

Annex I

Report of the Working Group on Stock Definition

Members: Lang (Convenor), Skaug (co-Convenor), Archer, Baird, Baker, Bengtson Nash, Bickham, Brierley, Brownell, Butterworth, Castro Ayala, Cipriano, Diallo, Donovan, Double, Fleming, Fortuna, Funahashi, Griffiths, Hancock-Hanser, Hoelzel, Iñíguez, Jackson, Johnson, K., Johnson, M., Ketele, Kitakado, Leslie, Lundquist, Manley, Mduduzi Seakamela, Melcón, Mesnick, Mikhno, Mizroch, Monnahan, Morin, Moronuki, Muraki, Murase, Natoli, Nda, Øien, Okazoe, Pampoulie, Paniego, Pastene, Pease, Perrin, Prewitt, Punt, Reeves, Robertson, Roel, Rosenbaum, Scordino, Simeone, Sitar, Slooten, Solvang, Thuok, Tiedemann, Uoya, Wade, Wang, D., Waples, Yoshida.

1. INTRODUCTORY ITEMS

1.1 Convenor's opening remarks

Lang welcomed participants.

1.2 Election of Chair and appointment of rapporteurs

Lang was elected as Chair, and Leslie and Cipriano acted as rapporteurs.

1.3 Adoption of Agenda

The adopted agenda is given in Appendix 1.

1.4 Review of documents

The documents identified as containing information relevant to the Working Group were: SC/66a/AWMP02, Pomilla *et al.* (2014), Alexander *et al.* (In review), Waples (2015), SC/66a/IA03-IA04, SC/66a/IA08-IA09, SC/66a/IA14, SC/66a/SD01-SD02, SC/66a/SD04-SD05, SC/66a/SH13, SC/66a/SH19, and SC/66a/SH29.

2. GUIDELINES AND METHODS FOR GENETIC STUDIES AND DNA DATA QUALITY

This agenda item relates to the two sets of guidelines that the Scientific Committee has requested the Working Group (hereafter SDWG) to develop for reference in the Committee's discussions of stock structure. Both sets are subject to ongoing update as appropriate.

The SDWG discussed how to increase awareness and thus the use of these guidelines. The DNA quality guidelines are currently included under the Scientific Committee Handbook section of the IWC website and may be difficult to find for some. It was suggested that the IWC website could be updated to include a page where all guidelines (e.g. DNA data quality guidelines, sighting survey guidelines, etc.) could be made available, and which could be linked to the homepage of the website to increase visibility. Lang offered to explore this possibility with the Secretariat.

2.1 Guidelines for genetic data analysis

Guidelines for some of the more common types of statistical analysis of genetic data that are employed in IWC management contexts are still not finalised. The main section is intended as guidance for managers and will also contain examples of management problems that are regularly faced by the Committee. There will also be an extensive appendix of genetic analysis techniques for specialist readers. This guidelines document is near completion and is expected to be available by SC/66b (see work plan).

2.2 DNA quality

The DNA data quality control guidelines are already available as a 'living document' on the IWC website¹. A section discussing SNP data will be developed intersessionally by Tiedemann, Cipriano, and Hoelzel and added to the data quality document after review at SC/66b.

In addition, the SDWG discussed whether the guidelines should be updated to include genomics data produced using next generation sequencing approaches. It was noted that not all of these approaches provide data that is useful in the IWC management context. The SDWG encouraged the submission of papers to SC/66b that may inform the development of guidelines for genomic data.

2.3 Other developments

SC/66a/SD02 reports on the inferred oceanic origins of 113 fin whale products purchased in Japanese markets from 1993 to 2009. For this, the authors used Random Forest, a classification algorithm, based on the largest reference dataset assembled to date for mtDNA sequences of fin whales from the three ocean basins: North Atlantic ($n=332$, haplotypes=35), North Pacific ($n=346$, haplotypes=31) and the Southern Hemisphere ($n=99$, haplotypes=48). First, using the reference dataset to create and validate the classification model, Random Forest showed 96% accuracy for re-assigning haplotypes to the ocean of known origin. Second, Random Forest was used to classify the mtDNA sequences of the market products to the most likely ocean of origin. The expectation was that the classification of the market products would reflect three oceanic sources, depending on date of purchase: the North Atlantic for special permit hunting by Iceland, which ended in 1989, and commercial whaling by Iceland in 2006 and 2009, with importation after 2008; the Southern Hemisphere for special permit hunting by Japan in the Antarctic (JARPA II), initiated in 2005/06 season; and, the North Pacific for bycatch in Japanese coastal waters. These expectations were not consistent with the results of the classification. Of the 44 haplotypes found among the 113 products, 16 were classified as North Atlantic and the remaining 28 as Southern Hemisphere. Most of the products represented by the 16 North Atlantic haplotypes were purchased from 1993 to 1999, roughly consistent with the reported 10-year maximum for storage of products from the Icelandic scientific whaling. Products represented by 19 of the Southern Hemisphere haplotypes were purchased after the hunting of fin whales in the Antarctic was initiated in the austral season of 2005/06. As reported previously (Steel *et al.*, 2009), these 19 haplotypes represented at least 19 individuals, exceeding the 15 reported from either JARPA II or as bycatch. Furthermore, products represented by 10 of the Southern Hemisphere haplotypes were purchased before the addition of this species to the JARPA II programme, some dating back to as early as 1993. Regardless of the inferred oceanic origins, SC/66a/SD02 notes that it is difficult to explain the sale of fin whale products from 2000-05, prior to the 2006 JARPA II hunt and after the 10-year storage limit for products from Iceland. Taken together with the results

¹<http://iwc.int/scientific-committee-handbook#ten>.

of the Random Forest classification, evidence points to an illegal, unreported or undocumented (IUU) source of fin whales from the Antarctic, similar to that of questionable sei whale products purchased in Japanese markets (SC/66a/IA04). Information on the mtDNA haplotypes from the Japanese and Icelandic DNA register would provide greater confidence in excluding bycatch and special permit whaling as sources of these questionable products.

Given that SC/66a/SD02 presents a new approach with utility in identifying diagnosable groups as well as in assigning samples of unknown origin to their source, the SDWG first discussed the methodology used before focusing on the results presented in the paper.

Archer presented a review of Random Forests (Breiman, 2001), which is an ensemble-based classification algorithm that extends the more familiar method of CART by adding several layers of stochasticity to the tree growing process. This permits the algorithm to fully explore the predictive capability of all variables, as well as producing an internally validated classifier. A Random Forest is a collection of bifurcating CART-like decision trees. In this implementation, the initial data is a set of samples represented by aligned mtDNA sequences, each grouped into some a-priori defined classes (e.g. ocean basins). In the algorithm, each nucleotide is used as a potential predictor. As an output, Random Forests produces a measure of model performance in the form of a 'confusion matrix' which describes the fraction of training samples that have been misclassified. The model can then be used to classify unknown samples and produces a probability of assignment to each class for each sample.

The SDWG thanked Archer for his overview of this method.

In discussion, it was noted that this approach treats variable sites within a sequence as unlinked, which in the case of single locus sequence data (e.g. mtDNA) is not true. However, this is not a violation of assumptions in Random Forests (RF). Unlike methods to construct phylogenetic trees, RF classifies sequences into clusters without relying on an underlying evolutionary model. This can be an advantage as sites that are only weakly informative individually can have a larger effect when combined together. The RF method is also able to evaluate diagnosability in cases where resolving phylogenetic relationships is difficult. An additional advantage is that RF is able to assign novel haplotypes into clusters and is thus not reliant on comprehensive sampling of source populations. One limitation, however, is that the phylogenetic information contained in the sequence data is not fully exploited.

It was noted that the probabilities generated using RF are relative rather than absolute probabilities; because the approach is not based on an underlying parametric or theoretical model it is not possible to calculate likelihoods. As with other classification methods that are constrained to assign samples into categories, the RF method can be misleading if the true source population of a sample is not represented, as it would have to be assigned to one of the existing categories.

The SDWG discussed whether increasing the length of sequence analysed would improve the performance of the RF approach. It was noted that model performance was driven by the ratio of information content to noise. While increased sequence length could increase the number of informative sites, it might also contribute noise that would interfere with model performance. On the other hand, the addition of samples generated from multiple sources can collapse sequences and remove variable sites. However increasing the number of individuals that define a cluster can increase the method's performance if sufficient information

content remains in the collapsed sequences. Homoplasy can become an issue when the number of variable sites is low.

One consideration in using the RF approach is that it is not designed for assigning individuals to stocks that exhibit only frequency-level differences, because it relies on identifying combinations of diagnostic sites to classify individuals to cluster membership. Thus the utility of this approach may be limited when addressing stock structure questions at demographic scales.

In discussion of the results of SC/66a/SD02, a question was raised regarding how the RF analysis results compared with those from the phylogenetic analysis that was previously conducted. It was noted that the RF method performed better, although some samples remained unassigned. When whole mitogenomes were used with this method (Archer *et al.*, 2013), the error rates were lower than when only the mtDNA control region was used, but there were still some North Pacific whales that were classified as being from the Southern Hemisphere. These samples belong to a clade that is thought to represent introgression of Southern Hemisphere whales into the North Pacific.

It was suggested that the addition of microsatellite loci to this analysis could provide more insight. It was noted, however, that while additional loci would increase power, it would be difficult to standardise microsatellite genotypes across labs, and that the samples that are in Japan's DNA register are only available on request. The advantages of using mtDNA sequence data are that it is highly transferable across labs, it works relatively well with degraded samples, and representative sets of reference sequences from several ocean basins exist.

In the review of stock structure related papers by the SDWG over the last few years, the utility of testing for departure from Hardy-Weinberg proportions (HWP) for nuclear loci has been highlighted. Waples (2015) provides a review of factors that can cause departures from HWP at individual loci and a guide to distinguishing between possible causes for the departure. One cause of this deficit is the Wahlund effect (Wahlund, 1928), which is present when the sample set analysed includes individuals from more than one population. A Wahlund effect results in a positive F_{IS} value, which reflects a deficiency of heterozygotes compared to the expected HWP. A positive F_{IS} value can also result from other factors, such as non-random sampling or apparent or real null alleles. However, the Wahlund effect is largest when mixture fractions are approximately equal and when allele frequencies differences between populations are large. Thus if a Wahlund effect is present under these conditions, the magnitude of F_{IS} should be greatest at the loci that show the largest allele frequency differences. This relationship, which was first proposed in Waples (2011), provides a way to test the hypothesis that two stocks may be present among a given sample set.

The SDWG thanked Waples for providing this overview. In discussion, it was noted that when the sample set contains roughly equal proportions of animals from two different stocks, there should be a linear relationship between F_{IS} and F_{ST} . This linear relationship can also result if fixed differences in alleles are present between two stocks. However, if positive F_{IS} values are the result of sampling of family groups (i.e. non-random sampling) or due to the presence of real or apparent null alleles, there is not expected to be any relationship between F_{IS} and F_{ST} .

Given the utility of F_{IS} to test stock structure hypothesis, the SDWG encourages reporting F_{IS} values in papers with relevance to stock structure.

3. STATISTICAL AND GENETIC ISSUES RELATING TO STOCK DEFINITION

The SDWG has the task of discussing high-priority stock related papers from other sub-committees and Working Groups, and then providing stock structure related feedback and recommendations to those sub-committees and Working Groups (IWC, 2012, Appendix 2). These discussions often refer to the genetic analysis guidelines and genetic data quality documents.

3.1 Population structuring and migration rates

3.1.1 Bowhead, right, and gray whales

SC/66a/SD04 reports the results of genetic studies on biopsies taken from western gray whales taken near Sakhalin Island in 2011, 2012 and 2013. The study is a collaboration between US and Russian laboratories. Data include molecular sexing and mtDNA control region (CR), cytochrome b (cyt b), and COI haplotype sequences of 32 western gray whales. As with previous studies of the genetics of this population, appreciable genetic variation was observed for mtDNA. Two control region haplotypes predominate in frequency, A and B, with many more haplotypes observed at very low frequencies. Many of the low frequency haplotypes are males. Haplotype networks confirm that the whales summering near Sakhalin Island do not comprise a specific maternal lineage. Statistically significant differences were observed in haplotype frequencies for the years 2012 and 2013 that might reflect groups of related individuals of unknown provenance. Future studies are planned including SNP development, and expanding the sample size to include biopsies collected in 2014 ($n=30$) and biopsies planned to be collected in 2015 ($n=30$).

In discussion, it was noted that the observed inter-year differences in the haplotype frequencies of the mtDNA COI and cytochrome B sequences could result from non-random sampling, such as collecting samples from a mother and her calf while together. However, photo-identification data suggests that mothers and their calves were not sampled during the same encounter. The high haplotype diversity combined with small sample sizes suggests the observed difference could easily be the result of sampling error.

In a small number of cases, genotyping of samples that were considered to be collected from the same individual based on photo-identification records revealed that the samples were obtained from different individuals. Such discrepancies could be resolved through comparison of the genetic data collected from these individuals with that collected from Sakhalin whales as part of a separate study (Lang *et al.*, 2011). This issue may also be resolved as additional nuclear genotyping of samples is conducted.

It was noted that three sets of samples of Sakhalin gray whales exist, including those analysed in SC/66a/SD04, those included in Lang *et al.* (2011), and those presented in Meschersky *et al.* (2015). While it is likely that some individuals are represented in multiple sample sets, the timing of sample collection efforts (e.g. 2011-13, SC/66a/SD04; 1995-2007, Lang *et al.*, 2011) suggests that these datasets likely also contain samples from unique individuals. Work is currently in progress by the authors of this paper, as well as by the SWFSC, to use next generation sequencing approaches to identify SNP loci in gray whales, which will facilitate the future integration of datasets across labs if warranted (SC/66a/Rep08).

3.1.2 In-depth Assessment

This year, the SDWG discussed three papers with relevance to the stock structure of sei whales in the North Pacific.

SC/66a/IA08 used 16 microsatellite DNA markers to analyse samples of sei whales collected widely from the North Pacific at the same time of the year in order to test spatial genetic heterogeneity in this ocean basin. This study is the first to utilise temporally similar (collected at the same year), yet geographically very different, samples. The study involved a total of 77 samples from IWC POWER surveys and 295 samples from JARPN II surveys covering the geographical area between 37-53°N and 145°E and 135°W. Therefore this study used samples collected from the northwestern (JARPN II surveys), north central (POWER surveys), and northeastern (POWER surveys) areas of the North Pacific in the same summer seasons in 2010, 2011 and 2012. No evidence of significant genetic differences between the samples from JARPN II and POWER in each of the three years were found. Each yearly sample was then combined as JARPN II as well as POWER samples, respectively. No significant genetic differences were detected between these two samples. Genotypic profiles of each whale in the IWC POWER biopsy samples were used to find any cases of matching to the individuals in the JARPN II samples, and no matching was found at all. In conclusion, this study failed to demonstrate evidence of multiple stocks of sei whales in the area of the North Pacific covered by this genetic survey.

The SDWG thanked the authors for this work, which builds on previous genetic analyses that have been presented in the past (Kanda *et al.*, 2009; Kanda *et al.*, 2013). In discussion, it was noted that a Wahlund effect would be expected if multiple stocks were present within the area in which samples are collected. No departures from Hardy-Weinberg equilibrium were identified among the loci and strata analysed in SC/66a/IA08. It was suggested that F_{IS} be calculated, especially given the variability in sample sizes between the strata compared. The magnitude of F_{IS} would be expected to be close to or vary around zero if samples were collected from the same stock.

SC/66a/IA14 explores the distribution, movements and population structure of sei whales (*Balaenoptera borealis*) in the North Pacific by analysing 20th century whaling data, location data from the placement and recoveries of 106 of 620 *Discovery*-type marks implanted in sei whales between 1949 and 1975 and sightings data from systematic sightings surveys starting in 1980. *Discovery* mark recoveries show that sei whales travelled great distances across the North Pacific basin, from low latitudes in winter to high latitudes in spring and summer, and across high latitudes during the spring and summer. Although pelagic and land station catch data showed widespread concentrations of sei whales both in coastal waters and on the high seas, systematic sighting surveys from 1980 through to the present indicate that sei whales are now only rarely seen in coastal areas where large numbers had been taken by whalers. Analysis of whaling and marking data suggest no obvious divisions between separate demes within the pelagic North Pacific, but does suggest a division between pelagic and coastal stocks. Based on this data, SC/66a/IA14 proposes that the North Pacific formerly contained multiple stocks of sei whales, including: (1) a North Pacific pelagic stock; (2) an Aleutians/Gulf of Alaska stock; (3) an eastern North Pacific migratory stock; (4) a southern North American coastal stock (coastal California); and (5) a Japanese coastal stock. The almost complete absence of sei whales in coastal areas suggest that the coastal stocks as well as the eastern North Pacific migratory stocks have remained depleted almost 40 years after whaling ceased. Bayesian analyses of catch and *Discovery* mark recovery data show that hunting effort and mortality greatly exceeded what

would have been sustainable levels for such a long-lived species with low reproductive rates. The analyses further suggest that the pelagic migratory stock, which had already been depleted by 1972, was likely reduced by a further 65% (95% CI 30-86%) from 1972-75 to around 4,000 animals.

In discussion, it was clarified that the gap in catches that can be seen between 150°E and 160°E does not represent a lack of whales in this area but is an artefact of government regulations restricting whaling in this area in order to provide a buffer zone between the coastal and pelagic whaling operations.

It was noted that discriminating between Bryde's whales and sei whales can be difficult. While mis-identifications among harvested whales would be unlikely, the data from sighting surveys might include some proportion of mis-identified whales. Some mis-identifications could also be present in the *Discovery* marking data, though the species identification of whales whose marks were recovered would have been confirmed upon harvest. Although species distributions may shift with environmental variation, the geographic location of sightings and catch records included in SC/66a/IA14 is consistent with the generally more northern distribution of sei whales. However, it was suggested that determining what criteria were used to discriminate between species during sighting surveys could be useful in better assessing this potential source of error.

The proportion of *Discovery* marks that are recovered is driven in part by the spatial and temporal extent of whaling effort subsequent to marking. A primary point of discussion was whether the patterns in mark recovery proportions and catch distributions presented in SC/66a/IA14 were influenced by geographical or temporal changes in whaling effort. In response, the author indicated that there was likely great heterogeneity in capture probabilities throughout the entire long time series, but that the quantitative analysis was restricted to a subset of years (1972-75) where capture probabilities could be estimated with great precision. Based on these analyses, the statistical test confirmed that the whales marked in coastal areas did not mix with the whales that had been marked in lower latitudes.

If shifts in catches reflect whale distribution and abundance, the generally southward shift in catches and the lack of mark recovery among coastally marked whales are consistent with the depletion of whales in coastal and high latitude areas. However, other explanations for this pattern are possible. One alternative hypothesis that was raised is that a range contraction may have occurred within a single pelagic stock. Other whale species are commonly observed feeding in areas that were historically used by sei whales, suggesting that these areas remain highly productive and raising the question of why sei whales would have abandoned these areas if the stock was not depleted.

In discussion, it was noted that the results of genetic analyses, in which no significant differences between areas were detected, were not inconsistent with the stock structure hypothesis generated based on the *Discovery* mark recovery and catch data if only the pelagic stock was sampled. Under the multiple-stock hypothesis, the areas where genetic samples have been collected would lie within the range of the pelagic stock and would thus be expected to support panmixia.

SC/66a/IA09 reviewed the information on movement, catch and sighting distribution, and genetics of sei whales in the North Pacific with the aim of proposing stock structure hypotheses of this species in this oceanic basin. Mark-recapture data based on *Discovery*-type tags suggested that whales from the same breeding area (whales marked

in low latitude in winter) distributed widely in higher latitude feeding areas in summer, in the longitudinal range between 140°E and 140°W, south of latitude 50°N. Catch distribution data based on past commercial and JARPN II surveys showed no geographical gaps through the North Pacific. An analysis of probability of occurrence based on sighting data obtained during JARPN II and IWC/POWER surveys suggested no obvious gaps in distribution although the probability of occurrence near the coast of Japan was relatively low. Genetic analyses have been based on mtDNA control region sequencing and microsatellite DNA and have been conducted on genetic samples collected during JARPN II, IWC/POWER and past commercial whaling. The genetic survey covered the area comprised between approximately 35°-50°N and between 142°E-135°W. No significant genetic heterogeneity has been found in this area. Based on the review of the information on movement, catch and sighting distribution and genetics, this study proposes the hypothesis of a single stock of sei whales in the North Pacific, in the area covered by this review.

In discussion, the difficulty of discriminating between these two hypotheses in the absence of genetic data from the coastal stocks proposed in SC/66a/IA14 was highlighted. Under the multiple-stock hypothesis, the coastal stocks are considered greatly depleted and potentially extirpated. Thus it is unlikely that contemporary samples could be obtained to test this hypothesis using genetic data. It was noted that some biological samples from California whaling stations were collected and sent to the Smithsonian, but they cannot currently be located. Some remnant material may also be available from Canadian whaling stations. In light of this limitation, the SDWG encouraged future survey effort in areas where sei whales were formerly abundant and the analysis of any samples (even from remnants like bones) that become available.

In summary, while the *Discovery* mark recovery and catch data appear to be consistent with the multiple stock hypothesis proposed in SC/66a/IA14, alternate explanations based on the presence of a single stock of sei whales in the North Pacific were also considered to be plausible.

3.1.3 Other Southern Hemisphere whale stocks

Pomilla *et al.* (2014) analysed 11 microsatellite markers and mitochondrial DNA sequences extracted from 67 Arabian Sea humpback whale tissue samples, and compared them to equivalent datasets from the Southern Hemisphere and North Pacific. Results show that the Arabian Sea population is highly differentiated; estimates of gene flow and divergence times suggest a southern Indian Ocean origin but indicate that it has been isolated for approximately 70,000 years, remarkable for a species that is typically highly migratory. Genetic diversity values are significantly lower than those obtained for Southern Hemisphere populations and signatures of ancient and recent genetic bottlenecks were identified. Many of these results were presented to this sub-committee previously (Pomilla *et al.*, 2010). New results from STRUCTURE and a Bayesian Skyline Plot in the published paper reinforced the previous results presented to the sub-committee. These findings suggest this is the world's most isolated humpback whale population, which, when combined with low population abundance estimates and anthropogenic threats, raises concern for its survival, particularly given the current and projected increase in anthropogenic activities.

Since most of the analyses included in Pomilla *et al.* (2014) have been reviewed in past sessions of the Scientific Committee, only new results were discussed by the SDWG.

In discussion, it was noted that the STRUCTURE results shown were based on two models, one which incorporated prior information on sampling location and assumed that $K=3$ and another that did not utilise information on sampling location and assumed $K=2$. It was noted that including the results where only one of these two parameters were changed could be informative in terms of evaluating the influence of these assumptions on the results.

Alexander *et al.* (In review) reports on the global population structure of sperm whales with an emphasis on regional populations in equatorial or temperate waters in each of the three ocean basins, including samples from the voyage of the *Odyssey*, a five-year circumnavigation of equatorial whaling grounds. A worldwide database of mitochondrial DNA (mtDNA) control region haplotypes (394bp) was assembled from 1,587 sperm whale samples, combining 1,091 previously published samples with newly obtained DNA profiles (mtDNA, sex, 13 microsatellite loci) from 55 stranded individuals, and 441 individuals biopsied in previously under-sampled equatorial waters. The dataset was used to investigate oceanic diversity and differentiation, population structure within oceans, and female philopatry. The overview focused on a few key conclusions of the extensive analyses, including the following.

- (1) mtDNA diversity of sperm whale is low, as reported previously, but sampling in the Indian Ocean did reveal new haplotypes, including 'private haplotypes'.
- (2) Despite the absence of a phylogeographic signal, there is strong differentiation in mtDNA haplotypes between oceanic populations and between many regions within population, with strong influence of regional fidelity in the previously unsampled Indian Ocean. There was also differentiation among social groups within regional populations, although most social groups include multiple matriline.
- (3) Finally, the results indicate that both geographic fidelity and social philopatry drive genetic structure in the sperm whale, but their relative importance differs by sex and by ocean, reflecting breeding behaviour, geographic features (e.g. marginal seas in the Atlantic) and perhaps a history of social disruption due to whaling in the Pacific.

In discussion, it was cautioned that, as noted in Alexander *et al.* (In review), the results of this and other genetic studies will need to be interpreted in the context of what is known about age and sex-based differences in sperm whale movement patterns (Dufault *et al.*, 1999; Jacquet *et al.*, 2003; Whitehead, 2001).

It was noted that both the locus-specific and the overall F_{IS} values calculated from the microsatellite data for each strata were all positive, indicating a deficit of heterozygotes. The interpretation of this result is complicated given that the strata contained different proportions of males and females. One possible explanation for such a deficit is that a Wahlund effect has resulted from mixing of different breeding populations within the areas sampled. This explanation was considered to be unlikely given that only low levels of nuclear differentiation have been observed between areas in this and other studies (Lyrholm *et al.*, 1999; Mesnick *et al.*, 2011). Another possible explanation for the positive F_{IS} values is that allelic dropout may have occurred, as some of the included samples were of low quality. Given what is known about sperm whale social structure, this finding may also have been driven by sampling of familial groups, which could result in a mild inbreeding effect.

SC/66a/SD05 provides an update on the progress of genetic analyses that are underway to evaluate the population structure and taxonomy of blue whales globally. The analyses reported in LeDuc *et al.* (2007), which evaluated population structure among Southern Hemisphere whales, have been expanded to incorporate samples from blue whales in the eastern North Pacific (ENP) and eastern Tropical Pacific (ETP). This work, which is near completion, suggests that while blue whales in the eastern South Pacific and eastern North Pacific are genetically differentiated, they are genetically more similar to each other than the ESP whales are to other Southern Hemisphere whales. Additional work, using next generation approaches to produce mitogenomic and SNP data, is underway. These analyses include a small number of samples collected during POWER cruises (2011-13) in areas thought to be used by central North Pacific blue whales, and thus may provide some insight into stock structure of blue whales within the North Pacific. An update on these analyses will be provided at SC/66b.

3.2 Population assignment and mixing

3.2.1 Aboriginal Subsistence Whaling Management Procedures

SC/66a/AWMP02 presented data on the timing and movement patterns of humpback whales from the southeast Caribbean. Animals from eastern feeding grounds were significantly over-represented in the southeast Caribbean, while those from western feeding areas were under-represented. This is in direct contrast to the pattern in the Dominican Republic. Supporting this finding, the proportion of whales showing visible scarring on the flukes from non-lethal attack by killer whales was substantially similar to that previously shown for Norway, yet dramatically lower than shown from western feeding areas. The seasonal pattern of distribution in the southeast Caribbean shows a peak of occurrence about six weeks later than in the Dominican Republic, and there is little overlap in the periods of greatest use. This is consistent with the pattern of sightings from historical whaling records in the southeast Caribbean. These results demonstrate that the humpbacks mating and calving in this region are not a representative subset of those that winter in the Dominican Republic. Given this, the widely-held idea that there is a single West Indies humpback whale breeding population is in need of reconsideration.

In discussion, it was noted that photo-identification comparisons between the southeastern Caribbean and the Dominican Republic have revealed few inter-area matches, suggesting that limited movements between these two breeding ground sub-regions occur. Further support for connectivity between the southeastern Caribbean and feeding areas in the northeastern Atlantic can be derived from tagging data showing movements of three whales tagged off Guadeloupe that appeared to subsequently migrate north, one of which was tracked to waters west of the Faroe Islands (Kennedy *et al.*, 2014). Photo-identification matches ($n=4$) between Guadeloupe and Cape Verde (Steivick *et al.*, In press) and a genetic match of a whale sampled off Trinidad with a sample collected off Norway (Bérubé *et al.*, 2004) are also consistent with the patterns identified in SC/66a/AWMP02.

It was suggested that genetic analyses may provide further insight into the patterns observed in the photo-identification data. While samples from humpback whales were collected from the West Indies as part of the YONAH (Palsbøll *et al.*, 1997; Smith *et al.*, 1999) and MONAH cruises (Clapham *et al.*, 2005), these cruises did not encompass effort outside of

the Dominican Republic and Puerto Rico, and the number of samples available from the southeastern Caribbean is very limited. Thus, additional sample collection would be necessary to make such comparisons.

The SDWG asked if the scars resulting from killer whale attacks become less visible over time, such that older whales might have scars that are difficult to detect. In response, the author noted that field observations indicate that these scars, most of which are acquired as calves, remain distinct over long time periods (several decades).

A small number of records of humpback whales in Venezuelan waters during the summer exist (Acevedo *et al.*, 2008) and correspond with the peak of abundance of whales off Abrolhos Bank, Brazil (Martins *et al.*, 2001). While this raises the possibility that some migration by Southern Hemisphere whales into the southeastern Caribbean could occur, currently there is no evidence of movement between these areas and additional studies would be needed to explore this possibility.

3.2.2 In-depth Assessment

During the SC/65b meeting in 2014, it was noted that phylogenetic analysis of the likely origin of sei whale market samples presented in Baker *et al.* (2014) would be strengthened by the inclusion of a more comprehensive set of reference sequences. As a result, a reciprocal exchange of mtDNA sequence data between the authors and the Institute of Cetacean Research was conducted under the Data Availability Agreement Procedure B data sharing protocol. Results presented in SC/66a/IA03 and SC/66a/IA04 represent a re-analysis of the likely origin of these market samples using this expanded reference sequence dataset, which includes the addition of sequences derived from 488 JARPN II samples, 29 from the 2011 POWER cruise, 304 from past commercial whaling and a small number of sequences from Southern Hemisphere whales.

SC/66a/IA03 used mtDNA control region sequences from market products and from sei whale samples of known origin ('ICR sample') to investigate possible stock origins of the market products. Sequences from 75 market products examined by Baker *et al.* (2014) were obtained under data access Protocol B through the Data Availability Group (DAG). The market products were purchased in Japan (71) and the Republic of Korea (4) (1997-2009). The 821 ICR sei whale samples were collected in the North Pacific: 488 from JARPN II (2002-07); 29 from the 2011 POWER cruise; and 304 from past commercial whaling (1972-73). The NJ-based phylogenetic tree of haplotypes showed clades specific to North Atlantic, North Pacific and Southern Hemisphere. With the exception of the North Atlantic, the clades were supported by low bootstrap values. Phylogenetic analysis suggested affinity of the market products with oceanic basins: 51 products (18 haplotypes) showed affinity with North Pacific haplotypes (all but two products involving a single haplotype showed exact matches to JARPN II haplotypes); three products (two haplotypes) showed affinity with North Atlantic haplotypes; the remaining 21 products (eleven haplotypes) showed an affinity with Southern Hemisphere haplotypes. Therefore most of the market products (68%) were of North Pacific origin and almost all of these can be explained by JARPN II samples. The statistical test comparing North Pacific JARPN II, commercial and POWER samples to market samples of North Pacific affinity showed no significant differences although the analysis of market samples was based on number of products rather than number of individuals. As noted by Baker *et al.* (2014) the occurrence of products

with North Atlantic affinity is explained by the catch and import to Japan of sei whales caught under special scientific permit in Iceland some 10 years ago. With regard to the 21 products with Southern Hemisphere affinity, and on the basis of the current phylogenetic analysis, we suggest that those products could be actually from Southern Hemisphere sei whales. The 21 market products of Southern Hemisphere origin were purchased at a single shop in Osaka, which was 'sampled' till 2007 more intensively than the other purchase locations in Baker *et al.* (2014). Based on a TRAFFIC East Asia report, a hypothesis is proposed that these products could have been stored from the end of commercial whaling in 1979 this is 18 years before the first sei whale market product was purchased in 1997 and 28 years before the last product was purchased in 2007. To elucidate this hypothesis interview with the owner of the single shop in Osaka would be useful, but the name and address of that shop has not been provided by Baker *et al.* (2014). However what is relevant and appropriate for discussion at the in-depth assessment of North Pacific sei whale is the issue of stock structure within the North Pacific, and the present genetic analyses of the relevant North Pacific samples provide no evidence to challenge the single stock hypothesis for this species in the North Pacific.

SC/66a/IA04 reports on continuing efforts to determine the stock origins of sei whales represented by 71 products purchased in Japanese markets from 1997 to 2009, and four products purchased in 2009 at a speciality restaurant in Seoul, South Korea. As described in Baker *et al.* (2014), phylogenetic reconstruction and matching of mtDNA control region sequences with available reference sequences suggested that the 75 market products showed affinities with three oceanic stocks of sei whales; three with the North Atlantic (all purchased prior to 2000), 51 with the North Pacific (all purchased after 2002, including the four products from Korea) and 21 with the Southern Hemisphere (purchased from 1997 to 2007). The comparison showed an exact match of the ICR haplotypes with 49 of the 51 market products previously attributed to the North Pacific, including the four products purchased in South Korea. The matching sequences are consistent with the assumption that these products originated from the JARPN II program. However, none of the three products previously attributed to the North Atlantic or the 21 attributed to the Southern Hemisphere were an exact match to the ICR haplotypes. Although the three products attributed to the North Atlantic could have arisen from Icelandic scientific whaling of sei whales, which ended in 1988, there is no known source for the 21 products attributed to the Southern Hemisphere. Based on this process of exclusion, SC/66a/IA04 concludes that these 21 products must have originated from an Illegal, Unreported or Unregulated (IUU) source. This comparison confirms the utility of the Japanese 'DNA register' for detecting IUU products and the relative ease by which mtDNA haplotypes of sei whales can be compared and standardised; however, the stock origin of the products remains uncertain. A revised phylogenetic reconstruction, including the ICR reference samples, showed strong support for a North Atlantic clade but only weak support for two groups of reference sequences from the Southern Hemisphere, exclusive of the North Pacific reference samples. More reference samples are needed to exclude the possibility of an origin from the North Atlantic or a coastal stock in the western North Pacific.

In discussion of both SC/66a/IA03 and SC/66a/IA04, the SDWG noted that the phylogenetic results of both studies were very similar. With the exception of the North Atlantic, bootstrap support for the remaining clades was low in both

studies. Similar patterns have been identified in other whale species, e.g. fin whales (Archer *et al.*, 2013), suggesting that the results are plausible. Of note, both studies indicated that 21 of the market products demonstrated an affinity with the Southern Hemisphere. This result suggests that these samples would not need to be considered in the context of the IA assessment of North Pacific sei whales.

While the number of haplotypes found among the market samples represents a minimum number of individuals taken, samples that share the same haplotype are not necessarily collected from the same whale and may instead represent different individuals. Although it might be possible to obtain a better estimate of the number of individuals represented in the market samples by integrating information on haplotype diversity, this would require assuming that the oceanic origins of the market products are known and would be limited by the lack of available reference data to characterise haplotype diversity among sei whales in the North Atlantic and the Southern Hemisphere.

From a methodological point of view, the SDWG agreed that it would be valuable to compare results generated by the phylogenetic approach used here with those that could be generated using the Random Forest method presented for fin whales in SC/66a/SD02. Of note, however, a larger number of sei whale reference samples would be needed for such a comparison.

3.2.3 Other Southern Hemisphere whale stocks

In SC/66a/SH13, sequence data of the mitochondrial DNA control region (mtDNA) from individual humpback whales in the Antarctic Peninsula (AP) is used to evaluate the population structure, genetic diversity and mixed-stock apportionments to breeding grounds E2, E3, F1, G and A. These AP samples, collected in 2014, were also compared to another AP dataset collected from 1996-99 in order to document any temporal changes in population composition. Three new haplotypes were identified for the South Pacific dataset that have also not been previously identified in Brazil. Feeding aggregations of humpback whales generally contain a number of haplotypes, and are not simply matrilineal in nature. When comparing the 2014 samples with previous samples collected in the same region (1996-98) from the same time of year they are not significantly different ($F_{ST}=0.00$), indicating that haplotype frequencies are similar within these whales over time. Using a Bayesian mixed-stock analysis, the vast majority were apportioned to Colombia, with very small percentages allocated to French Polynesia/American Samoa (FP/AS), and none to Brazil. This is similar to previous results from Albertson-Gibb *et al.* (2008). From genotype comparison, one positive match was made from the AP samples and a sample from French Polynesia, this is the first such match between this breeding and feeding ground to go along with two photographic matches that have been made. A whale sampled in 2014 was also matched with a 1996 sample collected in the same region. Together, these results improve our understanding of the feeding population of humpback whales around the AP and provide insights for future directions to try and compare samples with other South American regions.

The SDWG thanked the authors for their presentation and noted that this work illustrated the value of collaboration when addressing questions that necessitate combining samples over multiple studies.

In discussion, the value of using a Bayesian approach to incorporate uncertainty associated with un-sampled haplotypes and small sample sizes (Pella and Masuda, 2001), as done in SC/66a/SH13, was highlighted.

Multiple haplotypes were identified within each of the western AP feeding aggregations, suggesting that aggregations were not comprised of whales belonging to a single matrilineal lineage. However, two of the four aggregations appeared similar, with two haplotypes found in roughly similar frequencies in both groups. Although this could be an artifact of small sample size, it may also suggest that some degree of matrilineally driven structure is present on the feeding ground. Analysis of additional feeding ground samples may allow further exploration of this possibility.

In discussion, it was noted that the results suggest that a relatively small proportion of the whales sampled in the western AP utilise the FP/AS breeding ground. The confidence intervals surrounding this estimate encompassed zero, raising the possibility that no movements of whales between the FP/AS breeding ground and the western AP occur. However, it was noted that further support for a limited degree of connectivity between the western AP and FP/AS is provided by the identification of a genotype match between the two areas.

The need to interpret these results in the context of the relative abundance of whales in each area was highlighted. The number of whales utilising the FP/AS breeding ground is small, *ca* 850 (Albertson-Gibb *et al.*, 2009). If the number of whales feeding in the western AP is large, then a substantial proportion of the whales using the FP/AS breeding ground may feed in the western AP while only representing a small proportion of the whales in the feeding area.

Finally, it was noted that one challenge in using mixed stock analyses is that it is difficult to detect the contribution of a small source population to a large mixed-stock aggregation without very comprehensive sampling of the mixture area. This is a statistical issue rather than a genetic one but needs to be considered when using this type of analysis.

SC/66a/SH19 provides new information on the genetic identity of blue whale around New Zealand based on $n=9$ samples of blue whales collected in 2014 from the Taranaki Bight, a foraging area off western coast of the New Zealand North Island (about 40°S), three from biopsy samples collected elsewhere in New Zealand and $n=11$ from strandings collected over the last 20 years. An associated report, SC/66a/SH06, includes preliminary genetic analysis, as well as results of a multidisciplinary study of habitat use and population identity. Sequencing of the mtDNA control region from the 23 New Zealand samples resolved five haplotypes, the most common of which (haplotype d) is shared with both subspecies (at low frequencies) and all populations (except the small sample from the Maldives). The five mtDNA haplotypes from the 23 New Zealand samples were included in a phylogenetic reconstruction with published sequences from three other regions in the Southern Hemisphere: southeast Pacific Chilean coast ($n=113$), Australia ($n=28$) and the Southern Ocean (assumed to represent Antarctic blue whales, $n=183$). The New Zealand haplotypes grouped with other haplotypes were reported to be common in the sample from Australia. Despite the lack of phylogenetic distinctiveness, the New Zealand sample was highly differentiated from the southeast Pacific Chilean pygmy and Southern Ocean Antarctic blue whale population, but not from the Australian population.

To confirm the subspecies identity of the New Zealand samples, microsatellite genotypes ($n=14$ loci) were compared to those previously reported for the Antarctic blue whales (Sremba *et al.*, 2012) using the program STRUCTURE. The program gave highest likelihood to $K=2$ populations, corresponding to the New Zealand blue whales and the Antarctic blue whales. All the New Zealand whales were excluded from the population representing the

Antarctic blue whales but one individual considered to be an Antarctic blue in the IDCR/SOWER dataset appears to be misclassified and one appears to be a potential hybrid/admix of New Zealand and Antarctic. These require further investigation.

In discussion, it was noted that the lack of genetic differentiation between the blue whales sampled off New Zealand and those sampled off the southern and western coasts of Australia contrasts with the acoustic differences in song types that have been observed between these areas. In general, caution should be used when interpreting the significance of acoustic differences between regions, as evidence of horizontal transfer of songs between regions has been demonstrated in humpbacks (Garland *et al.*, 2011; Garland *et al.*, 2013). In blue whales, however, calls have been shown to be highly stereotypical and are known to remain stable over decades (McDonald *et al.*, 2006).

Unlike the LeDuc *et al.* (2007) analysis, the comparisons made in SC/66a/SH19 utilised only those samples collected off the southeastern Australian coast to represent Indian Ocean blue whales. The haplotypes frequencies identified in this sample set is strikingly similar to those identified among the New Zealand blue whales. Both of these areas are considered feeding grounds (Gill, 2002; Rennie *et al.*, 2009; Torres, 2013; SC/66a/SH06). It was noted that there is a general lack of information about blue whale breeding ground locations and usage, but a recent tagging study tracked blue whales from feeding areas in southeastern Australian waters to potential breeding areas in Indonesian waters (Double *et al.*, 2014).

It was noted that the genetic analyses in SC/66a/SH19 indicate that all of the samples collected from stranded New Zealand blue whales were pygmy-type blue whales. The authors are currently trying to identify whether morphological data for any of these whales was collected and could be compared with the genetic results.

Multiple labs are currently conducting genetic analyses of blue whales samples. The SDWG recommended that researchers in these labs work together to identify a standardised set of genetic markers that could be utilised in future studies. This effort would facilitate integration of and comparisons between datasets generated in different labs, providing a more complete picture of blue whale population structure world-wide.

SC/66a/SH29 presents the first genetically confirmed documentation of living Omura's whales, including descriptions of basic ecology and behaviour from northwest Madagascar. Species identification was confirmed through molecular phylogenetic analyses of biopsy samples from 23 animals. All individuals shared a single haplotype in a 402bp sequence of mtDNA control region, suggesting low diversity and a potentially small population. Sightings of 44 groups indicated preference for shallow-water shelf habitat with frequent observations of lunge feeding, likely on zooplankton. Observations of five mothers with young calves, and recordings of a stereotyped, repetitive song-like vocalisation uttered in choruses indicated reproductive behaviour. Social organisation consisted of loose aggregations of predominantly single individuals that were spatially and temporally clustered. Photographic recapture of an adult female re-sighted the following year with a young calf, and reports of continual presence at least from April to December, suggest a resident population. The results demonstrate that the species is a tropical whale without segregation of feeding and breeding habitat, and is likely non-migratory. The extension of the range of this rare whale into the western Indian Ocean fundamentally alters the

understanding of this potentially widely distributed species, and raises questions about the demography, dispersal, radiation and genetic continuity among populations.

In discussion, it was noted that future comparison of the mtDNA sequence derived from the Omura's whale that stranded off Mauritania (reported below in SC/66a/SD01) with the mtDNA sequence of the Omura's whales from northwest Madagascar could provide insight into the provenance of the stranded whale.

3.2.4 Other

SC/66a/SD01 reports on the finding of a 3.98m long, juvenile rorqual *Balaenoptera* sp. in advanced decomposition near Chott Boul (16°32.488'N, 016°27.0317'W), Mauritania in 2013. Photographs and skin samples were taken but the specimen could not be collected. Based on limited morphological evidence only *B. edeni* and *B. omurai* were plausible. Three mtDNA regions, i.e. parts of the *cox1* and the *cytb* genes as well as the D-loop, sequenced for a total of 2,636 bp (>16% of the mitogenome) unambiguously identified the specimen as an Omura's whale (*Balaenoptera omurai*), representing the first record in the Atlantic Ocean and at least 18,000km away from its closest known range in the (sub)tropical Indo-Pacific. The question whether the specimen is a vagrant or belongs to an unrecognised Atlantic population was discussed. Long-distance advection by currents or transport on a ship's bow bulb following collision was discarded. Circumstances (calf/juvenile status, great distance from Indo-Pacific, necessary interoceanic passage through cold temperate waters) may slightly favour the hypothesis that Omura's whale, if rare, could be autochthonous in the Atlantic.

The SDWG thanked Pastene for presenting this interesting finding on behalf of the authors.

4. TERMINOLOGY AND UNIT-TO-CONSERVE

Following a recommendation arising in 2011 (IWC, 2012), the SDWG began working on compiling a 'go-to' glossary of stock related terms, with the aim of encouraging consistent use of stock related terms within Scientific Committee reports and in papers submitted to the Scientific Committee. Initial work on this glossary focused on defining terms most commonly used in assessments of baleen whales. At SC/65b, a joint session of the SDWG and the Small Cetaceans sub-committee was held to evaluate how the terms in this glossary aligned with terminology used in the SM sub-committee discussions. Several concerns were raised (IWC, 2015) regarding the application of these terms to small cetaceans, largely due to differences in the behaviour and life history of small cetaceans relative to baleen whales.

This year, the SDWG held a second joint session with the Small Cetaceans sub-committee to evaluate how further progress could be made. After further consideration of the concerns raised at SC/65b, it was decided that one way forward would be to develop a 'Rosetta Stone' of stock structure related terms used by the different sub-committees and working groups as well as by relevant outside groups (e.g. the IUCN) that would identify equivalencies between terms. Once compiled, this 'Rosetta Stone' would highlight where changes in terminology might be made to improve consistency of usage. An intersessional email group was formed under Lang (see work plan, Item 7.2).

5. TOSSM (TESTING OF SPATIAL STRUCTURE MODELS)

TOSSM was developed with the intent of testing the performance of genetic analytical methods in a management

context using simulated genetic datasets (Martien *et al.*, 2009), and more recently the TOSSM dataset generation model has been used to create simulated datasets to allow the plausibility of different stock structure hypotheses to be tested (Archer *et al.*, 2010; Lang and Martien, 2012). The SDWG noted that TOSSM has been particularly valuable in informing the interpretation of results of stock structure related analyses, but it has not been widely utilised outside of the IWC SC.

The SDWG considered whether TOSSM might be used more frequently if it was available in a more user-friendly package. In its current format, the use of TOSSM requires at least a basic knowledge of the R language, which some potential users may be reluctant to tackle. Archer reported that he had attended a recent workshop focused on creating an R package that will guide users through the workflow of implementing simulations in population genetic questions. Rmetasim (Strand, 2002), which is the package that creates the density-dependent individual-based model used for generating simulated datasets in TOSSM, will be integrated into this more user-friendly package. A prototype is expected to be available in the next year or two and will have some overlap with the functionality of TOSSM. The SDWG expressed their appreciation for this effort and noted that this may allow the TOSSM framework to be utilised by a wider audience.

An additional limitation associated with the use of TOSSM is that it has not been updated to be compatible with the current version of R, and thus is no longer available on the SWFSC website or on the CRAN repository. The SDWG **recommended** that the TOSSM package be updated and made more easily accessible through the SWFSC TOSSM webpage. Lang noted that she would contact the TOSSM developers to initiate this process.

Finally, the SDWG noted that a wide-range of simulation-based software is currently available and may have utility to the group. As such, the SDWG's TOSSM agenda item should be expanded to include review of a wider range of simulation tools. As such, the SDWG looks forward to reviewing papers demonstrating the utility of such simulation-based software to stock structure issues in future sessions.

6. OTHER ISSUES

No other issues were discussed.

7. WORK PLAN

7.1 Genetic analysis guidelines

The genetic analysis guidelines are anticipated to be completed intersessionally (convened by Waples) and should be ready to circulate within the Scientific Committee at SC/66b.

7.2 Stock definition terminology

An intersessional email group was formed to identify stock-related terms used by different sub-committees and working groups as well as by relevant outside groups (e.g. the IUCN). Once a list of relevant terms has been compiled, equivalencies between terms can be identified and modifications to better align terminology used by the different sub-committees and working groups can be proposed. The group was convened by Lang and includes Cipriano, Fortuna, Natoli, Rodriguez-Fonseco and Tiedemann and will report on progress at SC/66b.

8. ADOPTION OF REPORT

This report was adopted at 15:00 on 30 May 2015.

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Appendix 1

AGENDA

1. Introductory items
 - 1.1 Convenor's opening remarks
 - 1.2 Election of Chair and appointment of rapporteurs
 - 1.3 Adoption of agenda
 - 1.4 Review of documents
2. Guidelines and methods for genetic studies and DNA data quality
 - 2.1 Guidelines for genetic data analysis
 - 2.2 DNA quality
 - 2.3 Other developments
3. Statistical and genetic issues relating to stock definition
 - 3.1 Population structuring and migration rates
 - 3.1.1 Bowhead, right, and gray whales
 - 3.1.2 In-depth assessment
 - 3.1.3 Other Southern Hemisphere whale stocks
 - 3.2 Population assignment and mixing
 - 3.2.1 Aboriginal subsistence whaling management procedure
 - 3.2.2 In-depth assessment
 - 3.2.3 Other Southern Hemisphere whale stocks
 - 3.2.4 Other
4. Terminology and unit-to-serve
5. TOSSM
6. Other issues
7. Work plan