

High plausibility of Hypothesis III for stock structure of the western North Pacific minke

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ABSTRACT

As part of the *Implementation* process for North Pacific common minke whales, one of the primary tasks is to assign relative plausibility to stock structure hypotheses. These plausibility rankings determine the weight each hypotheses (or ‘trials’) are given in determining which RMP *variants* are acceptable (an RMP *variant* consists of specifications for where and when whaling is to occur). There are three stock structure hypotheses that were considered plausible at the first intercessional workshop: Hypothesis I) a stock in the Sea of Japan and Yellow Sea and one in the Pacific Ocean; Hypothesis II) one stock each in the Yellow Sea, Sea of Japan, and Pacific Ocean; and Hypothesis III) one stock in the Yellow Sea, one in the Sea of Japan, a ‘J-like’ stock along the Pacific coast of Japan, and two ‘O-like’ stocks in the Pacific nearshore and offshore waters. We reiterate that finding conclusive evidence to fully resolve the stock structure is unlikely given that no samples have been collected on the putative breeding grounds during winter when presumably ‘pure’ stocks would exist. Instead, the primary information on population structure comes from biological information on conception dates and genetic data collected from year-round coastal bycatch and seasonal commercial and scientific hunting during migration. Whales in the Yellow Sea only have autumn conception dates, whales in the Sea of Japan and along the Pacific coast of Japan have a mix of autumn and winter conception dates, and whales from the rest of the Pacific only have winter conception dates. Hypotheses II and III are both equally consistent with data on conception date, but Hypothesis I is not, and so is considered Low plausibility. Results from both mtDNA and microsatellite genotypes show significant differences in most pairwise comparisons between spatial areas. Of primary importance for distinguishing Hypotheses II and III are the significant differences seen between three regions in the Pacific Ocean – the coast of Japan, nearshore waters >10nm from the coast, and offshore waters, as well as the significant differences seen between either coast of Japan. One explanation proposed for these significant differences is that there are differing proportions of just two stocks (‘J-stock’ and ‘O-stock’) in each of these four areas. However, allozyme and microsatellite allele frequencies only show strong evidence for mixing of stocks in other regions (i.e., along the Korean coast of the Sea of Japan, and north of Hokkaido). The four areas in question do not show strong evidence for mixing of stocks. Therefore, we consider Hypothesis II to have Low plausibility. Only Hypothesis III, which has differentiated stocks in each of these four locations, is in agreement with the genetic data, and therefore has High plausibility.

INTRODUCTION

The SC is conducting an *Implementation* for North Pacific minke whales. Under the Revised Management Procedure, the outcome of an *Implementation* will be recommendations to the Commission regarding *variants* of the RMP that can be used to set commercial catch limits for the species in the designated *Region*. An RMP *variant* consists of specifications for where and when whaling is to occur and how the catch limits will be calculated (from what spatial areas abundance will be used in the CLA, and other details). Simulation models (*Implementation Simulation Trials* or ISTs) are used to test different *variants*. *Implementations* are conducted under a specified process that starts with a *pre-implementation assessment* followed by a two-year *Implementation* that includes two intercessional workshops and two annual meetings (IWC 2005).

For North Pacific common minke whales the IWC has completed the *pre-implementation assessment* and the first intercessional workshop. The workshop (held in Busan, Korea, December 2010) represented the last point in the *Implementation* process where new stock structure hypotheses could be specified. It was agreed there that three stock structure hypotheses were plausible: Hypothesis I) a stock in the Sea of Japan and Yellow Sea (‘J-stock’) and one in the Pacific Ocean (‘O-stock’); Hypothesis II) one stock each in the Yellow Sea (‘Y-stock’), Sea of Japan (‘J-stock’), and Pacific Ocean (‘O-stock’); and Hypothesis III) one stock in the Yellow Sea (‘Y-stock’), one in the Sea of Japan (‘JW-stock’), a ‘J-like’ stock along the Pacific coast of Japan (‘JE-stock’), and two ‘O-like’ stocks in the Pacific nearshore (‘OW-stock’) and offshore (‘OE-stock’) waters. One of the primary tasks at the first intercessional workshop was to create a Trial structure (essentially a combination of a multi-population model and agreed data inputs and assumptions) to use to test different *variants*. The important point in this process is that no single stock structure hypothesis is selected and considered ‘best’. Instead, the *variants* are tested across all stock structure hypotheses that are given ‘High’ or ‘Medium’ plausibility. This is done in order to ensure that accepted RMP *variants* are robust to uncertainty in stock structure. One of the primary tasks to accomplish at the first annual meeting (this meeting, SC64 in Panama) is to assign those relative plausibility ranks to the stock structure hypotheses (and all other hypotheses, such as MSYR rates). The relative plausibility

of each hypothesis (or trial) determines what criteria must be met when examining the results of those trials. In this paper we concisely summarize the evidence for the relative plausibility of each of the stock structure hypotheses.

PLAUSIBILITY OF EACH STOCK STRUCTURE HYPOTHESIS

We reiterate that finding conclusive evidence to fully resolve the stock structure of western North Pacific minke whales is unlikely given that no samples have been collected on the breeding grounds during winter when presumably ‘pure’ stocks would exist. Instead, the primary data on population structure comes from samples collected from year-round coastal bycatch and seasonal commercial and scientific hunting during migration. The most important evidence regarding stock structure comes from pair-wise tests of mtDNA haplotypes and microsatellite allele frequencies, tests for Hardy-Weinberg disequilibrium for allozyme and microsatellite loci, and biological data on conception dates. A summary of the most important evidence within each area is as follows. We consider Hypothesis III to have the highest relative plausibility, and therefore summarize evidence regarding that hypothesis first. For clarity, where comparisons between areas are made the name of the stock in the area is provided in parentheses (e.g., ‘Y’ for ‘Y-stock’). New sub-area boundaries are shown in Fig. 1, and a visual depiction of Hypothesis III is shown in Fig. 2. Evidence for each stock division is summarized in Table 1.

Hypothesis III

1. Evidence for a Yellow Sea stock (‘Y-stock’)

- There are significant differences in microsatellite DNA between the Yellow Sea (‘Y’) and Sea of Japan (in winter) (‘JW’) based on bycatch samples (Kanda et al. 2010a).
- Whales in the Yellow Sea have only autumn conception dates (Wang 1985, de Moor 2011).
- There is evidence for Hardy-Weinberg disequilibrium along the Korean coast of the Sea of Japan in summer suggesting the Yellow Sea stock mixes with the Sea of Japan stock (Kanda et al. 2010a, Slikas and Baker 2011, Wade and Baker 2011).

2. Evidence for a Sea of Japan stock (‘JW-stock’)

- There are significant differences in mtDNA and microsatellite DNA between the Sea of Japan (‘JW’) and all areas in the Pacific, including Japanese coastal waters (‘JE’) (Fig. 3, Baker et al. 2010, 2010b, Kanda et al. 2010a, Park et al. 2010, Slikas and Baker 2011).
- Whales in the Sea of Japan have a mixture of autumn and winter conception dates (Kato 1992, de Moor 2011).

3. Evidence for a ‘J-like’ stock along the Pacific coast of Japan (‘JE-stock’)

- The bycatch samples along the Pacific coast (‘JE’) are significantly differentiated from Sea of Japan bycatch samples (‘JW’) based on mtDNA haplotype frequencies. The two stocks share several common haplotypes (at different frequencies), and consequently are referred to as a ‘J-like’ (as compared to ‘O-like’ stocks further offshore) (Kanda et al 2010a, 2010b, Baker et al. 2010, 2011, Slikas and Baker 2011).
- There are significant differences in mtDNA and microsatellite DNA between coastal bycatch samples (‘JE’) and nearshore whaling samples (‘OW’) in the Pacific (Fig. 3, Baker et al. 2011, Slikas and Baker 2011).
- There are unique haplotypes found along the Pacific coast of Japan (‘JE’) that are not found in the Sea of Japan (‘JW’) or further offshore (‘OW’ and ‘OE’) (Kanda et al 2010b, IWC 2011).
- There is no consistent Hardy-Weinberg disequilibrium along the Pacific coast of Japan (‘JE’), thus no evidence for a mixture of two stocks (Slikas and Baker 2011, Wade and Baker 2011).

4. Evidence for two ‘O-like’ stocks in the Pacific Ocean, one of which is more ‘nearshore’ (‘OW’) and one of which is found further offshore to the east (‘OE’).

- There are significant differences in mtDNA and microsatellite DNA between coastal bycatch samples (JE’) and ‘nearshore’ whaling samples from 7CS and 7CN (‘OW’) in the Pacific (Fig. 3, Baker et al. 2010, 2011). However, the two stocks share several common mtDNA haplotypes (at different frequencies), and consequently are referred to as ‘O-like’ (Kanda et al 2010a, 2010b, Baker et al. 2010, 2011, Slikas and Baker 2011).
- There are significant differences in mtDNA and microsatellite DNA between nearshore whaling samples in sub-areas 7CS and 7CN (‘OW’) and offshore whaling samples in sub-areas 8 and 9 (‘OE’) in the Pacific (Fig. 3, Baker et al. 2010, 2011, Kanda et al. 2009, Park et al. 2010, Slikas and Baker 2011, Gaggiotti and Gascuel 2010).
- There is no significant Hardy-Weinberg disequilibrium in a large number of samples collected during commercial whaling operations from coastal stations along the Pacific coast of Japan (i.e., Sanriku and

Kushiro) ('OW') based on allozyme loci (Wada 1991). This is consistent with a single stock in nearshore waters, as first suggested by Wada (1991), rather than a mixing of two stocks as proposed under Hypothesis II.

- There is no consistent Hardy-Weinberg disequilibrium based on microsatellite DNA in sub-areas 7CS or 7CN ('OW'), 7WR+7E, or 8+9 ('OE'), thus providing no evidence for a mixture of two strongly differentiated stocks, such as O and J, in the areas where 'O-like' whales primarily occur (Slikas and Baker 2011, Wade and Baker 2011).
- Whales in the Pacific Ocean have only winter conception dates (except in the coastal portion of sub-areas 7CS and 7CN that have a mixture of winter and autumn) (de Moor 2011).

Hypothesis I

1. Evidence against a single stock in the Yellow Sea and Sea of Japan ('J-stock')

- There are microsatellite DNA genetic differences between the Yellow Sea and Sea of Japan (in winter) based on bycatch samples (Kanda et al. 2010a).
- Whales in the Yellow Sea have only autumn conception dates whereas whales in the Sea of Japan have a mixture of both autumn and winter conception dates (Wang 1985, Kato 1992, de Moor 2011).
- There is significant evidence for Hardy-Weinberg disequilibrium along the Korean coast of the Sea of Japan in summer suggesting a mixture of two stocks there (Baker et al. 2011, Kanda et al. 2010a, Wade and Baker 2011).

2. Evidence against a single Pacific Ocean stock ('O-stock')

- See summary under Hypothesis II.

Hypothesis II

1. The Yellow Sea stock ('Y-stock')

- This portion of the hypothesis is consistent with evidence under Hypothesis III.

2. Evidence against a single stock in the Sea of Japan and coastal Pacific ('J-stock')

- The bycatch samples along Pacific coast of Japan are significantly different from Sea of Japan bycatch samples, so there cannot be a single J-stock that occurs on both coasts of Japan (Fig. 3, Kanda et al 2010a, 2010b, Baker et al. 2010, 2011, Slikas and Baker 2011).
- There are unique haplotypes found along the Pacific coast of Japan that are not found in the Sea of Japan or further offshore (Kanda et al 2010b, IWC 2011).
- There is no consistent Hardy-Weinberg disequilibrium along the Pacific coast of Japan, thus no evidence for a mixture of two stocks there (Slikas and Baker 2011, Wade and Baker 2011).

3. Evidence against a single Pacific Ocean stock ('O-stock')

- There are differences in mtDNA and microsatellite DNA between nearshore whaling samples (7CS and 7CN) and offshore whaling samples (8 and 9) in the Pacific (Fig. 3, Baker et al. 2010, 2011, Kanda et al. 2009, Park et al. 2010, Baker et al. 2011, Slikas and Baker 2011, Gaggiotti and Gascuel 2010).
- There is no significant Hardy-Weinberg disequilibrium in samples collected during commercial whaling operations from coastal stations along the Pacific coast of Japan (i.e., Sanriku and Kushiro) based on allozyme loci, consistent with a single stock in nearshore waters (Wada 1991).
- There is no significant Hardy-Weinberg disequilibrium based on microsatellite DNA in areas 7CS, 7CN, 7WR+7E, or 8+9, thus providing no evidence for a mixture of two strongly differentiated stocks, (e.g., 'O' and 'J') in the areas where 'O-type' whales primarily occur (Slikas and Baker 2011, Wade and Baker 2011). Therefore, the significant genetic differences seen between nearshore areas (7CS and 7CN) and offshore areas (8 and 9) represent two 'O-type' stocks.

CONCLUSIONS

Hypothesis I specifies only two stocks, a 'J-stock' in the Yellow Sea and Sea of Japan, and an 'O-stock' in the Pacific Ocean. Whales in the Yellow Sea only have autumn conception dates whereas whales in the Sea of Japan have a mix of autumn and winter conception dates, so there cannot be a single stock that occurs in both those areas. Additionally, there are significant differences in microsatellite DNA between the Sea of Japan (in winter) and the Yellow Sea. Therefore, Hypothesis I is not supported by the data, and is considered to have Low plausibility.

Hypothesis II modifies Hypothesis I to allow for separate stocks in the Yellow Sea and Sea of Japan. However, Hypothesis II (as well as Hypothesis I) specifies that the stock in the Sea of Japan is the same stock as that found along the Pacific coast of Japan. However, there are significant genetic differences in both mtDNA and

microsatellite DNA between the two coasts of Japan, discounting the hypothesis of a single stock that occurs on both coasts. Furthermore, Hypotheses II specifies that a single stock ('O-stock') occurs in the Pacific Ocean away from the coast. However, there are significant genetic differences in both mtDNA and microsatellite DNA between nearshore areas (>10nm from the coast in 7CS and 7CN) and offshore areas (8 and 9). Therefore, Hypothesis II is not supported by the data, and is considered to have Low plausibility. Note that these criticisms of Hypothesis II regarding stock structure in the Pacific Ocean apply to Hypothesis I as well.

Only Hypothesis III was found to be in agreement with the conception date and genetic data. Hypothesis III is the only hypothesis that accounts for the significant genetic differences seen between three regions in the Pacific Ocean – the coast of Japan ('JE-stock'), nearshore waters >10nm from the coast ('OW-stock'), and offshore waters ('OE-stock'). Hypothesis III is also the only hypothesis that accounts for the significant genetic differences seen between the Sea of Japan ('JW-stock') and the Pacific coast of Japan ('JE-stock'). One explanation given for these significant differences is that there are differing proportions of just two stocks in each of these four areas (the Sea of Japan coast of Japan, the Pacific coast of Japan, the nearshore Pacific >10nm from the coast, and the offshore Pacific). However, allozyme and microsatellite DNA data only show consistent evidence for mixing of stocks in other areas (i.e., along the Korean coast of the Sea of Japan, and north of Hokkaido). The four areas in question do not show strong evidence for mixing of stocks. Therefore, only Hypothesis III, which has differentiated stocks in each of these four locations, is in agreement with the genetic data, and therefore has High plausibility. It should also be noted that a review of the mixing matrix results by a genetics sub-group (SC/D11/NPM4) found that Hypothesis III was either consistent with the genetic data, or the samples sizes are too small to allow confidence in reaching any definite conclusion. A more extensive summary of the evidence for Hypothesis III can be found in Wade and Baker (2010, 2011). Further details regarding the biological and genetic evidence for Hypothesis III can be found in Baker et al. (2010, 2011), Slikas and Baker (2011), and Wade et al. (2010).

Implications

The process by which the results of the *Implementation Simulation Trials* are interpreted are specified in the *Requirements and Guidelines for Implementations under the Revised Management Procedure* (IWC 2005). To be accepted, an RMP *variant* must have 'acceptable' performance for conservation measures on all High plausibility trials, and 'borderline' performance on only a small number of Medium plausibility trials¹. If the SC cannot come to an agreement on whether a trial has High, Medium or Low plausibility, it is labelled as a "no agreement" trial, and is effectively treated as a trial with Medium plausibility. As an example of how *variants* can differ, in the previous North Pacific common minke whale *Implementation* the preferred whaling operation scenario expressed by Japan was a RMP *variant* where catches would only occur in the traditional coastal whaling areas of Sanriku, Kushiro, and north of Hokkaido (old sub-area 7W and sub-area 11), but the catch limits would be based on *catch-cascading* from the abundance found in a broad area that included sub-areas 7 and 8 in the Pacific and sub-areas 11 and 12 in the Sea of Okhotsk (IWC 2004). In contrast, other *variants* (that were more conservative regarding the potential depletion of coastal or nearshore stocks) specified that the catches would be taken throughout a broader region that included most or all of the sub-areas.

It should be reiterated that the *Implementation Simulation Trials* test the RMP *variants* (where and when whales are hunted) over all stock structure hypotheses considered to have High or Medium plausibility. In general, it is unnecessary to select a single stock structure hypothesis as the 'best' hypothesis, as the intent of the trials is to account for uncertainty in this, and other parameters. In the recent *Implementation* for North Atlantic fin whales, six stock structure hypotheses were considered to have High plausibility. A seventh hypothesis was given Medium plausibility because it was inconsistent with some allozyme and non-genetic data (IWC 2009, pg 95). In the recent *Implementation* for western North Pacific Bryde's whales, three stock structure hypotheses were given High plausibility (even though the second and third hypotheses were considered less plausible than the first), and a fourth hypothesis was given Medium plausibility because the genetic data did not provide support for that hypothesis (IWC 2007). For western North Pacific common minke whales, given that Hypotheses I and II are essentially nested within Hypothesis III, it is likely that any *variant* considered acceptable under Hypothesis III will also be considered acceptable under Hypotheses I and II, but this can be confirmed after the trials are run. Consequently, the relative plausibility given Hypotheses I and II may not be of consequence if Hypothesis III has High plausibility.

¹ *Variants* that have borderline performance on more than a small number of Medium plausibility trials, or 'unacceptable' performance on Medium plausibility trials, can be considered for acceptance if a 10-year research plan can be specified that has a good chance of further resolving whether the unacceptable trials really have Low plausibility.

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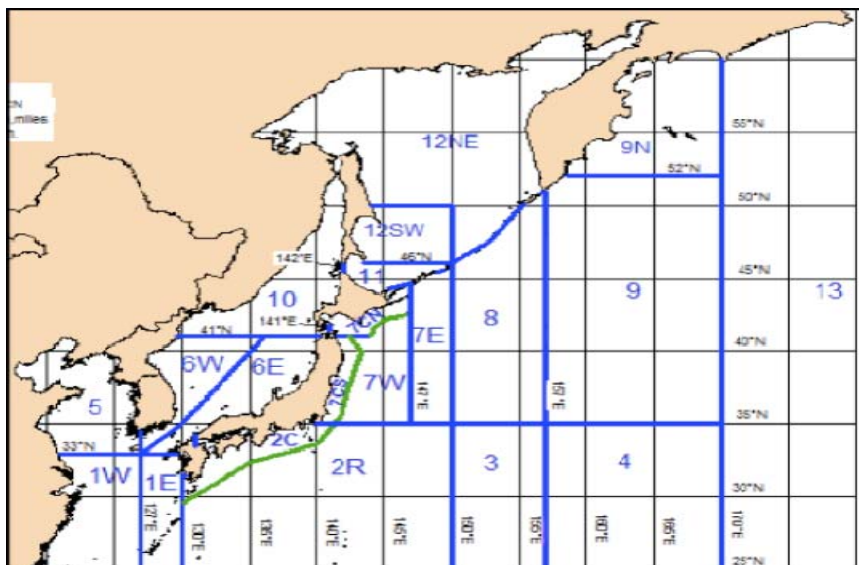


Figure 1. A map of the new sub-area designations. Note that '7W' is now referred to as '7WR' in the text.

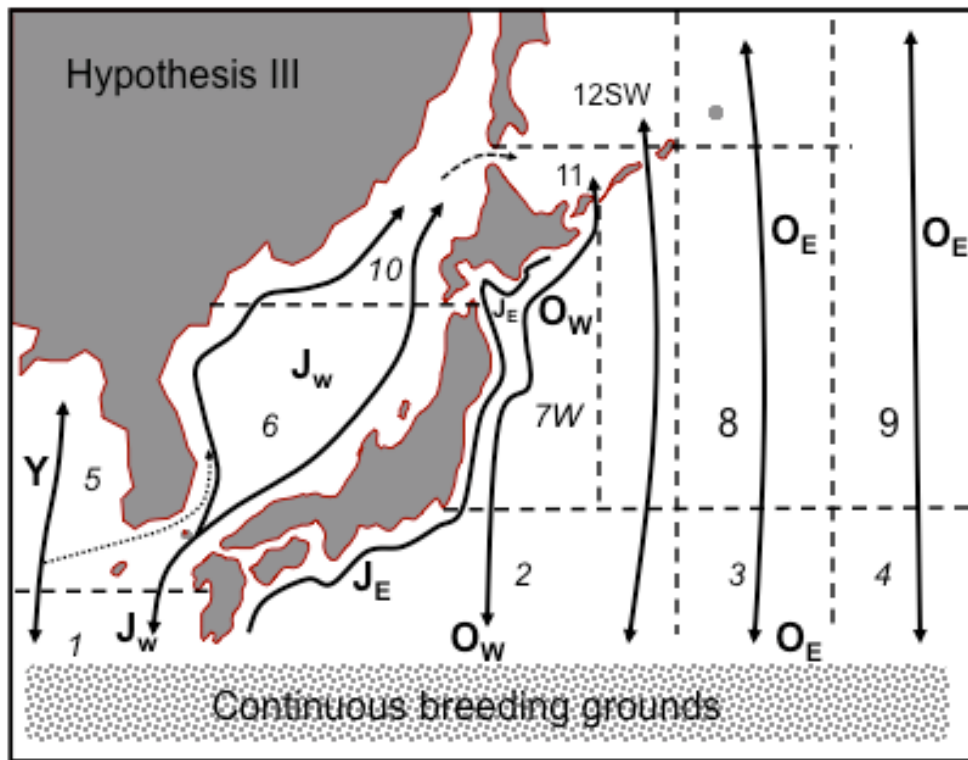


Figure 2. A conceptual depiction of the Stock Structure Hypothesis III showing migratory and non-migratory stocks (arrows indicate at least partial migration). Note that for clarity this figure does not show the new revised sub-area designations along the Pacific coast of Japan (shown in Figure 1) in what is labelled here as ‘7W’.

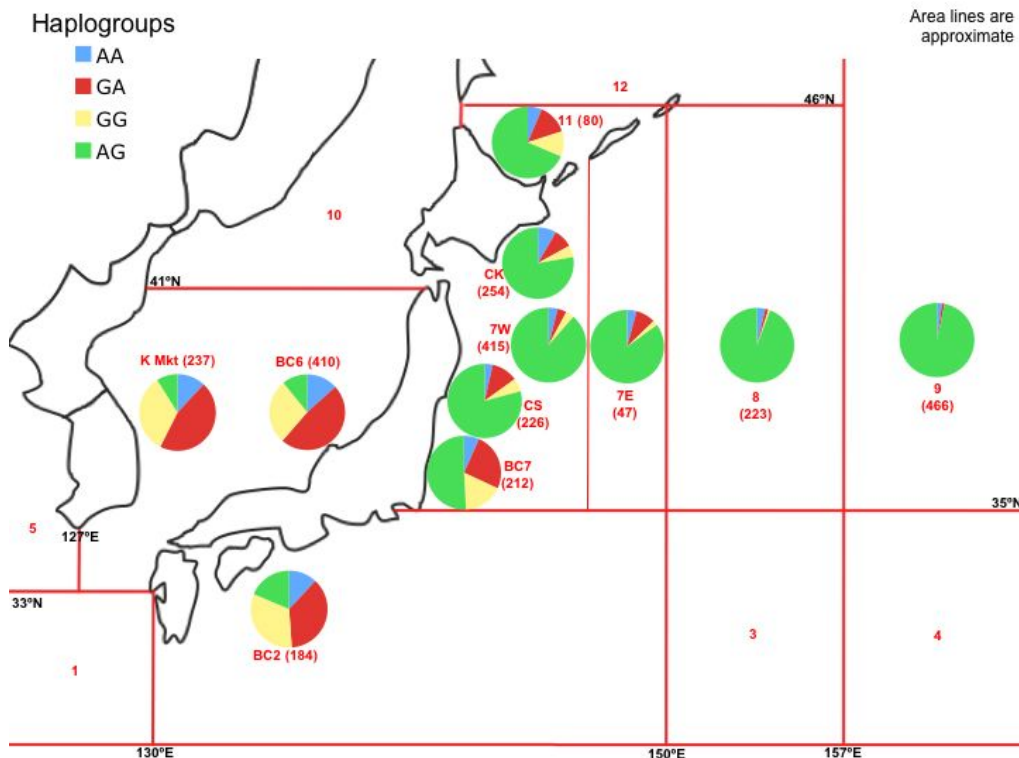


Figure 3. Frequencies of 4 ‘stock-informative’ mtDNA haplogroups for western North Pacific minke whales (Fig. 1 from Baker et al. 2010a). More detailed analyses were carried out on haplotype frequencies in Baker et al. (2011), but the haplogroup analysis is easier to visually depict.

Table 1. A summary of evidence for Stock Structure Hypothesis III. A dash ('-') indicates there was no information about stock structure from that type of data. In some cases the data were filtered or subdivided; 'all' means that all samples were included in the analysis, 'Without-J' means that whales thought to be 'J-type' were excluded (filtered) from the analysis, 'O-only' means that only whales thought to be 'O-type' were used in the analysis. It should be noted that there is no intention to imply that every data type (every row in the table) is equally important.

Source	Evidence for a Yellow Sea (YS) stock (Y-stock)	Evidence for a Sea of Japan (SOJ)-only stock (JW)	Evidence for a coastal J-stock on the Pacific-side of Japan (JE)	Evidence for nearshore (OW) and offshore (OE) stocks in the Pacific Ocean
microsatellite DNA Kanda et al. 2009 Pair-wise comp.	-	-	-	Differences (all) Differences ('Without-J')
microsatellite DNA Kanda et al. 2010a Pair-wise comp.	Differences between YS and SOJ (winter)	Differences between east and west coasts of Japan	-	-
microsatellite DNA Slikas and Baker 2011 Pair-wise comp	Differences between YS and SOJ (winter)	Differences between east and west coasts of Japan (SA 6E and 2)	Differences between Pacific coast bycatch samples and all other areas	Differences between all areas in the Pacific
microsatellite DNA Slikas and Baker 2011 Hardy-Weinberg	Evidence for mixing on Korean coast of SOJ	no H-W disequilibrium in SA 6E	no consistent H-W disequilibrium in SA 7CS, 7CN ('OW'), 7WR+7E, or 8+9 ('OE')	no consistent H-W disequilibrium in SA 7CS, 7CN ('OW'), 7WR+7E, or 8+9 ('OE')
mtDNA Park et al. 2010 Pair-wise comp.	No differences between YS and SOJ	Differences (all) between east and west coasts of Japan	-	Differences (all)
mtDNA Kanda et al. 2010b Additional information	-	unique haplotypes on west coast of Japan not found on east coast of Japan	unique haplotypes on Pacific coast of Japan not found further offshore	-
mtDNA Baker et al. 2011 Pair-wise comp.	No differences between YS and SOJ	Differences between east and west coasts of Japan (SA 6E and 2)	Differences between Pacific coast bycatch samples and all other areas	Differences between Sanriku/Kushiro samples and other areas incl. SA 8+9
mtDNA Baker et al. 2011 Additional information	-	SA 2C shares common haplotypes with 6E but with significantly different frequencies	SA 2C shares common haplotypes with 6E but with significantly different frequencies	-
mtDNA and microsatellite DNA Gaggiotti and Durand 2010, PCA and Boundary Rank	-	-	-	Differences (all) Differences ('O- only')
Allozymes Wada 1991 Hardy-Weinberg	-	-	-	No significant Hardy-Weinberg disequilibrium in whaling samples in Sanriku and Kushiro
Conception date Kato 1992, de Moor 2011	Differences between SOJ (small N) and YS	-	-	-
Distribution	Year-round presence in both YS and SOJ	Year-round presence on both coasts of Japan	Higher density in coastal waters	Higher density in coastal waters