Shortfin Mako Sharks in the Atlantic: Outline Design for Close-Kin Mark-Recapture

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Acknowledgements

Summary

Close-Kin Mark-Recapture (CKMR) could be a powerful tool for informing the sustainable management of Atlantic shortfin mako sharks, North and South, both in the short and long term. The payoff would be reliable estimates of key management parameters— in particular, of the absolute abundance and trend of spawning females, which cannot be sampled directly via the fisheries— without relying on fishery-derived data such as CPUE and its attendant complications. Data (tissue samples and lengths/ages of juvenile sharks) could be collected from existing fisheries, and there do not seem to be any obvious technical problems: the size-range in the catches, the spatial spread, and the basic biology is suitable for CKMR, and based on statistical calculations of expected precision, the sample size requirements seem modest for a program spread over the next few years. Age data from vertebrae— though certainly useful for CKMR, if it is available— does not appear to be essential, so that good length measurements alone could perhaps be enough (subject to further investigation); this may be a key point if no-retention policies becomes widely adopted. The next step would be a broader discussion of logistic options and design objectives.

1   Introduction

Pelagic sharks worldwide continue to be significantly impacted by fisheries (by)catch, but the severity and sustainability of impact is often hard to assess by conventional fisheries methods.

Direct surveys are precluded because of the wide distribution; tagging is always a logistic challenge and can be crippled by reporting rate problems; incoming fisheries data are often suspect (e.g. concerning species ID, misreporting, discards); and the degree to which CPUE reflects abundance can be especially tenuous because of patchy effort and variable targeting. While those issues are shared by many highly-migratory oceanic species including tuna, sharks are also less resilient to overfishing than most teleosts. There is a well-known literature on these points.

For shortfin mako sharks (*Isurus oxyrhinchus*; hereafter just "makos"; not to be confused with longfin mako shark *Isurus paucus*) in the North Atlantic, the most recent ICCAT assessment (ICCAT 2017a) concludes that the population is likely historically overfished and is still subject to overfishing. While this conclusion seems fairly clear, there are still substantial uncertainties within the assessment, e.g. concerning natural mortality and "resilience" (the strength of the density-dependent response to exploitation). For the future, there is a real concern that the "capital" in the adult (spawning) stock, which is largely safe from fishing, is dwindling because not enough juveniles are surviving the ages of high fishing exposure. Precisely because (female) adults are rarely caught in the main fisheries, there will be no direct way to tell from the existing data streams in the future how the spawning stock is going— e.g. whether any future management actions are succeeding. Further, if management actions such as no-retention policies come into force, then there may be changes in fisher behaviour and reporting adverse which further comprise the interpretability of fishery-derived data such as CPUE.

The status of the South Atlantic population(s) is even less well understood. Input data quality is worse, different assessment models are internally inconsistent and/or tell different stories, and ICCAT 2017a points at the fundamental inconsistency between the signal of increasing catches overall at the same time as increasing (reported) CPUE in certain fisheries. There is no reason to expect uncertainty to decrease in future merely through accrual from existing data streams in the South Atlantic— the issue is with interpretability, not quantity.

Against this background, the possibility of Close-Kin Mark-Recapture (CKMR; Bravington, Skaug, et al. 2016) as an independent and reliable data source becomes appealing. At least in principle, CKMR as it might be applied to makos delivers estimates of three key management-related quantities:

- absolute adult abundance, by sex;

- trend in the latter, as a time series;

- adult natural mortality rate

CKMR can deliver these estimates just using data collected in the fishery itself (i.e. fairly cheaply), but at the same time it is largely immune to biases caused by human behaviour, changes in species distribution, etc. It helps— though it is not essential— to have total catch-at-length data, but there is no need to use CPUE or length-compositions as indices related to abundance. (However,

CKMR can be combined with other data sources in a single assessment, if the other data sources are reliable enough.)

This information would be of great benefit for makos, but there are some requirements that have to be met if CKMR is to work:

- adequate sample sizes;

- adequate spread of covariates, e.g. wide length-range and several years of sampling;

- adequate measurement of covars: ideally age, or at least length if not;

- adequate spatial coverage (not all from one small part of the ocean)

- [adequate genotyping and "kinference", i.e. the process of finding kin-pairs from the genotypes of the samples.]

The final point is a technical one that can be addressed eventually, provided that the first four are met. This report therefore presents preliminary comments on what the above "adequates" might be for makos in the North and the South Atlantic, in order to estimate various quantities-of-interest such as current abundance, trend, and exploitation rate relative to reference points. Now that the basic code has been set up, it would be fairly easy to investigate other sampling scenarios and objectives. The data and modelling choices that I made in order to get everything running, may well not be the best or most up-to-date for mako sharks, and should certainly be gone over in detail in due course; for the South Atlantic in particular, sample size requirements are heavily dependent on assumptions about management targets that require collective input. This document is put forward not as a finished product, but in the spirit of a basis for further discussions about appropriateness of modelling assumptions, logistic feasibility of different sampling options, wider choice of scenarios to investigate, and objectives for a future-proofed fishery-independent way to monitor the status of mako sharks in the North and South Atlantic.

After a brief summary of recent CKMR applications next, this report briefly explains the principles of CKMR as they might apply to project design for makos (section 2). Section 3 explores various sample-size and sample-composition scenarios for makos in the North and South Atlantic, in terms of likely precision of estimated quantities. Section 4 briefly comments on other general aspects of CKMR— some of which are important for makos, other not so— and Section 5 provides a summary. The Appendices [not yet attached] describes the data sources— primarily ICCAT 2017a; ICCAT 2017b— and details of the population-dynamics and CKMR model.

1.1   Background: a brief history of CKMR

Although there are still rather few peer-reviewed papers on CKMR, there is now a considerable body of theoretical and practical experience across a range of species. Most of these are from

work at CSIRO (see below for references) but not exclusively; e.g. Ruzzante et al. 2019 report a successful application to Canadian brook trout, and Rawding et al. 2014 to salmon.

The idea of using close-kin to learn about spatial population structure goes back to the 1990s at least, but CKMR as a tool for abundance estimation was first suggested in Skaug 2001. Unfortunately, limitations in the genotyping techniques of the time, and of the specific "single sample" formulation of Skaug's model, did not make the approach generally viable. Nevertheless, the core idea— that each offspring tags its two parents, and that those tags can be found by comparing genotypes among large samples— had clear appeal for many other situations. While CKMR can be applied in a very simple way to a few special cases— notably to breed-then-die salmonids, as in Rawding et al. (2014) and Ruzzante et al. (2019)— more complicated biologies such as most marine teleosts and sharks require some fairly sophisticated modelling. At CSIRO, we started CKMR work on Southern Bluefin Tuna (SBT) in 2006, using Parent-Offspring Pairs (POPs) only, and by 2012 had successfully produced abundance estimates that were far more credible than anything available through other methods (Bravington, Grewe, et al. 2016). In about 2013, we started considering applications to endangered elasmobranchs. For many elasmobranchs, it turns out to be fairly easy to sample juveniles in quantity, but not adults— so POPs were not an option. However, by this time genotyping methods had advanced to the point of finding Half-Sibling Pairs (HSPs— two juveniles that share one mother, or one father), so that juvenile-only CKMR became possible, at least for certain life-histories including many elasmobranchs but not teleosts. We returned to SBT and changed our genotyping methods so that we could use both POPs and HSPs; it turns out the combination is remarkably powerful, and in fact is by far the best way to apply CKMR to teleosts (Davies et al. 2018). The CKMR datasets for SBT are updated annually with new samples, and this is now a core part of CCSBT management process.

Meanwhile, we applied CKMR to five species of elasmobranch (White Shark; Grey Nurse Shark; Northern River Shark; Speartooth Shark; School Shark), primarily just using HSPs. Only the White Shark results are so far published (Hillary et al. 2018— note that the sample size has been substantially increased since publication), but all the others are completed or in-review reports to Australian environment and fisheries-management agencies.

Amongst our six species completed to date, the one most similar to makos from a CKMR perspective is School shark (*Galeorhinus galeus*). This species used to be the mainstay of Australian domestic shark fisheries, but collapsed through overfishing in the 1990s. Management restrictions have given some breathing space, but the species is still by-caught and any recovery has been slow (inevitably, given the demographics). The CPUE data is no longer reliable because of management-driven changes, so there is no other good way to monitor the stock except CKMR. Adult abundance is a little lower than for North Atlantic makos; age at maturity is slightly younger; there is a moderate effect of body size on (female) fecundity; and the catch mostly consists of juveniles are caught. We achieved a sample size of about 3000 animals, and were able to get vertebrae for all them for ageing purposes; unfortunately, the ageing of adult school sharks turns out to be rather unreliable, which did impact substantially on the precision of our results. Nevertheless,

we obtained an absolute abundance with useful precision and free from dependence on CPUE, and data collection is ongoing so that trend can be estimated better in future. [Final report still in review.]

The best overview of CKMR is given in a fairly comprehensive theoretical paper (Bravington, Skaug, et al. 2016) which sets out the framework we have followed in all real applications, although it is geared to a statistical audience and is quite technical in places. As yet, there are no publicly-available examples of general-purpose CKMR code, though we expect this to change in the next couple of years— first for the technical step of kin-finding from genotypes, and then gradually for the modelling code through workshops and general diffusion into the stock assessment and statistical-ecology communities.

Worldwide interest in CKMR is considerable, and the experience gained during our CSIRO projects has refined our tools so that the process is much less daunting (and also cheaper) than it used to be. The technique is ready to be applied more widely, but the technical requirements are still demanding: in sampling, in genotyping, and in analysis ("modelling"). Since CKMR will fail altogether unless sampling is adequate, the first key to success is careful design *before* a sampling program is started.

2 Principles of HSP-only CKMR

The basis of HSP-based CKMR is shown in Figure 2.1, for a simple hypothetical population where all (female) adults are reproductively similar. The underlying principle, just as with POP-based CKMR, is that each animal had exactly one mother and one father alive at its birth (or fertilization, as appropriate). In HSP-based CKMR, the two "tags" that an offspring places into the adult population (i.e. its parents) are detected indirectly, by finding another offspring that has "tagged" one of the same parents; in POP-based CKMR, the tags are found directly, by sampling the adults.

In the Figure, the demographic probability that one juvenile from the first cohort and one from the second will be a (maternal) HSP, is made up of two parts: the first mother has to survive through to the second birthing occasion, and then the second juvenile's mother must happen to be one particular female (the first mother) out of all the female adults alive at the second occasion. In this case, the survival probability is 3/5, and there are 4 female adults alive at the second occasion, so the overall probability is $\frac{3}{5} \times \frac{1}{4} = \frac{3}{20}$. In the actual samples shown, there are 9 comparisons, of which only 1 (Lucy and Liz) happens to be a maternal HSP: $\frac{1}{9} = \frac{2}{18}$ which is not that far from $\frac{3}{20}$.

An exactly similar exercise can be conducted for *paternal* HSPs, i.e. linked thru the father. We can distinguish ♂HSP from ♀HSP genetically, by comparing mtDNA. Note that the sex of the juvenile samples is (usually) not relevant; the question is whether they share a father, or share a mother, or neither.

One difference from the POP-based cartoon (as shown in e.g. Bravington, Skaug, et al. 2016 section 3) is that even in the simplest HSP case, there are *two* parameters that drive each HSP

Figure 2.1: HSP-based CKMR
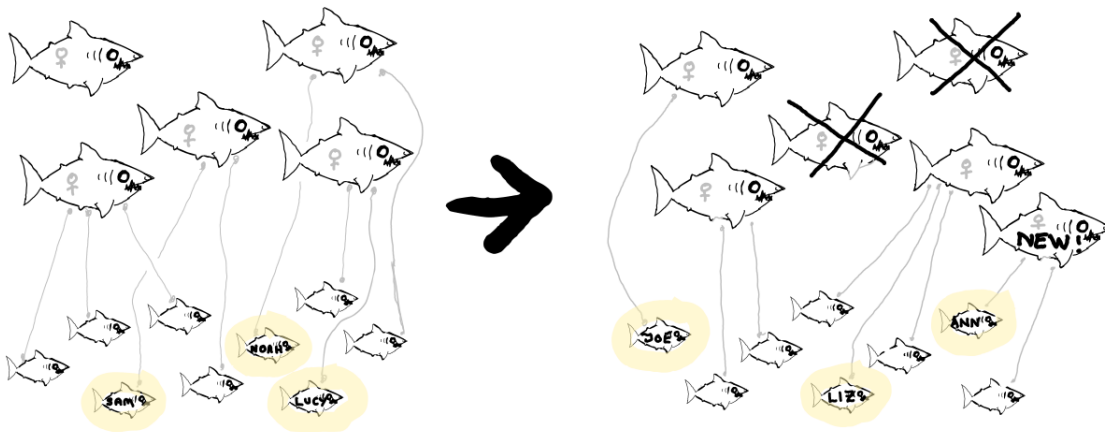
There is one population of adults, with *only* the females shown here; two cohorts of new-born juveniles are shown, on the left and right. The big arrow represents time between the two cohorts' birth-dates, during which two adults die and one new adult is recruited. The sample consists only of the highlighted and named juveniles; no adults are sampled directly.

probability (mortality as well as abundance) rather than just one; therefore there is no simple closed-form formula for estimating either abundance or mortality. However, in practice there will usually be a time-series of samples from different cohorts to be compared, and this allows us to disambiguate and estimate three different pieces of information (again, separately by adult sex if required, but it may be possible to share parameters across the sexes, e.g. natural mortality):

1. The *average rate* of HSP finding (i.e. proportion of comparisons that yield an HSP) is inverse to the average adult abundance;

2. How that rate changes for newer cohorts (as they get compared with previous cohorts) shows how fast the adult population is growing or shrinking;

3. The HSP-finding-rate will drop with increasing interval between cohorts. The speed at which this happens gives an estimate of the overall adult mortality rate.

In reality, the right way to use the data is to build a full population-dynamics model that estimates everything all at once and optimally, rather than to attempt a series of ad-hoc calculations. The probability that each comparison will yield a maternal or paternal HSPs can be computed using the above ideas; then the outcome of the comparison is checked using the genotypes, and the log-likelihood is formed by addin up the log-likelihoods of all these pairwise comparisons. All the calculations, whether POP- or HSP-based, fit quite naturally within an age-structured stock-assessment-style framework, just as is normally used for estimating demographic parameters; details are beyond this report, but see eg Brav 2016 or BSA 2016.

2.1 Complications

There are three or four complicating factors that often need to be allowed for with HSPs in CKMR. While all are reasonably important for makos, none of them seem to be limiting, so this section

2.1.1 Comparisons *within* a single cohort are not useful

The problem is that random variation in (surviving) litter sizes will systematically inflate the number of within-cohort HSPs. This problem goes away when only cross-cohort comparisons are considered (statistically speaking: "the product of an expectation is the expectation of the products, provided events are independent"). The simplest remedy— if age is known— is to simply exclude within-cohort comparisons. If age is uncertain, then it can be hard to exclude enough comparisons without depleting the "effective sample size", and it becomes necessary instead to introduce extra parameters to allow for "lucky litter" effects and various complications thereof. Although tedious for the modeller, in our experience this has not *usually* caused a major problem for the results, though it could do so if age is very uncertain. The Appendix to Hillary et al. (2018) contains further discussion.

2.1.2 Size-fecundity relationships

If there is variation in fecundity (i.e. expected reproductive output) between individuals, or within one individual's adult lifespan, then this will also inflate the number of HSPs. For female mako sharks, there is an appreciable effect of body-size on litter-size (not so for all shark species), and of course there is growth post maturation as well as systematic differences between individuals in size. In the context of the cartoon Figure 2.1: if the first mother does not die, then she will grow instead and become more fecund, so the "adult mortality" parameter actually becomes a composite of mortality-and-fecundity-growth.

As long as the effects are well-understood biologically (true for makos) and not too severe, it is possible to adjust the CKMR probability calculations to avoid bias, as we had to for school sharks. (For teleost fish, the lifetime variation in fecundity is so strong that HSPs alone are not much use for abundance or trend, because changes in the adult age composition will substantially affect the number of HSPs expected; it turns out that both POPs and HSPs are required for teleost CKMR.)

It turns out that the roughly 10% CV on length-at-age between individuals in mako sharks would contribute about a 5% bias to the number of HSPs expected. That is small enough to be ignored in the context of design. Individual growth may contribute a somewhat larger effect— based on the parameters used in the assessment, fecundity would nearly double between ages 20 and 40. This should really be incorporated into design calculations, but there has not yet been time to do so; however, it seems unlikely to have major effects on precision, which is the goal of design calculations.

Note also that body-size/relative-fecundity effects may be completely different in males— for whom there is usually no direct data, whereas e.g. embryonic litter size can often be measured directly for females. POP data also allow direct estimation of size/relative-fecundity relationships for both sexes, as we do with SBT, but this is unlikely to work for makos because large male adults are seldom caught. However, for makos, one might perhaps expect *a priori* no strong link between male body size and fecundity. Female makos grow much larger than males, so the males clearly have the capacity to grow bigger. Presumably they would, if growth gave an evolutionary payoff in reproductive success— but they evidently do not.

This report does not go into all these complications, but in a real CKMR study for makos the following would need to be considered:

- Adult mortality-and-fecundity-growth parameters should be sex-specific;

- Adult natural mortality can be estimated directly (after allowing for growth/fecundity effects in females, and after allowing for catches of younger male adults). For assessment, an estimate for juveniles is also necessary. This could be extrapolated from the adult-specific estimates, assuming no strong size-specific effects on natural mortality per se— as per the current ICCAT assessment.

- It may be reasonable to link the male and female parameters deterministically, using known data on female growth and litter size; or it may be best to just estimate them separately.

2.1.3 False-negative rate for HSPs

The process of finding HSPs reliably— i.e. of excluding other less-related kin— needs to be tightly controlled to avoid false-positives, which would otherwise lead to biased estimates. Consequently, a certain proportion of HSPs will be lost accidentally below whatever acceptance-threshold is used to exclude false-positives; for details, see Bravington, Thomson, et al. (2017) and Bravington, Skaug, et al. (2016). It is straightforward to allow for a known false-negative rate in CKMR models, so no bias should result; however, there is an impact on precision, because not all the true HSPs in the sample will be found. The false-negative rate can be estimated once a reasonable number of HSPs have been found, based on properties of their genotypes (but independently of how many HSPs there are, or which animals are involved); the rate will depend on the species and the genotyping technique, but in our studies has usually been around 15%, which is the figure assumed in this report.

2.1.4 Effects of age-uncertainty

Birth-year is central to the discussion above. Uncertainty about age means uncertainty about birth-year, and this will have two follow-on consequences for CKMR models, especially where HSPs are used:

- trying to estimate a rate-of-change— abundance, or mortality— gets more difficult as you become less sure about the duration of the interval (e.g. a gap between birth-years) over which the change is measured;

- same-cohort comparisons become unavoidable (unless very brutal restriction of possible comparisons is employed), requiring extra parameters to be estimated, and to some confounding (correlation) between estimates of abundance, trend, and mortality rate.

In general, these difficulties should be less apparent in longer studies, because small errors in the "location" of the ends of intervals ("location" being "birth-year" here) have less relative impact if the intervals are longer.

At a theoretical level, there is no particular difficulty in allowing for age-uncertainty within the CKMR model (i.e. for modelling in a way that will avoid bias), provided the extent of uncertainty is well-understood: given a pair of uncertain age estimates, the probabilities simply need to be averaged across all the possible true ages, according to the probability of true age given measured age. If length is being used in place of age, then there *should* be good data on length-at-age variability, so the calculations can be adjusted accordingly— as has been done in this report (though the details of my assumptions about ageing error may be a bit generous). However, even if the model is adjusted so as to avoid bias, there will inevitably be some loss in precision from imprecise ageing. Whether that loss matters in practice, depends on details of each situation.

2.2 Design

The aim of designing a CKMR study is to ensure that enough samples are collected to give a usefully precise result, without spending more money than is really required. The key determinant of precision is the number of kin-pairs found, not the actual sample size; it is statistically impossible to get a "stock-assessment-grade" CV with fewer than about 50 POPs for teleosts, or 50 HSPs for sharks, and aiming for 100 is probably safer. However, it is not just the number of kin-pairs that matters; for example, if the juvenile samples cover too small a range of cohorts, or if age is completely uncertain, or if there is a colossal spatial imbalance in the sampling (see section 4.3), then precision will be poor regardless of how many HSPs are found. A single "design" therefore amounts to specification of design parameters— e.g. total sample size, duration of study, range of sizes sampled, covariate information for each animal (e.g. length and its accuracy of measurement, age), etc; and then working out what precision is likely to be achieved, for various quantities of potential interest (e.g. absolute adult biomass). The whole "design process" leads to choosing a single design that is likely to answer management questions at lowest cost and satisfying logistic constraints.

Provided that there is a pre-existing stock assessment, then there are perhaps three stages in an ideal CKMR design process, as follows.

1. "Laugh test" of basic feasibility: for a few sampling patterns and sample sizes, predict the number of kin-pairs that would be found, and check that the sample size required to generate, say, 100 HSPs is not ridiculously high given the "value" of the problem.

2. Build a CKMR-based stock-assessment model for estimating demographic parameters that has the main features of whatever model would be used on real data, and use it to predict the variance of the estimates of those parameters for a few different designs.

3. Optimize the design using the model from step 2, given real-world logistic constraints, sampling costs (which may vary between different types of sample), assessment objectives, etc. The mathematics of CKMR optimization has been worked out, and there is prototype code, but it would be completely premature to try this for makos yet.

For teleosts, even the "laugh test" is quite complicated and requires special code, because the very strong age- (or size-) fecundity relationship means that that not all adults are equal. However, for sharks the laugh test can be remarkably simple, under simplifying assumptions: that all female adults have similar fecundity, and ditto for males; that adult mortality can be ignored (reasonable in a short period for a species with high survival); and that the adult abundance will not change much over the period (ditto). The 2019 North Atlantic mako assessment suggests there were about 150,000 female adults in 2014, and about 260,000 males. Therefore, each comparison between two juveniles has about a 1 in 150,000 chance of yielding a maternal HSP, and a 1 in 260,000 chance for paternal HSPs. These two events are independent[1], so the per-comparison probability of finding any HSP is about

$$\frac{1}{150,000} + \frac{1}{260,000} = 1.1 \times 10^{-5}$$

The expected total number of HSPs is the number of comparisons times the average per-comparison probability, and we need to choose the sample size S to get 100. About 15% of true HSPs will be lost to false-negatives, though, so we should aim for 115. With S samples, there are $S^2/2$ comparisons (avoiding double-counting), so we need to solve

$$\frac{S^2}{2} \times 1.1 \times 10^{-5} = 115$$
$$\implies S \approx 4800$$

If there was just one parameter to estimate (constant average adult abundance with known adult sex ratio)— and if the assumptions of the laugh test were met— then aiming for 100 HSPs would on average yield a CV of 10%, which would be very respectable. However, aside from its simplifying assumptions, and the fact that the per-comparison probabilities vary substantially depending on individual covariates, the laugh test ignores several factors which do matter: avoidance of

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[1] Or almost independent, for species that do not pair-bond and have long reproductive lives.

same-cohort HSP comparisons, and the need to estimate several parameters rather than just one "abundance". In practice, those factors mean that achieved CVs will be considerably higher. The only way to study that, is by moving to a much more detailed model, as in Step 2 and the rest of this report.

In principle, Step 2 could follow a traditional framework used widely in stock assessment:

- simulate CKMR data using population dynamics from known parameters, and a proposed sampling design;

- estimate the parameters with CKMR-based assessment;

- compute the variance of parameter estimates across repeat runs.

- adjust the sampling design and repeat, until satisfactory results are obtained.

This would be a mammoth task, but fortunately it turns out that the nature of CKMR data permits huge shortcuts, using some advanced statistical theory; remarkably, the simulate/estimate/ repeat step can be avoided entirely, at the expense of writing some fairly complicated "administrative" code. Mathematically, the results are guaranteed to be the same. Details are beyond the scope of this report (MS in preparation; some hints are given in Bravington, Skaug, et al. 2016 section 4), but that is how the numbers in the next section were generated.

Before going into details about Step 2 for makos, it is worth making a few overall comments on this design process. First, the pre-existing assessment might be quite wide-of-the-mark. In general, though, it still seems reasonable to design around that one assessment, given it is the current basis for management recommendations. If the true abundance is greater than the assessment, then there will be fewer HSPs than expected, so that the estimated abundance will be imprecise— but it will also be "good news", and loss of precision may not be so important. If the true abundance is lower than the assessment, there will be more HSPs than expected, and the bad news will at least be precise bad news. It is generally harder to start a CKMR program than to keep it going, so revised estimates of abundance and other demographic parameters can of course be used to refine the sampling design (and increase or even decrease sample sizes) en route.

Second, while the above approach can be applied directly to North Atlantic makos, in the South Atlantic there is no assessment to start from. Nevertheless, there is at least an existing agreed catch series. If one assumes that the current status is "not overfished/no overfishing", then it is possible to design a CKMR study aimed at verifying specifically that. If we use the catch series to reconstruct a population dynamic history in which current fishing levels are *just* sustainable (i.e. on the very edge of overfishing), then we can design a CKMR program that would give usefully precise results for that case. No fitting-to-data is involved. It is most unlikely that this particular history is actually where the stock really is, but that doesn't really matter. If the true status were much worse than the reconstruction— i.e. current abundance is much lower— then there will be plenty more HSPs than expected, and a precise model can be constructed. On the other hand, if

the true status were much better and catches are having little impact on a much larger stock, then there would be very few HSPs, but also a clear signal that current fishing levels were *not* causing a problem.

One major source of uncertainty in the above, is natural mortality. Different assumptions about m lead to quite different just-about-sustainable population-dynamic-histories, partly because the reconstructed demographics are different, and partly because the definition of "just about sustainable", which is based on SPRR, itself depends strongly on m. Therefore, I made four different reconstructions, for m-values between 0.06 and 0.12 (the North Atlantic assessment assumes $m = 0.08$). Designing for the "most challenging" reconstruction should be safe.

In principle, the reconstruction process could get quite complicated, bringing in not just natural mortality but also other structural uncertainties in the assessment— in particular, around DD and the stock-recruit relationship. Note that in South Atlantic, fishing pressure has increased over time; so if current F's were indeed still sustainable, then there would also be no reason to think that the stock would have reached overfished levels yet. Therefore, for the reconstruction, it is reasonable to use a simplified population dynamics model with constant recruitment from 1980 onwards. However, there is no particular reason to think the reconstruction is correct— it is just a device used for design purposes— so the actual CKMR model which is "fitted" to the data during design does allow for changing recruitment, just as in with North Atlantic.

2.3   Density dependence and management objectives for sharks

The most obvious products from a CKMR-based assessment are estimates of (adult) absolute current abundance and natural mortality. However, those in themselves are not the end-points of an assessment process. It is worth thinking a bit further about (1) how CKMR outputs might be used to achieve (and define) management goals, and also (2) about the implications of those goals for designing a CKMR study that will yield useful results. This raises two points:

1. It is useful to consider the precision (CV etc) with which can CKMR estimate not just abundance and mortality, but also derived quantities related to management, such as reference points and the TACs required to ensure long-term sustainability.

2. In the South Atlantic specifically, there is no assessment— so the only way to design a CKMR study is by considering scenarios about how the current catches *might* sit with respect to some reference point, and how big a sample size would be needed if that scenario happens to be true.

For this report, I focused on SPR (Spawning-per-Recruit-Ratio, Spawner-Per-Recruit, etc.) as a possible composite measure of direct relevance to management.

SPR is widely used as a basis for reference points for fisheries management: the aim is to ensure that the total fishing mortality, aggregated across all life stages, will not reduce the average

lifetime reproductive output of a newly-recruited-to-the-fishery female to below X% of what it would be in the absence of fishing. The *current* value of SPR in the fishery, or the value that it might take in the near future under some proposed management scenario, can be calculated from fairly simple assessment outputs, such as CKMR and/or other data might provide (see below); and the reference point (limit or target) of SPR to compare it with— the X%— is essentially based on meta-analysis of other depleted stocks. Target reference points of SPR proposed for teleosts are typically in the range 40–50% these days. Such values would not generally be appropriate for elasmobranchs, for which the capacity for density-dependent increases in productivity is much lower and perhaps more variable between species. Although the "ideal" choice of SPR target/ limit for an elasmobranch is perhaps more complicated than for teleosts (Brooks et al. 2009), for most elasmobranchs it is nevertheless clear that persistent fishing at a "teleost-friendly" rate corresponding to SPR of, say, 50% would reduce the stock to a point where not just spawning *per recruit* was substantially reduced, but also— unlike for most teleosts— the *number* of recruits in the first place. Indeed, the absolute limit SPR_{crash}— at which the density-dependent response is unable to compensate for fishing mortality even when abundance is very low, so that continued fishing pressure at that level would eventually lead to extinction— is certainly much higher for elasmobranchs than teleosts. Consequently, higher values of X such as 60–70% have been proposed for elasmobranchs (Clark 2002).

There is an appealing link between CKMR and SPR. Given adequate data, CKMR can directly estimate *all* the parameters required to compute the SPR, given any recent or proposed catch-at-age: female relative-fecundity-at-age and natural mortality rate[2], which are "constants"; and adult abundance and mean adult age, which summarize the current position of the stock. In a stock assessment based only on traditional fisheries data, on the other hand, relative-fecundity-at-age has to be assumed (e.g. proportional to weight post maturity) and natural mortality is notoriously difficult to estimate reliably. The estimates of natural mortality that CKMR provides only pertain directly for adults, but typically teleosts will mainly be caught as adults (SBTuna is an exception) and so the natural mortality rate estimated by CKMR is ideal. With elasmobranchs that are caught mostly as juveniles, such as makos, the quantity required for SPR calculations is *juvenile* natural mortality schedule across the (female) ages in the fishery. In ICCAT 2017a and ICCAT 2019, it is assumed that natural mortality is the same for adult as for juvenile makos (age 1 or greater), with value 0.08. Here I have also assumed that just one value applies to all age classes, but that it will be estimated as part of the CKMR analysis. It is important to note that CKMR permits *direct* estimation of the quantities needed for SPR calculations (with the sole caveat being that natural mortality is really being estimated for adults, not specifically for juveniles— the latter is a modelling assumption), rather than having to rely on indirect estimates based on cross-species life-history proxies. Indirect estimates— while unavoidable in the absence of an alternative— are inevitably vulnerable to "uncheckable" uncertainty because of species-to-species variation,

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[2]Actually it is *total* mortality rate z that gets estimated; however, if catch C is known and abundance N are also known/estimated, then natural mortality m could be estimated— conceptually and approximately— via $z = m + C/N$. In practice this is done automatically and properly inside the CKMR log-likelihood maximization.

something that does not improve with more data or with time. With direct data such as provided by CKMR, uncertainties can be reduced over time by collecting more data.

Even if this is on the low side for small juvenile sharks, and even though SPR calculations are somewhat sensitive to natural mortality rate (which is quite uncertain for makos),

For this document, I mostly assumed a target of 70% SPR for the South Atlantic, with one scenario using 60% target SPR as a sensitivity. Of course, ICCAT may eventually decide to use a different value of X%, or indeed a non-SPR based reference point, for makos; the precise choice would probably not have a great effect on CKMR sample size requirements. Note that the outputs of ICCAT 2017a imply that SPR is currently 21% for North Atlantic makos (based simply on the ratio of survival to female age-at-maturity of 18 with current Z, versus with natural mortality only). This seems well below any remotely acceptable limit reference point for sharks, let alone target reference point.

3 Results

For a design exercise like this, it is not necessary to accurately capture every detail of the full stock assessment; a simpler model is sufficient, provided it captures the important elements and produces similar numbers to the full assessment. With that in mind, the model is a slightly simplified version of standard age-structured population dynamics, using annual aggregate catch-at-age (or catch-at-length, in the case of South Atlantic) but with the only data signal coming from CKMR. That is, no CPUE data at all was used, and there was no fitting to length-frequencies— just the subtraction of known removals-at-size or age, from the dawn of time (1950 and 1980 in the N and South Atlantic respectively) until the present (2014). Population dynamics were then projected forwards until 2030 (the last year considered for sampling), assuming the same F-at-age as for the average across 2012—2014. An equal sex-ratio at birth is assumed, with knife-edge maturity at 8yo for males and 18yo for females.

Current assessment results suggest that average recruitment did not drop appreciably until around 2005 (Table 7, ICCAT 2017a). In this model, recruitment is treated as constant from year-to-year, except that the level (the "constant") is allowed to change from 2005 onwards to an estimated value. This is slightly simpler than embedding a stock-recruit relationship into the model, but should have basically the same effect as fitting an LFSR (Taylor et al. 2013; Kai et al. 2017) with one free parameter.

Note that the constant-recruitment assumption is a computational necessity during design for computational reasons, but it could be relaxed by allowing recruitment deviations as random-effects when fitting to real CKMR data (as we have with SBT, for example). The impact on CVs should not be severe.

One other important issue is ageing uncertainty. In the scenarios, I varied the proportion of the

samples that were aged (from vertebral sections), with only a length (and sex[3]) measurement available for the rest. The vertebral ages were treated as exact, which may be over-optimistic; and I made some particular assumptions about length and age (based on growth curve and CV of length-at-age in the assessment; see box below Table 1) which may or may not be optimistic about the extent of ageing uncertainty. These points should be discussed during follow-up work.

Overall, there are just 4 demographic parameters to estimate:

- initial adult abundance (1950 or 1980);

- natural mortality (assumed equal for all sexes and ages);

- reduction in average recruitment post 2005;

- "lucky-litter effect", i.e. extent to which within-cohort HSP frequency exceeds the cross-cohort frequency.

The quantities of most interest to management are typically different to the actual demographic parameters, but are of course derived from the estimated demographic parameters using the population-dynamics model itself. In the results below, I selected five quantities of possible interest: current SSF, trend, depletion, natural mortality rate, and SPRR, the current Spawner-Per-Recruit-Ratio. The latter provides a widely-used set of reference points for teleosts. In fact, for "typical" teleosts, POP-and-HSP-based CKMR alone (plus catch data) estimate all the ingredients of current SPRR, without needing external assumptions: adult natural and fishing mortality rates, relative fecundity at age.

With elasmobranchs, it is perhaps harder to define appropriate "target" for SPRR that will work well across species, but it is still a useful reference. Because DD response is much weaker in (most) elasmobranchs than in teleosts, any SPRR-based target or limit reference should be higher than for teleosts. For example, whereas fishing a teleost at SPRR of 60% would in the long-term send the SSB around 60% with little effect on recruitment, fishing a shark at the same SPRR is likely to drive the SSF substantially *below* 60% of unexploited, because the average recruitment itself will be substantially diminished along the way. In this draft report, I tentatively used SPRR of 70% as a "edge of sustainable" for South Atlantic reconstructions. Note that, according to the North Atlantic mako assessment, the SPRR in 2014 was about 21%.

Because (female) mako sharks are only subject to substantial fishing mortality while juvenile, SPRR depends only on the juvenile natural mortality, whereas CKMR only provides information on adult mortality. In order to link the two, I have assumed that the two rates are equal, just as the current ICCAT assessment does— but that may not be the case. There could be substantial implications for SPRR (and other related quantities, such as Replacement Yield), so this issue requires further discussion in any follow-up work.

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[3]Sex can be determined genetically for sharks, so even if it not recorded accurately when samples are collected, it can be inferred post hoc at the point of genotyping— we have done this for other shark species.

3.1 North Atlantic

Table 1 shows setup and results of several possible CKMR designs for North Atlantic makos. In all cases except the final row, the total sample size was 4800, but the scenarios vary in three other aspects:

- duration of the study (3–10yo);

- emphasis on sampling smaller or older sharks;

- proportion aged directly.

The age range in the samples is about 0–11yo so, even in a short study, enough cohorts are covered to make a defensible estimate of trend over a 10-year period. (In fact, since the CKMR data are embedded in a population dynamics model with strong assumptions about recruitment stability, it is technically possible to make inferences over much longer periods, right back to "B0" ; however, the *direct* statistical signal from CKMR only covers a shorter period.)

It would be a mistake to concentrate too hard on detailed results within Table 1: the scenarios are far from comprehensive, and many of the assumptions/implementation details should probably be improved. Perhaps the most surprising part is that results do not differ greatly— except for the last row, in which the sample size is doubled.

- The main effect on precision comes from the total sample size, which is the same in all scenarios except the last row where it is doubled (otherwise the same as the previous row). This halves all the CVs and SEs, and quadruples the expected number of HSPs.

- All other scenarios gave a CV of $N_{\female ad2020}$ of 15–20%;

- Short study (V_n3) is appreciably worse at estimating trend and SPRR;

- Longer studies (less sampling per year over more years) give better precision— but of course the results take longer to arrive;

- Lack of ageing made (surprisingly) little difference;

- Concentrating on young sharks worsens the ability to estimate m;

- The SE of SPRR is fairly wide— varying between 0.06 and 0.13. However, given the actual value is estimated only at 0.21, even an Upper Confidence Interval (optimistic) would clearly be undesirably low.

Scenario V_n7 was a "personal favourite": sampling in the first two years concentrated on large sharks, and with a high proportion aged (70%), so as to get a good historical range of birth-dates; then concentrating mostly on younger sharks for the remaining 8 years (with only 10% aged), to

Table 1: North Atlantic: expected precision for various designs, based on the current ICCAT assessment. Bold line shows actual values from (replicated) assessment. Non-bold entries; the column for N_FAd2020 shows CV, and the columns to the right show Standard Error (SE).

Scen	NY	SS_small	SS_big	paged	E_HSP_XC	N_FAd2020	depl_2020	logtrend_10yr	m	SPRR
Assessed						**135,000**	**0.39**	**-0.31**	**0.08**	**0.21**
V_n1	5	1774	3026	0.90	83	0.17	0.13	0.054	0.030	0.082
V_n2	5	1774	3026	0.10	89	0.16	0.12	0.063	0.027	0.099
V_n3	3	1774	3026	0.10	85	0.15	0.12	0.084	0.025	0.133
V_n4	5	3660	1140	0.10	97	0.17	0.16	0.050	0.038	0.073
V_n5	5	924	3876	0.10	88	0.15	0.11	0.078	0.025	0.123
V_n6	5	924	3876	0.70	84	0.16	0.12	0.067	0.027	0.105
V_n7	10	2733*	1851*	0.46	77	0.19	0.11	0.050	0.027	0.067
V_n8	10	1774	3026	0.10	93	0.18	0.12	0.049	0.030	0.064
V_n8$\times$2	10	3548	7052	0.10	372	0.09	0.06	0.024	0.015	0.032

*Bigger sharks at the start, smaller later on; see text

Key to columns	
NY	Number of years, starting from 2020 (equal sample sizes every year)
SS_small	Number of sharks under 125cm
SS_big	Number of sharks between 125cm and 200cm
paged	Proportion aged
E_HSP_XC	Expected number of cross-cohort HSPs
N_FAd2020	Number of female adults in 2020[2].
depl_2020	Spawning stock depletion, i.e. ratio of N_FAd2020 to N_FAd1950
logtrend_10yr	log(N_FAd_2025 / N_FAd_2015)
m	Natural mortality (assumed constant by sex and age)

[2]: This is a proxy for Total Reproductive Output or SSF etc. It should in principle reflect age-specific fecundity, but the actual code used here treats all female adults as equal. See section 2.1.2.

Sampling was length-based, according to 5cm bins centred on the mean lengths for ages 0–10 and uniform within each bin. Sharks with lengths between bins were not sampled (these would have higher age uncertainty). Some simulated sharks were also aged directly; if their ages fell in the range 0–10yo, they were used for CKMR, but older sharks were (somewhat arbitrarily) discarded. Length measurements were assumed accurate to the 5cm band, and age to the year. This is rather a "utopian" setup, which may understate the uncertainty associated not having direct age data; further discussion would be useful.

get the most up-to-date information on spawning stock and trend. It does indeed do well, despite generating the lowest overall total of HSPs, but the difference from the other results is not as big as I expected.

Remark 1. One apparent anomaly is that some scenarios with little direct ageing (e.g. V_n2) actually seem to perform *better* for certain parameters than otherwise-similar scenarios with more ageing (e.g. V_n1). This is probably due to an arbitrary quirk of the setup. If age data are available, then only sharks up to age 10 are used, with older samples being discarded; but if only length data are available, then the entire sample is up to 200cm is used, which brings in some extra fish older than 10yo. This means that more samples are available in V_n2 than V_n1, which is reflected in the number of expected HSPs (89 vs 83). In this particular case, the increase in HSPs seems to roughly compensate for the loss of age information, at least for several parameters— though not for SPRR or logtrend.

3.2 South Atlantic

Table 2 shows possible results for three design scenarios in the South Atlantic. Since no reliable age-structured assessment is available, results are presented under 4 different possible values for m (0.06, 0.08, 0.10, 0.12). For each m, the initial abundance of the stock (in, say, 1980) was calculated so that current F-pattern yields an SPRR of 70%— i.e. as if the current state of the stock is "not overfished, not overfishing", but just at the highest comfortably-sustainable level for an elasmobranch. The true situation may be very different.

If the working assumption of "just sustainable" is correct, then sample sizes in the South Atlantic need to be higher than in the North Atlantic to achieve reasonable precision. Scenario V_s1, with the same sample size of 4800 as the North Atlantic, gives for the case $m = 0.08$ a CV of 0.35, which is borderline useless. Scenarios V_s2 and V_s3 use a total sample size of 10000 instead, and are able to achieve reasonable CVs over a 5-year study. Of the two, V_s2 gives somewhat better precision; it concentrates on larger sharks than V_s3, but also has a much higher proportion of aged samples (70% vs 10%). The main reason that recommended South Atlantic sample sizes are higher, is the "just sustainable" working assumption, which would imply that the current Southern population is substantially larger than the Northern population, where the assessment strongly suggests that current fishing mortality is *not* sustainable. There is no particular reason to believe that the working assumption is actually correct; if in fact there is already substantial overfishing in the South Atlantic, then CKMR should yield a clear result well before a target of 10000 samples is reached.

The dominant feature of Table 2 is the effect of "true" m. Unsurprisingly, given that these particular reconstructions are constrained to the assumption that current SPRR=70%, higher m means lower N— and thus the higher-m reconstructions yield more HSPs and better precision for any given design scenario. At the sample sizes and assumptions of Table 2, there is unlikely to be enough

Table 2: South Atlantic: *if* current F-pattern is just about sustainable (70% SPRR). Bottom group of rows (*italics*) are a sensitivity if SPRR target is 60%, at natural mortality $m = 0.08$

Scen	m	NY	SS_small	SS_big	paged	E_HSP_XC	N_FAd2020	depl_2020	logtrend_10yr	m	SPRR
"True"							**780,000**	**0.78**	**-0.10**	**0.06**	**0.70**
V_s1		5	972	3828	0.1	15	0.42	0.188	0.40	0.076	0.209
V_s2	0.06	5	922	9078	0.7	63	0.20	0.094	0.20	0.038	0.101
V_s3		5	6159	3841	0.1	68	0.21	0.114	0.17	0.046	0.108
"True"							**470,000**	**0.75**	**-0.10**	**0.08**	**0.70**
V_s1		5	972	3828	0.1	22	0.34	0.169	0.37	0.066	0.141
V_s2	0.08	5	922	9078	0.7	92	0.16	0.084	0.19	0.033	0.068
V_s3		5	6159	3841	0.1	100	0.18	0.102	0.16	0.040	0.080
"True"							**300,000**	**0.73**	**-0.09**	**0.10**	**0.70**
V_s1		5	972	3828	0.1	30	0.29	0.153	0.36	0.060	0.109
V_s2	0.10	5	922	9078	0.7	125	0.14	0.076	0.18	0.030	0.053
V_s3		5	6159	3841	0.1	136	0.15	0.092	0.15	0.036	0.065
"True"							**210,000**	**0.71**	**-0.09**	**0.12**	**0.70**
V_s1		5	972	3828	0.1	40	0.25	0.138	0.36	0.056	0.092
V_s2	0.12	5	922	9078	0.7	164	0.12	0.069	0.18	0.028	0.045
V_s3		5	6159	3841	0.1	179	0.13	0.082	0.15	0.033	0.055
"True"							*310,000*	*0.67*	*-0.14*	*0.08*	*0.60*
V_s1		*5*	*972*	*3828*	*0.1*	*33*	*0.27*	*0.159*	*0.26*	*0.051*	*0.131*
V_s2	*0.08*	*5*	*922*	*9078*	*0.7*	*157*	*0.13*	*0.080*	*0.13*	*0.025*	*0.063*
V_s3		*5*	*6159*	*3841*	*0.1*	*150*	*0.14*	*0.097*	*0.10*	*0.032*	*0.079*

information to estimate *m* precisely purely from a South Atlantic program in the next few years. However:

1. If the South Atlantic is actually in a worse state than currently assumed, there will be a lot more HSPs found, leading to better precision;

2. Estimates of *m* could perhaps be pooled between North and South Atlantic CKMR programs;

3. Sampling can always be extended in future. Mako sharks are long-lived, and management needs tools for the long term.

3.3   What if the assessments or assumptions are wrong?

Assessments— even if they exist— are not always accurate. Therefore, with a CKMR program designed on the assumption that a particular assessment is correct, the actual results may turn out quite different. If the true abundance is higher than the assessment's estimate, then there will be fewer HSPs than designed-for, and the abundance estimate from CKMR will be imprecise. However, the lower confidence interval (LCI) on abundance still tends to increase with increasing true abundance— in other words, the CKMR data should reveal "good news", even if the actual amount of "goodness" will be uncertain. Conversely, if the true abundance is lower than the assessment's estimate, then there will be plenty of HSPs and the "bad news" will be more precise (lower CV) than expected from the design.

This "good news" situation is more-or-less what we found with SBT c. 2010. By then, we had genotyped enough SBT samples to start looking for POPs[4]— though still well below our original target sample size— and we found a lot fewer POPs than expected. It was clear that, if we had just proceeded to the original sample size, we would not get enough POPs to give a precise abundance estimate. However, it was also clear that SBT abundance must be considerably higher than had been suspected— and that increasing the sample size would deliver good news. This was enough motivation to deliver funds for increasing sample size was

Of course, depending on the results, it may well be desirable (in either case) to continue sampling— but that is not inevitable, at least for a bycatch species. In the "good news" case, if the LCI on abundance (or on SPRR) turns out to be sufficiently high, then there would be clear evidence that current exploitation rates are *not* a problem, and therefore that sampling levels could actually be reduced without jeopardy. Unfortunately, that outcome does not seem likely, at least not in the North Atlantic.

In the case of South Atlantic, there is no assessment. The "if just sustainable" design process suggested here simply assumes that the population and its demographic parameters are just sufficient to make current catch-rates safely sustainable. That may not be the case. If the true situation is substantially worse, then implementing the "if just sustainable" design should clearly reveal that there is a problem, and probably before the target sample size is reached. If the implementation finds very few HSPs, on the other hand, the implication would be that catch-rates in the South Atlantic are not currently of concern.

For the latter to be defensible, though, sampling levels do need to be high enough to give reasonable statistical power. If sample sizes are simply inadequate, then the point estimate may be encouragingly high (infinite, if no kin-pairs are found), but the LCI will still be in the danger zone— in other words, finding few kin pairs but based only an inadequate sample would give no justification for a claim of "precautionary management". Avoiding that kind of inadequacy is, of course, the point of doing design studies like this one.

4 Other considerations

4.1 Skip-spawning

Female mako sharks do not produce pups every year. In principle, this means that two makos born 1 year apart cannot be a Maternal HSP, i.e. they have an HSP-probability of 0; whereas two that are born 2 years apart (assuming a 2-year breeding gap) actually have a HSP-probability of about $1/\left(N_{\female}/2\right) = 2/N_{\female}$ (plus mortality allowance), because only half the female population will be in "breeding mode" in any one year. However, the models used in this report (and in all CKMR projects completed at CSIRO) do not bother to take account of skip-spawing, simply

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[4]At that point we were not yet using HSPs for SBT, but the principles here are the same.

using a probability of $1/N_{\female}$ (plus mortality allowance) throughout. Overall, about half of the comparisons will be separated by an even number of birth-years and about half by an odd year, so the "miscalculations" of HSP probabilities in the presence of skip-spawning basically cancel out. The CKMR model could in principle be reformulated to allow explicitly for skip-spawning; we might in future decide to do so when analysing some real datasets, but it does complicate the code and there is often no point.

In a CKMR study that spanned a very limited range of juvenile cohorts and if adult mortality was high, this simplification could lead to some bias; but with makos in particular, the range of cohorts would be wide, and adult (female) mortality is low. There should therefore be no concern on this point.

4.2 Genotyping and kinference

Cost-effective and reliable genotyping, combined with dedicated kin-finding processes that can basically eliminate false-positive HSP and estimate the proportion of false-negatives, are key to the success of any CKMR project. This report does not go details; see Bravington, Skaug, et al. (2016) section 5, and Bravington, Thomson, et al. (2017), for fairly recent summaries, though the technologies and algorithms are evolving fast. The salient points for Atlantic makos, and indeed for most species of teleost and elasmobranch fish, are:

1. HSPs can be found reliably and cheaply (i.e. at low unit cost), with only moderate loss to false-negatives, provided that a suitable genotyping method and suitable kinference software are used.

2. Picking the wrong genotyping method leads to disaster: inability to distinguish HSPs from other not-quite-as-close-kin, and/or an unnecessarily expensive price-tag that may kill feasibility. There are a lot of methods suitable for *other* problems (but not CKMR) which exhibit either too high an error rate, and/or too high a unit cost, and/or too high a development cost. The devil is in the detail.

3. If several countries collect samples, then genotyping needs to be done either centrally or at least in a way to ensure comparability of genotypes. If two countries each collect half of the necessary total sample size, but their genotypes were not compatible, then the effective sample size of the "combined" study would only be half of the necessary.

At CSIRO, we have developed a reliable pipeline based on DartCap developed by Dart Pty Canberra (ddRAD, plus "baits/capture-probes" to restrict sequencing to a chosen subset of SNPs of interest, typically 1500—2000, plus Dart's bioinformatic processing). There is little start-up cost (e.g. no requirement for a genome assembly), and unit cost from "extracted DNA" to "here is a genotype" are AUD20 or less. Of course there are extra costs associated with collecting samples and tissue preparation and extraction, but we do not generally budget more than AUD30–35 per

sample— from the fish thru to the genotype— overall. We continue to refine our processes to reduce both false-negative rates and unit costs, but we do not expect to switch to an entirely different genotyping method. While it is true that there are now other genotyping methods which *might* be able to do a similar job, it is also worth noting that it took us several years of hard work to become familiar enough with the detailed properties of DartCap to be able to use it more-or-less routinely for new projects; any new genotyping method may impose a similar burden. CKMR— particularly finding a small number of HSPs among a huge number of comparisons— is a demanding task, and up-skilling to the point where it becomes almost routine— which we are close to reaching at CSIRO— requires some dedication.

4.3   Spatial effects

Extensive tagging results have shown that mako sharks do move around a lot, including sometimes right across the North Atlantic— although apparently not across the equator. However, makos often tend to be restricted to a smaller area for several years— more so than blue sharks, for example. Therefore, it is possible that HSPs born just a few years apart will tend to come from the same part of the ocean and, depending on their age at sampling (which gives them further opportunities to move), the HSPs may still tend to be physically closer within-pair than for unrelated pairs among the samples. If such proximity is combined with heavily uneven sampling, and a naive CKMR model is nevertheless applied, then there is the possibility for bias in abundance estimates.

The good news is that, given decent sample sizes and overall numbers of HSPs and basic spatial spread, any such patterning should be clear in the data. It should also be more visible when the animals in the HSP are younger at capture, and when their birth-dates are closer in time. A CKMR study for makos should span many birth-years and many ages-at-capture, giving ample opportunity for movements to blur any patterning and to make spatial effects irrelevant. However, if a pattern does emerge, then there *is* a way to extend CKMR models to such cases, alluded to in BSA section 3— potentially incorporating tagging data as well as the CKMR patterns themselves.

To summarize,

- Make sure that substantial sampling happens on both sides of the Atlantic (whether North or South)— although it does not have to be "evenly distributed".

- Check whether there are any spatial patterns in the HSPs— for example, a disproportionately high proportion of E-E and W-W pairs compared to E-W pairs.

  – If not, there is no need to worry about spatial complications for Atlantic mako CKMR;

  – If there are patterns, then a more sophisticated model could be devised.

- Note that sampling and biology would both need to be unbalanced to give any risk of bias; for example, "cryptic" breeding stocks that are well-mixed at the location of sampling do not cause bias in CKMR when estimating aggregate abundance.

In the South Atlantic, there is the further possibility that some mixing may occur between the South Atlantic and Indian Oceans, around the tip of South Africa. If there was complete mixing, then a CKMR estimate based only on South Atlantic samples would in fact apply to both oceans combined. Unfortunately, though, the sample size proposals in this report would also be insufficient for that case (because the true abundance would be higher, and the rate of kin-finding per comparison would be lower).

Genetic stock structure results presented during the 2019 SCRS suggest that there is *not* one single stock covering the entire Indian and South Atlantic oceans, so it perhaps is reasonable to treat the South Atlantic as basically separate from the Indian Ocean for initial CKMR design purposes. However, there clearly is some mixing and spatial complexity, shown by genetic differences between South African and Uruguayan samples. The extent and implications of between-ocean mixing cannot be resolved just by sampling the South Atlantic alone (nor by conventional genetic stock structure studies, unless the results are extremely clear), but it is possible that a CKMR program may start in the IO as well. In that case, it would be simple to check for the extent of cross-ocean HSPs— provided that no huge basic mistakes are made, such as choosing incompatible genotyping methods for the same species in different oceans.

4.4   Impact of no-retention

If a policy of no-retention for makos is adopted, would there be implications for CKMR? Provided that it is still possible to collect samples from dead-at-the-boat animals, and/or during live-release, alongside reasonably accurate length measurements, then there should not be a major problem. The following comments may be relevant:

1. Although direct age data (i.e. from vertebrae, and i.e. from dead animals only) does help the models run better than length-only data, it appears not to be essential provided lengths are measured accurately (somewhat to the surprise of the author— and a caveat that there should be further checking of the design calculations, making sure that realistic assumptions are being made about the accuracy of length measurements).

2. Really inaccurate length measurements (e.g. if it is difficult to measure length during the messy process of live-release) could, however, be enough to wreck CKMR as a useful tool. Without *some* information on year-of-birth (ideally from direct age, but perhaps from length and a growth curve), the models just don't work regardless of the total number of HSPs found, because the correlations between the estimated parameters approach 100%.

3. A live-released juvenile could eventually become the *grandparent* of another juvenile sampled (much) later. Grandparent-Grandchild Pairs (GGPs) are genetically indistinguishable from HSPs, so there is potential for bias or at least modelling complications with live-release (whereas dead juveniles cannot go on to breed). However, on demographic grounds such GGPs will be much rarer than true HSPs until the birth-gap approaches twice the generation length, so (i) this will not be a problem for many years, and (ii) it is always possible to restrict the range of birth-gaps over which comparisons are made (i.e. simply not include the results of such comparisons in the model) so as to eliminate "GGP contamination".

4. It is *possible*— but this would need a lot more investigation— that genotyping of live-releases (and dead samples) with the main aim being CKMR, could also be used to directly estimate juvenile mortality (and even juvenile natural mortality, by allowing for known catches), via some kind of Brownie-type model (i.e. repeat tagging of a cohort). This kind of gene-tagging has the advantage of not relying on the vagaries of tag-return rates, albeit at the disadvantage of expense; however, if samples are being used for CKMR, then the marginal expense may not be great. Gene-tagging of 2yo SBT, recaptured during harvest at age 3, is now a core element of SBT management, because it provides information specifically on the size of each incoming cohort. For SBT, this is more expensive than CKMR (although very cheap compared to the value of the fishery), because it needs to be repeated afresh every year, and also because the average number of 2yo juvenile SBT is larger than the total adult abundance. With mako sharks, though, the focus would presumably be different: a single estimate of juvenile natural mortality (perhaps age-specific) to be constructed eventually using data from multiple years. Hence the overall sample size requirement may not be so large. Since juvenile m for mako sharks (which may be appreciably different to adult m) is such an important parameter for calculating key management statistics such as SPRR, the potential benefit to long-term management would be considerable. Quite how many samples might be needed is open, but a design approach similar to the one in this report could be used to investigate feasibility.

Finally, it is worth considering whether future no-retention and live-release policies could complicate the interpretation of catch data (let alone CPUE). For example, although post-release survival estimates are available under certain release conditions, perhaps there will be uncertainty about how carefully the release protocols are actually followed in the various fisheries. Here CKMR has a massive advantage compared to traditional assessment methods, in that CKMR can deliver an unambiguous signal on trends in adult abundance without needing any catch data at all.

5 Discussion

CKMR could be a powerful tool for informing the sustainable management of Atlantic mako sharks, North and South, both in the short and long term. There do not seem to be any scientific

problems (the size-range in the catches, the spatial spread, and the basic biology is suitable for CKMR), and the sample size requirements seem very modest. Age data from vertebrae— though certainly useful for CKMR, if it is available— does not appear to be essential, so that good length measurements alone could probably suffice. However, a little further work (prior to December 2019) is needed to confirm that.

In the North, it should be able to "anchor" the assessment (e.g. by giving a precise estimate of absolute adult abundance) within 5 years or less of sampling, and in addition to obtain valuable information on other parameters (e.g. adult m, which is closely linked to stock productivity) as time goes on. A reasonable total sample size (across animals up to about 200cm) would be 5000, which if spread over a 5-year project would amount to just over 1% of annual catches from the early 2010s. This seems quite modest. There is, however, little point in starting a program unless the long-term expected total sample size is at least close to that figure of 5000— there would simply not be enough kin-pairs found to reveal much.

In the South Atlantic, it is harder to produce a specific design because there is no assessment. However, if a management status of "not overfished, no overfishing" is correct, then it is possible (given a reasonably complete catch series) to work out how many samples would be needed to validate that conclusion via CKMR *if* the current state of the stock is just on the edge of sustainability. (The criterion suggested in this report, 70% Spawner-Per-Recruit-Ratio, could be modified if it is not thought to be appropriate; sample size requirements would be somewhat lower if a criterion of 60% SPRR was preferred, but would certainly not be halved, say.) In practice, the stock will be either substantially healthier or substantially worse. In either case, CKMR at the proposed sample size should give useful information— even if very few kin-pairs were found, so that no precise estimate could be made (without longer-term sampling), it would nevertheless be clear by virtue of the design that the stock is not *currently* experiencing a problem. Sample sizes required in the South Atlantic would probably need to be larger than in the North Atlantic, but still modest compared to the scale of catches. The sample size required in South Atlantic depends substantially on what is chosen as a in-principle sustainable criterion (e.g. 60% or 70% SPRR) rather than on assessment results, and consequently need further discussion— the indicative numbers for South Atlantic in this report are likely to change. Note if current fishing mortality in the South Atlantic is in fact not sustainable, then clear results should be visible well before a target of 10000 samples is reached.

In the longer term, CKMR would also provide an independent check on trends in the spawning stock in each hemisphere, and thus on whether management is succeeding, even in extreme cases of degraded data in future (e.g. if catch data become unreliable— let alone CPUE).

In both hemispheres, the next step would presumably be a more detailed investigation of logistic options and design objectives. Planning is vital to success in CKMR. Nevertheless, it is not essential to specify *every* design detail before a program starts. In particular, the main expense of CKMR usually lies in the sample preparation and genotyping. By starting to collect samples early, a sample bank can be built up that can be genotyped in future if and when the necessity arises.

This can allow a for a quick "retrospective sample size increase" if early CKMR results reveal a reality very different to prior expectations.

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A   Model details, data preparation

[Equations and other details to be added later. Standard age-structured stock assessment using historic catch-at-age reconstructions as per stock assessment inputs to 2019, plus CKMR data. Three (South) or four (North) parameters are estimated: initial abundance, natural mortality, and one nuisance parameter connected to litter size variability. In the North Atlantic, recruitment at age 1 is assumed to be steady until 2005— as per current stock assessment results— followed by an estimated step-change (the fourth parameter). This amounts to a rough but convenient version of a standard stock-recruit relationship.

For the South Atlantic, I used ICCAT SCRS documents to obtain nation-specific catch series, combined with recent nation-specific length compositions assumed to apply back thru time; since this is only for study-design, the series do not need to be exact. For the South Atlantic, I assumed *no* effect yet of spawning stock on recruitment, because of the working assumption of "just about sustainable".]