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Distribution, seasonal movements and habitat utilisation of an endangered shark, *Glyphis glyphis*, from northern Australia

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ABSTRACT: Euryhaline and freshwater elasmobranchs are considered amongst the most threatened groups of aquatic animals. The speartooth shark *Glyphis glyphis* has a distribution restricted to estuaries and rivers in northern Australia and Papua New Guinea. Due to this restricted range and threats from fisheries and habitat degradation, the species is currently listed as Endangered on the IUCN Red List. To inform and direct conservation management actions, we investigated the distribution and habitat utilisation of *G. glyphis* in the Wenlock River system, Queensland, Australia. Using acoustic transmitters and a network of fixed underwater acoustic hydrophones, the movements of 40 sharks (63 to 131.5 cm total length) were tracked over 22 mo, throughout 137 km of river and adjacent coastal embayment. Three broad zones were utilised by tagged *G. glyphis*, comprising a lower (0 to 23 km), mid (20 to 50 km) and upper (35 to 68 km upstream) estuary zone. Individual-based occupancy of these zones changed with seasonal changes in freshwater inflow. These results provide new insight into the habitat requirements of *G. glyphis*, the importance of natural eco-hydrological flows for the species, and the significance of the Wenlock River as a *G. glyphis* natal area.

KEY WORDS: Elasmobranch · Acoustic telemetry · Spatial ecology · Tropical tidal river · Conservation · Fisheries · River shark · *Glyphis* · Euryhaline

INTRODUCTION

The International Union for the Conservation of Nature (IUCN) has identified elasmobranchs as amongst the most threatened groups of animals, with 25% of the world's 1041 known species threatened with extinction (IUCN 2016). Overfishing, bycatch mortality, pollution, and habitat loss and degradation have been identified as the major threats to elasmobranch diversity (Hutchings 2000, Compagno 2002, Field et al. 2009). Compared to many other aquatic species, elasmobranchs are more susceptible to anthropogenic pressures due to their large body size, slow rate of maturity and low fecundity (Cortés 2000). Elasmobranchs inhabiting riverine habitats are particularly prone because they are less able to evade these threats due to the confined landward boundaries of their habitat (Compagno & Cook 1995, Martin 2005, Compagno et al. 2008). Human populations and activities are forecast to intensify along river boundaries and coastal regions over the next century, making thorough understanding of the distribution, seasonal movement and habitat utilisation of these species imperative for their long-term management and conservation (Small & Nicholls 2003, Lotze et al. 2006).

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The 'river sharks' (Family Carcharhinidae, genus *Glyphis*) are considered amongst the most threatened of the elasmobranchs (IUCN 2016). This genus comprises 4 confirmed species, all of which are found within tropical rivers, estuaries and/or coastal habitats of the Indian–West Pacific Oceans (Compagno 2002). The speartooth shark *Glyphis glyphis* is known only from southern coastal Papua New Guinea and river catchments in northern Australia. This includes 5 catchments in Northern Territory and 1 in northern Queensland (Pillans et al. 2009, Commonwealth of Australia 2015). Genetic analysis has revealed that there is very little genetic exchange between these catchments (Feutry et al. 2014) and *G. glyphis* is currently listed as Endangered on the IUCN Red List, and Critically Endangered under the Australian Government's Environmental Protection and Biodiversity Conservation Act 1999 (the EPBC Act). Previous research has been limited to fishing surveys (Peverell et al. 2006, Field et al. 2013, White et al. 2015) and short-term tracking of shark movements (Pillans et al. 2008, 2009). These studies showed that juvenile *G. glyphis* prefer turbid tidal rivers; however, nothing is known of how habitat use varies over extended periods of time, or if sharks regularly move into marine habitats. Furthermore, nothing is known of the occurrence of adult sharks and the timing and locations where they reproduce (White et al. 2015). The paucity of information currently limits our ability to develop policy structured to protect this rare and endangered species from anthropogenic threats.

Acoustic telemetry has revolutionised our ability to track aquatic organisms, providing detailed insight into species occurrence, habitat utilisation, connectivity and short- and long-term movement patterns (Heupel et al. 2006, Campbell et al. 2012a, Hussey et al. 2015). This information can prove invaluable in exposing times of year, life history stages or geographical areas where animals are at particular risk (Heupel et al. 2010, Simpfendorfer et al. 2010, Hussey et al. 2015). Telemetry can also be used to directly inform policy, such as the development of conservation areas (e.g. Lea et al. 2016). Such knowledge is becoming increasingly important as human activity expands and intensifies along systems where this species is known to occur.

The objective of this study was to identify critical areas and understand the seasonal movements and habitat utilisation of juvenile *G. glyphis* in the Wenlock River, Cape York Peninsula, Australia, using acoustic telemetry. We investigated the degree of movement between estuarine and adjacent habitats, and how habitat-use varied in response to environmental conditions and shark life history (i.e. shark size and gender). We discuss areas and times of year where there is increased potential for conflict, and provide recommendations with the aim of informing species management and conservation.

MATERIALS AND METHODS

Study area

The Wenlock River is located within the remote Cape York Bioregion in far north Queensland, Australia. The Wenlock and the Ducie River drain into Port Musgrave, a coastal embayment within the Gulf of Carpentaria (Fig. 1). These river systems are thought to be minimally impacted by human activities (Blackman et al. 1999, Woinarski 2007), maintaining natural ecological functions including intact hydro-ecological flows fed by perennial sandstone and bauxite springs (Leblanc et al. 2015). However, both rivers are fished recreationally and commercially, and sections of both catchments are contained within bauxite mining or mining exploration tenements, suggesting potential future conservation and management challenges.

The climate of the study area is tropical monsoonal, with strongly seasonal rainfall and high ambient air temperatures year round (mean minimum temperature: 21.9°C, mean maximum temperature: 32.8°C; Climate Stn 027045, 12.67° S, 141.92° E; Australian Government Bureau of Meteorology). The dry season extends from April/May until October, during which little or no measurable rain falls and no direct rainfall runoff occurs. October, November and December are transitional months, featuring increased temperatures and humidity with isolated to scattered showers and thunderstorm activity. The core part of the wet season extends between January and March, continuing some years into April, driven by a series of monsoonal rain events.

Animal capture and tracking

Fishing was conducted between 28 November 2012 and 9 November 2013 at selected points within the Wenlock River, Tentpole Creek and Hudson Creek, from the river mouth to 60 km upstream (Fig. 1). Sharks were captured using rod and reel with teleost baits. Six *Glyphis glyphis* were incidentally caught in recreational crab pots and 1 *G. glyphis* was inciden-

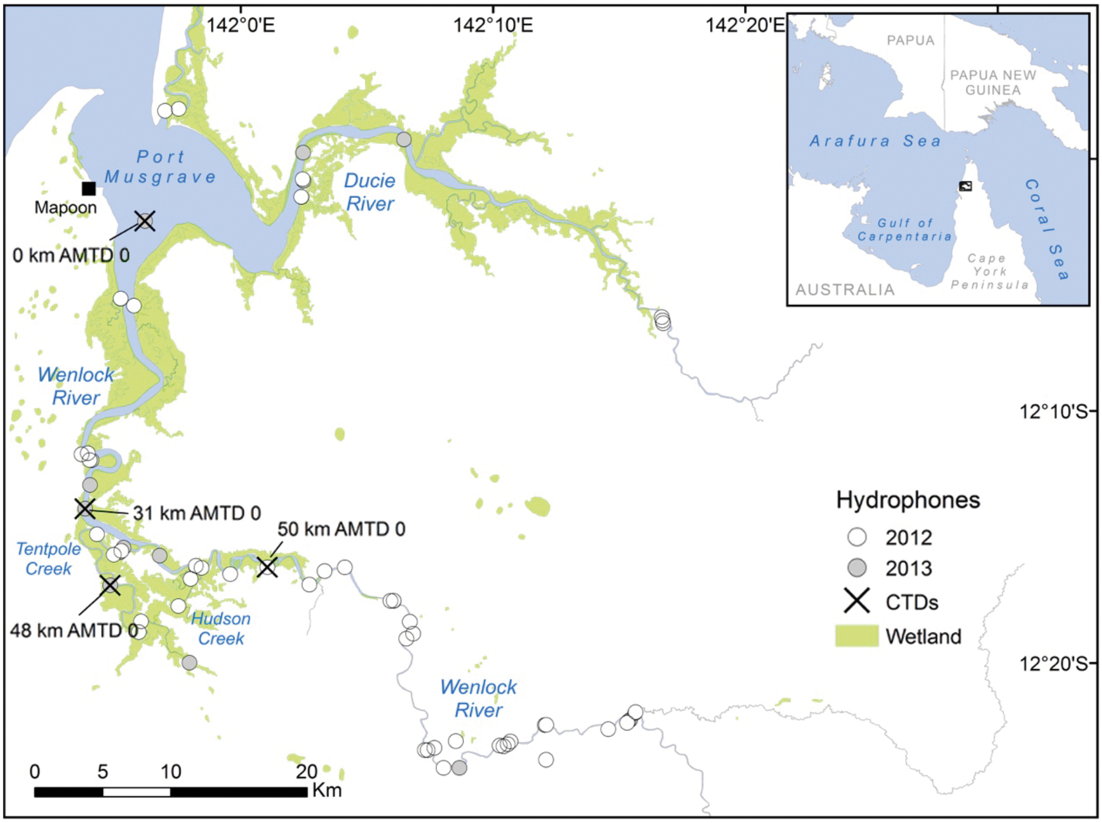

Fig. 1. Study location showing the array of acoustic hydrophones deployed in 2012, additional hydrophones deployed in 2013 and the locations of environmental loggers (CTDs) within the Wenlock and Ducie Rivers, Queensland, Australia. CTDs were attached to moorings also bearing an acoustic hydrophone

tally captured in a gill net set to catch bait. Shark gender was assessed by the presence/absence of external claspers. Neonates were assessed by the presence of fresh umbilical scars.

To track shark movements, a 69 kHz coded acoustic transmitter (VEMCO) was inserted surgically into the abdominal cavity of sharks (n = 54), and the wound closed using 2 or 3 sutures. Individuals <80 cm total length (TL) were implanted with VEMCO V9 transmitters (estimated battery life = 350 d), and individuals >80 cm were implanted with VEMCO V13 tags (estimated battery life = 700 d). Procedures took between 3 and 5 min and were undertaken with the shark securely held, ventral surface upwards, on soft foam slotted to accommodate the dorsal fin. Continuous gill irrigation of fresh river water was provided using a bilge pump and soft plastic hose. Following tagging, each shark was held upright by the dorsal fin in the river to assist with recovery and assess condition prior to release.

Between November 2012 and August 2013, shark movements were monitored using an array of 45 omnidirectional underwater hydrophones (VEMCO VR2-W; Fig. 1). In areas where the river was particularly wide, a cluster of hydrophones was deployed to enhance transmitter detectability. The array was expanded in August 2013 by an additional 9 hydrophones: 6 positioned in the Wenlock River system, 2 in the Ducie River and 1 in Port Musgrave. For our analyses, hydrophones <3 km apart were grouped to represent a single station, as not to over-represent parts of the river for our analysis of shark movements (Dwyer et al. 2015).

Movement analysis

In order to capture long-term, broad scale movements, only those tagged individuals with >5 mo (118 d) of continuous detection were included in our analysis. Detection data were downloaded and analysed for departure and arrival times when transmitters moved between the detection fields of adjacent hydrophones (or hydrophone clusters). This was performed using the V-Track package (Campbell et al. 2012b) in R (R Core Team 2015). Following Dwyer et al. (2015), the minimum distance travelled was calculated by summing all consecutive upriver and downriver movements of tagged sharks between hydrophones along the course of the river. The extents of river occupied by sharks were determined as the adopted middle thread distance (AMTD) between the farthest upstream hydrophone and the hydrophone closest to the river mouth (Dwyer et al. 2015). For the purpose of this study, AMTD 0 was taken as the hydrophone located at the mouth of the Wenlock River within Port Musgrave (S/N 123003 = PM2). The AMTD between hydrophone stations were calculated by first digitising satellite images of the river into a spatial lines object in ArcGIS 10.1 (ESRI), before estimating the least cost path and the AMTD in km between each hydrophone. If a tagged shark was detected in multiple branches of the river network, the extent of river occupied also included the distance between the main trunk and the most upstream hydrophone in the tributary. To investigate seasonal differences in shark movements and range use, and to reduce the bias of transmitter longevity on these measures, detections were subsampled into monthly intervals before distance travelled and extent of river utilised were estimated.

Differences in distances moved and home range according to life history characteristics were tested using linear mixed effect models (LMMs) via the 'nlme' package in R (Pinheiro et al. 2016). Monthly extent of river utilised (km) or minimum distance travelled (km) per month was the dependent variable and animal sex (factor), body size (factor; ≤100 or >100 cm TL), month (factor; Jan to Dec) and the 2-way interactions between these variables as the independent variables. Minimum distance travelled was square root transformed and extent of river was natural log transformed to meet model assumptions of homoscedasticity and normality of errors. Shark body size was discretised into 2 equal-width intervals using the 'cut()' function in R to assist with model interpretation. In both LMMs, Shark ID (i.e. the unique tag code of each shark's acoustic transmitter) nested within tracking year (2012/2013 or 2013/2014) were included as random effects to account for repeated measures from individual sharks and the expansion of the acoustic array in 2013. Full models including interaction terms were fitted initially, with nonsignificant interaction terms removed to simplify models according to the principle of parsimony based on corrected Akaike's information criteria (AIC).

Environmental monitoring

Daily river flow and river height measurements were obtained from Moreton Telegraph gauging station on the Wenlock River (Gauging Stn 027015; 12.45° S, 142.64° E; DNRM 2015). Mean annual rainfall at this location was 1887 mm yr^{-1} and mean annual discharge was 17 197 m^3 s^{-1}. Salinity data were obtained between December 2013 and March 2014 using 4 environmental loggers (CTD-Diver; Schlumberger Water Services) deployed on hydrophone moorings positioned at 0, 31, 48 and 50 km AMTD 0 (Fig. 1). Electrical conductivity readings in mS cm^{-1} were converted to salinity using the Practical Salinity Scale 1978 in the range of 2 to 42 (Fofonoff & Millard 1983). Salinities <2 were calculated using the extension of the Practical Salinity Scale (Hill et al. 1986) using the 'ws' package (Jassby & Cloern 2016) in R (R Core Team 2015). Salinities were expressed as mean hourly salinity weight of solute per thousand parts of solution. To investigate salinity preferences in *G. glyphis*, we extracted the timing when tagged sharks were detected at hydrophone moorings with attached environmental loggers and matched these detections to the transformed salinity values at that location. We then constructed a generalized linear model (GLM; binomial distribution and logit link) to compare salinities when tagged sharks were detected at hydrophones versus salinities when tagged sharks were not detected. Here, shark presence/absence was the dependent variable and salinity, and its quadratic term ($salinity^2$) was the independent variable. Models were run separately for each calendar month (December 2013 to March 2014), and the test statistic extracted for all variables for each temporal period. We then ran a randomisation test based on 9999 permutations of the data to compare the reference estimate of the test statistic to the reference distribution obtained under our null hypothesis (i.e. no preference towards salinity). To accommodate serial autocorrelation, randomisations were set to accommodate temporal ordering between 30 min salinity readings. The level of rejection of a null hypothesis was taken as $\alpha = 0.05$.

RESULTS

Animal capture and tracking

A total of 65 *Glyphis glyphis* (max. TL = 139 cm) were captured during fishing in the Wenlock River system between November 2012 and December

2013. Two juvenile bull sharks *Carcharhinus leucas* were also captured in this period. Of the 65 *G. glyphis* captured, 54 were implanted with acoustic transmitters and 40 had sufficient data with which to undertake our analysis of shark movements. These comprised 23 females and 17 males, ranging between 63 and 139 cm TL. Of these sharks, 35 were captured in Tentpole Creek and 5 in Hudson Creek (Fig. 1, Table 1). Over 22 mo, 154 686 detections were obtained from these 40 individuals (min. = 238, max. = 16 936 detections; Table 1, Fig. 2). The detection periods ranged between 118 and 669 d, with the greatest number of sharks detected in January (n = 38) and the fewest number in October (n = 22). There was no significant variation in TL between male (mean ± SE: 87. 0 ± 5.1 cm) and female sharks (88.5 ± 3.7 cm; Student's *t*-test, $t = -0.22$, df = 29, p = 0.80).

Table 1. Capture location, sex, length, deployment dates and detection information for acoustic tagged speartooth sharks *Glyphis glyphis* with >117 d of detection within the acoustic array. TP: animal captured in Tentpole Creek; H: animal captured in Hudson Creek

Transmitter code	Total length (cm)	Sex	Capture river	Capture date	Duration (d)	Acoustic detections
11713	64	Female	TP	6 December 2013	279.9	728
11715	68	Female	TP	5 December 2013	148.6	703
11716	65	Male	TP	5 December 2013	296.09	1074
11720	64	Male	TP	5 December 2013	283.94	792
11721	71.5	Female	TP	4 August 2013	337.4	512
11723	75.5	Female	TP	31 July 2013	394.07	743
11724	101	Female	TP	31 July 2013	424.92	2346
26569	100	Female	TP	5 December 2013	298.37	9692
27628	75	Female	TP	5 December 2013	298.66	3644
27630	84	Male	TP	5 December 2013	120.68	960
27641	78	Female	TP	10 August 2013	171.68	1368
27642	76.5	Female	TP	9 August 2013	416.09	11517
27643	79	Female	TP	9 August 2013	412.93	3536
27644	75	Male	TP	9 August 2003	261.42	4806
27647	79	Female	TP	2 August 2013	421.68	2483
27649	77	Male	TP	30 July 2013	176.83	1181
27652	69.5	Female	TP	30 July 2013	421.12	517
27653	75	Male	TP	30 July 2013	373.06	1861
27655	80	Male	H	29 July 2013	267.89	2535
27659	83	Female	TP	5 December 2013	296.26	965
27974	102	Female	TP	7 December 2013	286.33	2756
27979	83	Male	TP	8 December 2013	295.92	9637
27992	101	Female	TP	1 August 2013	295.23	4485
27993	110	Female	TP	5 December 2013	299.45	4538
28345	131	Female	H	9 December 2013	295.06	9418
28348	72	Female	TP	31 July 2013	423.04	9229
28349	139	Male	TP	31 July 2013	425.9	16936
28351	125	Male	TP	4 August 2013	421.28	5426
28353	99	Male	TP	31 July 2013	423.57	9823
29182	86	Male	H	28 November 2012	300.24	4655
29184	117	Male	H	28 November 2012	416.7	1011
29185	114	Female	H	28 November 2012	335.89	4224
29187	63	Male	TP	30 November 2012	139.51	1825
29188	78	Male	TP	30 November 2012	232.6	3284
29189	108	Female	TP	30 November 2012	117.82	1116
29191	106	Male	TP	30 November 2012	669.21	7195
29192	92	Female	TP	30 November 2012	344.24	3960
29193	63	Male	TP	1 January 2013	126.33	610
29774	96	Female	TP	2 August 2013	407.2	2357
29804	89	Female	TP	31 July 2013	403.21	238

Environmental drivers of space use

Between September (mid dry season) through early January (early wet season) in both study years, all tagged *G. glyphis* occupied an upper estuary zone within the Wenlock River system between 35 and 68 km upstream (Fig. 2). During this period, sharks exhibited a high degree of fidelity to their capture area, with individuals remaining within Tentpole Creek (n = 19 sharks), within Hudson Creek (n = 5 sharks), or moving between the 2 creek systems (n = 16 sharks). This period coincided with the lowest freshwater discharge rates at the tidal gauging station (min. = 1.0 Ml d^{-1}; Fig. 3A) and the highest salinity levels recorded in the upper estuary zone (CTD-Diver at 48 km AMTD 0: max. = 18.06 psu; Fig. 3B). Selection of salinities during December differed significantly from random (GLM with permutation test: quadratic estimate = −0.40, p < 0.0001; linear estimate = 11.24, p = 0.004), with sharks occurring at hydrophone moorings with attached environmental loggers when mean (±SD) salinities were approximately 13.83 ± 0.88 psu (Fig. 3C,D & Fig. S1 in the Supplement at www.int-res.com/articles/suppl/m573p203_supp.pdf).

All tagged sharks undertook a large-scale movement downstream from the upper estuary to the lower estuary (0 to 23 km) during January and February. Juveniles also moved into Port Musgrave (n = 27 sharks) and at least 25 km up the Ducie River (n = 6). Downstream movements occurred at the onset of sustained in-

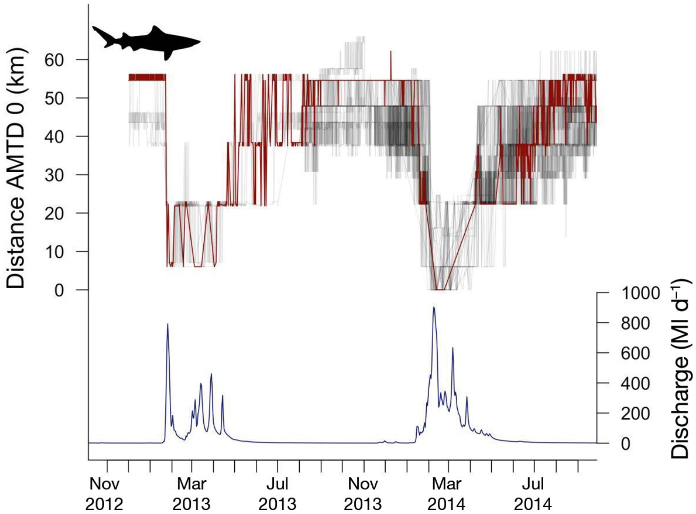

Fig. 2. Movements of 40 tagged *Glyphis glyphis* over a 22 mo period with respect to increases in freshwater discharge. Shark locations are quantified as the adopted middle thread distance in km between Port Musgrave (AMTD 0) and fixed hydrophone stations. Each grey line represents an individual shark and line transparency is used to visualise general patterns. Shark ID 29191 is highlighted in red. Water discharge (in Ml d^{-1}) was obtained from a tidal gauge located at Moreton telegraph station

creases in freshwater inflow (Figs. 2 & 3A) and a corresponding drop in salinity, particularly in upstream areas (Fig. 3B,C). During January, salinities selected by tagged sharks differed significantly from random (GLM with permutation test; quadratic estimate = –0.03, $p < 0.0001$; linear estimate = 0.69, $p = 0.0001$), with sharks present at hydrophone moorings with environmental loggers in mean (±SD) salinities of 10.24 ± 4.40 psu (Figs. 3D & S1). Tagged sharks remained in the lower estuary/coastal embayment habitat for the remainder of the wet season (late January to late March) where salinity at AMTD 0 varied between 0.18 psu (min.) and 11.55 psu (max.; Fig. 3B,C). During this time, sharks were present at AMTD 0 when mean (±SD) salinity was 2.74 ± 2.05 psu in February and 0.82 ± 0.62 psu in March (Fig. 3B). However, the low frequency of detection during this period suggests that sharks may have spent more time in areas not covered by our acoustic array. Salinities when tagged sharks were present did not differ significantly from random (February: GLM with permutation test: quadratic estimate = –0.19, $p = 1$; linear estimate = 1.55, $p = 0.291$; March: GLM with permutation test: quadratic estimate = –2.22, $p = 1$; linear estimate = 5.63, $p = 0.45$).

Between April and September, sharks moved upstream to occupy an estuarine zone between approximately 20 and 50 km within the Wenlock River, and the lower reaches of Tentpole Creek and Hudson Creek (Fig. 2). In total, 60% of tagged sharks returned to the area of river they resided in the previous year, and 4 of the 6 sharks that had moved into the Ducie River during the wet season returned to the Wenlock River.

Ontogenetic changes in space use

Of the 65 *G. glyphis* captured, 24 sharks (37%) had fresh umbilical scars indicative of a neonate life history stage. These individuals were caught only during November and December, and were found in the Wenlock River and Tentpole and Hudson Creeks between 40 and 58 km upstream from Port Musgrave (Fig. 1).

The cumulative distance tagged sharks moved between acoustic hydrophones varied significantly between survey months and according to shark body length (Table 2). The interaction between these terms was also significant (LMM: $F = 2.075$, $p = 0.022$). Juveniles >100 cm TL moved greater distances than smaller sharks, with distance moved estimates being lowest during February and March (Fig. 4A). Sex was not a significant predictor of minimum distances moved (Table 2). The total extent of river occupied within the Port Musgrave catchment by all sharks (including the main trunk of the Wenlock and Ducie Rivers and Tentpole and Hudson Creeks) was 137 km. As with distance travelled, the extent of river occupied by individual *G. glyphis* varied considerably between survey months (LMM: $F = 11.51$, $p < 0.0001$; Table 3). This varied between a mean (±SE) of 28.34 ± 1.88 km in January and 7.47 ± 1.43 km in October (Fig. 4B). Sharks occupied the greatest extent of river when a flood event stimulated a downstream migration (i.e. January) and when sharks were ranging between upstream and downstream sections (i.e. May). There was no significant effect of shark gender or size on the extent of river habitat occupied (Table 3).

DISCUSSION

Our study builds on previous understanding on the distribution of *Glyphis glyphis* within Australia and reinforces the Wenlock River as an import nursery site for the species. Juvenile *G. glyphis* were shown to be highly mobile and exhibited a strong seasonal migration between upper estuary and coastal embayment. Larger juveniles (>100 cm TL) moved greater distances than smaller juvenile sharks (≤100 cm TL). These movement patterns indicate a high degree of

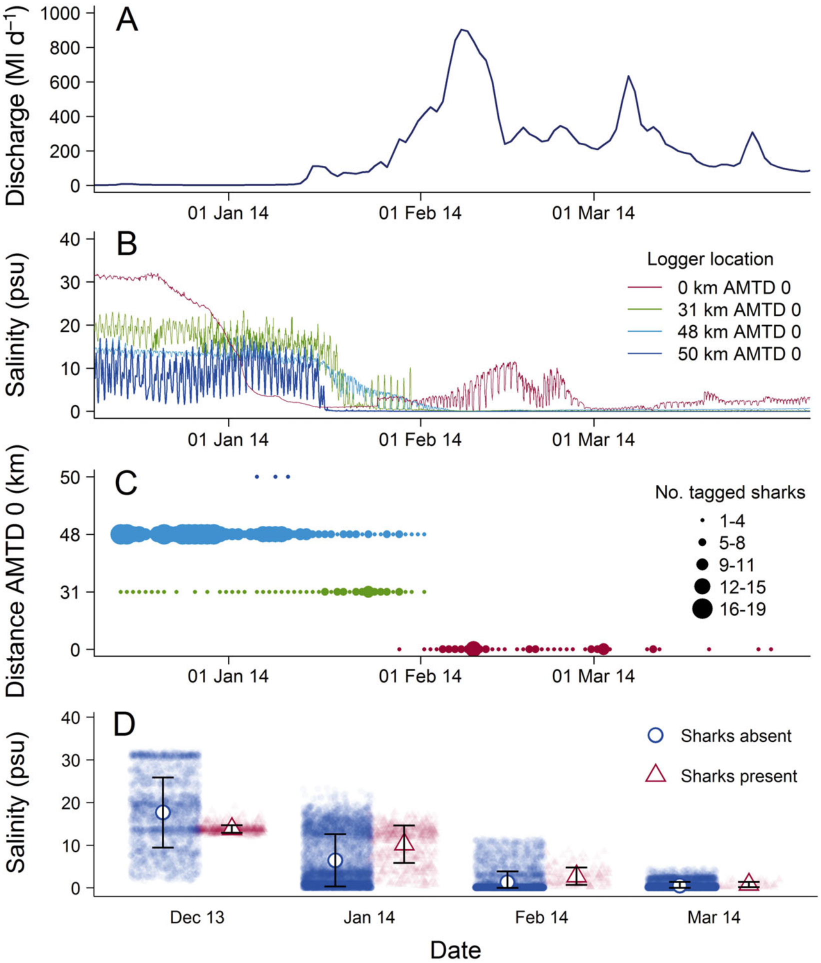

Fig. 3. Temporal variation in (A) instantaneous freshwater discharge, (B) environmental salinity (in per thousand parts of solution), and (C) daily detections of tagged *Glyphis glyphis* at hydrophone moorings fitted with environmental loggers. Distances are given as the adopted middle thread distance (AMTD) in km to the river mouth (AMTD 0). (D) Environmental salinity when sharks were absent or present within the detection fields of hydrophones at moorings fitted with environmental loggers; the mean and SD values are provided for each calender month (discrete), along with the raw data, which are scattered randomly on the *x*-axis to assist with data interpretation

connectivity between estuarine and inshore coastal habitats, promoting the transfer of energy between the 2 contrasting habitats and the potential for conflict between *G. glyphis* and local anthropogenic threats.

Effective species management relies on accurate knowledge of a species' distribution and the usage of habitats through time (Martin 2005, Simpfendorfer et al. 2010). Previous work on the distribution and habitat utilisation of *G. glyphis* relied on animal presence data only (Peverell et al. 2006, Pillans et al. 2009, Field et al. 2013, White et al. 2015) or short-term movement data restricted to 6 animals (Pillans et al. 2008, 2009). Our study, encompassing 40 individuals tracked over a 2 yr period, showed that *G. glyphis* utilised a maximum combined linear extent of at least 137 km of connected freshwater, estuarine and coastal habitat. This includes the Wenlock River (0 to 68 km upstream), the inshore coastal section of Port Musgrave, the Ducie River (0 to 23 km upstream) and Tentpole and Hudson Creek. We also showed that occupancy of these areas varied according to time of year, with presence coinciding with seasonal changes in freshwater inflow and salinity. Sharks exhibited a high degree of site fidelity to the upper estuarine reaches of the Wenlock River during the mid to late dry season period. Occupancy of the lower Wenlock, lower Ducie and Port Musgrave occurred during the core part of the wet season only (January to April), with no tagged *G. glyphis* detected in these areas for the rest of the year. This establishes the coastal embayment's role as critical wet season habitat for *G. glyphis*, while also highlighting the importance of Tentpole and Hudson Creeks as important dry season habitat. Temporal partitioning of habitat has been shown previously in other euryhaline elasmobranches (Heupel & Simpfendorfer 2008, Whitty et al. 2009, Yates et al. 2015). This ability of biotelemetry to obtain long-term and relatively unbiased location information highlights its capacity to identify threats and inform the spatial and temporal scale of management actions for mobile aquatic species.

Table 2. Linear mixed effects model of the response of the cumulative distance speartooth sharks *Glyphis glyphis* moved between hydrophones to month, body size (≤100 or >100 cm TL), sex and the 2-way interaction between these terms. AICc: corrected Akaike's information criterion. Significant effects shown in **bold**

Response	df	*F*	p	AICc	ΔAICc
Intercept	1	407.424	<0.0001	2636	
Month	**11**	**12.948**	**<0.0001**	**2732**	**+96**
Sex	1	0.027	0.871	2639	−3
Body size	**1**	**6.020**	**0.019**	**2640**	**+4**
Month:sex	11	1.225	0.269	2651	−15
Month:body size	**11**	**2.075**	**0.022**	**2636**	**0**
Sex:body size	1	0.831	0.368	2640	−4

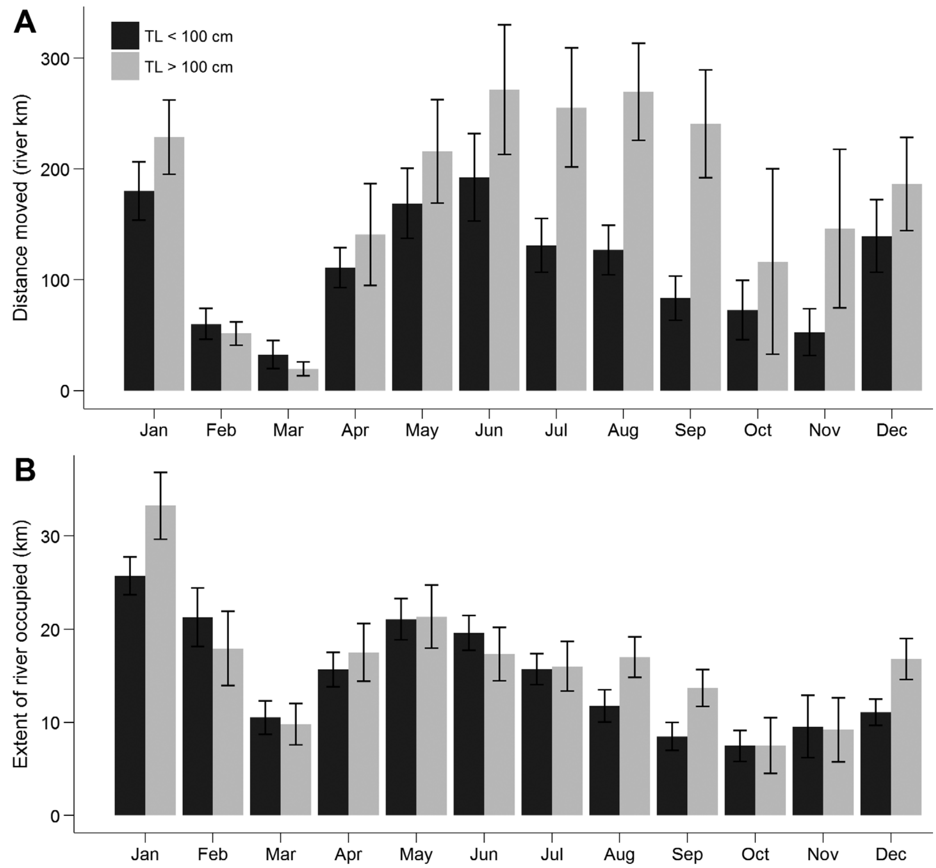

Fig. 4. Variation in (A) monthly distances travelled and (B) the extent of river occupied by *Glyphis glyphis* according to total body length (TL). Measurements are the adopted middle thread distance (AMTD) along the river in km; bars: means ± SE

Table 3. Linear mixed effects model of the response of extent of river occupied by speartooth sharks *Glyphis glyphis* to month, body size (≤100 or >100 cm TL), sex and the 2-way interaction between these terms. AICc: corrected Akaike's information criterion. Significant effects shown in **bold**

Response	df	*F*	p	AICc	ΔAIC_c
Intercept	1	1106.412	<0.0001	1527	
Month	**11**	**11.518**	**<0.0001**	**1615**	**+88**
Sex	1	0.869	0.358	1528	−1
Body size	1	1.672	0.204	1527	0
Month:sex	11	1.509	0.127	1535	−8
Month:body size	11	1.336	0.203	1537	−10
Sex:body size	1	1.307	0.261	1530	−3

G. glyphis has been identified previously as a euryhaline species, with juvenile sharks recorded in tidal, turbid estuarine habitats of low to moderate salinity with strong current flow (Peverell et al. 2006, Pillans et al. 2008). In this study, juvenile *G. glyphis* displayed a preference for habitats with salinities below 18 psu, while occupying upper estuarine reaches. However, tagged sharks appeared to tolerate more saline water (~23 psu) when migrating from upstream to coastal areas during the wet season. Prey access, predator avoidance, energetic costs of osmoregulation and mechanical challenges with buoyancy control have all been suggested as potential limitations for occurrence of euryhaline sharks (Pillans & Franklin 2004, Froeschke et al. 2010, Gleiss et al. 2015). The observation that sharks moved in response to changes in freshwater inflow and salinity supports the hypothesis that sharks are using behaviour to reduce metabolic demands, such as those affecting osmoregulation (Froeschke et al. 2010), or to avoid excessive negative buoyancy impacting swimming energetics (Gleiss et al. 2015). An observation during this and other studies (Field et al. 2013) was that juvenile *Carcharhinus leucas* were rarely captured in areas where juvenile *G. glyphis* were present. It has been previously established that juvenile bull sharks in other Australian rivers have a preference for freshwater in their early life history (Pillans & Franklin 2004, Pillans 2006). Further long-term, multi-species tracking studies could reveal the extent of this habitat partitioning and confirm whether salinity tolerances indeed limit shark distribution patterns in Northern Australian rivers.

The capture of sharks with open umbilical scars between November and December indicates that parturition may occur between September and November, most likely taking place within Port Musgrave and/or the river mouths. Furthermore, the capture of *G. glyphis* <80 cm TL, and their continued presence, confirms the Wenlock River as a nursery river for the species. This was assessed following the criteria outlined by (Heupel et al. 2007), where (1) juveniles were not found outside the study area, (2) juveniles remained in these areas for extended periods and (3) areas were used repeatedly across years by individual sharks. The absence of large sharks (i.e. TL > 140 cm) during our sampling also suggests that *G. glyphis* move into marine habitats prior to maturity. The protection of areas required by all life stages (including neonate, juvenile and adult sharks) is essential in facilitating conservation efforts (Knip et al. 2010). Further studies are needed to establish the migration routes, habitat preferences and breeding grounds of mature *G. glyphis* that inhabit the region.

For the size range of sharks tagged as part of this study (63 to 139 cm TL), animals used similar extents of river regardless of body size and gender. However, larger juvenile sharks covered greater linear distances and remained active in the lower estuary for longer than smaller sharks. Ontogenetic shifts in resource use and activity has been documented previously in other euryhaline elasmobranchs (Simpfendorfer et al. 2010). Here, smaller individuals were found to occupy the smallest home ranges with the lowest degree of movement within these areas. It may be that larger tagged sharks were moving and hunting more widely as part of a development phase prior to leaving the river. While it was not possible to test this in the current study, continued monitoring of these individuals with long-lived (>5 yr) tags would facilitate future investigation dispersal and survival in this little known shark.

Our findings that *G. glyphis* exhibit specific habitat requirements, high site fidelity and seasonal migratory movements have direct implications for species conservation. As all age-classes of this population inhabit one specific nearshore area (i.e. Port Musgrave), a direct impact such as habitat modification of this inshore habitat (e.g. dredging) may have major negative impacts on the species' persistence (Knip et al. 2010). Furthermore, indirect impacts in freshwater areas such as the installation of dams, large-scale water extraction or interference with permanent spring systems may have unforeseen impacts on river flow, turbidity and salinity characteristics that are important for *G. glyphis* and the ecological integrity of the river as a whole (Leblanc et al. 2015). The readiness for *G. glyphis* to take baited lines and the incidental capture of *G. glyphis* in crab pots and gillnets also supports existing concerns that mortality via bycatch is major threat to *G. glyphis* populations (Peverell et al. 2006, Field et al. 2013, Commonwealth of Australia 2015). Commercial barramundi *Lates calcarifer* and mud crab *Scylla serrata* fisheries currently operate within the Port Musgrave catchment under the Queensland Fisheries Act. Following the opening of the barramundi fishery (01 February), commercial fishers using gill nets in the Wenlock River typically target inshore coastal areas to avoid strong river flows and flood debris before directing their efforts further upstream as river flow decreases (J. Lyon pers. comm.). Commercial mud crab fisheries also operate throughout the extent occupied by tagged *G. glyphis*. We have demonstrated that these fisheries overlap with migrating *G. glyphis*, making the species highly susceptible to indirect capture. To reduce negative impacts, an education and awareness program identifying *G. glyphis*, its conservation status and correct handling procedures should be introduced. We encourage research into improved crab pot design and placement designed to minimise the potential for *G. glyphis* bycatch. Finally, seasonal habitat partitioning demonstrated by *G. glyphis* indicates the potential for spatio-temporal closure scenarios designed to reduce shark bycatch while limiting impacts on local fishers (Grantham et al. 2008).

This study provides the first insights into the long-term movement behaviour and habitat utilisation of a critically endangered river shark. Our results suggest that juvenile *G. glyphis* exhibit specific habitat requirements and predicable movement behaviours driven by seasonal changes in freshwater inflow. The knowledge gained provides the first steps in informing the development and implementation of conservation plans aimed at managing anthropogenic impacts on *G. glyphis* populations and habitats.

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