

REPLY COMMENT

Erring on the side of caution: Reply to Irion et al. (2017)

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ABSTRACT: Irion et al. (2017; Mar Ecol Prog Ser 577:251–255) disputed the population estimates of white sharks *Carcharodon carcharias* along the South African coastline as presented in Andreotti et al. (2016; Mar Ecol Prog Ser 552:241–253), claiming that both the genetic and the capture-mark-recapture results are poorly supported by the methods and data provided. Here, we provide additional analyses to refute the claims of Irion et al. (2017). We show that the integrated, balanced approach in Andreotti et al. (2016a) provides an objective and substantiated result.

KEY WORDS: *Carcharodon carcharias* · Effective population size · Capture-mark-recapture · White shark · South Africa · Conservation

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INTRODUCTION

In Andreotti et al. (2016a) we used a capture-mark-recapture (CMR) technique to estimate the population size (N) of white sharks *Carcharodon carcharias* in Gansbaai, South Africa. We also used a genetic technique and reported 2 estimates of the contemporary effective population size (CN_e) of white sharks: 1 for Gansbaai and 1 representing the South African coastline (5 aggregation sites). Although CMR and CN_e techniques differ markedly in model assumptions and sampling design, similar low population estimates between the 2 techniques were obtained in Andreotti et al. (2016a). The approach of integrating CMR and genetic analyses has been strongly advocated (Ovenden et al. 2016), since it is unlikely that the 2 techniques will reveal similar estimates by chance alone or because of methodological errors. In addition, information derived from each technique can be used to improve the development of popula-

tion genetic theories (Ovenden et al. 2016). For example, Andreotti et al. (2016a) presented a species-specific ratio of $N_e:N$ (the effective population size per generation:population size), which can be used to inform data modelling (Waples et al. 2013, Ovenden et al. 2016). The $N_e:N$ ratio observed by Andreotti et al. (2016a) also falls within the range observed for other sharks that have a long life span and late maturation (Dudgeon et al. 2009, Portnoy et al. 2009, Ovenden et al. 2016).

Andreotti et al. (2016a) found low population numbers—whether the calculations were done for 1 aggregation site (using CMR and genetic data) or the entire coastline (genetic estimate only)—and concluded that the size estimate of fewer than 500 individuals is likely to be representative of the entire population occurring along the South African coastline. This conclusion hinges on the tested assumption that aggregation sites of white sharks along the South African coastline are not significantly sub-

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structured at the genetic level (Andreotti et al. 2016b). The perception that intra-regional site fidelity exists, and the reported lower N than previously published for the Gansbaai population alone (Towner et al. 2013a) led Irion et al. (2017) to question and reject the multiple independent population estimates published in Andreotti et al. (2016a). Irion et al.'s (2017) major criticisms were: (1) the CMR population estimate (N) is unreliable, based on the failure to meet the CMR model assumptions, (2) the definition of the South African white shark population as panmictic is unrealistic and (3) selective choices of citations. We welcome the opportunity to respond to the specific criticisms.

THE CMR POPULATION ESTIMATE (N)

Before applying a CMR model, it is essential to collect a substantial amount of data (Sutherland 2006). Andreotti et al. (2016a) used the most comprehensive single South African white shark data set collected to date (4398 photographic identifications, 426 individual sharks, 298 sampling days over a 3 yr period). By making use of good quality photographs (Andreotti et al. 2014) and cross-checking among methods (cf. Fig. 2 in Andreotti et al. 2016a), we minimized the chance of false identifications. Thus we could be confident that the sharp decline in the number of newly identified sharks after 2 yr of sampling (once 400 individuals were catalogued; cf. Fig. 1 in Andreotti et al. 2016a) was due to data saturation and not mis-identification. Based on the time span of the study and the saturation in the sampling data, we considered the data set to be adequate for the CMR technique (Sutherland 2006, McCallum 2008).

We agree with the opinion of Irion et al. (2017) that researchers should account for uncertainty using information-theoretic approaches, such as the Akaike's information criterion (AIC; Bozdogan 1987, Akaike 1998). Accordingly, Andreotti et al. (2016a) initially employed all 8 different variations of the model by changing the settings of Φ (apparent survival rate), ρ (capture probability) and β (probability of entry into the population) to either constant (.) or time dependent (t) (Table 1). Instead of deciding the most likely CMR model ad hoc (based on biological assumptions that are difficult to validate; Grimm et al.

2014), the corrected AIC (AICc) selection criteria was used on all permutations, by including a correction for finite sampling sizes (as also suggested by Irion et al. 2017). Subsequently, the best CMR models were selected for presentation in Andreotti et al. (2016a) taking into account the available biological information on white sharks and while also considering the outcome of the RELEASE goodness of fit (GOF) test (applied to the monthly history of captures matrix). Since capture heterogeneity is likely to occur in most field studies (Pollock et al. 1990) and individual differences in catchability need to be accounted for (Andreotti et al. 2016a), models with non-constant capture probability were preferred over models with constant capture probability (Table 1).

We disagree with Irion et al. (2017) that the probability of the entry parameter should not be held constant ($\beta(\cdot)$) for white sharks. The longer the study is conducted, and the more comprehensive the sampling effort is, the less β influences the outcome, especially if the analysis is conducted on sharks captured yearly in the same peak season when sexes and sizes are not segregated (Towner et al. 2013b). Irrespective, the estimated point number (N) of white sharks was always below 500 in all 8 permutations (Table 1).

Based on a significant RELEASE GOF test reported in Andreotti et al. (2016a), Irion et al. (2017) rightly stated that model assumptions have not been met, but then wrongly concluded that any estimate of N is unreliable. They based their criticism on the combined results of Tests 2 and 3 where $\chi^2 = 251.95$, $p < 0.005$, applied to the history of monthly captures. When the results of Test 2 ($\chi^2 = 195.78$, $p < 0.005$) and Test 3 ($\chi^2 = 56.16$, $p = 0.145$) are considered

Table 1. Selected parameter estimates and model selection criteria for 8 POPAN model variants for the seasonal (winter) capture history matrix. Survival rate (ϕ), capture probability (ρ) and probability of entry into the population (β) are assumed to be either constant (.) or time dependent (t). The population estimate (N) and interval (N-i) are calculated with CI = 95%. The models are sorted by model likelihood (ML). AICc and Δ AICc are reported. The 3 variants included in Andreotti et al. (2016a) are in **bold** and the deviance = 0 in all instances

Model	AICc	Δ AICc	AICc weights	ML	N	N-i
$\{\phi(\cdot) \rho(\cdot) \beta(t)\}$	347.415	0.000	0.211	1.000	470	381–561
$\{\phi(\cdot) \rho(t) \beta(\cdot)\}$	347.555	0.140	0.197	0.932	438	353–522
$\{\phi(t) \rho(\cdot) \beta(t)\}$	347.759	0.344	0.178	0.842	471	381–561
$\{\phi(t) \rho(\cdot) \beta(\cdot)\}$	347.847	0.432	0.170	0.806	472	381–564
$\{\phi(\cdot) \rho(t) \beta(t)\}$	349.319	1.904	0.081	0.386	408	336–479
$\{\phi(t) \rho(t) \beta(\cdot)\}$	349.616	2.200	0.070	0.333	426	346–506
$\{\phi(\cdot) \rho(\cdot) \beta(\cdot)\}$	350.004	2.589	0.058	0.274	451	371–531
$\{\phi(t) \rho(t) \beta(t)\}$	351.034	3.618	0.035	0.164	382	333–431

separately, the individual differences in catchability (Test 2) (although not due to the capture technique) are the main reason for the high combined χ^2 value. The lower χ^2 value of Test 3 ($\chi^2 = 56.16$), by being not significant ($p = 0.145$), supported the assumption that most marked animals captured have the same probability of surviving to the next capture occasion, fitting the model assumption (the AICc also favoured models based on constant survival rate). The RELEASE GOF χ^2 on the monthly history of captures in Andreotti et al. (2016a) is also markedly similar to Rykklief (2012), who estimated $\chi^2 = 295.65$ ($p < 0.001$), suggesting that heterogeneous capture probability is present in both studies when monthly sampling is used.

Since model assumptions were not met when monthly captures were considered, Andreotti et al. (2016a) focused their discussion on the results obtained from the three winter season captures. This reduced the bias derived from seasonal heterogeneity in the capture probability (cf. Fig. S2 in Andreotti et al. 2016a). This adaptive sampling approach is preferred in CMR studies since it concentrates the sampling effort during times of high density, making the marking event more efficient (Sutherland 2006). Andreotti et al. (2016a) achieved comparable and fairly even number of captures of marked and unmarked animals across the three winter seasons ($N_{i_{2009}} = 121$; $N_{i_{2010}} = 90$; $N_{i_{2011}} = 114$). Since a RELEASE GOF test with only 3 occasions cannot be performed (G. White pers. comm.), a GOF test for the global model from the residuals of the $\{\Phi(\cdot) \rho(t)\}$ model was performed instead. This global model GOF test resulted in a much lower χ^2 value of 3.11, which was not significant ($p = 0.07$). This finding further supported the adaptive sampling choice employed by Andreotti et al. (2016a). In addition, since heterogeneity in capture probability can also be caused by differences in behavioural patterns of individuals (Sperone et al. 2010, Delaney et al. 2012, Jacoby et al. 2014) and the population is not residential within the study area, models with time dependent capture probability ($\rho(t)$) were preferred by Andreotti et al. (2016a).

The suggestion by Irion et al. (2017) of calculating and including the variance inflation factor (\hat{c}) to update parameter confidence limits is valid. The data set presented by Andreotti et al. (2016a) is characterised by $\hat{c} = 1.76$. In instances where $\hat{c} < 2$, the inclusion of the variance inflation factor is considered unnecessary (see Lebreton et al. 1992, White & Burnham 1999, Rykklief 2012) and was thus not presented in Andreotti et al. (2016a).

WHY IS THE SOUTH AFRICAN WHITE SHARK POPULATION REGARDED AS PANMICTIC?

Irion et al. (2017) provided an extensive discussion on the presence of temporary emigration from the area of Gansbaai, and also suggested that data collection from this area alone is not representative of the entire South African population. The major critique to our approach was based on the statement that ‘while some individuals do move between aggregation sites [...] many do not’ (Irion et al. 2017, p. 253). This statement by Irion et al. (2017) was based on data presented by Hewitt (2014), Kock et al. (2013), the satellite telemetry data available online (www.ocearch.org) and unpublished data from the SAIAB Acoustic Tracking Array Platform (Irion et al. 2017). Hewitt (2014) stated that 20% of individuals are common between the area of False Bay (S.Island) and Gansbaai (G.bay), based on a ‘preliminary comparison of identified sharks from S.Island with a catalogue from G.bay (2006–2009; Unpublished data)’ that ‘must still be rigorously tested’ (Hewitt 2014, p. 106). Kock et al. (2013) conducted a study in False Bay on 56 white sharks tagged with acoustic transmitters. The large majority of the sharks ($n = 51$, 91%) were not recorded to stay resident in False Bay for longer than 6 mo, and none stayed resident in False Bay for more than 282 d (~9.4 mo, Fig. 1). Further, 15 of the tagged sharks have been recorded in other areas by an array of acoustic receivers in Gansbaai, Mossel Bay and Algoa Bay. Thus, the data presented by Kock et al. (2013) do not support individual residency in False Bay (Fig. 1).

Irion et al. (2017, p. 253) indicated that ‘satellite telemetry data available online (www.ocearch.org, accessed 22 July 2016) and acoustic tagging data

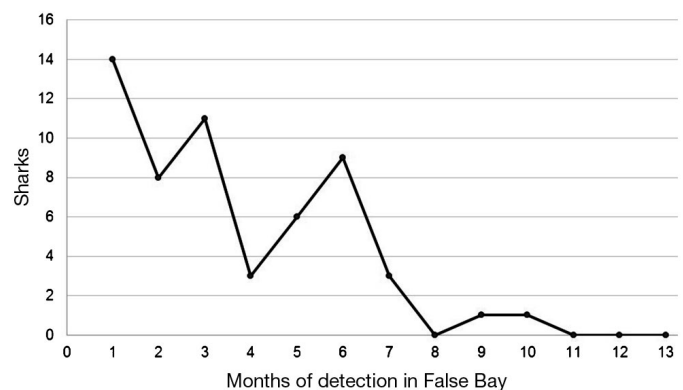


Fig. 1. The number of sharks detected in False Bay with acoustic transmitters (data obtained from Table 2 in Kock et al. 2013) support the notion that individual white sharks are not residential in the area of study. Most of the sharks ($n = 14$) were recorded in False Bay for a month

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)'. For the purpose of this Reply Comment, we conducted our own preliminary survey based on the data available on the Oearch website on 20 January 2017. Since our CMR study was conducted in Gansbaai, and to simplify the interpretations, we specifically investigated how many of the 33 sharks tagged in total along the South African coast were also recorded in Gansbaai and if there have been movements between Gansbaai and False Bay. After exclusion of 5 animals that lost their tag during the first 6 mo, a total of 79% (22 of 28) of the tagged sharks visited Gansbaai. In particular all of the sharks ($n = 4$) who retained their tags for longer than 1004 d (the time span of the study by Andreotti et al. 2016a) visited Gansbaai, indicating that the time span of the data collection of Andreotti et al. (2016a) was sufficient to allow for most of the sharks to visit the study area. In addition, of the 3 sharks tagged in False Bay (Lesley, ref: 035-150412; Edna, ref: 037-150412; Kathryn, ref: 038-150412), 2 were recorded in Gansbaai at a later stage, and the third shark (Edna) lost her tag after 53 d (rendering this observation data deficient). Based on the data presented in Kock et al. (2013) and our preliminary analyses of the satellite telemetry data, we argue that a more accurate statement would be: 'while *many* individuals do move between aggregation sites, *some* do not', a statement further supported by Bonfil et al. (2005) and the genetic data of Andreotti et al. (2016a,b).

Irion et al. (2017) cited Chapple et al. (2011), Dewar et al. (2013) and Burgess et al. (2014) to support a perception that, due to site fidelity among South African white shark aggregation sites, some individuals would be unavailable for sampling in a study based on a single site. None of the citations listed by Irion et al. (2017) investigated fine-scale site fidelity among populations sampled along the same coastline. Chapple et al. (2011), Dewar et al. (2013) and Burgess et al. (2014) all used the study of Jorgensen et al. (2011), who showed seasonal inshore-offshore white shark movements as well as interchange among aggregation sites distributed along the Californian coast (with a maximum residency of 107 d in one area). Irion et al. (2017) also suggested to compare the inbreeding coefficients among sampling sites to detect population structure, and indeed a comparison of F_{IS} values among areas where sample sizes are

>25 (Costa et al. 2015) revealed that the inbreeding coefficients in Andreotti et al. (2016a) do not differ significantly from each other and are close to 0 (Gansbaai $F_{IS} = -0.061$; Mossel Bay $F_{IS} = -0.065$). In agreement with Jorgensen et al. (2011), Andreotti et al. (2016b) confirmed site fidelity at a continental scale, and a lack thereof within the South African region (see Appendix S1 in Andreotti et al. 2016b). Specifically, Andreotti et al. (2016b) used structure analyses, the exact test of sample differentiation and the F -statistic approaches (Weir & Cockerham 1984) and found no clear evidence of site fidelity among the 5 aggregation sites (mtDNA $\phi_{ST} = 0.018$, $p = 0.71$; nDNA $F_{ST} = 0.0014$, $p = 0.38$). Furthermore, based on simulations on nuclear genotypes, Andreotti et al. (2016b) showed that an F_{ST} as low as 0.02 could be detected with 90.2% confidence. In addition, an F_{ST} of 0.001 implies a migration rate of $m = 0.5$ (using an optimistic $N_e = 500$; Wright 1938), which is well above the minimum considered threshold of $m = 0.1$ for panmixia (Waples 1998). Despite this, Irion et al. (2017) stated that the assertion of a lack of genetic structure in Andreotti et al. (2016b) is debatable and then cited O'Leary et al. (2015), who in fact did not test for panmixia among the South African aggregation sites. The sampling performed by O'Leary et al. (2015) was concentrated along the Kwazulu Natal coastline and this precluded any tests for genetic population structure among white shark aggregation sites (supplementary material in O'Leary et al. 2015). Irion et al. (2017) also cite Palsbøll et al. (2007) to support their statement that the rejection of significant population subdivision does not confirm demographic dependence. Palsbøll et al. (2007), however, make it clear that when structure is observed in the population, the amount of population genetic divergence is more important than simply a statistical rejection of panmixia. Since Andreotti et al. (2016a) did not detect any significant structure (see above), and used a model-based threshold for population genetic divergence (as advocated by Palsbøll et al. 2007), the support for white shark site fidelity—at such small geographic scale—is currently lacking.

Finally, Irion et al. (2017) questioned the outcome of the genetic estimate, based on the presence of 2 loci that showed a heterozygote deficit. Since both markers in question (Cca1072 and Ccar9) were designed for white sharks, we regarded the possibility of null alleles less likely. Potential null alleles were nonetheless handled following standard procedures (see Chapuis & Estoup 2006, Henriques et al. 2014). In addition, Waples (2006) and Waples & Do (2010) indicate that the linkage disequilibrium

method has little or no bias for a $p_{\text{crit}} \geq 0.05$. Comparison of CN_e values obtained at $p_{\text{crit}} = 0.05$ for 14 loci or 12 loci (excluding the 'problematic' loci) reveals nearly identical results (14 loci $CN_e = 374$; 12 loci $CN_e = 366$). At a lower (less suitable; Waples & Do 2010) $p_{\text{crit}} = 0.02$, and based on 12 loci only, $CN_e = 433$ which is still below the $N_e = 500$ threshold used by Andreotti et al. (2016a) to claim that the South African white shark population is in serious trouble.

SELECTIVE CHOICES OF CITATIONS

Irion et al. (2017) imply that the omissions of Dudley & Simpfendorfer (2006), Rykclief (2012), and Hewitt (2014) were one of the reasons why they consider the conclusions of Andreotti et al. (2016a) doubtful. Irion et al. (2017) are correct in pointing out that citing a popular science article (i.e. Peschak 2009) is not ideal. However, in this instance the Peschak (2009) popular science article was selected since it is the only reference that provides an actual number of white sharks catches as part of shark protection measures by the Kwazulu Natal Shark Board in South Africa ($n = 1063$). Both Dudley & Simpfendorfer (2006) and Cliff & Dudley (2011) provide average values of catches. Irrespective, human induced mortality of sharks is so widely published (van der Elst 1979, Ferretti et al. 2013, Worm et al. 2013) that, in this instance, including a popular science article rather than a peer reviewed reference does not affect the validity of the discussion. Rykclief (2012) and Hewitt (2014) were omitted since they both comprise MSc thesis dissertations that have not been subjected to the peer-review process. In our particular case, a citation of Rykclief (2012), who had a reasonable sampling effort, would have supported our own findings (super-population size estimated to be 389 sharks with a 95% CI of 351–428 sharks), while we are of the opinion that Hewitt (2014) probably overestimated the population size at 723 sharks due to a scattered sampling effort.

In conclusion, Andreotti et al. (2016a) used an integrated approach where 2 methods are employed in an attempt to improve the knowledge of population estimates of white sharks. A variety of different CMR models was also utilized, accounting for the criticisms raised by Irion et al. (2017). Due to the uncertainties associated with model selection (Sutherland 2006, McCallum 2008, Grimm et al. 2014), Andreotti et al. (2016a) chose the optimal model by also considering the results of the AICc, and specific care was taken not to extrapolate the results obtained from the

CMR method to the entire coastline. The extrapolation to the entire coastline was based on the genetic component as stated: 'the CN_e point estimates and the confidence intervals for including individuals from the entire coastline ($n = 233$) or just from Gansbaai ($n = 167$) were remarkably close (Coastline $CN_e = 333$ [...]; Gansbaai $CN_e = 351$ [...])' (Andreotti et al. 2016a, p. 250) and then 'If these values are correct, it seems reasonable to suggest that sharks sampled at Gansbaai over a 3 yr period are likely representative of the entire South African population' (Andreotti et al. 2016a, p. 250). Given the poor support for site fidelity at the regional scale, and since both the genetic estimates (from Gansbaai only or from the entire coastline) and the CMR estimate from Gansbaai are below 500 in all permutations of the model, it is reasonable to conclude that the results of Andreotti et al. (2016a) are robust. Under these circumstances surely the 'precautionary principle' should apply and it is thus reasonable to conclude that 'The survival of this population and the ecological structure of the coastline will be seriously compromised if management measures aimed at halting population declines are not improved in the short term and maintained into the future' (Andreotti et al. 2016a, p. 251).

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