COMMENT

Pessimistic assessment of white shark population status in South Africa: Comment on Andreotti et al. (2016)

Dylan T. Irion[1,*], Leslie R. Noble[2], Alison A. Kock[3,4], Enrico Gennari[1,4],
Matt L. Dicken[5,6], Adrian M. Hewitt[7], Alison V. Towner[8,9], Anthony J. Booth[8],
Malcolm J. Smale[10], Geremy Cliff[5,11]

[1]Oceans Research, PO Box 1767, Mossel Bay 6500, South Africa
[2]Institute of Biological & Environmental Sciences, University of Aberdeen, Aberdeen AB24 2TZ, UK
[3]Human Wildlife Institute, Department of Biological Sciences, University of Cape Town, Private Bag X3,
Rondebosch 7701, South Africa
[4]South African Institute for Aquatic Biodiversity (SAIAB), Private Bag 1015, Grahamstown 6140, South Africa
[5]KwaZulu-Natal Sharks Board, Private Bag 2, Umhlanga Rocks 4320, South Africa
[6]Department of Zoology and Entomology, University of Fort Hare, Alice 5700, South Africa
[7]Bransholme, Hull, HU7 4QB, UK
[8]Department of Ichthyology and Fisheries Science, Rhodes University, PO Box 94, Grahamstown 6140, South Africa
[9]Dyer Island Conservation Trust, PO Box 78, Keinbaai 7220, South Africa
[10]Department of Zoology, Institute for Coastal and Marine Research, Nelson Mandela Metropolitan University,
PO Box 77000, Port Elizabeth 6031, South Africa
[11]Biomedical Resource Unit, University of KwaZulu-Natal, Durban 4000, South Africa

ABSTRACT: Andreotti et al. (2016; Mar Ecol Prog Ser 552:241–253) estimate an abundance (N) of 438 white sharks *Carcharodon carcharias* and a contemporary effective population size (CN_e) of 333 individuals along the South African coast. N was estimated by using a mark-recapture analysis of photographic identification records from a single aggregation site (Gansbaai). CN_e was calculated based on the levels of pairwise linkage disequilibrium of genetic material collected from 4 aggregation sites across approximately 965 km of South African coastline. However, due to the complex stock structure of white sharks and the model assumptions made by Andreotti et al. (2016), the conclusions drawn cannot be supported by their methods and data.

KEY WORDS: White shark · *Carcharodon carcharias* · Abundance · Contemporary effective population size · Mark-recapture · POPAN · Linkage disequilibrium

INTRODUCTION

Results of a mark-recapture study and a genetic analysis are reported by Andreotti et al. (2016a) to support claims that the South African population of white sharks *Carcharodon carcharias* has experienced a recent drastic decline over the last few generations and could face a difficult future. The use of a combination of techniques to estimate abundance (N) has been previously suggested for improved monitoring of white shark populations (Burgess et al. 2014, Dewar et al. 2013). In contrast to the title of the

article however, the methods used by Andreotti et al. (2016a) do not reflect a truly integrated and independent approach in which separate datasets would be combined into a joint likelihood. The authors estimate N based on a photographic identification dataset and then seek out a link between their estimate of N and effective population size estimates (CN_e) from a genetic dataset. Few caveats are provided to explain discrepancies between the 2 datasets, except when to refute higher estimates. Several sources of uncertainty may explain the discrepancy between datasets, but are omitted in favour of a precautionarily low population estimate. This type of approach, termed the 'precautionary principle', has widely been accepted amongst policy makers for management of resources in the face of uncertain information (Cooney 2004). The principle, however, serves to guide policy makers in erring on the side of caution when facing uncertain risks, not as a means to draw conclusions from uncertain results (Kriebel et al. 2001).

MARK-RECAPTURE ANALYSIS

A primary source of uncertainty in the interpretation of mark-recapture results often stems from the need to identify the most parsimonious data representation—achieving an acceptable balance of structure and precision. This process is generally achieved through model selection, where the fully parametrised model can be compared to those in which nuisance parameters are constrained or grouped, allowing the researcher to account for uncertainty using an information-theoretic approach such as Akaike's Information Criterion (AIC) (Lebreton et al. 1992, Barker & White 2004). Paramount to the success of this method is the *a priori* identification of a set of candidate models that are biologically relevant (Mundry 2011). For instance, Jolly-Seber (JS) mark-recapture models (as implemented in the open population model POPAN in MARK; White & Burnham 1999), where the parameter representing probability of entry (β) is held constant (as in Andreotti et al. 2016a), rarely have any biological interpretation and are therefore usually modelled with a time-dependent parametrisation (e.g. Vasconcellos & Colli 2009, C. J. Schwarz pers. comm.). The use of a constant parametrisation for β in Andreotti et al. (2016a) without any biological explanation raises concerns about the authors' use of the methods employed there, and the associated underlying assumptions (Anderson & Burnham 2002).

Among the key requirements of JS studies is the assumption of homogeneous capture probability between marked and unmarked individuals at each sampling occasion; this assumption allows for the estimation of N (Seber 1982). Similarly important is the assumption of homogeneous probability of survival between marked and unmarked individuals and sampling occasions (Seber 1982). Andreotti et al. (2016a) provide the combined results of Test 2 and Test 3 from the goodness of fit tests within the programme RELEASE (available in MARK), which tests the null hypotheses that capture and survival probabilities are homogeneous, citing a test statistic of $\chi^2 = 251.9$ and $p < 0.005$. The test statistic is highly significant and the null hypotheses should be rejected, which indicates that either capture or survival probability is heterogeneous (Burnham et al. 1987). The model assumptions have not been met, in contrast to how Andreotti et al. (2016a) have interpreted their data. Any estimate of N in this case is unreliable and therefore not a suitable measure for determining management decisions (Fletcher et al. 2012).

For South African white sharks, heterogeneous capture probability has been identified at Seal Island and False Bay (Hewitt 2014), and heterogeneous capture and survival probabilities have been identified in Mossel Bay (Ryklief 2012), yet neither study is cited in Andreotti et al. (2016a). Heterogeneous survival probability was also reported by Towner et al. (2013b) in a previous estimate of white shark abundance at Gansbaai. Estimates of population size can be negatively biased when the capture probability is heterogeneous because the proportion of marked individuals in the sample is overestimated (Pollock et al. 1990). In practice the assumption of heterogeneous capture probability can be violated e.g. if (1) individuals that show a 'trap' response to the capture events are more or less likely to return for recapture (Laroche et al. 2007); or (2) behavioural differences between cohorts or individuals make certain members of the population more likely to be recaptured than others, such as the sex- and size-based segregation observed in white sharks along the South African coastline (Dicken & Booth 2013, Dicken et al. 2013, Kock et al. 2013, Towner et al. 2013a, Ryklief et al. 2014, Findlay et al. 2016). In each of the previous POPAN estimates for False Bay, Mossel Bay, and Gansbaai, a variance inflation factor was used to update parameter confidence limits and AICs, resulting in estimates of N = 723 (95% CI: 466–980; Hewitt 2014), N = 389 (95% CI: 351–428; Ryklief 2012) and N = 908 (95% CI: 808–1008; Towner et al. 2013b), respectively. More flexible model structures allowing for capture heterogeneity between co-

horts or seasons were used by Hewitt (2014) and Ryk-lief (2012). Hewitt (2014) additionally highlighted that due to model violations his estimate was likely biased low. Since Andreotti et al. (2016a) neither incorporated a variance inflation factor to account for overdispersion in the model nor structured the model to allow for flexibility in the recapture parameter, heterogeneous capture probability remains an unresolved issue in their study.

The presence of temporary emigration will also bias estimates of abundance in JS models by reducing recapture probabilities when individuals are temporarily outside of the sampling area (Burnham 1993, Kendall et al. 1997). Andreotti et al. (2016a) account for this issue by incorporating a time-dependent probability of recapture. However, while some individuals do move between aggregation sites (Bonfil et al. 2005, Kock et al. 2013) — a fact used by Andreotti et al. (2016a) to support their assertion that their sample is representative of the entire South African population — many do not. For example, satellite telemetry data available online (www.ocearch.org, accessed 22 July 2016) and acoustic tagging data from large-scale receiver arrays (SAIAB Acoustic Tracking Array Platform unpubl. data) show long-distance coastal and offshore movements in the region, yet very little movement between Gansbaai and False Bay, another well-known white shark aggregation site (Kock et al. 2013). This finding is further supported by a white shark population assessment of Seal Island, False Bay, which showed that only ~20% of white sharks identified at Seal Island also appeared in photo-identification records from Gansbaai during the same time period (Hewitt 2014). A lack of homogeneous mixing between aggregations suggests that some individuals show site fidelity to the False Bay region, and would be unavailable for sampling in a study based on a single site in Gansbaai, especially over only a 2.5 yr period. Site fidelity is not unique to False Bay and is likely also true for other aggregation sites in South Africa (Dewar et al. 2013, Burgess et al. 2014, Chapple et al. 2016). Unpublished telemetry data from the South African region (www.ocearch.org, accessed 22 July 2016) show transmissions that occur along approximately 5212 km of coastline; this observation, coupled with the aforementioned observations from False Bay, suggests that individuals migrate amongst aggregation sites with varying frequencies. Therefore, an estimate of N for a single aggregation site should not be extrapolated to represent the entire South African population, as highlighted in Hewitt (2014), Ryklief (2012), and Towner et al. (2013b). Future population

estimates should incorporate photo identification and other sources of data from as many aggregation areas as possible to overcome these shortcomings.

GENETIC ABUNDANCE ESTIMATES

Andreotti et al. (2016a) also conduct an estimation of effective population size using genetic material collected from individuals at 5 aggregation sites along the South African coastline and arrive at a value of $CN_e = 333$ (95% CI: 247−487). This estimate is similar to O'Leary et al.'s (2015) estimate of 364.6 (95% CI: 188.0−1998.3). However, O'Leary et al. (2015) highlight that because their sampling period (7 to 8 yr, i.e. triple that of Andreotti et al. 2016a) did not span an entire shark generation, it was not random and therefore their estimate of N_e was more representative of a cohort than of the entire population. Andreotti et al. (2016a) do not reference the findings of O'Leary et al. (2015).

Like mark-recapture studies, the estimation of effective population size also makes some assumptions about the population in question, such as the random sampling mentioned above. Other assumptions are that the population is at equilibrium, unstructured, and panmictic (Waples & Do 2010). Andreotti et al. (2016a) assert that the sampled population satisfies assumptions of panmixia. This statement is based on findings in Andreotti et al. (2016b), which suggested a lack of population subdivision in South Africa. However, the assertion of a lack of genetic structure in Andreotti et al. (2016b) is debatable (cf. O'Leary et al. 2015) because statistical rejection of significant population genetic subdivision does not confirm demographic dependence (Palsbøll et al. 2006). Determination of demographic dependence remains a controversial issue in population genetics, and it is appropriate to draw on ecological and life history data to assess whether apparent genetic panmixia may be consistent with demographic dependence (White et al. 2009). The assumption that a lack of significant population structure is indicative of random mating and unbroken population connectivity throughout the South African region is incautious (cf. Palsbøll et al. 2006 for an illustration of the effect of statistical power on acceptance or rejection of panmixia when the level of dispersal is not considered). Population heterogeneity may be reflected in estimates of inbreeding coefficients across the South African region. These measures indicate that sharks from Gansbaai are more inbred than those at other aggregation sites in South Africa (Andreotti et al. 2016b). The presence of regional inbreeding vio-

lates a major assumption of the bias-corrected single-sample molecular method based on linkage disequilibrium, a violation likely to introduce downward bias into estimates of N_e (Luikert et al. 2010). From a theoretical and applied perspective, defining marine 'populations' along the isolation-panmixia continuum is challenging, and estimates of their size and connectivity based on necessarily restricted sampling should be interpreted cautiously.

Further, Andreotti et al. (2016a) mention 2 problematic loci showing a heterozygote deficit that was deemed insignificant and retained them in the analysis. It is unclear if this heterozygote deficit is due to the presence of null alleles. The presence of null alleles can bias estimates of CN_e based on the single point linkage disequilibrium approach (Sved 2013), and it would have been informative to quantify the effect of excluding these loci in Andreotti et al. (2016a).

There is a lack of clear justification for the manner in which the CN_e estimate is linked with the results of the mark-recapture study in Andreotti et al. (2016a). The authors suggest that point estimates of N and CN_e reveal a 'gloomy picture for the future' of the species unless current management measures are improved (Andreotti et al. 2016a, p. 251). This revelation is drawn from the conclusion that discordance between CN_e and the number of observed mature adults in the study is suggestive of a recent drastic decline in numbers, ignoring the possibility that the South African region was insufficiently sampled for the mark-recapture study in Andreotti et al. (2016a). Interestingly, no note is made of recent population trends from the authors' own data during the time period of the mark-recapture study as in Hewitt (2014) or Ryklief (2012). The discussion instead makes reference to anthropogenic mortality in the form of catch statistics from a popular literature article (Peschak 2009), omitting scholarly data such as those of Dudley & Simpfendorfer (2006). Apparent survival (φ), a parameter estimated by the JS models used in Andreotti et al. (2016a), would elucidate the current health status of this subpopulation, revealing information about mortality and the population's immediate ability to recover or remain stable, but this parameter and others estimated by the most parsimonious model (probability of capture p, and probability of entry β) are not reported by the authors.

To conclude, failure to meet model assumptions, the unlikely representation of the entire South African white shark population, selective citations, and highly debatable and subjective interpretations of the results shed doubt on the validity of the conclusions presented by Andreotti et al. (2016a).

LITERATURE CITED

Anderson DR, Burnham KP (2002) Avoiding pitfalls when using information-theoretic methods. J Wildl Manag 66: 912–918

Andreotti S, Rutzen M, van der Walt S, von der Heyden S and others (2016a) 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

Andreotti S, von der Heyden S, Henriques R, Rutzen M, Meÿer M, Oosthuizen H, Matthee CA (2016b) New insights into the evolutionary history of white sharks, *Carcharodon carcharias*. J Biogeogr 43:328–339

Barker RJ, White GC (2004) Towards the mother-of-all-models: customised construction of the mark-recapture likelihood function. Anim Biodivers Conserv 27:177–185

Bonfil R, Meÿer M, Scholl MC, Johnson R and others (2005) Transoceanic migration, spatial dynamics, and population linkages of white sharks. Science 310:100–103

Burgess GH, Bruce BD, Cailliet GM, Goldman KJ and others (2014) A re-evaluation of the size of the white shark (*Carcharodon carcharias*) population off California, USA. PLOS ONE 9:e98078

Burnham KP, Anderson DR, White GC, Brownie C, Pollock KH (1987) Design and analysis methods for fish survival experiments based on release-recapture. American Fisheries Society, Bethesda, MD

Burnham KP (1993) A theory for combined analysis of ring recovery and recapture data. In: Lebreton JD, North PM (eds) Marked individuals in the study of bird population. Birkhäuser, Basel, p 199–213

Chapple TK, Chambert T, Kanive PE, Jorgensen SJ and others (2016) A novel application of multi-event modeling to estimate class segregation in a highly migratory oceanic vertebrate. Ecology 97:3494–3502

Cooney R (2004) The precautionary principle in biodiversity conservation and natural resource management: an issues paper for policy-makers, researchers and practitioners. IUCN, Gland

Dewar H, Eguchi T, Hyde J, Kinzey D and others (2013) Status review of the northeastern Pacific population of white sharks (*Carcharodon carcharias*) under the Endangered Species Act. NOAA, NMFS, SWFSC, La Jolla, CA

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

Dicken ML, Smale MJ, Booth AJ (2013) White sharks *Carcharodon carcharias* at Bird Island, Algoa Bay, South Africa. Afr J Mar Sci 35:175–182

Dudley SFJ, Simpfendorfer CA (2006) Population status of 14 shark species caught in the protective gillnets off KwaZulu–Natal beaches, South Africa, 1978–2003. Mar Freshw Res 57:225–240

Findlay R, Gennari E, Cantor M, Tittensor DP (2016) How solitary are white sharks: social interactions or just spatial proximity? Behav Ecol Sociobiol 70:1735–1744

Fletcher D, Lebreton JD, Marescot L, Schaub M, Gimenez O, Dawson S, Slooten E (2012) Bias in estimation of adult survival and asymptotic population growth rate caused by undetected capture heterogeneity. Methods Ecol Evol 3:206–216

Hewitt AM (2014) Demographics of a seasonal aggregation of white sharks at Seal Island, False Bay, South Africa. MSc thesis, University of Cape Town

Kendall WL, Nichols JD, Hines JE (1997) Estimating tem-

porary emigration using capture–recapture data with Pollock's robust design. Ecology 78:563–578

Kock A, O'Riain MJ, Mauff K, Meÿer MA, 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

Kriebel D, Tickner J, Epstein P, Lemons J and others (2001) The precautionary principle in environmental science. Environ Health Perspect 109:871–876

Laroche RK, Kock AA, Dill LM, Oosthuizen H (2007) Effects of provisioning ecotourism activity on the behaviour of white sharks *Carcharodon carcharias*. Mar Ecol Prog Ser 338:199–209

Lebreton JD, Burnham KP, Clobert J, Anderson DR (1992) Modeling survival and testing biological hypotheses using marked animals: a unified approach with case studies. Ecol Monogr 62:67–118

Luikart G, Ryman N, Tallmon DA, Schwartz MK, Allendorf FW (2010) Estimation of census and effective population sizes: the increasing usefulness of DNA-based approaches. Conserv Genet 11: 355–373

Mundry R (2011) Issues in information theory-based statistical inference — a commentary from a frequentist's perspective. Behav Ecol Sociobiol 65:57–68

O'Leary SJ, Feldheim KA, Fields AT, Natanson LJ and others (2015) Genetic diversity of white sharks, *Carcharodon carcharias*, in the Northwest Atlantic and Southern Africa. J Hered 106:258–265

Palsbøll PJ, Bérubé M, Allendorf FW (2006) Identification of management units using population genetic data. Trends Ecol Evol 22:11–16

Peschak T (2009) Shark nets — the real killers of the sea? Afr Geogr 17:36–44

Pollock KH, Nichols JD, Brownie C, Hines JE (1990) Statistical inference for capture-recapture experiments. Wildl Monogr 107:3–97

Ryklief R (2012) Population dynamics of the white shark, *Carcharodon carcharias*, at Mossel Bay South Africa. MSc thesis, Nelson Mandela Metropolitan University, Port Elizabeth

Ryklief R, Pistorius PA, Johnson R (2014) Spatial and seasonal patterns in sighting rate and life-history composition of the white shark *Carcharodon carcharias* at Mossel Bay, South Africa. Afr J Mar Sci 36:449–453

Seber GAF (1982) The estimation of animal abundance and related parameters. Charles Griffin & Co., London

Sved JA, Cameron EC, Gilchrist AS (2013) Estimating effective population size from linkage disequilibrium between unlinked loci: theory and application to fruit fly outbreak populations. PLOS ONE 8: e69078

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

Towner AV, Wcisel MA, Reisinger RR, Edwards D, Jewell OJD (2013b) Gauging the threat: the first population estimate for white sharks in South Africa using photo identification and automated software. PLOS ONE 8:e66035

Vasconcellos MM, Colli GR (2009) Factors affecting the population dynamics of two toads (Anura: Bufonidae) in a seasonal neotropical savanna. Copeia 2009:266–276

Waples RS, Do C (2010) Linkage disequilibrium estimates of contemporary N_e using highly variable genetic markers: a largely untapped resource for applied conservation and evolution. Evol Appl 3:244–262

White GC, Burnham KP (1999) Program MARK: survival estimation from populations of marked animals. Bird Study 46:S120–S139

White TA, Stefanni S, Stamford J, Hoelzel AR (2009) Unexpected panmixia in a long-lived, deep-sea fish with well-defined spawning habitat and relatively low fecundity. Mol Ecol 18:2563–2573