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Mixed-stock apportionment of humpback whales from feeding grounds to breeding grounds in the North Pacific based on mtDNA

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Abstract

The allocation of catches from the feeding grounds to breeding stocks is one of the objectives of the Comprehensive Assessment of humpback whales in the North Pacific. This catch allocation is complicated by the mixing of individuals from different breeding stocks on shared feeding grounds. Here we use mixed-stock analyses to estimate the apportionment of humpback whales from feeding areas to breeding regions (i.e., source stocks), as a proxy for allocation of historical catches. For this, we first updated the frequencies of mitochondrial DNA haplotypes from regional samples collected during the program *Structure of Populations, Levels of Abundance and Status of Humpback Whales* (SPLASH) from 2004-2006, adding nearly 1,000 additional samples to the 1,800 published previously (Baker et al. 2013). Most of these additional samples were collected in Mexico, a region known to have a complex pattern of interchange and varying migratory destinations. We then used the Statistics Programme for Analyzing Mixtures (SPAM) to estimate the contributions of breeding regions to feeding areas based on six scenarios. These six scenarios allowed for revised stratification of both breeding regions and feeding areas, as previously defined by the program SPLASH. The preferred scenario considered apportioning each of the 6 feeding areas to 5 breeding regions, Asia (the Philippines, Okinawa and Ogasawara), Hawaii, offshore Mexico (Revillagigedo Islands), mainland Mexico and Central America.

Introduction

The total number of humpbacks killed in the North Pacific during the 20th century is now estimated to be 29,103 whales (Ivashchenko et al. 2016). Most of these whales were killed in northern latitude feeding areas. The allocation of these historical catches from feeding areas to breeding stocks is one of the objectives of the Comprehensive Assessment of the North Pacific humpback whales. In previous discussion, the Sub-Committee on In-Depth Assessment has noted that DNA profiles include microsatellite loci suitable for population assignment procedures and mtDNA haplotype suitable for mixed-stock analyses (e.g., Albertson et al. 2017; Schmitt et al. 2014). A mixed-stock analysis can apportion feeding ground genetic samples to breeding grounds and estimate the probability of an individual from a feeding ground originating from a defined breeding stock. This apportionment or assignment can be used as a proxy for historical catch allocation in the assessment model for North Pacific humpback whales (IWC 2018).

Here we present mixed-stock estimation using mtDNA haplotypes from samples collected during the program *Structure of Populations, Levels of Abundance and Status of Humpback Whales* (SPLASH) from 2004-2006. We chose to focus on SPLASH because of the synoptic collection of samples from all known (at the time) breeding regions and feeding areas throughout the North Pacific (Figure 1; Calambokidis et al. 2008). We chose to focus on mtDNA because the distribution of this maternally inherited marker reflects patterns of maternal fidelity to migratory destinations (e.g., Baker et al. 2013). Additional analyses are ongoing to include microsatellite loci with the mtDNA haplotypes using the program ONCOR (Kalinowski et al 2007).

SPLASH database update

As a result of the collaborative effort to investigate stock structure for the SPLASH program, the Cetacean Conservation and Genomics Laboratory at Oregon State University adopted a standard DNA profile including sequencing of mtDNA haplotypes, molecular markers for sex and genotyping at 10 micro-satellite loci. This DNA profile was used to identify 1,805 individuals from 2,193 biopsy samples collected as part of the SPLASH program in 2004-2006 (Baker et al. 2013). Since this publication, our laboratory has continued to process SPLASH samples adding an additional 291 DNA profiles from the feeding areas. For the mixed-stock analysis presented here, we have also included haplotypes from an additional 757 samples representing the three regions of Mexico, as delimited in SPLASH (Calambokidis et al. 2008). These haplotypes are included in the PhD thesis of U. Gonzalez Peral but were not fully represented in Baker et al (2013) because they do not include microsatellite genotypes for individual identification. Instead, there was an effort to reduce the potential for replication of samples using the associated photo-identification records.

Revised stratification and mixed-stock scenarios

The original SPLASH program recognized 10 feeding areas and 8 breeding regions. Following discussion of the Working Group, we considered three revised stratifications of breeding regions representing the putative “pure stocks”, and two revised stratifications of feeding areas representing the “mixed-stocks”:

- B1) 4 Breeding regions (including Baja) - [OG+OK+ PHI], Hawaii, [MX-ML+MX-AR+MX-BC], Central America
- B2) 4 Breeding regions (excluding Baja) - [OG+OK+ PHI], Hawaii, [MX-ML+MX-AR], Central America
- B3) 5 Breeding regions (excluding Baja) - [OG+OK+PHI], Hawaii, MX-ML, MX-AR, Central America
- F1) 8 Feeding areas - [RUS+WAL], EAL, BER, WGOA, NGOA, [SEA+NBC], SBC-WA, CA-OR
- F2) 6 Feeding areas (see Figure 2) - [RUS+WAL], [EAL+BER+WGOA], NGOA, [SEA+NBC], SBC-WA, CA-OR

Together, the combination of the revised strata provide 6 Scenarios for mixed-stock analyses: B1/F1, B1/F2, B2/F1, B2/F2, B3/F1 and B3/F2. Note that the samples sizes of the revised strata are simply sums of the previous breeding regions and feeding areas used in SPLASH, except for the addition of new samples and the deletion of replicates within the revised strata (Table 1). For example, SEA includes haplotypes of samples not included previously in Baker et al. (2013) and

the revised stratum, NBC-SEA, includes only one record of an individual, if sampled in both feeding areas.

Note also that the B1 re-stratification is most similar to the 4 Distinct Population Segments currently recognized under the US Endangered Species Act in considering the three regions of Mexico as a single unit. The B2 and B3 strata exclude Baja California on the assumption that it is an area of mixing during migration, rather than a source stock. The B3 stratum recognizes mainland Mexico and the offshore Revillagigedo Archipelago as different breeding stocks based on significant differences in haplotype frequencies from biopsy samples (see Table 2) and migratory destinations from photo-identification (Calambokidis et al. 2008).

Tests of differentiation

The program Arlequin (Excoffier and Lischer 2010) was used to calculate F_{ST} and test for significant differentiation in haplotype frequencies among the breeding regions and among the feeding areas, based on the revised stratification (Tables 2 and 3). The significant differences observed for the breeding regions are consistent with the expectations for “pure” or source stocks. Note, however, there were significant differences in all three of the revised strata for Mexico.

Most of the feeding areas also differed significantly in haplotype frequencies with the exception of some comparison with the Bering, the Western Aleutians, the Western Gulf of Alaska and the Northern Gulf of Alaska. When the Bering, the Western Aleutians and the Western Gulf of Alaska are combined in the F2 stratum [BER+WAL+WGOA], all pair-wise comparisons of the feeding areas are highly significant. The frequencies of haplotypes are shown as pie charts for the B3/F2 stratum as an example (Figure 3). Sample sizes for these pie charts are included in Tables 2 and 3. The frequencies of each haplotype for each of the strata are available in an Excel file on request.

Mixed-stock apportionment

The program SPAM (Version 3.7) was used to estimate the mixing apportionments (Debevec et al. 2000), with implementation of a Bayesian option for baseline allele frequency distributions (Rannala and Mountain 1997). The 95% confidence limits were calculated using the symmetric percentile bootstrap option, following the guidance of the manual. The Standard Error and Coefficient of Variation from the SPAM output files are available in an Excel file on request.

Conclusion: A preferred Scenario?

The B3/F2 Scenario seemed most consistent with other evidence of stock structure in the North Pacific, especially in distinguishing between the migratory destinations of mainland Mexico and Revillagigedo Mexico (Tables 4 and 5). In this Scenario (Figure 4), the BER-EAL-WGOA feeding area received the highest apportionment from Revillagigedo Mexico (65.9%) and SBC-WA received the highest apportionment from Mainland Mexico (69.7%). The highest apportionment to SEA-NBC was from Hawaii (100%) and to RUS-WAL from Asia (68.6%) and Revillagigedo Mexico (26.7%). The apportionment for NGOA was 65.9% from Hawaii and 33.6% from Revillagigedo Mexico. The apportionment to CA-OR was 44.7% from Mainland Mexico and 55.4% from CentAm. The B3/F2 Scenario is shown in

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Figure 1: The distribution of SPLASH samples and the original stratification of 10 feeding areas and 8 breeding regions as described in Baker et al. (2013).

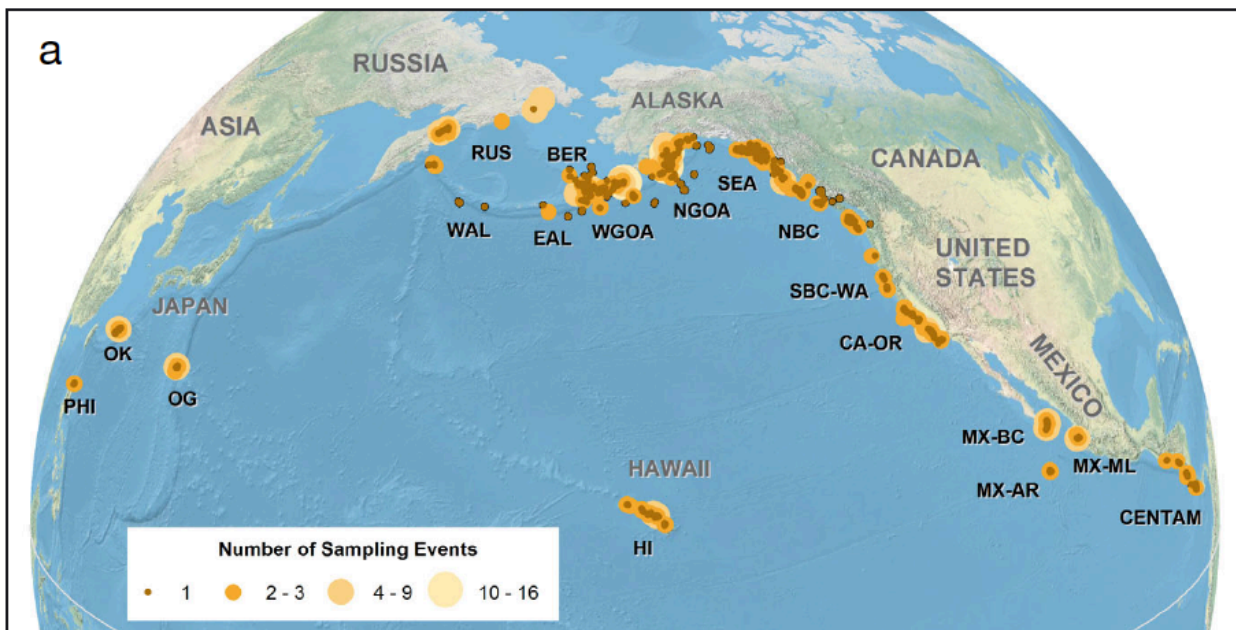


Figure 2: Regions considered in the Comprehensive Assessment of North Pacific humpback whales following discussion by the working group in January 2021 (courtesy of Y. Ivashchenko). The revised stratification of feeding areas shown here is most similar to the F2 stratum.

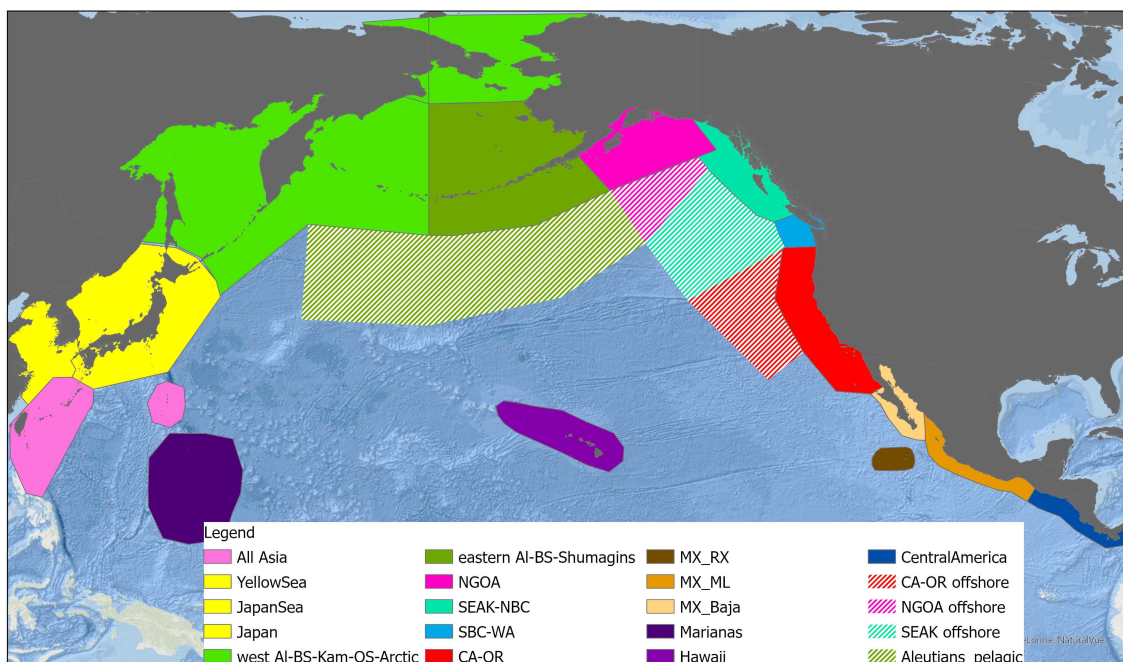
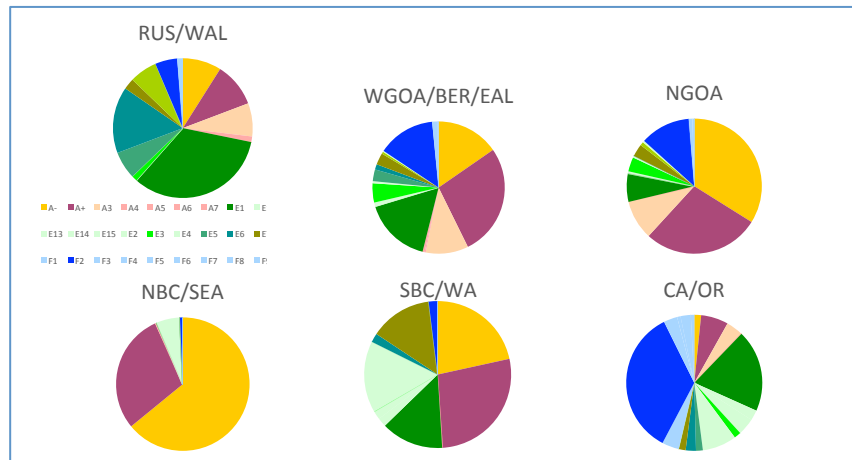


Figure 3: The frequencies of mtDNA haplotypes from samples collected in 6 feeding areas and 5 breeding regions, following Scenario, B3/F2. Samples sizes are reported in Tables 2 and 3.

Feeding areas (F2)



Breeding regions (B3)

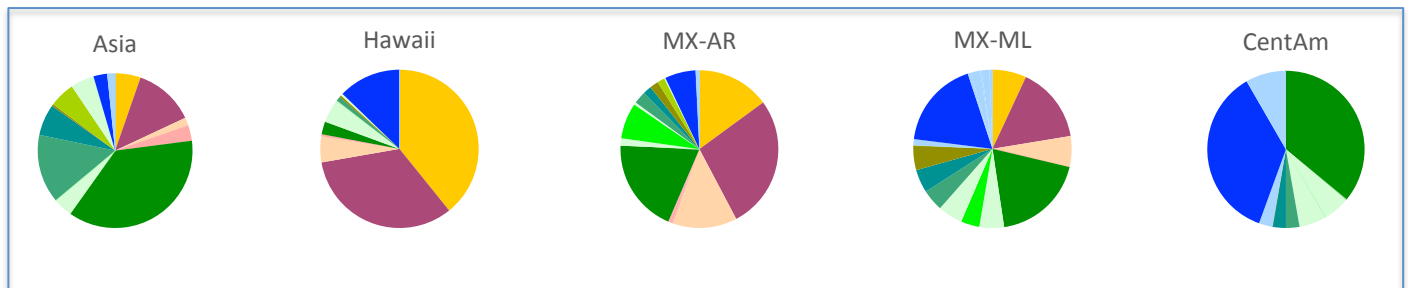


Figure 4: North Pacific humpback mixed-stock apportionment of breeding regions to feeding areas, as outlined in scenario B3/F2 (see Table 5).

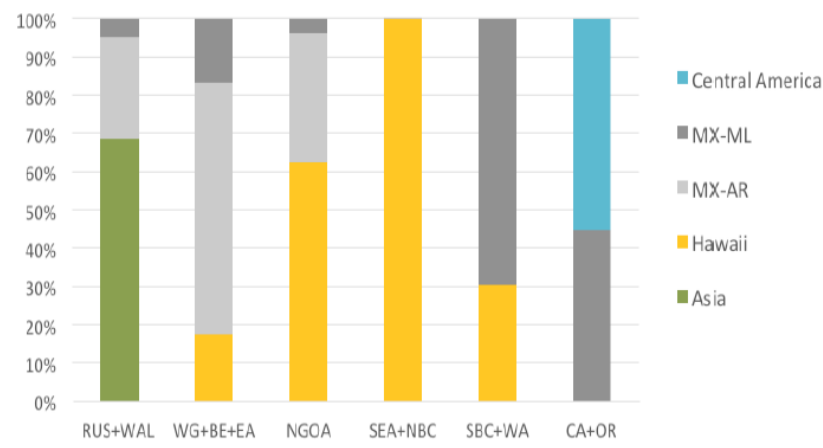


Table 1: The number of samples with mtDNA haplotypes as included in Baker et al. (2013) and as updated here with additional samples collected during SPLASH, from 2004-2006. Abbreviations follow those shown in Figure 1.

SPLASH strata		
Feeding areas	n (Baker et al. 2013)	n (updated)
Russia (RUS)	70	70
Western Aleutians (WAL)	8	8
Bering Sea (BER)	114	205
Eastern Aleutians (EAL)	36	36
Western Gulf of Alaska (WGOA)	96	143
Northern Gulf of Alaska (NGOA)	233	233
Southeast Alaska (SEA)	183	336
Northern British Colombia (NBC)	104	104
Southern BC-Washington (SBC-WA)	51	51
California-Oregon (CA-OR)	123	123
Breeding regions		
Philippines (PHI)	13	13
Okinawa (OK)	72	72
Ogasawara (OG)	159	159
Hawaii (HI)	227	227
Mexico-Revillagigedo (MX-AR)	106	323
Mexico-Baja (MX-BC)	110	317
Mexico-Mainland (MX-ML)	62	395
Central America (CENTAM)	36	36
Total	1,803	2,851

Table 2: Test of differentiation for the breeding regions based on three stratifications. F_{ST} values are below the diagonal, p values are above the diagonal. The revised stratum combining [PHI+OK+OG] is referred to here as Asia and the stratum combining the three regions of Mexico is referred to as MX-all.

a) B1 stratum

	N	Asia	Hawaii	MX-all	CentAm
Asia	244	-	<0.0001	<0.0001	0.0001
Hawaii	227	0.1675	-	<0.0001	<0.0001
MX-all	1035	0.0424	0.0712	-	<0.0001
CentAm	36	0.0801	0.2278	0.0771	-

b) B2 stratum

	N	Asia	Hawaii	MX-AR+ML	CentAm
Asia	244	-	<0.0001	<0.0001	0.0001
Hawaii	227	0.1675	-	<0.0001	<0.0001
MX-AR+ML	712	0.0440	0.0682	-	<0.0001
CentAm	36	0.0801	0.2278	0.0802	-

c) B3 stratum

	N	Asia	Hawaii	MX-AR	MX-ML	CentAm
Asia	244	-	<0.0001	<0.0001	<0.0001	<0.0001
Hawaii	227	0.1675	-	<0.0001	<0.0001	<0.0001
MX-AR	395	0.0560	0.0605	-	<0.0001	<0.0001
MX-ML	317	0.0432	0.0942	0.0233		0.0007
CentAm	36	0.0801	0.2278	0.1196	0.0444	-

Table 3: Test of differentiation for feeding areas based on two revised stratifications. F_{ST} values are shown below the diagonal, p values are above the diagonal.

a) F1 stratum

	N	RUS/WAL	BER	EAL	WGOA	NGOA	SEA/NBC	SBC/WA	CA/OR
RUS/WAL	78	-	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001
BER	205	0.0542	-	0.9072	0.0558	<0.0001	<0.0001	0.0009	<0.0001
EAL	36	0.0606	0.0000	-	0.5256	0.1318	<0.0001	0.0215	0.0015
WGOA	143	0.0365	0.0064	0.0000	-	0.0007	<0.0001	0.0253	<0.0001
NGOA	233	0.1050	0.0298	0.0107	0.0214	-	<0.0001	0.0032	<0.0001
SEA/NBC	440	0.3048	0.2131	0.2097	0.1818	0.0905	-	<0.0001	<0.0001
SBC/WA	51	0.0712	0.0375	0.0343	0.0178	0.0351	0.1802	-	<0.0001
CA/OR	123	0.0749	0.0625	0.0528	0.0717	0.1236	0.3468	0.1075	-

a) F2 stratum

	N	RUS/WAL	WG-BE-EAL	NGOA	SEA/NBC	SBC/WA	CA/OR
RUS/WAL	78	-	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001
WGOA-BER-EAL	384	0.0475	-	<0.0001	<0.0001	0.0018	<0.0001
NGOA	233	0.1050	0.0237	-	<0.0001	0.0028	<0.0001
SEA/NBC	440	0.3048	0.1831	0.0905	-	<0.0001	<0.0001
SBC/WA	51	0.0712	0.0291	0.0351	0.1802	-	<0.0001
CA/OR	123	0.0749	0.0642	0.1236	0.3468	0.1075	-

Table 4: Estimates for apportionment of mixed-stocks for humpback whales on the feeding areas of the North Pacific based on 3 Scenarios derived from re-stratification of breeding regions, B1/F1, B2/F1 and B3/F1. Apportionment estimates and 95% bootstrap CL calculated with SPAM 3.7, using mtDNA haplotypes from the SPLASH sample collections in 2004-2006.

B1/F1	RUS-WAL		BER		EAL		WGOA		NGOA		SEA-NBC		SBC-WA		CA-OR	
Source Pop	Estimate	95% CL	Estimate	95% CL	Estimate	95% CL	Estimate	95% CL	Estimate	95% CL	Estimate	95% CL	Estimate	95% CL	Estimate	95% CL
Asia+	0.702	0.46, 0.9	0.029	0, 0.13	0.026	0, 0.22	0	0, 0.02	0	0, 0.06	0	0, 0	0	0, 0	0	0, 0.04
Hawaii	0.001	0, 0.17	0.256	0.08, 0.44	0.429	0.04, 0.76	0.251	0.09, 0.41	0.686	0.55, 0.8	1	1, 1	0.172	0, 0.47	0	0, 0.05
MX-all	0.298	0.01, 0.52	0.715	0.45, 0.9	0.546	0.11, 0.89	0.749	0.57, 0.91	0.314	0.18, 0.44	0	0, 0	0.828	0.36, 0.99	0.327	0.24, 0.5
CentAm	0	0, 0.1	0	0, 0.1	0	0, 0.23	0	0, 0.04	0	0, 0.03	0	0, 0	0	0, 0.26	0.673	0.45, 0.7

B2/F1	RUS-WAL		BER		EAL		WGOA		NGOA		SEA-NBC		SBC-WA		CA-OR	
Source Pop	Estimate	95% CL	Estimate	95% CL	Estimate	95% CL	Estimate	95% CL	Estimate	95% CL	Estimate	95% CL	Estimate	95% CL	Estimate	95% CL
Asia+	0.681	0.43, 0.88	0.008	0, 0.11	0.018	0, 0.22	0	0, 0.01	0	0, 0.05	0	0, 0	0	0, 0	0	0, 0.04
Hawaii	0.001	0, 0.15	0.203	0.03, 0.41	0.39	0.02, 0.75	0.213	0.05, 0.38	0.665	0.52, 0.78	1	1, 1	0.148	0, 0.46	0	0, 0.05
MX-ML+AR	0.318	0.04, 0.54	0.789	0.51, 0.95	0.592	0.12, 0.92	0.787	0.6, 0.95	0.335	0.2, 0.47	0	0, 0	0.851	0.35, 1	0.32	0.23, 0.5
CentAm	0	0, 0.1	0	0, 0.09	0	0, 0.22	0	0, 0.04	0	0, 0.03	0	0, 0	0.002	0, 0.27	0.68	0.46, 0.7

B3/F1	RUS-WAL		BER		EAL		WGOA		NGOA		SEA-NBC		SBC-WA		CA-OR	
Source Pop	Estimate	95% CL	Estimate	95% CL	Estimate	95% CL	Estimate	95% CL	Estimate	95% CL	Estimate	95% CL	Estimate	95% CL	Estimate	95% CL
Asia+	0.686	0.42, 0.87	0	0, 0.1	0.003	0, 0.2	0	0, 0.01	0	0, 0.05	0	0, 0	0	0, 0	0	0, 0.04
Hawaii	0	0, 0.14	0.157	0, 0.37	0.341	0, 0.71	0.16	0, 0.35	0.625	0.46, 0.75	1	1, 1	0.303	0.08, 0.52	0	0, 0.06
MX-AR	0.267	0, 0.48	0.64	0.33, 0.88	0.602	0.14, 0.93	0.69	0.37, 0.92	0.336	0.16, 0.5	0	0, 0	0	0, 0.17	0	0, 0.09
MX-ML	0.047	0, 0.34	0.202	0, 0.4	0	0, 0.25	0.15	0, 0.39	0.039	0, 0.17	0	0, 0	0.697	0.36, 0.9	0.447	0.28, 0.7
CentAm	0	0, 0.13	0	0, 0.15	0.054	0, 0.27	0	0, 0.08	0	0, 0.04	0	0, 0	0	0, 0.19	0.553	0.27, 0.6

Table 5: Estimates for apportionment of mixed-stocks for humpback whales on the feeding areas of the North Pacific based on 3 Scenarios derived from re-stratification of breeding regions and feeding areas, B1/F2, B2/F2 and B3/F2. Apportionment estimates and 95% bootstrap CL calculated with SPAM 3.7, using mtDNA haplotypes from the SPLASH sample collections in 2004-2006.

B1/F2	RUS-WAL		BER-EAL-WGOA		NGOA		SEA-NBC		SBC-WA		CA-OR	
Source Pop	Estimate	95% CL	Estimate	95% CL	Estimate	95% CL	Estimate	95% CL	Estimate	95% CL	Estimate	95% CL
Asia+	0.702	0.46, 0.9	0.004	0, 0.08	0	0, 0.06	0	0, 0	0	0, 0	0	0, 0.05
Hawaii	0.001	0, 0.17	0.265	0.14, 0.39	0.686	0.55, 0.79	1	1, 1	0.172	0, 0.47	0	0, 0.05
MX-all	0.298	0.01, 0.52	0.731	0.57, 0.85	0.314	0.18, 0.44	0	0, 0	0.828	0.35, 0.99	0.327	0.24, 0.54
CentAm	0	0, 0.1	0	0, 0.05	0	0, 0.03	0	0, 0	0	0, 0.25	0.673	0.45, 0.74

B2/F2	RUS-WAL		BER-EAL-WGOA		NGOA		SEA-NBC		SBC-WA		CA-OR	
Source Pop	Estimate	95% CL	Estimate	95% CL	Estimate	95% CL	Estimate	95% CL	Estimate	95% CL	Estimate	95% CL
Asia+	0.681	0.43, 0.88	0	0, 0.06	0	0, 0.05	0	0, 0	0	0, 0	0	0, 0.04
Hawaii	0.001	0, 0.15	0.223	0.1, 0.35	0.665	0.52, 0.78	1	1, 1	0.148	0, 0.46	0	0, 0.05
MX-ML+AR	0.318	0.03, 0.55	0.778	0.61, 0.89	0.335	0.2, 0.47	0	0, 0	0.851	0.35, 1	0.32	0.23, 0.53
CentAm	0	0, 0.09	0	0, 0.05	0	0, 0.03	0	0, 0	0.002	0, 0.27	0.68	0.46, 0.75

B3/F2	RUS-WAL		BER-EAL-WGOA		NGOA		SEA-NBC		SBC-WA		CA-OR	
Source Pop	Estimate	95% CL	Estimate	95% CL	Estimate	95% CL	Estimate	95% CL	Estimate	95% CL	Estimate	95% CL
Asia+	0.686	0.42, 0.87	0	0, 0.06	0	0, 0.05	0	0, 0	0	0, 0	0	0, 0.04
Hawaii	0	0, 0.14	0.176	0.04, 0.32	0.625	0.47, 0.75	1	1, 1	0.303	0.08, 0.53	0	0, 0.05
MX-AR	0.267	0, 0.48	0.659	0.43, 0.83	0.336	0.15, 0.5	0	0, 0	0	0, 0.16	0	0, 0.09
MX-ML	0.047	0, 0.34	0.166	0, 0.32	0.039	0, 0.16	0	0, 0	0.697	0.37, 0.9	0.447	0.29, 0.72
CentAm	0	0, 0.12	0	0, 0.11	0	0, 0.04	0	0, 0	0	0, 0.2	0.553	0.27, 0.67