On the plausibility of stock structure hypotheses of western North Pacific common minke whale

Luis A. Pastene¹, Jung Youn Park², An Yong Rock² and Naohisa Kanda¹

¹The Institute of Cetacean Research, Toyomi 4-5, Chuo-ku, Tokyo 104-0055, Japan 2Biotechnology Research Center, National Fisheries Research and Development Institute, Busan, Korea

ABSTRACT

To assist the IWC SC in the assignment of plausibility to hypotheses on stock structure in the western North Pacific common minke whale we summarized and discussed here two kinds of information a) the work conducted since 2003 to refine previous hypotheses based on O and J stocks, which derived into current Hypotheses A and B, and b) our view and differences regarding the main arguments presented in support of Hypothesis C (Wade and Baker, 2011). There are two components that separate those hypotheses, first the question of J/O against the JW/JE and OW/OE sub-divisions, and second the occurrence or not of a different stock in the Yellow Sea (Y stock). The first component separates Hypotheses A and B from Hypothesis C, the second one separate Hypothesis A from Hypotheses B and C. Regarding the first component current Hypotheses A and B were refined based on new genetic analyses that followed a process and recommendations from the IWC SC through the years, e.g. genetic separation of J/O stocks, hypothesis testing on separated J and O stock samples, examination of the statistical power, etc. In contrast, Hypothesis C that has to demonstrate division into JW/JE in the J stock and OW/OE in the O stock, derived from genetic analyses conducted on total samples (pooled samples of the O and J stocks), and no analytical effort was made to discriminate further the samples. Following advice from the IWC SC several non-genetic data were examined by the proponents of Hypotheses A and B and comparative analyses were conducted separately for J and O stock samples. Despite that the proponents of Hypothesis C argued initially that several non-genetic data supported their division into JW/JE and OW/OE, finally the only evidence cited by those proponents was conception date, which is not a strong argument as explained in this document. Responding to recommendations from the IWC SC for specific analyses is important. One of the most relevant recommendations from the IWC SC was to conduct analyses separately for J and O stock samples. The proponents of Hypotheses A and B and other SC workers did. The proponents of Hypothesis C did not. We believe that further analyses and scientific evidences are necessary for the actual use of Hypothesis C in the RMP Implementation. Regarding to the second component, we can not deny the possibility of additional structure in the Yellow Sea (e.g. Y stock), however the current scientific evidences (conception date and microsatellite) are weak and much more work is required on those data to confirm the possibility of additional structure. Therefore we believe that the plausibility of Hypothesis A should be higher than that of Hypothesis B.

KEYWORDS: COMMON MINKE WHALES, *IMPLEMENTATION*, WESTERN NORTH PACIFIC, STOCK STRUCTURE HYPOTHESES, PLAUSIBILITY

INTRODUCTION

Three stock structure hypotheses (Hypotheses A, B and C) were proposed and specified on the new sub-areas (Figure 1) for the current western North Pacific common minke whale *Implementation*.

Stock structure hypotheses A and B are refinement of the previous Hypotheses A and B of the 2003 *Implementation*, with some elements of these hypotheses (e.g. Y stock in Hypothesis B) mimicing some of the aspects of the sensitivity tests considered during the 2003 *Implementation* (IWC, 2004). A difference between current and previous Hypotheses A/B is the more extensive distribution of J stock animals in the Pacific side of Japan and the spatial and temporal mixing of J and O stock animals in sub-areas 7CS and 7CN is now more documented under Hypotheses A and B. Stock structure Hypothesis C is a new one, derived basically from genetic analyses on pooled samples of the J and O stocks, which proposes new stocks e.g. JW and JE and OW and OE.

Descriptions of the three hypotheses were given in Appendix F of IWC (2011a). Our summary of the scientific evidences pro- and against those hypotheses and our plausibility ranking were already presented during the 2011 IWC SC meeting (Pastene and Hatanaka, 2011; Pastene *et al.*, 2011). We concluded that Hypothesis A should be assigned a 'High' plausibility ranking and Hypotheses B and C a 'Low' ranking (Pastene *et al.*, 2011).

To assist the IWC SC in the assigning of plausibility to stock structure hypotheses at the 2012 IWC SC meeting we summarized and discussed here two kind of information a) the analytical work conducted since 2003 to refine previous hypotheses based on O and J stocks, which derived into the current Hypotheses A and B, and b) our view and differences regarding the main arguments presented in support of Hypothesis C (based on the latest paper by Wade and Baker, 2011).

There are two main components that separate those hypotheses, first the question of J/O against the JW/JE and OW/OE sub-divisions, and second the occurrence or not of a different stock in the Yellow Sea (Y stock). The first component separates Hypotheses A and B from Hypothesis C, the second one separates Hypothesis A from Hypotheses B and C. The first component is examined in the next two sections below while the second component is examined in the third section below.

Regarding the first component in 2010 the IWC SC noted that much of the remaining disagreement about competing stock structure hypotheses centres on the question of whether minke whales in subarea 7 and 2 represent a mixture of 'O' and 'J' stock animals or a single stock with intermediate characteristics. It agreed that trying to resolve this issue should be a top priority using both genetic and non-genetic data (IWC, 2011b).

REFINEMENT OF PREVIOUS HYPOTHESIS BASED ON O AND J STOCKS

Table 1 shows examples of genetic analyses conducted by Japanese scientists to examine and refine previous hypotheses based on O and J stocks, which followed advices from the IWC SC. Results of those analyses were used to propose the current Hypotheses A and B in the current *Implementation*. Detailed results of these analyses were already presented in Appendix F of IWC (2011a) and Pastene *et al.* (2011). The next paragraphs summarize only the key elements.

Genetic analyses conducted separately for J and O stocks

During the previous *Implementation* of western North Pacific common minke whale, the IWC SC had recommended genetic analyses separately for J and O stocks, and specifically recommended the use of alternative methods for exclusion of 'J' stock animals (IWC, 2003). This would facilitate the interpretation of results. Then the first task by Japanese scientists was to identify a genetic method able to discriminate individual J and O stocks.

Kanda *et al.* (2009a) used 16 microsatellite loci and the program STRUCTURE to discriminate individual J and O stocks in a large sample from JARPN and JARPN II and from by-catches (n=2,542). The animals with the membership probability of over 90% for either two stocks were assigned as 'pure' individuals. A total of 2,302 animals (91%) were assigned as the pure individual to the either stock (770 to the J stock and 1,532 to the O stock). There were a 9% of unassigned animals.

During the 2009 annual meeting the IWC SC welcomed these results and recommended several additional analyses based on STRUCTURE, particularly to elucidate the problem of 'unassigned' animals (IWC, 2010a). Some of the recommended analyses were made and presented to the 2010 IWC SC by Kanda *et al.* (2010a). Basically the results of the additional analyses failed to detect evidence of additional stock structure and they suggested that unassigned individuals were probably either J or O stocks.

After examining the extensive discussions by the IWC SC on this particular topic we believe that there is agreement in the Committee that the approach used by Kanda *et al.* (2009a) is useful to assign individuals to stock differentiated at the level of O and J stocks (e.g. Fst= 0.04-0.05) and that there is remaining questions on whether the approach can assign individuals to less differentiated stocks. Therefore we consider that any genetic study focused to investigate additional genetic structure within the J and O stocks should start separating the O and J stocks animals as in Kanda *et al.* (2009a). Other more sensitive approaches could be tried then on the discriminated samples of J and O stock animals.

For example several genetic analyses based on hypothesis testing and mtDNA and microsatellite were conducted separately for O and J stocks (Table 1; see also Appendix F of IWC, 2011a and Pastene *et al.*, 2011). None of these analyses showed significant heterogeneity within the J and O stock samples. Another example is the Principal Component Analysis (PCA) used by Gaggiotti and Gascuel (2011), which was applied on samples of J and O stocks discriminated by the approach of Kanda *et al.* (2009a) (see discussion on the PCA results below).

However despite these methodological advances in separating O and J stocks animals, which were recognized by the IWC SC, the proponents of Hypothesis C conducted genetic analyses based on pooled samples of O and J stocks. Interpretations of results derived from such analyses are very difficult (see section below). No analytical effort was made by those proponents to demonstrate subdivision in the J and O stocks using the genetic data.

Examination of the statistical power

The IWC SC had recommended analysis of the statistical power of the hypothesis testing (IWC, 2010b). Japanese scientists presented results of the power analyses at the 2009 IWC SC annual meeting (Kanda *et al.*, 2009b). The study suggested high statistical power providing confidence to the conclusion of a single O stock. The IWC SC noted that the work was a direct response to a suggestion by the JARPN II Panel (IWC, 2010b), and thanked the authors for the substantial work involved in conducting the power analyses and agreed that the results represented a very valuable contribution (IWC 2010a).

Examination of non-genetic information for O and J stock

Other of the recommendations of the IWC SC was the analyses of non-genetic data in addition to genetic data. The IWC SC had made this recommendation several times, the last being in 2010 (IWC, 2011b). Several analyses of non-genetic data (morphometric, flipper color pattern, fluke color pattern, conception date) were conducted separately for J and O stock samples (Table 1). None of these analyses showed significant heterogeneity within the J and O stocks although in some cases the sample size was small (see results in Appendix F of IWC, 2011a and Pastene *et al.*, 2011).

EXAMINING THE SCIENTIFIC BASIS FOR THE SUB-DIVISION OF JW/JE AND OW/OE STOCKS

Spatial genetic heterogeneity of pooled J and O stock samples

The analytical approach used by the proponents of Hypothesis C to examine genetic data was different from that followed by the proponents of Hypotheses A and B and other IWC SC workers. The proposal for the division of the J stock into JW and JE and of the O stock into OW and OE was based on genetic analyses around the Japanese coast that considered all samples of O and J stocks pooled.

Our fundamental concern here is that the proponents of Hypothesis C did not take advantage of the approach previously used to separate J and O stock animals. As noted earlier there is agreement that the approach used (STRUCTURE) can assign individuals to stocks differentiated at the level of J and O stock. New genetic analyses could start from this point as Gaggiotti and Gascuel (2011) did. As a consequence of using pooled samples for the genetic analyses the proposal of JW/JE and OW/OE is not based on hard genetic information, and then the proposal is highly speculative.

As noted above the mtDNA analysis by Baker *et al.* (2010) and the microsatellite analysis by Slikas and Baker (2010) in the Pacific side of Japan were conducted for all J and O stock animals combined. As expected several 'significant' differences among sub-areas were found. The proponents of Hypothesis C provided two explanations for their results, one was that the significant differences found derive from differing proportion of just two stocks (J and O stocks) in each of the sub-areas examined, the other was that there are differentiated stocks in these sub-areas (Wade and Baker, 2011). They finally favored the latter explanation but conducted no further analyses or showed no evidence to justify such preference.

In favoring the second explanation of additional stock structure, the proponents of Hypothesis C alleged that allozyme and microsatellite allele frequencies only showed strong evidence for mixing of stocks (evidenced by HW disequilibrium) along the Korean coast of the Sea of Japan, and north of Hokkaido and that the areas in the Pacific side of Japan do not show strong evidence for mixing of stocks (e.g. J and O stocks) (Wade and Baker, 2011).

Notwithstanding our fundamental differences on the approach used in the genetic analysis by the proponents of Hypothesis C, we discussed below the interpretation of the proponents of Hypothesis C on the results of HW tests.

Results of the HW disequilibrium test

The argument given by the proponents of Hypothesis C is based on the allozyme results obtained by Wada (1991) who found no Hardy-Weinberg deviations in samples from small-type coastal whaling sub-area 7W (current 7CS, 7CN, 7WR) based on a single locus. According to the proponents of Hypothesis C, this result provides no support for the mixing of two stocks (J and O stocks) in that sub-area.

However Kanda *et al.* (2011a) examined a large number of samples from recent by-catch and JARPN/JARPN II samples in the same sub-area 7W (n= 1,106) with 16 microsatellite loci. Four of the 16 loci showed significant deviation from the Hardy-Weinberg expected genotypic proportion. The same result was found for all loci combined. The authors noted that these significant differences were due to the homozygote excess, which support the mixture of two stocks in that sub-area (including 7CS, 7CN and 7WR).

We believe that, in examining the plausibility of hypotheses, the IWC SC should discuss and conclude on these two different results. After all the results of Wada (1991) of no HW deviation in sub-areas 7W is being used by the proponents of Hypothesis C in support of their preferred explanation for their genetic results (e.g. that additional stocks occur in that sub-area).

One of the elements that the IWC SC could consider is the distribution of the samples used in both analyses. We know for sure about the distribution of the samples used in the analysis by Kanda *et al.* (2011a), which occur from very near the coast to more offshore waters. On the other hand there is agreement in the Committee that the distribution of J stock animals is within the 10n. miles from the coast, but concentrated mainly within 3n. miles (Kanda *et al.*, 2011b). The results of Wada (1991) could be explained by either the few commercial catches taken in very coastal waters, where the fraction of J stock animals is high (see maps in Kanda *et al.*, 2011b), or simply by the low power of the allozyme analysis.

Other genetic analyses that apparently support Hypothesis C

Gaggiotti and Gascuel (2011) used PCA to study the heterogeneity within J and O stock animals, respectively, as defined by STRUCTURE analyses of Kanda *et al.* (2009a). Two clusters separated clearly J and O stock animals. The authors found some degree of heterogeneity within the O stock samples, but none between J stock samples from the east and west coasts of Japan.

Whether or not such heterogeneity within the O stock could be associated to OW and OE stocks of Hypothesis C is unclear as the precise geographical specification is not possible based on PCA analysis (IWC, 2011c). Furthermore heterogeneity detected is not necessarily related to additional stock structure. It could be explained for example for pairs of closely related samples (kinship).

Gaggiotti and Gascuel (2011) noted that the structuring within the O stock was not related with body length and geographical position, and that such results do not have clear biological interpretation.

We believe that the results by Gaggiotti and Gascuel (2011) on the O stock, at least at this stage, can not be used in support of the idea of additional structure within this stock as proposed in Hypothesis C.

'Pure stock' and mixing proportion

Proponents of different hypotheses have defined 'pure' stock samples with the aim of estimating mixing proportion in sub-areas. In the case of Hypothesis C the 'pure' samples for the OW and JE stocks is as follow:

OW: whales in sub-area 7CN in June (>8.8n. miles) OE: whales in sub-area 8 and 9 (all months) (excluding 9W in 1995) JW: whales in sub-area 6E (all months) JE: whales in sub-area 2C in July-December First there is no scientific evidence supporting these definitions as 'pure' stocks, even thought as a proxy. If these definitions represent the best proxy for the 'pure' stocks, then at least significant differences should be found in the comparison between OW/OE and JW/JE. However this is not the case.

Results of a heterogeneity test for these 'pure' samples based on 16 microsatellites were the following: OW against OE (P=0.554); JW against JE (P=0.393). The implication of this result is that the estimates of mixing proportion in sub-areas e.g. 7WR (OW and OE mixing in April-September) or in sub-area 11 (mixing of JW, OW and OE in April-September), are of limited value as there is not significant differences among the baseline samples.

In summary we believe that there are no strong or conclusive genetic information supporting the JW/JE and OW/OE divisions.

Non-genetic data

Conception date

Initially several non-genetic data were presented in support of the stock divisions proposed under Hypothesis C (Table 1 in Wade and Baker, 2010). However recently, the conception date is the only non-genetic data mentioned by the proponents of Hypothesis C to support their hypothesis (Wade and Baker, 2011).

Regarding conception date, initially Wade and Baker (2010) claimed that different J stocks distribute on each side of Japan because whales in the Sea of Japan had bimodal (autumn and winter) distribution of conception date and single winter peak in Sanriku. Bando *et al.* (2010) demonstrated that J stock whales in sub-area 7W have also bimodal distribution of conception dates. Furthermore this author showed that the conception date of O stock animals in sub-area 7W and sub-areas 7E, 8 and 9 have similar conception date (winter).

Recently the proponents of Hypothesis C noted that under their hypothesis the rationale for JE vs JW does not depend heavily on differences in conception dates (IWC, 2011c).

Other non-genetic data

Another of the questions that the proponents of Hypothesis C have failed to respond appropriately is on the completeness of their proposed stocks. Analyses of length composition and sex ratio in the Pacific side of Japan and Sea of Japan were conducted separately for J and O stocks (Kanda *et al.*, 2010b). At the Pacific side of Japan O stock immature animals distributed mainly in coastal areas whereas O stock mature animals distribute mainly in offshore areas, which is consistent with a single O stock with spatial segregation by sex and maturity classes. J stock animals from the Sea of Japan and Pacific coast showed quite similar characteristics in the data. It should be noted that these analyses were based on large sample sizes.

The proponents of Hypothesis C suggested that stock OW and JE distributed along the Japanese coast year round. The question here is how is it possible that a stock will be composed by a single reproductive class, only immature animals in this case? In the case of their OE stock, how is it possible that a stock will be composed only by mature animals?

In summary contrary to initial allegations by the proponents of Hypothesis C that there are several nongenetic data supporting their hypothesis, our conclusion is that there is no non-genetic data supporting the division of JW/JE and OW/OE.

EXAMINING THE SCIENTIFIC BASIS FOR THE Y STOCK

Data that apparently support of additional stock structure in the Yellow Sea (Y stock) come from genetics and conception date.

There is a evidence of microsatellite differences between the Yellow Sea and Sea of Japan whales in winter (Kanda *et al.*, 2010a) and for HW disequilibrium along the Korean coast of the Sea of Japan in summer (Slikas and Baker, 2011). However in the latter case the deviations was very strong compared to slight or not differences (based on *Fst*) found between sub-areas 5 (Yellow Sea) and 6 (Sea of Japan) for both mtDNA and microsatellites. We believe that the genetic evidences are very preliminary in

nature, and obviously additional work is required to get final conclusions on differences between the Yellow Sea and Sea of Japan. For example the differences in the results between the mtDNA and microsatellite should be appropriately interpreted. Also the strong deviation from HV equilibrium in relation to the very low *Fst* should be appropriately explained.

It has been suggested that the Yellow Sea have only fall conception dates whereas whales in the Sea of Japan have a mixture of both autumn and winter conception date (Wang, 1985). However the quality of the data used by this author has been questioned in that a number of small foetuses could have been missed in the commercial whaling samples (e.g. whales with conception date in winter could have been missed) (Bando, 2011). Without further information on the collection method of the samples used in Wang (1985) it will be very difficult to get a conclusion on the conception date for the whales in the Yellow Sea. The possibility of collecting new conception date data from stranded or incidentally caught common minke whales in the Yellow Sea should be considered and evaluated.

The IWC SC has put particular emphasis in the examination of the quality of the genetic data used for management advice. We believe that the quality of non-genetic data used for management advices should be also considered by the IWC SC.

CONCLUDING REMARKS

- Genetic analyses conducted by the proponents of Hypotheses A and B to refine their hypothesis of single J and O stocks followed a process and recommendations from the IWC SC through the years (see Table 1). The genetic analyses conducted by the proponents of Hypothesis C in support of their JW/JE and OW/OE sub-divisions were based on pooled samples of the J and O stocks, which are of limited utility.
- Because the nature of the genetic analyses by the proponents of Hypothesis C, several interpretations on stock structure of O and J stocks emerged. The proponents selected one of the interpretations (additional stock structure) but they did not provide a strong rational for such preference. The absence of HW disequilibrium in sub-area 7W based on allozyme data is not a strong argument for the reasons given in this document.
- Several non-genetic data were examined by the proponents of Hypotheses A and B, and comparative analyses were conducted within the J and O stock samples. Despite the fact that the proponents of Hypothesis C argued initially that several non-genetic data supported their JW/JE and OW/OE sub-divisions, finally the only evidence presented was conception date, which is not a strong argument for the reasons given in this document.
- While the possibility of the occurrence of stock Y in the Yellow Sea can not be denied at this stage, the genetic results are very preliminary and contradictory, and further analyses are necessary to confirm this possibility. Further the quality of conception date data available for the Yellow Sea should be further examined.
- Responding to recommendations from the IWC SC for specific analyses is important. One of the most relevant recommendations from the IWC SC was to conduct analyses separately for J and O stock samples. The proponents of Hypotheses A and B and other SC workers did. The proponents of Hypothesis C did not. We believe that further analyses and scientific evidences are necessary for the actual use of Hypothesis C in the RMP *Implementation*. Given the preliminary and contradictory nature of the available evidences on the Y stock, we believe that the plausibility of Hypothesis A should be higher than that of Hypothesis B.

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Table 1. Examples of analyses conducted following suggestions and recommendations from the IWC
SC to refine previous stock structure hypothesis based only on O and J stocks

Suggestions/recommendations from	Reference	Response	Reference
the IWC SC Conduct genetic analyses separately for J and O stock animals	IWC (2003)	Analyses with 17 loci and program STRUCTURE	Kanda et al. (2009a)
Conduct genetic analyses separately for J and O stock animals	IWC (2003)	Hypothesis testing on O stock samples (microsatellite; mtDNA)	Kanda <i>et al.</i> (2009b); Goto et al. (2009)
Conduct genetic analyses separately for J and O stock animals	IWC (2003)	Hypothesis testing on J stock samples (microsatellite; mtDNA)	Kanda <i>et al.</i> (2010a); Park <i>et al.</i> (2010)
Conduct additional STRUCTURE runs and Principal Coordinate Analyses (PCA)	IWC (2010a)	Additional STRUCTURE runs and PCA	Kanda <i>et al.</i> (2010a)
Conduct power analysis	IWC (2010b)	Statistical power for the hypothesis testing analysis on O stock based on microsatellites	Kanda <i>et al.</i> (2009b)
Conduct analyses on non-genetic data	IWC (2011b)	Morphometry, flipper color pattern, fluke color pattern, conception date	Hakamada and Bando (2009); Kanda <i>et al.</i> (2010c); Bando <i>et al.</i> (2010)

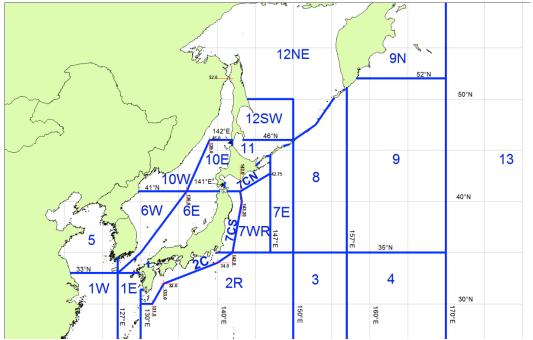


Figure 1. New sub-areas defined in the current RMP *Implementation* of western North Pacific common minke whales