

## Some inferences from an overview of genetic and other information regarding some key aspects of *M. paradoxus* stock structure off South Africa and Namibia

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### Summary

Genetic data, while compatible with the hypothesis of a single *M. paradoxus* stock off Namibia and South Africa, does not exclude the possibility of two *M. paradoxus* stocks with a soft boundary somewhere between Saldanha Bay and the Orange River. The same conclusion follows from the survey catch-at-length distribution information available. Thus, while a single *M. paradoxus* stock hypothesis likely remains the most plausible, the possibility of two stocks of this species (with no need for their joint management by South Africa and Namibia) remains. Some suggestions are made for further work in the short term which may throw more light on this issue.

### Introduction

Three key documents with discussion and/or results pertinent to this topic would seem to be Dunn *et al.* (2014), Henriques *et al.* (2016) and Stromme *et al.* (2016). Excerpts from these documents and their implications are discussed below.

### A summary from genetics

A key conclusion from the 2014 international review of hake stock structure by Dunn *et al.* (2014), which examined the available data (particularly genetics) related to stock structure was that: “*The most likely hypothesis is that there is a single [breeding] stock off Namibia and South Africa*”. Other pertinent comments in that report are:

The 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.

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).

The stock structure hypotheses that should be included the second stage of future modelling work include that for *M. paradoxus*, one or more multi-stock hypotheses based on the results of the GeoPop analyses. 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.

In a document published subsequent to that report, Henriques *et al.* (2015) state that: “Assessment of contemporary patterns of genetic differentiation based on microsatellite loci revealed evidence of panmixia in *M. paradoxus*”. Although some mtDNA variation had been observed, the authors ascribed this to the mechanism suggested above; importantly this variability seemed temporal – there was no consistent spatial pattern.

### Is the possibility of more than one *M. paradoxus* stock excluded by the genetics data?

Figure 2 of Dunn *et al.* (2014), reproduced below, addresses this question (though in a manner that is not exact, given the simplicity of the underlying model used). To explain the lower of the two plots, consider a fixed value of the effective population size ( $N_e$ ), and the implications of different migration rates ( $m$ ) between potentially two stocks. If  $m$  is sufficiently high (above the horizontal dotted line in that Figure), the fact that two breeding stocks are actually present would not matter from a management viewpoint, as interchanges between the two would be sufficiently rapid that their demographic behaviour would be indistinguishable from that of a single population (because depletion of one by harvesting would simply be adjusted by immigration from the other to re-equilibrate the two).

The inclined lines on the Figure indicate the power of what the microsatellite DNA data then available were able to distinguish. Below those lines the migration rate is sufficiently small that these data would be able to determine that more than one than one stock was present if this were the case. However, above those lines, two stocks with independent dynamics at a demographic (and hence relevant-to-management) level could be present, but such genetic data would not be able to detect that presence.

At the time the discussions at the 2014 international workshop took place, no estimate of  $N_e$  for hake was available. However, such estimates were subsequently developed, and are reported in Table 4 of Henriques *et al.* (2016), which is reproduced below. These suggest that the value of  $N_e$  for *M. paradoxus* is of the order of  $10^3$  to  $10^4$ , or higher. **Hence the effective population size ( $N_e$ ) for *M. paradoxus* lies in a range where two demographically independent stocks of the species could be present, but the then existing genetic data would not be able to differentiate them.**

### Other information

Fig. 2 from Stromme *et al.* (2016), based on length distribution data collected over a long time series of trans-boundary research survey cruises in the January-February period each year, suggests a single smaller fish nursery are for the *M. paradoxus* fished off both South Africa and Namibia which is adjacent to the South African coast between Saldanha and Hondeklip bays off South Africa, with the larger *M. paradoxus* found both to the north (extending into Namibian waters) and south of that area.

Clearly this is compatible with the hypothesis of a single *M. paradoxus* stock. However, it doesn't exclude other possibilities, such as two separate "north - Namibian" and "south - South Africa" *M. paradoxus* stocks with a common nursery area, each with movement dynamics as indicated by the arrows that have been superimposed on that Fig. 2 plot. Note also that although Stromme *et al.* (2016) report that *M. paradoxus* spawning has been observed only between Elands Bay and the Agulhas Bank, which are off south Africa and further south than the nursery area suggested, their observations apply only to a limited (the months of January-February) period of the year.

The South African fishery for hake takes place in the main fairly close to Cape Town, with little fishing in the area in Fig. 2 indicated as the *M. paradoxus* nursery area, so that the hypothesis that a "north-Namibian" *M. paradoxus* stock is virtually unaffected by the South African hake fishery is not inconsistent with the results presented by Stromme *et al.* (2016).

### In conclusion

While the conclusion offered by Dunn *et al.* (2014) that the hypothesis of a single stock of *M. paradoxus* off South Africa and Namibia is the most plausible probably remains the case, the commentary above suggests that a two-stock hypothesis for *M. paradoxus* also remains a plausible alternative. This hypothesis could, in turn, be compatible with the absence of any need to manage the South African and Namibian hake fisheries jointly (at least as far as the *M. paradoxus* component is concerned, though (in context) it is the *M. paradoxus* species and its possible stock structure that most motivates arguments for a potential need for joint management of the two fisheries).

For the near future, further work that might assist towards resolution of this debate would be use of the larger genetic datasets now available, and quantification of the proportion of the South African hake catch in various latitudinal bands between Saldahna Bay and the Orange River (to specify more accurately what South Africa might be catching from a potential “north – Namibian” *M. paradoxus* stock).

### **Acknowledgements**

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### **References**

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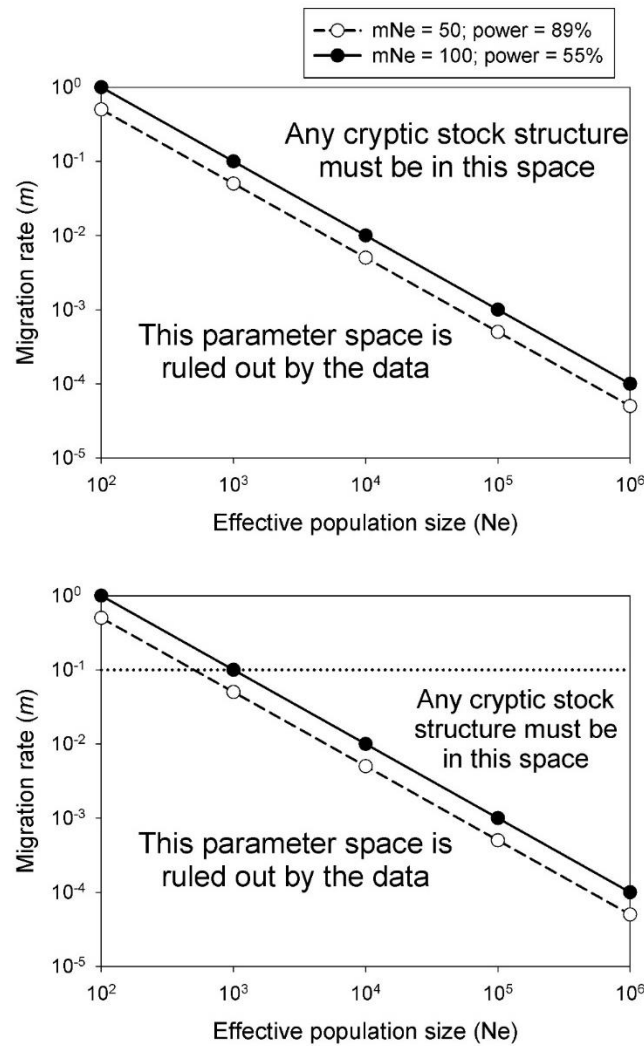
Figure 2 from Dunn *et al.* (2014)

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  $F_{st}$  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  $F_{st}$  [ $E(F_{st}) \approx 1/(1+4mNe)$ ] 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,  $F_{st}$  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  $E(F_{st}) \approx t/(2Ne)$ , where  $t$  is elapsed time in generations since the populations diverged. For example,  $F_{st} = 0.01$ , 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.

Table 4 from Henriques *et al.* (2016)

**Table 4** Estimates of current effective population size for populations of *M. paradoxus* and *M. capensis*, per year, based on nine microsatellite loci, for two critical allelic frequencies: 2% and 1% (95% confidence interval)

Species/Population	2012		2013		2014		Overall	
	0.02	0.01	0.02	0.01	0.02	0.01	0.02	0.01
<i>M. paradoxus</i>	4221 (1244-∞)	3759 (1194-∞)	∞	7177 (1437-∞)	15701 (1407-∞)	∞	10722 (2283-∞)	16730 (3274-∞)
<i>M. capensis</i> NAM	3176 (283-∞)	∞	2520 (330-∞)	4957 (271-∞)	331 (161-3546)	485 (263-2117)	2077 (709-∞)	4559 (1504-∞)
<i>M. capensis</i> SA	606 (297-6172)	1359 (622-∞)	410 (234-1169)	622 (335-2587)	1695 (377-∞)	485 (253-2626)	8870 (1777-∞)	7158 (2227-∞)

Figure 2 from Stromme *et al.* (2016)

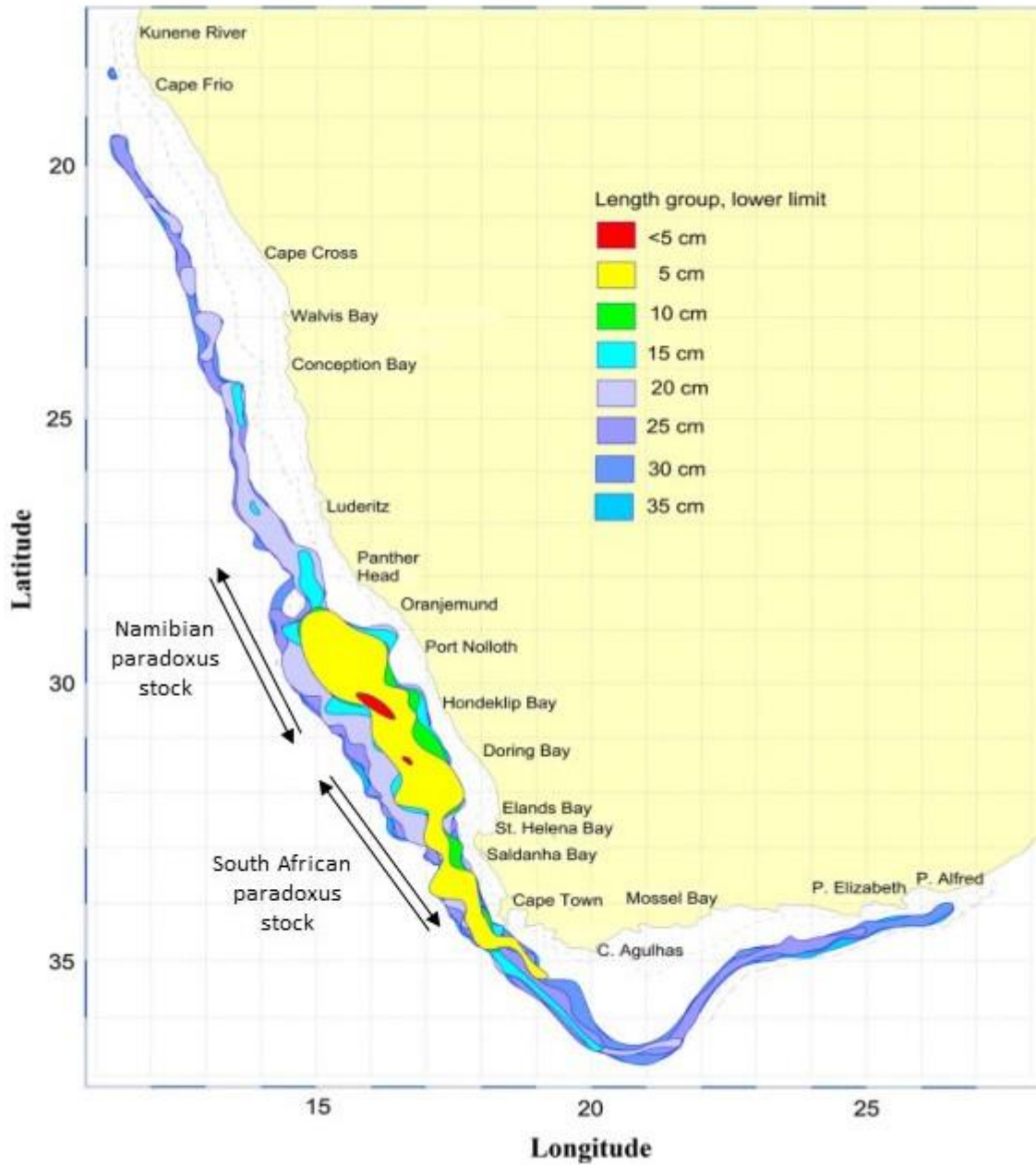


Fig. 2 Transboundary distribution of *Merluccius paradoxus* in January–February 2010 by size classes. The smaller fish are overlaid on the bigger fish, demonstrating expansion from a central area (Saldanha–Hondeklip Bay). Note that the arrows and associated labelling inside the plot are overlays on top of the original Figure.