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Original Article

Partial female migration and cool-water migration pathways in an overfished shark

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Knowledge about reproductive movements can be of important conservation value for over-exploited species that are vulnerable when moving between and within key reproductive habitats. Lack of knowledge persists around such movements in the overfished school shark *Galeorhinus galeus* in Australia. Management assumes all pregnant females migrate between adult aggregations in the Great Australian Bight, South Australia, and nursery areas around Bass Strait and Tasmania. We tracked 14 late-term pregnant females tagged in South Australia using satellite-linked pop-up archival tags to investigate extent, timing, and routes of migrations. We found partial migration, with some females ($n = 7$) remaining near aggregating areas throughout the pupping season, some migrating to known nursery areas ($n = 3$), and one migrating ~3 000 km to New Zealand. We conclude female movements and pupping habitats are less spatially constrained than assumed and propose females use cool-water routes along the shelf break to reduce energy costs of migration. Migrating females using these routes faced greater fishing pressure than sharks in inshore areas and were not protected by inshore shark fishing closures designed to protect them. This study demonstrates the complexity of reproductive movements that can occur in wide-ranging species and highlights the value of explicit movement data.

Keywords: behavioural plasticity, bioenergetics, fishing pressure, *Galeorhinus galeus*, large-scale movements, PSAT, soupfin shark, tope.

Introduction

Partial migration, whereby migratory behaviour varies producing migrants and residents within populations, has been reported in all major vertebrate taxa including birds (Lack, 1943; Lundberg, 1985; Adriaensen and Dhondt, 1990), mammals (Talbot and Talbot, 1963; Maddock, 1979; Ball *et al.*, 2001), and fishes (Jonsson and Jonsson, 1993; Wroblewski *et al.*, 1994; Papastamatiou *et al.*, 2013). The drive to migrate may arise through reproductive philopatry (Hendry *et al.*, 2003), genetic predisposition (Biebach, 1983), or individual choice weighing the benefits of migration against the costs of residency (Chapman *et al.*, 2011). Such decisions may be condition-dependent, e.g. fish in good condition can be more likely to migrate than those in poorer condition (Brodersen *et al.*, 2008). While varying participation and movements associated with partial migration can confer population-level resilience, it may also complicate conservation planning, e.g. through varying vulnerability to human impacts in different areas (Secor *et al.*, 2001; Parsons *et al.*, 2011).

Where species have been depleted by human interference, knowledge about reproductive movements can be of important conservation value, allowing for protection of critical habitats such as birthing or nesting areas (Myers *et al.*, 1987; Webster *et al.*, 2002; Martin *et al.*, 2007). Sanctuary or no-take zones are increasingly being used as a conservation tool to protect important habitats for fishes (Bohnsack and Ault, 1996; Beck *et al.*, 2001; Edgar *et al.*, 2014) including sharks (Carrier and Pratt, 1998; Escalle *et al.*, 2015; Speed *et al.*, 2018). Many marine vertebrates, however, have life-histories punctuated by migrations, e.g. between foraging and reproductive habitats or between areas associated with different stages of ontogenetic development (Johannes, 1978; Shillinger

Figure 1. Pregnant female *G. galeus* aggregate in the Great Australian Bight (diamond, upper left) in austral spring and are assumed to migrate (dashed line) to nursery areas around Bass Strait and Tasmania (e.g. Port Phillip Bay, Westernport, Port Sorell, Georges Bay, Pittwater) to give birth in austral summer. Line along coast denotes shark fishing closure from Kangaroo Island (to ∼2 km from shore) to Bass Strait (to ∼6 km from shore along mainland) designed to protect migrating *G. galeus*. Shark sanctuary zones designed to protect *G. galeus* pupping activity in Tasmania are also marked. Shaded area is the continental shelf. Inset: map area (boxed) relative to Australia.

et al., 2008; Grüss *et al.*, 2011). The efficacy of no-take zones may therefore be reduced if animals are captured en route during migrations from other habitats (Gerber *et al.*, 2005; Shillinger *et al.*, 2008; Costa *et al.*, 2012). Furthermore, in species where movements are commonly greater than the distance between sub-populations, the incorporation of up-to-date and informative movement data into management models is essential to produce effective, spatially explicit management policies and assessments (Walker *et al.*, 2008; Goethel *et al.*, 2011; Braccini *et al.*, 2016).

The school shark *Galeorhinus galeus* (also: soupfin shark, tope) is broadly distributed in temperate waters globally and has been overfished throughout its range, e.g. in California, Great Britain, and Australia (Walker, 1998; Molfese *et al.*, 2014). Like many sharks, *G. galeus* shares life history traits inhibiting recovery from population depletion, e.g. slow growth (reaching 60 years and ∼175 cm in Australia), late maturity (8–10 years), long reproductive cycles (2–3 years), discrete reproductive seasons (pupping in November–January in Australia), and selective use of reproductive habitats (Olsen, 1954; Walker, 1999). In Australian waters, *G. galeus* is Conservation Dependent after over-exploitation until the 1990s, and has not recovered despite fisheries management and conservation efforts introduced since the early 2000s (AFMA, 2009; Huveneers *et al.*, 2013; McAllister *et al.*, 2018). No-take zones designed to protect *G. galeus* migrations and recruitment are in place along the coastal strip from central South Australia to Bass Strait (to ∼6 km from shore) and in known nursery areas (Figure 1). However, a national recovery plan highlighted an important knowledge gap around critical reproductive habitats and movements for the species (AFMA, 2009).

Although wide-ranging and formerly common, >90% of *G. galeus* pupping in Australia is estimated to occur in unknown areas (Stevens and West, 1997). In the 1950s, spring aggregations of pregnant females were found in the Great Australian Bight, South Australia, in the northwest of the species' range, while nursery areas used in summer were found in Tasmania and Bass Strait in the southeast (Olsen, 1954) (Figure 1). Obligate female migrations between these areas were assumed, an assumption that persists and has shaped management of the species (Walker *et al.*, 2008), despite evidence that pupping may also occur close to aggregating areas in South Australia (Prince, 1996; Rogers *et al.*, 2017; McMillan *et al.*, 2018). Given genetic evidence for a single stock throughout this range (Hernández *et al.*, 2015), pupping near the northwest range of the species would entail partial female migration and present different challenges for conservation and fisheries management than the current model of reproductive movement and habitat use.

Temperature is a key driver of movement and habitat use in ectothermic fishes (Brett, 1971; Bernatchez and Dodson, 1987; Tanaka *et al.*, 2000); sharks have been proposed to select areas of favourable water temperature to behaviourally thermoregulate (Carey *et al.*, 1990; Thums *et al.*, 2012; Andrzejaczek *et al.*, 2018), conserve energy (Sims *et al.*, 2006), and assist digestion (Papastamatiou *et al.*, 2015). There is potential that behaviour of female *G. galeus* is likewise driven by thermal constraints, e.g. aggregating in warm areas to promote growth and gestation, and using cool waters to lower metabolic costs during migrations. We used satellite-linked pop-up archival tags (PSATs) to investigate extent, timing, and routes of migrations of pregnant *G. galeus* from aggregating sites in the Great Australian Bight. We aimed to address the knowledge gap around pupping movements and areas outlined in the national recovery plan for *G. galeus* (AFMA, 2009), and seek to understand potential drivers behind the aggregating and migratory behaviours of female *G. galeus* that may also be applicable to other wide-ranging ectothermic species.

Methods

Tagging

Tagging was undertaken in two different locations at different times. First, inshore near the head of the Great Australian Bight (Figure 2a) in early December 2015 at the start of the pupping season targeting females immediately prior to pupping (capture depth: 33 m, $n = 8$). Second, offshore southwest of Kangaroo Island, South Australia (Figure 2b) in October 2017 prior to the pupping season targeting migrating females (capture depth: 110–143 m, $n = 5$). A further female was tagged inshore in the Great Australian Bight in November 2017 (capture depth: 40 m) (shark x3: Supplementary Table S1). In 2015, females were caught by angling, using 50 kg braid and wire trace to 10/0 circle hooks set on the bottom and baited with Australian herring *Arripis georgianus.* In 2017, females were caught aboard commercial longlining vessels using 7 mm sinking rope main lines with up to 1 500 ∼40 cm long traces of 2 mm monofilament to 10/0 circle hooks at ∼7 m intervals and baited with slimy mackerel *Scomber australasicus.*

Only lively females (i.e. exhibiting strong, active, or responsive movements) free of injury to major organs (e.g. the gills) were selected for pregnancy examination and tagging. Selected females were kept oxygenated by pumping seawater over the gills via a hose inserted in the mouth and a moist cloth was placed over the eyes to reduce stress. Rolling females onto their back on a moistened rubber mat induced a tonic state whereby sharks became calmer, facilitating inspection, and tagging. Pregnancy was determined by visual inspection based on the characteristic triangular shape of late-term gravid females and *in-utero* movements of embryos that could be seen or felt externally. In 2017, ultrasound (Easi-Scan, BCF Technology Ltd, Livingston, UK) was used to validate the visual inspection method. Total length was also recorded to the nearest cm. All procedures were carried out under a research permit (S-2015–162) issued by the University of Adelaide Animal Ethics Committee in accordance with the Australian code for the use and care of animals for scientific purposes (NHMRC, 2013).

Wildlife Computers MiniPAT tags (Wildlife Computers, Redmond, WA, USA) programmed for 120-day deployments to cover the pupping season were deployed, fixed to either plastic umbrella or titanium anchor darts via 12 cm plastic coated wire tethers. Tag darts were inserted adjacent to the base of the first dorsal fin using an applicator cleaned with alcohol swabs before and after applications. Care was taken to insert the applicator at a sufficiently shallow angle and remain lateral to the vertebral column to avoid injury to vital organs. Time on deck ranged from 1.5 to 3 min, depending largely on sea conditions and liveliness of sharks. Sharks were swum next to the vessel into the current for up to 30 s until they swam away. Release location and capture depth were then recorded.

Data retrieval and analysis

Tags were programmed to record swimming depth and temperature at 5-min intervals along with daily summaries of thermal mixed layer depth and temperature, and light-based geolocation estimates at dawn and dusk. Upon tag detachment, data were transmitted to the ARGOS satellite network in a randomized manner until remaining battery power was exhausted, such that any gaps in transmission were distributed throughout the dataset rather than concentrated in any one period. Data were retrieved from the ARGOS platform then processed and exported using the Wildlife Computers DAP Processor software v 3.0. Kernel density distributions of swimming depth, temperature, and thermal mixed layer depth were plotted in R (R Core Team, 2013) using the *sm* package (Bowman and Azzalini, 2014). Environmental data were retrieved from the Kangaroo Island Integrated Marine Observing System (IMOS) monitoring station near our 2017 offshore tagging area and compared between tagging years to assess whether environmental conditions varied between years, including sea surface temperature, current speed, current direction, and sub-surface water temperature.

Raw geolocation estimates were refined using the Wildlife Computers GPE3 hidden Markov model fitting location estimates derived from dawn-dusk light levels against known sea surface temperature (SST) and depth data to generate maximum likelihood positions. Model parameters included a swimming speed of $1\ \mathrm{m\ s^{-1}}$ (consistent with other pelagic sharks: Queiroz *et al.*, 2010) and reference data sets were NOAA OI SST V2 high resolution for SST and ETOPO1-Bedrock for bathymetry. Here, we present horizontal movement tracks only for individuals that moved >150 km from tagging sites, since GPE3 geolocation error can exceed actual movements in deployments covering short distances (Braun *et al.*, 2018; Hueter *et al.*, 2018). Pop-up locations are accurate to within 1.5 km (ARGOS, 2016). Resident vs. transient habitat use was explored using the Panoply software v 4.8.10 to extract residency distributions based on 0.25° grid squares from GPE3 outputs. Residency distributions were calculated using a hidden Markov model smoothing approach to state space modelling that uses the posterior distribution of an individual's state to estimate probabilities of behavioural shifts between residency and migration (Pedersen *et al.*, 2011). Movement tracks were plotted against *G. galeus* commercial catch data from shark longline, gillnet, and trawl vessels during tag deployment periods in the Great Australian Bight (December 2015–March 2016) and between Kangaroo Island–Bass Strait (October–November 2017) to relate shark movements to fishing pressure.

Results

Data from three deployments were excluded from analyses due to a mortality based on 3 days of inactivity after release (shark x1: possible wounding based on presence of a mako shark *Isurus oxyrinchus* immediately after release), a premature detachment after 6 days (shark x2), and a tag reporting failure (shark x3) (Supplementary Table S1). Of the remaining eleven tags, six tags (55%) remained deployed for the full scheduled 120 days and deployments spanned a total of 1 083 days (mean ± *SD*: 99 ± 30 days) (Supplementary Table S1). All females tagged in December 2015 ($n = 6$: inshore and early in the pupping season) remained in South Australia, while of those tagged in October 2017 ($n = 5$: offshore and >1 month prior to the pupping season), one remained in South Australia, three migrated to Bass Strait and Tasmania, and one migrated to New Zealand (Figure 2). Some females moved short distances, remaining resident near tagging sites (e.g. 6 km in 80 days [shark S6] or 12 km in 77 days [shark S1]: Supplementary Table S1), while others made long and rapid dispersive movements (e.g. 2 908 km in 120 days [shark S11]: Supplementary Table S1) (Figure 2). One female tagged in the Great Australian Bight in 2015 was captured by a commercial fisher after 80 days at liberty ∼6 km from the tagging location prior to tag detachment (shark S6). Another shark from this group was captured by commercial fishers the following pupping season (January 2017) south of Avoid Bay, South Australia

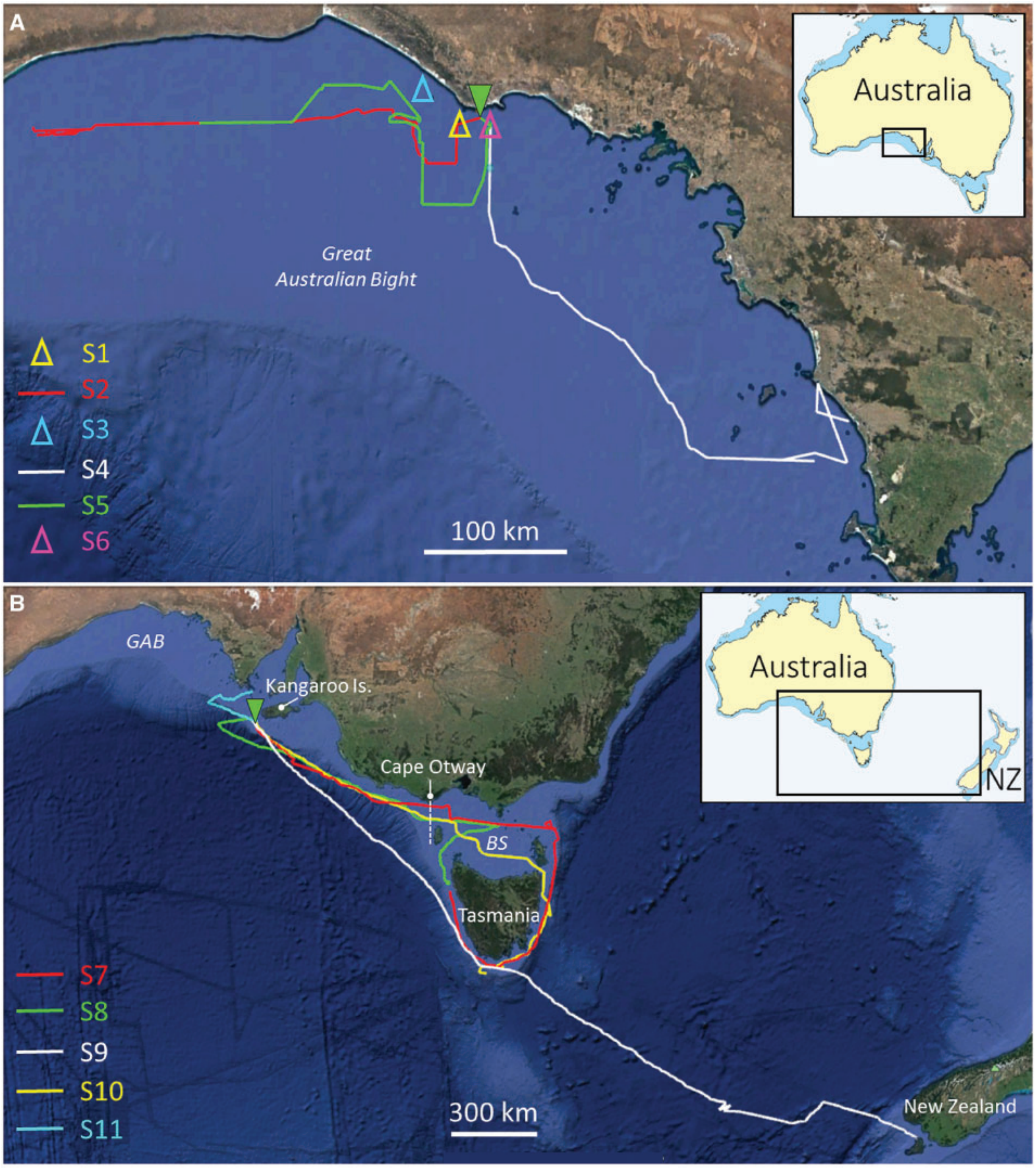

Figure 2. Movements of pregnant *G. galeus* tagged with PSATs in southern Australia in December 2015 ($n = 6$; a) and October 2017 ($n = 5$; b). Estimated movement tracks based on maximum likelihood locations are shown (lines) where sharks moved >150 km from tagging sites. Green inverse triangles = deployment sites. Terminal ends of tracks = pop-up locations (error: <1.5 km). Only pop-up or recapture locations are shown (hollow triangles) where sharks moved <150 km. Insets show study areas (boxed) relative to Australia. GAB, Great Australian Bight; BS, Bass Strait; NZ, New Zealand. Scale bars differ between panels.

~420 km from the tagging location, however it could not be identified as only the titanium anchor dart and tether remained *in situ* and total length was not recorded at recapture.

Residency distributions revealed strong plasticity in behaviour among sharks. Maximum probabilities of resident behaviour ranged from <0.1 to 0.9, where the highest probability of residence = 1 (Figure 3). Sharks tagged inshore in the Great Australian Bight in 2015 were more likely to exhibit semi-resident or resident behaviour (maximum residency probabilities: 0.2–0.9, mean: 0.4 ± 0.3) associated with their short movements, while sharks tagged off Kangaroo Island in 2017 were more transient (maximum residency probabilities: <0.1, mean: 0.04 ± 0.02)

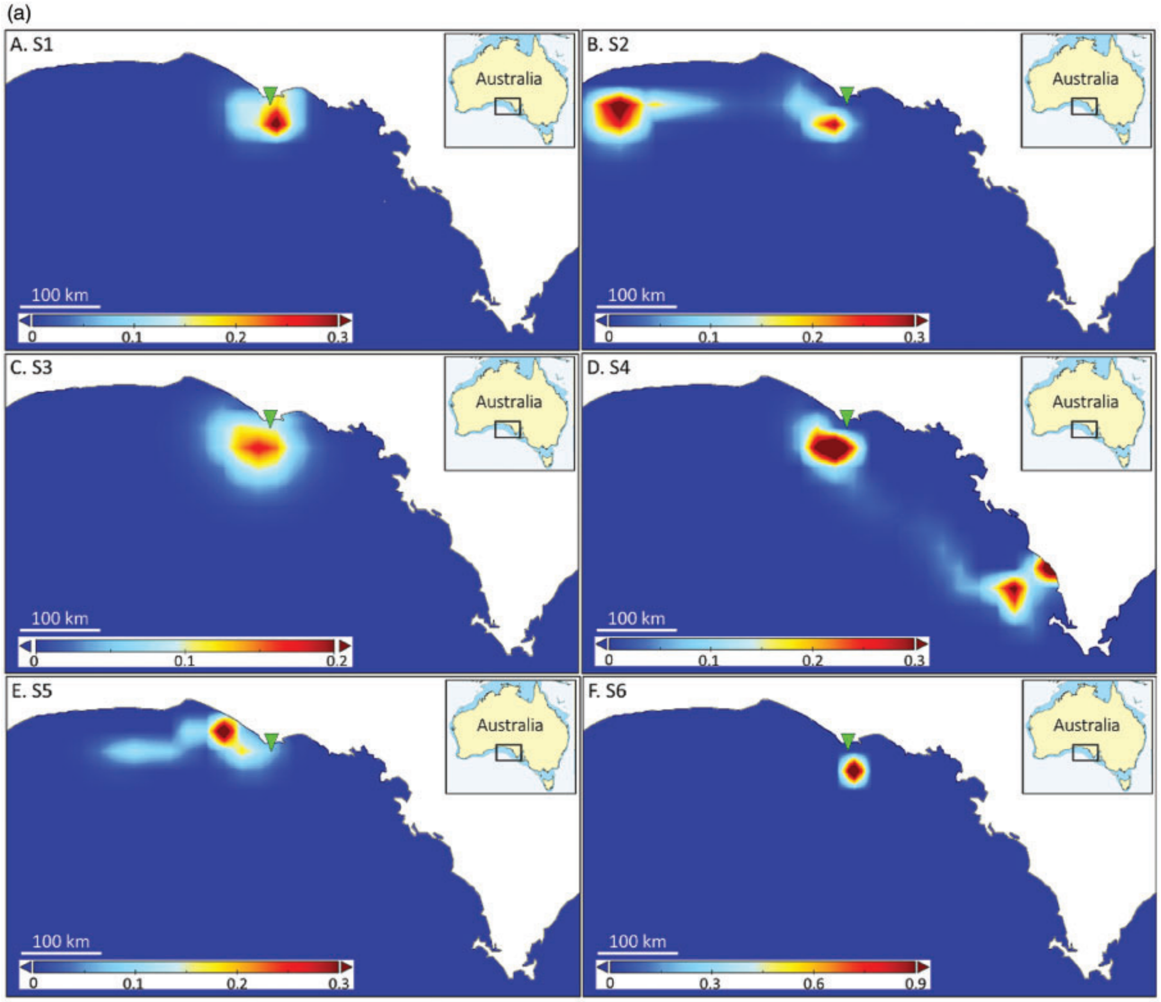

Figure 3. (a) Habitat use by pregnant *G. galeus* tagged in the Great Australian Bight in December 2015 at the start of the pupping season shown by residency distributions, i.e. probability of resident vs. transient behaviour based on 0.25° grid squares. Probability scales differ according to degree of residency in individual sharks (range: 0.2–0.9), maximum residency probability = 1. Inverse triangles = tagging locations. Scale bars differ among panels. Insets show study areas (boxed) relative to Australia. (b) Habitat use by pregnant *G. galeus* tagged offshore from Kangaroo Island in October 2017 prior to the pupping season shown by residency distributions, i.e. probability of resident vs transient behaviour based on 0.25° grid squares. Maximum residency probability = 1. Inverse triangles = tagging locations. Scale bars differ among panels. Insets show study areas (boxed) relative to Australia.

(Figure 3). Environmental conditions were broadly similar in both tagging periods. Sea surface temperature was similar throughout the study area during October (i.e. during our offshore tagging period) with no significant intrusion of the Leeuwin current from Western Australia in the Great Australian Bight (Supplementary Figure S1). Water temperature near the offshore tagging site off Kangaroo Island was also similar in this period (mean ± *SD*: 2015 = 14.5 ± 1.2°C, 2017 = 14.7 ± 0.9°C), as were current speed ($2015 = 0.4 \pm 0.3\ \mathrm{m\ s^{-1}}$, $2017 = 0.4 \pm 0.3\ \mathrm{m\ s^{-1}}$), and current direction (2015 = 179 ± 11°, 2017 = 171 ± 19°). A paired *t*-test showed mean monthly water temperatures at this site were also similar throughout September–December (i.e. when pupping migrations are undertaken) in 2015 (mean ± *SD*: 14.7 ± 0.2°C) and 2017 (mean ± *SD*: 15 ± 0.1°C, $t_3 = -2.9$, $p = 0.06$).

Three females that migrated to Bass Strait followed close to the shelf break (depth: 115–200 m) with excursions onto the slope, rather than via the inshore no-take zone (depth: generally <50 m though <80 m near Portland and Cape Otway), reaching mean daily maximum depths of 170 m (Figure 2b, Supplementary Figure S2). Females following this migration pathway (all tagged southwest of Kangaroo Island in early October) passed Cape Otway and were into Bass Strait prior to the end of November (Figure 2b). In contrast, females that remained in the Great Australian Bight reached mean daily maximum depths of only 43 m and spent more time (67% of observations) in the thermal mixed layer than migrating females (55% of observations) (Figure 4). Temperatures encountered ranged from 8 to 22°C and differed between residents and migrants ($t_9 = -4.2$, $p < 0.01$), with migrating females generally experiencing colder temperatures (mean: 14°C, range: 8–18°C) than those that remained resident in the Great Australian Bight (mean: 18°C, range: 13–22°C) (Figure 4). Although migrants maintained highly transient behaviour throughout the tracking period with probability of resident behaviour < 0.1, they appeared to select slightly warmer waters

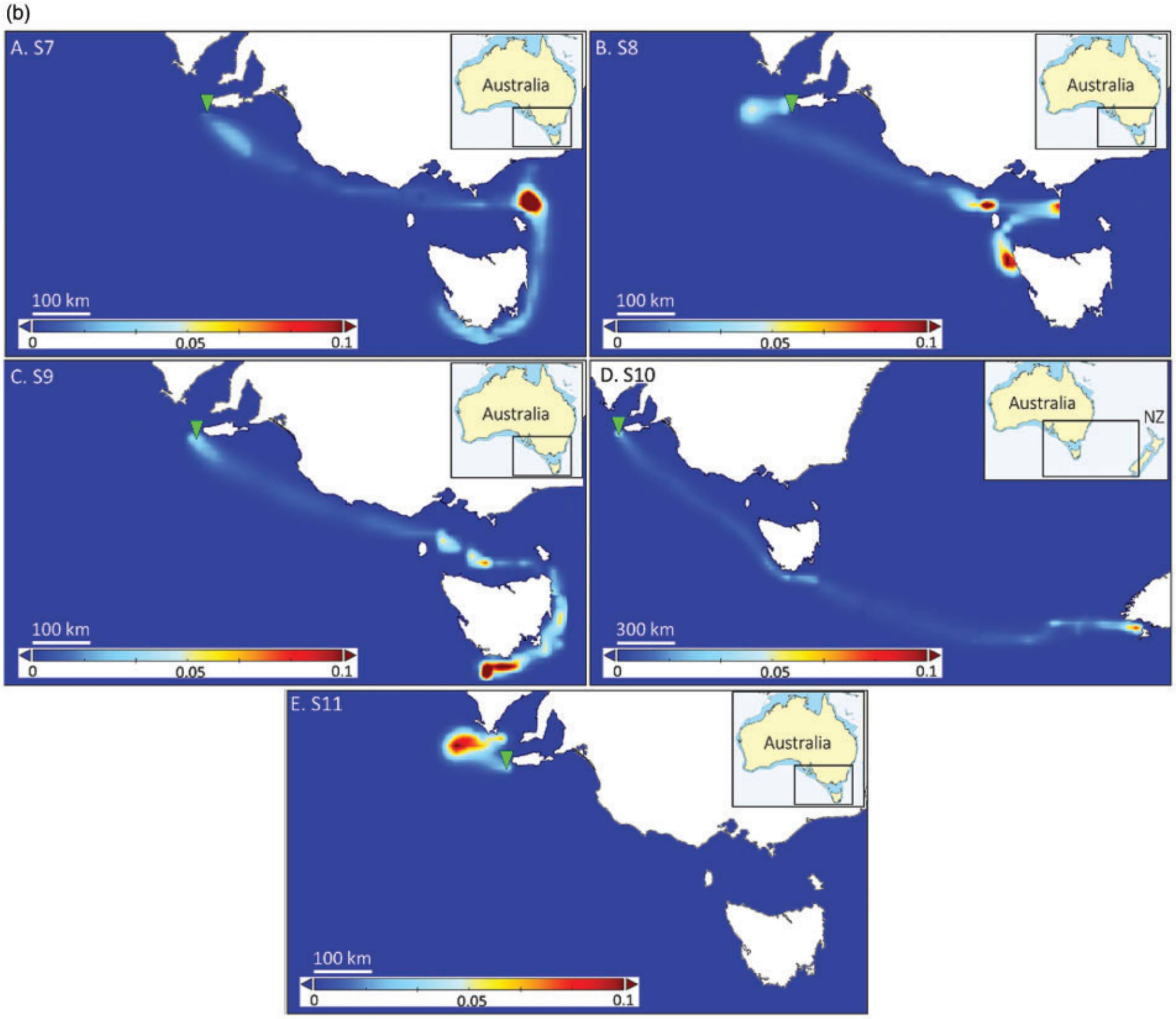

Figure 3. Continued.

during brief periods where residency probability was ≥ 0.05 (mean ± $SD = 15.3 \pm 1.5$°C) compared to periods where residency probability was < 0.05 (mean ± $SD = 14 \pm 1.7$°C), however a paired *t*-test found these differences were not statistically significant ($t_3 = -1.7$, $p = 0.19$). Migrating females moving along the outer shelf from Kangaroo Island to Bass Strait were exposed to greater fishing pressure than females that remained inshore (Figure 5). Vertical migrations were ubiquitous, continuing even during long-range movements >500 km (Supplementary Figure S2). The furthest moving female (shark S11 to New Zealand: 2 908 km) reached the maximum dive depth (536 m), and recorded the fastest swimming speed (>500 km: 24 km day^{-1}).

Discussion

We found partial female migration in Australian *G. galeus*, with some females remaining resident close to tagging locations (<15 km) over the pupping season in November–January and others migrating long distances to New Zealand (~3 000 km) (Figure 2). One female was also in western South Australia during two consecutive pupping seasons (tagged in December 2015 and recaptured January 2017). Pupping in South Australia (and thus partial female migration given the mixed nature of the stock) is also supported by recent evidence, such as capture of neonates there (Rogers *et al.*, 2017; McMillan *et al.*, 2018) and use of different pupping areas by South Australian and Bass Strait populations revealed by postnatal vertebral element signatures (McMillan *et al.*, 2018). Dispersive female *G. galeus* thus appear to migrate north from Tasmania and Bass Strait to overwinter in South Australia (Olsen, 1954; Punt *et al.*, 2000) before returning south to pup, while some pregnant females remain resident in South Australia throughout the pupping season. Behavioural plasticity among sharks tagged inshore at the start of the pupping season (December 2015) and those tagged offshore prior to the pupping season (October 2017) was marked by divergent modes of resident vs. transient habitat use. This was consistent with advice from experienced fishers who insist they encounter *G. galeus* in the same areas that differ in behaviour, colouration, and ectoparasite loads, which they relate to differences between resident and transient sharks.

Inshore shark fishing closures are in place along the coast to ~6 km offshore from Kangaroo Island running east along the mainland into Bass Strait to protect migrating *G. galeus*.

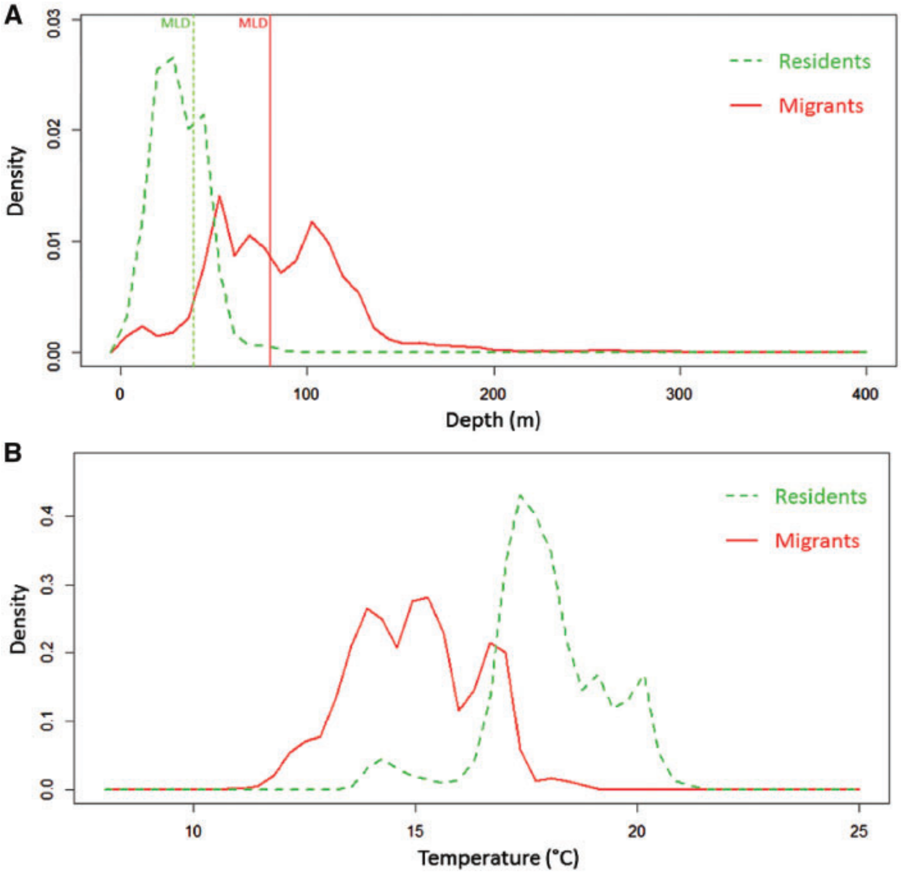

Figure 4. Density distributions showing time-at-depth (a) and time-at-temperature (b) for pregnant *G. galeus* that remained resident in the Great Australian Bight (dashed lines) and migrated to Bass Strait (solid lines). Vertical lines on upper panel (a) denote mean thermal mixed layer depth (MLD) for residents (dashed: 39 m) and migrants (solid: 80 m).

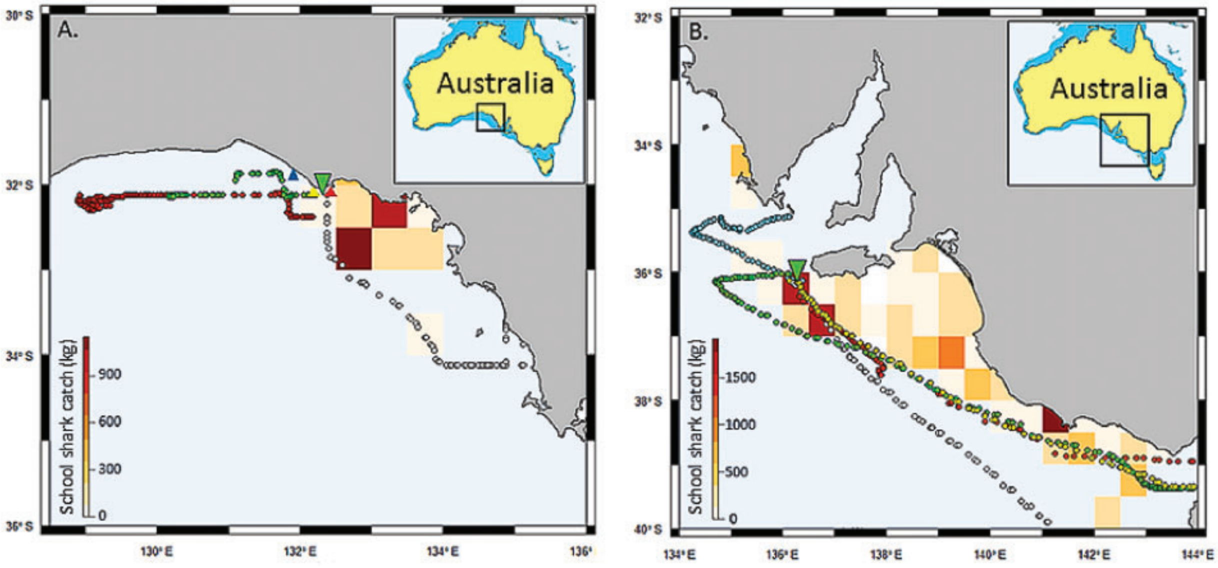

Figure 5. Movement tracks of tagged pregnant *G. galeus* relative to fishing pressure in the shark fishery off southern Australia. Density of *G. galeus* commercial catch (kg 0.25° grid square-1) is shown during periods of tag deployment from December 2015 to March 2016 in the Great Australian Bight (a) and from October to November 2017 on the migration pathway between Kangaroo Island and Bass Strait (b). Inverse triangles = deployment sites. Track IDs as for Figure 2. Catch data courtesy: Australian Fisheries Management Authority.

However, migrating females in this study favoured an offshore migration pathway close to the shelf break en route to Bass Strait, swimming at mean daily maximum depths of 170 m with excursions into deeper water on the continental shelf slope. While existing closures may benefit females moving close inshore during pupping runs, females migrating in deeper waters remain unprotected and exposed to fishing pressure. Migrating females faced greater fishing pressure from longline, gillnet and trawl vessels along this route than individuals remaining in shallower inshore areas (Figure 5). Given sharks' reliance on internal fertilization and thus limited fecundity, exposing mature female sharks to fishing pressure can impact heavily on population resilience (Ford, 1921; Mucientes *et al.*, 2009). The failure of current protections to cover migrating females may therefore limit the efficacy of terminal sanctuaries in south-eastern nursery areas (Gerber *et al.*, 2005; Costa *et al.*, 2012).

Migrating in deep, cool waters may reduce energetic costs of migration. Marine ectotherms can receive large energetic rewards, i.e. reduced energy costs, by moving to deep, cold waters (Steffensen, 2005; Seibel and Drazen, 2007). Metabolic demands of the related leopard shark *Triakis semifasciata*, decreased by a factor of 2.51 per 10°C decrease in temperature (Miklos *et al.*, 2003). Female *G. galeus* migrated in cool, deep water en route to Bass Strait and New Zealand (mean temperature: 14°C, range: 8–18°C). Migration along the shelf break may also be assisted by favourable currents. The eastward flowing South Australian current flows along the shelf break from the Great Australian Bight to the western edge of Bass Strait (Ridgway and Condie, 2004). The underlying Flinders current flows parallel at >400 m depth in the opposite direction pushing cool water up the shelf slope (Middleton and Bye, 2007). The shelf break may thus provide a convergence of favourable current direction and cool waters to lower metabolic costs. Despite using greater depths than residents, migrants maintained vertical foraging excursions into the warm thermal mixed layer (Supplementary Figure S2), where productivity is high and prey more abundant (McGowan and Hayward, 1978; Brainerd and Gregg, 1995). In contrast, sharks remaining in the Great Australian Bight stayed in warmer, inshore waters (Figure 4). Of six females tagged in the Great Australian Bight (mean temperature: 18°C, range: 13–22°C), only one (which moved the furthest: 334 km) swam in water <14°C (mean: 16°C), further suggesting that large-scale movements occur in cool waters potentially to reduce transport costs. Distribution of *G. galeus* on the shelf may be driven by interactions among shelf water masses (Jaureguizar *et al.*, 2018); future availability of detailed bottom temperature and other environmental data in the Great Australian Bight may allow any such relationships to be explored.

It is unclear whether female migrations are driven by philopatry, genetic predisposition, or condition-dependent choice. Philopatry could have important repercussions for conservation, e.g. disproportionate female mortality on certain migration routes could drive local population declines (Prince, 2005). Alternatively, if migration is a condition-dependent choice, numbers of migrants may vary over time. Environmental conditions (temperature, current speed, and current direction) were similar between tagging periods on the migration pathway and thus appear unlikely to have influenced resident vs. migratory behaviour. Prey abundance can drive shark movements (Sims, 2003; Hussey *et al.*, 2009; Speed *et al.*, 2010) and female *G. galeus* from southern latitudes are thought to pursue key prey species, e.g. jack mackerel *Trachurus declivis* as they move north into South Australia in winter with the highly productive subtropical convergence (Harris *et al.*, 1992; Punt *et al.*, 2000). However, while resource-driven migrations make sense for females from the southeast, they do not for females from South Australia where productivity remains comparatively high year round, enhanced by winter intrusions of the subtropical convergence and summer upwellings supporting vast shoals of sardines *Sardinops sagax* (Ward *et al.*, 2006), important prey for *G. galeus* (Ripley, 1946; Freer, 1992). The role of temperature as an ecological resource may also be important. Ectothermic fishes are known to use warm temperatures as a resource to maximize growth and fitness (Magnuson *et al.*, 1979; Brandt, 1993; Wirsing *et al.*, 2006). There is thus biological sense in mature females aggregating in the relatively warm waters of the Great Australian Bight over cooler months to maximize growth and fitness of themselves and their young, as has been suggested in other sharks (Hight and Lowe, 2007; Speed *et al.*, 2012), while building energy stores before dispersing to their respective pupping areas.

Partial migration is consistent with the current state of knowledge around *G. galeus* population dynamics in Australia. Demographic connectivity among populations has long been established by mark–recapture studies (Olsen, 1954; Brown *et al.*, 2000; Walker *et al.*, 2008) and genetic connectivity has been established more recently (Hernández *et al.*, 2015). However, the fact that new, apparently virgin populations were encountered as the fishery expanded westward after denuding previously fished populations (Olsen, 1959; Prince, 1996), is difficult to reconcile with a model of obligate female migration and a fully mixed stock. Partial migration explains both the established connectivity between populations and the capacity for populations to be locally over-exploited. Regional variations in resource availability over time may offer partially migratory species population-level resilience by benefiting migrants and residents at different times (Kerr *et al.*, 2009; Gillanders *et al.*, 2015). However, differences in movements and habitat use may also expose partially migratory populations to different threats, e.g. overharvesting or habitat degradation in different areas (Secor *et al.*, 2001; Parsons *et al.*, 2011). Where partial migration is occurring, it should therefore be identified and incorporated in conservation and management models. In addition, direct evidence of reproductive connectivity between Australia and New Zealand complements recent evidence of genetic connectivity (Hernández *et al.*, 2015; Bester-van der Merwe *et al.*, 2017), supporting a single panmictic stock. Consideration should therefore be given to trans-national management of the Australia–New Zealand school shark stock as a single management unit to best incorporate spatial modelling into fisheries management (Guan *et al.*, 2013; Secor, 2013; Braccini *et al.*, 2016).

Pregnant *G. galeus* in Australia thus undertake partial female migrations, with migrants using potentially predictable offshore migration pathways and timings. Pupping habitats are also likely less spatially confined than currently assumed, stretching from the Great Australian Bight to New Zealand rather than being concentrated in Bass Strait and Tasmania. This behaviour is analogous to that of many birds, dispersive contingents of which migrate to warmer climes from higher latitudes during winter while those from lower latitudes remain resident (Adriaensen and Dhondt, 1990; Berthold, 1991; Newton, 2010). These findings demonstrate the value of spatially explicit data from archival tags to refine information elicited from conventional mark–recapture studies. Our finding of partial migration may help clarify difficulties the current management model encounters in explaining serial depletion of the *G. galeus* stock in different areas, which appears incompatible with the assumption of obligate migration (R. Thomson, pers. comm.). In *K*-selected taxa with limited numbers of offspring, fulfilment of reproductive behaviours and movements by mature females is critical to population recovery and resilience. Spatially and temporally explicit movement information, as presented here, may thus assist conservation and fisheries managers in enabling fulfilment of key reproductive tasks by females of such taxa.

Supplementary data

Supplementary material is available at the *ICESJMS* online version of the manuscript.

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