

Distribution and movement of a stocked freshwater fish: implications of a variable habitat volume for stocking programs

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Abstract. Fish are commonly stocked into impoundments globally, yet their patterns of habitat use in this variable environment are rarely incorporated into the management of stocking density. The movement and distribution of Australian bass *Macquaria novemaculata* (Percichthyidae) were monitored in two impoundments to assess whether: (1) impoundment populations exhibit behaviour typical of wild or riverine percichthyids; (2) changing gradients of temperature and dissolved oxygen influenced distribution; and (3) the volume of available habitat should be incorporated into the management of these fisheries. Habitat use was determined with a combination of gill netting and ultrasonic telemetry using depth-coded tags. Tagged fish displayed both crepuscular and migratory behaviour typical of the Percichthyidae, but also showed a previously unobserved division between littoral and pelagic foraging strategies. Australian bass showed no obvious thermal preferences, but avoided areas with dissolved oxygen $<4 \text{ mg L}^{-1}$. In one impoundment, a combination of hypoxia and water extraction reduced the volume of available habitat to 15% of maximum in March 2009, which coincided with increased catch per unit effort (CPUE) and decreased fish condition. The adaptive behaviour of Australian bass makes them well suited to the variability of impoundments, but annual and stochastic events of habitat reduction should be considered when planning stocking regimes for these fisheries.

Additional keywords: acoustic tags, CPUE, extraction, Fulton's K , habitat availability, hypoxia, Percichthyidae, tracking.

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Introduction

Identifying the distribution of fishes in relation to environmental variation is an important component of fisheries management (Hayes *et al.* 1996; Rice 2005). For fisheries that are enhanced or maintained through stocking, this knowledge is essential for developing responsible stocking strategies (Cowx 1994; Taylor *et al.* 2005). Of relevance to stocked fisheries is how much habitat of sufficient quality is actually available to stocked fish and how this varies temporally. This is observed in models that include a spatial component to estimate a carrying capacity (Luo *et al.* 2001) or determine an optimal stocking density (Taylor and Suthers 2008). In particular, a variable habitat volume is potentially an important factor affecting the success of stocking programs and warrants further investigation. The

movement, habitat use and home range of fishes is also important information for the management of stocked or wild fisheries and can be used to identify refuge areas (Taylor *et al.* 2006; Taylor and Ko 2011) and foraging behaviours (Kobler *et al.* 2009). However, this information is unknown for many stocked species.

Identifying the environmental variables associated with the limits of a species' distribution is essential when explaining broad distribution patterns (Swales 2006) and for predicting the volume of available habitat in stocked fisheries. Interactions between habitat quality and species-specific preferences can drive the fine-scale distribution of fish in their natural environment (Hayes *et al.* 1996; Rosenfeld 2003). However, on a broader scale, the abiotic requirements and physiological

tolerances of a species can determine the amount of habitat that is actually available. Two abiotic factors that influence habitat availability in closed waters are dissolved oxygen (DO) and temperature (Coutant 1985; Dillon *et al.* 2003). Closed waters such as impoundments are frequently subject to thermal stratification in the warmer months, which can create a hypoxic bottom layer under a warm surface layer (Summerfelt 1999). If the thermal and DO conditions exceed a species' tolerance levels, then these areas become unavailable to fishes (Coutant 1985; Roberts *et al.* 2009), which can increase fish density in remaining habitats. Hypoxia is a particularly effective determinant of the vertical distribution of fishes because physiological limits determine the lower DO threshold for a species (Pollock *et al.* 2007). Environmental thresholds have been closely examined for many species but their importance in influencing the habitat availability of stocked fisheries remains largely unexplored. In addition to these abiotic stressors, variations in flow regime and impoundment releases can result in large and rapid fluctuations in the water level of closed waters. These fluctuations can be a key driver of impoundment ecology (Welcomme *et al.* 2010), yet the potential impacts on stocked or wild fish populations have rarely been examined, with the exception of spawning success in the littoral zone (Zalewski *et al.* 1995; Kahl *et al.* 2008).

The impoundments of eastern Australia are often stocked with native members of the family Percichthyidae, including the Australian bass *Macquaria novemaculeata*, yet the distribution and movement of percichthyids is known mostly from riverine studies (but see Ebner *et al.* 2010; Ebner *et al.* 2011). Despite the obvious value of describing the determinants of habitat availability for the management of stocked fish, an analysis of the minimum habitat requirements for a stocked percichthyid is lacking. Ultrasonic transmitters capable of transmitting depth information, which have been used to assess the association of individual fish with the thermocline (Nowak and Quinn 2002), were used in the current study to determine the availability of habitat for stocked fish. Depth tags also improve the resolution of individual foraging strategies by enabling the identification of associations between tagged fish and the benthic and surface zones in addition to the pelagic and littoral zones.

The objectives of this study were to quantify the volume of habitat used by Australian bass and to examine the implications of thermal stratification, hypoxia and variation in impoundment volume on habitat availability. Specifically, we aimed to address whether: (1) the home range and movement patterns of Australian bass in impoundments are typical of the Percichthyidae; (2) the stratification of impoundments influence the volume of available habitat for Australian bass, based on their specific requirements of temperature and DO; and (3) variation in an impoundment's available habitat volume can have a measurable impact on the density and condition of a stocked fish.

Materials and methods

Species and study areas

Australian bass (*Macquaria novemaculeata*) is an Australian percichthyid and a popular native sport fish. Impoundment populations of this species form important recreational fisheries

that are maintained solely through stocking, because Australian bass is catadromous and cannot reproduce in fresh water (Harris 1986). Approximately 300 000–500 000 Australian bass are released to maintain impoundment fisheries in eastern Australia each year (C. Westaway, personal communication).

This study was conducted in Danjera Dam (34.920°S, 150.385°E) and Brogo Dam (36.491°S, 149.740°E), in NSW, Australia (Fig. 1). The telemetry component of the study was undertaken in Danjera Dam, which is a storage for residential water supply (7800 ML capacity, 0.9 km² surface area) and has a maximum depth of 30 m. Gill netting and electric fishing were undertaken in Brogo Dam, which is a storage for mainly agricultural water supply (9000 ML capacity, 1 km² surface area) and has a maximum depth of 25 m. Both impoundments are stocked intermittently with Australian bass to maintain recreational fisheries and other than short-finned eels (*Anguilla australis*), there are no other large predatory fish found in either dam. Brogo Dam can experience high levels of water extraction and had large fluctuations in total volume during this study (20–100% capacity).

Telemetry

Telemetry was used in Danjera Dam to estimate the home range and movement patterns of Australian bass and to record their association with the stratified zone. Eleven Australian bass (135–696 g) were fitted with ultrasonic transmitters in September 2009. Fish were captured at one of two sites (Fig. 1) using gill netting (<30 min soak time) and monitored for 30 min before tagging. Sonotronics IBT tags (Sonotronics Inc., Tuscon, AZ, USA) were implanted in fish that displayed no obvious adverse effects of capture. Three different tag sizes were used to enable the tagging of a range of fish sizes and to meet the temporal and spatial requirements of the study. Three small fish (<230 g) were tagged externally with small transmitters with a 3 week battery life (model IBT-96-1-I, Table 1). These transmitters were attached using t-bar tags (Bradford *et al.* 2007) with the transmitter bound and glued to the trailer. Five fish were tagged externally using the same method with transmitters that also transmit depth information with a 10 day battery life (model IBDT-97-1-I, Table 1), enabling the resolution of vertical movement. Three large fish were tagged with transmitters with a 5 month battery life (model IBT-96-5-I, Table 1). These larger transmitters enabled the tracking of individuals over a period of months and were implanted surgically. Fish were anaesthetised using Aqui-S 60 mg L⁻¹ (Barker *et al.* 2002) and surgery was performed according to the method by Taylor *et al.* (2006). Surgery took <5 min, at which point the fish was returned to a tank containing fresh dam water. All fish visibly recovered within 10 min and were observed in captivity for 1 h before they were released at the point of capture.

Each transmitter had a unique pulse rate/frequency combination to allow identification of individual fish and the IBDT transmitters had an additional pulse string, which transmitted their depth by varying the pulse interval time. Fish were manually tracked using a boat-based acoustic receiver (Sonotronics USR-96; Sonotronics Inc.) and directional hydrophone (Sonotronics DH-4) mounted facing-forward on the starboard bow and signal codes interpreted aurally through headphones.

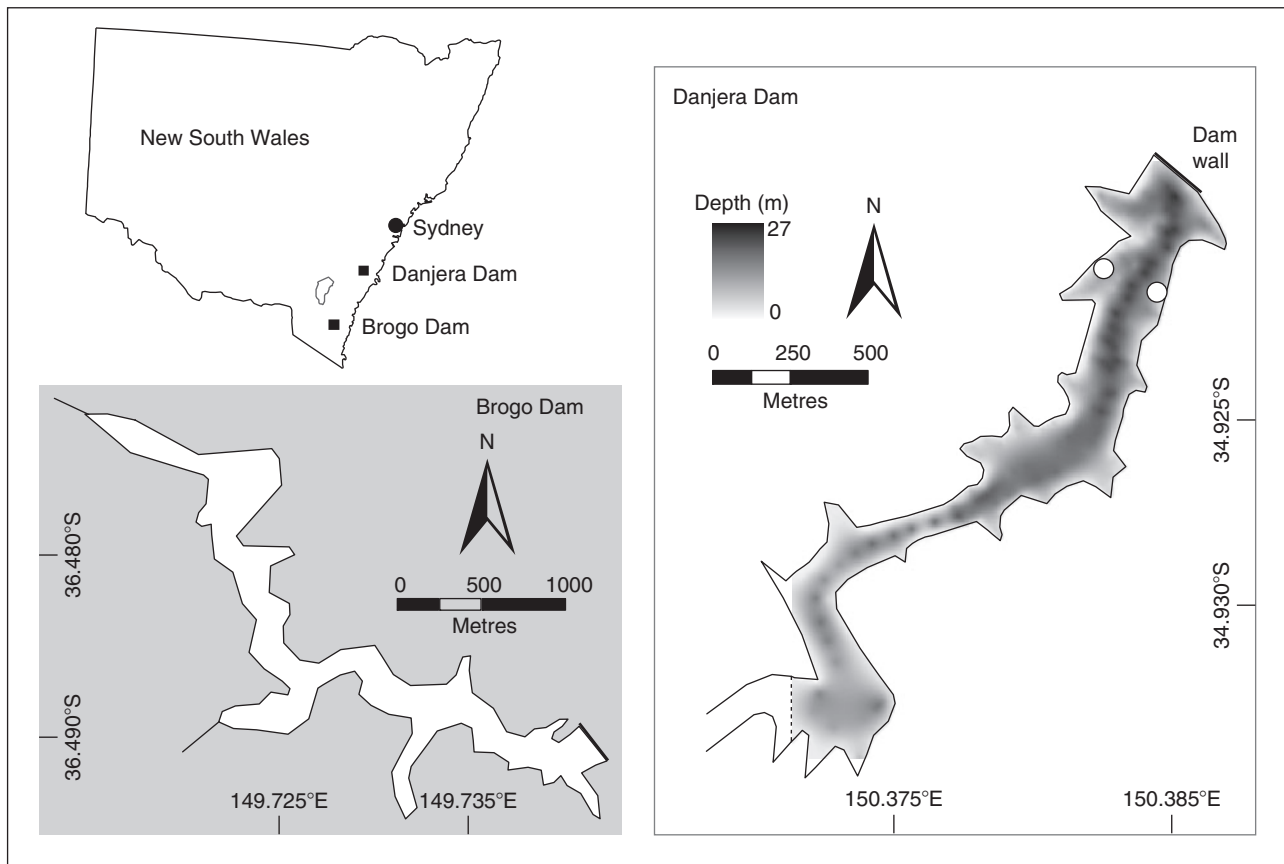


Fig. 1. Maps of the two study sites and the bathymetry of Danjera Dam, NSW, Australia. The dotted line represents the upper limit to the tracking area in Danjera Dam and the white circles represent the two capture and release points. In Danjera Dam, the depth ranges from ~0 m (light grey) to 27 m (dark grey).

Table 1. Biometric and movement information for tagged Australian bass at time of tagging
Movement values are mean (s.e.); MAI, minimum activity index (m h^{-1})

Fish identity number	Total length (mm)	Mass (g)	Movement (s.e.) (m)	MAI (s.e.) (m h^{-1})	Core (50%) home range (m^2)	Total (95%) home range (m^2)	50 : 95 Ratio	Home range volume (m^3)
1 ^B	320	466	800.3 (155.3)	39.1 (5.8)	20 923	80 784	0.259	
2 ^A	267	231			Fate unknown			
3 ^B	335	563	519.4 (113.4)	37.3 (9.1)	8857	43 242	0.205	
4 ^C	348	696			Moved out of tracking area on day 2			
5 ^B	349	633	712.0 (105.8)	39.3 (4.8)	28 378	99 828	0.284	
6 ^C	260	240	385.1 (55.9)	23.3 (6.6)	12 537	50 418	0.249	291 080
7 ^C	350	650	394.8 (67.3)	16.1 (3.0)	7427	45 506	0.163	231 171
8 ^C	231	170	773.8 (88.9)	37.7 (4.2)	21 708	66 583	0.326	769 255
9 ^A	224	150	1062.9 (40.5)	43.7 (14.1)		Moved out of tracking area on day 3		
10 ^C	240	192	1031.7 (149.4)	44.3 (6.1)	31 198	101 059	0.309	1 158 810
11 ^A	214	135			Fate unknown			
Average	285	375	710.0	35.1	18 718	69 631	0.256	612 579

^AFish tagged with 3 week tags.

^BFish tagged with 5 month tags.

^CFish tagged with depth tags.

The method used for manually locating fish was the same as in Taylor *et al.* (2006). The described technique had a horizontal accuracy of 4.8 m. Initially, fish were located every 3 h for 6 days after release. In addition, the three fish tagged with

5 month tags also had their locations recorded once a month for the following 2 months. Tracking was restricted to between the Danjera Dam wall and ~2.3 km upstream (Fig. 1). When IBDT tags were detected, the duration of the pulse string indicating

depth was recorded three times using a stopwatch and the average used to calculate the interval duration. A relationship between depth (D) and interval duration (I) is provided by Sonotronics Inc., but a regression was created independently for the method used in this study, by suspending an IBDT tag at known depths ($D = 194.6I - 105.5$, $n = 12$, $R^2 = 0.995$). The accuracy of depth measurements using this regression was 1.1 ± 0.6 m (mean \pm s.d.), with 90% of the estimates within 2.1 m of the true depth. Vertical temperature and dissolved oxygen profiles were constructed every ~ 12 h to enable the association of these parameters with fish depth.

Fish sampling

To assess the temperature and DO requirements of Australian bass, gill netting at discrete depths (Kahl and Radke 2006) was conducted in Brogo Dam in May, August and December 2008 and in March 2009. The depths of fish were compared with water quality profiles, made using a hand-held water quality meter (Hydrolab Datasonde 4, Hach Hydromet, Loveland, CO, USA). Horizontal multi-mesh gill nets (15 m and 30 m length, 2 m drop) were either sunk to sample the 2 m above the benthos at various depths, or floated to sample the surface 2 m. The mesh sizes ranged from 25 to 100 mm and regularly caught fish > 100 mm. The depths of submerged nets were measured using a sounder and were recorded every 5 m along the net. Nets were submerged for between 60 and 90 min. When a fish was caught, it was weighed (± 1 g) and measured (± 1 mm) and its point of capture recorded as a distance along the gill net and a height within the gill net, which were used to estimate the 2 m depth range at which the fish was caught. This method is unsuitable for mid-depth areas more than 2 m away from the bottom or surface. Catch per unit effort (CPUE) was calculated as the number of fish caught per 10 square metres of net per hour (fish $10 \text{ m}^{-2} \text{ h}^{-1}$). In every sampling period, sites were haphazardly selected and sampling effort was spread equally across all depths so that total CPUE estimates were representative of fish presence throughout the entire dam.

To sample additional fish for the estimation of fish condition, electric fishing was used in Brogo Dam during May and December 2008, March 2009 and May 2010. Electric fishing was done using a 5 m aluminium boat fitted with a Smith-Root 7.5 GPP unit (Smith-Root, Vancouver, WA, USA), operating at 600–800 V DC, 5 A, 25% duty cycle and 120 pulses s^{-1} . Approximately 4400 s electric fishing and $1000 \text{ m}^2 \text{ h}^{-1}$ gill netting were conducted in each sampling period and an effort was made to sample with equal effort during the day and after sunset.

Analysis

Home range was calculated by fixed kernel density estimation using the extension Hawth's Analysis Tools ver. 3.27 (Beyer 2007), which estimates a probability density function based on a finite number of detections. The home range (m^2) was defined as the area within a contour incorporating 95% of the kernel density and the core area of the home range as that within the 50% contour (Taylor *et al.* 2006). No suitable method was found in the literature to calculate a three-dimensional home range (m^3), so, for each of the four fish with sufficient depth data, an

estimate was calculated by assuming the home range volume approximates an oblate spheroid:

$$V = \frac{2}{3}\pi r^2 d, \quad (1)$$

where V is the estimated volume of the total home range (m^3), d is the observed depth range and r is calculated:

$$r = \left(\frac{A}{\pi}\right)^{\frac{1}{2}}, \quad (2)$$

where A is the area specified by the two-dimensional 95% kernel density contour. An oblate spheroid was chosen because the extremities of the 95% kernel density contour are defined by fewer detections, meaning a shape such as a cylinder would overestimate the volume at the edges of the home range.

Movement patterns were quantified using the minimum activity index (MAI, m h^{-1}) and through the assessment of diel activity. The MAI was calculated by dividing the distance between detections by the time elapsed during the detections, thus representing a minimum estimate of activity (Taylor and Ko 2011). Distances between waypoints were calculated using ArcGIS ver. 9.3.1 (ESRI, Redlands, CA, USA). If this distance intersected the edge of the impoundment, the distance was recalculated as the minimum non-intersecting distance. Diel activity patterns were examined using a proportional distance value, which partitioned the total distance moved during the experiment among eight daily tracking periods. Proportions were used for this analysis because they removed any inherent differences in overall activity between individuals. To reduce the bias of unknown movement, only MAI and proportional distance values calculated from consecutive detections were analysed. ANOVA was used to test for differences in the proportional distance values between the daily tracking periods and Tukey's HSD test was used to examine differences between specific periods. The data were not transformed, as the inspection of box-plots and normal probability plots showed sufficient homoscedasticity and normality of the data.

The association of Australian bass with specific habitat zones, including the stratified zone, was assessed using the relative-depth plot. Tracking data can be used in these plots, assuming the bathymetry and the depth of the fish is known. The relative-depth plot can identify associations not only the littoral and pelagic zones, which are often used to define variation in habitat use (Biro *et al.* 2003b; Kobler *et al.* 2009), but also the surface and epibenthic zones, which are not distinguished using two-dimensional tracking data. Bathymetric information for use in these plots was created by interpolating ~ 800 global positioning system (GPS) waypoints and associated depth readings throughout the Danjera Dam tracking area (ArcGIS ver. 9.3.1).

To examine the impact that variations in habitat volume might have on Australian bass, gill netting CPUE and fish condition were compared with the volume of available habitat in Brogo Dam for each sampling period. CPUE was calculated as an average of all individual gill net deployments within each sampling period. Available habitat was calculated as the volume between the surface and the depth at which dissolved oxygen

dropped to 4 mg L^{-1} and is given as a percentage of maximum impoundment volume. This volume was calculated using a volume–depth profile (Plumb and Blanchfield 2009) and the impoundment volume at each sampling period, both of which were obtained from the NSW Office of Water (personal communication). Fish condition was calculated using a modified Fulton's K , discussed by Cone (1989):

$$K = \frac{W}{L^b} \times 10^n, \quad (3)$$

where K is the index of fish condition, W is the mass of a fish, L is its length, n is a scaling integer ($n = 100$) and b is the exponent of the length–weight least-squares regression:

$$W = aL^b, \quad (4)$$

where W and L are as above and a is a constant. The regression was calculated using Australian bass caught in all five sampling periods by gill netting and electric fishing and the resultant b was used to calculate fish condition for all five sampling periods ($b = 2.995$, $R^2 = 0.995$, $n = 764$). For analysis, 92 fish (the minimum number caught in a sampling period) were selected at random from each period. Fish weighing less than five grams were excluded from the length–weight regression and condition calculations due to considerable uncertainty in their masses ($\pm 1 \text{ g}$). ANOVA and Tukey's HSD test were used on untransformed data to examine the differences in fish condition between sampling periods. CPUE was not analysed, as no transformation was found to meet the assumptions of a parametric analysis and non-parametric tests were deemed

unsuitable. All statistical tests were performed in JMP (7.0, SAS Institute, Cary, NC, USA).

Results

Home range and movement patterns

Australian bass moved, on average, a minimum of 700 m day^{-1} , at an average speed of $\sim 35 \text{ m h}^{-1}$ in Danjera Dam (Fig. 1; Table 1). After the six tracking days, fish had an average core home range of $18\,700 \text{ m}^2$ and an average total home range of $69\,600 \text{ m}^2$, or ~ 2 and 8% of the dam's surface area respectively. The core range was $\sim 25\%$ the size of the total home range. The total range volume for those fish with depth tags was an average of $612\,579 \text{ m}^3$ (612.6 ML), or $\sim 8\%$ of the dam's capacity. The core range was variably made up of 1–3 separate areas (Fig. 2), to which fish showed varying degrees of fidelity. Fish 1, 3 and 5, which were all fitted with longer duration tags, were observed within their same core ranges in the 2 months following the tracking study. Fish movement was elevated during dawn (around 0600 hours) and to a lesser extent dusk (1800 hours), with proportionally greater movement than other periods of the day (ANOVA, $F_{7,47} = 5.04$, $P < 0.001$; see Fig. 3 for results of Tukey's HSD test). The midday period showed the least amount of proportional movement (Fig. 3).

Not all tagged fish were continually located during the entire study (Table 1). Two fish disappeared from the main tracking area after 12 h and only two detections each (fish 2 and 11). Both were implanted with the smaller tags (IBT-96-1-I tags) and it is possible the tags failed or that the fish exited the tracking area within a 3-h period. Fish 4 and 9 were suspected of leaving the tracking area on the second and third days respectively (Table 1),

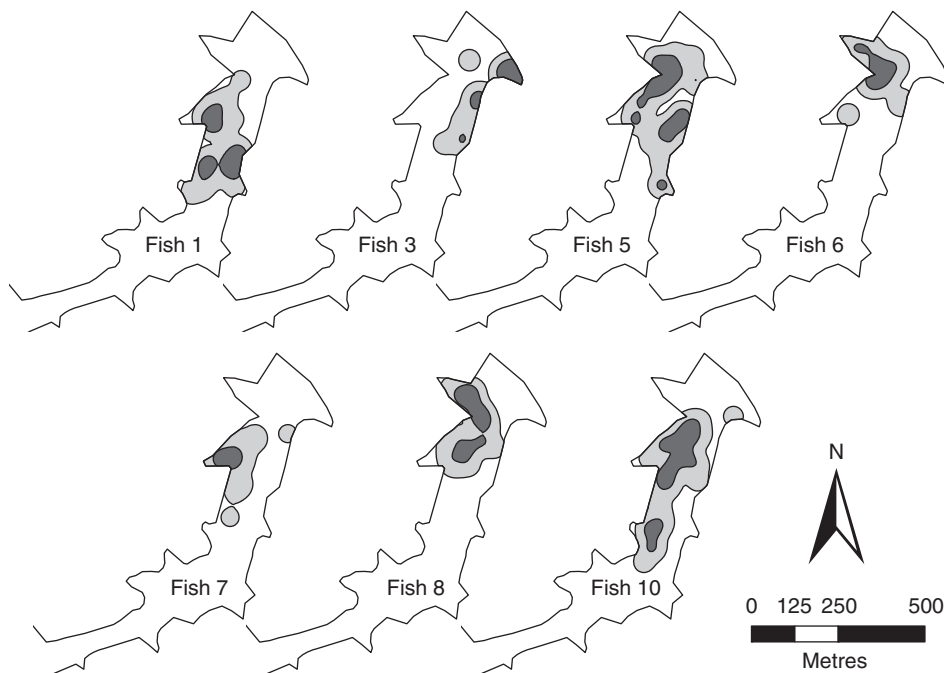


Fig. 2. Home ranges of individual Australian bass in Danjera Dam, NSW, Australia. The dark grey area represents the core range (50% kernel density) and the dark and light grey area represents the total range (95% kernel density). Values correspond with those presented in Table 1.

as the final detections of these fish were near the upstream boundary of the tracking area. There were insufficient detections to calculate a home range for fish 4 or 9, or movement indices for fish 4.

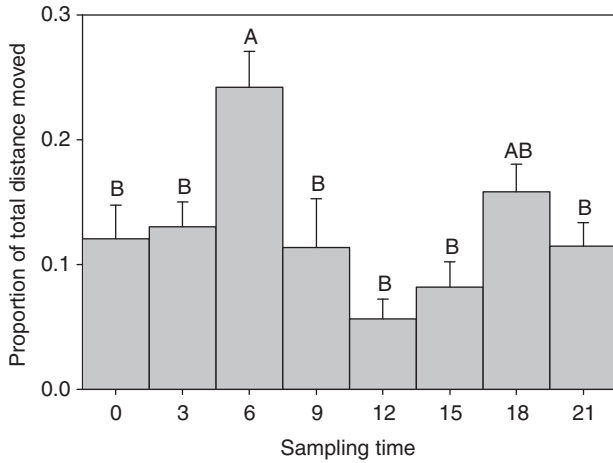


Fig. 3. Mean movement (+s.e.) of individuals expressed as the proportion of distance travelled over a 24-h period. Sampling time is the approximate time detections were made ('0' is midnight). Data include distances calculated using only consecutive detections. The results of Tukey's HSD test are given (times not sharing a letter are significantly different).

Relative-depth plots (of fish 6, 7, 8, 10) show individual variation in habitat zone association (Fig. 4). Fish 8 and 10 were either pelagic or benthic. These fish moved into deeper sections during the day but avoided the surface. Fish 6 and 7 preferred littoral and surface zones and only moved into the pelagic zone at night.

Abiotic variability and habitat availability

Fish were caught from all sampled depths in Brogo Dam when no stratification was present (August 2008) (Fig. 5). The vertical distribution of Australian bass was more restricted during periods with stratification and no fish were collected below the thermocline where DO was less than 4 mg L⁻¹. Acoustic telemetry in Danjera Dam showed that some fish briefly tolerated DO of 2–4 mg L⁻¹ (Fig. 4). Australian bass were associated with a range of different temperatures (9–21°C), including a range of 10–20°C within the same sampling period (December 2008) (Fig. 5).

The percentage volume of available habitat in Brogo Dam varied substantially due to stratification and a fluctuating impoundment volume. The impoundment volume for each sampling period, in chronological order, was 97, 100, 62 and 25% (Fig. 6). The volume had returned to 100% capacity by May 2010. Average CPUE from gill netting did not show a clear relationship with habitat volume, but did increase more than 4-fold in March 2009, when the volume of available habitat reduced to 15% (Fig. 6). Fish condition decreased substantially

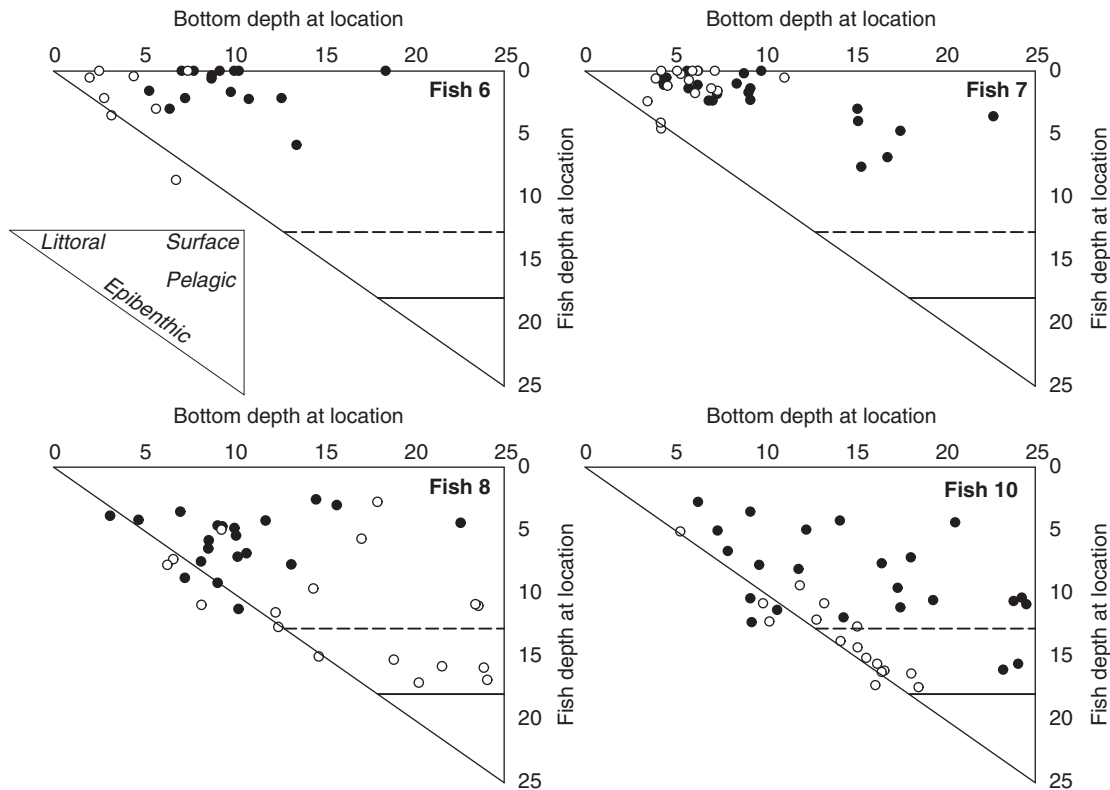


Fig. 4. Relative-depth plots, indicating fish depth and bottom depth during the day (white) and night (black), for the four fish with sufficient telemetry data. The dashed line represents the depth at which dissolved oxygen equals 4 mg L⁻¹ and the solid line 2 mg L⁻¹. The different habitat zones represented by different areas of the plot are given.

at this time (Fig. 7) and was significantly lower than other sampling periods except for August 2008 (ANOVA, $F_{4,455} = 11.95$, $P < 0.001$; Fig. 7).

Discussion

Home range and movement patterns

Impoundment populations of stocked Australian bass had home ranges and movement patterns typical of the Percichthyidae, but tracking with depth tags revealed traits previously unobserved in this family. These behavioural differences are most likely driven by unique features of the impoundment environment, rather than an inherent difference between stocked and wild fish. The total home range for Australian bass was similar in size to that observed for wild Macquarie perch (Percichthyidae) in a reservoir, tracked for approximately the same duration (Ebner *et al.* 2011). These home ranges in impoundments appear larger than those of a similar species in riverine environments (Thiem *et al.* 2008; Ebner and Thiem 2009). This may be the result of consistently larger home ranges in impoundment environments (Minns 1995), or due to difficulties calculating home range areas in convoluted riverine systems (Ebner *et al.* 2010). The distance moved per day, however, seems to be similar between the Australian bass in the current study and some riverine percichthyids (Simpson and Mapleston 2002; Koehn *et al.* 2009). Australian bass were also observed to have multiple core

areas within a home range, in a similar manner to those observed in impoundment populations of wild Macquarie perch (Ebner *et al.* 2011). The total range for Australian bass was 8% of the impoundment, both in surface area and volume, which suggests Australian bass are consistent users of both the horizontal and vertical habitat.

The ratio of core range to total range in the current study (25.6%) is similar to the ratio observed for wild Macquarie perch in an impoundment (20.8%; Ebner *et al.* 2011), which is almost certainly due to crepuscular foraging in these species. Crepuscular movements of Australian bass were strongly observed, with peaks in activity occurring at dawn and, to a lesser extent, dusk. Crepuscular predation was a suspected trait of Australian bass (Harris 1985), but from mostly anecdotal evidence. Dawn and dusk as periods for peaks in activity is often observed in other fish species (Ng *et al.* 2007), including some percichthyids (Thiem *et al.* 2008; Ebner *et al.* 2009a, 2009b). Crepuscular foraging is a common strategy for species that prey on vertically-migrating zooplankton or zooplanktivorous fish (Reebs 2002) and Australian bass are known to consume both prey types (Harris 1985; Smith *et al.* 2011).

Migratory diel movements were observed in Australian bass, which is a novel finding for this species and is probably the result of predatory behaviour by Australian bass. The relative-depth plots show the two pelagic/epibenthic fish moving up in the water column at night and the two littoral fish moving out from

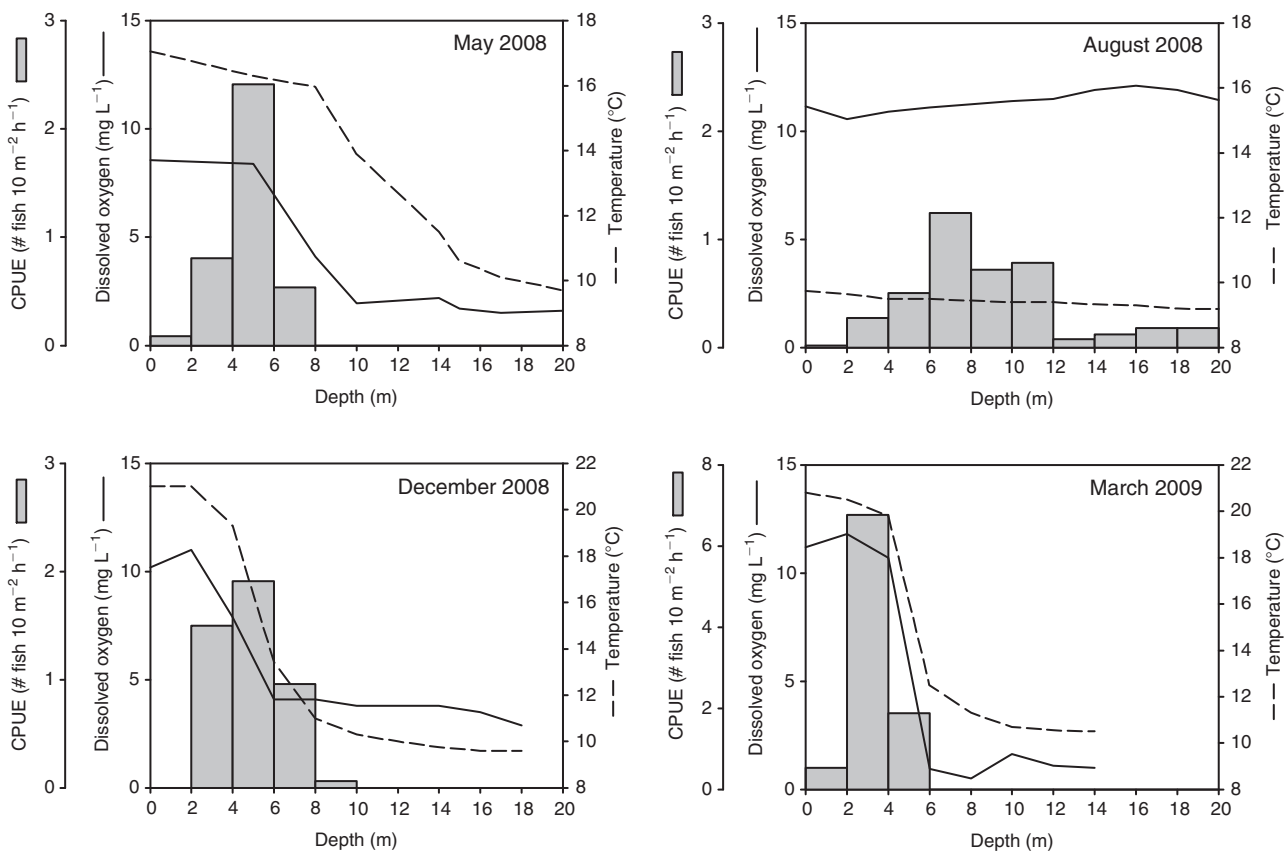


Fig. 5. Vertical distribution of Australian bass in Brogo Dam, NSW, Australia, observed with gill netting, expressed as the total number of fish caught in each depth bin in each sampling period, standardised to effort in that depth bin (catch per unit effort, CPUE).

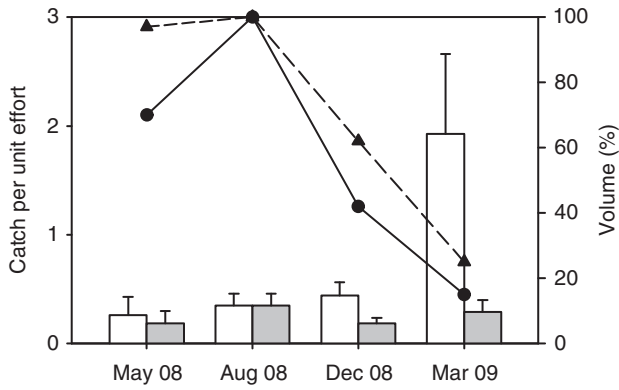


Fig. 6. Average catch per unit effort (CPUE) (+s.e.) using gill netting (fish per 10 m² h⁻¹). The white bars represent the actual CPUE and the grey bars represent the CPUE standardised to the volume of available habitat (i.e. the likely CPUE given 100% available habitat). The volume of available habitat (line) and impoundment volume (dashed line) as a percentage of maximum impoundment volume are given.

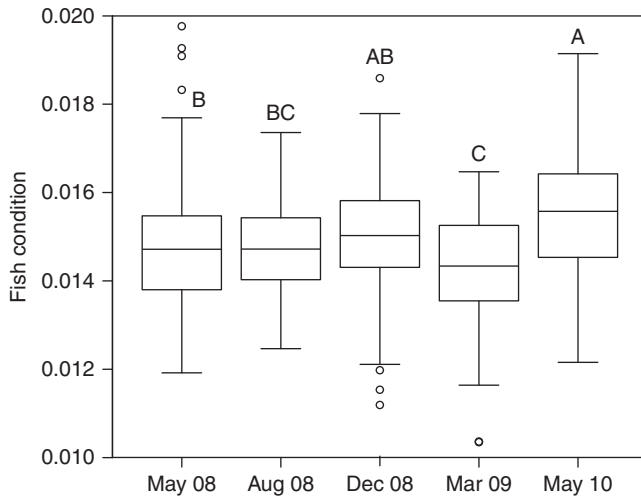


Fig. 7. Boxplots of fish condition in Brogo Dam, NSW, Australia, for the four sampling periods. The results of Tukey's HSD test are given (periods not sharing a letter are significantly different).

the littoral zone at night. These movements coincide with the movement of migratory prey. Zooplankton often migrate vertically on a daily basis, moving up into the shallow pelagic zone at night (Lampert 1993), which can drive a similar migration in their teleost predators, both vertically (Lieschke and Closs 1999) and horizontally (Wurtsbaugh and Li 1985). This indicates that both the crepuscular foraging and pelagic migrations in Australian bass could be driven by the behaviour of their prey. Although crepuscular foraging is also observed in riverine percichthyids (e.g. Ebner *et al.* 2009b), the diel migrations by Australian bass may be more likely in impoundments because of the importance of zooplankton in these environments. A previous study found that riverine Murray cod generally avoided the pelagic zone (Koehn 2009), which supports this assertion.

Significant individual variation in the use of the available spatial niche was observed from depth tag data. Two fish were consistently found in the littoral/surface zones and two were

found consistently in the pelagic/epibenthic zones, with few excursions out of these areas. Such separation between littoral and pelagic foraging strategies may be particularly indicative of stable intra-population niche partitioning, as these two zones can show distinct food chains (Meredith *et al.* 2003; Quevedo *et al.* 2009). The tagging of more individuals is needed to quantify the extent of spatial niche partitioning in Australian bass, but there is strong evidence that consistent separation of the spatial niche can occur between competing species (Werner and Hall 1979; Kahl and Radke 2006) and between individuals of the same species (Armstrong *et al.* 1999; Keeley 2001; Laurel *et al.* 2007). This possible association of Australian bass with specific foraging zones supports the idea that the species exhibits strong inter-individual variation in foraging behaviour (Smith *et al.* 2011).

Two Australian bass were suspected of exiting the tracking area during the study. Such movements can indicate the search for new home ranges (Ebner and Thiem 2009) and a consistent proportion of 'nomadic' individuals in a population has been observed in numerous percichthyid species (Simpson and Mapleston 2002; Crook 2004; O'Connor *et al.* 2005; Koehn *et al.* 2009). The presence of non-settled individuals is considered an important mechanism for dealing with temporally or spatially variable resources (Switzer 1993; Crook 2004) or heterogeneous habitat quality (Switzer 1993). Occasional migration appears to be a consistent trait of the Percichthyidae in both impoundment and riverine ecosystems.

The post-operative recovery time in this study was minimal (1 h), which may have influenced the behaviour of tagged fish. The similar patterns of movement between this study and other percichthyid studies with longer recovery times (e.g. Ebner *et al.* 2009b, 2011) do suggest, however, that tagging did not have a large effect on behaviour. Australian bass tagged with t-bars can show quick recovery and little inflammation after 1 week, although fish tagged internally can show greater signs of inflammation and eventual tag rejection (Butler *et al.* 2009). The time taken for the resumption of foraging behaviour post tagging is uncertain, but the percichthyid Macquarie perch has been shown to resume normal feeding behaviour 2 days after implantation of an internal tag (Broadhurst *et al.* 2009). Tracking studies examining the influence of post-tagging recovery time on fish behaviour are needed if the results of studies such as this one are to be correctly interpreted.

Abiotic variability and habitat availability

Stratification restricted the volume of habitat available for Australian bass in this study, but it was driven by the requirements for DO rather than temperature. Australian bass were observed in a wide range of temperatures within the same sampling period (e.g. 10–20°C in December 2008), which suggests that the boundaries for thermal tolerance lie outside this range. Other species of fish in closed waters show thermal boundaries outside this range, such as striped bass (25°C, Coutant 1985). The correlation between DO and temperature can make interpretation of thermal boundaries difficult and, without observing Australian bass in a wider range of temperatures, we cannot identify the boundaries of thermal tolerance. The data do indicate, however, that Australian bass tolerate most temperatures likely to occur in their temperate

Australian impoundments, which means that bottom hypoxia is of greater concern in these environments.

Both impoundments in this study experienced bottom hypoxia and in Brogo Dam, changes in the depth of stratification were associated with changes in the vertical distribution of Australian bass. The minimum DO required for fish survival is often around 2–3 mg L⁻¹ (Coutant 1985; Suthers and Gee 1986; Swales 2006), but fish behaviour may be affected as DO drops below 5–6 mg L⁻¹ (Dillon *et al.* 2003; Plumb and Blanchfield 2009). For Australian bass, hypoxia appears to exist when DO drops below 4 mg L⁻¹, as fish in this study were not caught below this concentration using depth-specific gill netting. The Australian bass fitted with acoustic depth tags, however, showed that some individuals did access habitat with DO <4 mg L⁻¹, if only occasionally. Other species have been observed to enter the hypoxic zone briefly to a search for prey (Swales 2006; Roberts *et al.* 2009), including at levels of DO below their survival threshold (Swales 2006). It seems likely that Australian bass make similar movements as part of a foraging strategy, which may be part of a pelagic/epibenthic strategy. The lack of fish caught with gill nets in water below the 4 mg L⁻¹ threshold may be due to fewer fish making these movements, or reduced activity in hypoxic water (Kramer 1987), either of which would reduce the likelihood of a fish encountering a gill net. Despite the evidence of some individuals moving into areas with DO <4 mg L⁻¹, the consistent lack of fish observed in this study below 4 mg L⁻¹ suggests this threshold has a strong influence on a population's distribution.

A reduced impoundment volume had a significant impact on Australian bass during this study. A decline in the volume of Brogo Dam combined with bottom hypoxia to reduce the volume of available habitat by 85% in March 2009. This coincided with a greatly increased CPUE and significantly decreased fish condition. This increase in gill netting CPUE approximates the relative decrease in the available habitat volume, which is observed in the reasonably consistent standardised CPUE values. When this impoundment was almost full (May 2008), severe bottom hypoxia reduced the volume of available habitat by only 30% and CPUE and condition showed no obvious change. This may suggest that that the bottom 30% of a dam can become temporarily unavailable with little observable impact on the stocked populations of Australian bass.

The main assumption of standardised sampling in this study was equal average catchability of the population between sampling periods. If this was met, then the CPUE values are an accurate approximation of relative density (Hubert and Fabrizio 2007). Sampling with identical multi-panel gill nets was aimed at meeting this assumption, but it must be accepted that the growth of fish during the study and variation in temperature-dependent activity may have contributed to some variation in the relative catch rates. Sampling at all depths with equal effort should mean that gill netting CPUE approximated the relative density of fish in the entire dam. If the assumption of equal catchability was not met and, for example, fish increased their activity rates with increasing density (Marchand and Boisclair 1998; Biro *et al.* 2003a), then the standardised catch rates could overestimate the actual density of fish. Regardless of the exact relationship between habitat volume and density, the observed 4-fold increase in relative density, associated with a

reduction in the available habitat volume from 100% to 15%, must be considered an indicator of a population under stress. There was no significant increase in relative density among the other three sampling periods, but it is interesting to note that the highest standardised CPUE was associated with full habitat availability (August 2008).

The observed decline in fish condition when the volume of available habitat was lowest may be due to a chronic exposure to high population density (Fagerlund *et al.* 1981). The decline in condition during March 2009 coincided with 15% available habitat volume and presumably a much higher population density than if the impoundment was full. Density-dependent growth, therefore, may have caused this decline in condition (Refstie and Kittelsen 1976), but equally, a reduced prey supply (Vanderploeg *et al.* 2009), decreased water quality (Hayes *et al.* 1999), or decreased habitat quality may have all contributed. The lower condition at the end of winter (August 2008) probably indicates a normal over-winter depletion of fat reserves, which is not uncommon (Booth and Keast 1986). Conversely, the greatly increased condition in May 2010 (~3 months after the rapid re-filling of Brogo Dam) is probably due to the abatement of the stressors listed above and possibly a trophic upsurge, which can occur when an impoundment refills after a protracted period of reduced volume (Summerfelt 1999). Gonadal development, which occurs in this species between July and September (Harris 1986), can increase body mass in female Australian bass (Harris 1987). The condition values for the August sampling period, therefore, may actually overestimate the nutritional condition during this period. There is also some evidence of sexual dimorphic growth in Australian bass in wild populations (Harris 1987), although there is no evidence for sex-biased allometry. In any case, if the sex ratio of fish remained constant between sampling periods, then the condition values are robust to sexual dimorphic growth (Leclercq *et al.* 2010).

Conclusions and management implications

Australian bass is a flexible species, shown by the variation in the use of the foraging zones (this study) and by differences in the dietary niche (Smith *et al.* 2011). There is also evidence for flexible behaviour in other percichthyids (Crook 2004; Howell *et al.* 2004; Sternberg *et al.* 2008). Adaptive behaviour, or 'ecological flexibility' (Werner and Hall 1979), is an ideal behaviour for variable environments (Dill 1983), which makes the Percichthyidae suited to stocked recreational fisheries in the variable impoundments of Australia. Although the behavioural flexibility of these species may delay the onset of density-dependent effects due to stratification, habitat restriction was observed to affect Australian bass, meaning site-specific information on habitat availability should still be incorporated into stocking regimes. Information on habitat availability could aid stocking through the elucidation of relationships between environmental variables and stocking rates (Cowx 1994; Jacobson and Anderson 2007), or through the direct estimation of a system's carrying capacity (Li 1999; Arahamian *et al.* 2003).

Although the use of available habitat volumes in production-based stocking models (e.g. Taylor and Suthers 2008) may be of limited use without precise knowledge of the relationship between habitat volume and productivity, at the very least the

availability of habitat should be incorporated into a stocking regime in a risk-management capacity (Arahamian *et al.* 2003). For example, an impoundment that is known to lose ~50% of its volume to hypoxia should be stocked at lower densities than one which loses ~20%, all else being equal. Likewise, an impoundment that experiences high variation in flows could be stocked at densities proportional to the trade-off between the severity of a 'drought' event and its likelihood. In fact, an ideal factor for deciding upon the goal for a stocked fishery, i.e. to produce a few large fish, or many small ones (Walters and Post 1993), could be based on the expected environmental variability. Brogo Dam, for example, which experiences a decline in total volume to below 50% every 2–5 years (NSW Office of Water, personal communication), would be best stocked as a trophy fishery, with low densities that are unlikely to experience severe density-dependent limitations at times of reduced habitat volume. The current study demonstrates that habitat availability should be included in the management of stocked fisheries. Quantitatively, this would require the use of spatially explicit stocking models, but, even without these, a qualitative consideration of habitat availability should be included in stocking management plans.

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