Acoustic monitoring reveals the broad-scale movements of commercially important sharks

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ABSTRACT: Information on broad-scale movements is required for spatial management and improved conservation of large marine predators. We studied the mobility of the 4 most commercially important shark species of Western Australia (WA) using a network of acoustic receivers. Dusky sharks *Carcharhinus obscurus* showed very high mobility across WA. Sandbar *C. plumbeus*, gummy *Mustelus antarcticus* and particularly whiskery *Furgaleus macki* sharks were less mobile but can still move over long distances. The proportion of monitored time within different fisheries management zones varied among species. Dusky sharks showed the highest interconnectivity among these zones, reflecting the high mobility and complex movement patterns of this species. Sandbar, gummy and whiskery sharks followed, showing less movement among zones. Our study demonstrates how acoustic telemetry can be used to determine the movement patterns of species at the scale of fisheries management and therefore contribute to improved management and sustainability.

KEY WORDS: Shark fisheries · Sustainability · Tagging · Residency · Management · Conservation

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INTRODUCTION

Broad-scale movements can delineate population structure through spatial and temporal organizations such as size, age and/or sexual segregation (Whitehead et al. 2008). Although migrations and largescale displacements are increasingly reported for many marine taxa, in general the study of movement remains challenging, particularly for species that are difficult to observe, such as large marine predators (Heupel et al. 2015). This information, however, is required for determining the scale at which to manage these species, and it can allow a better representation of their population dynamics (Hilborn 1990). Large-scale movements are increasingly being reported for sharks, so a better understanding of their movement patterns is required to define the appropriate scale for assessing and managing shark populations (Braccini et al. 2016). Despite the recent increase in electronic tagging research for monitoring shark movement (Speed et al. 2010), the use of these

data for informing population modelling and deriving management advice remains rare for sharks (but see Graham et al. 2016 and Queiroz et al. 2016 for an example of recent applications of electronic monitoring for advising shark conservation).

Gummy Mustelus antarcticus, dusky Carcharhinus obscurus, whiskery Furgaleus macki and sandbar *C. plumbeus* sharks compose the bulk (~80%) of the catch of the Temperate Demersal Gillnet and Demersal Longline Fisheries (TDGDLF) the main shark fisheries of Western Australia (WA) and one of the main shark fisheries of Australia (McAuley & Simpfendorfer 2003). Although previous research allowed setting sustainable harvest levels for these target species, it also identified a number of information gaps and potential sustainability risks relating to stocks' temporal and spatial dynamics. For example, very low levels of cryptic fishing mortality on adult and sub-adult dusky and sandbar sharks would jeopardise stock sustainability (McAuley et al. 2007).

The fishery biology of these species is relatively well understood (Simpfendorfer et al. 1996, 1999, McAuley et al. 2005); however, uncertainty regarding their movement patterns remains a significant caveat to ensuring their sustainability. Dusky and sandbar shark stocks are distinctly size-segregated (Simpfendorfer et al. 1999, McAuley et al. 2005, Braccini & Taylor 2016). Juveniles are targeted by demersal gillnet and longline fishers off the lower-west and south-west coasts, hundreds of kilometres south of the primary distribution of adults (Simpfendorfer et al. 1996, 1999, McAuley et al. 2005). To maintain adequate recruitment, shark fishing has been prohibited in the north-west of WA (Ningaloo Closure; Fig. 1) to protect adult sharks. However, the extent to which adults remain vulnerable to capture during their southerly natal migrations is unknown due to insufficient knowledge on their movement patterns. In turn, understanding gummy and whiskery shark movements will contribute to improving their recovery from historical periods of overfishing.

Understanding the broad-scale movement dynamics of dusky, gummy, sandbar and whiskery sharks off WA would therefore allow the incorporation of

movement information into their management and conservation. This study uses detection data from a network of acoustic receivers deployed across WA to improve understanding of the movement patterns of these 4 target species. In particular, we studied the proportion of time spent per management zone, the degree of connectivity among zones, residency and roaming patterns, and the extent of shark movement within WA.

MATERIALS AND METHODS

Data

Movements of dusky *Carcharhinus obscurus*, sandbar *C. plumbeus*, gummy *Mustelus antarcticus* and whiskery *Furgaleus macki* sharks were studied using a network of acoustic receivers deployed across WA consisting of 3 large arrays (Ningaloo Reef, Perth and Southern Lines arrays) (Fig. 1). Detection data were collected from up to 455 Vemco VR2W and VR4G acoustic receiver stations deployed as gates (7 lines) or clusters by the Department of Fish-

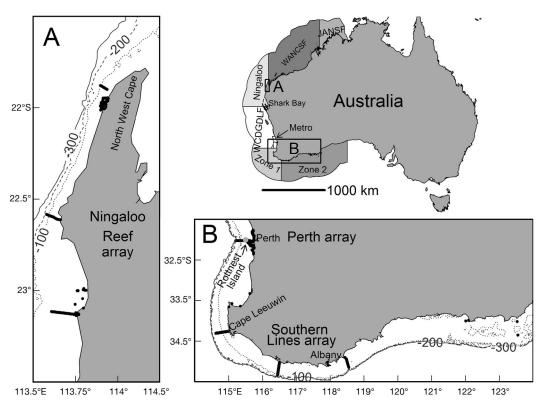


Fig. 1. Location of acoustic receivers (black dots). (A) Ningaloo Reef array. (B) Perth and Southern Lines arrays. Also shown are the fishery management zones: Joint Authority Southern Demersal Gillnet and Demersal Longline Fishery (JASDGDLF, Zones 1 and 2); Metro Closure (Metro); West Coast Demersal Gillnet and Demersal Longline Fishery (WCDGDLF); Ningaloo Closure (Ningaloo); West Australian North Coast Shark Fishery (WANCSF); Joint Authority Northern Shark Fishery (JANSF)

eries (DoF), the Australian Animal Tracking and Monitoring System and the Ocean Tracking Network. Acoustic receivers were downloaded approximately once per year; shallow water receivers (<30 m) were retrieved by SCUBA divers, whereas deep water receivers (>30 m) were retrieved by a combination of acoustic release mechanisms and a remotely operated vehicle. Combined data from these multiinstitutional arrays allowed monitoring of animals' distributions, movements and migration routes within and between management zones (Joint Authority Southern Demersal Gillnet and Demersal Longline Fishery: JASDGDLF, Zones 1 and 2; Metro Closure: Metro; West Coast Demersal Gillnet and Demersal Longline Fishery: WCDGDLF; Ningaloo Closure: Ningaloo; West Australian North Coast Shark Fishery: WANCSF; Joint Authority Northern Shark Fishery: JANSF) (Fig. 1). (N.B. refer to McAuley et al. (2015) for a description of the management measures in place in the different zones.)

Tagging involved implanting uniquely coded acoustic transmitters (Vemco V16-5H and V16-6H) into sharks' body cavities via a small incision on the ventral surface using standard surgical procedures (Heupel et al. 2004). All personnel involved in tagging were previously experienced or trained by experienced researchers prior to conducting tagging procedures. The acoustic tags had a transmission interval of 75 to 150 s for gummy and whiskery sharks and of 100-200 s for sandbar and dusky sharks. (It must be noted that transmitter emission rate may affect the mean duration of detections for each species.) Sharks were also fitted with conventional Jumbo Rototags on the first dorsal fin to allow their visual identification and the reporting of re-capture details. During tagging, sharks were measured to the nearest cm (fork length, FL) and sexed. Date and GPS coordinates were also recorded. A total of 6 fishery-independent research cruises (2 per year) aimed at tagging sandbar and large dusky sharks in northern WA were conducted between May 2011 and August 2013 on board DoF's R/V 'Naturaliste'. In addition, several days of shark longlining and drumlining aimed at tagging large dusky sharks were opportunistically conducted during receiver maintenance cruises in southern WA between 2012 and 2013. Gummy and whiskery sharks were mostly tagged during 51 trips on-board TDGDLF gillnet vessels operating in southern WA between May 2012 and October 2013. To maximise sharks' chances of surviving the tag and release process, gillnet-caught sharks were selected for tagging according to their apparent vigour and absence of obvious injuries.

Analyses

Acoustic tagging data were analysed to investigate broad-scale movement patterns. All analyses and data manipulations were conducted in the statistical package R (R Development Core Team 2014).

Minimum linear displacement (in km) was calculated as the straight-line distance between receivers with consecutive detections. To minimise movement trajectories crossing over land, 3 fixed GPS co-ordinates (off North West Cape, Shark Bay and Cape Leeuwin) were used as arbitrary turning points, and an algorithm containing these points was computed for consecutive detections by different receiver lines which would cross land if connected with a straight line. Minimum speed was then determined as the minimum linear displacement divided by the time (d) between those consecutive detections. Because the majority of the receivers were deployed in lines, the actual position of a shark could not be determined using centre-of-activity as typically done for grid arrays. Hence, we only calculated minimum linear displacements and speed for long-distance trajectories (>100 km).

For each detected individual, the proportion of time spent within each management zone during the monitoring period (i.e. the number of days between release and last detection) was calculated. This required information on the complete movement trajectory of each individual. Because acoustic tagging only provides information on the presence/absence of tagged individuals within the detection range of a receiver, trajectories were reconstructed assuming straight line movement among detections in different receivers. For this, the position between consecutive detections in different receivers was interpolated (avoiding crossing over land) and the amount of time spent between these detections was split proportionally to the distance between the receivers. As for the calculation of minimum linear displacement and speed, for this analysis, we had to assume straightline movement between consecutive detections. For example, if a tagged shark was detected by one receiver within the Ningaloo Reef array, then not detected for some time and then detected again by one of the Ningaloo Reef array receivers, the assumption is that the shark stayed within the Ningaloo zone. To study residency patterns within management zones, the proportion of time spent per zone within each year was used as the response variable of a generalised linear model (GLM) with a binomial distribution. Model predictors included species, size, sex, year, and release zone. Analyses were done for each

zone separated. The WANCSF zone was not included in this analysis due to the very small number of observations.

To determine the extent of shark movement among the array lines, a roaming index was calculated as the number of array lines visited in a year divided by the total number of array lines. A GLM with a binomial distribution was used to test the effects of species, size, sex, year and release zone on the roaming indices. For all GLM analyses, term interactions were not considered due to the highly unbalanced sampling designed.

RESULTS

In total, 103 dusky Carcharhinus obscurus, 101 sandbar C. plumbeus, 100 gummy Mustelus antarcticus and 40 whiskery Furgaleus macki sharks were implanted with acoustic transmitters (Table 1). The location and year of tagging of each individual is shown in Fig. S1 in the Supplement at www.int-res.com/ articles/suppl/m577p121_supp.pdf). For the 4 species, sex ratio was biased towards females, and the size of tagged individuals was approximately the female size at 50% maturity (254, 130, 111 and 112 cm FL for dusky, sandbar, gummy and whiskery sharks; Braccini et al. 2015). Of the tagged sharks, 68 dusky, 57 sandbar, 33 gummy and 14 whiskery sharks were

detected and monitored intermittently for up to 1460, 1725, 1087, and 1591 d, respectively. These individuals showed a similar sex ratio and mean FL as the tagged population (Table 1). On average, sandbar and dusky sharks were monitored for longer periods (994 and 697 d) than gummy (377 d) and whiskery (362 d) sharks. Dusky sharks were detected by the largest number of receivers, followed by gummy, sandbar and whiskery sharks. However, sandbar sharks had the largest number of detections followed by dusky sharks, whereas gummy and whiskery sharks had considerably less detections.

For dusky, gummy and whiskery sharks, the proportion of time detected within the monitored period was generally low (Fig. S2). For sandbar sharks, the proportion of time detected was also generally low; however, the several individuals that were monitored for a substantial period of time were detected regularly.

Table 1. Data summary for all individuals of the 4 main commercial shark species tagged in Western Australia. Also shown is a summary of long-distance displacements (>100 km) between consecutive detections in different arrays and between detections and reported recapture. FL: fork length

Variable	Dusky	Sandbar	Gummy	Whiskery			
Tagged							
No. of ind.	103	101	100	40			
Mean FL (SD)	242(32)	141(8)	102(10)	112(9)			
Sex ratio (male:female)	1:1.8	1:1.8	1:3.2	1:2.3			
Sex rutto (mare.remare)	1.1.0	1.1.0	1.0.2	1.2.0			
Detected							
No. of ind.	68	57	33	14			
Mean (cm) FL (SD)	242(33)	142(9)	103(10)	110(9)			
Sex ratio (male:female)	1:1.8	1:2.7	1:7.2	1:2.5			
,							
No. days monitored							
Minimum	1	1	9	1			
Mean (SD)	697(446)	994(537)	377(312)	362(491)			
Maximum	1460	1725	1087	1591			
No. of detections							
Total	12847	152022	2451	490			
In the Ningaloo array	8602	151969	0	0			
In the Perth array	1130	6	44	0			
In the Southern Lines array	3115	47	2407	490			
1							
Total no. of receivers	228	73	106	35			
detecting individuals							
S .							
Long-distance displacements (>100 km)							
Total number of trajectories	402	46	82	9			
Total number of sharks	60	27	27	7			
Mean displacement	421(416)	270(287)	237(121)	282(151)			
distance (km) (SD)				` '			
Maximum displacement	2098	1409	969	606			
distance (km)							
Mean speed (km d ⁻¹) (SD)	32(26)	13(17)	22(18)	13(18)			
Maximum speed (km d ⁻¹)	107	63	65 [′]	4 5			
- '							

Sandbar sharks were detected in all 3 arrays but predominately in the Ningaloo Reef array. Dusky sharks showed a more even number of detections across the 3 arrays. Gummy and whiskery sharks are temperate shark species, so as expected, they were not detected in the Ningaloo Reef array. Most gummy sharks were detected in the Southern Lines array, although 5 individuals (44 detections) were detected in the Perth array. Whiskery sharks were only detected in the Southern Lines array (Table 1).

For the Ningaloo Reef array, dusky and sandbar sharks were detected in all of the 3 lines and across most receivers. For the Perth array, detections of dusky sharks were fairly evenly distributed across the offshore receivers (>50 m deep), with a slightly higher number at the outermost receivers. For sandbar sharks, there were only 6 detection events, all at receivers moored at >50 m deep. No detections for

dusky or sandbar sharks were recorded in shallower waters. Detections of gummy sharks were spread across both inshore receivers and receivers extending out to Rottnest Island (Fig. 1) as well as west of Rottnest Island up to approximately the 100 m isobath. All species were detected in the Southern Lines array, although detections were limited for sandbar (n = 47) and whiskery (n = 490) (Table 1). For dusky, gummy and whiskery sharks, detections were distributed across the 3 receiver lines. Gummy sharks had a high number of detections on the eastern-most line (line 3) at receivers closest to the coast, just past the 50 m isobath. Sandbar sharks were only detected in the western-most line, adjacent to Cape Leeuwin (Fig. 1), at deepwater receivers.

For long-distance displacements (>100 km), dusky sharks showed the fastest speeds with a top of 107 km d⁻¹. Gummy and sandbar sharks followed, with maximum speeds of >60 km d⁻¹. The fastest speed recorded for whiskery shark was 45 km d⁻¹ (Table 1). For dusky sharks, 60 individuals (402 trajectories) undertook long-distance displacements. The longest displacement between receivers was 2098 km. For gummy and sandbar sharks, 27 individuals undertook long-distance displacements, with the longest displacement between receivers being 969 and 1490 km, respectively. For whiskery sharks, 7 individuals undertook long-distance displacements, each of up to 606 km.

Dusky sharks had substantially more individuals detected in >1 array than the other 3 species (Table S1). For dusky sharks, 13 individuals were detected in the 3 arrays, and several individuals were detected in 2 arrays. In addition, 15 individuals (10 females and 5 males) completed round-trip long-distance migrations between the Ningaloo Reef array and the Perth/Southern Lines arrays. For sandbar sharks, only 1 individual was detected in the 3 arrays, and only 1 or 2 individuals were detected in 2 arrays. For gummy sharks, 4 individuals were detected in the Perth and Southern lines arrays. No whiskery shark was detected in >1 array.

Dusky sharks showed the highest mobility of the 4 species with sharks spending substantial time across all fishery zones (Fig. 2). Sandbar and gummy sharks followed, showing less movement among zones. Whiskery sharks were the least mobile species, spending most the monitored time within the release zone. For dusky sharks, most individuals moved beyond their release zone, revealing a high degree of inter-zone connectivity. Most individuals released in Ningaloo spent a considerable proportion of the time in zones south of Ningaloo. Similarly, individuals

released in other fishery management zones spent a considerable amount of the monitored time in other zones. For sandbar sharks released in Ningaloo, the vast majority of the individuals remained within the release zone with the exception of 1 individual which spent ~30% of the time in WANCSF and 2 individuals that spent a considerable amount of time south of Ningaloo. For individuals released in WANCSF, most of them spent most the monitored time in Ningaloo. For gummy sharks, most individuals released in Zone 2 remained within that zone, with the exception of 3 individuals which were also detected in Zone 1 (3 individuals) and in Metro (1 individual). Most individuals released in Zone 1, in contrast, spent a considerable amount of time in Metro and particularly Zone 2. For whiskery sharks, most individuals remained within the release zone, with the exception of 2 individuals released in Zone 1 which were detected for a considerable proportion of the monitored time in Zone 2 and 2 individuals released in Zone 2 which were detected in Zone 1.

Dusky sharks showed the lowest proportion of individuals remaining within the release zone with only about 18% of males and 47% of females remaining where they were tagged (Fig. S3). For sandbar sharks, a very high proportion, particularly for males, remained within the release zone. Gummy and whiskery sharks also showed a high proportion of individuals remaining within the release zone, particularly male gummy and male and female whiskery sharks.

The number of individuals of each species that moved to adjacent zones and non-adjacent zones at different time scales (Fig. S4) provides further evidence of the differences in species' mobility. Dusky sharks had the highest number of individuals moving to adjacent and non-adjacent zones. In addition, dusky sharks took considerably less time to undertake these movements than the other 3 shark species.

The models used for testing the effects of several predictors on residency and roaming explained between 26 and 58% (Table 2) and 20% (Table 3) of the deviance, respectively. For both indices, species explained most of the deviance, followed by release zone (residency index only for Metro and Zone 2 zones). Other significant terms explained a very small percentage of the deviance. Dusky and sandbar sharks showed high residency to Ningaloo, particularly sandbar sharks, and lower residency to other zones (Fig. 3). Gummy sharks showed high residency to Zone 2 and lower residency to other zones, whereas whiskery sharks showed high residency to Zone 1 and Zone 2 (Fig. 3). All species showed low residency to Metro, which is the smallest zone included in the

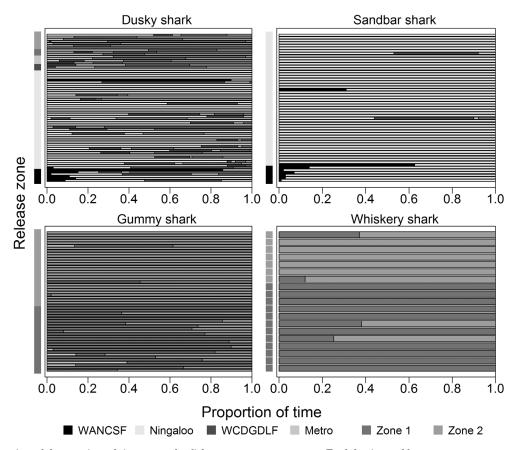


Fig. 2. Proportion of the monitored time spent by fishery management zone. Each horizontal bar represents a tagged individual. The analysis includes detected individuals as well as non-detected individuals that were recaptured. Joint Authority Southern Demersal Gillnet and Demersal Longline Fishery (Zones 1 and 2); Metro Closure (Metro); West Coast Demersal Gillnet and Demersal Longline Fishery (WCDGDLF); Ningaloo Closure (Ningaloo); West Australian North Coast Shark Fishery (WANCSF)

Table 2. Deviance explained for the GLM models fitted to the residency data for each zone. FL: fork length; WCDGDLF: West Coast Demersal Gillnet and Demersal Longline Fishery management zone

	Species	Release zone	Year	FL	Sex	Total
Ningaloo Dev. explained (%)	25.4 <0.001	2.23 <0.001	8.02 <0.001	4.02 <0.001	0.55 <0.001	40.21
WCDGDLF Dev. explained (%) p	20.4 <0.001	7.79 <0.001	6.21 <0.001	0.94 <0.001	1.07 <0.001	36.42
Metro Dev. explained (%) p	2.02 <0.001	21.86 <0.001	0.8 <0.001	0.5 <0.001	0.45 <0.001	25.63
Zone 1 Dev. explained (%) p	34.22 <0.001	2.78 <0.001	5.65 <0.001	5.17 <0.001	1.03 <0.001	48.86
Zone 2 Dev. explained (%) p	32.33 <0.001	21.31 <0.001	3.63 <0.001	0.12 <0.001	1.09 <0.001	58.47

analyses. Dusky sharks showed significantly higher roaming than the other shark species (Fig. 4).

DISCUSSION

Acoustic tagging studies have traditionally been done at short spatial and temporal scales on species likely to show strong aggregation/residency to an area (but see Heupel et al. 2015 and Espinoza et al. 2016 for recent examples of the use of acoustic receiver networks for monitoring the broad-scale movements of sharks). In this study, the most commercially important shark species of WA were monitored across multiple temporal and spatial scales. This allowed the construction of a more thorough picture of the species' movement behav-

Table 3. Deviance explained for the GLM models fitted to the roaming data. FL: fork length

Term	Roaming			
	Dev. explained (%)	p		
Species	17.85	< 0.001		
Release zone	0.60	0.88		
Year	1.63	0.25		
FL	0.07	0.61		
Sex	0.04	0.70		
Total	20.18			

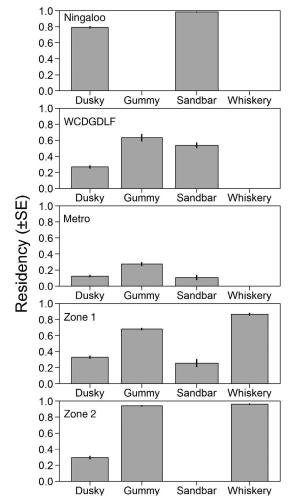


Fig. 3. Predicted mean (±1 SE) residency by species and zone: Joint Authority Southern Demersal Gillnet and Demersal Longline Fishery (Zones 1 and 2); Metro Closure (Metro); West Coast Demersal Gillnet and Demersal Longline Fishery (WCDGDLF); Ningaloo Closure (Ningaloo)

iours than could have been obtained from traditional experimental designs. Another important aspect of our study is that most individuals were large juveniles or adult individuals, which allows a better understanding of this stage of the life history of these shark

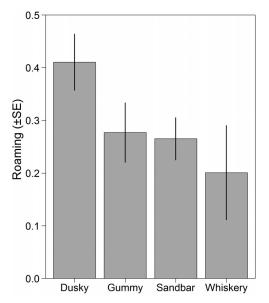


Fig. 4. Predicted mean (±1 SE) roaming by species

species, particularly in relation to their exposure to fishing pressure. For example, fishing mortality rates of as little as 1 to 2% on adult and sub-adult sandbar Carcharhinus plumbeus and dusky C. obscurus sharks would be sufficient to cause declining recruitment to these stocks (McAuley et al. 2007). Although adults predominantly reside in areas closed to commercial shark fishing (Ningaloo) or where commercial shark fishing effort has not been exerted since 2009 (WANCSF), they undertake seasonal migrations to commercial fishing grounds (Simpfendorfer et al. 1996, 1999, McAuley et al. 2005). Several dusky shark and some sandbar shark individuals spent a considerable proportion of the monitored time outside Ningaloo and WANCSF and, therefore, were potentially exposed to fishing mortality. Similarly, although whiskery Furgaleus macki and gummy Mustelus antarcticus sharks are commercially fished in WCDGDLF, Zone 1 and Zone 2, fishing mortality in these zones should vary, given the different spatial distribution of fishing effort (McAuley et al. 2015). The movement information generated in our study could be used in a spatial population dynamics model to make predictions of age-specific fishing mortality by zone and make a spatially explicit assessment of stock sustainability.

Dusky sharks were the most widely distributed of the 4 species, showing the most extensive displacements throughout WA. This, in part, could be due to the larger size of dusky sharks, which would allow them to be more mobile than the other 3 species. Tagged individuals did not reside within a detection array for very long, and 15 individuals completed round-trip long-distance migrations between northern and southern WA (M. Braccini pers. obs.). Satellite and conventional tagging studies in South Australia (Rogers et al. 2013), the Gulf of Mexico (Hoffmayer et al. 2014) and South Africa (Hussey et al. 2009) also indicate that dusky sharks are capable of long-distance displacements and of maximum displacements on the order of 100s to 1000s of km at maximum speeds (based on minimum linear displacement) on the order of 10s to 100 km d⁻¹ (Hussey et al. 2009, Rogers et al. 2013, Hoffmayer et al. 2014, present study). Hence, dusky sharks are highly mobile species with broad-scale movements.

Sandbar sharks spent most of the monitored time in Ningaloo. In WA, sandbar sharks exhibit a considerable degree of spatial segregation, with adults being more abundant north of 26°S latitude and juveniles occurring predominantly in deeper continental-shelf waters south of 26°S (McAuley et al. 2005). Based on conventional tagging, juveniles remain in temperate waters for several years and slowly migrate northwards to join the breeding stock while adults migrate south to temperate waters to give birth. Several reported recaptures of conventionally tagged adults and sub-adults partly support this hypothesis (Mc-Auley et al. 2005). In North America, sandbar sharks are highly migratory (Kohler et al. 1998) with adults annually migrating along the eastern coast from overwintering areas as far south as the Gulf of Mexico to summer nurseries as far north as Great Bay, New Jersey, USA (Rechisky & Wetherbee 2003). In our study, however, only 2 individuals released in northern WA (2 females larger than the length at 50% maturity) were detected south. These detection events occurred between February and April by receivers located in deep water. The lack of detections south, however, could be an artefact resulting from the limited depth distribution of the receivers (<200 m) because large sandbar sharks were observed while retrieving deepwater receivers using the ROV, and commercial catches of large sandbar sharks in south-western WA occur in deep waters (DoF unpubl.). Therefore, it is unclear to what extent the observed patterns are representative of the broad-scale movements of sandbar sharks in WA, so no inferences on migratory movements can be drawn for this species.

Gummy and whiskery sharks were considerably less mobile than dusky sharks, particularly whiskery sharks. This pattern is consistent with conventional tagging studies (Simpfendorfer et al. 1996, Brown et al. 2000). Gummy sharks in south-eastern Australia showed average displacements in the order of 100 to 250 km with a maximum displacement of >2500 km (Brown et al. 2000). Comparably, in this study, gummy

sharks showed average long-distance displacements of 238 km with a maximum displacement of >900 km. For whiskery sharks, conventional tagging in southwestern WA showed that most tagged individuals were recaptured within 50 km of the point of release, even after long periods at liberty, although 3 individuals (out of 17 recaptures) showed displacements of between 120 and 384 km (Simpfendorfer et al. 1996). In our study, average long-distance displacements were larger (>240 km), but the maximum displacement recorded was similar (374 km).

CONCLUSIONS

This study tagged and monitored an unprecedented number of individuals from the main commercial shark species of WA, revealing their complex and broad-scale movement patterns, particularly for male and female dusky sharks. Sandbar sharks were expected to show comparable broad-scale movements to dusky sharks, though tagged individuals were mostly detected at Ningaloo. These findings, however, must be interpreted with caution as they could be an artefact from the depth distribution of the acoustic receivers. Gummy and particularly whiskery sharks showed relatively less movement, although these species are still capable of relatively large-scale displacements.

The observed movement patterns of dusky sharks are driven by reproduction, with large females, which occur mostly in northern WA, moving south to give birth (McAuley et al. 2005). For the other species, an explanation of the observed species-specific movements remains purely speculative. Size is likely to play a role, with larger species being naturally capable of larger displacements. However, other life history traits, such physiological requirements/capabilities, and several environmental factors (e.g. temperature gradients or changes in prey density) may also be important. Whether the observed differences in movement patterns are associated directly or indirectly with these factors remains unclear; further information is needed to avoid spurious correlations.

The broad-scale movement information generated in this study provides the basis for modelling movement among management zones, allowing the spatial quantification of fishing mortality. In summary, our study demonstrates how acoustic telemetry can be used to determine the movement patterns of species at the scale of fisheries management and therefore contribute to improved management and sustainability.

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LITERATURE CITED

- Braccini M, Taylor S (2016) The spatial segregation patterns of sharks from Western Australia. R Soc Open Sci 3: 160306
- Braccini M, Brooks EN, Wise B, McAuley R (2015) Displaying uncertainty in the biological reference points of sharks. Ocean Coast Manag 116:143–149
- Braccini M, Aires-da-Silva A, Taylor I (2016) Incorporating movement in the modelling of shark and ray population dynamics: approaches and management implications. Rev Fish Biol Fish 26:13–24
 - Brown L, Bridge N, Walker T (2000) Summary of tag releases and recaptures in the Southern Shark Fishery. Report No. 18. Marine and Freshwater Resources Institute, Queenscliff
- Espinoza M, Heupel MR, Tobin AJ, Simpfendorfer CA (2016) Evidence of partial migration in a large coastal predator: opportunistic foraging and reproduction as key drivers? PLOS ONE 11:e0147608
 - Graham F, Rynne P, Estevanez M, Luo J, Ault JS, Hammerschlag N (2016) Use of marine protected areas and exclusive economic zones in the subtropical western North Atlantic Ocean by large highly mobile sharks. Divers Distrib 22:534–546
- Heupel MR, Simpfendorfer CA, Hueter RE (2004) Estimation of shark home ranges using passive monitoring techniques. Environ Biol Fishes 71:135–142
 - Heupel MR, Simpfendorfer CA, Espinoza M, Smoothey AF, Tobin A, Peddemors V (2015) Conservation challenges of sharks with continental scale migrations. Front Mar Sci 2:1–7
- Hilborn R (1990) Determination of fish movement patterns from tag recoveries using maximum likelihood estimators. Can J Fish Aquat Sci 47:635–643
- Hoffmayer ER, Franks JS, Driggers WB, McKinney JA, Hendon JM, Quattro JM (2014) Habitat, movements and environmental preferences of dusky sharks, *Carcharhinus obscurus*, in the northern Gulf of Mexico. Mar Biol 161:911–924
- Hussey NE, McCarthy ID, Dudley SFJ, Mann BQ (2009) Nursery grounds, movement patterns and growth rates of dusky sharks, Carcharhinus obscurus: a long-term tag

- and release study in South African waters. Mar Freshw Res 60:571–583
- Kohler NE, Casey J, Turner PA (1998) NMFS cooperative shark tagging program, 1962-93: an atlas of shark tag and recapture data. Mar Fish Rev 60:1–87
- McAuley R, Simpfendorfer C (2003) Catch composition of the Western Australian temperate demersal gillnet and demersal longline fisheries, 1994 to 1999. Fisheries Research Report No. 146, Department of Fisheries, Perth
- McAuley R, Lenanton R, Chidlow J, Allison R, Heist E (2005) Biology and stock assessment of the thickskin (sandbar) shark, *Carcharhinus plumbeus*, in Western Australia and further refinement of the dusky shark, *Carcharhinus obscurus*, stock assessment. Fisheries Research and Development Corporation Project No. 2000/134. Fisheries Research Report No. 151, Department of Fisheries, Perth
- McAuley R, Simpfendorfer C, Hall N (2007) A method for evaluating the impacts of fishing mortality and stochastic influences on the demography of two long-lived shark stocks. ICES J Mar Sci 64:1710–1722
- McAuley R, Braccini M, Newman SJ, O'Malley J (2015) Temperate demersal gillnet and demersal longline fisheries status report. In: Fletcher WJ, Santoro K (eds) Status reports of the fisheries and aquatic resources of Western Australia 2014/15. The state of fisheries. Department of Fisheries of Western Australia, Perth, p 261–272
- Queiroz N, Humphries NE, Mucientes G, Hammerschlag N and others (2016) Ocean-wide tracking of pelagic sharks reveals extent of overlap with longline fishing hotspots. Proc Natl Acad Sci USA 113:1582–1587
 - R Development CoreTeam (2014) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna
- Rechisky E, Wetherbee B (2003) Short-term movements of juvenile and neonate sandbar sharks, *Carcharhinus plumbeus*, on their nursery grounds in Delaware Bay. Environ Biol Fishes 68:113–128
- Rogers P, Huveneers C, Goldsworthy SD, Mitchell JG, Seuront L (2013) Broad-scale movements and pelagic habitat of the dusky shark *Carcharhinus obscurus* off southern Australia determined using pop-up satellite archival tags. Fish Oceanogr 22:102–112
 - Simpfendorfer CA, Lenanton RCJ, Unsworth P (1996) Stock assessment of large coastal and demersal sharks. Fisheries Research and Development Corporation Project No. 93/067. Fisheries Department of Western Australia, Perth
 - Simpfendorfer CA, McAuley R, Chidlow JA, Lenanton R, Hall N, Bastow T (1999) Biology and stock assessment of Western Australia's commercially importat shark species. Fisheries Research and Development Corporation Project No. 96/130. Department of Fisheries of Western Australia, Perth
- Speed CW, Field IC, Meekan MG, Bradshaw CJA (2010) Complexities of coastal shark movements and their implications for management. Mar Ecol Prog Ser 408: 275–293
 - Whitehead H, Coakes A, Jaquet N, Lusseau S (2008) Movements of sperm whales in the tropical Pacific. Mar Ecol Prog Ser 361:291–300

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