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A synthesis of the work conducted on stock structure of western North Pacific common minke whale in response to recommendations from the IWC Scientific Committee

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ABSTRACT

A brief summary of the updated analyses on the stock structure of western North Pacific common minke whale conducted following recommendations from the IWC SC is presented. The refined analyses provide strong support to stock structure hypothesis A (proposing only J and O stocks), with a single O stock exhibiting a pattern of sexual and age segregation during migration. Hypothesis C (proposing two J stocks and two O stocks) is contradicted by the data, and consequently such hypothesis should now be rejected.

INTRODUCTION

Discussions on the stock structure of the western North Pacific common minke whale have taken place at the International Whaling Commission Scientific Committee (IWC SC) since 1993, with the latest discussions occurring during the JARPNII final review workshop (IWC, 2017a) and during the 2016 IWC SC Annual Meeting (IWC, 2017b).

Genetic analyses on stock structure by Japanese scientists have been conducted following specific recommendations from the JARPNII mid-term review (IWC, 2010). Results of the analyses were reviewed by the JARPNII final review workshop (IWC, 2017a) and by the subsequent IWC SC in 2016 (IWC, 2017b). The JARPNII final review workshop report states: 'agree that most of the recommendations and suggestions proposed in 2009 Panel have been *addressed…*' (IWC, 2017a).

This document presents a synthesis of the refined analyses conducted in response to the recommendations from the IWC SC, together with an evaluation of the plausibility of the stock structure hypotheses used in the latest RMP Implementation in 2013.

RESULTS

A large number of analyses on stock structure of the western North Pacific common minke whale have been conducted following recommendations from the JARPNII mid-term review (IWC, 2010) and JARPNII final review (IWC, 2017a) workshops.

Assignment test

Pastene *et al.* (2016a) examined a total of 4,275 western North Pacific common minke whales with a set of 16 microsatellite DNA loci and the program STRUCTURE (Pritchard *et al.*, 2000) to assign whales to either J or O stocks. Regarding the unassigned whales in the STRUCTURE analyses, a simple simulation exercise showed that the number of unassigned whales decreased with the increase in the number of microsatellite loci used, and that they were widely distributed geographically (Figures 1a and 1b). The authors concluded that the unassigned whales are not related with the occurrence of additional stock structure.

Tamura *et al.* (2017) reported some additional analyses on the unassigned whales. According to their report, a total of 217 common minke whales was selected among whales in sub-areas 6 and 7 in order to ensure a dataset with a nearly equal proportion of J and O stock whales, which were genotyped with additional 10 microsatellite loci (GATA97408, GATA91083, GATA43950, GATA38314, GATA6059012, GATA5946992, GATA6063862, GATA6064765, GATA5943219 and GATA5890064). PCR amplifications for these loci were performed under the same condition as in Pastene et al. (2016a). Thus, the total sample of 217 whales were genotyped at 26 microsatellite loci. The genotyped whales were assigned to J/O stocks by applying the Bayesian clustering approach to each dataset with randomly selected 8, 11, 14, 17, 20, 23 and 26 microsatellite loci in the program STRUCTURE. These analyses were conducted with ten independent runs for $K = 2$ without information on sampling locations. All runs were performed with 100,000 Markov chain Monte Carlo repetitions and 10,000 burn-in lengths using the admixture model which assumes whales may have mixed ancestry, and with correlated allele frequencies which assumes frequencies in the different stocks are likely to be similar due to migration or shared ancestry.

Whale assignment was conducted using respective membership probabilities of more than 90%, 80% and 70%, and the number of unassigned whales for each number of microsatellite loci was examined. As expected, the number of unassigned whales decreased with the increase in the number of microsatellite loci used (Figure 2), which confirms that the number of loci used for assignment to the J/O stock is one of factors leading to the unassigned individuals in the STRUCTURE analysis of common minke whale. This was also supported by the previous study suggesting that the accuracy of the assignments depends in practice on the number of loci (Prichard et al., 2000). For the three membership probabilities (70%, 80% and 90%), the trend was the same, with the trend for the 70% probability approaching zero when the number of loci was 26. It is reasonable to assume that the same result would be obtained for 80% and 90% probabilities if the number of loci is increased further.

Based on these results, the authors considered that only the whales assigned to the O stock with assignment probability greater than 90% could be used to investigate additional structure with the O stock using alternative analytical approaches.

Hypothesis testing

Pastene *et al.* (2016b) examined the genetic population structure of ‘O’ stock common minke whale in the western North Pacific based on mitochondrial DNA (mtDNA) control region sequencing (487bp) and microsatellite DNA (16 loci). Whales used in the tests of homogeneity were obtained during the surveys of the JARPN and JARPNII in sub-areas of the Pacific side of Japan between 1994 and 2014 (n= 2,071 for microsatellite; n=2,070 for mtDNA). Whales were assigned to the ‘O’ stock by the analysis of STRUCTURE presented in Pastene *et al.* (2016a). Tests based on both genetic markers and different grouping of the samples showed no evidence of sub-structuring in the ‘O’ stock common minke whale on the Pacific side of Japan. A simulation exercise showed that the statistical power of the homogeneity test was high.

DAPC analysis

A Discriminant Analysis of Principal Components (DAPC) based on the total whale samples used in Pastene *et al.* (2016a) showed clear differentiation between J and O stock whales but no evidence of sub-structuring within the O stock whales (Pastene *et al*., 2016b).

Morphometric analysis

Bando and Hakamada (2016) conducted a morphometric analysis to examine stock structure of western North Pacific common minke whales by using external measurement data collected during the 1994-2014 JARPN and JARPNII surveys. External measurements of mature males were first compared between O and J stock whales using the Analysis of Covariance (ANCOVA) and Discriminant Analysis (DA). Then only O stock whales were compared among sub-areas. These analyses showed that J stock whales had a longer head region compared to O stock ones but no significant differences were found within O stock whales.

Catch-at-age analysis

Kitakado and Maeda (2016) used catch-at-age data for common minke whales in the western North Pacific provided by the JARPN/JARPNII program to refine existing RMP *Implementation Simulation Trials* (*ISTs*) in a simple way so as to investigate the relative plausibility of the single and two (Ow and Oe) stock hypotheses for the O stock whales in the Pacific side of Japan. While the single stock scenario seems consistent with these age data, it is difficult to reconcile the two stock hypothesis with these data because of the relative absence of particularly younger whales in a supposedly separate discrete Oe stock.

Kinship analysis

Tiedemann *et al.* (2017) used a dataset of complete genotypes at 16 microsatellite loci of 4,554 North Pacific common minke whales, accompanied by mtDNA and biological information to infer Parent-Offspring relationships using a Maximum-Likelihood approach. A total of 75 pairs were confirmed, among them 26 pairs were mother-fetus. Most of the matches between sub-areas for O stock whales were between adult offshore fathers and coastal offspring, providing support to the previous view of sexual and age segregation during migration of this stock.

CONCLUSIONS

A substantial amount of new information on stock structure of common minke whale has been accumulated since the last *Implementation Review*, which was based on data collected until 2007. In particular this includes a larger number of new samples (around 1,700), new analytical procedures (DAPC, kinship, statistical power of the heterogeneity test, etc.), and the availability of age data.

Most of the analyses in the documents summarized above responded to recommendations made during the 2009 mid-term and the 2016 final reviews of JARPNII. A parsimonious and consistent interpretation of all different refined analyses and results points to a single O stock distributed from the Japanese coast to approximately 170°E. Also the available information provides evidence for a single J stock around Japan.

Stock structure hypothesis C, which proposes a coastal (Ow) and an offshore (Oe) stocks, is very difficult to reconcile with the current genetic and non-genetic evidence summarized above. In particular, this hypothesis cannot be reconciled with the finding of Tiedemann et al. (2017) showing a substantial number of Parent-Offspring matches between offshore (Oe) and coastal (Ow) areas.

Tables 1A and 1B show the number of Parent-Offspring pairs observed by sub-area pairings for O and J stock whales, respectively. The different colors show which sub-areas pairings are and are not consistent in terms of the Hypothesis C mixing matrices for the assumed Ow/Oe and Jw/Je stocks. Table 1A indicates 20 examples of Parent-Offspring pairs that are inconsistent with the Hypothesis C split of O whales into Ow and Oe stocks. Table 1B indicates two examples of Parent-Offspring pairs that are inconsistent with the Hypothesis C split of J whales into Jw and Je stocks.

Hypothesis C is also hardly consistent with the available age information (Kitakado and Maeda, 2016). The missing younger whales from the 'Oe stock' raise further serious questions about the plausibility of the hypothesis C.

In summary, the latest scientific information is consistent with a single J stock and a single O stock which is sexually segregated during the migration, with younger animals migrating mainly along the coast and mature animals mainly through offshore areas; this new evidence necessitates the rejection of Hypothesis C.

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Table 1A. The number of Parent-Offspring pairs of O stock whales within and between sub-areas (from Table 2 of Tiedemann *et al*., 2017). The blue color indicates those sub-area pairings that are not consistent with the Hypothesis C mixing matrices for the assumed Ow/Oe stocks; the orange color indicates those sub-areas that are not inconsistent with this hypothesis.[1]

O stock

	1E	2C	6E	7CN	7CS	7WR	7E	8	9	11
1E				1						
2C				1						
6E										
7CN				1	7	1		3	7	1
7CS					5	1		1	6	
7WR										
7E									2	
8									2	
9									1	
11										

Table 1B. The number of Parent-Offspring pairs of J stock whales within and between sub-areas (from Table 2 of Tiedemann *et al*., 2017). The blue color indicates those sub-area pairings that are not consistent with the Hypothesis C mixing matrices for the assumed Jw/Je stocks; the orange color indicates those sub-areas that are not inconsistent with this hypothesis.

J stock

	2C	6E	7CN	7CS
2C				
6E		4		2
7CN			1	
7CS				2

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[1] Rev1 differs from the original version of the paper only in that the color coding of the 2C-7CN cell and the 7CN-11 cells in Table 1a were changed from blue to orange.

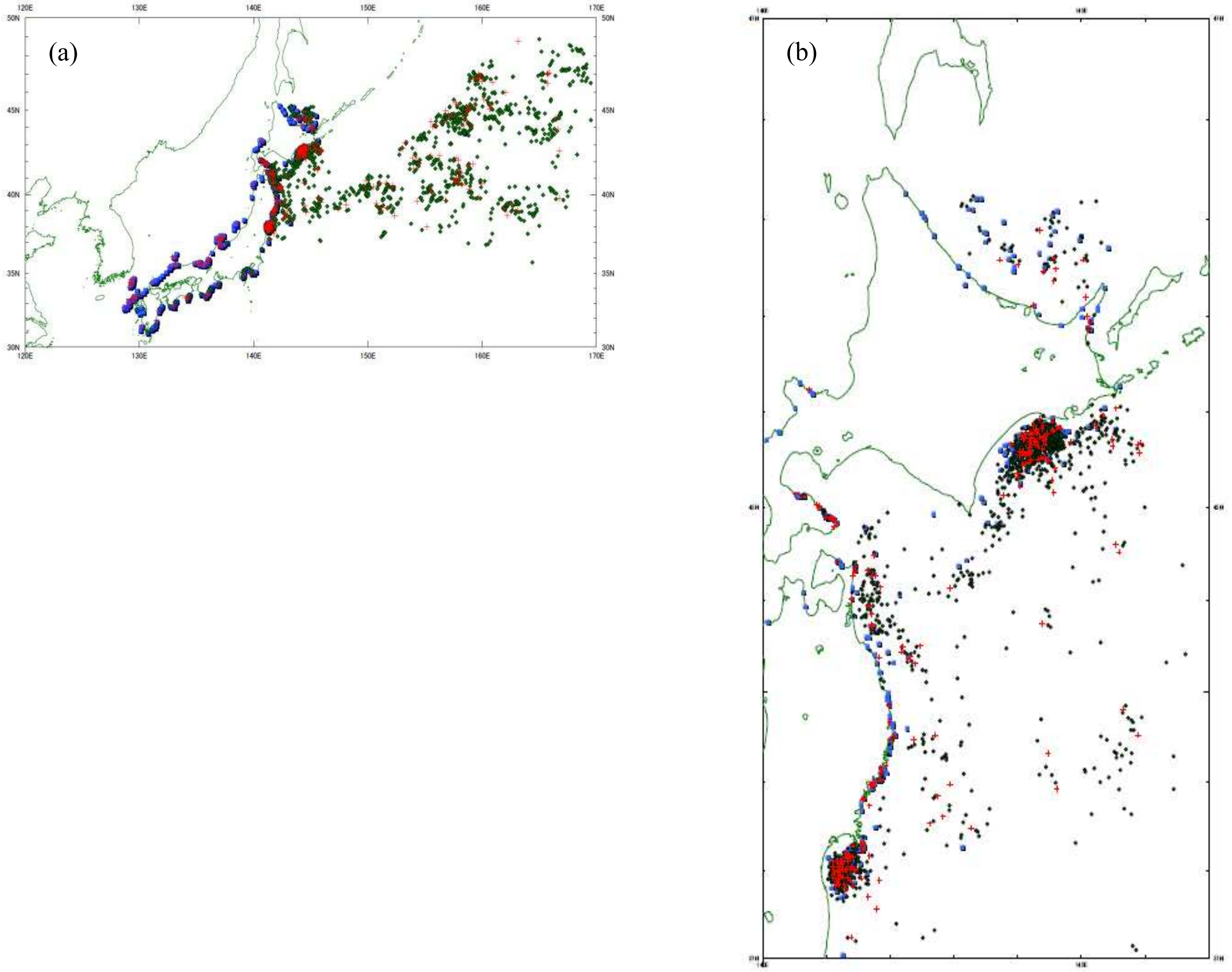

Figure 1. Locations of the common minke whales used in the different analyses on stock structure in the western North Pacific. Stock assignment is according to the STRUCTURE analysis: O-stock (green), J-stock (blue) and unassigned (red); (a) whole sampling area; (b) enlarged map of the coastal area

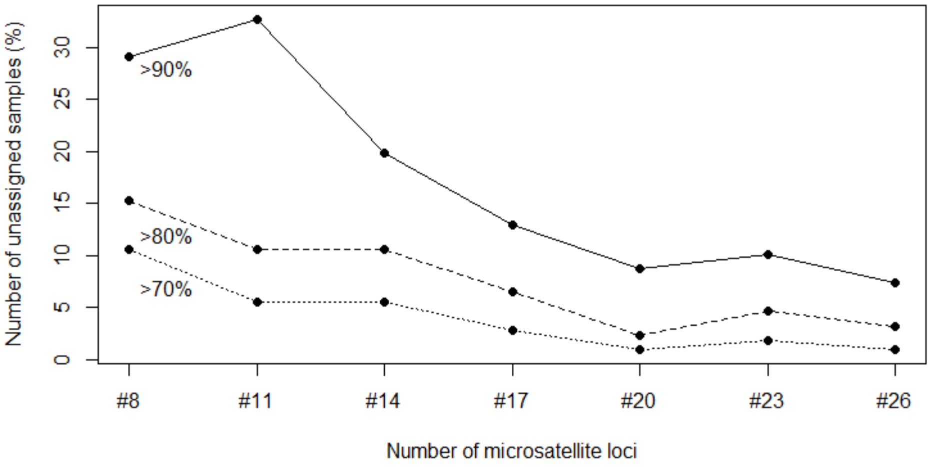

Figure 2. Change in the proportion of unassigned individuals in relation to the number of microsatellite loci used in each assignment criteria.