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Genetic identity of North Pacific minke whales from Korean bycatch and market surveys with progress on quality control review

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Abstract
We report on progress with data quality review and analyses of genetic datasets made available courtesy of the Cetacean Research Center, National Fisheries Research and Development Institute, for North Pacific minke whales taken in Korean bycatch, as reported in SC/D10/NPM2. Information on genetic identity, including mtDNA haplotypes, sex and microsatellite genotypes (up to 11 loci) for 477 samples collected from Korean bycatch was received on 15 September 2010. The bycatch database, referred to as KBC, was first reviewed for data quality and internal consistencies and then compared for external consistency to DNA profiles of 90 individual NP minke derived from independent surveys of commercial markets, referred to as Kmk. Following discussion of data quality issues at the intercessional meeting in December 2010, a revised dataset with minor corrections was received on 15th April 2011 but did not influence the primary conclusions of SC/D10/NPM2.

Tests of differentiation between the 3 Korean populations represented in the KBC dataset confirmed previous reports (SC/62/NPM11) – the Yellow Sea (subarea 5) and the East Sea (subarea 6W) showed significant differences in allele frequencies for microsatellites but not for haplotype frequencies of mtDNA. To investigate previous reports of a strong deviation from HW equilibrium in KBC samples from East Sea (subarea 6W), we simulated a mixed stock using available samples from Yellow Sea stock (assumed to be pure Yellow Sea stock) and subarea 6E (assumed to be pure J stock). The results provided no evidence of a detectable deviation from HW due to a mixing of these two hypothetical stocks, questioning the interpretation that the observed deviation in subarea 6W is due to a Wahlund effect.

We investigated agreement between the KBC and Kmk datasets at two levels: population sampling and individual sampling. At the population level, there were no significant differences in haplotype frequencies or allele frequencies at the 3 microsatellites (after approximate calibration for allele binning). Compared to the market individuals, the sex ratio of the bycatch was significantly more male biased in the 'sry sex' identification and somewhat less male biased in the 'sex' identification. At the individual level, we compared the DNA profiles of bycatch from the years 2003, 2004 and up until 11 February 2005, to the intensive market survey from 2004 and February 2005. Bycatch for this period was represented by 154 samples, presumably including all of the 148 individuals in national Progress Reports for 2003 and 2004. Market surveys included 160 products of 90 market individuals. A comparison of genotypes resulted in likely matches of 49 market individuals to one or more bycatch samples. However, 19 of these 49 putative replicates mismatched for mtDNA haplotypes, suggesting that only 30 of the 90 market individuals were represented in samples of the official bycatch. In summary, market surveys and official bycatch collections are sampling the same population or stock of minke whales but not necessarily the same individuals. This could be explained by market samples originating from unreported bycatch or other forms of IUU exploitation.

Background

Information on genetic identity, including mtDNA haplotypes, sex and microsatellite genotypes (up to 11 loci) for 477 samples collected from Korean bycatch of North Pacific (NP) minke whales, was first made available, courtesy of the Cetacean Research Center (CRC), National Fisheries Research and Development Institute, Korea, through the IWC Data Availability Group on 15 September 2010 (DAG DNA bycatch.xls). The bycatch database, referred to as KBC, was first reviewed for data quality and internal consistencies. The KBC database was then compared for external consistency to DNA profiles of 90 individual NP minke derived from independent surveys of commercial markets in Busan, Ulsan and Pohang from February 2004 to February 2005. The market database, referred to as Kmk, includes mtDNA haplotypes, sex and microsatellite genotypes (5-6 loci), as first described in (SC/62/NPM26).

Initial review of data quality revealed potential errors within the KBC dataset. Internal matching of bycatch genotypes revealed 6 pairs of samples that matched at 9 or 10 of the 11 microsatellite loci, but did not match at mtDNA haplotypes; comparison of mtDNA haplotypes to haplotypes from Korean or Japanese market surveys and from ICR samples of Japanese bycatch and scientific hunting showed 9 potential 'singleton' sequencing artifacts; and there was significant disagreement between the data field labeled 'sex' (presumably visual inspection) and the

field labeled 'sry sex' (presumably a y chromosome marker). Requests for clarification on these potential quality control issues were communicated to the data owners on 26 September 2010 and in summary on 27 October 2010.

Results from analyses and quality control review were reported in SC/D10/NPM2 and discussed at the December 2010 workshop in Busan, Republic of Korea. A revised dataset was received from the Cetacean Research Center (CRC), National Fisheries Research and Development Institute, Korea, on the 15th April 2011 (DAG DNA Korea Revised.xlsx). The new bycatch database, referred to as KBCr1, was again first reviewed for data quality and internal consistencies and then compared to Kmk.

Databases and Methods

Korean bycatch data revised (KBCr1). The revised Korean database received on 15th April 2011 (DAG DNA Korea revised.xlsx) included information on up to 11 microsatellite loci, sex (2 data fields), mtDNA control region sequences (487 bp), and haplotype codes, for 477 samples with associated information on location, date and IWC area (5E and 6W). The mtDNA haplotype codes appeared to be standardized with those in the ICR dataset (Vs2.0 and 3.0). Corrections had been made to 4 samples from 3 replicate pairs (02KBC17, 04KBC53 06KBC50 and 06KBC51) compared with the initial dataset received in August 2010 (KBC). These corrections included changes to collection information (location, date and length), sex (first data field only), mtDNA control region sequence, mtDNA haplotype code and some microsatellite alleles. Corrections had been highlighted in red. Additionally it was noted that the subarea designations had changed from YS (Yellow Sea), ES (East Sea) and KS (Korean Strait) to the IWC Areas 5E and 6W. This change was not included in the email communications.

Korean market data (Kmk). The Korean market data included DNA profiles of 90 'market individuals' derived from 160 whale-meat products purchased during market survey from February 2004 to February 2005, as described in SC/62/NPM26.

Analyses. Analyses involved the programs Micro-checker (Oosterhout *et al.*, 2004), GenAlex (Peakall, Smouse, 2006), Genepop (Rousset, 2008), Cervus (Kalinowski *et al.*, 2007) and Structure (Falush *et al.*, 2003).

Data quality review and analysis of Korean Bycatch

Comparison of KBC to KBCr1: Corrections had been made to 4 samples in the original KBC dataset and resulted in the identification of 3 duplicate samples (02KBC17 = 02KBC18, 04KBC53 = 04KBC44 and 06KBC51 = 06KBC50). These duplicates were 3 of the 6 pairs of possible matches found in our review of the KBC dataset (SC/D10/NPM2). The following samples within each of these pairs, 02KBC17, 04KBC53 and 06KBC51, were removed for all following analyses leaving 474 samples within KBCr1.

mtDNA haplotypes: Initial review of the 39 haplotypes in the KBC data showed matches with 27 haplotypes found in market samples from Korea (Kmk) and Japan or reported in ICR samples of Japanese bycatch and scientific whaling. Of the 12 unshared haplotypes, 9 were apparent 'singletons' (i.e., found in only one sample of the KBC dataset). These unshared singletons were noted and discussed at the Busan workshop. Corrections within the KBCr1 dataset resulted in changes in frequency to 6 of the 39 haplotypes (haplotypes 1, 22, 63, 64, 86 and 95). None of the 9 apparent "singletons" found in KBC were involved in the corrections.

Sex identification: Both the KBC and KBCr1 dataset report 2 data fields referred to as 'sex' and 'sry sex'. We assume that 'sex' was visually determined in the field and that 'sry sex' was the result of a Y chromosome marker. Comparison of the 2 data columns within the KBC dataset showed disagreement in sex identification for 143 of the 424 samples for which information was available in both columns. Corrections within the KBCr1 dataset had only been made to the 'sex' data column for 3 samples. Therefore removal of these 3 replicates did not significantly change the results with 143 of 421 samples for which information was available in both columns showing disagreement (Table 1). While it appears that there is an increase in reporting or identification of sex in the field for the later years (2004 onwards) there is no apparent trend in agreement/disagreement between the two identification techniques. This indicates that there has been no improvement in sry sex identification and that the high level of disagreement is not due to older less reliable techniques. For both datasets the largest disagreement was found for samples identified as females by 'sex' and males by 'sry sex'. This could indicate the need for training of inspectors for visual identification or a systematic error in the sex marker, perhaps due to amplification of a *sry* gene on the X chromosome.

Microsatellites and test of Hardy Weinberg equilibrium. The Korean bycatch revised dataset includes 11 microsatellite loci, 9 of which are dinucleotide repeats and 2 are tetranucleotide repeats. Subarea designations had been changed between KBC and KBCr1 from YS, ES and KS to the IWC Areas 6W and 5E. We choose to use the initial designations with the 3 replicates removed. Initial review of KBCr1 genotypes with Micro-checker showed some evidence of null alleles or homozygote excess for 2 loci (EV21 and GT195) for the East Sea sample but not for the Yellow Sea or Korea Strait. There was no significant evidence of stutter or large-allele dropout in any of the 3 population samples. However, analysis of HW using a two-tailed probability test in Genepop revealed a number of loci showing significant heterozygote deficiency for the East Sea population (Table 2). Such a large number of loci showing heterozygote deficiency could be evidence of a Wahlund effect (i.e., a mixing of the putative Yellow Sea and East Sea J stocks). However, this interpretation is somewhat at odds with the very small effect size of the test of differentiation and the null results of Structure (see below). Alternative explanations for the heterozygote deficiency include inbreeding (including a biased sampling of close relatives) or genotyping error (null alleles or allelic dropout).

To further investigate the strong HW disequilibrium we attempted to simulate a mixing of pure Yellow Sea and pure J stocks. This simulation was done with the KBC dataset and has not yet been repeated with KBCr1. We generated 5 replicate "mixed populations". Each replicate included all the available Yellow Sea genotypes (n=47) and an identical number of randomly-selected subarea 6E genotypes, the latter representing pure J stock. We expected that a 50:50 mix of these samples should reflect the maximum Wahlund effect possible along the East Sea coast of Korea. We tested Hardy-Weinberg equilibrium using a two-tailed probability test in Genepop (option 1.3) (Table 2). Only one locus in one of the 5 simulations approached significance after a simple Bonferroni correction (GATA417). Otherwise, we found no loci out of HWE for any of the 5 simulated mixed populations, suggesting that a Wahlund effect is unlikely to explain the deviation from HWE at multiple loci observed in the East Sea population

Test of differentiation and Structure. Tests of differentiation among the 3 Korean populations represented in the KBC dataset confirmed previous reports – significant differences in allele frequencies were found for microsatellites but not for haplotype frequencies of mtDNA (Table 3). However, the effect size, as measured by F_{ST} was low for both markers and analysis of genotypes with the program Structure failed to reveal evidence of more than a single population (k=1) in Korean waters, i.e., the level of differentiation in microsatellites is too low to be detected in the Bayesian grouping analysis.

Internal matching of Korean Bycatch genotypes and haplotypes

To assess the internal consistency of the KBC data, we sorted samples for matching genotypes using the program Cervus, allowing for up to 2 mismatching loci. The results of this internal matching revealed no matching samples. This was consistent with the expectation that KBC represents only a single sample of each whale killed as bycatch. However, the review did reveal 6 pairs of 'near matches' within the KBC dataset (Table 4). This was unexpected given that the average probability of identity varied from 7.29×10^{-6} to 9.75×10^{-9} for 8 loci (depending on loci and population) and from 3.01×10^{-8} to 1.04×10^{-9} for 10 loci. All 6 pairs of 'near matches' also mismatched for mitochondrial control region haplotype, excluding the possibility that the near matches were close maternal kin.

Of the 6 pairs of near matches, 3 pairs matched at 10 loci and mismatched at 1 locus. Of these, 2 mismatches could be explained by allelic dropout (i.e., the absence of an allele). The other was a 'hard mismatch' at one allele (Table 4). Two pairs matched at 9 loci and mismatched at 2 loci. Of these, 1 mismatch could be explained by allelic dropout. The remaining 3 are hard mismatches with 2 of the samples sharing one allele at both mismatching loci. There was a further pair of samples that matched at 8 loci and mismatched at 2 loci, both of these are hard mismatches with alleles shared at only one locus. Samples in 2 of the pairs came from different areas; one of the pairs was sampled in different years.

The revised KBC dataset, KBCr1, had corrections to 4 samples within 3 of the possible matching pairs (Table 4). Corrections had been made to mtDNA haplotype information, geographic location and to 4 microsatellite loci. Two of these pairs originally matched at 10 loci and mismatched at 1 locus, both potentially explained by allelic dropout. The corrections to both of these samples changed a heterozygote to a homozygote indicating that the initial error was actually a false allele, not allelic dropout. The remaining pair originally matched at 9 loci and mismatched at 2 loci with 1 mismatch explained by allelic dropout and the other a hard mismatch at both alleles. Corrections to both of these samples showed that one of the initial errors was dropout (homozygote was changed to a heterozygote) and

the other mismatch was due to two errors, a false allele (heterozygote changed to homozygote) and an unknown error which had resulted in complete mismatch.

The remaining 3 near matches identified in the KBC dataset remain in KBCr1; 1 pair matching at 10 loci and mismatching at 1 locus, 1 pair matching at 9 loci and mismatching at 2 loci and 1 pair matching at 8 loci and mismatching at 2 loci. All of these mismatches (5 over all pairs) are hard mismatches , there is one shared allele within 4 of the mismatches and the remaining mismatch differs at both alleles. These pairs also have different mtDNA haplotypes. These remaining near -matches can be explained by two scenarios. First, these samples are truly from the same individual, in which case the mismatching alleles are due to genotyping error and the mismatching haplotypes are a misallocation of data to sample, possibly as a result of a sorting error in the Excel spreadsheet. Second, the KBCr1 dataset contains some closely related individuals, none of which are cow-calf pairs.

Population comparison of KBCr1 and Kmk

Given the differences in time periods of the KBCr1 and Kmk samples, we standardized our initial comparison to the bycatch samples reported from the years 2003, 2004 and up until 11 February 2005 (referred to as KBCr103_04). This period pre-dates and overlaps with the intensive market survey from February 2004 and February 2005 (SC/62/NPM26). Market surveys during this period included 160 products of 90 market individuals. Bycatch for this period was represented by 154 samples, presumably including all of the 148 individuals in national Progress Reports for 2003 and 2004.

mtDNA haplotypes frequencies. The KBCr103_04 datasets included 26 haplotypes, 18 of which were found in the Kmk surveys (Figure 1). Comparison of haplotypes frequencies from KBC03_04 to Kmk showed no significant differences ($p= 0.88$, modified Fisher's exact test).

Sex identification. Both KBCr103_04 and Kmk showed a male bias but KBCr103_04 showed a significantly greater male bias for the variable 'sry sex' but not 'sex' in comparison to Kmk (Table 5).

Microsatellites allele frequencies. Of the 11 loci included in KBCr1, only 3 overlapped with the 6 loci included Kmk market, GT211, GATA98 and GATA417. Comparison of allele frequencies for the 3 overlapping loci showed similarities in the shape of the frequency histograms but differences in allele sizes bins (Figure 2). Using the similarities in allele frequencies we attempted a 'frequency-based calibration' to adjust our allele bins to correspond with those of KBCr103_04. After this adjustment, the market dataset contains all the common alleles of the KBCr1 dataset but, as expected for the smaller sample size, is missing a few of the rare alleles. A test of differentiation showed no significant differences in allele frequencies between KBCr103_04 and Kmk at any of the 3 loci ($p>0.05$).

Individual comparison of genotypes and haplotypes

Given the close agreement of the 'frequency-based calibration' for the 3 overlapping loci, we considered it reasonable to search for matching genotypes between KBCr103_04 (n=154) and Kmk databases (n=90). The comparison resulted in matches of 49 market individuals to one or more bycatch samples at 2 or 3 overlapping loci. Although the 3 loci were not sufficient for confident identification ($pID= 2.4 \times 10^{-3}$), these matching genotypes represent potential replicate samples of the same individual as the whale meat is distributed through the market distribution chain. However, 19 of these 49 putative replicates mismatched for mtDNA haplotypes, suggesting that only 30 of the 90 market individuals could be represented in the 154 samples of the official bycatch and some of these potential matches could be the result of false inclusion.

Again, there are several potential reasons for the low rate of 'recapture' between KBCr103_04 and Kmk. First, error in the allele size calibration could be resulting in false exclusion. Second, genotype errors (e.g., allelic dropout) could be resulting in false exclusion. Third, sorting error or misallocation could be resoling in mismatching of genotypes and haplotypes. Finally, it is possible that reporting of bycatch is incomplete and that market surveys include whale taken through other forms of IUU exploitation.

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Table 1: Agreement and disagreement of sex identification by year for the Korea bycatch revised dataset KBCr1. The fields are ordered 'sex'/'sry sex' i.e., F-M is number of samples identified as female in the 'sex' field and as male in the 'sry sex' field. X means no sex ID for that field for that sample. All samples were sex ID'd for 'sry-sex'.

Year	F-F	M-M	F-M	M-F	X-F	X-M	Total
1999	6	1	4	1	4	9	25
2000		2	2		1	3	8
2001	2	3	8		1	5	19
2002	15	22	12	2		9	60
2003	12	45	12	3		16	88
2004		34	25				59
2005	8	48	37	1		2	96
2006	5	43	15				64
2007	1	31	19	2			55
Total	49	229	134	9	6	44	474

Table 2: Test for HWE in Korean bycatch revised samples and in simulated mixed populations of pure Y (Yellow Sea) and J (subarea 6E) stocks, with F_{IS} estimates using the Robertson and Hill (1984; R&H) method as implemented in Genepop. Significant values are shown in bold, those still significant after applying a Bonferroni correction are shown with an asterisk*. No loci are out of HWE for any simulated population, after applying Bonferroni-corrected significance levels for loci within each resampling.

	East Sea		Korean Strait		Yellow Sea		Simulated mixed	
Locus	P val	F_{IS}	P val	F_{IS}	P val	F_{IS}	P val (range)	F_{IS} (mean)
Ev1	0.276	0.008	**0.031**	0.037	0.191	0.073	0.079-0.508	0.084
Ev94	**0.048**	0.186	**0.032**	0.092	0.700	0.062	0.072-0.463	0.175
GT23	**0.038**	-0.005	0.643	-0.041	0.051	0.043	**0.019**-0.373	0.096
GT195	**0.000***	0.202	0.351	0.073	**0.029**	0.011	**0.025**-0.359	0.238
Ev21	**0.000***	0.422	0.708	0.043	0.199	0.124	0.531-1.000	0.085
GT575	0.383	0.025	**0.012**	0.010	1.000	0.007	0.117-0.555	0.032
GT211	0.690	0.000	0.440	0.014	0.156	0.020	0.098-0.832	0.069
DlrFCB14	0.963	0.002	0.821	0.021	1.000	-0.026	0.058-0.954	0.129
GATA98	**0.004***	0.170	0.515	0.040	0.781	-0.071	0.077-0.605	-0.095
GATA417	**0.010**	0.222	0.168	0.073	0.250	0.086	**0.007**-0.915	0.082
Ev37	**0.000***	0.166	0.062	0.000	0.183	0.022	0.205-0.590	0.055

Table 3: Regional differentiation of Korean bycatch revised samples based on A) 11 microsatellite loci and B) mtDNA. Pairwise F_{ST} values shown below diagonal and p values above diagonal, as implemented in Genepop. Significant values are shown in bold.

A) Microsatellite	East Sea	Korean Strait	Yellow Sea
East Sea	-	0.3416	**0.0003**
Korean Strait	0.0007	-	0.1393
Yellow Sea	0.0053	0.0008	-

B) mtDNA	East Sea	Korean Strait	Yellow Sea
East Sea = 366	-	0.763	0.426
Korean Strait = 64	-0.0003	-	0.437
Yellow Sea = 47	0.0014	0.0038	-

Table 4: See next page

Table 5: Comparison of sex identification Korea bycatch (KBCr103_04) and Korean market (Kmk) for A) 'sex' and B) 'sry sex'.

A)'Sex'	F	M
KBCr103_04	50	87
Kmk	20	57

Fisher's exact test, two-tailed p= 0.1305

B) 'sry sex'	F	M
KBCr103_04	15	139
Kmk	20	57

Fisher's exact test, two-tailed p=0.0018

Table 4: Pairs of 'near matches' revealed in the internal matching of microsatellite genotypes from Korean bycatch samples dataset (KBC) and the 4 corrected samples from the revised dataset (KBCr1). Mismatching alleles are shown in bold, matching alleles at mismatching loci are italicized, corrected information is underlined, corrected genotypes are marked with an asterisk*. Loci for which there is no information are shown by -. Genotype matching implemented in CERVUS, allowing for 2 mismatches. Note that the mismatching of mtDNA precludes maternal kinship, unless haplotypes have been misallocated.

Sample code	Area	EV1	EV94	GT23	GT195	EV21	GT575	GT211	DlrFCB14	GATA98	GATA417	EV37	mtDNA Haplotype
02KBC18	KS	**149/*149***	207/211	099/105	169/169	112/114	155/157	098/110	261/263	089/089	210/214	179/199	95
02KBC17	YS	**141/*149***	207/211	099/105	169/169	112/114	155/157	098/110	261/263	089/089	210/214	179/199	64
*02KBC17r	KS/6W	149/149	207/211	099/105	169/169	112/114	155/157	098/110	261/263	089/089	210/214	179/199	95
02KBC32	ES	147/159	207/209	***099*/107**	167/169	112/112	153/155	098/098	261/261	085/085	210/214	179/179	3
02KBC60	ES	147/159	207/209	**093/*099***	167/169	112/112	153/155	098/098	261/261	085/085	210/214	179/179	127
04KBC44	ES	149/149	209/211	099/105	165/167	112/112	155/159	098/100	261/261	089/097	**214/*214***	179/205	1
04KBC53	YS	149/149	209/211	099/105	165/167	112/112	155/159	098/100	261/261	089/097	***214*/218**	179/205	86
*04KBC53r	ES/6W	149/149	209/211	099/105	165/167	112/112	155/159	098/100	261/261	089/097	214/214	179/205	1
03KBC52	ES	149/171	**209/*211***	113/115	165/167	112/112	155/155	**098/*106***	261/261	089/093	214/218	179/199	64
03KBC53	ES	149/171	***211*/213**	113/115	165/167	112/112	155/155	**102/*106***	261/261	089/093	214/218	179/199	46
06KBC50	ES	149/149	211/211	107/109	169/169	112/114	**149/157**	098/098	261/263	***089*/093**	206/210	179/179	63
06KBC51	ES	149/149	211/211	107/109	169/169	112/114	**153/155**	098/098	261/263	***089*/089**	206/210	179/179	22
*06KBC50r	ES	149/149	211/211	107/109	169/169	112/114	155/155	098/098	261/263	089/093	206/210	179/179	63
*06KBC51r	ES/6W	149/149	211/211	107/109	169/169	112/114	155/155	098/098	261/263	089/093	206/210	179/179	63
02KBC11	ES	133/149	209/211	**099/103**	167/169	112/112	155/157	***102*/110**	261/261	089/089	210/214	179/199	64
03KBC83	ES	133/149	209/211	**107/111**	-	112/112	155/157	**098/*102***	261/261	089/089	210/214	179/199	72

Figure 1: Frequencies of 26 mtDNA haplotypes found in Korean bycatch for 2003 and 2004 (KBCr103_04, n=154) compared to Korean market surveys in 2004 (Kmk, n=85). X axis refers to haplotype codes used in the KBCr1 dataset of the CRC. Fisher's exact test, p = 0.88.

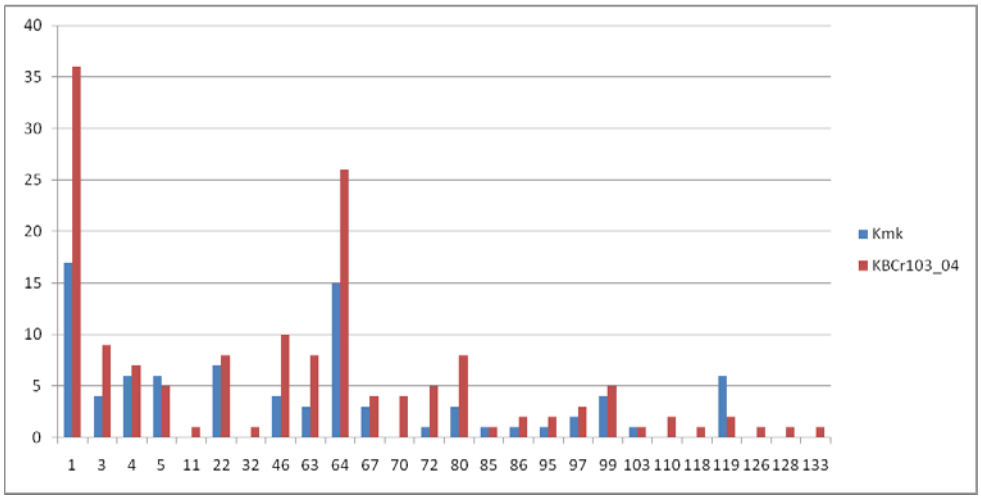
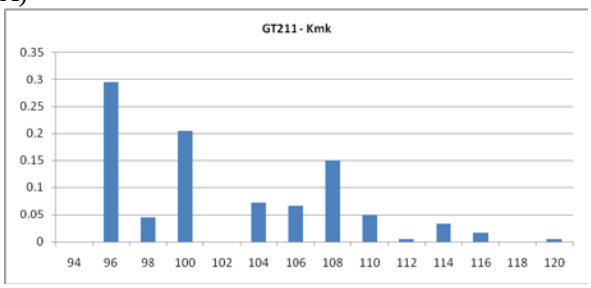
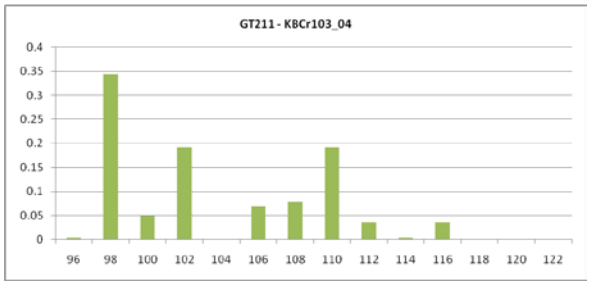


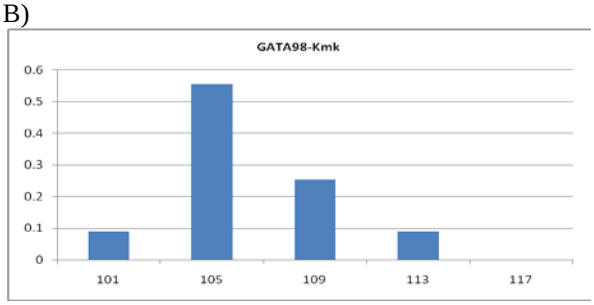
Figure 2: Comparison of allele frequencies of 3 microsatellite loci from Korean market surveys for the year 2004, n=85 (blue) and Korean bycatch revised for years 2003-2004, n=155 (green) prior to frequency-based calibration of allele size bins.

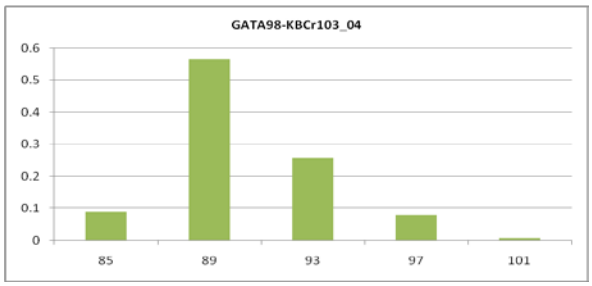
A)





B)





C)