A review of the plausible range of stock structure hypotheses of western North Pacific minke whales using genetic and other biological information

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Introduction

The population structure of minke whales has previously been examined from the perspective of examining differences between the Sea of Japan ("J-stock") and the Pacific Ocean ("O-stock"). These include genetic differences, and also the timing of conception or breeding season, coloration patterns of the flipper and baleen, scarring/parasite patterns, and chemical analyses of Persistent Organic Pollutants (POPs) and heavy metals. Apart from the differences noted between those two broad regions, most other genetic and biological studies have mainly examined hypotheses of possible population structure within the western Pacific Ocean, such as the possibility of one stock in sub-area 7 and a second stock in sub-areas 8-9 (Fig. 1, bottom right panel).

Recent genetic analyses have indicated there may be population structure within the area thought to be occupied by the putative J-stock, and that what are thought of as 'J-type' whales may occur outside the Sea of Japan, so the picture is more complicated than a simple 2-stock scenario of a Sea of Japan stock versus a Pacific Ocean stock. Genetic evidence has shown that 'J-type' whales are found along the Pacific coast of Japan, and there are other indications of possible genetic differences between the Yellow Sea, the Korean coast of the Sea of Japan, and the Japanese coast of the Sea of Japan. In light of these recent genetic results, seven new hypotheses (Fig. 1) were proposed regarding population structure of minke whales in the Yellow Sea, Sea of Japan, and Pacific Coast of Japan (IWC 61, 2010, Annex G1, Appendix 8). In the past, when genetic differences have been found between different sampling locations (such as coastal Pacific versus offshore Pacific Ocean), these differences have been interpreted as being due to a mixture of J and O-type whales occurring in the coastal area. Some of the previous genetic analyses attempted to 'filter' the data prior to comparisons between spatial areas to (for example) remove all 'J-type' whales prior to comparisons on the Pacific side of Japan. An alternate view is that some areas may contain only a single distinct stock characterised by intermediate haplotype frequencies. Stocks characterized by intermediate haplotype frequencies are well described in humpback whales, where stock divisions are supported by multiple lines of evidence (e.g., photo-ID records).

Although the seven hypotheses depicted in Fig. 1 appear complicated, they simply represent different permutations of four main uncertainties. Investigations of these four issues will help resolve stock structure of minke whales in the western North Pacific, particularly in the Yellow Sea, the East Sea/Sea of Japan, and the Pacific coast of Japan:

1) *Are whales in the Yellow sea part of the same population that migrates into the Sea of Japan?*
2) *Are whales along the Korean coast part of the same population as whales that migrate along the Japanese coast?*
3) *Are whales on the east coast of Japan the same population as on the west coast of Japan?*
4) *Is there a coastal population in Subarea 7 (east of Hokkaido and northern Honshu) that is different from offshore minke whales in the Pacific Ocean, even after accounting for some Sea of Japan whales that might migrate into this area?*

In this paper, we summarize and synthesize genetic and other biological data from western North Pacific minke whales in order to more closely examine population structure within the Yellow Sea, Sea of Japan, and Pacific coast of Japan, and we also review genetic and other biological data relevant to population structure in the Pacific Ocean and Sea of Ohkotsk, where many of the whales have been hunted during the last decade. For non-genetic information we primarily use the review of Wade et al. (2010); for simplicity and conciseness here we do not cite the primary source for all information summarized here and refer the reader to that paper for complete citations. For genetic information we primarily use the most recent results presented to the SC (Baker et al. 2010, Park et al. 2010, Gottiago and Durand 2010, Kanda et al. 2010, Kanda et al. 2009). Information from these papers is summarized in Table 1, which provides the support for the verbal narratives about stock structure that follow.

Conclusions

Here we examine whether available data are provide evidence for or against the four uncertainties described above.

1) ***Are whales in the Yellow Sea part of a population that migrates into the Sea of Japan?***
Minke whales migrate north into both the Yellow Sea and the Sea of Japan, and mature whales as well as cow/calf pairs are seen in the Yellow Sea in summer, indicating it is possible a separate stock exists in the Yellow Sea. Most significantly, Yellow Sea whales have only autumn conception dates, whereas minke whales in the northeastern Sea of Japan appear (from a small sample) to have a bimodal distribution of conception dates, with peaks in both autumn and winter, suggesting either different stocks in the two areas, or, alternatively, a mixture of two stocks in the northeastern Sea of Japan (with whales with winter conception dates entering there from the Sea of Okhotsk). Kanda et al. (2010) found differences between the Yellow Sea and the Korean coast in the Sea of Japan in microsatellite DNA from bycatch samples. In contrast, using essentially the same data, Park et al. (2010) did not find differences in mtDNA between those same two areas. On the Korean coast of the Sea of Japan there was some evidence for a mixture of two stocks (Baker et al. 2010), and microsatellite DNA showed differences between winter Sea of Japan samples and the Yellow Sea but not between summer Sea of Japan samples and the Yellow Sea (Kanda et al. 2010); this could be explained by a Yellow Sea stock moving northward along the Korean coast of the Sea of Japan in summer. In summary, the available data suggest there may be a stock of minke whales in the Yellow Sea that differs from the stock in the Sea of Japan.

2) ***Are whales along the Korean coast part of the same population as whales along the eastern Japanese coast?***
Survey data show minke whales distributed throughout the Sea of Japan so there is no obvious hiatus in distribution between the two coasts. On the other hand, it is conceivable that whales on the Korean coast migrate north into feeding grounds in the northern Sea of Japan and adjacent Sea of Okhotsk and that whales along the Japan coast migrate north into feeding grounds in the Pacific Ocean through the Tsugaru Strait between the islands of Honshu and Hokkaido. No data on conception dates are available from the southern Sea of Japan; whales in the northeast Sea of Japan appear (from a small sample) to have a bimodal distribution of conception dates, with peaks in both autumn and winter. Two different flipper colour patterns are also seen in the northeast Sea of Japan. For both the conception date and flipper colour pattern, the data could represent a mixture of two stocks from either side of the Sea of Japan, but an alternative explanation is that this is due to a mixture of whales coming into the northeast Sea of Japan from the Sea of Okhotsk. Genetic differences were found between bycatch samples from Korea and Japan in both mtDNA (Park et al. 2010) and microsatellite DNA (Kanda et al. 2010). No genetic differences were found in a haplogroup analysis (Baker et al. 2010) or in a clustering analysis using program *Structure* (Kanda et al. 2010); both analyses likely have less statistical power or resolution to find differences that the other two analyses. As mentioned above, there is some evidence for a mixture of two stocks along the Korean coast of the Sea of Japan (Baker et al. 2010), which could be explained by Yellow Sea whales appearing there in summer. No sex bias or haplogroup-by-sex differences were found for Japanese Sea of Japan bycatch, suggesting a possible year-round presence of a non-migratory coastal stock (Baker et al. 2010). In summary, it is plausible there are different stocks on either side of the Sea of Japan, but the data are somewhat contradictory or are lacking in sufficient resolution or spatial extent to make definitive conclusions.

3) ***Are so-called 'J-type' whales on the east coast of Japan the same population as on the west coast of Japan?***
A major recent finding was that whales thought to be 'J-type' whales (thought to occur in the Sea of Japan) also occur along the Pacific coast of Japan, so it is possible that those whales are part of the Sea of Japan stock but it is also possible they are a separate stock. It appears that coastal whales on either side of Japan may (at least partially) migrate to different feeding grounds, with Sea of Japan whales moving into the northern Sea of Japan (but maybe also the Pacific) and coastal Pacific whales migrating north to coastal areas east of northern Honshu and Hokkaido; another hypothesis is that a coastal Pacific population in southern Japan (subarea 2) stays in the Kuroshio Current and does not migrate further north than central Hokkaido (~34 or 35 degrees N. latitude). Sea of Japan bycatch samples show a sex ratio close to 50% whereas Pacific Ocean bycatch samples have a majority of females, particularly in the south (>70%). Whales from Sanriku along the Pacific coast of Japan have only winter conception dates, whereas minke whales in the northeast Sea of Japan appear (from a small sample) to have a bimodal distribution of conception dates, with peaks in both autumn and winter. The proportions of flipper colour type in the Sea of Japan whales were significantly different from the proportions seen in the Sanriku catches, which could also indicate differences between coastal whales on either side of Japan. An alternative explanation for the observed pattern of conception dates and flipper colours in the northern Sea of Japan is that this is due to a mixture of Korean or Pacific Ocean whales in that area. There are differences in microsatellite DNA between either coast of Japan when all samples are used (Kanda et al. 2010), but not when the analysis is filtered to remove what are thought to be 'O-type' whales (Kanda et al. 2010). Baker et al. (2010) also found differences between the two coasts in mtDNA when using all samples. No differences were seen when all samples from the Western pacific were analyzed using program *Structure* (Kanda et al. 2010). The southern Pacific coast bycatch (subarea 2) is also genetically different from bycatch along the northern Pacific coast of Japan (subarea 7), suggesting a Pacific coastal stock might be distributed only in the Kuroshio current,

and does not occur further north in the Oyashio current. In summary, a comparison between the two coasts of Japan is complicated (in part because of the lack of data and the possible mixing of stocks in some coastal areas), but it is plausible that there are different coastal stocks on either coast of Japan, and some evidence suggests this is the case.

4) ***Is there a coastal population in Subarea 7 (east of Hokkaido and northern Honshu) that is different from offshore minke whales in the Pacific Ocean, even after accounting for Sea of Japan whales that might migrate into this area?***

The general view in the past has been there was a separate stock of minke whales in the Pacific Ocean ('O-type' whales) and the Sea of Japan ('J-type' whales). From genetics, there are many studies showing significant differences between coastal and offshore waters when all samples are included (Park et al. 2010, Kanda et al. 2010, Baker et al. 2010, Gaggiota and Durand 2010). This different genetic signal in Pacific coastal waters off northern Honshu and Hokkaido (subarea 7W) has been interpreted to be a mixture of 'J-type' whales from the Sea of Japan and the 'O-type' whales (e.g., Kanda et al. 2010, Park et al. 2010). This view has been supported by analyses that show when what are thought to be 'J-type' whales are excluded, many (but not all) of the genetic differences go away. An alternate view is that this area contains a distinct stock characterised by intermediate haplotype frequencies (Baker et al. 2010). Stocks characterized by intermediate haplotype frequencies are well described in humpback whales, where stock divisions are supported by multiple lines of evidence (e.g., photo-ID records). Although it is possible that the haplotype frequencies of subarea 7W could be explained by a complex seasonal, sex- and age-biased mixing of 2 stocks, e.g., a 'core J' and a 'core O', it may be less parsimonious than the hypothesis of a distinct stock with intermediate haplogroup frequencies. The absence of a strong haplogroup-by-sex interaction in coastal waters is inconsistent with the prediction of a sex-biased mixing of two stocks (Baker et al. 2010). In particular, the analysis of Gaggiota and Durand (2010) concludes there is genetic heterogeneity in the Pacific Ocean, and their conclusions still hold when the analysis is restricted to what are thought to be 'O-only' type whales.

Information from non-genetic minke whale biology suggests the possibility of two stocks, but some of the information can also be explained by a mixture of a 'core J' and a 'core O'. Densities of minke whales are much higher along the Pacific coast than in offshore waters; this density pattern could be consistent with a coastal stock but could also be consistent with a single stock that occurs at higher densities near the coast. One striking diffence between coastal and offshore Pacific waters is that catches from coastal waters (bycatch or small-type whaling catches from the Sanriku and Kushiro grounds) have a much higher percentage of females, whereas offshore catches are heavily dominated by males. The offshore waters are so dominated by males in summer they cannot represent a complete stock; one explanation is that females are further north in summer, and higher ratios of females have been observed (for example) in the Sea of Okhotsk. One study found morphometric differences between near-shore and offshore waters, but other studies have not found differences. Coastal animals have fewer body scars from cookie cutter shark bites than offshore animals, suggesting a lack of complete mixing offshore, though this may be confounded by inshore waters having a higher percentage of juvenile animals (which have fewer scars). Some differences in contaminant values have been found between nearshore and offshore waters but other studies show no differences. In summary, a comparison between the coastal and offshore waters in the Pacific is complicated, in part because of the lack of data such as samples from the breeding grounds that could prove the existence of a 'core J' and a 'core O' stock. It is not possible to come to definitive conclusions about minke whale stock structure in the Pacific Ocean east of Japan, but it is plausible that the unique genetic signal seen in coastal waters of the Pacific coast of Japan is due to the existence of a distinct coastal stock, rather than a mixture of a 'core J' and a 'core O' stock.

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Table 1. A summary of evidence for or against the four uncertainties about stock structure in the Yellow Sea, Sea of Japan, and the Pacific coast of Japan (see text for a description of the four questions being addressed). 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; some types of data (such as genetic comparisons) are particularly important.

	Q1. Yellow Sea vs Sea of Japan	Q2. Korea coast vs west Japan coast	Q3. West coast Japan vs. east coast Japan	Q4.Coastal Pacific vs Offshore
microsatellite DNA Kanda et al. SC/61/JR8 Pair-wise comp.	-	-	-	Differences (all) Differences ('Without-J') No differences ('O-only')
microsatellite DNA Kanda et al. SC/61/JR8 Test of "baseline C"	-	-	-	Differences (all) No differences ('Without-J')
microsatellite DNA Kanda et al. SC/62/NPM11 Pair-wise comp.	Differences	Differences	Differences (all) No differences ('J-type' only)	-
microsatellite DNA Kanda et al. SC/62/NPM11 *Structure* analysis	No differences	No differences	No differences	No differences
mtDNA Park et al. SC/62/NPM21 Pair-wise comp.	No differences	Differences	-	Differences (all) No differences ('Without-J')
mtDNA Baker et al. SC/62/NPM20 Pair-wise comp.	-	No differences	Differences (all)	Differences (all)
mtDNA and microsatellite DNA Gaggiotti and Durand SC/62/NPM30 PCA and Boundary Rank	-	-	-	Differences (all) Differences ('O-only')
Conception date	Differences	Consistent with 1 or 2 stocks	Differences	No Differences
Flipper colour	-	Consistent with 1 or 2 stocks	Differences	No Differences
Morphometrics	-	-	Differences	Mixed Results
Cookie cutter scars	-	-	-	Differences
Contaminants	-	-	-	Differences
Feeding grounds	Differences	Consistent with 1 or 2 stocks	Consistent with 1 or 2 stocks	Differences
Migration patterns	Differences	Consistent with 1 or 2 stocks	Consistent with 1 or 2 stocks	Consistent with 1 or 2 stocks
Whale density	-	-	-	Differences

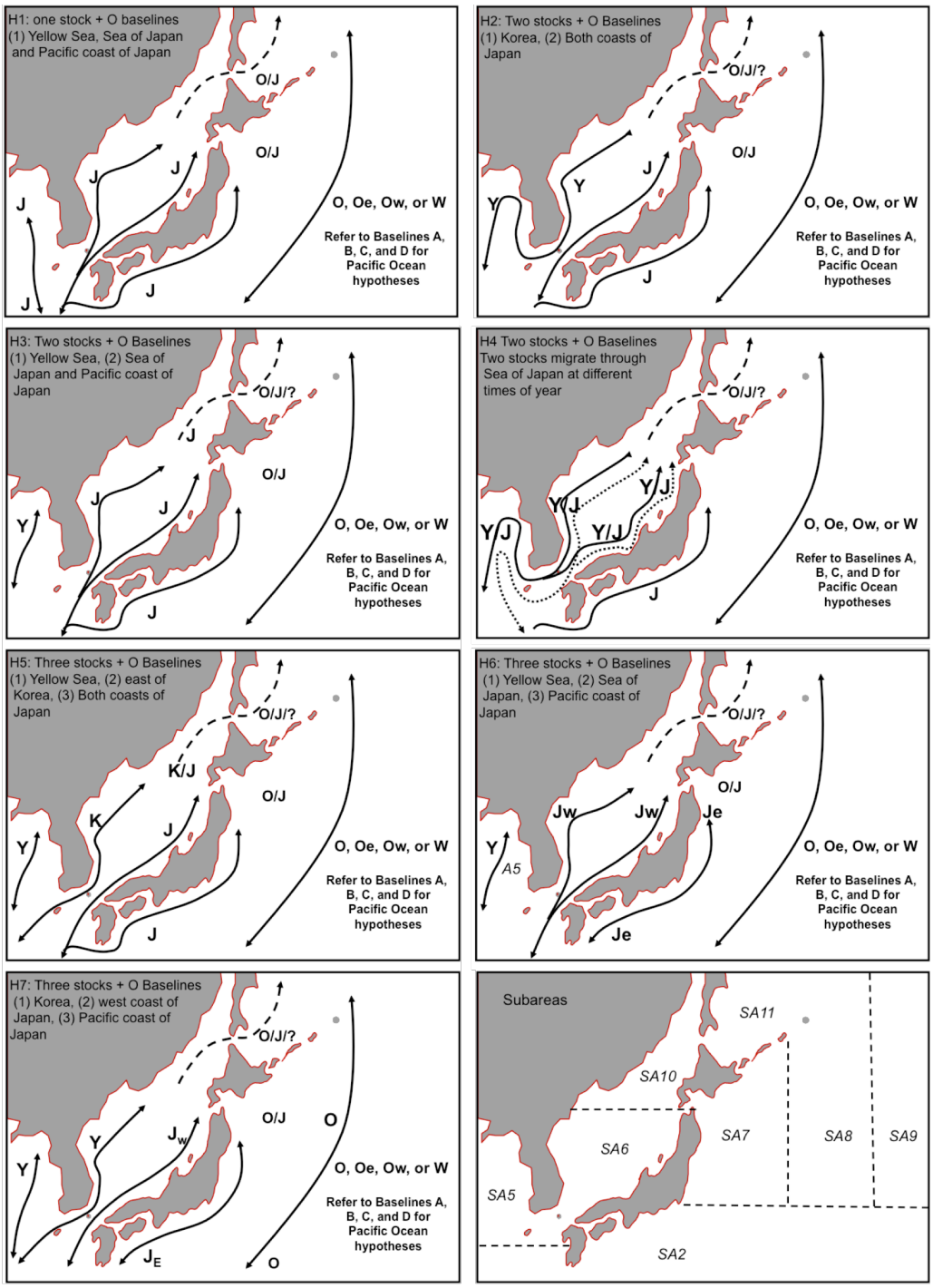

Figure 1. A description of 7 hypotheses for the stock structure of minke whales in the western North Pacific. Note that all permutations of stock structure in the Pacific Ocean are not shown; hypotheses of stock structure in the Pacific have previously been described as Baselines A, B, C, and D. Note that the hypothesis of a coastal stock on the east (Pacific) coast of Japan ('J_E') may or may not be similar to the hypothesis of a coastal Pacific Ocean stock ('O_E"). Sub-areas 2, 5, 6, 7, 8, 9, 10, and 11 are shown in the lower right panel; sub-area boundaries are approximate.