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Genetic analyses on stock structure of fin whales in the Indo Pacific region of the Antarctic feeding grounds

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ABSTRACT

The stock structure of fin whales in the Indo Pacific region of the Antarctic feeding grounds was investigated using 478bps mitochondrial (mtDNA) control region sequences and genotypes at sixteen microsatellite loci for a total of 108 genetic samples collected in Areas III-VIW under the JARPA, JARPAII, NEWREP-A and SOWER cruises. The observed haplotype diversity was extremely high (0.993 across all samples) with large number of singletons, and mtDNA diversities represented by haplotype (0.984-1.000) and nucleotide (0.0111-0.0115) diversities were comparable among three sample populations, i.e., POP1 (-70°E), POP2 (70°E-160°E) and POP3 (160°E) which were defined based on the genetic analyses without *a prior* population grouping, *i.e.*, STRUCTURE, PCA and geographic cline of genetic variations. In addition, insignificant departures from Hardy-Weinberg equilibrium and F_{IS} estimates observed in each sample population and across all samples suggested a lack of genetic structure of this species. This was supported by hypothesis tests, *i.e.*, heterogeneity tests and pairwise F_{ST} estimates, among the sample populations using both markers. This inference was also consistent with the haplotype network with no distinct clusters of samples corresponding to sampling localities. On the other hand, the geographical cline of F_{IS} estimates gradually shift to the positive in the east of 130°E, which implied a mixing of different stocks in the eastern part of the present survey area. Taking this observation together with the findings suggesting a lack of genetic structure of this species, further consideration with a greater number of samples, particularly in Areas I, V and VI, will be needed to conclude the genetic structure of the Antarctic fin whales.

KEYWORDS: ANTARCTIC, GENETICS, FIN WHALE, JARPA, JARPAII, NEWREP-A, SOWER

INTRODUCTION

Little information is currently available on the stock structure of fin whales in the Antarctic. As in the case of the blue whale, earlier mark-recapture analysis showed that most whales return to the same part of the Antarctic year after year (Brown, 1954). Subsequent mark-recapture studies conducted by Brown (1962) suggested that the six whaling areas are probably more valid for blue and humpback whales than for fin whales (see also Mackintosh, 1965). The past information suggested there was certain segregation of fin whales in the feeding ground between certain longitudes in four sectors which lie: South of the Atlantic Ocean, South of the Indian Ocean, South of Western South Pacific Ocean and South of Eastern South Pacific Ocean (Mackintosh, 1965). South of the Indian Ocean correspond approximately to JARPAII Areas IIIE and IV and South of Western South Pacific to JARPA and JARPAII Areas VIW and V. It is important to investigate whether such geographical segregation is supported by genetic differences.

Wada and Numachi (1991) conducted allozyme analysis using North Pacific, Spanish coastal and Antarctic fin whales. They showed significant allele frequency differences between Hemispheres. However, they could not detect evidence of more than one stock within the Antarctic or within the North Pacific fin whales.

First study based on JARPA biopsy samples and mtDNA has been conducted to examine genetic differences between the whales from IIIE+IV and VW (Pastene *et al*., 2005). Although the authors found no evidence of the genetic differences between IIIE+IV and VW, the sample size was too small (8 and 15, respectively) to make a firm conclusion on stock structure of this species in the Antarctic.

A subsequent genetic study based on JARPA biopsy and additional JARPAII research take and biopsy samples from Areas IIIE (n = 6), IV (n = 23), V (n = 24) and VIW (n = 2) were conducted with two genetic markers, mtDNA control region sequencing and 16 microsatellite DNA loci, to investigate stock structure of this species (Goto *et al*., 2014). This study found no statistical significant difference in mtDNA haplotype frequencies between Areas IIIE+IV and Areas V+VIW, but showed a significant differences in the microsatellite allele frequency between Areas IV and V with a significant deviation from the Hardy-Weinberg equilibrium (*HWE*) in Area V. Based on these findings, Goto *et al*. (2014) suggested the possibility of genetic structuring of fin whales in the JARPAII survey area, which should be further explored with the analyses of a large number of samples.

In this study, mtDNA and microsatellite analyses were conducted, using 53 additional biopsy samples newly obtained under the JARPAII, NEWREP-A surveys and the SOWER cruises after the work by Goto *et al*. (2014) in combination with the samples used in the work by Goto *et al*. (2014), to investigate further stock structure of fin whales in Areas III−VIW.

MATERIALS AND METHODS

Samples and laboratory and laboratory procedures

Genetic samples were available from fin whales caught by JARPAII surveys between 2005/06 and 2010/11 and from biopsies obtained from the sighting surveys of the JARPA, JARPAII, NEWREP-A and SOWER cruises, on an opportunistic basis.

The IWC guidelines for DNA data quality (IWC, 2009) were followed as much as possible (see Kanda *et al*., 2014). Genomic DNA was extracted from all individuals, which were sequenced for the partial mtDNA control region and genotyped for sixteen nuclear microsatellite loci: EV1, EV14, EV21, EV94, EV104 (Valsecchi and Amos, 1996), GT011 (Bérubé *et al*., 1998), GT23, GT211, GT271, GT310, GT575 (Bérubé *et al*., 2000), GATA28, GATA53, GATA98, GATA417, GGAA520 (Palsbøll *et al*., 1997), and DlrFCB17 (Buchanan *et al*., 1996). The details of laboratory procedures are available in Goto *et al*. (2014).

Statistical analysis

We screened parent-offspring pairs or resampled whales using the microsatellite profile and mtDNA haplotypes in the present dataset, and found four whales re-sampled and two calves sampled together with their mother from all data analyses. The six samples were excluded from all subsequent analyses to ensure an independence of the dataset. Table 1 and Figure 1 show the number and geographical position of the genetic samples used in the data analyses, by sampling source and Area.

In order to confirm the possibility of genetic differentiation between Areas IV and V shown by Goto *et al*. (2014) with larger sample size, two Area groups, *i.e.*, Area III+IV and Area V+VIW, were defined (Figure 1). Subsequently, a further genetic structure was explored without *a prior* population grouping.

The False Discovery Rate (FDR) approach (Benjamini and Yekutieli, 2001) was used for adjustment of *P*-value in case of multiple comparisons.

Genetic variations

MtDNA

Haplotype (h) (Nei, 1987) and nucleotide (π) (Nei, 1987: equation 10.5) diversities with sample standard deviations were calculated for each sample population and the entire data set, using the program ARLEQUIN ver. 3.5.2.2 (Excoffier and Lischer, 2010).

Microsatellites

The number of alleles (A) in each locus and across loci was estimated using the ARLEQUIN. The inbreeding coefficient (F_{IS}; Weir and Cockerham, 1984) in each locus and across loci was estimated using the R package '*Demerelate*' (Kraemer and Gerlach, 2017). The departure from *HWE* was tested in each locus using the R package '*HWxtest*' (Engels, 2009), and a global test across loci combining the observed *P*-values in each locus by Fisher's method was performed using the R package '*metap*' (Dewey, 2018). All statistics were calculated in each sample population and the entire data set.

Genetic differentiations

MtDNA

The difference in mtDNA haplotype frequencies among the sample populations was tested using the randomized chi-square Test of Independence (Roff and Bentzen, 1989). In each test, a total of 10,000 permutations of the original data were performed. A *P*-value smaller than 0.05 was used as a criterion to reject the null hypothesis of panmixia. To measure the mitochondrial differentiation between the sample populations, the pairwise conventional F_{ST} and Φ_{ST} were calculated using 10,000 random permutations of the original dataset in the ARLEQUIN.

Microsatellites

Probability test (or Fisher's exact test) implemented in GENEPOP 4.0 (Rousset, 2008) was used to conduct the heterogeneity tests. Statistical significance was also determined using the chi-square value obtained from summing the negative logarithm of p-values over the 16 microsatellite loci (Sokal and Rohlf, 1995). A *P*-value smaller than 0.05 was used as a criterion to reject the null hypothesis of panmixia.

Exploring genetic structure without a priori population grouping

In order to investigate if there is a geographical cline of the genetic variations within the survey area, changing of genetic variations, *i.e.*, h, π and F_{IS} estimates, were calculated for 30° longitudinal intervals and plotted as moving averages over

60° intervals. The intervals were set considering a geographical distribution gap of this species in the Antarctic around between 100°E and 160°E shown by Miyashita *et al*., 1995, based on the Japanese Scouting Vessel data during 1965-1987/88 (Appendix 1).

Bayesian clustering analysis was performed using microsatellite data to infer the most likely number of clusters using STRUCTURE 2.3.4 (Pritchard *et al.,* 2000). The analysis was conducted with ten independent runs for K = 2 and 3. All runs were performed without information on their geographic origins, using 100,000 Markov chain Monte Carlo repetitions and 10,000 burn-in length using the admixture model with correlated allele frequencies. The web-based program STRUCTURE HARVESTER (Earl and vonHoldt, 2012) was used to estimate the mean posterior probability of data.

The Principal Component Analysis (PCA) was also performed using the microsatellite data, and the first two principal components (PCs) were plotted.

Preliminary phylogeographic analyses

A statistical minimum spanning network (Bandelt *et al*., 1999) was constructed with a 95% connection limit using the computer program PopART (Leigh and Bryant., 2015) to infer phylogenetic relationships among mtDNA haplotypes. The five most frequent haplotypes of fin whales in each of the North Atlantic and the North Pacific found in Archer *et al*. (2013) were used as out groups.

Mismatch distribution analysis (Rogers and Harpending, 1992; Excoffier, 2004) was conducted with 10,000 bootstrap replications in the ARLEQUIN, to infer historical sudden population expansion of the Antarctic fin whale. The observed distribution of pairwise nucleotide differences among individuals was compared with the expected distributions under the Sudden Expansion model (Rogers and Harpending, 1992; Rogers, 1995), and evaluated with goodness-of-fit tests (sum of squared deviations: Schneider and Excoffier, 1999). Fu's F_S (Fu, 1997) was also calculated to test for the selective neutrality.

RESULTS

Genetic variations

A segment of 478bp of the mtDNA control region was sequenced for all samples. A total of 45 polymorphic sites identified a total of 80 unique haplotypes in a total of 108 fin whales, and 60 haplotypes of which were singleton. Except for two transversion sites, all substitutions were transitions. The h and π for the entire sample were 0.993 ± 0.003 and 0.0111 ± 0.0060, respectively (Table 2).

All sixteen microsatellite loci were polymorphic and A ranged from 5 at TAA31 to 28 at EV94. Significant deviations from *HWE* was not shown at any loci as well as across loci for the entire data set implying that fin whales used in the present study derived from a single breeding population (Table 3).

Genetic differentiation between Area groups III+IV and V+VIW

The h was 0.9949in Area III+IV and 0.9894 in Area V+VIW, and the π was 0.0113 in Area III+IV and 0.0107 in Area V+VIW (Table 1 in Appendix 2). These diversities were comparable between Area groups. Significant deviations from *HWE* were not observed at any loci and across loci in each Area group after FDR correction, which suggested the samples in each sample population derived from a single breeding population (Table 2 in Appendix 2). Heterogeneity test showed no significant differences in the haplotype (χ^2 = 75.72, P = 0.754) and microsatellite allele (χ^2 = 34.45, df = 32, P = 0.351) frequencies between the Area groups, which was consistent with the pairwise F_{ST} estimates suggesting insignificant differentiation between the groups for both markers (Tables 3a and 3b in Appendix 2).

Exploring genetic structure without *a priori* population grouping

The clustering patterns in each K estimated by the program STRUCTURE did not show a distinct genetic structuring of this species (Figure 3). This was confirmed by the results of PCA showing a geographical overlap of samples on the coordinate plane (Figure 4). On the other hand, the trend of h and F_{IS} slightly changed around the area between 70°E and 160°E (Figure 2). Taking all findings together, hereafter, a further genetic structure was investigated with the alternative sample populations, *i.e.*, POP1 (-70°E), POP2 (70°E-160°E) and POP3 (160°E-) (Figure 1).

Genetic differentiation among alternative population definition

MtDNA

The h and π in each sample population ranged from 0.9842 to 1.0000 and from 0.0111 to 0.0115, respectively (Table 2), which were comparable with each other. The chi-square statistical comparison showed no significant differences in the haplotype frequency among three sample populations (χ^2 = 156.40, P = 0.650). The pairwise conventional F_{ST} and Φ_{ST} also showed no statistically significant differentiation between sample populations (Table 4a).

Microsatellites

Significant deviations from *HWE* were not observed at any loci and across loci in each sample population and the entire data set after the FDR correction (Table 3), which suggested that the samples in each sample population derived from a

single breeding population (Table 3). Heterogeneity test showed no significant differences in microsatellite allele frequencies among sample populations ($\chi^2 = 33.24$, $df = 32$, $P = 0.407$), which was consistent with the pairwise F_{ST} estimates suggesting insignificant differentiation between sample populations (Table 4b).

Preliminary phylogeographic analyses

A minimum spanning network based on 80 mtDNA haplotypes found in the Antarctic Ocean with the five most common haplotypes in each of the North Pacific and the North Atlantic showed a distinct separation of the Antarctic fin whales from the North Pacific and the North Atlantic whales by several mutation steps (Figure 5). The haplotype network revealed one of the Pacific haplotypes, Haplotype 89, is separated from the Antarctic haplotype, Haplotype 54, only by three mutational steps, while all Atlantic haplotypes were separated from the Antarctic ones at least by five mutational steps. The network also showed that the distinct geographic concordance of the network was not observed within the Antarctic and some frequent haplotypes, *e.g.*, Haplotypes 24 and 33, were shared among the sample populations.

The mismatch distribution analyses showed a unimodal distribution, with comparable τ ranging from 4.0 to 5.5, in all sample populations (Figures 6a-6c) and the entire data set (Figure 6d), which was supported by each of the significant negative Fu's F_S. However, the goodness-of-fit tests suggested that the observed mismatch distributions significantly deviated from the simulated distribution under the Sudden Expansion model in each of POP1 and POP2 and the entire data set (Table 2).

DISCUSSION

Genetic variations and stock structure

The present study did not indicate a genetic differentiation between Area III+IV and Area V+VIW for both markers. This observation was inconsistent with the previous study showing a significant difference in microsatellite allele frequency between Areas IV (Indian Ocean) and V (Pacific Ocean) (Goto *et al*., 2014). Although the number of samples was a nearly two-fold increase in total in this study, most of them were collected in the Area III+IV (Goto *et al*. (2014): n = 29, this study: n = 70) and that in Area V+VIW had almost not increased (Goto *et al*. (2014): n = 26, this study: n = 28). If weak differentiated stocks are mixed around Area V as suggested by Goto *et al*. (2014), the different results in heterogeneity tests between the studies might be caused by the uneven sample size between Area groups. Furthermore, considering small sample size in Area V+VI, the geographical mixing stocks could also explain the fact that statistical significance in *HWE* tests in Area V, observed in Goto *et al*. (2014), disappeared in this study because of only one additional sample from Area VI.

The present genetic analyses without *a prior* population grouping, *i.e.*, STRUCTURE analysis, PCA analysis, genetic variations in each *post-hoc* sample population and across all samples, heterogeneity test and pairwise F_{ST} estimates, suggested a lack of genetic differentiation among the Antarctic fin whales at least within the survey area. This inference was also supported by the haplotype network indicating that there were no distinct clusters of samples corresponding to sampling localities with sharing some frequent haplotypes among sample populations. These results did not consistent with the segregation hypothesis of fin whales in the Antarctic feeding grounds proposed by Mackintosh (1965), at least between two, *i.e.*, South of the Indian Ocean and South of Western South Pacific Ocean, of the four areas. A possible explanation for this discrepancy includes geographical mixing of stocks weakly differentiated in a part of the survey area. Pastene and Goto (2016) indicated that two differentiated stocks of Antarctic minke whale, which was another abundant baleen whale in the Antarctic Ocean, are distributed with geographical overlapping around between 130°E-165°E in the Antarctic feeding grounds. Given that the geographical cline of F_{IS} estimates gradually shift to the positive in the east of 130°E, although only a few numbers of samples from the east of 130°E was used in this study, the mixing hypothesis in the area may be true of the Antarctic fin whales. Taken this together with the observations suggesting a lack of genetic structure of this species aforementioned, further consideration with a greater number of samples, particularly in Areas I, V and VI, will be needed to conclude the genetic structure and the mixing hypothesis of the Antarctic fin whales.

MtDNA analysis consistently showed no genetic structure of this species in the previous (Goto *et al*., 2014) and present studies. This might be associated with the extremely high *h* close to 1 due to the large number of haplotypes represented by a single individual (singletons). In general, it is considered that too high *h* is not an informative measure of polymorphism, and is not useful in the discrimination of different populations (Li, 1997). The previous studies for other abundant large cetaceans in the Antarctic Ocean showed distinct genetic structure, using mtDNA control region sequences with lower variations than for the Antarctic fin whales, *e.g.*, 0.980 for the Indian sector and 0.975 for the Pacific sector of Antarctic minke whales (Pastene and Goto, 2016) and 0.975 in humpback whales (Schmitt *et al.*, 2014). In population genetic analyses of this species, it is necessary to use other mtDNA region with lower variations that the control region, or to combine routinely the mtDNA control region with other genetic markers.

Preliminary phylogeographic inferences

The haplotype network revealed one of the Pacific haplotypes is separated from the Antarctic haplotype only by three mutational steps, although the distinct geographic clade corresponding to each of the ocean basins. Archer *et al*. (2013) revealed that the North Pacific fin whales was genetically closer to the Southern Hemisphere than the North Atlantic based

on the complete mitogenome, and suggested a possibility that at least one female from the Southern Hemisphere immigrated to the North Pacific approximately 0.37 Ma. The pattern of relationships among haplotypes at inter-oceanic level in the present study was consistent with this finding. The possible gene flow between the North Pacific and the Southern Hemisphere could explain the observed large polyatomic tree of the Antarctic fin whales with the high level of *h*.

The mismatch distribution analysis showed a unimodal distribution in all sample populations and the entire data set, suggesting a historical population growth of this species. This inference was supported by the Fu's *F*s showing significant negative values in all sample populations and the entire data set. On the other hand, *SSD* estimates suggested that the observed mismatch distribution was significantly deviated from the expected under the Sudden Expansion model in POP1 and POP2 as well as across all samples. These results would imply that the Antarctic fin whales undergo the population expansion in the past but the expansion process did not follow the Sudden Expansion model.

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Table 1. Sample size used for data analyses in this study by sampling area and source. Left: number of samples for mtDNA analyses, right: number of samples for microsatellite data analyses.

Source	III		IV		V		VI		Total	
JARPA/JARPAII	6	5	23	23	25	25	2		56	53
NEWREP-A			15	15			1	1	16	16
SOWER	34	34	2	2					36	36
Total	40	39	40	40	25	25	3	1	108	105

Table 2. Summary statistics for mtDNA analyzed in the Antarctic fin whale. SSD: Sum of Squared deviation in the Test of goodness-of-fit. Bold means the significant difference.

	n	No. of Hap	h	SD	π	SD	Tau	SSD	Fu's Fs
POP1	40	40	1.0000	0.0056	0.0111	0.0061	5.000	**0.0092**	**-25.42**
POP2	48	40	0.9929	0.0056	0.0111	0.0061	4.000	0.0049	**-25.45**
POP3	20	17	0.9842	0.0205	0.0115	0.0064	5.000	**0.0303**	**-9.74**
Total	108	80	0.9929	0.0026	0.0111	0.0060	5.526	**0.0029**	**-25.36**

Table 3. Summary statistics for 16 microsatellite loci analyzed in the Antarctic fin whale.

Microsatellites	POP1 (n=39)			POP2 (n=48)			POP3 (n=18)			Entire (n=105)		
	A	HWE	F_{IS}	A	HWE	F_{IS}	A	HWE	F_{IS}	A	HWE	F_{IS}
EV37	20	0.443	-0.033	16	0.831	-0.050	15	0.046	0.120	23	0.764	-0.018
EV1	23	0.663	-0.027	22	0.937	-0.058	17	0.924	-0.005	23	0.956	-0.033
GT310	15	0.956	-0.014	15	0.879	-0.067	11	0.930	-0.095	16	0.753	-0.057
GATA28	14	0.550	-0.020	15	0.890	-0.070	11	0.126	0.178	16	0.682	-0.005
GT575	11	0.369	0.011	9	0.956	-0.079	8	0.857	-0.106	11	0.968	-0.052
EV94	23	0.390	0.106	26	0.094	-0.003	15	0.296	0.141	28	0.072	0.062
GT23	15	0.471	-0.008	11	0.441	0.017	14	0.366	0.099	16	0.479	0.019
GATA98	7	0.478	-0.077	7	0.171	0.049	5	0.032	0.039	7	0.007	0.009
EV104	6	0.980	-0.073	5	0.165	0.137	4	0.754	0.076	6	0.714	0.045
GATA417	12	0.706	0.017	17	0.264	-0.035	11	0.896	-0.009	19	0.415	-0.014
GT211	11	0.518	0.017	12	0.323	0.019	10	0.377	0.099	12	0.776	0.032
EV21	4	1.000	0.011	4	0.419	-0.089	6	0.357	0.152	6	0.778	-0.005
DlrFB14	4	0.016	-0.218	8	0.035	0.253	5	0.455	0.158	8	0.068	0.076
EV14	10	0.067	-0.131	11	0.970	-0.032	10	0.093	-0.002	12	0.805	-0.064
GT195	12	0.556	-0.063	10	0.791	0.136	9	0.494	0.122	13	0.822	0.055
TAA31	5	0.201	0.228	3	0.341	-0.196	4	0.010	0.072	5	0.075	0.000
Overall		0.529			0.536			0.078			0.389	

Table 4. Pairwise F_{ST} estimates between sample populations for the Antarctic fin whale: (a) mtDNA and (b) microsatellites. Upper and lower diagonals for mtDNA show the conventional F_{ST} and Φ_{ST} estimates.

(a)

	POP1	POP2	POP3
POP1		-0.0038	0.0002
POP2	-0.0146		0.0020
POP3	-0.0041	-0.0078	

(b)

	POP1	POP2	POP3
POP1		-0.0001	-0.0056
POP2			0.0008
POP3			

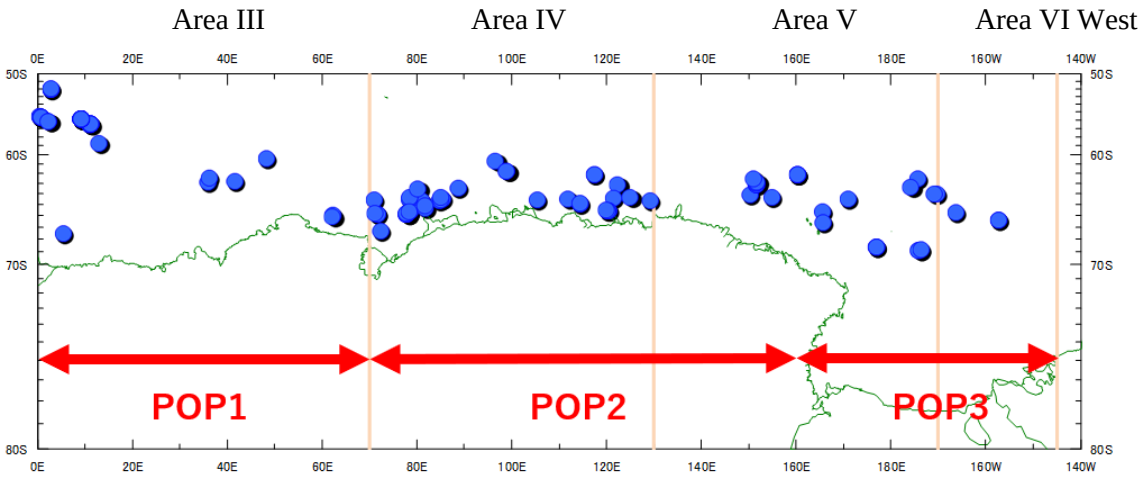

Figure 1. Sampling location of fin whales used in this study.

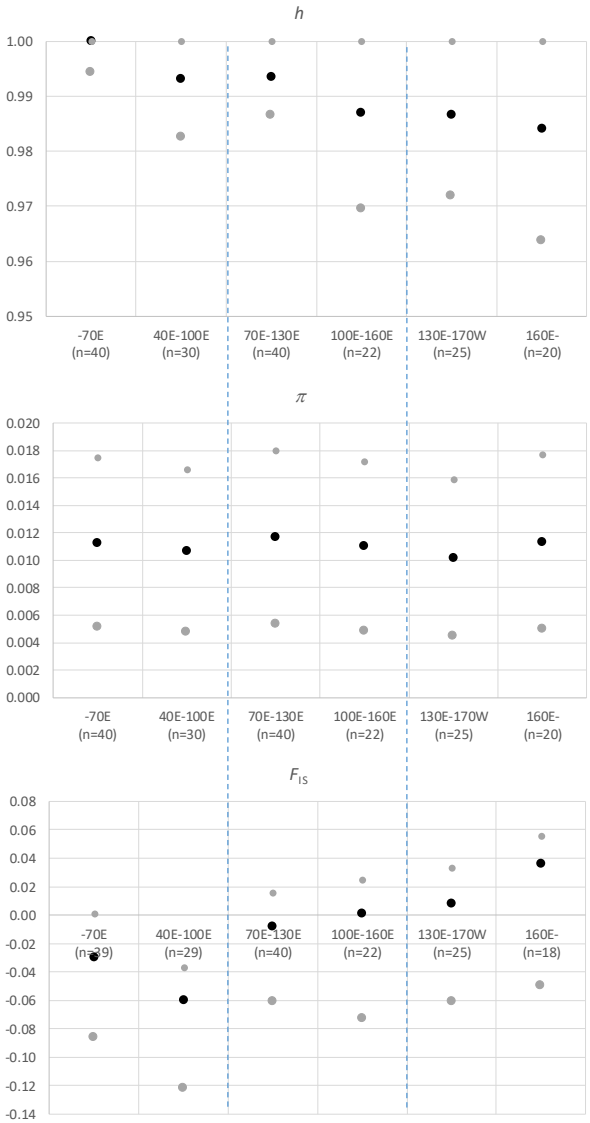

Figure 2. Changing of genetic variations, i.e., haplotype diversity, nucleotide diversity and F_{IS} estimates, along a longitudinal cline of Antarctic fin whales, which were calculated for 30° longitudinal intervals and plotted as moving averages over 60° intervals. Gray points in haplotype diversity, nucleotide diversity indicate the standard deviations, and in F_{IS} estimates indicate upper and lower 95% confidence intervals.

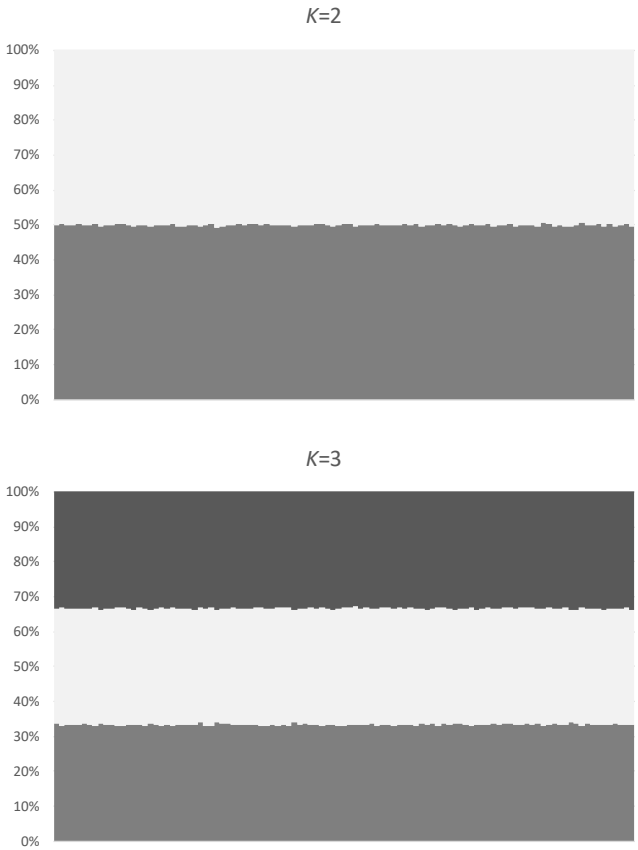

Figure 3. Bar plot of membership probabilities at *K*=2-3 for Antarctic fin whales estimated by the program STRUCTURE. Each individual is characterized by a thin vertical line, which is divided into *K* colored segments on the basis of the individual's membership fractions in *K* clusters.

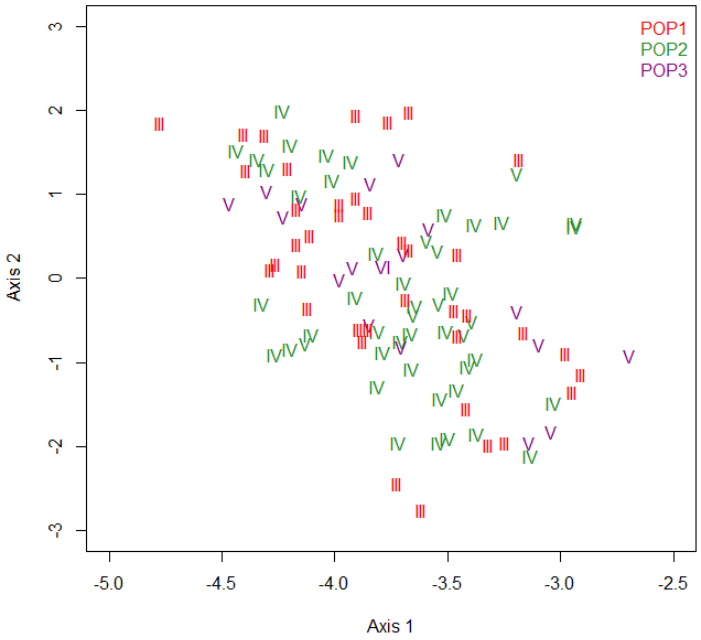

Figure 4. Plot of the first two principal components of principal component analysis representing the 16 microsatellite loci data. Letter indicates the management area defined by the IWC.

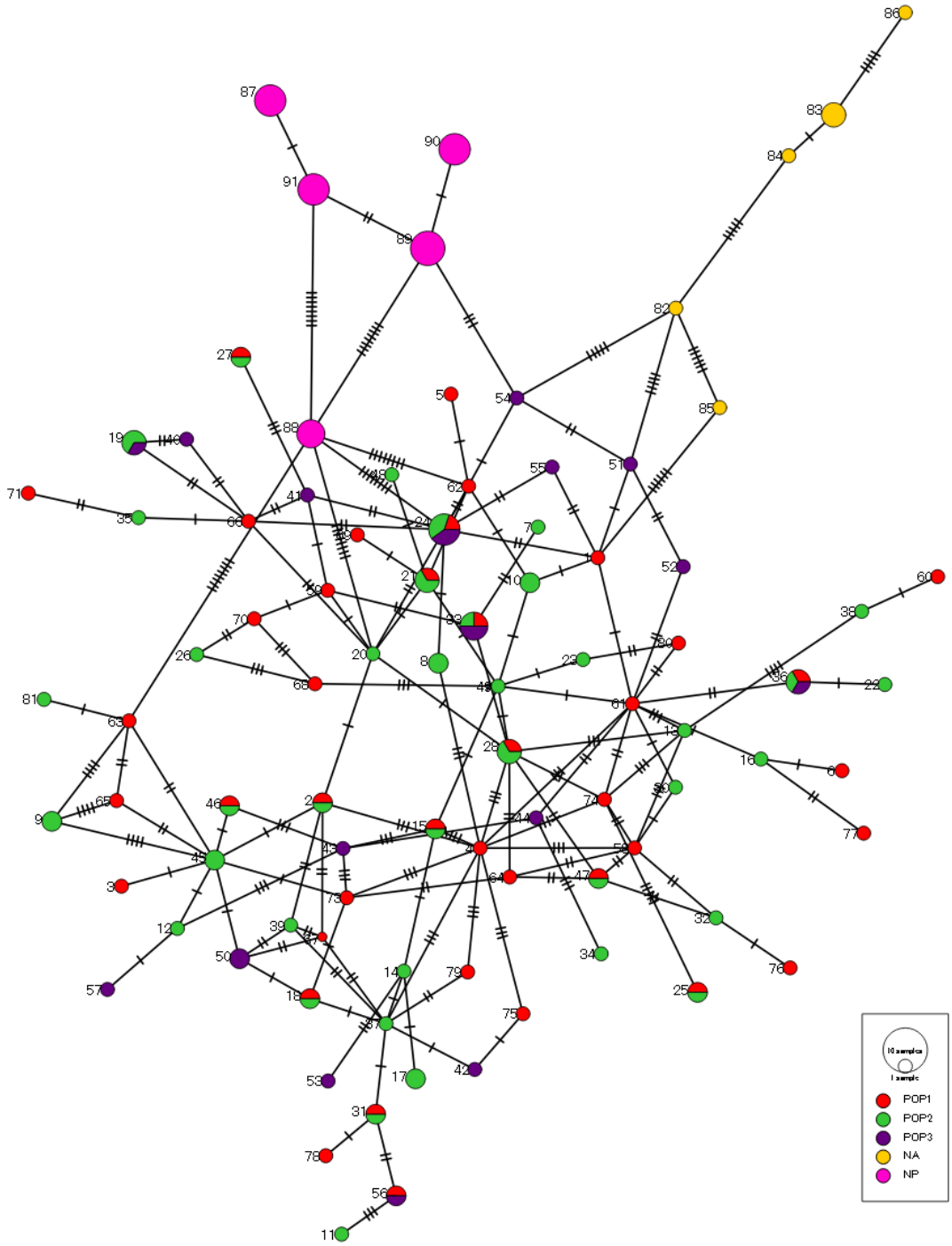

Figure 5. Statistical parsimony network based on 80 mtDNA haplotypes of Southern fin whales. Each line and circle indicate a single mutational step and haplotype. Cross-dash indicates inferred but not found haplotype in this study. Circle size refers to haplotype abundance. Ten haplotypes from the North Pacific (NP) and North Atlantic (NA) deposited in the DDBJ by Archer *et al.* (2013) were used as out groups: Haplotype 82, KC572708; Haplotype 83, KC572709; Haplotype 84, KC572714; Haplotype 85, KC572825; Haplotype 86, KC572826; Haplotype 87, KC572713; Haplotype 88, KC572718; Haplotype 89, KC572719; Haplotype 90, KC572720; Haplotype91, KC572736.

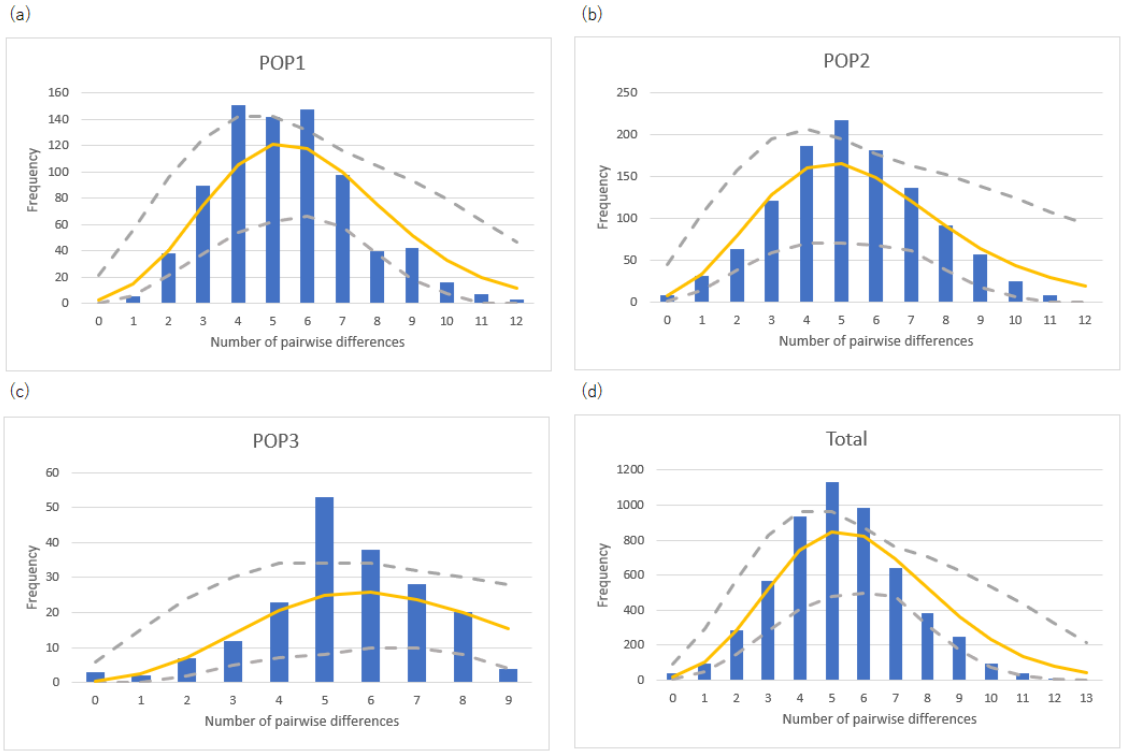

Figure 6. Mismatch distributions under the sudden expansion model: (a) POP1, (b) POP2, (c) POP3 and (d) entire data set. The bar and yellow line show the observed and expected distributions, respectively, and dashed lines indicate upper and lower 95% confidence intervals around the expected distribution.

Appendix 1

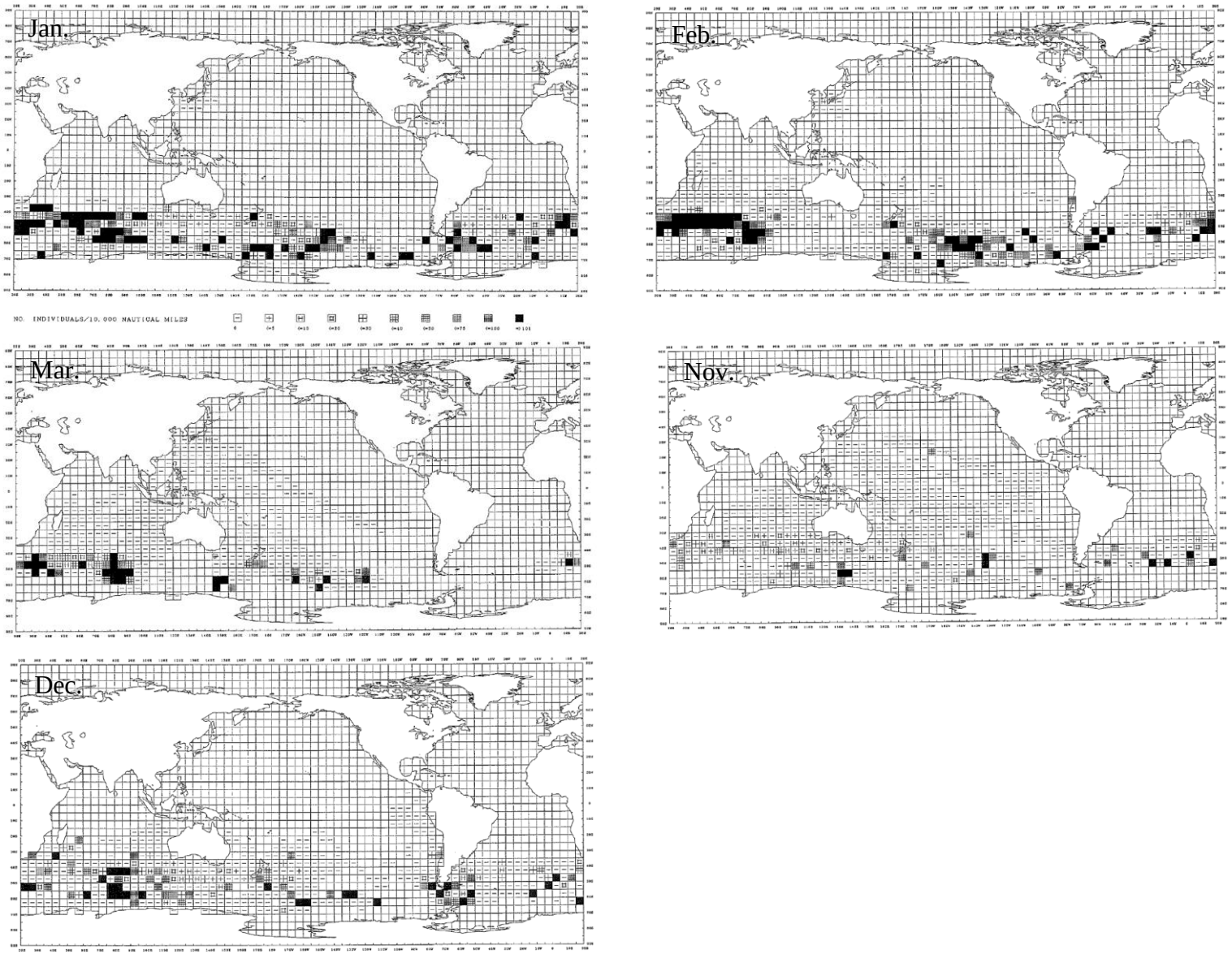

Figure 1. Number of fin whales sighted per 10,000 nautical miles during 1965/66 to1987/88 from the Japanese Scouting Vessel (JSV) data (Miyashita *et al.* 1995). Only months with sighting efforts in the Antarctic Ocean were extracted.

Appendix 2

Table 1. Summary of No. of samples, No. of haplotype, haplotype diversity (*h*) and nucleotide diversity (π) devided by 130° E for mtDNA analyzed in the Antarctic fin whale.

	n	No. of Hap	*h*	SD	π	SD
III+IV	80	65	0.9949	0.0028	0.0113	0.0061
V+VI	28	24	0.9894	0.0123	0.0107	0.0060
Total	108	80	0.9929	0.0026	0.0111	0.0060

Table 2. Summary statistics devided by 130° E for 16 microsatellite loci analyzed in the Antarctic fin whale.

Microsatellites	III+IV (n=79)			V+VI (n=26)			Entire (n=105)		
	A	HWE	F_{IS}	A	HWE	F_{IS}	A	HWE	F_{IS}
EV37	22	0.916	-0.048	17	0.084	0.086	23	0.764	-0.018
EV1	23	0.891	-0.040	22	0.935	-0.008	23	0.956	-0.033
GT310	16	0.950	-0.037	13	0.911	-0.105	16	0.753	-0.057
GATA28	16	0.658	-0.044	12	0.492	0.106	16	0.682	-0.005
GT575	11	0.762	-0.047	9	0.921	-0.067	11	0.968	-0.052
EV94	28	0.148	0.056	19	0.343	0.073	28	0.072	0.062
GT23	15	0.740	0.008	14	0.185	0.058	16	0.479	0.019
GATA98	7	0.140	-0.034	7	0.004	0.147	7	0.007	0.009
EV104	6	0.661	0.052	5	0.451	0.033	6	0.714	0.045
GATA417	17	0.565	-0.018	14	0.970	0.003	19	0.415	-0.014
GT211	12	0.712	0.006	11	0.349	0.093	12	0.776	0.032
EV21	4	0.726	-0.017	6	0.788	0.033	6	0.778	-0.005
DlrFB14	7	0.077	0.034	7	0.444	0.180	8	0.068	0.076
EV14	12	0.538	-0.082	11	0.397	0.001	12	0.805	-0.064
GT195	13	0.517	0.061	10	0.962	0.044	13	0.822	0.055
TAA31	5	0.626	0.062	4	0.003	-0.165	5	0.075	0.000
Overall		0.903			0.091			0.389	

Table 3. Pairwise F_{ST} (upper diagonal) and Φ_{ST} (lower diagonal) estimates for mtDNA (a) and microsatellites (b) between Area groups devided by 130° E for the Antarctic fin whale.

(a)

	III+IV	V+VI
III+IV		-0.0012
V+VI	-0.0091	

(b)

	III+IV	V+VI
III+IV		-0.0020
V+VI		