1 2 **Convoluted shorelines confound diel range estimates of radio-tracked fish**

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16 **Abstract.** Understanding the spatial ecology of animals is an important part of
17 conserving biodiversity. In this context, manual radio-tracking is a primary means for
18 understanding the movement of freshwater fish. Our aim was to determine the
19 suitability of using linear or area-based estimates to quantify diel use of space by
20 Macquarie perch, *Macquaria australasica* (Percichthyidae), in a reservoir. Area-based
21 estimates were calculated as minimum convex polygons (MCPs). Four-hourly radio-
22 tracking of 23 adults within diel periods resulted in 136 pairs of linear and area-based
23 estimates. We encountered problems with MCPs that were not associated with
24 outlying radio-fixes. MCPs were more likely to overlap with land as the extent of an
25 individual's range increased. Corrections were applied to account for land intersecting
26 with MCPs (33.1% of cases) however, underestimates of diel range occurred in most
27 of these cases. MCPs were also small despite substantial movement along one
28 dimension if individuals only occupied straight-edged sections of the reservoir and did
29 not traverse bays or peninsulas (8.1% of estimates). Mean ($\pm$ s.e.) diel range length
30 was 516 m $\pm$ 89 (n = 23) and records varied from 6 to 1972 m. In waterways with
31 convoluted shorelines, linear estimates of diel range are more reliable than area-based
32 estimates derived from manual radio-tracking.

Additional keywords: bias, minimum convex polygon, radio-tracking, threatened species, Percichthyidae, reservoir.

Running headline: diel range estimation

Introduction

Globally, freshwater fishes and freshwater ecosystems are confronted with a range of anthropogenic impacts, with habitat loss a major issue (Maitland 1995; Abell *et al.* 2008). Consequently, an understanding of the spatial ecology of threatened freshwater fishes is an important part of biodiversity conservation and fisheries management (Fausch *et al.* 2002; Rice 2005). Observational studies have been used to compile detailed records of the spatio-temporal behaviour of fishes in high-visibility aquatic systems (e.g. Jones 1984; Nakano 1995). In freshwater environments, including in low-visibility conditions or where a species is highly mobile, radio-tracking has proven useful for recording the behaviour of large-bodied freshwater fishes and has contributed to an increase in understanding of fish movement at the individual and population level. Radio or acoustic tracking studies of fishes in lotic environments customarily report home-range or diel range as the distance occupied along the longitudinal dimension of the stream (e.g. Bunnell *et al.* 1998; Crook 2004*a, b*) and/or as area-based estimates (e.g. Thiem *et al.* 2008). In contrast, area-based estimates are common in tracking studies of lentic fishes (e.g. Guy *et al.* 1994; Paukert *et al.* 2004; Mlewa *et al.* 2005). This difference in reporting linear versus area-based estimates of range has the potential to bias our understanding of the spatial behaviour of fishes (Thiem *et al.* 2008). For instance, focusing on longitudinal movement in lotic waters ignores the importance of lateral movement in these environments. Conversely, resolving the lateral position of fishes in linear (often lotic) systems can be difficult and therefore costly, and may be of no immediate value in a particular study (e.g. in migrational studies).

A home-range is often defined as the area repeatedly used by an individual in regular day-to-day activity (e.g. Gerking 1953, Mace and Harvey 1983). However, studies of the movements of riverine fish generally measure home-ranges at arbitrary temporal scales, including among a few days (e.g. Thiem *et al.* 2008), seasonally (e.g.

Snedden *et al.* 1999) or on an annual scale (e.g. Hesthagen 1990). The temporal scale and resolution of a study has major bearing on the measurement of home-range size (Baras 1998, Ovidio *et al.* 2000, Börger *et al.* 2006a,b). Where the functional scale of home-range measurement has been determined post-hoc, it is underpinned by an environmental driver such as photoperiod (Börger *et al.* 2006a,b).

Fishes commonly exhibit diel activity patterns relating to the cycle of day and night (Reebs 2002). Diel range estimates indicate the spatial scale of fish movement within the cycle of day and night (e.g. Bunnell *et al.* 1998; Thiem *et al.* 2008). Temporal sampling resolution affects estimates of diel range and has practical implications for manual radio-tracking exercises (Ryan *et al.* 2008; Ebner *et al.* 2009a). Diel range can be measured in terms of length (diel range length) or area (diel range area) of space used in a 24-hour period (Bunnell *et al.* 1998; Thiem *et al.* 2008; Ryan *et al.* 2008). Manual and remote telemetry-based methods are useful for repeatedly locating the position of fishes on this time scale and minimising observer effects without relying on animal recapture (Cooke 2008; Ryan *et al.* 2008). Furthermore, minimising recapture can be especially important in studies of threatened species (e.g. Ryan *et al.* 2008). During a radio-tracking study of an endangered fish in Cotter Reservoir, Australian Capital Territory (ACT), we became aware of individual differences in scale of diel movement and in occupation of bays and straight-edged sections around the shoreline of a reservoir. This led us to hypothesise that metrics used to compare the diel range of fish in such an environment may be confounded by the sinuosity of the shoreline. Subsequently, our aim was to compare the suitability of using linear versus area-based estimates of the diel range of an endangered fish Macquarie perch, *Macquaria australasica* (Percichthyidae) in a reservoir.

Materials and methods

The study was conducted in Cotter Reservoir (35°19'S, 148°55'E) (500 m asl, 4.7 GL, surface area = 52 ha) on the Cotter River, 10 km west of Canberra, ACT. The reservoir is relatively narrow and sinusoidal with a bed dominated by soft sediment. Emergent macrophytes (*Typha*, *Phragmites*, and *Eleocharis*) occupy the reservoir edge, particularly in the shallow upstream third of Cotter Reservoir (water depth <5

m), whereas the downstream two-thirds of the reservoir is deep (to 23 m) with numerous steep rocky banks with emergent macrophytes restricted to shallow inlets (Ebner *et al.* 2007).

Adult Macquarie perch were collected in gill nets and fyke nets, and then radio-tagged and released in spring 2001 (n = 10), autumn 2002 (n = 11) and spring 2002 (n = 20), respectively (details of the capture and tagging method Ebner *et al.* (2009b)). The sex of individuals could often be determined from observation of ovaries during implantation of radio-tags, whereas, males could not be determined reliably. Forty individuals were radio-tagged during the study, including an individual that was radio-tagged a second time after having rejected the original radio-tag (Ebner 2009b).

A two-person crew undertook manual radio-tracking surveys from a 3-m aluminium punt (powered by an 8-hp outboard motor), with fish locations obtained by directly positioning over the top of a radio-transmitter or, where this was not possible, by triangulating. Individuals were located by scanning receiver (R4100, Advanced Telemetry Systems, Isanti, MN, USA) and a three-element Yagi antenna (Titley Electronics, Ballina, Australia or Advanced Telemetry Systems, Isanti, MN, USA). The location of each individual was recorded by obtaining three waypoints with a hand-held Global Positioning System (GPS) device (Garmin GPSII Plus) in GDA94 format (with a Figure of Merit ≤ 5.0 equating to an accuracy of ≤ 10.0 m). Four-hourly radio-tracking of Macquarie perch was conducted within 20 diel periods commencing at 10:00 am and finishing at that same time the following day on each occasion (three diel tracking periods in summer 2001, eight in autumn 2002, nine in spring/summer 2002). This resulted in seven fixes per individual per diel period. In a subset of cases, radio-tracking was conducted on two consecutive diel periods in autumn 2002. Data from 23 individuals that were radio-tracked on at least one diel period was used for calculation of diel range. Diel range was calculated as an area-based estimate from minimum convex polygons (MCPs) (diel range area) and in terms of the maximum linear dimension (diel range length), using the spatial analyst tool in a Geographical Information System (Arcview 3.1). A total of 136 diel range estimates were available for analysis based on each of the linear and area-based calculations (Table 1).

Where land intersected with MCPs, only the components of the MCP overlaying water were included in the estimate. Occurrences of two or more fragments of an MCP representing the diel range of an individual as a result of land completely crossing the MCP ('landmass-affected') were distinguished from single MCPs ('landmass-unaaffected'). The shortest pathway by water between the two most distant fixes was used in calculating diel range length.

Initially, extremely small diel range area values were visually inspected to determine if human error had occurred in selecting fragments of MCPs in the geographic information system. This led us to record occurrences of the chance alignment of all 7 fixes of an individual within a diel period (termed 'aligned' and equating to less than 2° deviation from a midline between the two most distant points of seven fixes recorded per diel period). Diel range area was plotted against diel range length based on the 136 estimates coded for records of aligned, landmass-affected and landmass-unaaffected estimates. Linear regression was used to determine if mean diel range length was related to the total length of adults. The process was repeated for the subsample of known females and for the subsample of individuals of unknown sex.

Results

Mean diel range length was 516 ± 89 m (s.e.) (136 diel tracks from 23 individuals) and ranged between 6–1972 m (Table 1). Twenty-two individuals were tracked for more than one diel period, facilitating calculation of mean diel range. The mean diel range length used by each individual ranged from 149 to 1212 m (Table 1) and was not linearly related with total length ($r^2 = 0.010311$, $n = 22$, $p = 0.65297$), for known females ($r^2 = 0.00039141$, $n = 15$, $p = 0.94421$) or those of unknown sex ($r^2 = 0.0073022$, $n = 7$, $p = 0.85546$). Mean diel range area across all individuals was 1.6 ± 0.2 ha (s.e.) ($n = 23$). The mean diel range area used by each individual ranged from 0.05 to 6.5 ha (Table 1, $n = 22$). Records of diel range varied from 15 m² to 15.2 ha (Table 1, Fig. 1). However, diel range area was an inconsistent indicator of diel range and led to underestimates in two types of circumstance (Fig. 1). First, a diel range was broken into two or more fragments as a result of individuals occupying aquatic locations either side of at least one landmass (i.e. a peninsula, an island) without an intermediate location (e.g. Fig. 2a). This occurred in 33.1% of diel range estimates

(based on 136 diel range estimates) and was common in diel ranges of length > 500 m (Fig. 1). Second, when all locations were aligned by chance (e.g. Fig. 2b), very small ratios of area to length were obtained. This occurred in 8.1% of diel range estimates and is typified by estimates along or close to the X-axis in a plot of diel range area against diel range length (Fig. 1). Both chance alignment of seven radio-tracking locations within a diel period and landmass effects occurred in 2.2% of cases. Neither problem occurred in 61.0% of cases.

Discussion

The current study has identified two circumstances under which area-based estimates of diel range are biased. Underestimation of diel range area in a reservoir occurs when MCPs are bisected by land and the area of reservoir linking the two (or more) aquatic fragments is unknown. Furthermore, this differentially affects estimates corresponding to individuals with large rather than small ranges. This bias would be reduced by more frequently radio-tracking individuals within diel periods, either manually (e.g. Bunnell *et al.* 1998; Ryan *et al.* 2008) or through applications of automated telemetry (e.g. Hanson *et al.* 2007). However, more frequent manual radio-tracking is demanding of human and financial resources, has sample size tradeoffs, and may increase the likelihood of introducing behavioural effects (Ryan *et al.* 2008; Thiem *et al.* 2008). Automated telemetry is unlikely to entirely replace manual tracking at this stage as the former has some deficiencies (e.g. high cost and lower precision of location data). A similar problem has been encountered in home-range studies of riverine fishes and has been partly dealt with by subtracting terrestrial portions from all home-range estimates and using a river midline to infer mobility between radio-tracking fixes (Hodder *et al.* 2007; Ebner and Thiem 2009; Knight *et al.* 2009).

Alignment of all of the fixes of an individual per diel period produced very small estimates of diel range area in the current study. It can be argued that this does not represent a bias since the spatial arrangement of the fixes is real. However, it did contrast with substantially larger diel range area estimates corresponding to individuals that traversed similar lengths of littoral zone but have comparatively inflated area estimates as a function of the geometry of the fixes. Specifically, where

individuals cross the thalweg of the reservoir or MCPs incorporate bays, large proportions of limnetic zone are incorporated into estimates even though radio-tracking fixes are confined to the littoral zone. These non-linear diel range shapes potentially bias towards an overestimate of the space used by an individual. The effect of available habitat shape on MCPs has been identified by others (e.g. Burgman and Fox 2003, Simaika and Samways 2010). This bias would be removed or reduced by more frequently radio-tracking individuals within diel periods since the shape of the diel range would more accurately approximate the true range of the individual. However, given the impracticality of more frequent manual radio-tracking within a diel period, solutions include a) not using area-based estimates and simply using linear estimates of diel range, or b) multiplying linear range by a pre- or post-determined width as is often done in calculating the amount of stream occupied by an animal (e.g. Gust and Handasyde 1995). For a species occupying the littoral zone of a reservoir, the horizontal dimension of an individual's range could be based on its median distance from shore or based on a set depth contour (e.g. 5 m). However, as the spatial behaviour of a species can vary between sexes, studies, sites, seasons and habitats, the determination of which fixed factor to use in combination with diel range length is problematic.

We conclude that estimates of diel range arising from manual radio-tracking of highly mobile fishes should be interpreted with caution. Our findings are unlikely to be unique to Macquarie perch and are probably relevant to any species that moves at a comparable scale or greater than that of the convolution of a shoreline. This problem is less relevant to species with small ranges relative to the scale in sinuosity of a stream or lake edge. Linear range estimates are likely best for comparing high and low mobility species or where the shoreline has different scales of sinuosity in the shoreline across studies (as is likely when comparing lentic and lotic systems). Alternatively, remote telemetry arrays (e.g. Hanson *et al.* 2007) could facilitate accurate calculation of area-based estimates of diel range by providing high temporal resolution.

The linear estimates of diel range obtained in the current study represent the first estimates relating to the endangered Macquarie perch. These estimates show that adults, on average, range over 500 m along the littoral zone of Cotter Reservoir per diel period (Table 1). Furthermore, the largest diel ranges recorded in the current study approach the linear extent of the reservoir (~2 km) and it would be interesting to

determine if the diel range of Macquarie perch remains the same in much larger reservoirs.

The scale of diel movement recorded in the current study is generally greater than that reported for other large-bodied percichthyids in rivers where identical radio-tracking schedules (or higher temporal resolution) have been used (Thiem *et al.* 2008; Ebner *et al.* 2009a). For instance, the mean diel range of bluenose cod, *Maccullochella macquariensis* is generally less than 100 m (Thiem *et al.* 2008; Ebner *et al.* 2009a). Furthermore, the diel range of Macquarie perch in the current study is actually comparable or greater than the home-range size reported from radio-tracking percichthyids weekly or monthly across seasons (Simpson and Mapleston 2002; Jones and Stuart 2007; Nicol *et al.* 2007; Koehn *et al.* 2008).

The apparently large diel range of Macquarie perch relative to other percichthyids may relate to species-specific trophic ecology. Macquarie perch generally feed on macroinvertebrates (e.g. Cadwallader and Eden 1979), whereas, other large-bodied percichthyids are generally higher-order, ambush predators (Ebner 2006; Baumgartner 2007). Alternatively, the apparently large range of Macquarie perch may simply be an artefact of the current study being conducted in a lentic as opposed to a lotic system (*cf.* Minns 1995). Additionally, many radio-tracking studies of percichthyids have sampled at a coarse temporal resolution to develop an understanding of home-range or migration patterns and have therefore been based on locating individuals once or twice within any diel period (Crook *et al.* 2001; Simpson and Mapleston 2002; Crook 2004a, b; Jones and Stuart 2007; Nicol *et al.* 2007; Koehn *et al.* 2008). More intensive radio-tracking may reveal that these other large-bodied percichthyids have diel ranges comparable to that recorded of Macquarie perch in the current study.

While diel ranges of Macquarie perch and two species of *Maccullochella* have been estimated (Thiem *et al.* 2008; Ebner *et al.* 2009a; Butler 2001, this study), it would be beneficial for conservation purposes to determine the diel range of the other large-bodied percichthyids. Both the diel range and home-range of Macquarie perch also remain unknown in lotic habitats, and this should be rectified to better manage populations of this endangered species. In general, linear rather than area-based estimates of diel range are recommended where manual radio-tracking is used for estimating diel range and when making comparisons within and among species of freshwater fish from lentic and lotic systems.

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Table 1 Linear and area-based diel range estimates resulting from radio-tracking 22 adult Macquarie perch over two or more diel radio-tracking periods. *Individual rejected original radio-tag and was radio-tagged a second time.

Identity	TL (mm)	Wt. (g)	Sex	No. of diel periods			Linear diel range		Diel range area (ha) $\pm$ s.e.
				spring–summer 2001	autumn 2002	spring 2002	mean (m) $\pm$ s.e.	Total	
A1*	297	416	♀	1	5		351 $\pm$ 90.3	6	1.3 $\pm$ 0.59
A2	289	358	♀	3			1087 $\pm$ 175	3	1.4 $\pm$ 0.68
A4	297	369	♀	3			995 $\pm$ 7.21	3	3.8 $\pm$ 1.4
A6	281	342	♀	2			1053 $\pm$ 35	2	5.6 $\pm$ 2.2
A10	394	830	♀	3	9	8	454 $\pm$ 68.8	20	2.4 $\pm$ 0.47
B1	403	1026	♀		9		390 $\pm$ 135	9	1.5 $\pm$ 0.92
B2	275	333	?		9		649 $\pm$ 206	9	0.9 $\pm$ 0.44
B3	310	418	♀		9		364 $\pm$ 23.8	9	1.3 $\pm$ 0.19
B6	340	615	♀		3		406 $\pm$ 121	3	0.6 $\pm$ 0.22
B9	263	250	♀		4		494 $\pm$ 108	4	2.2 $\pm$ 0.61
C2	417	1209	♀			3	1212 $\pm$ 389.9	3	6.5 $\pm$ 4.4
C3	420	1382	♀			3	713 $\pm$ 391	3	1.3 $\pm$ 0.64
C5	395	953	♀			8	417 $\pm$ 191	8	1.8 $\pm$ 1.5
C6	360	763	?			6	428 $\pm$ 44.3	6	1.5 $\pm$ 0.32
C7	356	747	?			8	255 $\pm$ 48.6	8	0.4 $\pm$ 0.12
C8	330	627	?			4	397 $\pm$ 203	4	0.9 $\pm$ 0.80
C9	279	332	♀			6	198 $\pm$ 33.7	6	0.1 $\pm$ 0.02
C10	267	305	?			3	450 $\pm$ 151	3	1.0 $\pm$ 0.52
C12	386	869	♀			6	195 $\pm$ 52.8	6	0.6 $\pm$ 0.28
C13	322	528	♀			8	241 $\pm$ 40.8	8	0.2 $\pm$ 0.10
C15	266	279	?			6	149 $\pm$ 76.7	6	0.05 $\pm$ 0.02
C16	257	274	?			6	179 $\pm$ 90.7	6	0.3 $\pm$ 0.16

Fig. 1. Reduced estimates of diel range area arising from complete division by landmasses (i.e. peninsula or island)(landmass-affected) or the chance linear alignment of all seven locations resulting from four-hourly radio-tracking (aligned) compared with those estimates unaffected by landmass (landmass-unaffected).

Fig. 2. Examples of underestimation of diel range area based on four-hourly radio-tracking where a) fragmentation of the diel range area by landmasses occurred, or b) all seven fixes were aligned (Note: two radio-tracking fixes had an identical location).