Excerpts from the 2014 International Review Panel Report for the 2014 International Stock Assessment Workshop.

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Note: This document contains excerpts from the 2014 panel report[6] relevant to hake discussions at the 2019 International Stock Assessment workshop.

General Hake Comments

The process implemented following the 2013 review involved biologists and modellers collaborating to synthesize multiple sources of information for hake off South Africa and Namibia to identify plausible stock structure hypotheses. It also identified the data that might be used to fit models based on those hypotheses. This process has been very successful. The hypotheses identified through this process, while not yet final, represent an effective synthesis of a diverse set of information. The Panel recommends reducing the number of hypotheses considered during the initial stages of modelling transboundary hake issues, owing to problems that some of the analyses identified during the review.

Model formulations have been developed to conduct assessments of the hake off South Africa and Namibia that take spatial structure into account. These formulations range from those representing spatial structure using fishery selectivity, to ones which model spatial structure explicitly. The initial fits of the latter class of model are currently poor, and much work likely remains before a model is found which provides an adequate fit to all of the data when they are represented spatially.

Hake Recommendations

Stock structure

B.1 (*) Genetic data provide evidence related to what might be termed “breeding stocks” – that is, these data provide insights into the degree of reproductive isolation over space and time. In general, neutral genetic markers will not be able to evaluate another class of scenario that might be of interest to management: breeding occurs randomly in a single location, but portions of the progeny either passively drift or actively migrate into two or more geographic areas, where they then grow and mature. If the areas differ in environmental features, this could produce differences in growth rate, parasite load, age at maturity, or other phenotypic characteristics that might be interpreted as evidence for multiple stocks. Such scenarios should be considered when evaluating management options, even though they would not include more than a single breeding population.

B.2 (*) The stock structure hypotheses that assumed a hard boundary between the stocks of *M. capensis* and *M. paradoxus* (C2d and P2b) within Namibia should be assigned low priority for implementation. This is because the basis for the hypotheses (Reimer, 1993) was largely qualitative – retrieving the original data and conducting appropriate statistical analysis would be necessary before these data could be used to derive stock structure hypotheses. The

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assumption of a northern stock of *M. paradoxus* off Namibia that is separate from a southern stock, which underlies hypothesis P2b, is problematic given the perceived lack of spawning of this species in Namibia. Further, the assumption of a hard boundary between two stocks of *M. capensis* is inconsistent with the mixing that can be inferred from the genetics studies.

B.3 (*) The discrepancy between the mtDNA results for 2005 and for 2012-13 for *M. paradoxus* has not been resolved. The hypothesis that the different results were due to different sampling locations in the earlier and later time periods is not consistent with the assumption of a single panmictic population. Under those conditions, it should not matter from where the samples are taken, as they all should be derived from the same random-mating population. However, such results can occur if, for example, animals from the same family or cohort are found and sampled together. This can lead to a "chaotic" pattern of statistically significant results that do not provide consistent results over time (Planes and Lenfant 2002; Iacchei *et al.* 2013).

B.4(*) Figure 2 uses results of the power analyses conducted by Henriques *et al*. (unpublished data) to depict levels of stock differentiation of *M. paradoxus* that can and cannot be excluded based on available genetic data. If cryptic stock structure (more than a single stock) exists, it must be characterized by combinations of migration rate (*m*) and effective population size (*Ne*) that produce *Fst* values too small to detect with available data. As illustrated in Figure 2, how confident one can be that the power analyses of genetic data can rule out more than one population of *M paradoxus* depends on how large *Ne* is. Two general approaches can be used to estimate recent or contemporary *Ne*. First, one can use genetic methods (reviewed by Luikart *et al*. 2010) to estimate *Ne* based on any of several indices. However, because all of these indices are sensitive to a signal proportional to 1/*Ne*, they are most effectively used to study relatively small populations, particularly those of conservation concern. Once *Ne* reaches 10^3 or 10^4, 1/*Ne* is so small that it becomes difficult to distinguish between values that are "large," "very large," and "very very large" (Waples and Do 2010). Therefore, although genetic methods have considerable power to detect relatively small *Ne*, they have difficulty distinguishing between values in the range $10^3 – 10^4$ and higher. Second, one can use the ratio *Ne/N* estimated for other species, together with a species-specific estimate of *N* (number of mature adults), to derive an estimate of *Ne*. However, published estimates of the ratio *Ne/N* in marine species span such a wide range (about 10^{-1} to 10^{-6}; see review by Hauser and Carvalho 2008) that considerable uncertainty would still remain after application of this approach.

B.5 (*) Further review of the data on which the GeoPop model results used to develop stock structure hypotheses are based suggests that the boundary at the Olifants River for *M. paradoxus* does not appear in the raw survey data for South Africa nor the model output. This strongly suggests that stock structure hypotheses for *M. paradoxus* based on GeoPop output should not be taken forward at present, and any future attempt to develop stock structure hypotheses using GeoPop should utilize plots of the raw data, as well as the predicted distribution of abundance by age-class.

B.6 (*) The following stock structure hypotheses should form the basis for initial stages of future modelling work:

- *M. paradoxus*. The most likely hypothesis is that there is a single stock off Namibia and South Africa (hypothesis P1).
- *M. capensis*. The most likely hypothesis based on the genetics data is that there are two stocks off Namibia and South Africa (hypothesis C2c). There are northern and southern stocks and an area of mixing.

The stock structure hypotheses that should be included the second stage of future modelling work are:

- *M. paradoxus*. One or more multi-stock hypotheses based on the results of the GeoPop analyses (see recommendation B.9). The group developing stock hypotheses based on GeoPop should consider that one interpretation of the genetics data is a single breeding stock with sub-stocks that have different migration patterns.
- *M. capensis*. One or more multi-stock hypotheses based on the results of the GeoPop analyses (see recommendation B.9) and a three-stock hypothesis if the analyses of genetics data supports such a hypothesis.

B.7 (H) Genetic data for *M. capensis* provide convincing evidence for more than one stock. Results from the STRUCTURE analysis conducted by Henriques *et al.* (unpublished data) are most compatible with two stocks, which have an area of mixing that varies across years within the approximate range (28-33 lat). Fitting the STRUCTURE results to a scenario involving three populations does not provide convincing evidence for the existence of another stock. However, because it is well known that clustering programs such as STRUCTURE respond primarily to the strongest genetic signal and hence might miss a weaker signal of less-well differentiated stocks, two additional analyses should be conducted to further explore the potential for more than two stocks of *M. capensis*.

- Using the data for all three years and a STRUCTURE run with $k = 2$, select those individuals assigned with high confidence to the “northern” stock. Run STRUCTURE with k set to 2 and evaluate evidence for an additional stock that is genetically similar to the “northern” stock. Repeat the above using just the individuals assigned with high confidence to the “southern” stock. Removing the main signal of north *vs* south might reveal cryptic structure within either of those “stocks”.
- Using all the data for all three years, conduct a principal components analysis as described in Patterson *et al*. (2006), which provides a formal statistical test of the number of gene pools in a mixed sample.

B.8 (H) Use the DNA already extracted from the 2005 samples to generate microsatellite data comparable to those that are available for the 2012-2014 samples. This will provide a multi-generation perspective on the stability of the mixing pattern of putative stocks seen in the more recent samples.

B.9 (H) Establish a group under the auspices of ECOFISH to review the GeoPop model in greater depth. This review should consider whether the model output is consistent with the raw survey data (and any commercial catch-rate data, even if such data cannot be included in the GeoPop analyses). It should then use the model output to identify stock structure hypotheses, including potential migration routes for putative stocks.

B.10 (H) Although microsatellite data for *M. paradoxus* do not provide evidence for more than a single stock, results of a “factorial component” analyses conducted by Henriques *et al.* (unpublished data) show a few individuals as substantial outliers. Is it possible that those are mis-identified *M. capensis*? Repeating the same analyses with simulated data for a single, random-mating population would provide a useful context for interpreting this result.

B.11 (M) Efforts should be made to determine whether historical collections of scales or otoliths exist. Several published examples exist where scientists have been able to extract DNA from samples up to a century old, and this can provide a very valuable temporal dimension to information related to stock structure.

B.12 (M) Develop next-generation DNA sequencing markers to further evaluate evidence for stock structure in *M. capensis* and *M. paradoxus*. With 10^3 to 10^5 new markers, it should be possible to considerably increase power to detect weak population structure. Furthermore, it might be possible to identify markers in or closely linked to genes under selection, which would provide information about the extent of local adaptation.

B.13 (L) The ability to develop and compare stock structure hypothesis would be enhanced if spatial data on age and growth and maturity curves were available. In addition, the use of parasite studies and the application of otolith microchemistry approaches, morphometric analyses and meristic methods have the potential to inform the selection and weighting of stock structure hypotheses. However, the data required are currently not available. There is a consequently a need to evaluate (and implement) the sampling schemes that could inform future discussions regarding stock structure.

Population dynamics modelling

B.14 (*) The proposed schedule for model development in MARAM/IWS/DEC14/Hake/P10 is an appropriate way to move forward. However, taking account of mixing in a "fleets as areas" model will be difficult. Consequently, it may be best to move from Stage 1 directly to Stage 3.

B.18 (H) Development of a spatial model for hake requires catch data split to species, and ideally to depth strata. Such data already exist for South Africa but were not available for Namibia. A group of scientists, and others with appropriate expertise, should be convened under the auspices of BCC to develop catch series by the spatial strata in the spatial models.

B.19 (H) The current fit of the hake explicit movement model (MARAM/IWS/DEC14/Hake/P5) to the survey data by stratum is very poor. An evaluation of whether reasonable fits to these data are possible in principle should be conducted by (a) fitting a fleets-as-areas model to data disaggregated to the same extent as are used in the spatial model, and (b) increasing the weight applied to the fits to the survey data in the spatial model.

B.20 (H) Some of the predicted movement directions in the movement model appear to be biologically unrealistic. A group of scientists should be established to provide guidelines for the appropriate qualitative structure of the movement matrices, such as that movement is towards deeper water with age.

B.21 (H) Identify the spatial strata that need to be implemented for the full set of movement models. This information is needed to allow the data used for fitting purposes (survey, catch, composition) to be extracted for use in these models.

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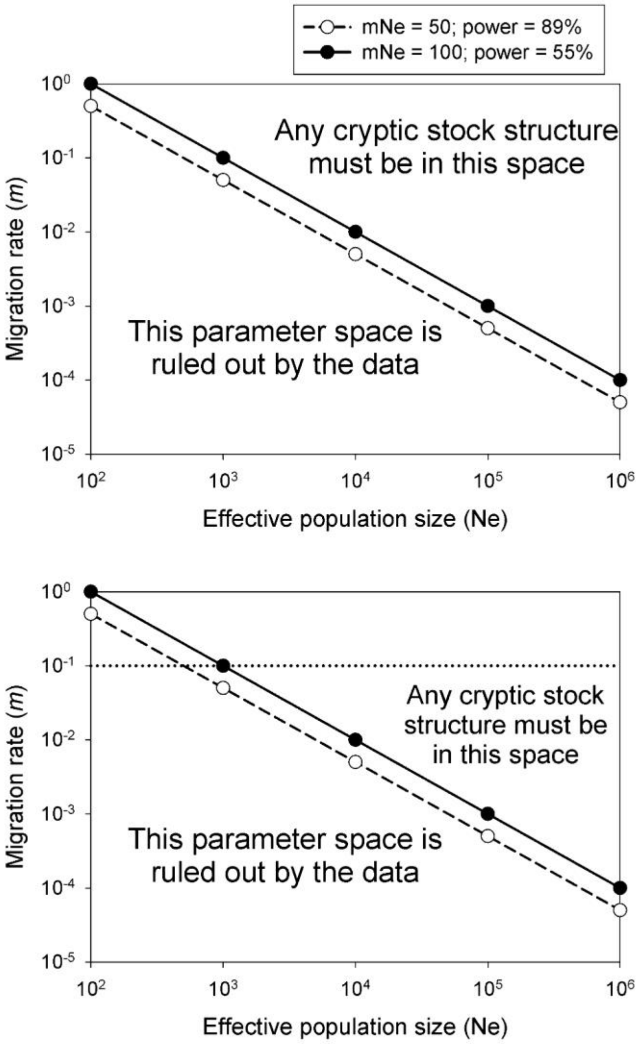

Figure 2. Graphical depiction of the parameter space that is and is not compatible with more than one stock of *M. paradoxus*. The lines plot combinations of effective population size (*Ne*) and migration rate (*m*) that are expected to produce *Fst* values of 0.005 (*mNe* = 50) and 0.0025 (*mNe* = 100). The values from the power analysis come from Henriques *et al.* (unpublished data). The parameter space below the lines can be ruled out as implausible with specified probabilities based on genetic data. The bottom figure shows that the parameter space consistent with multiple stocks is further constrained if one assumes that separate stocks must exchange migrants at a rate below a certain threshold (in this case $m = 0.1 = 10\%$ per generation). Two caveats about the above relationships between *m*, *Ne*, and power: 1) They are based on a widely-used but somewhat simplistic relationship between *mNe* and *Fst* [$E(Fst) \approx 1/(1+4mNe)$] developed by Wright (1931). The relationships shown above are probably qualitatively robust but caution should be used in quantitative applications. 2) Wright's relationship assumes that an equilibrium has been reached between the homogenizing effects of migration (*m*) and divergence due to genetic drift (indexed by *Ne*). Under an alternative scenario, *Fst* can be modeled as a value that increases over time in a system in which populations are completely isolated. A comparable figure could be developed based on the relationship $E(Fst) \approx t/(2Ne)$, where *t* is elapsed time in generations since the populations diverged. For example, $Fst = 0.01$, which produced 100% power according to Henriques *et al.* (unpublished data) , could be achieved if 2 populations of size $Ne = 1000$ each were isolated for 20 generations, if two populations of size 100,000 were isolated for 2000 generations, or any other combination of *t* and *Ne* that satisfied the above relationship. This means that very large populations might have to be isolated for large numbers of generations before a detectable signal of genetic differentiation develops.