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Contribution to the Theme Section 'Biologging technologies: new tools for conservation'

Observations on the distribution, biology, short-term movements and habitat requirements of river sharks *Glyphis* spp. in northern Australia

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ABSTRACT: The genus *Glyphis* comprises a group of rare and poorly known species. *G. glyphis* and *G. garricki* are found in northern Australia, and both species are listed as Critically Endangered C2a(i) on the International Union for Conservation of Nature (IUCN) Red List of Threatened Species. We collated all available records of *G. glyphis* and *G. garricki* in Australia to gain an understanding of the species' distribution and biology. All records of *G. glyphis* (n = 106) were confined to 9 tropical rivers and estuaries north of 15° S. *G. garricki* (n = 32) were captured in 4 rivers and estuaries as well as in marine environments north of 18° S. Both species can be classified as euryhaline elasmobranchs. Parturition is thought to occur in October to December, and size at birth for both species is around 50 to 65 cm total length (TL). Two male *G. garricki* were mature at 142 and 144 cm TL, 2 females of 177 and 251 cm TL were mature, with the smaller animal having 9 early-stage embryos *in utero*. No mature *G. glyphis* have been recorded to date. Short-term movement patterns of 3 *G. glyphis* were investigated in the Adelaide River (Northern Territory) using acoustic tags. Animals were tracked for 27.8, 27.0 and 50.2 h respectively and displayed up- and downstream tidally assisted movement, moving on average 10 to 12 km per tide. The limited distribution, specific habitat requirements and repeated use of available habitat make *Glyphis* species particularly vulnerable to localised overfishing and habitat degradation. These findings highlight the need for additional research and the implementation of national recovery plans for both species.

KEY WORDS: *Glyphis* spp. · Australia · Euryhaline · Elasmobranch · Acoustic telemetry

INTRODUCTION

The river sharks (genus *Glyphis*) comprise poorly known, cryptic sharks of the family Carcharhinidae with patchy Indo-West Pacific distributions in tropical riverine and coastal habitats (Compagno 1984, Last & Stevens 2009). *Glyphis* appears to comprise 5 species (Compagno et al. 2005, 2008). The Ganges shark *G. gangeticus* (Müller & Henle, 1839) is definitely known from the Ganges-Hooghly river system in India and possibly Pakistan. The Irrawady River shark *G. siamensis* (Steindachner, 1896) is known from a single specimen from the Irawaddy River mouth, Burma (Compagno et al. 2005). The speartooth shark *G. glyphis* (Müller & Henle, 1839) was described from a single specimen, but without locality, and has recently been shown to be synonymous with the Bizant River shark (formally *Glyphis* sp. A sensu Compagno et al. 2005). *G. glyphis* is known from Queensland (Qld) and the Northern Territory (NT) in northern Australia and also from Papua New Guinea (Compagno et al. 2008). The Borneo River shark *Glyphis* sp. B (sensu Compagno et al. 2005) is recorded from the Kinabatangan River in Sabah, Malaysian Borneo (Compagno 1984, Manjaji 2002). The northern river shark *G. garricki* Compagno, White & Last 2008, formerly *Glyphis* sp. C (sensu Compagno et al. 2005), has been recorded in Papua New Guinea (Compagno et al. 2005) and north-

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ern Australia, where it is found in NT and Western Australia (WA) (Taniuchi et al. 1991, Thorburn & Morgan 2004, Last & Stevens 2009).

Glyphis glyphis was first recorded in Australia in 1982 when 2 small (70 to 75 cm total length [TL]) specimens were captured 17 km upstream in the Bizant River, Qld (Last 2002). One of these specimens was subsequently used in the description of *G. glyphis* (see Compagno et al. 2008). From 1983 to 2002, only 21 specimens of *Glyphis* spp. were recorded from Australia, with all records coming from NT. These included the first record of *G. garricki* from the Adelaide River, NT in 1989 (Taniuchi et al. 1991). A survey of elasmobranchs in rivers and estuaries in northern Australia in 2002, which sampled 147 sites in 39 rivers and creeks, did not record any species of *Glyphis* (Thorburn et al. 2003). Since 2002, a further 104 specimens of *Glyphis* spp. have been recorded from northern Australia, including the first record of *G. garricki* in WA (Thorburn & Morgan 2004) as well as records of *G. glyphis* in the eastern Gulf of Carpentaria, Qld (Peverell et al. 2006).

Almost all aspects of the life-history and habitat requirements of *Glyphis* spp. in Australia and worldwide are unknown. In Australia, the lack of data combined with river sharks' limited distribution and rarity is reflected in their conservation status. *G. glyphis* is listed as Critically Endangered (CR) by both the International Union for Conservation of Nature (IUCN; Cavanagh et al. 2003) and the Australian Commonwealth Environmental Protection and Biodiversity Conservation Act 1999 (EPBC Act) while *G. garricki* is listed as CR by the IUCN and Endangered by the EPBC Act. Data are urgently required to facilitate the development of a recovery plan for *G. glyphis* and *G. garricki.*

Given the lack of data on the distribution, biology and habitat requirements of *Glyphis* spp. in Australia, the present study aims to (1) summarise all available records of *Glyphis* spp. from Australia and provide data on their distribution, habitat type and salinity tolerance, (2) provide data on the biology of *Glyphis* spp., (3) gain an understanding of short-term movement patterns of *G. glyphis* in the Adelaide River using acoustic telemetry, and (4) summarise these data with respect to the conservation and management of *Glyphis* spp. in Australia.

MATERIALS AND METHODS

Distribution and biology. Validated *Glyphis* spp. records with accompanying location data were collated and mapped using GIS. Data on habitat type, salinity and turbidity, and size, sex, maturity and reproductive status of animals were also collected. Information sources included published data from scientific surveys (Taniuchi et al. 1991, Taniuchi & Shimizu 1991, Larson 2002, Last 2002, Thorburn & Morgan 2004, Peverell et al. 2006), unpublished data from unrelated research (H. Larson, Museum and Art Gallery of the Northern Territory, pers. comm.; T. Berra, Ohio State University, pers. comm.), verified records from the public, and unpublished data from CSIRO Marine and Atmospheric Research.

Acoustic tracking of *Glyphis glyphis*. *Study site:* Sampling for *Glyphis* spp. was carried out from 9 to 20 December 2004 in Marrakai Creek, about 96 km upstream from the mouth of the Adelaide River. The Adelaide River is a highly flushed, turbid, tidal river located east of Darwin (mouth = 12° 13′ 18.0″ S, 131° 13′ 6.6″ E). Salinity and flow varies seasonally, with >95% of flow occurring in the wet season (December to April). During the present study, the wet season had not yet commenced and the current was driven by large tides of 3.5 to 7.5 m (resulting in periods of slack tide of <10 min). The banks were dominated by mangroves and the bottom substratum was fine mud throughout. Turbidity was extremely high (Secchi disc reading: 4 to 40 cm; T. Berra pers. comm.).

Capture and tagging: The majority of specimens were captured using either a 60 m monofilament gill net with a 4 m drop and a stretched mesh of 15.2 cm, or a 30 m net with a 2 m drop and a stretched mesh of 10.2 cm. The net was set during the day and checked every 10 minutes, or when fish were seen to hit the net. Gill nets were mostly set across the creek except when the tidal flow was too great; at these times the net was set parallel to the banks or fishing was carried out with rod and line. Captured *Glyphis* were identified to species, measured (TL), sexed, sampled for genetic analysis (fin clip) and released if they were not tracked. For those animals to be tracked, acoustic tags were attached with dissolving sutures, one end through the leading edge of the first dorsal fin and the other through the dorsal musculature.

Telemetry: Sharks were tracked using acoustic telemetry equipment comprising a Vemco VR-60 receiver, a V-10 hydrophone and either Vemco V22TP-01, V16P-5HR transmitters with a depth sensor, or a Sonotronics CHP-87S transmitter with no depth sensor. Tracking was carried out from a 4 m aluminium boat. The hydrophone was mounted on a pole and rotated manually to maximise signal strength. The tags had a range of ~1.0 km and a battery life of ~14 d. Depth from the tag, together with position from a Garmin GPS 12, was assumed to be the position of the shark and was recorded every 15 to 30 min. Tracking was continuous apart from periods when it was necessary to change personnel or seek shelter from thunderstorm activity. After these periods the shark was re-located by systematically searching the area of last contact. When these periods exceeded 30 min, these data were not used to calculate rate of movement (ROM). Bottom depth was recorded using a lead line (marked off in 1 m intervals). Temperature and salinity were measured on the surface and on the bottom using a WTW LF340 salinity/conductivity meter throughout the track at the position of the shark. There was no noticeable difference in surface and bottom salinity or temperature and all data presented are from the surface readings.

Data analysis: Recorded positions were plotted using ArcView GIS. Distance between successive positions was calculated following the contours of the river, using the 'measure distance' tool in ArcView GIS. Rate of movement was calculated by dividing the distance between points (m) by the sampling interval (s) to give ROM in m s^{-1}. Data from the first ebb tide (5 to 7 h) was not used in calculations of ROM due to increased activity during this period, presumably due to capture and handling stress. Due to the highly directional (either upstream or downstream) movement of sharks in the present study, we assumed that point-to-point measures accurately reflected ROM. Day and night ROM were based on local times of sunrise and sunset. Movement over a tidal cycle refers to 1 run of the tide, i.e. the time from low tide to high tide or vice versa. The average time between low and high tide from this region during the month of December 2004 was used to calculate the length of tidal cycle.

To determine the influence of time of day and tide on movement, pooled ROMs were compared using a Mann-Whitney *U*-test which was also used to test for differences in ROM between successive tidal cycles. Depth profiles were only obtained from 1 shark due to malfunction of the other depth tags. Depth of the shark and water depth were recorded at the same time as position. A Mann-Whitney *U*-test was used to test for differences in shark depth in relation to bottom depth between time of day and tide. Significance levels were set at $p < 0.05$.

RESULTS

Distribution and biology

Glyphis glyphis

Over 7 d between 9 and 20 December 2004, 28 *Glyphis glyphis* between 50 and 165 cm TL were caught in the Adelaide River. A total of 106 *G. glyphis* have now been recorded from freshwater and estuarine reaches of 9 rivers and estuaries in NT and Qld (Fig. 1). An additional 18 sharks identified as *Glyphis* spp. were reported in the Normanby, Bizant, Hey and Embley Rivers, Qld by Peverell et al. (2006) from historical records compiled between 1979 and 1985. We

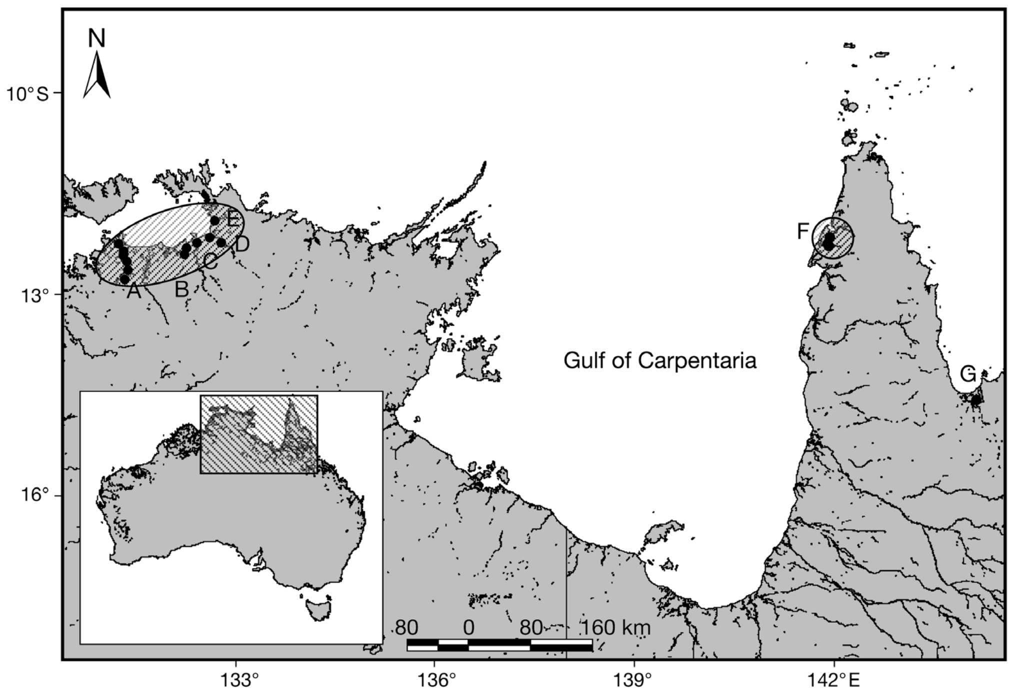

Fig. 1. *Glyphis glyphis*. Map showing all documented records in Australia (n = 106). Hatched areas represent the likely range; circles (●) are capture locations. A = Adelaide River (n = 84), B = West Alligator River (n = 3), C = South Alligator River (n=1), D = East Alligator River (n = 4), E = Murganella Creek (n = 1), F = Wenlock River, Ducie River and Port Musgrave (n = 11), G = Bizant River (n = 2 prior to 1983, no records since)

have not included these 18 animals due to the lack of taxonomic resolution and the fact that *Glyphis* spp. have not been recorded from any of these river systems since 1985.

Glyphis glyphis have not been recorded from marine environments outside river mouths. In NT, 93 *G. glyphis* were recorded from the tidal reaches (salinity 3.0 to 25.8) of the Adelaide River, South, East and West Alligator Rivers and Murganella Creek. The majority of these animals (n = 84) were recorded from the Adelaide River. The length-frequency of 75 animals captured in the Adelaide River, including those captured in December 2004, is shown in Fig. 2. Animals captured 0 to 20 km from the mouth of the Adelaide River (mean ± 1 SD = 117.4 ± 37.0 cm TL, n = 19) were significantly larger ($p < 0.0001$, Student's 2-tailed *t*-test) than animals captured 80 to 100 km upstream (mean ± 1 SD = 70.9 ± 26.1 cm TL, n = 36). In Qld, 13 *G. glyphis* were recorded from the tidal reaches (salinity 0.8 to 28.0) of the Wenlock and Ducie Rivers and Port Musgrave (the estuarine system of these 2 rivers) as well as the Bizant River. All *G. glyphis* were captured in highly turbid (Secchi disc reading: 5 to 40 cm), tidally influenced rivers and estuaries with fine muddy substrate and temperatures of 25 to 33°C (Larson 2002, Peverell et al. 2006, R. D. Pillans unpubl. data).

The smallest free-swimming *Glyphis glyphis* was 50 cm TL, and along with several others between 58 and 65 cm TL, it had open umbilical scars, suggesting that size at birth is 50 to 65 cm TL. Animals with open umbilical scars were recorded from October to December, suggesting parturition occurs around this time. The largest recorded *G. glyphis* was a 175 cm TL female. This animal was released and the reproductive status was not assessed. Based on the condition of their reproductive organs, all females <120 cm TL were immature; however, no larger females were examined. The largest males examined were between 147 and 157 cm TL and, based on non-calcified claspers, were not classified as sexually mature.

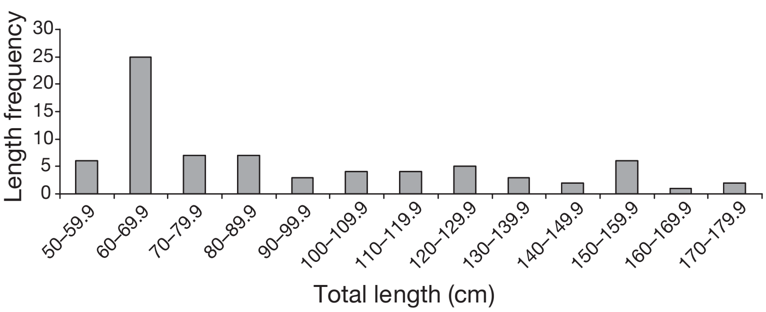

Fig. 2. *Glyphis glyphis*. Length frequency of individuals captured between 5 and 100 km upstream of the mouth of the Adelaide River between 1991 and 2005

Glyphis garricki

Thirty-two *Glyphis garricki* have been recorded from marine, estuarine and freshwater habitats in WA and NT (Fig. 3). Neonates, juveniles and sub-adults (<135 cm TL) have been recorded in freshwater (Adelaide River, salinity 2) estuarine (Ord and King Rivers, South and East Alligator Rivers, salinity 7 to 21) and marine environments (King Sound, salinity 32 to 36). Sexually mature adults (>140 cm TL) have only been recorded in marine environments (King Sound, Joseph Bonaparte Gulf, WA; Wessell Islands, NT).

The smallest free-swimming *Glyphis garricki* was 58 cm TL, but this animal was not assessed for the presence of an umbilical scar. Maximum recorded size was 251 cm for females and 142 cm TL for males. A 177 cm TL female was sexually mature and contained 9 early-stage embryos in the uteri. A female of 251 cm TL captured in October had recently given birth, based on the presence of distended uteri and uterine scars. Based on the presence of fully calcified claspers 2 male sharks (both 142 cm TL) were classified as sexually mature; however, a 135 cm TL male did not have calcified claspers, and was thus immature.

Acoustic tracking of *Glyphis glyphis*

Three female *Glyphis glyphis* were tracked for periods between 27 and 50.2 h, displayed net downstream movements, an overall ROM of between 0.45 and 0.52 m s^{-1}, and encountered increases in environmental salinity of 12.0 to 14.3 (Table 1). All 3 sharks were tagged in Marrakai Creek, a tributary of Adelaide River, ~96 km from the mouth of the river. All sharks were tagged shortly after the tide began to ebb, and after tagging moved downstream in the main channel of the Adelaide River. The movement of all sharks was strongly correlated to tide, with sharks generally moving downstream and upstream with ebb and flood tides, respectively. The average distance ± SD travelled per tidal cycle for the 3 tracked sharks was 11.7 ± 0.9 km.

Shark 1 showed the least variation in ROM over successive ebb and flood tides; only during the first flood tide was ROM significantly lower ($p = 0.008$) than during all other tides (Fig. 4). There was no significant difference in ROM between day (0.55 ± 0.44 m s^{-1}) and night (0.35 ± 0.23 m s^{-1}) ($p = 0.18$). Sharks 2 and 3 displayed similar movement patterns, with mean ROM during the ebb tide being significantly faster than ROM during the flood tide ($p < 0.0001$). This difference was largely due to the ROM of both sharks during the first ebb

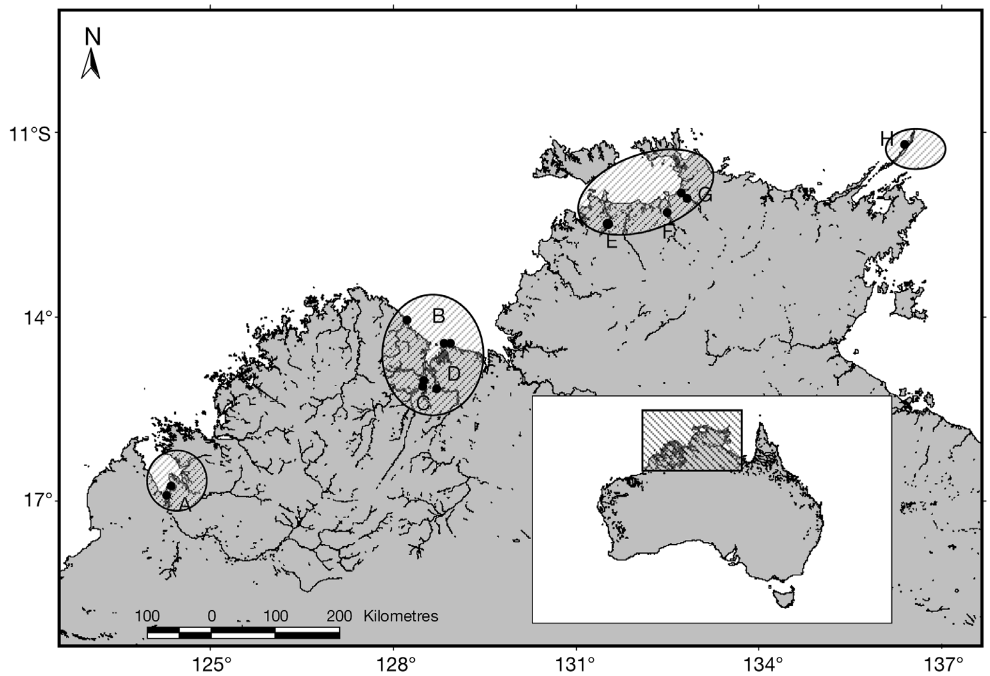

Fig. 3. *Glyphis garricki*. Map showing all documented records in Australia (n = 32). Hatched areas represent the likely range; circles (●) are capture locations. A = King Sound (n = 13), B = Joseph Bonaparte Gulf (n = 6), C = Ord River (n = 2), D = King River (n = 3), E = Adelaide River (n = 4), F = South Alligator River (n = 1), G = East Alligator River (n = 2), H = Wessel Islands (n = 1)

tide being significantly faster than during all other tides (Fig. 4). This was further compounded by ROM during the first flood tide being slower for both sharks than during all other tidal cycles (Fig. 4). There was no difference in ROM between day (0.46 ± 0.42 and 0.57 ± 0.26 m s^{-1}) and night (0.44 ± 0.47 and 0.50 ± 0.32 m s^{-1}) for both Sharks 2 and 3, respectively ($p > 0.5$).

The movement patterns of all 3 sharks were strongly influenced by the tidal cycles, with animals predominantly moving upstream with the flood tide and downstream with the ebb tide. There was a net downstream movement, with sharks being between 28.9 and 34.8 km downstream of the tagging position when tracking was terminated (Figs. 5 & 6). This downstream movement resulted in animals encountering a significant increase in environmental salinity over a 24 h period. After 24 h, Sharks 1, 2 and 3 had encountered a salinity increase of 12.0, 13.1 and 14.3, respectively (Fig. 5).

Table 1. *Glyphis glyphis*. Summary of 3 females tracked in the Adelaide River in December 2004. ROM = rate of movement; TL = total length

Track	Size (TL; cm)	Duration (h)	Distance travelled (km)	Mean ± SD ROM (m s^{-1})	Salinity range
1	66.5	27.8	53.1	0.52 ± 0.40	3.7–15.7
2	165.0	27.0	53.9	0.45 ± 0.43	3.9–17.0
3	158.5	50.2	84.1	0.51 ± 0.28	4.8–19.1

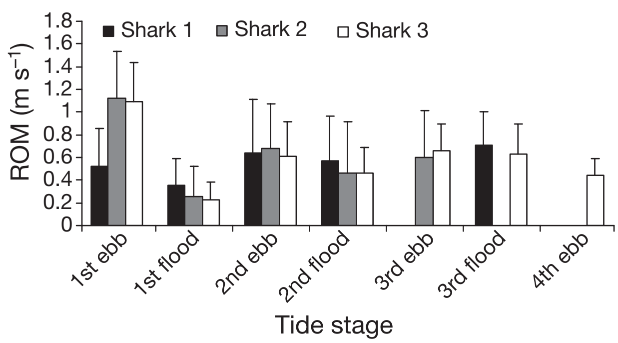

Fig. 4. *Glyphis glyphis*. Mean ± SD rate of movement (ROM) during ebb and flood tides throughout the track of 3 females in the Adelaide River

Shark 1 was tagged at 09:15 h, ~30 min after high tide, and tracked intermittently (due to adverse weather conditions) for a total track of 27.8 h over a 60.5 h period. The net movement during this time was 27.6 km downstream from the point of capture (Fig. 5a).

Shark 2 was tracked continuously for 27.0 h, after which the tag detached prematurely. Shark 2 was captured at 14:58 h, ~1 h after the tide began to ebb, and moved steadily downstream for 4.2 h, travelling a distance of 17.9 km. During the first

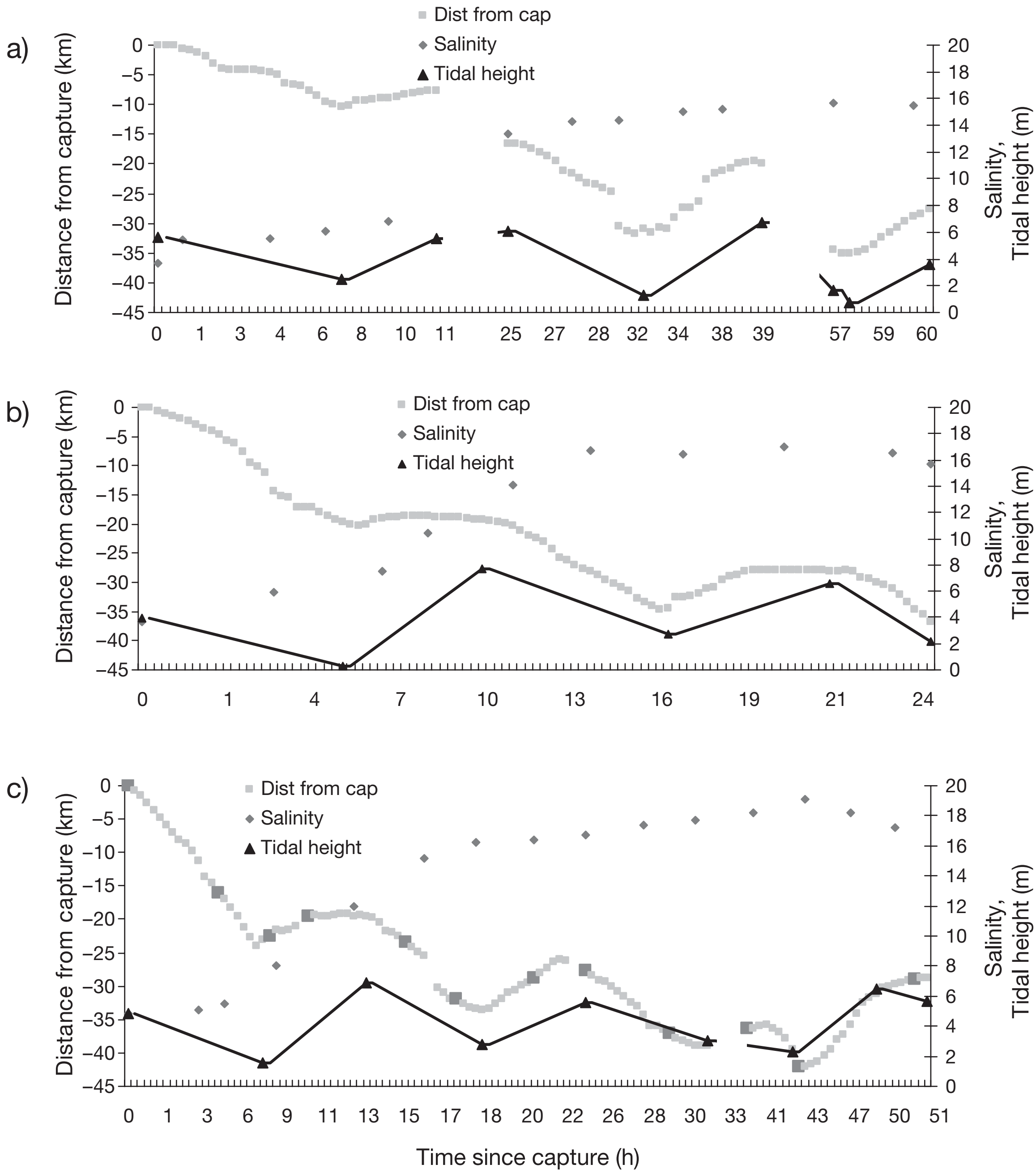

Fig. 5. *Glyphis glyphis*. Tracks of individuals, showing distance moved from site of capture (Dist from cap) over time including tidal height and salinity, for (a) Shark 1, (b) Shark 2, and (c) Shark 3. ■ = position of Shark 3 in Fig. 6

flood tide, the shark moved slowly upstream for 1.7 km over 3.2 h before spending the remainder of the flood tide in a small stretch of river around a bend (Fig. 5b). The shark repeated this pattern, moving 15.5 km downstream and only 6.5 km upstream in the next ebb and flood tide, respectively. During the flood tide, the shark spent 2.4 h near a larger eddy in a bend of the river and moved only 0.4 km further upstream during this time. The net movement during the track was 36.7 km downstream from the point of capture (Fig. 5b).

Shark 3 was tracked for 50.2 h before tracking was stopped (Figs. 5c & 6). Shark 3 was captured at 15:15 h, ~0.5 h after high tide, and moved 24.5 km downstream over 6.8 h during the ebb tide. Shark 3 also displayed greater downstream than upstream movements and spent long periods of the flood tide in eddies, moving as little as 4.1 km during a flood tide. However, during

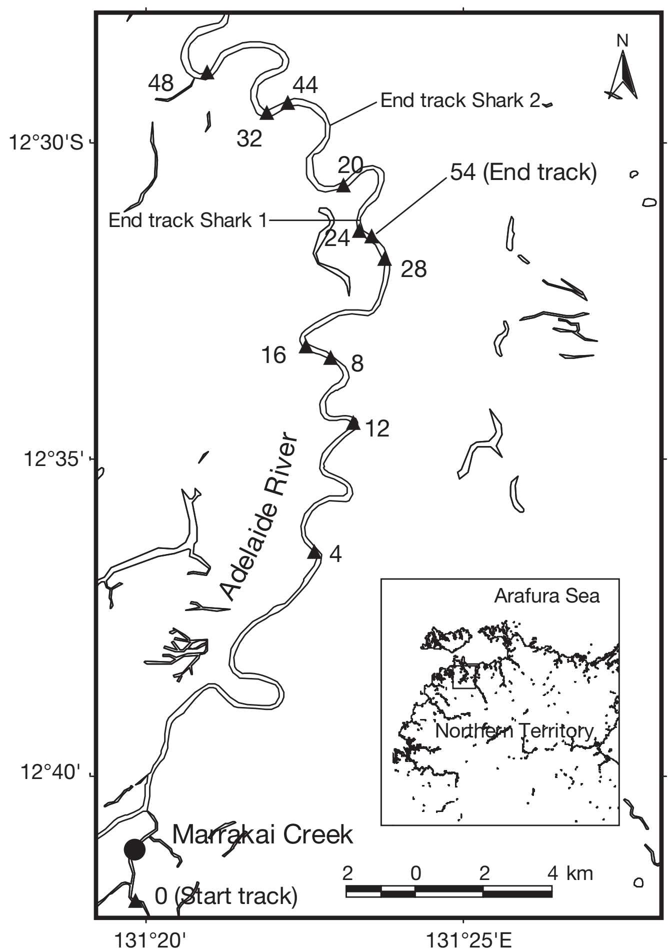

Fig. 6. *Glyphis glyphis*. Track of a 158.5 cm total length female (Shark 3) in the Adelaide River. ▲ = position every 4 h, with adjacent number representing the time (h) since the track began. ■ in Fig. 5 correspond to ▲ here to illustrate distance downstream from capture and time since capture. ● = starting point of Shark 1. Shark 2 was tagged in the same position as Shark 3. The position of Sharks 1 and 2 at the end of their tracks is also shown. All sharks were tagged in Marrakai Creek

the third flood tide, the shark moved 12 km upstream and despite the tide starting to ebb, continued to move upstream for 0.7 km until the track was terminated (Fig. 5c). At the end of the track, the shark was 29.8 km downstream from where it was tagged (Fig. 6).

Bottom depth and swimming depths (shark depth) of Shark 2 in relation to temporal cycles are shown in Fig. 7. There was no detectable pattern in shark depth and no difference in shark depth in relation to bottom depth between day and night or tidal cycle ($p > 0.4$). The only period when shark depth was relatively constant was the 5 h period after tagging. This period coincided with the fastest ROM during the first ebb tide and was attributed to post-capture stress and was thus omitted from the statistical analysis.

DISCUSSION

Distribution and biology

Investigation of records of *Glyphis* spp. in Australia revealed 106 *G. glyphis* and 32 *G. garricki* recorded between 1982 and 2006. Prior to 2002, only 21 specimens of *Glyphis* spp. were recorded in Australia, despite dedicated surveys for these species (Thorburn et al. 2003). The increase in records since 2002 represents increased awareness and better identification by commercial and recreational fishers and research organisations, which has led to surveys targeting this species (Thorburn & Morgan 2004, Peverell et al. 2006). The recent records in WA, NT and the Gulf of Carpentaria (Qld) suggest that there is no direct evidence of a decline in the extent of occurrence west of Cape York. No specimens of *Glyphis* spp. have been recorded on the east coast of Australia since 1983. Given the consistent commercial fishing effort that occurs in these river systems and the adjacent coastline, combined with research surveys and observer programs occurring in these systems, we would expect *G. glyphis* to have been recorded since 1983 if it still occurred in these rivers. The lack of specimens suggests that this species may have been extirpated on the east coast of Qld, representing a significant retraction in range. Despite their limited distribution, neonate and juvenile *G. glyphis* appear to be locally abundant within the Adelaide River in NT and the Wenlock and Ducie River system in Qld.

Glyphis glyphis have only been recorded in 9 highly turbid, tidal rivers and estuaries with fine muddy substrates in northern Australia. Animals have been recorded from inside river mouths to ~100 km upstream in salinities of 0.8 to 28.0 and temperatures of 27 to 33°C. No specimens have been recorded outside of rivers or estuaries. Unlike bull sharks *Carcharhinus leucas* (Valenciennes, Müller & Henle, 1839), which are often captured in freshwater billabongs or sections of river isolated from the main tidal stream (R. D. Pillans unpubl. data), *G. glyphis* and *G. garricki* have not been recorded in isolated water holes or billabongs. Presumably, the strong tidal currents combined with easily resuspended fine muddy or silty substrate cause the highly turbid waters in which these species occur.

There was some evidence that *Glyphis glyphis* display size segregation within rivers. The average size of *G. glyphis* captured 0 to 20 km from the mouth of the Adelaide River was significantly larger than that of animals captured 80 to 100 km upstream. This increase in size closer to the river mouth is similar to that displayed by bull sharks, which utilise rivers and estuaries as nursery areas (see Thorson et al. 1973, Simpfendorfer et al. 2005, Pillans 2006) and suggests

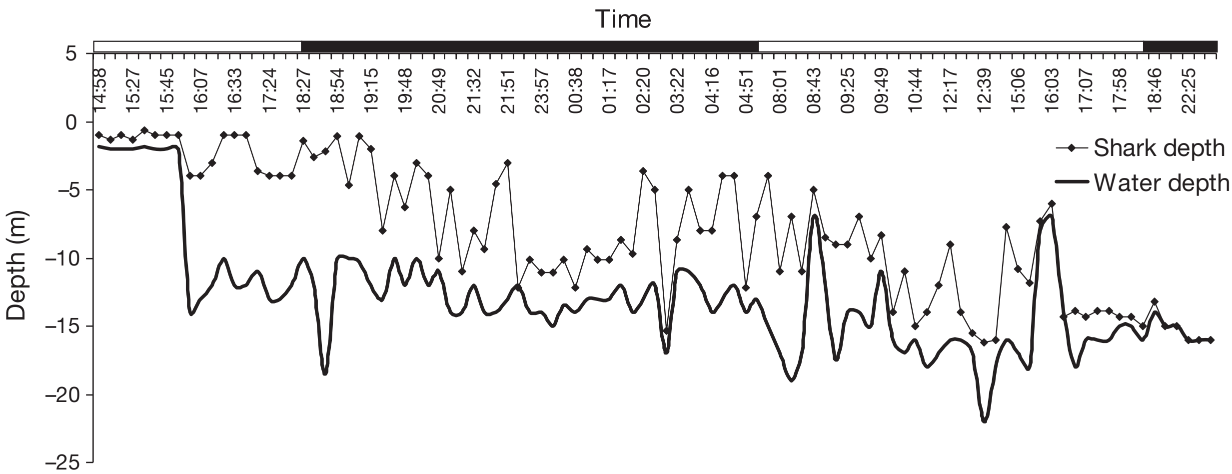

Fig. 7. *Glyphis glyphis*. Shark depth and bottom depth throughout the track of a 165 cm (TL) female (Shark 2) in the Adelaide River. Light and dark shading on the horizontal axis indicates day and night respectively. The last hour of the track shows bottom depth equal to shark depth indicating the time when the tag detached from the animal

that this species has a similar life history, with neonates and juveniles living in rivers and estuaries, and adults presumably living outside of rivers in a coastal marine environment. No sexually mature specimens of *G. glyphis* have been recorded and the distribution and habitat preferences of adults remain a critical gap in our knowledge of this species.

Glyphis garricki occur in a few large tropical river systems and macrotidal embayments, as well as coastal marine habitats in northern WA and NT. These habitats are defined by large tides (up to 11.8 m in King Sound), fine muddy or silty substrate and high turbidity. Neonates, juveniles and sub-adults were captured in freshwater, estuarine and marine environments (salinity 2 to 36), whereas sexually mature animals have only been recorded in marine environments. The overlap of all size classes in marine environments may indicate a reduced dependence on rivers and estuaries for neonates, juvenile sharks and sub-adult sharks; however, more data are required to determine the degree of ontogenetic shifts in habitat utilisation.

Worldwide, most records of *Glyphis* spp. have come from turbid, tidal rivers in the tropics, and the genus is thought to include both euryhaline and obligate freshwater species (Compagno 2002). Both *G. glyphis* and *G. garricki* were originally classified as obligate freshwater species by Last (2002); however, recent records of both species indicate that they should be classified as euryhaline.

Limited reproductive data and the presence of free-swimming neonates suggest that both *Glyphis glyphis* and *G. garricki* give birth around October, prior to the wet season (generally December to April). The lack of yolky ova in the ovaries of a shark that had recently given birth suggests that *G. garricki* may breed every second year as in other medium-to-large carcharhinid sharks such as sandbar shark *Carcharhinus plumbeus* (Nardo, 1827) (McAuley et al. 2007b), *C. leucas* (Jensen 1976, Cliff & Dudley 1991) and blacktip shark *C. limbatus* (Valenciennes, Müller & Henle, 1839) (Dudley & Cliff 1993). As in other carcharhinids, the reproductive mode is placental viviparity. Based on data from 1 individual, litter size in *G. garricki* was observed to be 9. *G. garricki* mature at a smaller size than *G. glyphis*, suggesting that *G. glyphis* attain a larger maximum size. Both species appear to have similar sizes at birth, maturity and maximum size as *C. plumbeus*, which is a species particularly vulnerable to overexploitation as a result of its low rate of population increase (McAuley et al. 2007a).

Short-term movements

Movement patterns of animals tracked in the Adelaide River showed that they were capable of moving up to 25 km in an ebb or flood tide and generally displayed a cyclic up- and downstream movement pattern. On average, sharks moved 11.7 km per tidal cycle, resulting in animals repeatedly utilising small sections of the available habitat.

All 3 tracked animals showed similar movement patterns, moving upstream with the flood tide and downstream with the ebb tide. All sharks showed a net downstream movement, which was largely due to all animals being tagged at the beginning of the ebb tide. This downstream movement was further enhanced by faster ROM in Sharks 2 and 3 during the first tidal cycle, which was attributed to post-capture stress. Post-capture stress has been shown to occur in other elasmobranchs, with animals diving to deeper water (Sciarrotta & Nelson 1977, Holts & Bedford 1993) or undertaking a rapid departure from the tagging site (Nelson 1990, Nelson et al. 1997). All sharks in the present study appeared to return to 'normal' behaviour following the first tide change, 4 to 6 h after tagging.

Sharks in the present study moved in the same direction as the strong tidal current and used this current to assist upstream and downstream movement. Movement against the tide or maintaining a position in the river occurred primarily during slack water or when the animals were in a large eddy near a bend in the river. Similar directional movements interspersed with periods of holding a position against the tidal flow were observed in the thin-lipped mullet *Liza ramado* Risso, 1810 (Almeida 1996) and allowed animals to preferentially move in one direction over successive tidal cycles. In the Adelaide River, maximum tidal velocity was measured with partially submerged objects and was between 0.6 and 0.8 m s^{-1} for at least 70% of a flood or ebb tide. Considering that average ROM for all 3 *Glyphis glyphis* was <0.52 m s^{-1}, animals were using the current to passively move up- and downstream, presumably to conserve energy while searching for food. Medved & Marshall (1983) observed a similar behaviour in juvenile *Carcharhinus plumbeus*, which drifted passively with the current except when feeding. Leopard sharks *Triakis semifasciata* Girard, 1854 also showed directional movement positively related to the tide (Ackerman et al. 2000).

Tidally assisted movements in rivers and estuaries have been demonstrated in several euryhaline teleosts such as *Liza ramado* (Almeida 1996), spotted grunter *Pomadasys commersonnii* Lacepède, 1801 (Childs et al. 2008), coho salmon smolts *Oncorhynchus kisutch* Walbaum, 1792 (Miller & Sadro 2003) and summer flounder *Platichthys flesus* Linnaeus, 1758 (Wirjoatmodjo & Pitcher 1984). These studies all suggest that animals were utilising the tide to move up and down rivers and estuaries in order to minimise energy expenditure. Elasmobranchs in estuaries do not always display tidally related movement, with no tide-related patterns observed in bat ray *Myliobatis californicus* Gill, 1865 (Matern et al. 2000) or cownose ray *Rhinoptera bonasus* Mitchill, 1815 (Collins et al. 2007). Although Matern et al. (2000) found no relationship between movement and tidal stage, *M. californicus* showed a significant diel pattern which was attributed to behavioural thermoregulation to aid digestion.

In the case of *Glyphis glyphis* in the Adelaide River, lower ROM is probably related to higher energy expenditure in order to stay within a particular section of the river, possibly due to high prey concentrations. The high reliance on tidal currents for up- and downstream movement suggests that *G. glyphis* are relatively sluggish. This is supported by observations of captured animals that were noticeably less active than similar-sized bull sharks (R. D. Pillans pers. obs.).

There was no evidence of a diurnal change in ROM in *Glyphis glyphis*. Similarly, swimming depth of Shark 2, the only animal with a depth tag, did not change. ROM has been shown to increase after sunset in some species (see Sciarrotta & Nelson 1977, McKibben & Nelson 1986, Parsons & Carlson 1998, Ackerman et al. 2000) but remain unchanged in others (see Yano & Tanaka 1986, Gruber et al. 1988, Holland et al. 1993, Rechisky & Wetherbee 2003). Yano & Tanaka (1986) tracked needle dogfish *Centrophorus acus* Garman, 1906 at depths >220 m and found no diurnal change in ROM, a finding which they attributed to constant darkness.

The swimming depth of Shark 2 showed that it spent the majority of time swimming well above the river bed and appeared to vary its swimming depth independently of bottom depth. Secchi depths in this section of the Adelaide River were between 10 and 40 cm. Using the equation $I_d = I_0 \exp(-kd)$ where I_d = irradiance at depth d, I_0 = irradiance at depth 0, k = 1.7/Secchi depth (m), d = depth internal (m), a maximum Secchi depth of 0.4 m would result in 99% of light being lost below 1 m. Therefore sharks swimming below 1 m would be in constant darkness. Given that the average swimming depth of Shark 2 was 7.7 m, it is not surprising that no diurnal changes in swimming depth or ROM were observed. Given the highly turbid conditions, it is likely that *Glyphis glyphis* relies heavily on an elaborate ampullary electroreceptor system to detect low-frequency bioelectric fields from its prey (see Hueter et al. 2004). The swimming depth of this animal is consistent with a benthopelagic habitat, supported by gut contents such as bony bream *Nematolosa erebi* (Günther, 1868), king salmon *Polydactylus macrochir* (Günther, 1867) and catfish (Ariidae) (Thorburn & Morgan 2004, Peverell et al. 2006).

The limited data on the distribution of *Glyphis glyphis* suggest that this species' distribution within rivers is limited by both upstream and downstream environments. Salinity is unlikely to influence the distribution of these species on a broad scale (i.e. which rivers this species occurs in) given their wide salinity tolerance (0.8 to 28 and 2 to 36 for *G. glyphis* and *G. garricki*, respectively). Tracked *G. glyphis* showed rapid movements across salinity gradients, providing additional evidence that this species is capable of osmoregulating in a range of salinities and probably osmoregulates in a similar manner to bull sharks (Pillans & Franklin 2004, Pillans et al. 2005, 2006).

Turbidity appears to play an important role in the distribution of *Glyphis* spp., in particular for *G. glyphis*.

Evidence of this comes from the presence of this species in one river system and its absence in adjacent river systems of similar size, salinity, temperature and tidal regimes but differing in bottom substrate and therefore turbidity. Within the Adelaide and Wenlock rivers, *G. glyphis* are confined to the turbid regions within freshwater reaches, whereas bull sharks occur further upstream in the less turbid reaches (R. D. Pillans unpubl. data). In both the Wenlock and Adelaide rivers, bull sharks are found further upstream but the 2 species do not overlap. Indeed, bull sharks have been recorded in all rivers and estuaries where *Glyphis* spp. occur (Thorburn et al. 2003, Last & Stevens 2009); however, the species have not been recorded together, indicating some degree of niche separation. Given the presence of bull sharks in most rivers and estuaries throughout northern Australia (Last & Stevens 2009) and the rarity of *G. glyphis*, it is evident that *Glyphis* spp. have more specific habitat requirements. While we cannot rule out variables such as dissolved oxygen and pH, due to a lack of measurements, turbidity appears to be an important factor. However, more data are required to explain the limited distribution of *Glyphis* spp.

CONCLUSIONS

It is well established that elasmobranchs living in rivers and estuaries are bound by physical constraints and are therefore less able to evade pollution, habitat destruction and fisheries (Compagno & Cook 1995). Both *Glyphis glyphis* and *G. garricki* are confined to a few highly turbid, tidal rivers and estuaries in tropical Australia. Although *G. garricki* has been recorded in marine environments, it appears to be reliant on rivers and estuaries for at least part of its lifecycle. The limited distribution of both species indicates that they have very specific habitat requirements. Movement patterns of *G. glyphis* indicate that animals are capable of covering ~25% of known available habitat in <7 h and that small sections of available habitat are utilised repeatedly as a result of tidally influenced movements. These factors combined with their biology make *Glyphis* spp. particularly vulnerable to overexploitation by commercial and recreational fishing gear such as gill nets and baited hooks. The lack of *G. glyphis* records from areas on the east coast of Qld where the species was previously recorded suggests that it may have been extirpated from this region. Given the localised movement patterns of the animals in the present study, spatial management combined with education of recreational and commercial fishers would prove an effective management tool. Despite positive results in the Wenlock and Ducie rivers, where commercial fishers are releasing captured *G. glyphis*, this species has a high mortality rate when captured in gill nets, making spatial management a more effective option.

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