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ABSTRACT

Currently, six stocks of harbor porpoise are recognized in the Pacific Stock Assessment Reports: Morro Bay, Monterey Bay, San Francisco-Russian River, Northern California/Southern Oregon, Oregon/Washington Coast, and Washington Inland Water stocks. The current stock boundaries were identified primarily as a result of a genetic study published in 2002, which provided evidence for relatively fine-scale structure of demographically independent stocks. In the published study, the Oregon/Washington Coast and Washington Inland Water stock boundary at Cape Flattery was supported by the genetic analyses, but stock structure along the Oregon/Washington Coast was unresolved because sample sizes for the genetic study were limited, and similarly, data about animal distribution and density along the Oregon/Washington coast were limited. Sample collection efforts continued after publication of the 2002 paper to increase sample size overall and to collect samples from previously unrepresented areas inhabited by harbor porpoise off the coasts of California, Oregon and Washington. Here, we present results from analyses of the expanded mitochondrial DNA control region sequence data set (n=375). All specimens were assigned to putative stocks prior to analyses. Evidence of genetic distinctness was detected among putative stocks, which included two putative stocks within the currently recognized Oregon/Washington Coast stock and two within the Washington Inland Water stock. While continuing to collect samples and generate additional genetic data will continue to facilitate resolving harbor porpoise stock structure, the accumulation rate of samples for the genetic study has been slow and collecting enough samples to conduct additional meaningful analyses will likely take another decade. Therefore, we recommend stock boundary revisions be considered for the Oregon/Washington Coast stock at this time and propose additional research to resolve boundaries within the Washington Inland Water stock.

INTRODUCTION

The objective of this study was to analyze additional genetic data to resolve stock boundaries off the coasts of Oregon (OR) and Washington (WA) for harbor porpoise (*Phocoena phocoena*). The data set analyzed here expanded that of Chivers et al. (2002) by including samples from additional sampling sites and adding samples to previously sampled sites.

Chivers *et al*. (2002) published evidence of fine-scale structure for eastern North Pacific Ocean harbor porpoise, and this information combined with data on harbor porpoise distribution and abundance resulted in a re-alignment of stock boundaries off the coast of California (CA). However, data on genetics, abundance and seasonal movements of harbor porpoise off OR and WA were insufficient to resolve whether changes in boundaries were warranted.

There are six stocks of harbor porpoise recognized for management off the CA, OR and WA coasts (Carretta *et al*., 2006). They are the (1) Morro Bay Stock, (2) Monterey Bay Stock, (3) San Francisco-Russian River Stock, (4) Northern California/Southern Oregon Stock, (5) Oregon/Washington Coast Stock, and (6) Washington Inland Waters Stock. None of these stocks are classified as 'strategic,' because the best available data indicate that the incidental fishery mortality is less than the estimated number of 'potential biological removals' (PBR) the stocks can withstand. However, the average fishery mortality estimates have been > 10% of PBR for several stocks: (1) Morro Bay, (2) Monterey Bay and (6) Washington Inland Waters (Carretta *et al*., 2006). Because harbor porpoise are vulnerable to coastal gillnet fisheries, continuing analyses to resolve stock structure is particularly important to ensure that these assessments are as accurate as possible.

Because the results presented by Chivers *et al*. (2002) and other population structure studies using molecular markers indicate that the mitochondrial DNA (mtDNA) marker is sufficient to reveal appropriate levels of genetic differentiation to meet the management objectives of the Marine Mammal Protection Act (MMPA), we expanded the harbor porpoise genetic data set by only sequencing the mtDNA control region for samples collected since the 2002 paper. The mtDNA marker is maternally inherited, which means that the effective population size is approximately a quarter that of nuclear markers and relatively more rapid differentiation of population subunits will occur, primarily due to genetic drift, when gene flow is limited (*i.e*., negligible movement of breeding females). Analyses of the mtDNA marker reveal patterns of gene flow that can be used to infer movement and dispersal patterns of the breeding portion of the population studied, and thus provide evidence of stock structure. Stocks are defined for the purposes of management as demographically independent population sub-units. That is, a stock's population dynamics are essentially independent of those for neighboring stocks. Analyses of mtDNA data can reliably detect near zero dispersal rates, but when dispersal low but demographically significant (*i.e*., 1-3%), analyses may fail to reject the null hypothesis of panmixia (Dizon *et al*., 1995; Mills and Allendorf, 1996; Taylor *et al*., 1997). The statistics used for analyses have inherently low power to detect low dispersal rates, and in marine mammal stock structure studies, the ability to detect evidence of demographically independent sub-units is typically further confounded by small sample size. However, detecting low dispersal rates between population sub-units is needed to meet the management objectives of the MMPA (Taylor, 1997; 2005).

Here, we present analyses of the mtDNA control region sequence data to measure genetic differentiation between putative stocks defined *a priori*. This study improves our understanding of harbor porpoise stock structure by expanding the molecular genetic data set to include more samples from more areas inhabited by harbor porpoise along the CA, OR and WA coasts than were in the Chivers *et al*. (2002) study.

MATERIALS AND METHODS

The samples

Samples used in this study were collected along the west coast of the US (including Alaska) and Canada between 1984 and 2005 from animals incidentally taken in fisheries, stranded on the beach, or biopsied at sea (Fig. 1; Table 1). The samples collected were predominantly skin tissue (88% skin; 6% muscle or internal organ tissue; 6% teeth

or bone) preserved in a 20% dimethylsulphoxide solution saturated with NaCl (Amos and Hoelzel, 1991; Amos, 1997). All samples are stored in the Southwest Fisheries Science Center's Genetic Tissue Archive (contact author SJC for information).

Laboratory Methods

The 5' end of the hypervariable mtDNA control region was amplified from extracted genomic DNA using standard protocols (Saiki *et al*., 1988; Palumbi *et al*., 1991) and primers L15812 (5'-cctccctaagactcaagg-3') (Chivers *et al*., 2002) or L15926 (5'-acaccagtcttgtaaacc-3'), and H16498 (5'-cctgaagtaagaaccagatg-3') (Rosel *et al*., 1994), which are named according to their position in the mtDNA sequence of the fin whale (Árnason *et al*., 1991). DNA was extracted from most tissue samples using a CTAB (cetyltrimethylammonium bromide) protocol (Winnepenninckx *et al*., 1993), a lithium chloride protocol (Gemmell and Aikiyama, 1996), and a silica based capture protocol (either a Dneasy tissue kit, Qiagen, Maryland, USA, catalog # 69506, or Xtractor Gene kit, Sigma Co. catalog #XTR2-1KT), but when DNA yield was initially low, a phenol-chloroform technique was used for a second extraction (Sambrook *et al*., 1989). DNA was extracted from the tooth and bone samples using a modification of Hagelberg's (1994) phenol-chloroform method. Both strands of the amplified DNA product of each specimen were sequenced independently as mutual controls using standard protocols on the Applied Biosystems Inc. (ABI) model 373, 377 and 3100 automated sequencers. Most sequences were generated on the ABI 377. All sequences were aligned using SEQED, version 1.0.3 software (Applied Biosystems Inc., 1992), or Sequencher V4.1 (Gene Codes Corp, Ann Arbor, MI). The final aligned sequences were 393 base pairs long.

Additional detail about the methods was published in Chivers *et al*. (2002).

Analytical Methods

Genetic variation

Genetic variation of the control region was characterized by the number of unique haplotypes present and by estimates of haplotypic and nucleotide diversity (Nei and Tajima, 1981; Nei, 1987).

Population Structure

Conventional analyses designed to detect intra-specific structure are based on *a priori* stratification of the samples using non-genetic criteria (e.g. a distributional hiatus or geographic barriers). Therefore, we further analyzed our data with *a priori* stratifications that subdivided the data set based on sampling discontinuities, the putative populations identified in Chivers *et al.* (2002), and the current management scheme. Different schemes were tested, because results from these analyses are fundamentally dependent on decisions about stratification.

Since Chivers *et al.* (2002), additional samples were collected from Morro Bay, CA (n=3), Northern CA (n=28), Central WA (n=4), Sekiu River, WA (n=23), and Puget Sound, WA (n=4). Northern CA and Sekiu River, WA represent previously un-sampled regions within the distribution of eastern North Pacific Ocean harbor porpoise. The samples collected from the Morro Bay were excluded from analyses, because they are inadequate to represent the stock. The samples collected from Central WA were pooled with the samples collected around the Columbia River mouth based on the distribution and density information available from past aerial surveys. The Puget Sound samples were also excluded from analyses because based on their past history of exploitation and the relatively fine-scale structure that has been documented for harbor porpoise in the region suggest they may represent a separate demographically isolated population.

Samples collected off the coast of Alaska were also excluded, because they are not pertinent to the question we are addressing here and are too few to address stock structure around Alaska.

Our first *a priori* stratification of the data set recognized current CA management units (Carretta *et al*., 2006) and discrete sampling sites as putative populations: (1) Monterey Bay, (2) San Francisco and Russian River, (3) Northern CA (new), (4) Oregon, (5) Columbia River, (6) Spike Rock, (7) Vancouver Island, (8) Sekiu River (new), (9) San Juan Islands, and (10) Strait of Georgia. As in Chivers *et al*. (2002), the San Juan Islands stratum

includes animals collected in the eastern part of the Strait of Juan de Fuca (*i.e.*, principally off Victoria, Vancouver Island) and throughout the San Juan Islands region.

Our second *a priori* stratification was defined based on results from analyses of the first stratification. In this analysis, we recognized the following as putative populations: (1) Monterey Bay, (2) San Francisco Bay and Russian River, (3) Northern CA/ Oregon, (4) Columbia River and Spike Rock, (5) Vancouver Island, (6) Sekiu River, (7) San Juan Islands, and (8) Strait of Georgia (Fig. 1).

Using the mtDNA data, we tested the null hypothesis of panmixia for intra-specific structure using both χ^2 and Φ_{ST}, because each statistic characterizes a unique aspect of genetic differentiation. The χ^2statistic detects differences in haplotype frequencies between strata and makes no assumptions about the evolution or relatedness of haplotypes (Rolf and Bentzen, 1989) while Φ_{ST} detects differences in the relatedness of haplotypes between strata. That is, statistically significant Φ_{ST} values mean that haplotypes within a stratum are more closely related to each other in an evolutionary context (*i.e.*, have a smaller genetic distance or are more genetically homogenous) than to those found in other strata. This statistic uses genetic distance to measure the genetic differences between haplotypes. We used the number of homologous nucleotide differences between two individuals as the measure of genetic distance. Φ_{ST} is analogous to the more familiar F-statistic but is modified for pairwise comparisons of genetic distance data and tests significance with a non-parametric permutation method in an analysis of variance framework (AMOVA; Excoffier *et al*., 1992). Although χ^2 is generally more powerful than distance based statistics (Hudson *et al*., 1992), poor performance can be expected when genetic diversity is high relative to sample size resulting in poor characterization of haplotype frequencies (Dizon *et al*. 1995; Taylor *et al.* 1997). Given the low sample size for most strata, we anticipate that such is the case here. Therefore, results from both statistics are presented, and the lowest p-value of either statistic is used to decide whether to reject the null hypothesis. The significance criterion was $\alpha = 0.05$.

RESULTS

There were 83 haplotypes among the 431 mtDNA control region sequences in our data set for harbor porpoise, which includes samples collected north of WA, off British Columbia, Canada and Alaska (Table 2). Nucleotide diversity was 1.46% (S.E. = +/- 0.77%), and the mean number of pairwise differences between haplotypes was 5.72 (S.E. = +/- 2.75). Within the 393 base pair sequences, there were 98 polymorphic sites including 96 substitutions, 63 transitions, 44 transversions and 3 indels.

Results of the analyses supported recognition of the current CA stocks, and the addition of samples from Northern CA stratum (Table 3) as well as the addition of samples to OR and WA strata facilitated examination of the stock boundaries for the Oregon/Washington Coastal stock. The Northern CA stratum was only statistically distinguishable from its most distant neighbors, and the distribution of harbor porpoise suggests these animals may be part of a larger population to the north. Therefore, the Northern CA stratum was combined with OR in the second analysis. Although more samples were added to the Columbia River stratum, it was also not statistically distinguishable from its nearest neighbors (Table 3), and therefore, the stratum was combined with the Spike Rock stratum. However, the newly added Sekiu River stratum was statistically distinguishable from neighboring strata (Table 3), which suggests demographic independence of the population these samples may represent.

The second stratification tested combined neighboring strata that were not genetically distinguishable by χ^2 or Φ_{ST} (Table 4). In these analyses, all strata were statistically distinguishable by at least one of the statistics. Combining the Northern CA and Southern OR strata for analyses means that the current genetic data set does not support a stock boundary at Cape Blanco, OR but does support a stock boundary north of Cape Blanco and south of the Columbia River. The stock boundary at Cape Flattery, WA that separates the Oregon/Washington and Washington Inland Waters stocks is again supported in these analyses. The genetic distinctness of the Sekiu River stratum suggests there is more than one stock within the Washington Inland Waters stock. Additional analyses of all available data relevant to stock identification are needed to resolve whether there are multiple demographically isolated populations within the inland waters and to determine the location of potential stock boundaries.

Although our analyses make many pairwise comparisons, we did not apply a multiple-test correction factor. This is in part because (1) multiple-test correction factors are inherently conservative, (2) the statistics we use have inherently low power, and (3) harbor porpoise are distributed essentially linearly along the coast. The third point means that harbor porpoise movements are well described by a stepping-stone model, and therefore, not all pair-wise comparisons are biologically plausible. That is, rather than 45 comparisons being made in Table 3, there are 10

as indicated by the bordered cells in the table. We present the results for all pairwise comparisons, however, because the results are informative. Specifically, they help us to empirically assess the power of our data set. For example, in Table 4, we see an example of what we would interpret as a false negative. The comparison of Northern CA and Oregon to the Strait of Georgia is not significant, but given the geographic distance between the strata, we would expect the comparison to be statistically significant. This result is likely due to the small sample size representing the Strait of Georgia.

DISCUSSION

Analyses of the expanded mtDNA control region sequence data set support the principal conclusion of Chivers *et al.* (2002), which was that harbor porpoise are organized into relatively small demographically-isolated populations. Specifically, the analyses support the re-alignment of stock boundaries off California that followed publication of the 2002 paper. The addition of the Northern CA and Sekiu River strata as putative populations provide additional information about structure for harbor porpoise off CA, OR and WA and support for additional stock boundary changes (Chivers *et al*., 2007).

Northern CA was one area known to be inhabited by large numbers of harbor porpoise that was not represented in the Chivers *et al.* (2002) study. Although evidence of genetic distinctness for this stratum was not detected in our analyses, when combined with the neighboring stratum to the north, pairwise comparisons using at least one test statistic were statistically significant ($P < 0.05$). Thus, the current stock boundary at Cape Blanco, OR is not supported.

The Sekiu River stratum was also new and was represented by samples collected from animals captured as part of a telemetry study to quantify seasonal movements. In our analyses, this stratum was genetically distinct in all pairwise comparisons with $P < 0.05$ using one or both statistics, which suggests that more than one stock of harbor porpoise may inhabit the inland waters off WA. The telemetry data showed that the tagged animals remained in the Strait of Juan de Fuca and moved east and west of their capture site near the mouth of the Sekiu River. Because the San Juan Islands stratum included animals that stranded off Victoria, Vancouver Island, it may have included animals that lived in the Strait, we split the San Juan Islands stratum in two: Eastern Strait of Juan de Fuca and San Juan Islands for analyses. In these comparisons, the Sekiu River stratum was statistically distinguishable from the Eastern Strait of Juan de Fuca stratum ($n = 25$) but not the San Juan Islands stratum ($n=20$) (Table 5). This apparently counter-intuitive result may be due to small sample size or animals from potentially different stocks stranding at the same locale. The Sekiu River samples were also collected differently than samples representing all other strata, because they were collected from animals live-captured over a relatively short time (*i.e*., 2001-2003). Additional analyses are needed to determine whether the evidence presented here supports recognition of more than one stock within the Washington Inland Waters stock.

The analyses presented here are based on samples collected opportunistically from discrete locales within the harbor porpoise population's range. While difficulty collecting samples continues to limit the extent to which genetic data alone can be used to identify stocks, results from the genetic analyses provided the essential information that gene flow is limited over relatively small geographic distances. Furthermore, the genetic results prompted us to review old data in new ways and to test new hypotheses. The available data on porpoise distribution, abundance and seasonal movements from line-transect and telemetry studies (NMFS, AKFSC and NWFSC, unpublished data) corroborate the genetic results and support the conclusion that demographically isolated populationss of harbor porpoise are structured on a relatively fine geographic scale in the eastern North Pacific Ocean.

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Table 1. Summary of *a priori* strata and sample size represented in the stock structure analyses: (1) in the 2002 paper and (2) in the current study. Two new strata were added to the analyses since the 2002 paper: Northern California, central Washington and Sekiu River, Washington. In the analyses, central Washington samples were combined with the Columbia River stratum samples. Although our total data set now includes sequences for 431 harbor porpoise, the additional samples collected at Morro Bay, California, Puget Sound, Washington and multiple sites in Alaska were excluded from these analyses (see text for explanation). The final data set analyzed and presented in this paper included sequences for 375 harbor porpoise.

LOCATION	2002 Sample Size	2002 No. of Haplotypes	Current Sample Size	Current No. of Haplotypes
Monterey Bay, California	36	13	95	18
San Francisco Bay and Russian River, California	17	12	42	20
Northern California (new)			28	13
Oregon	17	8	32	12
Columbia River, Oregon (includes 4 samples from the Central WA coast)	20	12	25	13
Spike Rock, Washington	42	14	42	14
Inland waterways, Washington and British Columbia: Sekiu River, Washington (new)			23	8
San Juan Islands & Inland Strait of Juan de Fuca	35	15	45	16
Strait of Georgia, British Columbia	24	5	25	5
Vancouver Island, British Columbia (western shore)	18	10	18	10
Copper River Delta, Alaska	16	10		

Table 2. The haplotype frequencies for each strata represented in the analyses.

Haplotype	Monterey Bay, CA (n=95)	San Francisco & Russian River, CA (n=42)	Northern California (n=28)	Oregon (n=32)	Columbia River, OR (n=25)	Spike Rock, Washington (n=42)	Vancouver Island, British Columbia (n=18)	Sekiu River, WA (n=23)	San Juan Islands, WA (n=45)	Strait of Georgia, British Columbia (n=25)
1	19	10	11	15	7	11	8	4	10	19
2	23	5	4	0	3	7	0	0	3	0
3	0	1	2	3	4	3	1	12	8	2
4	7	2	0	1	0	3	2	1	3	0
5	16	2	0	0	0	0	0	0	0	0
6	12	3	0	0	0	0	0	0	0	0
7	0	1	0	0	1	2	1	2	2	0
8	0	0	0	2	2	1	0	1	2	0
9	1	0	1	1	0	3	0	0	0	0
10	5	3	0	0	0	0	0	0	0	0
11	0	0	2	3	0	0	0	1	2	0
12	1	2	0	0	0	3	0	0	0	0
13	1	1	1	2	1	0	0	0	0	0
14	1	2	0	0	0	1	0	0	1	0
15	0	0	0	0	0	3	0	1	0	0
16	0	0	0	0	0	0	0	0	4	0
17	0	0	0	0	0	0	0	0	3	1
18	1	1	0	0	0	0	0	0	0	2
21	1	0	0	0	0	0	0	0	0	0
22	2	1	0	0	0	0	0	0	0	0
23	0	0	1	1	0	1	0	0	0	0
24	0	0	0	0	1	2	0	0	0	0
25	0	2	0	0	0	0	0	0	0	0
26	0	0	0	1	0	1	0	0	0	0
27	0	0	0	0	0	0	0	0	2	0
28	0	0	0	0	0	0	0	1	1	0
29	1	0	0	1	0	0	0	0	0	0
40	1	0	0	0	0	0	0	0	0	0
41	1	0	0	0	0	0	0	0	0	0
42	1	0	0	0	0	0	0	0	0	0
43	0	1	0	0	0	0	0	0	0	0
44	0	1	0	0	0	0	0	0	0	0
45	0	1	0	0	0	0	0	0	0	0
46	0	1	0	0	0	0	0	0	0	0
47	0	0	1	0	0	0	0	0	0	0
48	0	0	0	1	0	0	0	0	0	0
49	0	0	0	1	0	0	0	0	0	0
50	0	0	0	0	1	0	0	0	0	0
51	0	0	0	0	1	0	0	0	0	0
52	0	0	0	0	1	0	0	0	0	0
53	0	0	0	0	1	0	0	0	0	0
54	0	0	0	0	1	0	0	0	0	0
55	0	0	0	0	0	1	0	0	0	0
56	0	0	0	0	0	0	0	0	1	0
57	0	0	0	0	0	0	0	0	1	0
58	0	0	0	0	0	0	0	0	1	0
59	0	0	0	0	0	0	0	0	1	0
60	0	0	0	0	0	0	1	0	0	0
61	0	0	0	0	0	0	1	0	0	0
62	0	0	0	0	0	0	1	0	0	0
63	0	0	0	0	0	0	1	0	0	0
64	0	0	0	0	0	0	1	0	0	0
65	0	0	0	0	0	0	1	0	0	0
66	0	0	0	0	0	0	0	0	0	1
74	0	0	1	0	0	0	0	0	0	0
75	0	0	1	0	0	0	0	0	0	0
76	0	0	1	0	0	0	0	0	0	0
77	0	0	1	0	0	0	0	0	0	0
78	0	0	1	0	0	0	0	0	0	0
79	0	0	0	0	1	0	0	0	0	0
81	0	1	0	0	0	0	0	0	0	0
82	1	0	0	0	0	0	0	0	0	0
83	0	1	0	0	0	0	0	0	0	0

Table 3. Results from analyses of the mitochondrial DNA (mtDNA) marker for harbor porpoise using χ^2 (above the diagonal) and Φ_{ST} (below the diagonal with P-values in parentheses) are presented here for the current, expanded data set. In these analyses, all sampling strata were defined as putative populations. The strata recognized here differ from those in the 2002 paper: Northern California and Sekiu River, Washington were added, and the San Juan Islands stratum was split: Strait of Juan de Fuca and San Juan Islands. Bold print of the text in cells highlights the comparisons with $P \leq 0.05$. Nearest neighbor strata comparisons are the bordered cells.

	1. Monterey Bay, CA	2. San Francisco and Russian River, CA	3. Northern California	4. Oregon	5. Columbia River, Oregon	6. Spike Rock, Washington	7. Vancouver Island, British Columbia	8. Sekiu River, Washington	9. San Juan Islands, Washington	10. Strait of Georgia, British Columbia
2002 mtDNA: n=	36	17		17	20	42	18		35	24
Current mtDNA: n=	95	42	28	32	25	42	18	23	45	25
1. Monterey Bay, CA	-	**0.0290**	**<0.0001**	**<0.0001**	**<0.0001**	**<0.0001**	**0.0004**	**<0.0001**	**<0.0001**	**<0.0001**
2. San Francisco and Russian River, CA	0.014 (0. 146)	-	0.0768	**0.0012**	0.0710	0.0538	0.1868	**<0.0001**	**0.0014**	**0.0048**
3.Northern California	**0.099 (0.007)**	0.015 (0.185)	-	0.4846	0.4234	0.1096	0.1168	**0.0010**	**0.0280**	**0.0204**
4. Oregon	**0.142 (0.001)**	0.044 (0.050)	-0.023 (0.910)	-	0.1062	**0.0118**	0.1792	**0.0034**	**0.0192**	0.0878
5. Columbia River, OR	0.036 (0.067)	0.004 (0.283)	0.025 (0.116)	**0.056 (0.033)**	-	0.1768	0.1572	0.0666	0.1998	**0.0016**
6. Spike Rock, Washington	**0.043 (0.026)**	-0.005 (0.462)	-0.0004 (0.347)	0.029 (0.109)	-0.002 (0.392)	-	0.0804	**0.0030**	**0.0080**	**0.0002**
7. Vancouver Island, British Columbia	**0.218 (0.0007)**	**0.106 (0.012)**	0.032 (0.103)	0.022 (0.156)	**0.097 (0.012)**	**0.096 (0.019)**	-	**0.0062**	0.0836	**0.0324**
8. Sekiu River, WA	**0.133 (0.0013)**	**0.105 (0.009)**	**0.124 (0.011)**	**0.162 (0.008)**	0.036 (0.111)	**0.078 (0.024)**	**0.220 (0.002)**	-	0.3288	**<0.0001**
9. San Juan Islands, WA	**0.085 (0.001)**	0.018 (0.108)	-0.006 (0.504)	0.007 (0.218)	0.004 (0.306)	0.0002 (0.345)	0.036 (0.076)	**0.054 (0.039)**	-	**0.0018**
10. Strait of Georgia, British Columbia	**0.210 (<0.001)**	**0.100 (0.013)**	0.010 (0.239)	-0.008 (0.448)	**0.107 (0.014)**	**0.086 (0.018)**	0.0004 (0.389)	**0.231 (0.002)**	0.036 (0.063)	-

Table 4. Combined results from analyses of the mitochondrial DNA (mtDNA) marker for all pairwise comparisons of the eight putative stocks using χ^2 and Φ_{ST} are presented. The strata shown here were revised following the analyses presented in Table 3. For these analyses, the Northern California and Oregon strata, Columbia River and Spike Rock strata, and Strait of Juan de Fuca and San Juan Islands strata were combined. The Φ_{ST} test statistic and P-value for each comparison is printed in the lower diagonal and the P-value for χ^2 is printed in the upper diagonal. Nearest neighbor strata comparisons are the bordered cells.

	1. Monterey Bay, California	2. San Francisco & Russian River, California	3. Northern California & Oregon	4. Columbia River, OR & Spike Rock, WA	5. Vancouver Island, British Columbia	6. Sekiu River, Washington	7. San Juan Islands, Washington	8. Strait of Georgia, British Columbia
Current mtDNA: n=	95	42	60	67	18	23	45	25
1. Monterey Bay, California	-	**0.0262**	**<0.0001**	**<0.0001**	**0.0002**	**<0.0001**	**<0.0001**	**<0.0001**
2. San Francisco, California	0.014 (0.145)	-	**<0.0001**	**0.0090**	0.1806	**<0.0001**	**0.0004**	**0.0030**
3.Northern California & Oregon	**0.132 (<0.001)**	**0.039 (0.041)**	-	**0.0172**	**0.0488**	**0.0014**	**0.0022**	0.1832
4. Columbia River, Oregon & Spike Rock, WA	**0.039 (0.012)**	-0.001 (0.368)	**0.032 (0.024)**	-	0.0788	0.0524	**0.0074**	**0.0062**
5. Vancouver Island, British Columbia	**0.219 (<0.001)**	**0.106 (0.009)**	0.034 (0.091)	**0.092 (0.007)**	-	**0.0088**	0.0814	**0.0268**
6. Sekiu River, Washington	**0.133 (0.001)**	**0.105 (0.005)**	**0.155 (<0.001)**	**0.057 (0.025)**	**0.220 (<0.001)**	-	0.3322	**<0.0001**
7. San Juan Islands, Washington	**0.085 (0.001)**	0.018 (0.109)	0.009 (0.167)	0.003 (0.288)	0.036 (0.082)	**0.054 (0.043)**	-	**0.0016**
8. Strait of Georgia, British Columbia	**0.210 (<0.001)**	**0.100 (0.015)**	0.004 (0.275)	**0.081 (0.008)**	0.0004 (0.395)	**0.231 (0.002)**	0.036 (0.062)	-

Table 5. Results from analyses of the mitochondrial DNA (mtDNA) marker for harbor porpoise using χ^2 and Φ_{ST} are presented here with one change from stratification scheme number one (Table 3). The analyses differed in that the San Juan Islands stratum was split in two: the Strait of Juan de Fuca and the San Juan Islands. Bold print of the text in cells highlights the comparisons with $P \leq 0.05$. Nearest neighbor strata comparisons are the bordered cells.

	1. Monterey Bay, California	2. San Francisco, California	3. Northern California	4. Oregon	5. Columbia River, Oregon	6. Spike Rock, Washington	7. Vancouver Island, British Columbia	8. Sekiu River, Washington	9. Strait of Juan de Fuca	10. San Juan Islands, Washington	11. Strait of Georgia, British Columbia
mtDNA: n=	36	17		17	20	42	18		22	13	24
Current mtDNA: n=	95	42	28	32	25	42	18	23	25	20	25
1. Monterey Bay, CA	-	**0.0276**	**0.0002**	**<0.0001**	**<0.0001**	**<0.0001**	**<0.0001**	**<0.0001**	**<0.0001**	**<0.0001**	**<0.0001**
2. San Francisco, CA	0.014 (0. 410)	-	0.0794	**0.0022**	0.0778	0.0568	0.1794	**<0.0001**	**0.0370**	**0.0094**	**0.0026**
3.Northern California	**0.099 (0.005)**	0.015 (0.174)	-	0.4752	0.4198	0.0982	0.1154	**0.0014**	0.1080	**0.0130**	**0.0184**
4. Oregon (south)	**0.142 (0.000)**	0.044 (0.057)	-0.023 (0.909)	-	0.1092	**0.0092**	0.1692	0.1560	**0.0212**	**0.0276**	0.0870
5. Columbia River, OR	0.036 (0.070)	0.004 (0.272)	0.025 (0.111)	**0.056 (0.037)**	-	0.1770	0.1560	0.0692	0.1844	0.4194	**0.0016**
6. Spike Rock, Washington	**0.043 (0.031)**	-0.005 (0.449)	0.000 (0.340)	0.028 (0.108)	-0.002 (0.397)	-	0.0812	**0.0038**	0.0522	**0.0108**	**0.0002**
7. Vancouver Island, British Columbia	**0.218 (0.000)**	**0.105 (0.011)**	0.032 (0.106)	0.021 (0.147)	**0.097 (0.008)**	**0.096 (0.015)**	-	**0.0070**	0.1080	0.0508	**0.0290**
8. Sekiu River, WA	**0.132 (0.002)**	**0.105 (0.008)**	**0.123 (0.013)**	**0.161 (0.002)**	0.035 (0.109)	**0.078 (0.027)**	**0.219 (0.003)**	-	**0.0144**	0.6642	**<0.0001**
9. Strait of Juan de Fuca	**0.088 (0.008)**	0.013 (0.187)	-0.013 (0.620)	0.000 (0.367)	0.017 (0.162)	0.000 (0.364)	0.027 (0.130)	**0099 (0.017)**	-	0.1602	**<0.0001**
10. San Juan Islands, WA	**0.091 (0.010)**	0.026 (0.112)	0.009 (0.257)	0.028 (0.141)	-0.018 (0.679)	0.007 (0.271)	0.054 (0.071)	0.007 (0.271)	-0.001 (0.368)	-	**0.0022**
11. Strait of Georgia, British Columbia	**0.210 (<0.001)**	**0.100 (0.013)**	0.010 (0.216)	-0.008 (0.445)	**0.107 (0.008)**	**0.085 (0.019)**	0.000 (0.397)	**0.230 (0.002)**	0.036 (0.101)	**0.063 (0.047)**	-

Figure 1. Sample collection locations and names of strata used in analyses of the mitochondrial DNA control region marker for eastern North Pacific harbor porpoise. The Sekiu River stratum is labeled as Neah Bay in this figure.

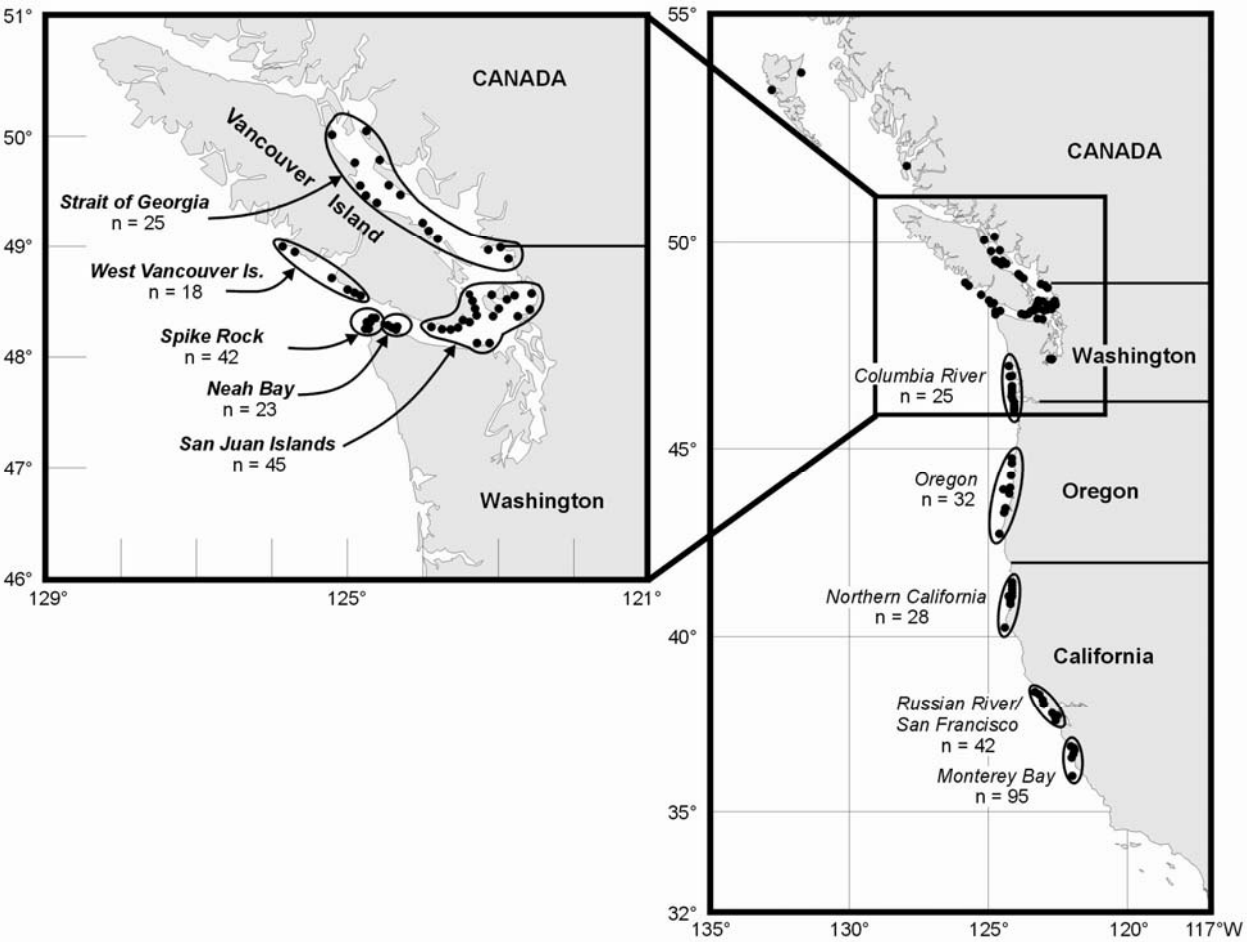

Figure 2. Shown here is the design of the 2002 aerial survey and the strata designations used to estimate harbor porpoise population abundance. The planned survey lines are shown for each of the strata. Strata B, D, E-G are composed of inshore and offshore sub-strata. The offshore strata were generally sampled at a lower rate in anticipation of lower porpoise densities. Strata I and J were split into US and Canadian sub-strata. For each stratum, the estimates of porpoise density (D) and the number of genetic samples (N) we had available for the genetic analyses are displayed. The correspondence between the strata recognized for abundance estimation and our genetic sampling strata is as follows: strata B and C correspond to the Oregon stratum, E to Columbia River, G to Spike Rock, I to Sekiu River, J to the San Juan Islands, and K to the Strait of Georgia (Figure 1).