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Natural tags reveal populations of Conservation Dependent school shark use different pupping areas

M. N. McMillan[1,*], C. Huveneers[2], J. M. Semmens[3], B. M. Gillanders[1]

[1]Southern Seas Ecology Laboratories, School of Biological Sciences and Environment Institute, University of Adelaide, Adelaide 5005, Australia
[2]School of Biological Sciences, Flinders University, Bedford Park 5042, Australia
[3]Institute for Marine and Antarctic Studies, University of Tasmania, Taroona 7053, Australia

ABSTRACT: Knowledge of reproductive movements and sources of recruitment in highly mobile species is important to understand population-level resilience and to manage recovery in populations depleted by human interference. Management of the school shark *Galeorhinus galeus* (Linnaeus, 1758), a Conservation Dependent species in Australia subject to a national recovery strategy after stock collapse from overfishing, has long assumed obligate female migration to pupping areas in the southeast of their range. We used post-natal elemental signatures of individuals from 3 cohorts born in 1996 to 1998 as a proxy to test whether females use common pupping areas. Environmental or biological factors that differ among pupping areas can give rise to unique trace element signatures in shark vertebrae that act as natural tags and can be used to assess relative contributions from recruitment sources to adult populations. We compared post-natal signatures from sharks caught in 2 regions, South Australia in the northwest of the species' range and Bass Strait in the southeast, using laser ablation inductively coupled mass spectrometry. Signatures were similar between regions for 1 cohort, suggesting high use of shared or similar pupping areas, but differed for the 2 remaining cohorts. Region of capture could also be accurately predicted (>75%) based on post-natal signatures, refuting the long-held view that all females use common pupping areas. We conclude that female movements and reproductive strategies are likely more plastic than previously assumed, highlighting the need to clarify them and their potential effects on resilience and conservation.

KEY WORDS: Behavioural plasticity · Laser ablation inductively coupled mass spectrometry · LA-ICP-MS · Partial migration · Reproductive strategies · Recovery · Resilience

INTRODUCTION

Migratory species present considerable challenges for conservation management (Thirgood et al. 2004, Martin et al. 2007, Dulvy et al. 2008) that are amplified when variability in migrations occurs and direct observations are difficult or impossible to make. Knowledge about spatial ecology, e.g. connectivity among populations and sources of recruitment, is central to conservation planning (Webster et al. 2002, Simpfendorfer et al. 2011), particularly for managing the recovery of species depleted by overharvesting or habitat degradation (Martin et al. 2007, Petitgas et al. 2010). Furthermore, conservation efforts can be confounded where there is incomplete knowledge about reproductive movements; adult migrations to recruitment areas may be modeled on incomplete information. Widespread use of nursery areas by sharks (Feldheim et al. 2002, Heupel et al. 2007) can magnify the importance of knowledge about repro-

*Corresponding author: matthew.mcmillan@adelaide.edu.au

ductive migrations for conservation efforts. Many sharks and other elasmobranchs are unique in the marine realm for combining internal fertilisation with limited parental care, investing substantial resources into small numbers of offspring for which they select pupping habitats providing shelter, food, and protection from predators to maximise recruitment (Branstetter 1990, Simpfendorfer & Milward 1993).

School shark *Galeorhinus galeus* were heavily exploited in one of Australia's oldest commercial fisheries from the 1920s to the 2000s, leading to stock collapse, by which time stock size had declined to <14 % of original pup production levels (McLoughlin 2007). The species was listed as Conservation Dependent under the Environment Protection and Biodiversity Conservation Act 1999. A stock rebuilding strategy was introduced after the stock failed to recover, despite no longer being targeted commercially (AFMA 2009, Huveneers et al. 2013, McAllister et al. 2017). School shark are long-lived, ~60 yr (Walker 1999), and reach lengths up to 174 cm (Olsen 1954) in Australia. They have low reproductive capacity arising from late onset of maturity (>120 cm for males and >135 cm for females, equating to ages of ~8 and 11 yr, respectively), low fecundity (~28 pups), and a bi-annual reproductive cycle (Olsen 1954, Walker 1999), leading to a limited recovery potential. Despite these conservation challenges, a lack of knowledge about their reproductive movements and pupping areas persists.

Seventeen pupping areas were identified in the southeast of the species' range in the 1950s with help from the established commercial fishery in the region, while the fishery to the northwest in South Australia (SA) was in its infancy and had yet to locate such areas (Olsen 1954). However, productivity varied widely among these sites and more recently is concentrated in a handful of estuaries and sheltered bays (Stevens & West 1997) (Fig. 1). Combined with the absence of mature females from the southeast of their range during winter when they aggregate in SA, this led to a belief that persists today that all pregnant females migrate to southeastern pupping areas to pup during summer (Olsen 1954, Punt et al. 2000, Walker et al. 2008). However, recruitment from recorded pupping areas is vastly insufficient to support the population (Prince 1996, Stevens & West 1997, Walker 1999); >90 % of pupping activity is occurring elsewhere (Stevens & West 1997). Despite limited scientific investigation of other potential pupping areas since the 1950s, recent evidence of pupping in SA has emerged and includes presence of neonates <45 cm up to >1500 km from recorded nurseries (Knuckey et al. 2014, Rogers et al. 2017), presence of late-term pregnant females (Prince 1996, West & Stevens 2001, M. N. McMillan unpubl. data), and presence of females in immediate post-partum condition (Braccini et al. 2009). If females also pup in SA, the currently assumed obligate female migration must be inaccurate, instead entailing partial female migration.

Differences among pupping areas give rise to unique elemental signatures retained throughout the lives of sharks in the post-natal portion of their calcified vertebrae that may be driven by differences in water chemistry, diet, or environmental factors moderating elemental uptake (e.g. temperature or salinity) (Smith et al. 2013, McMillan et al. 2017a). These signatures act as natural tags present in all individuals that allow demographic connectivity among populations to be assessed at ecological timescales (Tillett et al. 2011, Lewis et al. 2016, Smith et al. 2016). The present study aimed to investigate (1) the validity of the obligate female migration hypothesis in *G. galeus* by analysing post-natal natural tags in

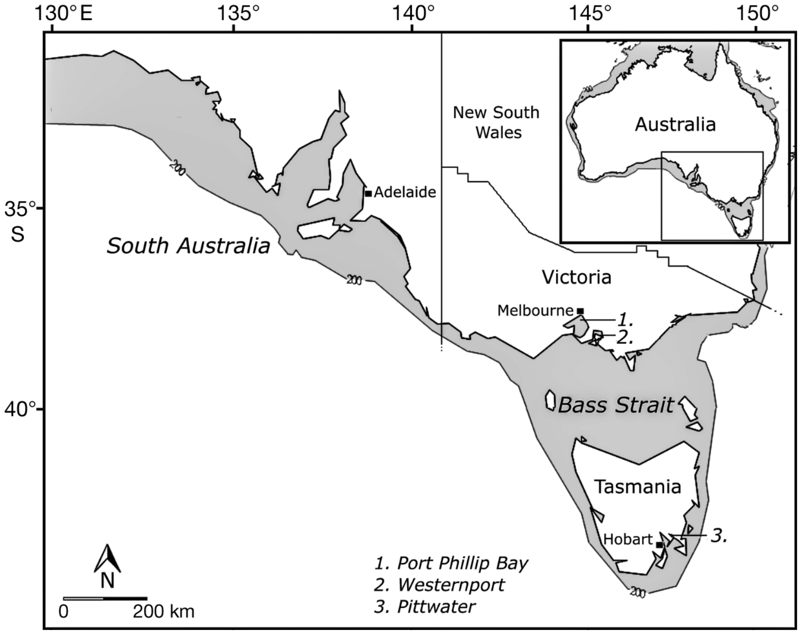

Fig. 1. Study area in southeastern Australia. The area depicted covers the core range of *Galeorhinus galeus* in Australian waters, although individuals are sometimes encountered further north and west. Main recorded nursery areas are numbered (1–3). Samples were compared between sharks caught in South Australia and Bass Strait. Inset shows study area (boxed) relative to Australia

vertebrae as a proxy of female reproductive movements and (2) whether sharks from SA and Bass Strait (BS) demonstrated evidence for use of common or different pupping areas. We predicted that post-natal elemental signatures would be similar for sharks caught in both regions if females from across their range undertake obligate migrations to common pupping areas in the southeast of their range. If post-natal signatures differed between regions, this would suggest that pupping areas differ between SA and BS and that pupping is likely not as spatially confined as currently assumed.

MATERIALS AND METHODS

Experimental design and sample collection

Cervical vertebral centra from 154 individuals were sourced from archival collections available at the Commonwealth Scientific and Industrial Research Organisation (CSIRO), Hobart. Vertebrae were collected from 2000 to 2003 and stored frozen until processed for age determination. Processing involved removal of adjoining tissue by immersion in bleach solution (active ingredients: 42 g l^{-1} sodium hypochlorite and 9 g l^{-1} sodium hydroxide) for up to 40 min. Bleaching of *Galeorhinus galeus* vertebrae using this method does not affect trace element concentrations for a range of elements (Ba, Li, Mg, Mn, Pb, Sr, Zn; exception Na) (McMillan et al. 2017a). Na was therefore not analysed in the present study.

Several cervical vertebrae were sampled from each shark, one of which was selected for age determination and embedded in polyester resin and then cut sagittally through the vertebral focus into 250 µm thick sections. Age was estimated by counting growth increments under a dissecting microscope using transmitted light and elevated contrast and used to determine birth year since year of capture was known. Age determination using this method has been validated for *G. galeus* <140 cm total length (TL) (Walker et al. 2001), and increment counts do not vary among adjacent vertebrae (Officer et al. 1996). Age estimation was conducted by 2 readers with precision of age estimates between readers well within acceptable limits (CV = 2.7%) (Chang 1982, Campana 2001). Samples from 3 cohorts (birth years: 1996, 1997, and 1998) were selected for further analysis (Table 1). Specimen size ranged from ~82 to 138 cm TL and age from 2 to 7 yr. In Australia, *G. galeus* have a well-defined pupping season beginning in November, peaking in December or January, and concluding by February (Olsen 1954, Stevens & West 1997), with neonates dispersing from pupping areas from March to June (McAllister et al. 2015). An arbitrary birth date of 1 January is thus assigned to *G. galeus* in the southern hemisphere (Moulton et al. 1992, Francis & Mulligan 1998); a shark of the 1996 cohort would therefore be considered 1 yr old at 1 January 1997, having been born in austral summer 1995–1996, and any migrations to pupping grounds by its mother would have occurred in 1995.

Table 1. Summary of sampling information and biological data including region of capture, cohort (birth year), sample size (n), sex ratio (male:female, M:F), age range, and total length (TL) range

Region	Cohort (birth year)	n	Sex (M:F)	Age (yr)	TL (cm)
South Australia					
	1996	27	1:1.25	4–6	90–131
	1997	27	1:0.93	3–5	88–121
	1998	25	1:2.13	2–4	82–117
Bass Strait					
	1996	24	1:0.71	4–7	92–138
	1997	26	1:1.36	3–6	85–138
	1998	25	1:1.08	2–5	86–126

Sample preparation for laser ablation

After individuals were assigned to cohorts, one of the remaining vertebral centra from each shark was embedded in an epoxy resin and cut sagittally into 500 µm thick sections with a low-speed diamond saw. Sections were polished with lapping film of decreasing grade (30, 9, and 3 µm) before rinsing in ultrapure water and air drying in a fume cupboard. Sections were then mounted onto glass microscope slides using thermoplastic glue. Birth bands were identified using transmitted light and elevated contrast under a dissecting microscope and marked by etching the adjacent resin to allow for accurate location of post-natal tissue during laser ablation.

Laser ablation inductively coupled mass spectrometry

Element concentrations were assayed using laser ablation inductively coupled mass spectrometry (LA-ICP-MS) employing a New Wave 213 laser coupled to an Agilent 7500cx mass spectrometer. Ca was used as an internal standard at a percent mass composition of 43% (equivalent to other carcharhiniform sharks from temperate Australian waters, e.g. *Carcharhinus brachyurus*: McMillan et al. 2017a). Transects of 200 µm length were ablated across the corpus calcareum perpendicular to its axis and immediately distal to the natal band, representing approximately the first month of growth after birth (Fig. 2). Transects were checked post ablation to ensure that only post-natal material was sampled. Transects were scanned at a speed of 5 µm s^{-1}, a width of 80 µm, and a frequency of 10 Hz. Glass reference standards (NIST 612) were ablated before and after each session and periodically after every 10 samples to account for any instrument drift. Elements analysed included ^{7}Li, ^{24}Mg, ^{55}Mn, ^{88}Sr, ^{138}Ba, and ^{203}Pb as well as ^{43}Ca against which element:Ca ratios could be calculated for statistical analysis by normalising raw element count data to Ca (mmol mol^{-1}). Element concentrations for all samples were detected at levels >3 SDs greater than mean limits of detection calculated for each session. CVs were calculated for each session and were <5% for all elements (range: 0.7–4.8%).

Statistical analysis

Element:Ca ratios were log(x + 1) transformed to normalise elemental distributions and ensure all elements were on a similar scale to relativise effects of abundant elements and then analysed using the PRIMER Permanova software package. To determine if differences occurred between regions and birth year, the multi-element signature (all 6 element:Ca ratios) was analysed using permutational MANOVAs (Anderson 2001) with both factors treated as fixed factors; a Euclidean distance matrix was used. Where significant differences were found, post hoc *t*-tests were used to determine which region or birth years differed. Similar analyses were used for individual elements using univariate ANOVAs. Canonical analysis of principle coordinates (CAP) (Anderson & Willis 2003) was used to assess spatial variation among regions using a leave-one-out approach to predict the region of origin of samples based on their post-natal signatures.

RESULTS

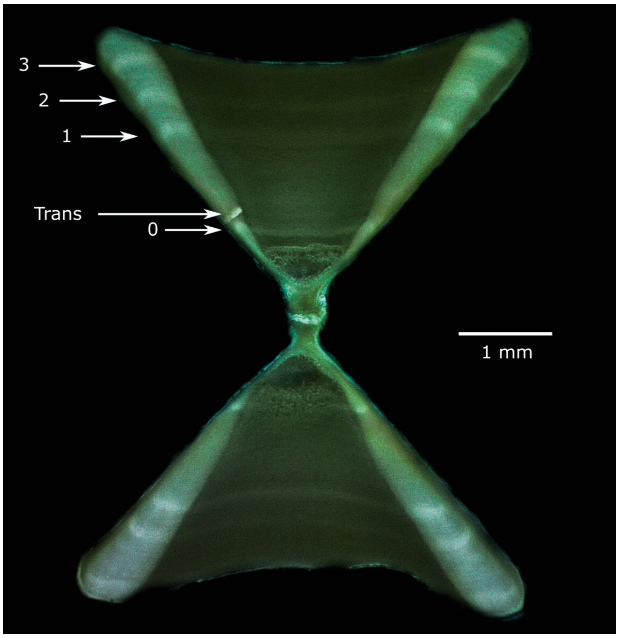

Fig. 2. Sectioned vertebral centrum of a 3 yr old school shark showing the ablated 200 µm laser transect (Trans) used to sample natal elemental signatures immediately distal to the birth band (0). Annual growth bands are numbered 1 to 3. Scale bar = 1 mm

Significant variation in post-natal elemental signatures in vertebrae of sharks occurred with interactions between year and region (Table 2). Sharks born in 1996 caught in both regions (SA and BS) had similar multi-element signatures ($t = 0.41$, $p = 0.74$), while corresponding signatures of sharks born in 1997 and 1998 differed between regions (1997: $t = 2.70$, $p < 0.01$ and 1998: $t = 2.29$, $p = 0.03$). There were also differences in multi-element signatures between regions (with sharks from all cohorts pooled: Table 2) and between years (1996–1997: $t = 2.08$, $p = 0.04$ and 1997–1998: $t = 2.11$, $p = 0.04$), validating the approach of comparing post-natal signatures within cohorts. The interaction between year and region observed for the multi-element signature (Table 2), indicating variation among years for spatial patterns, was reflected by a corresponding interaction for Mg:Ca that was similar for sharks born in 1996 ($t = 0.39$, $p = 0.71$) but that differed for sharks born in 1997 ($t = 2.73$, $p < 0.01$) and 1998 ($t = 2.30$, $p = 0.03$) (Table 2). Concentrations of Mg, Mn, and Li all varied between regions (Table 2), with Mn:Ca and Li:Ca generally higher in sharks caught in SA and Mg:Ca higher in sharks caught in BS born in 1997 and 1998 (Fig. S1 in the Supplement at www.int-res.com/articles/suppl/m599p147_supp.pdf). There was no significant variation in signatures between sexes ($F_{1,152} = 0.02$, $p = 0.96$).

CAP successfully predicted the region of capture for 75.3% of sharks based on their post-natal signatures (72.2% of sharks caught in SA and 78.7% of

Table 2. Permutational MANOVA results for the multi-element signature (Multi) and univariate ANOVAs for individual elements (Element:Ca) with region (i.e. South Australia vs. Bass Strait), cohort (birth years 1996, 1997, and 1998), and interactions thereof as factors. Significant differences ($p < 0.05$) are in **bold**

Element	Region			Cohort			Cohort × Region			Residual	
	df	MS	p	df	MS	p	df	MS	p	df	MS
Multi	1	0.501	**0.003**	2	0.198	**0.042**	2	0.189	**0.046**	148	<0.01
Li:Ca	1	<0.001	**<0.001**	2	<0.001	0.32	2	<0.001	0.412	148	<0.01
Mg:Ca	1	0.496	**0.002**	2	0.191	**0.038**	2	0.187	**0.046**	148	0.06
Mn:Ca	1	0.002	**0.016**	2	<0.001	0.306	2	<0.001	0.987	148	<0.01
Sr:Ca	1	0.003	0.241	2	0.006	**0.038**	2	0.002	0.289	148	<0.01
Ba:Ca	1	<0.001	0.116	2	<0.001	**0.022**	2	<0.001	0.947	148	<0.01
Pb:Ca	1	<0.001	0.450	2	<0.001	0.695	2	<0.001	0.570	148	<0.01

sharks caught in BS). Multi-element signatures showed considerable mixing of sharks from both regions in quadrant I of the CAP plot, whereas quadrants II and III were dominated by sharks caught in SA and quadrant IV was dominated by sharks caught in BS (Fig. 3). When individual cohorts were isolated from the CAP plot, similar patterns were discernible in all plots; however, signatures for sharks born in 1996 (Fig. 4A) were more clustered than for those born in 1997 (Fig. 4B) and 1998 (Fig. 4C).

DISCUSSION

Our results showed that sharks from both regions came primarily from different pupping areas in 2 years (1997 and 1998) and similar pupping areas in another year (1996). It is unclear whether the similarity of signatures from 1996 arose from use of common or similar pupping areas for this cohort. In relatively homogeneous marine environments, where most *Galeorhinus galeus* pupping likely occurs (Stevens & West 1997), there may be little variation in elemental signatures among regions. Where no differences exist, this should not automatically be taken for evidence of a single group, since the drivers of variability in signatures are not known (Campana et al. 2000). In marine environments, differences may emerge at broad regional scales such as in the present study, which may be of particular ecological relevance for studying wide-ranging species (Smith 2013, McMillan et al. 2017b). To date, little experimental work has validated drivers of elemental signatures in elasmobranchs (but see Smith et al. 2013). Such drivers may include regional differences in water chemistry, diet, temperature, salinity, physiology, or ontogeny (Smith et al. 2013). Ontogeny, however, is unlikely to have influenced differences in signatures here since all signatures were derived from the same cohort. Knowledge about specific drivers of elemental signatures is not required to distinguish groups of fish where the aim is simply to determine if such differences exist (Thorrold et al. 1998).

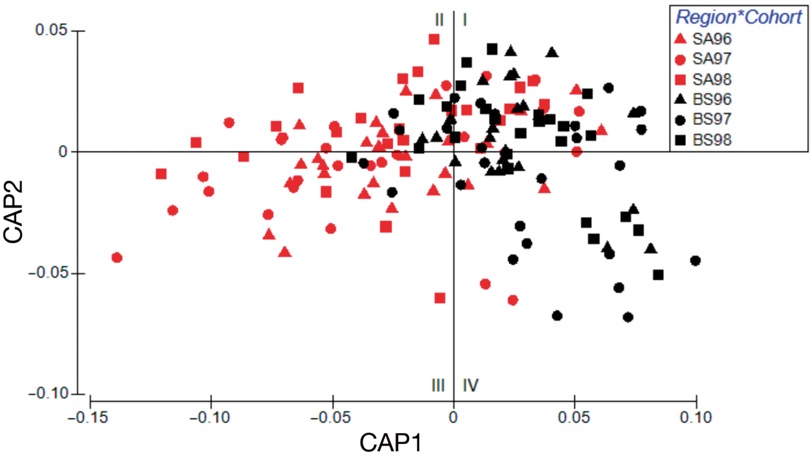

Fig. 3. Canonical analysis of principle coordinates (CAP) plot with cohorts (1996: triangles; 1997: circles; 1998: squares) pooled by region. Red and black symbols denote sharks caught in South Australia (SA) and Bass Strait (BS), respectively. Quadrants are numbered I to IV

Differences in post-natal signatures between regions indicate different pupping areas make major contributions to the SA and BS populations, at least in some years. One possibility is that pupping remains restricted to the southeast of the species' range but that females bearing pups destined for SA or BS select different pupping sites in the same general region. Alternatively, undiscovered pupping areas in other locations may make major contributions to the SA population, e.g. in

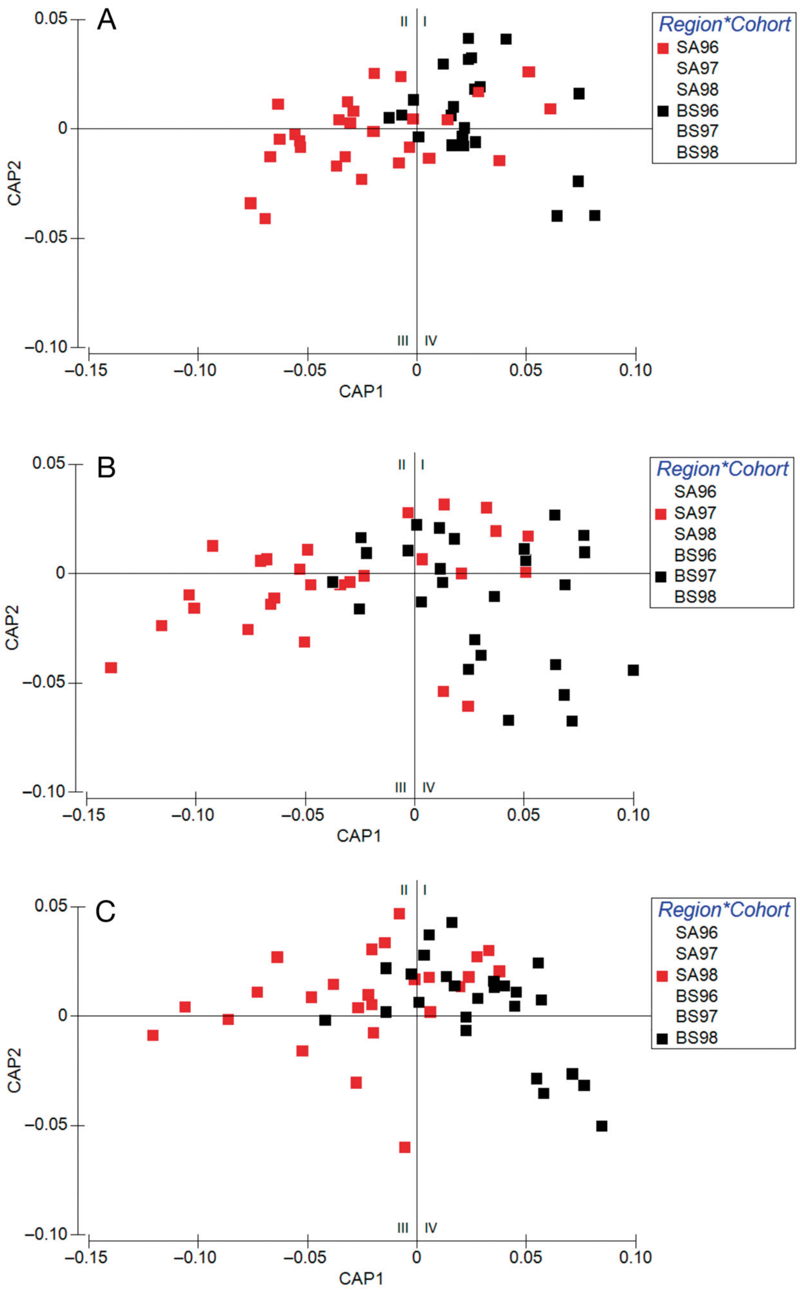

Fig. 4. Individual cohorts (A) 1996, (B) 1997, and (C) 1998, isolated from the canonical analysis of principle coordinates (CAP) plot of pooled cohorts (Fig. 3). Red and black symbols denote sharks caught in South Australia (SA) and Bass Strait (BS), respectively. Quadrants are numbered I to IV

Western Australia or New South Wales at the fringes of the species' range, although there is no evidence for pupping in these areas. Recruits from New Zealand (NZ) may also contribute to differences in post-natal signatures between SA and BS. Recent genetic evidence has established the Australian and NZ populations form a connected panmictic stock (Hernández et al. 2015, Bester-van der Merwe et al. 2017) and individuals from NZ move to Australia; 8 to 10% of recaptures of sharks tagged in NZ occurred in Australia (Hurst et al. 1999, Francis 2010). However, movements to Australia appear to increase with age (Francis 2010) and NZ emigrants appear to be roughly equally distributed throughout the Australian population (Hurst et al. 1999), suggesting they are probably not responsible for differences in post-natal signatures observed between SA and BS.

A more likely driver of differences is that pupping occurs in SA, as has long been considered plausible (Stevens & West 1997) or likely (Prince 1996). Discovery of pupping areas in the southeast in the 1950s led to a concentration of scientific effort there, e.g. a large-scale investigation of potential pupping areas in the 1990s consisted of >1300 scientific longline and gillnet sets surveying areas in BS and Tasmania, compared to only 7 in SA (all opportunistically and without scientific observation: Stevens & West 1997). Most pups born in southeastern pupping areas mix completely throughout the BS population (Olsen 1954, Stevens & West 1997) where juveniles form large aggregations, e.g. in eastern BS (Olsen 1954, Walker 1999). Juveniles in this region typically move short distances, e.g. tagged individuals <65 cm in BS and Tasmania travelled a mean distance of 22 ± 10 km at recapture (Brown et al. 2000), and the majority of sharks aged 0+ to 3 yr remain within 100 km of pupping areas (Stevens & West 1997). Although some dispersive individuals make long movements, e.g. as far as central SA (Olsen 1954, McAllister et al. 2015), movements >100 km generally do not occur until 3 to 4 yr of age (Stevens & West 1997). There is some recent evidence that neonates from Tasmania may disperse further from pupping areas than previously thought, however mostly northwards toward BS and NSW (J. M. Semmens unpubl. data). Yet, juveniles of these age classes are not uncommonly caught in SA, typically forming schools of similarly sized individuals (Fig. 5A), e.g. around Pearson Island in western SA

Fig. 5. (A) Juvenile school sharks caught near Pearson Island, western South Australia, in October 2017. Individuals this size rarely move more than 100 km from pupping areas. (B) Neonate school shark caught in Marion Bay, South Australia, in early February 2017, when neonates are yet to disperse from pupping areas

and off the Coorong, suggesting pupping likely occurs within 100 km of these areas.

Presence of neonates (Fig. 5B; see also Rogers et al. 2017), females in immediate post-partum condition (Braccini et al. 2009), and late-term pregnant females (Prince 1996, West & Stevens 2001), including late-term pregnant females remaining in SA throughout the peak pupping season in December and January (M. N. McMillan unpubl. data), also supports undiscovered pupping areas in SA. In addition to post-natal signatures differing between regions, region of capture was predicted for >75% of sharks based on post-natal signatures (where prediction by chance alone would equal 50%: White & Ruttenberg 2007), suggesting different sources of recruitment for most sharks in each region with some mixing of dispersive individuals. Such a model is consistent with the experience in NZ, where most individuals (76%) make localised movements <500 km with long distance movements by a minority of dispersive individuals (Hurst et al. 1999). In Australia, comprehensive tagging in the 1990s (the first to include all of SA) also found that most individuals of the size classes examined in this study (<140 cm TL) travelled <500 km at recapture (Brown et al. 2000), again suggesting mostly relatively localised movements for these age classes with a minority of dispersive individuals. Although knowledge about drivers of element incorporation in elasmobranch vertebrae is currently limited, incorporation of Mn increased and Mg decreased in response to increasing temperature in another elasmobranch, the round stingray *Urobatis halleri* (Smith et al. 2013). Elevated Mn:Ca and lower Mg:Ca in vertebrae of SA sharks would therefore be consistent with pupping in SA, where lower latitudes give rise to generally warmer coastal water temperatures than those in BS during the summer pupping season (Fig. S2). Pupping in SA would entail partial female migration, whereby some pregnant females remain resident in SA over the pupping season while others migrate to southeastern Australia or NZ pupping areas.

One of the key drivers of pupping site selection is predator avoidance (Branstetter 1990, Morrissey & Gruber 1993, Heupel et al. 2007). Shallow estuaries provide scarcity of predators and turbidity refuges, making them attractive nurseries for many fishes (Blaber & Blaber 1980). While some female *G. galeus* select such habitats, leading to high densities of pups in confined areas, others may employ more dispersed pupping in coastal marine habitats as an alternative strategy, relying on benthic cover and dispersal of young to limit predation. Use of alternative pupping strategies may confer population-level resilience; if one strategy fails, the other may still yield recruits. Habitat availability is known to drive reproductive strategies in sharks; the same species may pup in estuarine or marine habitats depending on availability (Knip et al. 2010). Marine pupping areas are used by *G. galeus* throughout their global range including in California (USA) (Ripley 1946), NZ (Hurst et al. 2000), South Africa (Freer 1992, M. McCord pers. comm.), and Argentina (G. Chiaramonte pers. comm.). The use of marine pupping areas thus appears to be an underinvestigated source of recruitment in Australia, particularly in SA, where all neonate records derive from marine areas (Fig. 5B; see also Knuckey et al. 2014, Rogers et al. 2017). Vertebral Sr concentrations have been used as a salinity tracer and found to decline with decreasing salinity in elasmobranchs, e.g. bull sharks *Carcharhinus leucas* (Tillett et al. 2011) and smalltooth sawfish *Pristis pectinate* (Scharer et al. 2012). However, in the present study, Sr:Ca did not differ between regions, supporting the idea that most pupping may occur in relatively homogeneous marine habitats. Due to the large extent of marine habitat available, marine pupping areas may yield lower densities of pups than estuaries, making them less conspicuous and less likely to be detected than within-estuarine pupping areas, but occur over larger areas and could therefore yield more biomass. This may explain why recruitment from recorded estuarine pupping areas is estimated at <10% of that required to maintain the population (Stevens & West 1997). Female reproductive behaviour therefore appears divided between alternate pupping strategies; the impacts of these strategies on the resilience of the species and on the ability to accurately monitor its status should be better understood to best manage the species' recovery.

Divergent modes of movement and habitat use across a species' range may be a bet-hedging strategy (Kerr et al. 2010, Chapman et al. 2011). Temporal fluctuations in resource availability may offer benefits to both migrants and residents at different times, potentially conferring long-term resilience (Gillanders et al. 2015). Varying degrees of mixing from year to year, driven by opportunistic exploitation of regional fluctuations in prey abundance, may also allow for replenishment of overexploited populations from source populations (Secor et al. 2001). However, variable patterns of movement may also lead to differing vulnerability among regions to stressors, e.g. overharvesting or habitat loss, and variable capacity among sub-populations to recover from population depletions (Secor et al. 2001, Parsons et al. 2011). This may explain the apparent loss of a population of *G. galeus* formerly present off New South Wales or account for the varying abundances noted between SA and BS over time (Punt et al. 2000). At any rate, our findings provide evidence that contributions to the populations in SA and BS derive largely from different pupping areas, at least in some years, with probable admixture of some dispersive individuals. If, as recent evidence suggests, pupping is also occurring in SA, this is not consistent with the current model under which recovery of *G. galeus* is managed in Australia, which assumes obligate female migration with all pupping occurring in the southeast of their range (Punt et al. 2000, Walker et al. 2008). Our evidence suggests female movements are likely more plastic than previously assumed and that, in concert with a preponderance of anecdotal and emerging scientific evidence, sources of recruitment remain unaccounted for, particularly in SA. Greater understanding of the species' reproductive strategies and habitats should therefore be sought to best direct and improve conservation measures, specifically via rigorous and overdue investigation of pupping activity in SA. Our study illustrates the complexity and variability of reproductive strategies that can occur in highly mobile species, presenting challenges for managing the conservation and recovery of such species depleted by human interference.

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