African Journal of Marine Science
Publication details, including instructions for authors and subscription information:
http://www.tandfonline.com/loi/tams20

Spatial and seasonal patterns in sighting rate and life-history composition of the white shark Carcharodon carcharias at Mossel Bay, South Africa

R Ryklief[ab], PA Pistorius[a] & R Johnson[b]

[a] Department of Zoology, Nelson Mandela Metropolitan University, Port Elizabeth, South Africa

[b] Oceans Research, Mossel Bay, South Africa

Published online: 07 Nov 2014.

African Journal of Marine Science 2014: 1–5
Printed in South Africa — All rights reserved

AFRICAN JOURNAL OF
MARINE SCIENCE
ISSN 1814-232X EISSN 1814-2338
http://dx.doi.org/10.2989/1814232X.2014.967296

Spatial and seasonal patterns in sighting rate and life-history composition of the white shark *Carcharodon carcharias* at Mossel Bay, South Africa

R Ryklief[1,2]*, PA Pistorius[1] and R Johnson[2]

[1] *Department of Zoology, Nelson Mandela Metropolitan University, Port Elizabeth, South Africa*
[2] *Oceans Research, Mossel Bay, South Africa*
* *Corresponding author, e-mail: rabia.ryklief@gmail.com*

White sharks *Carcharodon carcharias* aggregate at specific times of the year at localities along the South African coast. At Mossel Bay, on the southern Cape coast, four sites were sampled (Seal Island, Hartenbos, Kleinbrak and Grootbrak) to investigate spatial and seasonal patterns in relative abundance and life-history composition. These are known aggregation sites within the bay, each having particular physical and/or biological characteristics. Sightings-per-unit-effort data were collected from February to December 2008–2010. Sighting rates demonstrated significant seasonal and interannual variation at the four sites. The highest mean sighting rate was recorded at Seal Island and the lowest at Hartenbos, which might be a consequence of differences in prey availability. The greatest interannual variability was recorded at Kleinbrak, followed by Seal Island, with little variability at Grootbrak and Hartenbos. White sharks appeared to concentrate at Grootbrak and Kleinbrak in summer and autumn, at Seal Island in winter, and at Hartenbos and Seal Island in spring. All life-history stages were present year-round but their occurrence was influenced significantly by season ($p < 0.05$), although not site. Few adults (325–424 cm total length) were seen, with the highest frequency being in spring, whereas that of young-of-the-year (≤174 cm) was in autumn. Juveniles (175–324 cm) constituted 78% of the animals sighted, indicating that Mossel Bay is an important aggregation site for this life-history stage.

Keywords: adults, Agulhas system, habitat use, juveniles, relative abundance, young-of-the-year

Introduction

The white shark *Carcharodon carcharias* is a coastal apex predator that has a circumglobal distribution, occurring largely in temperate systems but also visiting tropical and subtropical waters (Compagno 1997). Its distribution includes South African waters, where it is a protected species (RSA 1998). Specific localities along the South African coast have been identified as aggregation sites, including False Bay, Gans Bay and Mossel Bay in the Western Cape province (Kock and Johnson 2006; Kock et al. 2013; Towner et al. 2013) and Algoa Bay in the Eastern Cape province (Dicken et al. 2013).

The white shark is characterised by a K-selected life-history strategy and thus has a low intrinsic rate of increase, making it particularly susceptible to exploitation (Hoenig and Gruber 1990; Baum et al. 2003). Given its role as a predator, knowledge of top-down effects and degree of interdependency is key to understanding ecosystem functionality (Stevens et al. 2000; Myers et al. 2007; Ferretti et al. 2010). Determination of patterns in temporal occurrence and relative abundance provides insight into the species' influence on community structure (Ferretti et al. 2010). Such patterns include spatio-temporal habitat preferences or habitat requirements for different sexes and size classes (Heithaus et al. 2007). The insight derived facilitates the effective conservation and management not only of the species but also of the ecosystem of which it is a part (Wirsing et al. 2007; Jorgensen et al. 2010).

The main objective of this study was to identify spatial and seasonal patterns in the relative abundance of white sharks at Mossel Bay. A secondary objective was to define the population structure in terms of life-history stage.

Material and methods

Study area

Mossel Bay (34°11' S, 22°08' E) is situated centrally within the warm-temperate Agulhas marine bioregion (Lombard et al. 2004) on the southern Cape coast. It is influenced by the southwestward-flowing Agulhas Current that transports warm water from the tropics (Lutjeharms 1998). During summer, coastal upwelling occurs occasionally in the vicinity of Mossel Bay, bringing nutrient-rich waters to the surface (Scott 1951; Schumann et al. 1982). It is a shallow, semi-enclosed bay with a flat bottom composed largely of exposed reef or sand (Johnson et al. 2009). The Hartenbos, Kleinbrak and Grootbrak rivers empty into the bay (Figure 1). Cape St Blaize is a rocky peninsula at the south-western edge. The most notable feature within the bay is Seal Island, a rocky outcrop 800 m from the shore. This island is a protected nature reserve and hosts a colony of Cape fur seals *Arctocephallus pusillus pusillus*, consisting of over 4 000 individuals (Johnson et al. 2009). There were four sampling sites: Seal Island, and the region immediately offshore of the surf zone off the mouths of the

Hartenbos, Kleinbrak and Grootbrak estuaries, all of which lie above the 15 m isobath (Figure 1). They were selected on the basis of being known aggregation sites for white sharks within the bay (Johnson et al. 2009).

Field sampling

Data were collected at each of the four sites in every month from February to December 2008–2010. A combination of chum and bait was used to attract white sharks to the boat (see Johnson et al. 2009). Once a shark arrived, its total length was estimated by experienced observers when it swam next to a 2 m length of pipe that was attached parallel to the boat. Also, the dorsal fin was photographed for individual identification. Photographs were taken only when the shark was in close proximity to the boat and the dorsal fin was perpendicular to the sea surface. All photographs were uploaded into Adobe Photoshop Lightroom 2 – a photographic cataloguing program. Standardised keywords were applied to the photographs and were used later to filter for potential matches. Keywords indicated the presence of partial amputations (of dorsal, caudal or pectoral fins), black or white pigmentation (dorsal fin), notches (trailing edge of dorsal fin) and artificial tags (acoustic or satellite), and whether the left or right side of the dorsal fin was photographed. Individual sharks were identified and matched using a combination of dorsal fin features (Anderson et al. 2011), namely the notch structure along the trailing edge as well as black or white pigmentation, if present. Identification and matching of individual sharks was performed manually by a single observer.

Data analysis

For each sampling trip, sightings-per-unit-effort (SPUE) was calculated as the number of individual white sharks sighted, divided by the number of hours spent sampling. Because sampling trips occurred both in the morning and in the afternoon, a Student's *t*-test was used to test for any significant variation in diurnal activity patterns. SPUE data were analysed using two-way ANOVA, with factors being (a) site and season and (b) site and year, to investigate variation in relative abundance. Seasons were categorised as summer (December–February), autumn (March–May), winter (June–August) and spring (September–November). All assumptions associated with the performance of an ANOVA were met. To determine composition by life-history stage, identified individuals were placed into life-history stages defined by size class: young-of-the-year (YOY; ≤174 cm), juvenile (175–324 cm), and adult (≥325 cm). These size classes approximate those defined in the literature; females mature at c. 450 cm (Francis 1996) and males at c. 360–380 cm (Pratt 1996; Malcolm et al. 2001) and YOY are generally regarded as being 120–150 cm (Francis 1996). Variation in size composition by site and season was assessed using Chi-square (χ^2) and contingency table analysis. To prevent pseudo-replication, only individuals that could be uniquely identified per sampling session were used for the analysis.

Results

In total, 717 sampling trips to the four sites were undertaken (Table 1). Total observation effort was 1 758 h and 20 min, with a mean of 2 h and 49 min per trip. A total of 2 648 white shark sightings were recorded. The highest mean sighting rate of 1.51 ind. h^{-1} (SD 1.38) was recorded at Seal Island, and the lowest of 0.96 ind. h^{-1} (SD 1.12) at Hartenbos. The mean sighting rates for the morning and afternoon trips were 1.34 ind. h^{-1} (SD 1.42) and 1.31 ind. h^{-1} (SD 1.34), respectively. There was no difference in diurnal activity patterns (t = 0.26, df = 692, p > 0.05), so the data were pooled for subsequent analysis. Relative abundance at each site was influenced significantly by season ($F_{(9,705)}$ = 6.1288, p < 0.05; Figure 2). Grootbrak and Kleinbrak exhibited similar seasonal patterns, peaking in summer and autumn. Similarly, Hartenbos and Seal Island exhibited seasonal peaks in spring. Seal Island also exhibited a pronounced winter peak. Year also had a significant influence on relative abundance across sites ($F_{(6,709)}$ = 7.0631, p < 0.05; Figure 3). Kleinbrak showed a high degree of interannual variation, with the relative abundance decreasing from 2.71 ind. h^{-1} (SD 2.17) in 2008 to 0.20 ind. h^{-1} (SD 0.37) in 2010, but there was little variation at the other three sites (Figure 3).

For the analysis of life-history composition, data from 481 sampling trips were used, during which a total of 1 548 sightings were recorded. In all, 261 unique individuals were identified, encompassing a broad size spectrum that ranged from 125 to 424 cm. All life-history stages were present year-round and size composition was influenced significantly by season (χ^2 = 31.21, df = 6, p < 0.05; Figure 4). The YOY

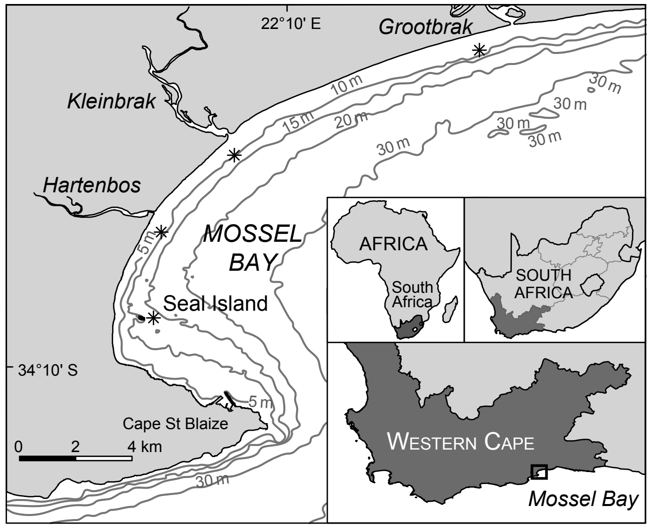

Figure 1: Map of Mossel Bay, South Africa, showing the four sampling sites

Table 1: Summary of sampling effort and mean sightings-per-unit-effort (SPUE) for each site sampled at Mossel Bay during 2008–2010

Site	Number of trips	Total effort (h)	Mean SPUE (ind. h^{-1})
Seal Island	337	956.70	1.51 (SD 1.38)
Hartenbos	154	358.37	0.96 (SD 1.12)
Kleinbrak	55	138.87	1.13 (SD 2.02)
Grootbrak	171	521.92	1.38 (SD 1.37)

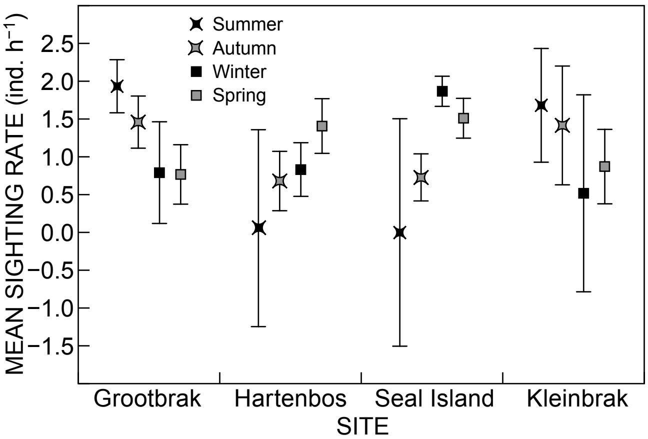

Figure 2: Seasonal patterns in relative abundance based on sightings-per-unit-effort (SPUE) for each site sampled at Mossel Bay, 2008–2010. Vertical bars denote 95% confidence intervals

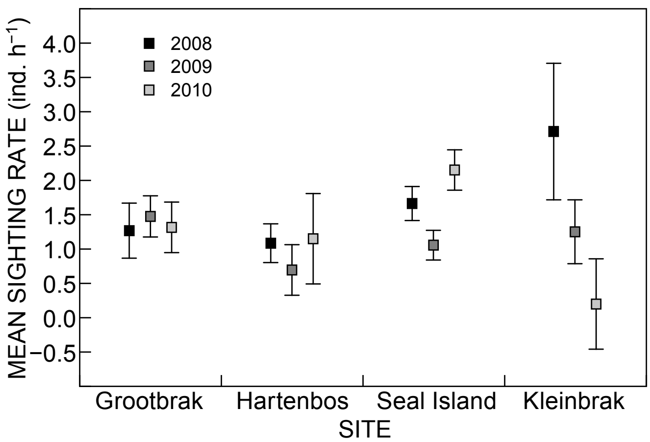

Figure 3: Interannual patterns in relative abundance based on sightings-per-unit-effort (SPUE) for each site sampled at Mossel Bay, 2008–2010. Vertical bars denote 95% confidence intervals

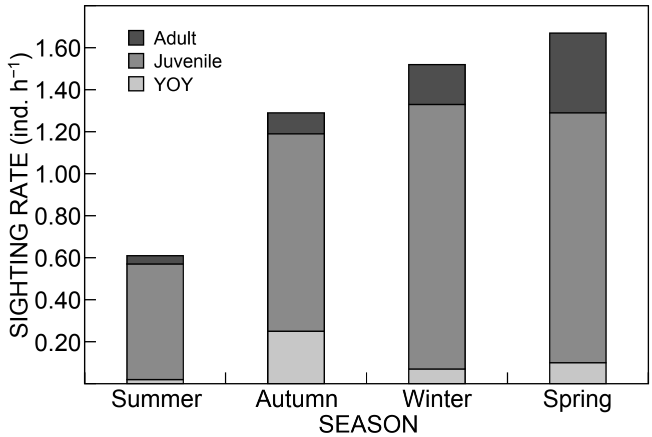

Figure 4: Sighting rate of life-history stages (young-of-the-year [YOY], juvenile and adult) of white sharks sampled in each season at Mossel Bay, 2008–2010. Life-history stages are defined in the text

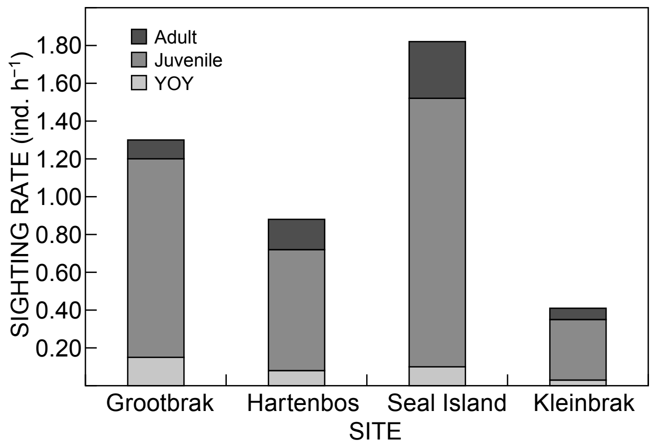

Figure 5: Sighting rate of life-history stages (young-of-the-year [YOY]; juvenile and adult) of white sharks sampled at four sites in Mossel Bay, 2008–2010. Life-history stages are defined in the text

(14% of those recorded) sharks peaked in autumn, whereas adults (23%) peaked in spring. Overall, juveniles (78%) dominated the demographic structure of the sharks under study. Site had no significant influence on size composition ($\chi^2 = 9.32$, df = 6, $p < 0.05$; Figure 5). The YOY sharks contributed the highest percentage at Grootbrak (12%), and adults (18%) the highest at Hartenbos. Similarly, the YOY sharks (5%) were not commonly found at Seal Island and adults (7%) were sighted infrequently at Grootbrak.

Discussion

A sound understanding of habitat use is essential for effective population management (Kareiva and Wennergren 1995). Habitat use can be related to three main factors: (i) prey availability, (ii) reproduction and (iii) shelter (Barnett et al. 2010). Prey abundance and movement have been linked to the distribution of sharks (e.g. Sims and Quayle 1998; Sims 2003; Dicken et al. 2006), including white sharks (Ainley et al. 1985; Martin et al. 2005; Kock and Johnson 2006; Dicken and Booth 2013; Kock et al. 2013). In Mossel Bay, given the low number of sexually mature individuals and YOY, reproduction seems unlikely to be a driving force associated with habitat use.

Seal Island had the highest mean sighting rate of white sharks, followed by Grootbrak, Kleinbrak and lastly Hartenbos. White sharks frequently prey on Cape fur seals at rookeries off southern Africa and particularly so during winter, when juvenile seals leave to forage offshore for the first time, rendering them vulnerable to predation by white sharks (e.g. Martin et al. 2005; Hammerschlag et al. 2006; Kirkman et al. 2006). Similarly, Ainley et al. (1981, 1985) observed that white shark occurrence coincided with the presence of juvenile northern elephant seals *Mirounga angustirostris* at the South Farallon Islands, USA. Cape fur seals have been shown to be targeted by white sharks in the vicinity of Seal Island (Johnson et al. 2009). Hartenbos lies just to the north of the hunting grounds and is generally used as a resting area for white sharks (Johnson et al. 2009). Hence the low sighting rate there is likely to be due to sharks being less active than at other sites. The Kleinbrak and Grootbrak study sites are characterised both by reef systems and by estuary mouths, with the mouths representing typical nursery areas for a number of estuarine-dependent marine fish species (Houde and Rutherford 1993; James and Harrison 2008). The large biomass of fish present at these sites (James and Harrison 2008) represents potential non-mammal prey. The second lowest sighting rate of white sharks was recorded at Kleinbrak, where fish are less abundant than at Grootbrak (James and Harrison 2008). Seasonal shifts in prey abundance may cause white sharks to switch their diet between marine mammals (e.g. pinnipeds) and demersal teleost or chondrichthyan species (Martin et al. 2005; Bruce et al. 2006). Through such feeding activities white sharks potentially play a large role in influencing ecosystem dynamics through direct and indirect predation effects (Stevens et al. 2000; Heithaus et al. 2002; Myers et al. 2007), supporting the suggestion of Ferretti et al. (2010) that predators utilising large areas are important because they usually prey on multiple species in different systems and/or habitats. This was observed in the present study in which sighting rates for white sharks were high at Seal Island in the winter and at Kleinbrak and Grootbrak in the summer.

Only sharks larger than 300 cm are considered capable of consuming large marine mammals such as seals (Tricas and McCosker 1984; Klimley 1985; McCosker 1985; Cliff et al. 1989; Estrada et al. 2006). Hartenbos is near to Seal Island and hence the presence of seals at Seal Island may explain why these two sites host the greatest proportion of adult sharks. In Spencer Gulf, South Australia, Strong et al. (1996) found that small white sharks appeared to limit their spatial use to reduce direct interactions with larger conspecifics. This may explain why Grootbrak, the farthest site in terms of proximity to Seal Island, had the highest sighting rate of YOY sharks. Surprisingly, however, Seal Island had the second highest sighting rate of YOY sharks. Life-history stages were significantly influenced by season and not site, and hence the rocky reefs of Seal Island may attract YOY sharks when adult sharks are not present.

Mossel Bay provides sheltered conditions throughout most of the year (Jewell et al. 2013) and hosts a diverse array of prey species that collectively represent potential prey for all life-history stages of white sharks (James and Harrison 2008; Johnson et al. 2009). However, despite the wide size range of sharks observed in our study (124–424 cm), a large proportion (78%) were between 175 and 324 cm, suggesting preferential use of the bay by juveniles. The size composition of white sharks on the South African coastline appears to increase from east to west. Algoa Bay (33°50' S, 26°17' E) seems to host the greatest proportion of YOY sharks, Gans Bay (34°68' S, 17°41' E) hosts a similar size composition to Mossel Bay – although with a greater proportion of subadults – and the greatest proportion of adults is found in False Bay (34°04'–34°23' S, 18°26'–18°51' E) (Kock and Johnson 2006; Dicken et al. 2013; Towner et al. 2013).

Our study provides information on the relative abundance and seasonal and spatial distribution of different life-history stages of white sharks within Mossel Bay, and identifies some factors that potentially explain the observed patterns. In addition, it demonstrates the importance of Mossel Bay as an aggregation site for juvenile white sharks, in particular. This provides a basis for ensuring that the ecosystem health of the bay is maintained, as part of the network of aggregation sites for this protected species.

Acknowledgements — We thank DT Irion for assistance with the map and E Gennari for support during this project. We acknowledge the support of Oceans Society and Petro SA for partial project funding. Oceans Research is thanked for the use of research boats and logistical support. The Department of Agriculture, Forestry and Fisheries and the Department of Environmental Affairs are acknowledged for the issuing of research permits. We thank two anonymous reviewers whose comments and suggestions improved the quality of an earlier version of the manuscript.

References

Ainley DG, Henderson RP, Huber HR, Boekelheide RJ, Allen SG, McElroy TL. 1985. Dynamics of white shark/pinniped interactions in the Gulf of the Farallones. *Memoirs of the Southern California Academy of Sciences* 9: 109–122.

Ainley DG, Strong CS, Huber HR, Lewis TJ, Morrell SH. 1981. Predation by sharks on pinnipeds at the Farallon Islands. *Fishery Bulletin* 78: 941–945.

Anderson SD, Chapple TK, Jorgensen SJ, Klimley AP, Block BA. 2011. Long-term individual identification and site fidelity of white sharks, *Carcharodon carcharias*, off California using dorsal fins. *Marine Biology* 158: 1233–1237.

Barnett A, Stevens JD, Frusher SD, Semmens JM. 2010. Seasonal occurrence and population structure of the broadnose sevengill shark *Notorynchus cepedianus* in coastal habitats of south-east Tasmania. *Journal of Fish Biology* 77: 1688–1701.

Baum JK, Myers RA, Kehler DG, Boris W, Harley SJ, Doherty PA. 2003. Collapse and conservation of shark populations in the northwest Atlantic. *Science* 299: 389–392.

Bruce BD, Bradford RW. 2012. Habitat use and spatial dynamics of juvenile white sharks, *Carcharodon carcharias*, in Eastern Australia. In: Domeier ML (ed.), *Global perspectives on the biology and life history of the white shark*. Florida: CRC Press. pp 225–254.

Bruce BD, Stevens JD, Malcolm H. 2006. Movements and swimming behaviour of white sharks (*Carcharodon carcharias*) in Australian waters. *Marine Biology* 150: 161–172.

Cliff G, Dudley SFJ, Davis B. 1989. Sharks caught in the protective gill nets off Natal, South Africa. 2. The great white shark *Carcharodon carcharias* (Linnaeus). *South African Journal of Marine Science* 8: 131–144.

Compagno LJV, Marks MA, Fergusson IK. 1997. Threatened fishes of the world: *Carcharodon carcharias* (Linnaeus, 1758) (Lamnidae). *Environmental Biology of Fishes* 50: 61–62.

Dicken ML, Booth AJ. 2013. Surveys of white sharks (*Carcharodon carcharias*) off bathing beaches in Algoa Bay, South Africa. *Marine and Freshwater Research* 64: 530–539.

Dicken ML, Smale MJ, Booth AJ. 2006. Spatial and seasonal distribution patterns of the ragged-tooth shark *Carcharias taurus* along the coast of South Africa. *African Journal of Marine Science* 28: 603–616.

Dicken ML, Smale MJ, Booth AJ. 2013. White sharks *Carcharodon carcharias* at Bird Island, Algoa Bay, South Africa. *African Journal of Marine Science* 35: 175–182.

Estrada JA, Rice AN, Natanson LJ, Skomal GB. 2006. Use of isotopic analysis of vertebrae in reconstructing ontogenetic feeding ecology in white sharks. *Ecology* 87: 829–834.

Ferretti F, Worm B, Britten GL, Heithaus MR, Lotze HK. 2010.

Patterns and ecosystem consequences of shark declines in the ocean. *Ecology Letters* 13: 1055–1071.

Francis MP. 1996. Observations on a pregnant white shark with a review of reproductive biology. In: Klimley AP, Ainley DG (eds), *Great white sharks: the biology of* Carcharodon carcharias. San Diego: Academic Press. pp 157–172.

Hammerschlag N, Martin RA, Fallows C. 2006. Effects of environmental conditions on predator-prey interactions between white sharks (*Carcharodon carcharias*) and Cape fur seals (*Arctocephalus pusillus pusillus*) at Seal Island, South Africa. *Environmental Biology of Fishes* 76: 341–350.

Heithaus MR, Burkholder D, Hueter RE, Heithaus LI, Pratt HL, Carrier JC. 2007. Spatial and temporal variation in shark communities of the lower Florida Keys and evidence for historical population declines. *Canadian Journal of Fisheries and Aquatic Sciences* 64: 1302–1313.

Heithaus MR, Dill LM, Marshall GJ, Buhleier B. 2002. Habitat use and foraging behavior of tiger sharks (*Galeocerdo cuvier*) in a seagrass ecosystem. *Marine Biology* 140: 237–248.

Hoenig JB, Gruber SH. 1990. Life-history patterns in the elasmobranchs: implications for fisheries management. In: Pratt HL, Gruber SH, Taniuchi T (eds), *Elasmobranchs as living resources: advances in the biology, ecology, systematics, and the status of the fisheries*. NOAA Technical Report NMFS 90. Springfield, Virginia: US Department of Commerce.

Houde ED, Rutherford ES. 1993. Recent trends in estuarine fisheries: prediction of fish production and yield. *Estuaries* 16: 161–176.

James NC, Harrison TD. 2008. A preliminary survey of the estuaries on the south coast of South Africa, Cape St Blaize, Mossel Bay – Robberg Peninsula, Plettenberg Bay, with particular reference to the fish fauna. *Transactions of the Royal Society of South Africa* 63: 211–217.

Jewell OJ, Johnson RL, Gennari E, Bester MN. 2013. Fine scale movements and activity areas of white sharks (*Carcharodon carcharias*) in Mossel Bay, South Africa. *Environmental Biology of Fishes* 96: 881–894.

Johnson R, Bester MN, Dudley SFJ, Oosthuizen WH, Meÿer M, Hancke L, Gennari E. 2009. Coastal swimming patterns of white sharks (*Carcharodon carcharias*) at Mossel Bay, South Africa. *Environmental Biology of Fishes* 85: 189–200.

Jorgensen SJ, Reeb CA, Chapple TK, Anderson S, Perle C, Van Sommeran SR, Fritz-Cope C, Brown AC, Klimley AP, Block BA. 2010. Philopatry and migration of Pacific white sharks. *Proceedings of the Royal Society Biological Sciences* 277: 679–688.

Kareiva P, Wennergren U. 1995. Connecting landscape patterns to ecosystem and population processes. *Nature* 373: 299–302.

Kirkman SP, Oosthuizen WH, Meÿer MA. 2006. The seal population of Seal Island, False Bay. In: Nel DC, Peschak TP (eds), *Finding a balance: white shark conservation and recreational safety in the inshore waters of Cape Town, South Africa*. WWF South Africa Report Series – 2006/Marine/001. Cape Town: WWF. pp 83–94.

Klimley AP, Anderson SD. 1996. Residency patterns of white sharks at the South Farallon Islands, California. In: Klimley AP, Ainley DG (eds), *Great white sharks: the biology of* Carcharodon carcharias. San Diego: Academic Press. pp 365–373.

Kock A, Johnson R. 2006. White shark abundance: not a causative factor in numbers of shark bite incidents. In: Nel DC, Peschak TP (eds), *Finding a balance: white shark conservation and recreational safety in the inshore waters of Cape Town, South Africa*. WWF South Africa Report Series – 2006/Marine/001. Cape Town: WWF. pp 1–19.

Kock A, O'Riain MJ, Mauff K, Meÿer M, Kotze D, Griffiths C. 2013. Residency, habitat use and sexual segregation of white sharks, *Carcharodon carcharias* in False Bay, South Africa. *PLoS ONE* 8: e55048.

Lombard AT, Strauss T, Harris J, Sink K, Attwood C, Hutchings L. 2004. *South African National Spatial Biodiversity Assessment 2004: Technical Report. Volume 4: Marine Component*. Pretoria: South African National Biodiversity Institute.

Lutjeharms JRE. 1998. Coastal hydrography. In: Lubke R, de Moor I (eds), *A field guide to the eastern and southern Cape coasts*. Cape Town: University of Cape Town Press. pp 50–61.

Malcolm H, Bruce BD, Stevens JD. 2001. *A review of the biology and status of white sharks in Australian waters*. Hobart, Tasmania: CSIRO Marine Research.

Martin RA, Hammerschlag N, Collier RS, Fallows C. 2005. Predatory behaviour of white sharks (*Carcharodon carcharias*) at Seal Island, South Africa. *Journal of Marine Biological Assessment UK* 85: 1121–1135.

McCosker JE. 1985. White shark attack behaviour: observations of and speculations about predator and prey strategies. *Memoirs of the Southern California Academy of Sciences* 9: 123–135.

Myers RA, Baum JK, Shepherd TD, Powers SP, Peterson CH. 2007. Cascading effects of the loss of apex predator sharks from a coastal ocean. *Science* 315: 1846–1850.

Pratt HL. 1996. Reproduction in the male white shark. In: Klimley AP, Ainley DG (eds), *Great white sharks: the biology of* Carcharodon carcharias. San Diego: Academic Press. pp 131–138.

RSA (Republic of South Africa). 1998. Regulations in terms of the Marine Living Resources Act (Act No. 18 of 1998). *Government Gazette, South Africa* 39(19205).

Schumann EH, Perrins LA, Hunter IT. 1982. Upwelling along the south coast of the Cape Province, South Africa. *South African Journal of Science* 78: 238–242.

Scott P. 1951. Inshore fisheries of South Africa. *Economic Geography* 27: 123–147.

Sims DW. 2003. Tractable models for testing theories about natural strategies: foraging behaviour and habitat selection of free-ranging sharks. *Journal of Fish Biology* 63: 53–73.

Sims DW, Quayle VA. 1998. Selective foraging behaviour of basking sharks on zooplankton in a small-scale front. *Nature* 393: 460–464.

Stevens JD, Bonfil R, Dulvy NK, Walker PA. 2000. The effects of fishing on sharks, rays, and chimaeras (chondrichthyans), and the implications for marine ecosystems. *ICES Journal of Marine Science* 57: 476–494.

Strong WR, Bruce BD, Nelson DR, Murphy RC. 1996. Population dynamics of white sharks in Spencer Gulf, South Australia. In: Klimley AP, Ainley DG (eds), *Great white sharks: the biology of* Carcharodon carcharias. San Diego: Academic Press. pp 401–414.

Towner AV, Underhill LG, Jewell OJD, Smale MJ. 2013. Environmental influences on the abundance and sexual composition of white sharks *Carcharodon carcharias* in Gansbaai, South Africa. *PLoS ONE* 8: e71197.

Tricas TC, McCosker JE. 1984. Predatory behaviour of the white shark (*Carcharodon carcharias*) with notes on its biology. *Proceedings of the California Academy of Sciences* 43: 221–238.

Wirsing AJ, Heithaus MR, Dill LM. 2007. Can measures of prey availability improve our ability to predict the abundance of large marine predators? *Oecologia* 153: 563–568.

Manuscript received August 2014, revised August 2014, accepted September 2014