Stuart, 2009; Conallin *et al.*, 2012) and are supported by this study. The floodplain together with the floodplain channels was used to some degree by all species in this study. Although floodplain use was predominantly undertaken by *C. carpio* and *M. ambigua*, additional records are provided for *M. macquariensis* and *M. peelii*. Koehn (2009*a*) reported habitat selection of the main river channel and use of the floodplain channels for *M. peelii* but provided only two records of this species using the nearby floodplain. Leigh & Zampatti (2013)

found *M. peelii* movement patterns similar to this study, with extensive movements between main and anabranch channel habitats but no use of the ephemeral floodplain. The additional records of floodplain use for these native species add support for the need for flooding of floodplain areas, something that has been much reduced in this regulated reach of the Murray River (Close, 1990), and for access which has often been blocked by regulators of road crossings, with all species in this study having been recorded to be trapped in a floodplain refuge behind a regulating structure (Jones & Stuart, 2008). Floodplain access may be particularly important for *M. ambigua* as the collection of young *M. ambigua* on floodplains indicates the possible use as either a spawning or rearing habitat (Rolls & Wilson, 2010).

Having an informed model of fish movements is a key component to planning river restoration (Palmer *et al.*, 2005; Mallen-Cooper & Brand, 2007) and imperative for providing adequate fish passage for all species and life stages (Barrett & Mallen-Cooper, 2006; Stuart *et al.*, 2008). Results from this study have added to the knowledge of the movements of the four species studied and have important implications for the conservation and management of potamodromous fish populations. Management strategies should not only appropriately recognize more complex movement models for a range of species that include large-scale movements, but also consider the more common, smaller movements that occur in both upstream and downstream directions. For example, the limited movements of *M. macquariensis* indicate a limited ability of adults to colonize new habitats or to recolonize following catastrophic events compared with the other species; potentially accounting for their fragmented distribution and heightened conservation status (Lintermans, 2007). In contrast, the greater propensity for larger movements by *C. carpio* indicates their high ability for dispersal which is evident by their rapid colonization of the MDB (Koehn *et al.*, 2000). Similarly, it highlights the potential ability of *M. ambigua* to colonize new habitats across large scales. This attribute is particularly important for species in highly variable environments where recolonization of river reaches from drought refuge pools is not an uncommon occurrence. To date, much of the restoration focus for connectivity has centred upon construction of fishways to facilitate upstream passage (Barrett & Mallen-Cooper, 2006). The prevalence of downstream movements observed for all species in this study strongly suggests that attention must also be given to restoring safe downstream movement pathways around instream barriers for potamodromous fishes (O'Connor *et al.*, 2006; Agostinho *et al.*, 2007; Stuart *et al.*, 2010), despite this potentially posing difficult solutions (Keefer *et al.*, 2013). Data from this study indicate that utilization of floodplain habitats has been underestimated for the native species and improved access must be considered (Jones & Stuart, 2008). The use of statistically robust, predictive models (Lucas & Baras, 2001; Patterson *et al.*, 2008) could be incorporated into the management of movement pathways (*e.g.* for invasive species; Conallin *et al.*, 2012) or connectivity between habitat patches (Galpern *et al.*, 2011).

This study provides a new perspective on the management of multiple freshwater fish species, supporting the need for greater connectivity and improved conceptual models of movements. Data from the study indicate that species mostly use small movements, but can transition to larger movement to new areas. This supports the 'home range shift' hypothesis of Crook (2004) which should be further developed to provide a more informed model for management that captures the diversity of movements for large potamodromous fishes in semi-arid ecosystems across a range of species. In this model, fish movements can contain core habitat areas where the majority of normal

activities occur (*e.g.* foraging and resting), intermediate areas where normal activities are undertaken less frequently and outer areas where infrequent exploratory behaviour occurs. Extended periods of core habitat occupation can be interspersed by relatively short periods of mobility and a shift to new locations (Crook, 2004). Range shifts may occur following specialized movements associated with the species' life history, such as spawning or feeding migrations or occupation of overwintering habitats (West *et al.*, 1992; Crook, 2004) and this occurred for species in this study. Generalizing the hypothesis to include 'temporary home ranges' that may be occupied for a short period of time before individuals return to their previous 'core' area would provide a more comprehensive model describing the movement ecology of large-bodied potamodromous fishes.

This study has highlighted the gradient of movements among large fish species, and the variables have provided a comparative 'mobility ranking' at the river-reach scale: *M*. *macquariensis* (least mobile), *M*. *peelii*, *C*. *carpio* and *M*. *ambigua* (most mobile). Such movement abilities should be taken into account when managing these sympatric species for issues such as recolonization or the utilization of new habitats, where accommodating the needs of the least mobile species is likely to provide for the other species.

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