



Decline or shifting distribution? A first regional trend assessment for white sharks (*Carcharodon carcharias*) in South Africa

Heather D. Bowlby^{a,*}, Matt L. Dicken^{b,c,1}, Alison V. Towner^{d,e,f}, Sarah Waries^{g,h}, Toby Rogers^{g,h}, Alison Kock^{i,j}

^a Fisheries and Oceans Canada, Bedford Institute of Oceanography, Dartmouth, Nova Scotia B2Y 4A2, Canada

^b KwaZulu-Natal Sharks Board, Umhlanga Rocks, South Africa

^c Institute for Coastal and Marine Research (CMR), Ocean Sciences Campus, Nelson Mandela University, Gqeberha 6031, South Africa

^d Department of Ichthyology and Fisheries Science, Rhodes University, Makhanda, South Africa

^e Dyer Island Conservation Trust, Kleinbaai, South Africa

^f South African International Maritime Institute, Ocean Sciences Campus, Gqeberha 6001

^g Institute for Communities and Wildlife in Africa (iCWILD), University of Cape Town, Cape Town 7701, South Africa

^h Shark Spotters, Cape Town 7945, South Africa

ⁱ South African National Parks, Cape Research Centre, Cape Town 7701, South Africa

^j South African Institute for Aquatic Biodiversity (SAIAB), Private Bag 1015, Makhanda 6140, South Africa

ARTICLE INFO

Keywords:

Conservation status
Abundance indices
Movement patterns
Ecological factors

ABSTRACT

Unprecedented levels of change in ocean ecosystems bring an ever-increasing need for re-analyses of existing data to explore pressing conservation questions. Substantial declines in white shark (*Carcharodon carcharias*) presence at two primary aggregation sites have raised concerns about the species' status throughout South Africa. Using the most comprehensive suite of abundance indices compiled to date, we evaluated temporal trends and the strength of evidence for regional redistribution. Individual indices from all primary aggregation sites in South Africa were highly variable. The overall temporal trend from a log-linear Generalized Additive Model was relatively flat, indicating largely unchanged abundance throughout South Africa since protection in 1991. However, reports of human-shark incidents showed a general shift from the Western to the Eastern Cape. Correlations among individual abundance indices demonstrated that movements were not as simple as animals leaving one site to inhabit another. Further research is needed to explore the effect of movement on monitoring data. Our results reaffirm the need for better standardization in data collection methods to generate abundance indices and to develop long-term monitoring programs on the Eastern Cape. Ideally, environmental or operational factors affecting abundance indices should also be explored in future status assessments at a regional level. Our results provide a baseline for future work, directing research to understand drivers of localized and regional changes and focusing management on reducing anthropogenic sources of mortality within their Southwest Indian Ocean range.

1. Introduction

White sharks (*Carcharodon carcharias*) in Southern Africa occur throughout the Southwest Indian Ocean and undertake extensive coastal and offshore migrations (Bonfil et al. 2005; Kock et al., 2022). In South Africa, several known large aggregation sites exist, namely, False Bay, Gansbaai, Struisbaai and Mossel Bay in the Western Cape and Plettenberg Bay and Algoa Bay in the Eastern Cape. Most aggregation sites,

especially in the Western Cape, have been the focus of research since the early 1990s and are locations for white shark cage diving and viewing tourism (Johnson and Kock 2006). Significant declines in the sightings of white sharks at aggregation sites in False Bay and Gansbaai since 2015 and 2017, respectively, have caused conservation concerns for the species (Hammerschlag et al. 2019, 2022; Towner et al. 2022a). The extended absence of white sharks in False Bay and Gansbaai has resulted in several changes in ecosystem structure, namely the increased

* Corresponding author.

E-mail address: heather.bowlby@dfm-mpo.gc.ca (H.D. Bowlby).

¹ ORCID: 0000-0001-9779-2347.

<https://doi.org/10.1016/j.ecolind.2023.110720>

Received 4 May 2023; Received in revised form 20 July 2023; Accepted 22 July 2023

Available online 30 July 2023

1470-160X/Crown Copyright © 2023 Published by Elsevier Ltd.

This is an open access article under the CC BY-NC-ND license

(<http://creativecommons.org/licenses/by-nc-nd/4.0/>).

prevalence of sevengill cow sharks (*Notorynchus cepedianus*) at Seal Island, False Bay (Hammerschlag et al. 2019) and bronze whaler sharks (*Carcharhinus brachyurus*) in Gansbaai and False Bay (Towner et al. 2022a; Shark Spotters unpublished data). The absence of white sharks has also had substantial socioeconomic impacts on the white shark cage diving industry and associated leisure and travel industries, which rely on viewing white sharks to attract tourists (DFFE 2020). However, white sharks do not appear to be absent across their entire South African range, in that anecdotal sightings are regularly reported in Mossel Bay, Plettenberg Bay, Algoa Bay and other Eastern Cape sites. The factors causing the disappearance at two major Western Cape aggregation sites have been the subject of much debate within scientific and stakeholder communities, presenting no clear direction for management authorities responsible for white shark conservation.

The urgent need for the conservation and management of global white shark populations is further hindered by gaps in our understanding of population status and species biology (Bowlby and Gibson 2020; Jorgensen et al. 2022). Applied research to address threats or threat mitigation (e.g., Morris and Doak 2002) requires information on relative or absolute abundance to determine population status (Dulvy et al., 2021). Yet developing an index of abundance that represents trends for a widely distributed population is challenging (Maunder et al. 2006; Gwinn et al. 2019). This is particularly true for protected shark species that are rarely intercepted as bycatch and are assessed primarily through sightings at localized aggregation sites and/or from tagging information. Although these non-traditional data sources are recognized as having the potential to address data deficiencies for population assessment (Huveneers et al. 2018, Jorgensen et al. 2022), individual indices represent a tiny proportion of the total range for most species due to costs and logistical challenges associated with monitoring. For highly mobile populations with the ability to redistribute among diverse habitats, localized monitoring is unlikely to consistently sample the same component of the population. Similar to how changes in catchability affect the proportionality assumption in catch-per-unit-effort indices (Maunder and Punt 2004; Maunder et al. 2006), movement associated with environmental change would introduce annual variability in the proportion of the population available to monitoring (Gwinn et al. 2019). Thus, combining multiple indices from the same population can better represent overall trends in abundance by reducing the uncertainty associated with individual indices (Gwinn et al. 2019; Thompson et al. 2022).

Before substantial management action is taken in South Africa, it is important to investigate the status of white sharks at a regional level by evaluating a broader suite of monitoring indices. To this end, we compiled sightings data, recreational captures and interactions with a bather protection programme, representing information collected throughout South Africa. These abundance indices are the largest white shark dataset yet compiled for the region and were combined in a regression analysis to assess temporal trends. To determine if specific locations may be connected by movement, we also evaluated the strength of correlation among detrended monitoring indices and looked at geographical patterns in the frequency of human-shark interactions. By assessing the strength of evidence for changes in regional status and/or for systematic redistribution of white sharks from the Western to the Eastern Cape, we can provide trend information to management authorities at the optimal spatial scale (throughout South Africa) as well as inform the design of future monitoring to index trends. This will be key to better tracking of changes in the status of white sharks in South Africa and provide meaningful guidance for future management.

2. Methods

2.1. Abundance indices

The available information to assess white shark trends included three vessel-based sightings per unit effort (SPUE) indices collected during

white shark ecotourism operations in Gansbaai and Mossel Bay or research-focused trips in False Bay, one index of incidental captures by shore-based recreational anglers in Algoa Bay, and two indices derived from the KwaZulu-Natal bather protection programme (KZNSB; Fig. 1). To improve comparability among different data types (sightings, captures), all raw data were summarized as an annual mean for analyses, scaled by effort (Table 1).

The methods used to collect vessel-based sightings data from white shark ecotourism operations in Gansbaai are outlined by Towner et al. (2022a) and were comparable to those used by ecotourism operators in False Bay and Mossel Bay (Hewitt et al. 2018; Towner et al. 2013). In all three locations, multiple trips of several hours duration were undertaken daily, and the number of white shark sightings were recorded without consistent identification of individual sharks. Therefore, sightings-per-unit-effort (SPUE) represented the annual average sightings per hour, uncorrected for overestimation due to repeated sightings of individual animals. During preliminary analyses, long-term sightings data from a shark safety program (Shark Spotters; Engelbrecht et al., 2017) were also considered. However, these sightings were largely duplicated with the sightings data from the False Bay region and were thus excluded to avoid pseudo-replication. Due to the reduced presence of white sharks in False Bay, observation effort was discontinued in 2019. Incidental captures in Algoa Bay were documented from voluntary interviews with four anglers, identified as those with the necessary knowledge of when and where incidental catches of white sharks occurred (Dicken and Booth 2013). Because of general consistency among participants in fishing locations and the number of days fished per annum (~100), we used the capture data as a proxy for catch-per-unit-effort (CPUE). However, we recognize that external factors such as improved technology, increased skill and/or knowledge of the anglers could affect capture success. Similarly, systematic changes have occurred in gear deployments from the KZNSB bather protection program, with a substantial reduction in the number of nets being deployed annually and their partial replacement with drumlines (Cliff and Dudley 2011; Dicken et al. 2016, 2018). Given the expectation of differences in catchability from these two gear types, catch-per-unit-effort indices were derived separately from the netting and drumline components.

We used mean annual sightings per hour (SPUE), total captures per fishing season (CPUE), and incidental captures per km of net or the number of drumlines (CPUE) as indices for analysis (Table 1). As is common when data are derived from different sources (Lawler et al. 2002), individual indices showed different trends over time and were expressed in different units (Table 1). We normalized the available indices relative to their maximum for analyses, which standardized values within a [0, 1] interval to ensure comparability. For each series, all available years from the beginning of monitoring to 2021 were included. However, to evaluate the sensitivity of our results to noteworthy changes in monitoring programs, we also truncated the data to 2019, given substantial logistical challenges and the resulting reduction in monitoring effort associated with Covid-19 pandemic restrictions in 2020 and 2021 (Government Notice No R. 480, 2020). We also evaluated the sensitivity of our results to normalizing the individual series relative to mean as opposed to maximum values. The ecological conclusions did not change in either instance.

2.2. Analyses

To estimate overall trends, we fitted Generalized Linear or Generalized Additive regression models (GLM or GAM) to all series combined using 'year' as a continuous predictor and assuming a Gamma distribution for the response. Combining the data this way assumes that each series is equally informative about overall trends, although longer series would have more influence on the fit. We did not add a categorical fixed effect or a random effect for 'series' because of the sparseness of the data and the diversity in individual trends (e.g. roughly linear for False Bay vs. quadratic for Gansbaai). We compared the relative support for a

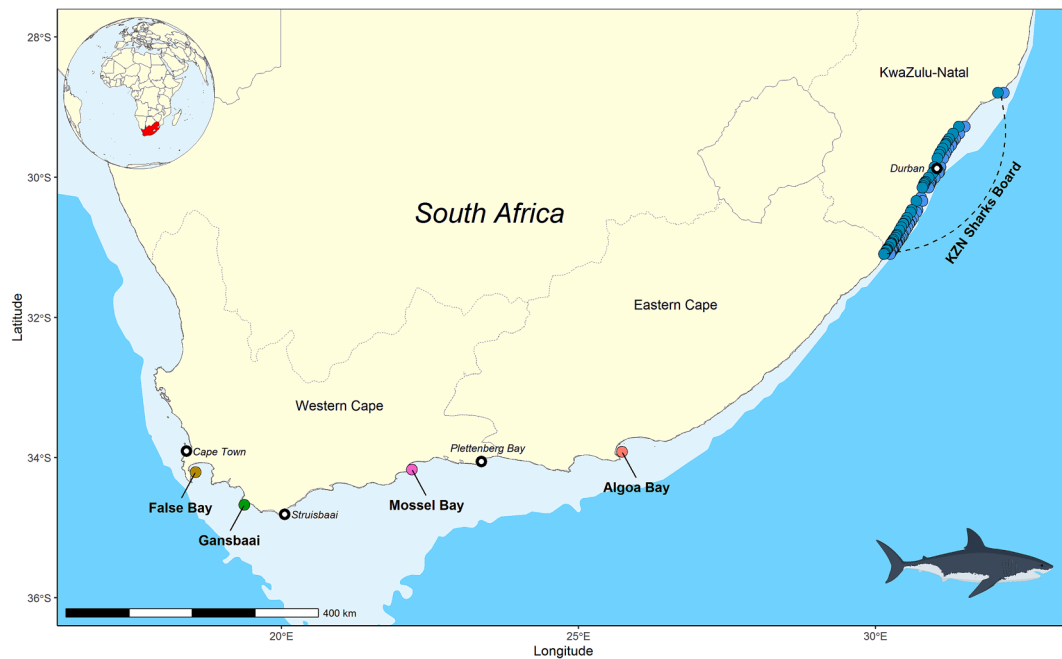


Fig. 1. Monitoring locations (solid circles) within South Africa that were used to develop the sightings-per-unit-effort or catch-per-unit-effort abundance indices. Three general regions are identified by grey lines: Western Cape, Eastern Cape and KwaZulu-Natal coastline.

Table 1
Characteristics of the monitoring indices derived for white sharks in South Africa.

| Location | Time Period | Site | Data type | SPUE or CPUE Index |
|-----------------|-------------|------------------|--------------------------------------|--------------------------------------|
| False Bay | 2000–2018 | Aggregation site | Sightings; research baited survey | annual mean number per hour |
| Gansbaai | 2007–2020 | Aggregation site | Sightings; cage diving baited survey | annual mean number per hour |
| Mossel Bay | 2001–2019 | Aggregation site | Sightings; cage diving baited survey | annual mean number per hour |
| Algoa Bay | 2013–2019 | Aggregation site | Recreational captures | annual total incidental captures* |
| KZNSB nets | 1991–2021 | Beach protection | Incidental captures | annual catch per km of net |
| KZNSB drumlines | 1991–2021 | Beach protection | Incidental captures | annual catch per number of drumlines |

*Information from 4 respondents, each fishing a season of approximately 100 days per year.

linear or quadratic GLMs and non-linear GAMs based on approximated AIC from Restricted Maximum Likelihood (REML) fits using the ‘mgcv’ R package (Wood 2011). The effective degrees of freedom were set at $k = 10$, after preliminary evaluation of multiple values. We assessed the validity of underlying model assumptions from the visual evaluation of diagnostic plots.

We evaluated the potential for redistribution from geographic trends in provoked and unprovoked white shark bite incidents in South Africa. Official reporting to the International Shark Incident File has been conducted by the KZNSB since 1974. An incident is defined as any physical contact between the shark and the victim, or any equipment used by the victim (e.g. a surfboard). As much information as possible is gathered to try to ascertain the species of shark responsible for the incident, including when and where the incident occurred, the time of day, water depth, water clarity, victims’ activity and clothing, as well as photographs of bite wounds and collection of embedded teeth fragments. The accuracy and completeness of the incident file depends on reporting by the victims and/or eyewitnesses to questions on a standardized shark incident questionnaire. Most incidents are investigated directly by the staff of the KZNSB, assisted by scientists from other organizations or research institutes. These analyses are based on all incidents (unprovoked and provoked) attributed to a white shark between 2000 and 2022. To evaluate geographic pattern, all locations were expressed as the relative distance in kilometers along the coast from the Mozambique/South African border (Dunlop et al. 2013; Rogers et al. 2022) and categorized into incidents on the Western Cape (WC), Eastern Cape (EC), and KwaZulu-Natal (KZN) coastline. While the extremely low

annual number of white shark incidents is positive in the context of human-shark co-existence, we recognize that such small numbers complicate robust statistical evaluation. As such, we did not fit a model to the annual number of incidents to assess trends.

In addition to the regional patterns assessed above, we used a pairwise correlation analysis to investigate the potential for smaller-scale associations among monitored locations. We measured the strength of pairwise correlations among the detrended monitoring indices with Kendall’s τ coefficient and used a one-sided test of association to evaluate significance. Kendall’s τ is a rank-based metric of association that is appropriate if the underlying relationship is unlikely to be linear. If animals tended to leave a specific site for an alternate site (for instance, animals leave False Bay to preferentially reside in Algoa Bay), there would be the expectation of a negative correlation.

3. Results

The individual indices used to assess trends demonstrated varying patterns over time, which were the most divergent during the last five years (Fig. 2). Captures in the KZNSB bather protection programme declined from a maximum of 1.79 animals/km of net in 1978 to 0.73 animals/km in 2021. It is important to recognize that monitoring in 2019–2021 used <12 km of netting while all other years had >20 km deployed, meaning that chance captures of single animals would have a proportionately greater effect on CPUE in recent years. CPUE from drumline deployments fluctuated above and below 0.6 captures/drumline from 2010 onwards, with the fourth highest value observed in 2021.

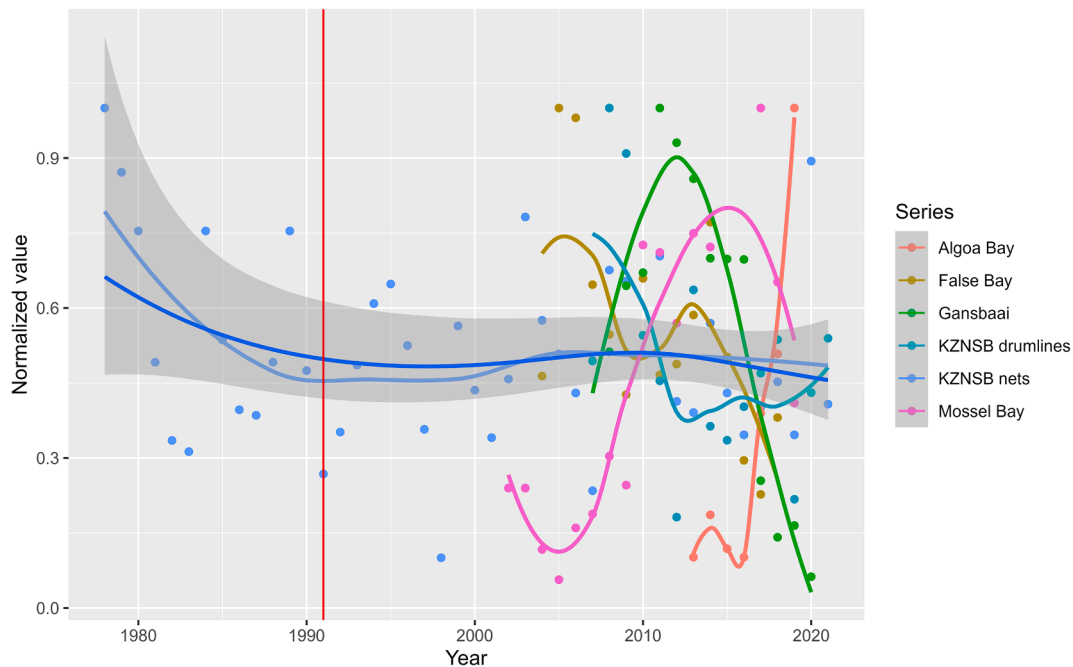


Fig. 2. A comparison of the data series used to assess trends in abundance for South African white shark, with all indices normalized by their maximum value. A loess smooth line was added to individual indices to make annual changes more apparent. The fit of a GAM model to the combined data is overlaid in dark blue with the confidence intervals shown as grey shading. Vertical red line denotes the year (1991) white sharks were protected in South Africa. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Shore angler captures in Algoa Bay increased dramatically from six individual sharks/season in 2013 to 59 in 2019. Mean annual SPUE in Mossel Bay strongly increased from 2002 to 2017, peaking at 2.8 individuals/hour before declining to 1.1 in 2019. Conversely, sightings in False Bay declined from an annual mean of 2.5 individuals/hour in 2005 to 0.6 in 2017, while interactions in Gansbaai peaked in 2011 at 3.8 sightings/hour and declined to 0.2 in 2020.

3.1. Abundance trends

While the GAM better described long-term trends compared to a simple linear or polynomial GLM, the deviance explained by the fitted model was very low (5.4%). This suggests that the majority of variability in abundance indices was not explained by the temporal trend and could be strongly related to unmodelled predictors. The smooth term demonstrated some non-linearity in relative abundance over time (edf = 3.074), yet the coefficient was not significant (p -value = 0.194). Following a slight decline during the initial years of monitoring, the overall fitted trend remained relatively constant over time (Fig. 2). Given the variability in the individual indices, there is no evidence of systematic changes in relative abundance across the full South African region.

3.2. Geographic distribution

There was a geographic pattern in the shark incident file. Within the Western Cape, the distribution of white shark incidents shifted easterly from 2000 to 2022 (Fig. 3; top panel), coincident with a slight reduction in the number of incidents in the Western Cape (Fig. 3; bottom panel). There was no evidence of a geographic pattern or a corresponding increase in the total number of incidents over time in the Eastern Cape or KZN regions. Among specific locations, correlation coefficients between detrended monitoring indices tended to be very low, with a single value $> |0.5|$ (-0.67 between Algoa Bay and Mossel Bay; Fig. 4). Locations linked by systematic, directional movement would be expected to have a negative correlation, yet most coefficients were positive. Additionally,

testing for association between the paired samples demonstrated that none of the correlations were significant at a 95% confidence level from a one-sided test. Removing the years of data collection affected by Covid restrictions (2020 onwards), lagging data by one year when paired with False Bay or Gansbaai, and/or using a different normalization method as sensitivity analyses did not change overall conclusions.

4. Discussion

White sharks were formally protected from exploitation in 1991 in South Africa (Cliff et al. 1996). Yet, their population status appears largely unchanged thirty years later despite the substantial reduction in occurrence in False Bay and Gansbaai in the last five years (Hammerschlag et al. 2019, 2022; Towner et al. 2022a). Our prediction arose because there was no overall consistency in the individual monitoring indices, with declines at some sites seemingly corresponding to increases at others in the same year. The magnitude of annual variability demonstrates that factors other than abundance influenced trends. For example, it is not biologically possible for reproduction to account for an 8-fold increase over four years in Algoa Bay (Bowlby et al. 2022). When evaluating monitoring data, movement would represent process error or a biological process causing variation in relative abundance at specific locations. The second source of variability is observation error, or variation in the methodology used to obtain the monitoring index. There were documented changes in the design and/or efficacy of monitoring in most time series, which would be expected to introduce variability in detection efficiency (Dénes et al., 2015). Furthermore, CPUE indices derived from positive catches only (discounting absence data) regularly exhibit hyperstability in catch rates as abundance declines (Langley 2019). However, movement and redistribution cannot be ignored when monitoring changes in relative abundance from localized indices, particularly in light of the geographical pattern in white shark incidents. For the status of white sharks in South Africa to remain unchanged, the population must have redistributed along the South African coastline. Shifts in occupancy at small spatial scales were not evident from correlation analyses, which suggests that the variability in movement

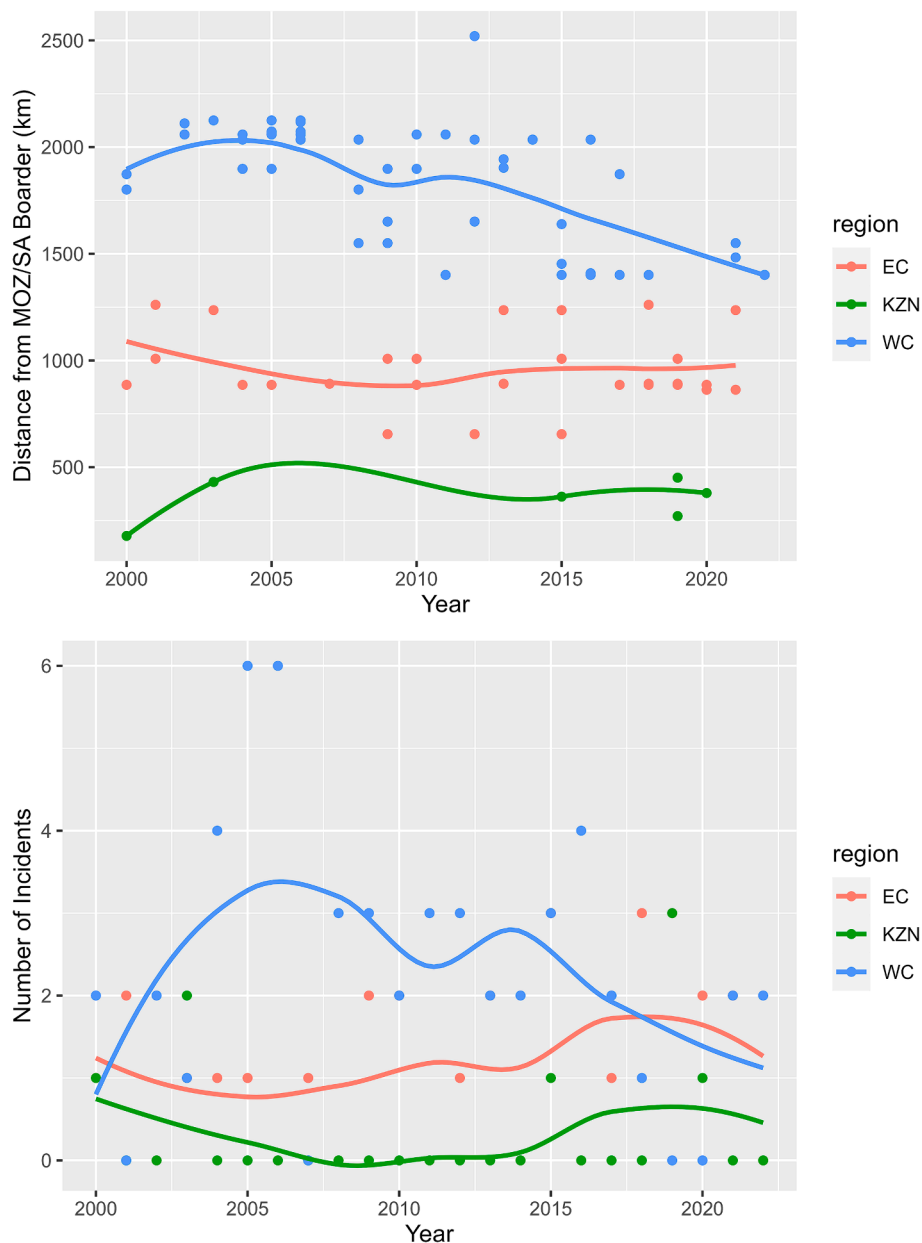


Fig. 3. Geographical distribution of provoked and unprovoked white shark incidents in South Africa over time (top panel), and the number of incidents per year (bottom panel). Incidents were categorized into Eastern Cape (EC), Western Cape (WC) and KwaZulu-Natal coastline and a loess smooth was fit to data in each category to show general patterns.

behaviour and habitat use among ontogenetic stages and sexes (Kock et al. 2013, 2022; French et al. 2018; Pardini et al. 2001; Dicken et al. 2013; Hoyos-Padilla et al. 2016) results in complex rather than unidirectional linkages among monitored locations. The hypothesis best supported by the shark incident file is that white sharks have partially shifted their distribution away from the Western Cape.

Individual white sharks are highly mobile and regularly exhibit transient movements interspersed with periods of residency at specific aggregation sites and/or localized regions (Skomal et al. 2017; Duffy et al. 2012; Jorgensen et al. 2010; Franks et al. 2021; Kock et al. 2022). Prey availability is a key driver for movement and occurrence of predators, including white sharks (Brown et al. 2010; Hoyos-Padilla et al. 2016; Kock et al. 2013). Historically, the availability of young Cape fur seals was thought to be one of the primary drivers for white shark occurrence in False Bay and Gansbaai during winter (Kock et al. 2013; Towner et al. 2016). A substantial body of evidence demonstrated the importance of seals in the white sharks' diet, especially for white sharks

> 3 m in length (Hussey et al. 2012; Kock et al. 2013; Martin et al. 2005). However, seal populations are stable in False Bay and Gansbaai (Pfaff et al. 2019) and offer an abundant and predictable food source in time and space. The fact that white sharks have been absent even when naïve, young-of-the-year seals are abundant suggests that prey availability is not the primary reason for their near-complete absence around the seal colonies during winter.

In the austral spring and summer months, white sharks are more often found at nearshore sites where they have been observed feeding on seasonally abundant fish, sharks and rays. Studies on the South African white shark diet have identified these generalist predators feeding on at least 40 different species from four main functional groups: cephalopods, elasmobranchs, teleosts and marine mammals (Hussey et al. 2012; French et al., 2018). Thus, white sharks are highly adaptive and likely prey upon species most abundant and accessible in time and space, albeit with dietary specialization differing between sexes (French et al., 2018). Some white shark scientists and cage diving industry

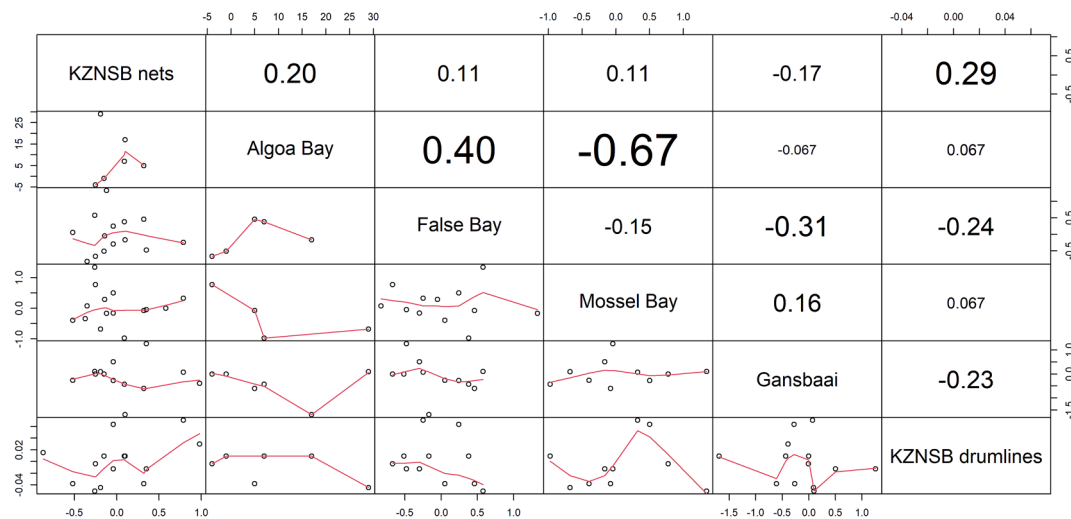


Fig. 4. Pairwise correlations (Kendall's τ) among abundance indices, with the monitoring site identified on the diagonal, the strength of the correlation in the top triangle and the data (open circles) used in each comparison in the bottom triangle. Red lines represent a loess smooth. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

representatives hypothesized that the substantial declines of formerly abundant demersal shark populations, particularly the smoothhound (*Mustelus mustelus*) and soupfin shark (*Galeorhinus galeus*), were responsible for the decline of white sharks in the Western Cape (DFFE 2020). However, demersal sharks are only one component of the white sharks' generalist diet (Hussey et al. 2012; French et al., 2018), and reconstructed catch records dating to the 1950s suggest the steep decline in soupfin sharks predates the disappearance of the white sharks at False Bay and Gansbaai (DFFE 2020, Winker et al. 2019, da Silva et al. 2019). Furthermore, despite higher fishing mortality of demersal sharks (specifically smoothhounds) in Mossel Bay, Plettenberg Bay and Algoa Bay, white shark occurrence and abundance have persisted (DFFE, 2020). Therefore, declines in demersal shark populations cannot explain the pattern of occurrence observed for white sharks in this study.

An alternative theory proposed for the disappearance of white sharks from False Bay and Gansbaai is the recent appearance of a pair of killer whales specializing in hunting large, coastal sharks. This killer whale pair was first documented in False Bay in 2015, preying upon sevengill sharks, which coincided with their disappearance from a large aggregation site in False Bay (Engelbrecht et al. 2019). In 2017, the same killer whale pair were suspected of preying upon at least five large white sharks in Gansbaai, ranging in size from 2.6 to 4.9 m total length (Towner et al. 2022a). Since that time, additional mortalities have been recorded in Mossel Bay from a greater number of killer whales (Towner et al. 2022b). These mortalities were not restricted to juvenile animals, but included juveniles, subadults and adults (Towner et al. 2022a, Towner et al. 2022b). The number of predation events by killer whales is likely more frequent than documented, as not all white shark carcasses would have washed ashore and been recorded. In addition to the direct effects of predation, the indirect effect of predation (or the fear of predation) profoundly influences animal behaviour (Laundré et al. 2010; Zanette and Clinchy 2020). Following these predation events, white sharks fled the area and remained absent for extended periods (Towner et al. 2022a). The significant impact of killer whales on white sharks is evident elsewhere. At the Southeast Farallon Islands in North America, brief and occasional visits by killer whales close to the island resulted in white sharks fleeing the immediate area and decreased predation by white sharks on pinnipeds during years killer whales were present (Jorgensen et al. 2019). Therefore, the increased presence of such specialist predators may explain why white sharks have remained absent in False Bay and Gansbaai, but continue to occupy Mossel Bay, Plettenberg Bay and Algoa Bay, where killer whales are less often observed. However, killer whales have recently started preying upon white sharks

in Mossel Bay, resulting in flight responses from the site (Towner et al. 2022b).

By necessity, our evaluation of regional trends was very simple due to the nature of the available data. If monitoring information had been collected over a longer time-period for most indices, dynamic factor analysis (DFA) might have been a preferred method to evaluate temporal trends (e.g., Peterson et al. 2021). Developed specifically for multivariate time series data, DFA can detect common patterns and evaluate the effects of explanatory variables (Zuur et al. 2003). Alternately, monitoring data are typically standardized using operational (e.g. vessel) or environmental (e.g. temperature) covariates to reduce variability in relative abundance indices prior to input in stock assessment (Maunder and Punt 2004; Maunder et al. 2006). For long-lived species protected from exploitation, changes in relative abundance would be expected to be gradual and could easily be masked by inter-annual variability or noise. A better characterization of changes in relative abundance at a regional level will only become possible from the continuation and better standardization of long-term monitoring at multiple locations, ideally coupled with an increased recording of potential covariates. In particular, increasing monitoring effort in non-traditional areas along the Eastern Cape will be critical to assess future status and inform management of white sharks in South Africa. Such monitoring would help substantiate anecdotal reports from shark incident victims and other marine user groups (fishermen, spearfishers, paddle skiers and fishing skiers) of markedly increased sightings and interactions with white sharks along the Eastern Cape during the last five years.

4.1. Conclusions

This study represents the most thorough analysis of white shark abundance indices in South Africa. Combining information from all primary aggregation sites substantially improves our understanding of the current population status and distribution of white sharks in South Africa. Although white sharks are inherently vulnerable to exploitation (Bowlby et al. 2022), the regional results provide an alternate and more comprehensive perspective on their status in South Africa compared to research focused on the Western Cape (Andreotti et al. 2016; Hamerschlag et al. 2019, 2022; Towner et al. 2022a). Although it is encouraging that there is no evidence of a population decline for this species across their entire South African range, changes in geographical distribution need to be closely monitored due to their socioeconomic impact on cage diving activities, tourism and risk of human-shark

incidents, as well as ecosystem effects on fish community structure. However, it remains a concern that there has been no evidence of population increase following protection in 1991 (this study) and that the mean size of female white sharks caught in the KZNSB bather protection program has declined. Both would be indicative of a population under pressure. Simulation modelling of four life-history scenarios (different productivity and population size) suggested that currently known white shark removals may prevent population recovery in South Africa (Bowlby et al. 2022), consistent with the lack of trend in relative abundance that we describe. Information provided in this study can be used to improve the conservation of this species by providing a baseline for future monitoring, reaffirming the need to assess the population at a regional and not a local level. Research needs to be directed towards understanding drivers of localized and regional abundance change, and management focused on reducing anthropogenic sources of mortality within their Southwest Indian Ocean range.

CRedit authorship contribution statement

MD, AK and AT conceptualized research, MD, AK, AT, and SW acquired funding and administered data collection. HB and TR undertook investigation and developed methodology. HB wrote the original draft. All authors participated in review and editing the final version.

Declaration of Competing Interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: The authors declare that no funds, grants, or other support were received during the preparation of this manuscript. Interests: All authors declare no relevant financial interests. Sara Waries and Toby Rogers are supported by Shark Spotters and Matt Dicken is employed by the KZN Sharks Board. Heather Bowlby and Alison Kock declare no relevant non-financial interests. The research was conceived by Matt Dicken. Data collections were performed by Matt Dicken, Alison Towner, Sara Waries, and Alison Kock. Analyses were performed by Toby Rogers and Heather Bowlby. The first draft of the manuscript was written by Heather Bowlby and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript. The datasets generated during and/or analyzed during the current study are available from the collaborating authors upon reasonable request. The corresponding author will facilitate data access.

Data availability

Data will be made available on request.

Acknowledgements

We gratefully acknowledge the Department of Fisheries, Forestry, and the Environment (DFFE) for granting research permits and Sarika Singh (DFFE) for facilitating logbook data access from Mossel Bay. We thank Shark Spotters, Marine Dynamics and White Shark Africa for providing research platforms in False Bay, Gansbaai and Mossel Bay. We also acknowledge the invaluable contributions of field assistants, crew members, and researchers in data collection. Finally, we thank the anonymous reviewers for their insightful feedback.

The Save Our Seas Foundation funded the white shark research in False Bay from 2003 – 2017. Research permits were granted to co-authors Alison Kock, Alison Towner and Matt Dicken and issued by the Department of Forestry, Fisheries and the Environment (ex-MCM/DEA/DFFE RES2003-RES2021) for all years of study.

References

- Andreotti, S., Rutzen, M., van der Walt, S., Von der Heyden, S., Henriques, R., Meyer, M., Oosthuizen, H., Matthee, C.A., 2016. An integrated mark-recapture and genetic approach to estimate the population size of white sharks in South Africa. *Mar. Ecol. Prog. Ser.* 552, 241–253. <https://doi.org/10.3354/meps11744>.
- Bonfil, R., Meyer, M., Scholl, M.C., Johnson, R., O'Brien, S., Oosthuizen, H., Swanson, S., Kotze, D., Paterson, M., 2005. Transoceanic migration, spatial dynamics, and population linkages of white sharks. *Science* 310 (5745), 100–103. <https://doi.org/10.1126/science.1114898>.
- Bowlby, H.D., Gibson, A.J.F., 2020. Implications of life history uncertainty when evaluating status in the Northwest Atlantic population of White shark (*Carcharodon carcharias*). *Ecol. Evol.* 10, 4990–5000. <https://doi.org/10.1002/ece3.6252>.
- Bowlby, H.D., Hammerschlag, N., Irion, D.T., Gennari, E., 2022. How continuing mortality affects recovery potential for prohibited sharks: the case of white sharks in South Africa. *Front. Conserv. Sci.* 3 <https://doi.org/10.3389/fcosc.2022.988693>.
- Brown, A.C., Lee, D.E., Bradley, R.W., Anderson, S., 2010. Dynamics of white shark predation on pinnipeds in California: effects of prey abundance. *Copeia*. 2010 (2), 232–238. <https://doi.org/10.1643/CE-08-012>.
- Cliff, G., Dudley, S.F., 2011. Reducing the environmental impact of shark-control programs: a case study from KwaZulu-Natal, South Africa. *Mar. Freshwater Res.* 62 (6), 700–709. <https://doi.org/10.1071/MF10182>.
- Cliff, G., Dudley, S.F.J., Jury, M.R., 1996. Catches of white sharks in KwaZulu-Natal, South Africa and environmental influences. In: Klimley, K.A., Ainley, D.G. (Eds.), *Great White Sharks: the Biology of Carcharodon Carcharias*. Academic Press, San Diego, California, pp. 351–362.
- da Silva, C., Winker, H., Parker, D., Kerwarth, S.E., 2019. Assessment of smoothhound shark *Mustelus mustelus* in South Africa. Technical Report FISHERIES/LSWG/#04/2019. Department of Agriculture, Forestry and Fisheries. Cape Town, South Africa.
- Dénes, F.V., Silveira, L.F., Beissinger, S.R., Isaac, N., 2015. Estimating abundance of unmarked animal populations: accounting for imperfect detection and other sources of zero inflation. *Methods Ecol. Evol.* 6 (5), 543–556.
- DFFE (Department of Forestry and Fisheries, and the Environment), 2020. Review of the South African National Plan of Action for the Conservation and Management of Sharks. https://www.dffe.gov.za/sites/default/files/reports/sharksconservationmanagement_nationplanofaction_review2020october.pdf [accessed April 13, 2023].
- Dicken, M.L., Booth, A.J., 2013. Surveys of white sharks (*Carcharodon carcharias*) off bathing beaches in Algoa Bay, South Africa. *Mar. Freshwater Res.* 64 (6), 530–539. <https://doi.org/10.1071/MF12336>.
- Dicken, M.L., Smale, M.J., Booth, A.J., 2013. White sharks *Carcharodon carcharias* at Bird Island, Algoa Bay, South Africa. *African J. Mar. Sci.* 35 (2), 175–182. <https://doi.org/10.2989/1814232X.2013.800579>.
- Dicken, M.L., Cliff, G., Winker, H., 2016. Sharks caught in the KwaZuluNatal bather protection programme, South Africa. 13. The tiger shark *Galeocerdo cuvier*. *African J. Mar. Sci.* 38, 285–301. <https://doi.org/10.2989/1814232X.2016.1198276>.
- Dicken, M.L., Winker, H., Smale, M.J., Cliff, G., 2018. Sharks caught in the KwaZulu-Natal bather protection programme, South Africa. 14. The smooth hammerhead shark *Sphymazyaena* (Linnaeus). *African J. Mar. Sci.* 40 (2), 157–174.
- Duffy, C.A.J., Francis, M.P., Manning, M.J., Bonfil, R., 2012. Regional population connectivity, oceanic habitat, and return migration revealed by satellite tagging of white sharks, *Carcharodon carcharias*, at New Zealand aggregation sites. In: Domeier, M.L. (Ed.), *Global Perspectives on the Biology and Life History of the White Shark*. CRC Press, Boca Raton, FL, pp. 301–318.
- Dulvy, N.K., Pacoureau, N., Rigby, C.L., Pollom, R.A., Jabado, R.W., Ebert, D.A., Finucci, B., Pollock, C.M., Cheok, J., Derrick, D.H., Herman, K.B., Sherman, C.S., VanderWright, W.J., Lawson, J.M., Walls, R.H.L., Carlson, J.K., Charvet, P., Bineesh, K.K., Fernando, D., Ralph, G.M., Matsushiba, J.H., Hilton-Taylor, C., Fordham, S.V., Simpfendorfer, C.A., 2021. Overfishing drives over one-third of all sharks and rays toward a global extinction crisis. *Curr. Biol.* 31 (21), 4773–4787.e8.
- Dunlop, S.W., Mann, B.Q., Van der Elst, R.P., 2013. A review of the Oceanographic Research Institute's Cooperative Fish Tagging Project: 27 years down the line. *African J. Mar. Sci.* 35 (2), 209–221. <https://doi.org/10.2989/1814232X.2013.769909>.
- Engelbrecht, T., Kock, A., Waries, S., O'Riain, M.J., Patterson, H.M., 2017. Shark spotters: successfully reducing spatial overlap between white sharks (*Carcharodon carcharias*) and recreational water users in False Bay, South Africa. *PLoS One* 12 (9), e0185335.
- Engelbrecht, T.M., Kock, A.A., O'Riain, J., 2019. Running scared: when predators become prey. *Ecosphere* 10 (1), e02531.
- French, G.C., Rizzuto, S., Stürup, M., Inger, R., Barker, S., van Wyk, J.H., Towner, A.V., Hughes, W.O.H., 2018. Sex, size and isotopes: cryptic trophic ecology of an apex predator, the white shark *Carcharodon carcharias*. *Mar. Biol.* 165, 102. <https://doi.org/10.1007/s00227-018-3343-x>.
- Government Notice No R. 480 of 29 April 2020. Disaster management Act, 2022, Amendment of regulations issued in terms of Section 27(2). https://www.gov.za/sites/default/files/gcis_document/202203/46127rg11413gon1941.pdf [accessed April 11, 2023].
- Gwinn, D.C., Bacheler, N.M., Shertzer, K.W., 2019. Integrating underwater video into traditional fisheries indices using a hierarchical formulation of a state-space model. *Fish. Res.* 219, 105309 <https://doi.org/10.1016/j.fishres.2019.105309>.
- Hammerschlag, N., Williams, L., Fallows, M., Fallows, C., 2019. Disappearance of white sharks leads to the novel emergence of an allopatric apex predator, the sevengill shark. *Sci. Rep.-UK* 9, 1908. <https://doi.org/10.1038/s41598-018-37576-6>.
- Hammerschlag, N., Fallows, C., Meyer, M., Seakamela, S.M., Orndorff, S., Kirkman, S., Kotze, D., Creel, S., 2022. Loss of an apex predator in the wild induces physiological

- and behavioural changes in prey. *Biol. Lett.* 18 (1), 20210476. <https://doi.org/10.1098/rsbl.2021.0476>.
- Hewitt, A.M., Kock, A.A., Booth, A.J., Griffiths, C.L., 2018. Trends in sightings and population structure of white sharks, *Carcharodon carcharias*, at Seal Island, False Bay, South Africa, and the emigration of subadult female sharks approaching maturity. *Environ. Biol. Fish.* 101 (1), 39–54. <https://doi.org/10.1007/s10641-017-0679-x>.
- Hoyos-Padilla, E.M., Klimley, A.P., Galván-Magaña, F., Antoniou, A., 2016. Contrasts in the movements and habitat use of juvenile and adult white sharks (*Carcharodon carcharias*) at Guadalupe Island, Mexico. *Anim. Biotelemetry* 4, 1–4. <https://doi.org/10.1186/s40317-016-0106-7>.
- Hussey, N.E., McCann, H.M., Cliff, G., Dudley, S.F., Wintner, S.P., Fisk, A.T., 2012. Size-based analysis of diet and trophic position of the white shark (*Carcharodon carcharias*) in South African waters. In: Domeier, M.L. (Ed.), *Global Perspectives on the Biology and Life History of the White Shark*. CRC Press, Boca Raton, FL, pp. 27–49.
- Huveneers, C., Apps, K., Becerril-García, E.E., Bruce, B., Butcher, P.A., Carlisle, A.B., Chapple, T.K., Christiansen, H.M., Cliff, G., Curtis, T.H., Daly-Engel, T.S., Dewar, H., Dicken, M.L., Domeier, M.L., Duffy, C.A.J., Ford, R., Francis, M.P., French, G.C.A., Galván-Magaña, F., García-Rodríguez, E., Gennari, E., Graham, B., Hayden, B., Hoyos-Padilla, E.M., Hussey, N.E., Jewell, O.J.D., Jorgensen, S.J., Kock, A.A., Lowe, C.G., Lyons, K., Meyer, L., Oelofse, G., Oñate-González, E.C., Oosthuizen, H., O'Sullivan, J.B., Ramm, K., Skomal, G., Sloan, S., Smale, M.J., Sosa-Nishizaki, O., Sperone, E., Tamburin, E., Towner, A.V., Wicisel, M.A., Weng, K.C., Werry, J.M., 2018. Future research directions on the “elusive” white shark. *Front. Mar. Sci.* 5 <https://doi.org/10.3389/fmars.2018.00455>.
- Johnson, R. and Kock, A., 2006. South Africa's White Shark cage-diving industry-is their cause for concern? In: Nel DC and Peschak TP (eds). *Finding a balance: White shark conservation and recreational safety in the inshore waters of Cape Town, South Africa*. Proceedings of a specialist workshop. WWF South Africa Report Series - 2006/Marine/001 (2006). <http://www.oceans-research.com/wp-content/uploads/2014/03/johnson-2006.pdf> [accessed April 11, 2023].
- Jorgensen, S.J., Reeb, C.A., Chapple, T.K., Anderson, S., Perle, C., Van Sommeran, S.R., Fritz-Cope, C., Brown, A.C., Klimley, A.P., Block, B.A., 2010. Philopatry and migration of Pacific white sharks. *P. Roy. Soc. B-Biol. Sci.* 277 (1682), 679–688.
- Jorgensen, S.J., Anderson, S., Ferretti, F., Tietz, J.R., Chapple, T., Kanive, P., Bradley, R. W., Moxley, J.H., Block, B.A., 2019. Killer whales redistribute white shark foraging pressure on seals. *Sci. Rep-UK* 9 (1). <https://doi.org/10.1038/s41598-019-39356-2>.
- Jorgensen, S.J., Micheli, F., White, T.D., Van Houtan, K.S., Alfaro-Shigueto, J., Andrzejczek, S., Arnoldi, N.S., Baum, J.K., Block, B., Britten, G.L., Butner, C., Caballero, S., Cardenosa, D., Chapple, T.K., Clarke, S., Cortés, E., Dulvy, N.K., Fowler, S., Gallagher, A.J., Gilman, E., Godley, B.J., Graham, R.T., Hammerschlag, N., Harry, A.V., Heithaus, M.R., Hutchinson, M., Huveneers, C., Lowe, C.G., Lucifora, L.O., MacKeracher, T., Mangel, J.C., Barbosa Martins, A.P., McCauley, D.J., McClenachan, L., Mull, C., Natanson, L.J., Pauly, D., Pazmiño, D.A., Pisteos, J.C.A., Queiroz, N., Roff, G., Shea, B.D., Simpfendorfer, C.A., Sims, D.W., Ward-Paige, C., Worm, B., Ferretti, F., 2022. Emergent research and priorities for shark and ray conservation. *Endanger. Species Res.* 47, 171–203.
- Kock, A.A., Lombard, A.T., Daly, R., Goodall, V., Meyer, M., Johnson, R., Fischer, C., Koen, P., Irion, D., Gennari, E., Towner, A., Jewell, O.J.D., da Silva, C., Dicken, M.L., Smale, M.J., Photopoulou, T., 2022. Sex and size influence the spatiotemporal distribution of white sharks, with implications for interactions with fisheries and spatial management in the southwest Indian Ocean. *Front. Mar. Sci.* 9, 811985 <https://doi.org/10.3389/fmars.2022.811985>.
- Kock, A., O'Riain, M.J., Mauff, K., Meyer, M., Kotze, D., Griffiths, C., Klimley, A.P., 2013. Residency, habitat use and sexual segregation of white sharks, *Carcharodon carcharias* in False Bay, South Africa. *PLoS one* 8 (1), e55048.
- Langley, A.D., 2019. An investigation of the performance of CPUE modelling approaches—a simulation study. *New Zealand Fisheries Assessment Report*. 2019/57. <https://docs.niwa.co.nz/library/public/FAR2019-57.pdf> [accessed April 11, 2023].
- Laundré, J.W., Hernández, L., Ripple, W.J., 2010. The landscape of fear: ecological implications of being afraid. *Open Ecol. J.* 3, 1–7. <https://doi.org/10.2174/1874213001003030001>.
- Lawler, J.J., Campbell, S.P., Guerry, A.D., Kolozsvary, M.B., O'Connor, R.J., Seward, L. C., 2002. The scope and treatment of threats in endangered species recovery plans. *Ecol. Appl.* 12, 663–667. [https://doi.org/10.1890/1051-0761\(2002\)012\[0663:TSATOT\]2.0.CO;2](https://doi.org/10.1890/1051-0761(2002)012[0663:TSATOT]2.0.CO;2).
- Martin, R.A., Hammerschlag, N., Collier, R.S., Fallows, C., 2005. Predatory behaviour of white sharks (*Carcharodon carcharias*) at Seal Island, South Africa. *J. Mar. Biol. Assoc. UK* 85, 1121–1135. <https://doi.org/10.1017/S002531540501218X>.
- Maunder, M.N., Punt, A.E., 2004. Standardizing catch and effort data: a review of recent approaches. *Fish. Res.* 70, 141–159. <https://doi.org/10.1016/j.fishres.2004.08.002>.
- Maunder, M.N., Sibert, J.R., Fonteneau, A., Hampton, J., Kleiber, P., Harley, S.J., 2006. Interpreting catch per unit effort data to assess the status of individual stocks and communities. *ICES J. Mar. Sci.* 63, 1373–1385. <https://doi.org/10.1016/j.icesjms.2006.05.008>.
- Pardini, A.T., Jones, C.S., Noble, L.R., Kreiser, B., Malcolm, H., Bruce, B.D., Stevens, J.D., Cliff, G., Scholl, M.C., Francis, M., Duffy, C.A.J., Martin, A.P., 2001. Sex-biased dispersal of great white sharks. *Nature*. 412 (6843), 139–140.
- Peterson, C.D., Courtney, D.L., Cortés, E., Latour, R.J., Anderson, E., 2021. Reconciling conflicting survey indices of abundance prior to stock assessment. *ICES J. Mar. Sci.* 78 (9), 3101–3120.
- Pfaff, M.C., Logston, R. C., Raemaekers, S. J. P. N., Hermes, J. C., Blamey, L. K., Cawthra, H. C., et al., 2019. A synthesis of three decades of socio-ecological change in False Bay South Africa: setting the scene for multidisciplinary research and management. *Elementa: Science of the Anthropocene*. 7, 32. doi: 10.1525/elementa.367.
- Rogers, T.D., Kock, A.A., Jordaan, G.L., Mann, B.Q., Naude, V.N., O'Riain, M.J., Simpfendorfer, C., 2022. Movements and growth rates of bronze whaler sharks (*Carcharhinus brachyurus*) in southern Africa. *Mar. Freshwater Res.* 73 (12), 1450–1464.
- Skomal, G.B., Braun, C.D., Chisholm, J.H., Thorrold, S.R., 2017. Movements of the White shark *Carcharodon carcharias* in the North Atlantic Ocean. *Mar. Ecol. Prog. Ser.* 580, 1–16. <https://doi.org/10.3354/meps12306>.
- Thompson, K.A., Switzer, T.S., Christman, M.C., Keenan, S.F., Gardner, C.L., Overly, K.E., Campbell, M.D., 2022. A novel habitat-based approach for combining indices of abundance from multiple fishery-independent video surveys. *Fish. Res.* 247, 106178 <https://doi.org/10.1016/j.fishres.2021.106178>.
- Towner, A.V., Underhill, L.G., Jewell, O.J.D., Smale, M.J., Tsikliras, A.C., 2013a. Environmental influences on the abundance and sexual composition of white sharks *Carcharodon carcharias* in Gansbaai, South Africa. *PLoS one* 8 (8), e71197.
- Towner, A.V., Wicisel, M.A., Reisinger, R.R., Edwards, D., Jewell, O.J.D., Russo, D., 2013b. Gauging the threat: the first population estimate for white sharks in South Africa using photo identification and automated software. *PLoS one* 8 (6), e66035.
- Towner, A.V., Leos-Barajas, V., Langrock, R., Schick, R.S., Smale, M.J., Kaschke, T., Jewell, O.J.D., Papastamatiou, Y.P., Hopkins, W., 2016. Sex-specific and individual preferences for hunting strategies in white sharks. *Funct. Ecol.* 30 (8), 1397–1407.
- Towner, A.V., Watson, R.G.A., Kock, A.A., Papastamatiou, Y., Sturup, M., Gennari, E., Baker, K., Booth, T., Dicken, M., Chivell, W., Elwen, S., Kaschke, T., Edwards, D., Smale, M.J., 2022. Fear at the top: killer whale predation drives white shark absence at South Africa's largest aggregation site. *African J. Mar. Sci.* 44 (2), 139–152.
- Towner, A.V., Kock, A.A., Stopforth, C., Hurwitz, D., Elwen, S.H., 2023. Direct observation of killer whales preying on white sharks and evidence of a flight response. *Ecology* 104 (1). <https://doi.org/10.1002/ecy.3875>.
- Winker, H., Parker, D., da Silva, C. and Kerwath, S., 2019. First comprehensive assessment of soupfin shark *Galeorhinus galeus* in South Africa. Technical Report FISHERIES/LSWG/#05/2019. Department of Agriculture, Forestry and Fisheries. Rogge Bay, South Africa.
- Wood, S.N., 2011. Fast stable restricted maximum likelihood and marginal likelihood estimation of semiparametric generalized linear models. *J. Roy. Stat. Soc. B* 73(1), 3–36. doi: 10.1111/j.1467-9868.2010.00749.x.
- Zanette, L.Y., Clinchy, M., 2020. Ecology and neurobiology of fear in free-living wildlife. *Ann. Rev. Ecol. Evol. System.* 51, 297–318. <https://doi.org/10.1146/annurev-ecolsys-011720-124613>.
- Zuur, A.F., Tuck, I.D., Bailey, N., 2003. Dynamic factor analysis to estimate common trends in fisheries time series. *Can. J. Fish. Aquat. Sci.* 60 (5), 542–552. <https://doi.org/10.1139/f03-030>.