

**Reevaluation of the DPS Designation for Hawaiian
(now Main Hawaiian Islands)
Insular False Killer Whales¹**

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INTRODUCTION AND BACKGROUND

On October 1, 2009, the National Marine Fisheries Service (NMFS) received a petition from the Natural Resources Defense Council (NRDC) requesting that the insular population of Hawaiian false killer whales (*Pseudorca crassidens*) be listed as an endangered species under the Endangered Species Act (ESA). On January 5, 2010, NMFS determined that the petition presented substantial information indicating that the petitioned action may be warranted and published the finding in the *Federal Register* (75 FR 316; Tuesday, January 5, 2010).

A biological review team (BRT) was established to complete a status review of the insular population of Hawaiian false killer whales to determine if listing under the ESA was warranted. The BRT conducted an analysis to determine if the insular population qualified as a distinct population segment (DPS) as a result of being both discrete and significant relative to the taxon to which it belongs (61 FR 4722; February 7, 1996). Using the best available data at the time, the BRT determined that the Hawaiian insular false killer whales were discrete because they were markedly separated from other false killer whales based on behavioral and ecological factors. After the BRT determined that Hawaiian insular false killer whales were discrete, the Team assessed the population for its biological and ecological *significance* to the species. The BRT determined that Hawaiian insular false killer whales were significant to the global taxon based on their persistence in a unique ecological setting, their marked genetic characteristics, and cultural factors. In August 2010, the BRT completed a status review report (Oleson et al. 2010) which found that the Hawaiian insular false killer whale was a DPS, and presented the scientific foundation on which to base a listing decision.

After reviewing the DPS' extinction risk, the factors causing its decline, and efforts being made to conserve the species, the NMFS determined that listing of this DPS as endangered was warranted. On November 17, 2010, the NMFS published in the *Federal Register* a proposed rule to list the Hawaiian insular false killer whale DPS as endangered (75 FR 70169; NMFS 2010). Although a final determination on whether to list the Hawaiian insular false killer whale DPS was due on November 17, 2011, as of October 1, 2012, a final decision has not yet been made.

Since the publication of the proposed rule in November 2010, a previously unrecognized Northwestern Hawaiian Islands (NWHI) population of false killer whales has been identified (Figure 1; Carretta et al., 2012). Preliminary analyses of available data from satellite tagging, photographic identification, and genetics suggest some separation between the NWHI population and the Hawaiian insular population proposed for listing. To ensure that the final listing decision is based on the best available scientific information, NMFS reconvened the BRT to evaluate whether the Hawaiian insular DPS remains a DPS, separate from both the new NWHI population and other pelagic false killer whales. The BRT was instructed by NMFS that a DPS finding should be supported by a consensus decision. Consensus is determined by 5/8 agreement within the BRT.

The original BRT members have been reconvened via a series of teleconferences to evaluate new information available since publication of the 2010 Status Review on Hawaiian insular false killer whales and identification of the newly recognized NWHI population. In addition to new information on the genetics of Hawaiian insular and NWHI false killer whales, more information has become available on the movements and range of both populations and the

social structure and habitat preferences of the Hawaiian insular population. Additional literature reviews were also conducted on the ecology and oceanography of the main Hawaiian Islands (MHI) and NWHI. The existence of an apparently island-associated population of false killer whales in the NWHI has necessitated a more precise designation of the Hawaiian insular DPS, which is now recognized by the BRT as Main Hawaiian Islands insular false killer whales. All original arguments supporting the MHI insular false killer whale DPS finding were revised to reflect the new information considered by the BRT.

This report summarizes new scientific information that has become available since the completion of the Status Review in 2010. In light of this new information and other information, the BRT evaluated whether the MHI insular false killer whale population proposed for listing continues to meet both the discreteness and significance criteria under the DPS policy. The BRT implemented a structured decision-making process similar to that used for the 2010 Status Review. In its deliberations, the BRT acknowledged the considerable uncertainty surrounding all aspects of MHI insular false killer whale biology, abundance, trends in abundance and threats. As such, the Team continued to treat the uncertainty explicitly by identifying where it exists and using a point system to weigh various plausible scenarios, thereby making the reevaluation process as transparent as possible and ensuring that the Team was basing its decisions on a full evaluation and common understanding of the evidence. The process is described in greater detail later in this report.

Following evaluation of all available information on MHI insular, NWHI, and other false killer whales, the BRT has found, by consensus, that the MHI insular population of false killer whales continues to meet the discreteness and significance thresholds to be considered a DPS under the ESA. The BRT found strong support for discreteness based on behavioral factors. The BRT also found strong support for significance based on marked genetic differences between MHI insular false killer whales and their conspecifics in other areas. Ecological and cultural factors still support the significance finding, although the evidence was considerably weaker and more uncertain. The BRT also found that all factors taken together increased confidence and strengthened the significance finding. The significance finding clearly represents a consensus but was not unanimous. Both majority and dissenting opinions are presented in this report.

In issuing this report, the BRT is not making a recommendation on listing status and the conclusions presented here do not represent conclusions regarding listing status of MHI insular false killer whales under the ESA.

Update on Hawaiian False Killer Whale Taxonomy, Biology, and Ecology

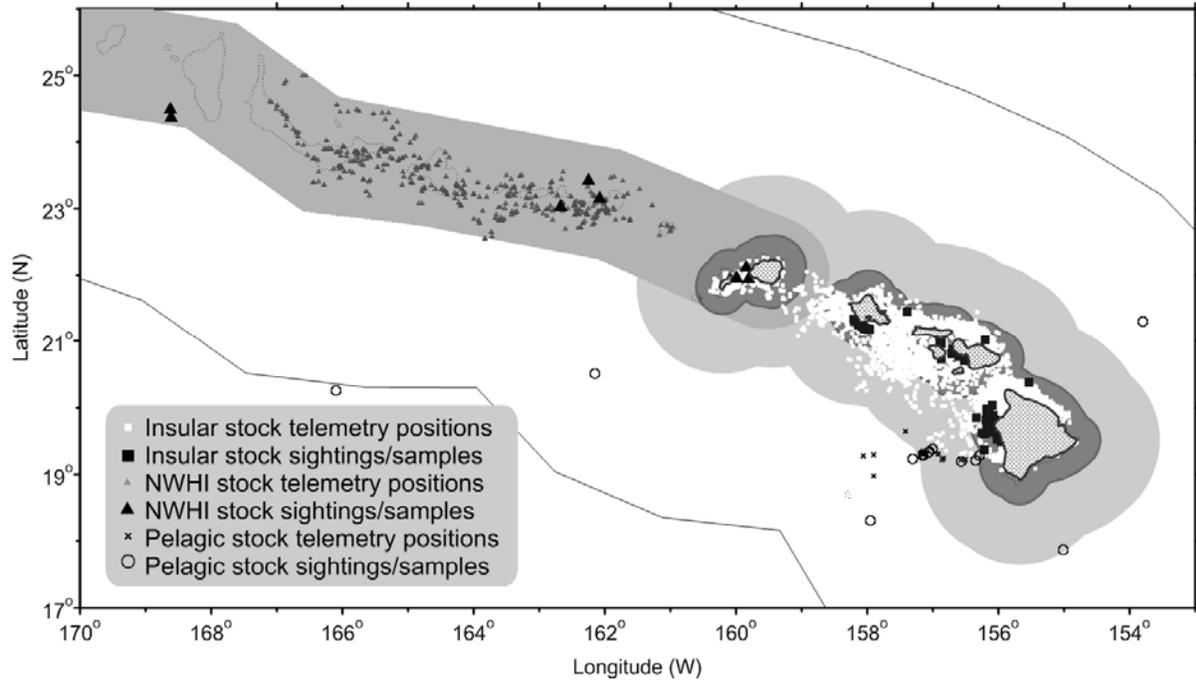


Figure 1. From Carretta et al, (2012). Sighting, biopsy, and telemetry records of false killer whales identified as being part of the MHI insular (square symbols), NWHI (triangle symbols), or pelagic (open and cross symbols) stocks. The dark gray area is the 40-km MHI insular core area; light gray area is the 40–140-km MHI insular-pelagic overlap zone; medium gray is the 50-nmi (93-km) Monument boundary extended to the east to encompass Kauai, representing the NWHI stock boundary. The MHI insular, pelagic, and NWHI stocks overlap in the vicinity of Kauai.

New survey information on false killer whales

In the summer and fall of 2010, a large-scale visual and acoustic line-transect survey for cetaceans (HICEAS II) was conducted within the U.S. Exclusive Economic Zone (EEZ) around the Hawaiian Islands. Although the survey was intended to provide the data necessary to estimate abundance for all Hawaiian cetaceans, false killer whales were of particular importance, with extra time dedicated to photograph and biopsy as many false killer whales as possible from each observed group. Satellite telemetry tags also were available to deploy on individual false killer whales to better understand movements outside of the main Hawaiian Islands. During 14 visual encounters with false killer whales during the survey, 91 false killer whales from 11 groups were photographed for individual identification; 48 false killer whales from 7 groups were sampled for genetic analysis; and two false killer whales from one group were satellite-tagged for evaluation of movements (Bradford et al. 2012). Analyses of the photo-ID, genetics, and movement data collected during HICEAS II suggest that a previously unrecognized population of false killer whales exists within the NWHI.

Re-sightings of individual false killer whales were documented among 3 encounters, all in the NWHI within the eastern portion of the Papahānaumokuākea Marine National Monument (Baird et al., accepted). During the first of these encounters (on 26 September 2010) satellite tags were deployed on two false killer whales. Information from the satellite tags was used to direct one of the research vessels in the survey to the general area occupied by the tagged whale approximately one month after it was tagged, resulting in the two additional encounters in which there were re-sightings of individual false killer whales documented during the 26 September encounter. Matches of distinctive false killer whales linked all three encounters. There were no re-sightings of individual false killer whales from the remaining groups photographically documented during HICEAS II. Further, no matches were found between HICEAS II photos and any insular or pelagic false killer whales already within the Hawaiian false killer whale photo-ID catalog, except for some false killer whales previously documented off Kauai whose population identity was not known.

During the 2010 Status Review, it was unclear whether the false killer whales seen near Kauai were part of the MHI insular population as they had not been associated with any other MHI insular group. The combination of photo-ID, movement (Baird et al. accepted), and genetics data (below) indicates that these whales are part of a NWHI population. The range of the NWHI population overlaps partially with the MHI insular population as satellite-tagged false killer whales from that population have been documented off the western side of Kauai and Niihau (Baird et al. 2012). Three populations of false killer whales are now recognized within Hawaiian waters: the Hawaii pelagic population, the MHI insular population, and the new NWHI population (Carretta et al. 2012). Abundance of the NWHI population was estimated to be 552 (CV = 1.09) based on the HICEAS II sightings (Bradford et al. 2012).

In June 2012, small-vessel surveys conducted off Kauai resulted in 2 encounters with false killer whales. During the encounters, 29 false killer whales were photo-identified, 11 were sampled for genetic analysis, and three false killer whales were satellite tagged (Baird 2012). Two false killer whales were seen over 2 survey days; however, there were no matches to any other false killer whales in the Hawaii false killer whale photo-ID catalog. Given the number of identified false killer whales compared to the number of catalog entries for each population, this suggests the groups encountered were either from the NWHI insular or pelagic populations (Baird 2012). Satellite-tag results suggest these false killer whales were part of the NWHI population given their island-associated movements near Kauai and within the eastern portion of the NWHI out to Gardner Pinnacles. Median distance from shore and depth usage by these whales was similar to observations of these characteristics for the animals tagged off Nihoa in 2010 (Baird 2012).

Update on MHI insular false killer whale habitat and social structure

Satellite tag data are now available from 27 MHI insular false killer whales (Baird et al. 2012). Using data from 22 independent tag records, where animals traveling together were excluded from the analysis, areas of frequent usage by the tagged whales were investigated to better understand habitat preferences. Baird et al. (2012) found 3 areas of frequent use by this population: the north side of the island of Hawaii (both east and west sides), a broad area extending from north of Maui to northwest of Molokai, and a small area to the southwest of Lanai. This analysis has also yielded a more precise evaluation of the depths most frequently

used by the MHI population. Although depth at the location of satellite receptions ranged from 10 m to 4900 m, the depth distribution for high-use areas was much better defined with a mean depth of 623 m, relative to an overall median depth of 1679 m (Figure 2). Tagged false killer whales spent slightly more time on the windward sides of the islands (52.2%) than the leeward sides (47.8%). Chlorophyll-*a* concentration was also significantly higher in high-density cells (cells with high false killer whale occupancy) than in low-density cells.

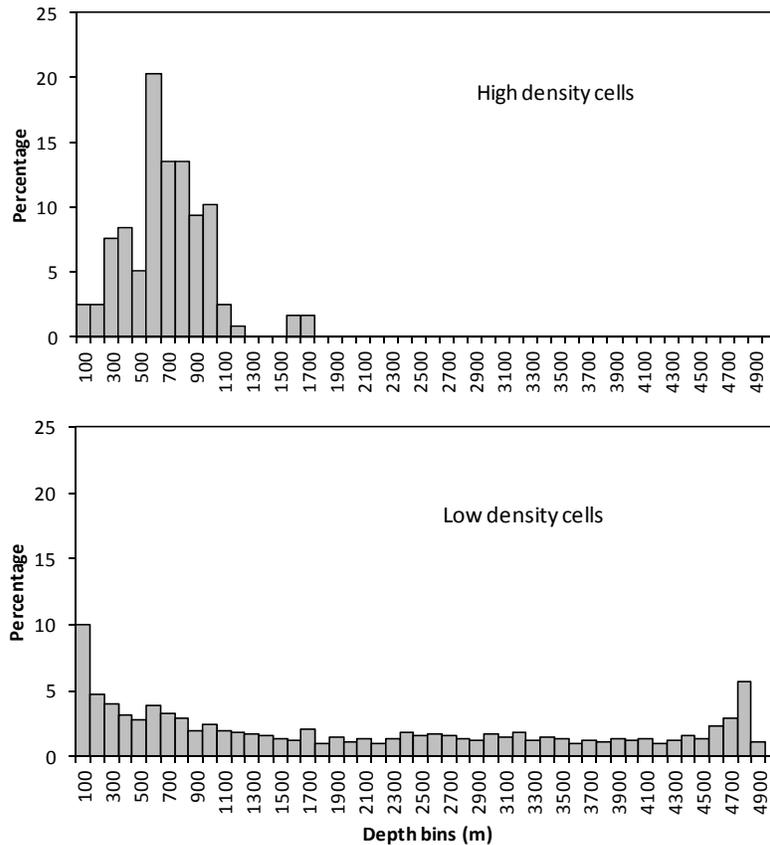


Figure 2. Depth use by MHI insular false killer whales in high-density versus low-density cells. From Baird et al. (2012).

The addition of many new photos, including several re-sightings for a number of false killer whales, has allowed a reevaluation of social structure of this population through construction of a new social network diagram (Whitehead 2008) (Figure 3). The new social network indicates that the population can be broadly divided into at least three primary social clusters where clusters are considered significant when network modularity (0.67 for this network) exceeds 0.3 (Newman 2006). A number of false killer whales either belong to other undersampled clusters, have been seen too infrequently for the analysis to place them in a specific cluster, or have undergone an undetected mark change such that they are represented more than once within the diagram. False killer whales from two of the three social clusters have been satellite-tagged, and analysis of their movements suggests different patterns of habitat use within the MHI. False killer whales from cluster 1 used all 3 of the high-density areas (north and northwest of Molokai,

southwest of Lanai, north end of Hawaii Island), while false killer whales from cluster 3 primarily use the area from north of Maui to northwest of Molokai (Figure 4). Further, when the observed number of sightings was compared with the number of sightings expected given the distribution of effort around each island, more sightings of cluster 2 false killer whales were recorded off the island of Hawaii than expected, and fewer sightings than expected were recorded off Oahu or Maui. Sightings of cluster 1 and cluster 3 false killer whales by island did not differ from expected frequencies (Baird et al. 2012). The genetics and mating patterns for these social clusters were also evaluated and are discussed below.

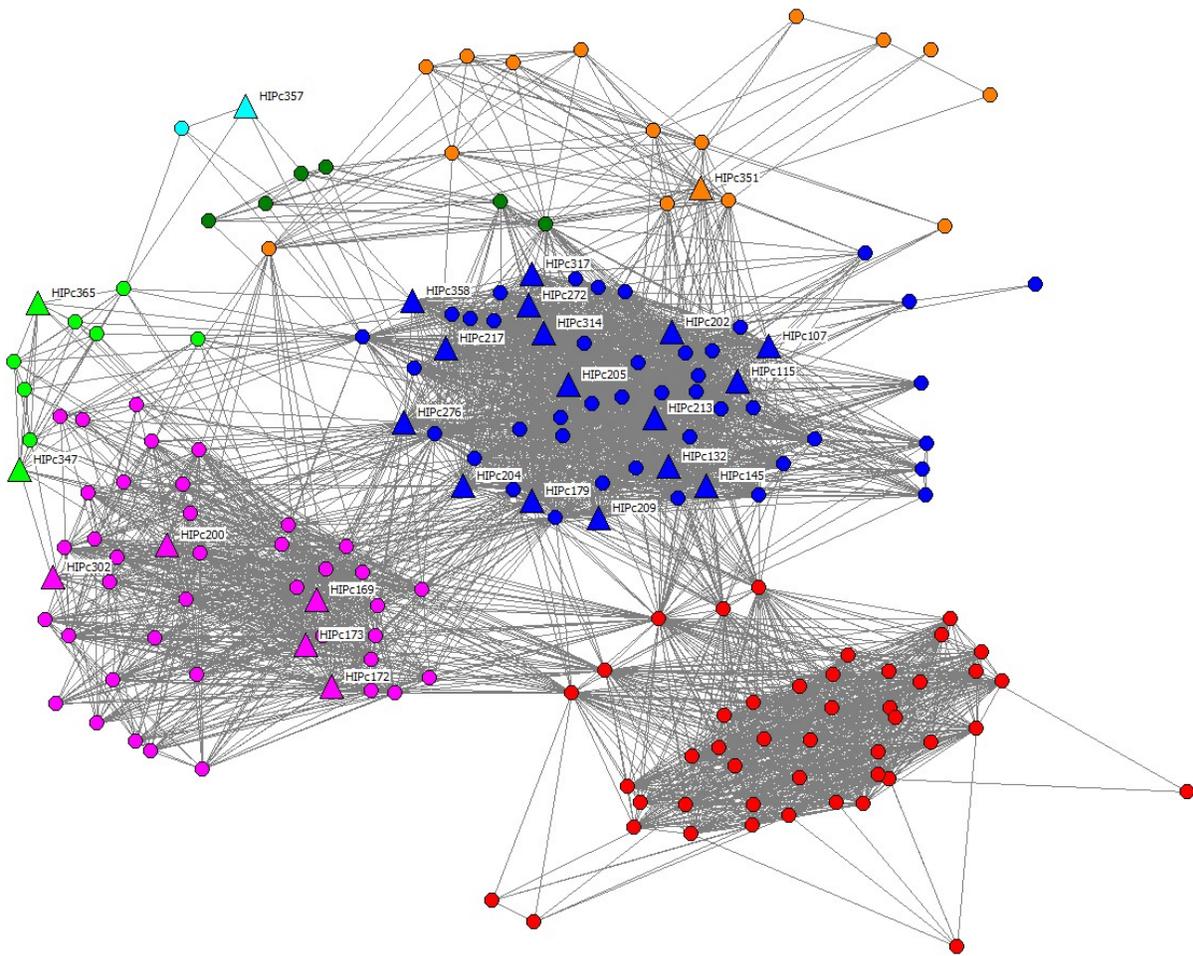


Figure 3. A social network diagram of distinctive and very distinctive Hawaiian insular false killer whales based on photo-identification data available from 2000 through 2011. Cluster membership was determined using a network modularity technique and is indicated by color coding: cluster 1 – blue; cluster 2 – red; cluster 3 – pink; other clusters not named. Satellite-tagged false killer whales are highlighted with large triangles and ID labels.

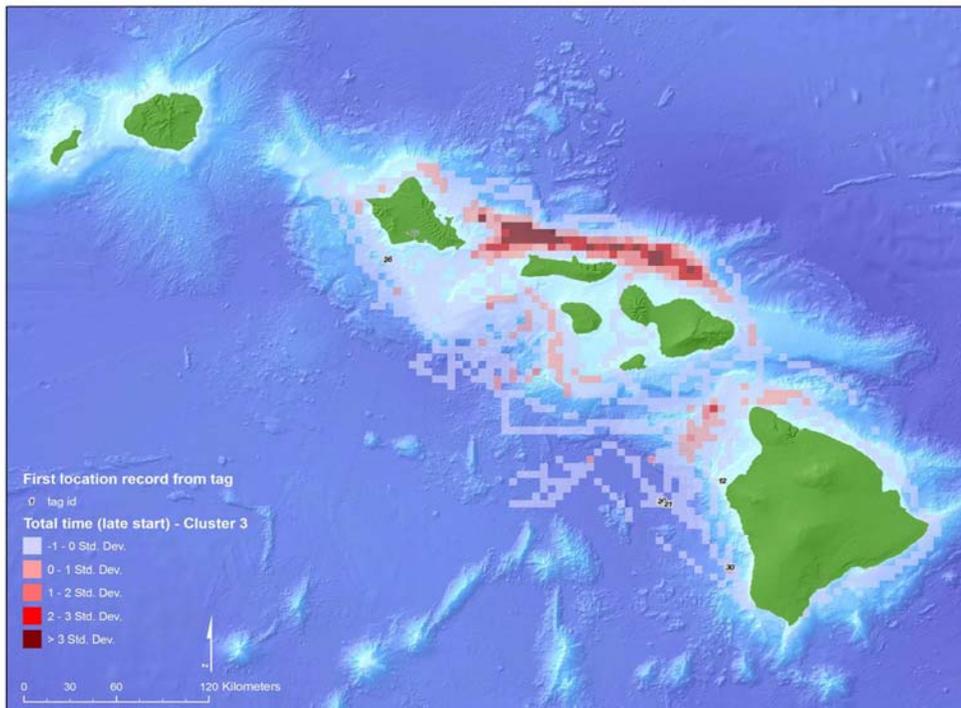
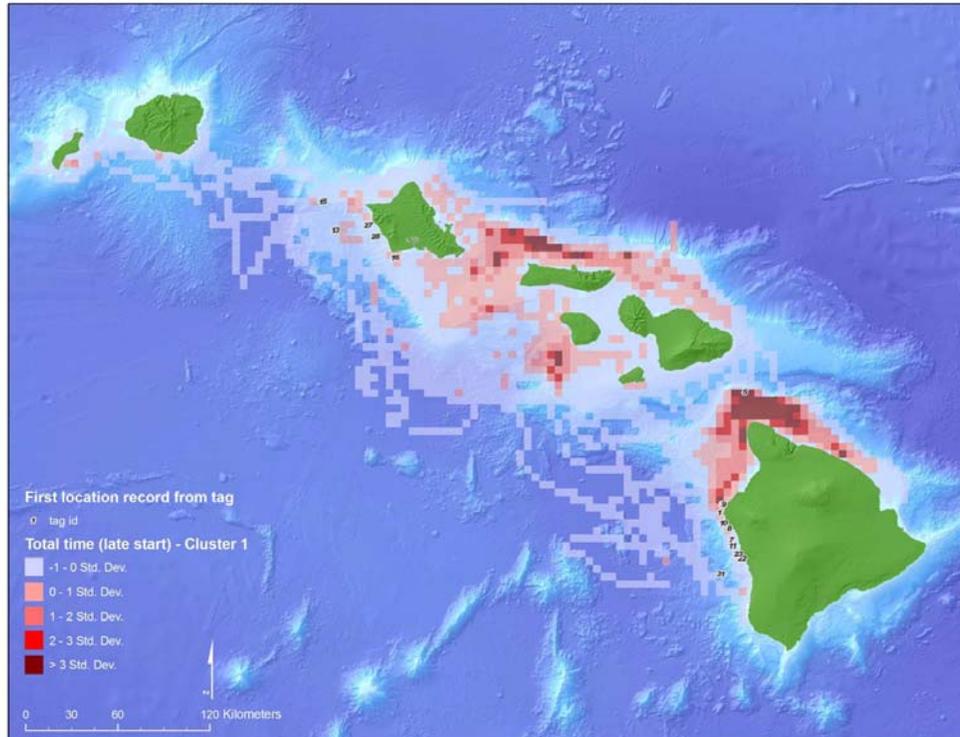


Figure 4. Density maps of MHI insular false killer whales: top –false killer whales from cluster 1; bottom –false killer whales from cluster 3. No false killer whales from cluster 2 have been tagged.

Update on the genetics of false killer whales in Hawaiian waters

Significant progress on understanding the genetics of false killer whales was reported in Chivers et al. (2010) and evaluated by the BRT in the 2010 Status Review. Readers of this update on new genetics findings should refer to the latter document for descriptions of the marker types (mitochondrial DNA (mtDNA) and microsatellites, henceforth referred to as nuclear DNA (nucDNA)), the basic analytical methods and how inferences from those methods relate to interpreting genetic data for various management questions. Case studies for other cetaceans found in Hawaiian waters (e.g., pilot whales, spinner dolphins, etc.) were also discussed within the 2010 Status Review and help develop a context; these studies will be referred to here but not repeated in full. Here, we focus on new data that were reviewed at the 2011 Pacific Scientific Review Group meeting (i.e., Martien et al. 2011, Chivers et al. 2011).

Since the status review was published, new genetic samples have been added to the data set in the MHI, the NWHI and nearby central North Pacific (CNP) waters. Martien et al. (2011) focused on comparing the MHI and NWHI using mtDNA sequence data (947 base pairs of the control region) and 16 dinucleotide microsatellite loci. This paper also used new data on social networks (Baird et al. 2012) to examine social structure within the MHI (see Fig. 3 above). Samples in the NWHI ($n = 21$) were obtained from four encounters during HICEAS II (Figure 5). The first three encounters were linked via a false killer whale that was satellite-tagged on the first encounter and seen on the second and third encounters. The fourth encounter is not photographically linked to the others but involved false killer whales with the most common insular Hawaii mtDNA haplotype. It is likely that these sampling events are of two social clusters.

Hawaiian insular false killer whales (MHI and NWHI) are characterized by 4 haplotypes: 1, 2, 5 and 31 (Table 1). The most common is haplotype 1 followed by haplotype 2, which differs by 2 mutations. The other two haplotypes are represented by only a single individual within each of the insular populations. Haplotype 5, which is also found in Australia, was an individual that was sampled off the island of Hawaii and was seen only on that single occasion. The individual with haplotype 31, which differs from haplotype 1 by a single mutation, was sampled on two occasions in the NWHI. The closest haplotype found in the CNP samples (including pelagic Hawaii whales) differed by 4 mutations from haplotype 1. Note that the Hawaiian insular haplotypes are all closely related to one another and have not been found elsewhere, with the exception of haplotype 5. This differs from most other cetaceans in Hawaii, including spotted, spinner and bottlenose dolphins that have distantly related haplotypes (see summary and figures in Oleson et al. 2010). The only other similar cetacean in Hawaiian waters is the pilot whale.

The mtDNA median joining network (Figure 6) indicates that MHI and NWHI false killer whales represent their own mtDNA lineage that has diverged considerably from other false killer whales, including CNP and eastern North Pacific (ENP) pelagic samples. This divergence indicates that there has been no movement of females between MHI and NWHI populations and all other false killer whale populations for a substantial period of time. The large difference in haplotype frequencies between MHI and NWHI populations, along with the presence of a unique haplotype (31) in the NWHI, suggests that females have not dispersed between the MHI and the NWHI populations for a considerable time, although the separation of these groups from other false killer whales has occurred over a much longer time scale. This conclusion includes the

assumption that the presence of haplotype 5 in the MHI population represents a recent immigrant of a single male animal from the pelagic population (see below), as there is no other logical conclusion to be made from the mtDNA network (Figure 6). Although the sample size for the NWHI population is not large, the presence of a unique haplotype (31) in that population is of particular interest because that haplotype was not found in the MHI population despite a substantial sample size.

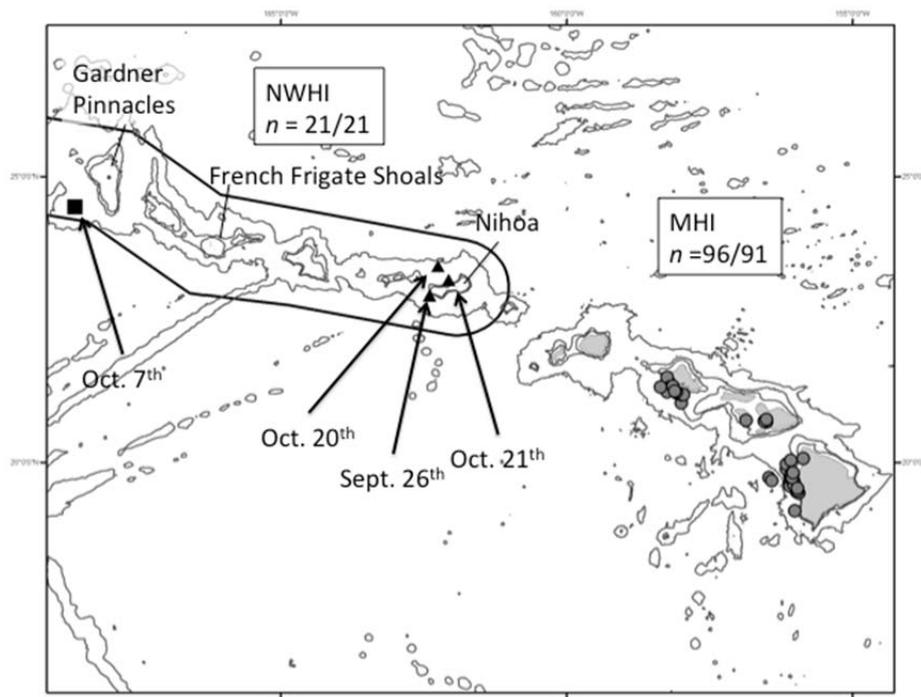


Figure 5. Map showing the locations of new false killer whale samples evaluated in Martien et al. (2011). Samples were stratified into main Hawaiian Islands (MHI; gray circles) and Northwestern Hawaiian Islands (NWHI; black symbols). Sample sizes (n) are given for the mtDNA/nucDNA data sets. The encounters within the NWHI are labeled according to the date they occurred. The three encounters marked by triangles were identified by Baird et al. (Accepted) as representing a previously undocumented island-associated population. Depth contours represent 400 m, 1000 m, and 4000 m. The black line shows the boundary of the Papahānaumokuākea Marine National Monument.

Social structure within the MHI

Recent additions to the Hawaiian false killer whale photo-identification catalog (Baird et al. 2008) and new social network analyses revealed the existence of three large, distinct social groups within the population (Baird et al. 2012). Table 1 reveals that social cluster 3, with quite good sampling ($n = 23$), has no haplotype 2 false killer whales despite that haplotype being quite common in the MHI overall. Significant differences were found in both mtDNA and nucDNA between social cluster 3 and clusters 1 and 2, but no differences were found between clusters 1 and 2 (see Table 2 below in the section *NWHI in relation to MHI*.)

Martien et al. (2011) also used parentage analyses to evaluate social structure within the MHI. They found that both males and females exhibit strong fidelity to natal social groups and that mating occurs within and between social groups. Such a mating system could result in inbreeding depression, further imperiling a population that we estimate has an effective population size of only 50.5 false killer whales. The parentage analysis also revealed that the single individual male with haplotype 5 is likely to have fathered a male offspring.

Table 1. Haplotype frequencies for each stratum. The accuracy of the assignment of false killer whales to a social cluster is dependent on the number of sightings for each individual. Not all false killer whales within the MHI are assigned to social clusters 1, 2 or 3 (Baird et al. 2012), likely due in part to infrequent sightings of those false killer whales. It is also possible that other social clusters exist within the MHI.

Stratum	N	Haplotype			
		1	2	5	31
NWHI	21	20	0	0	1
MHI	96	73	22	1	0
Social cluster 1	30	17	13	0	0
Social cluster 2	12	6	5	1	0
Social cluster 3	23	23	0	0	0

NWHI in relation to MHI

Chivers et al. (2011) compared the NWHI to the MHI populations in the larger context of other pelagic strata (shown in Figure 7). They used standard statistics (F_{st} and F'_{st} for mtDNA and nucDNA, respectively) to test the null hypothesis of no population structure. We have selected the most pertinent comparisons and coupled them with the comparisons of social clusters from Martien et al. (2011) to provide the best context for interpretation (Tables 2 and 3). Nearly all of the comparisons between MHI insular, NWHI, and other false killer whales are statistically significant for both the mtDNA and nucDNA datasets. The only exception is the comparison of MHI social clusters 1 and 2 (Tables 2A and 3A) to each other. In the mtDNA dataset the magnitude of differentiation (F_{st}) is greater when comparing the insular populations (MHI or NWHI) to the other strata (see rows 2 and 3 in Table 2B) than comparisons between the MHI and NWHI or between the social clusters, which is not unexpected given their likely divergence from the same founding group.

In contrast, the nuclear data strongly suggest that there is very little gene flow between the MHI and all other strata, including the NWHI (Table 3B). Differentiation between the MHI and the NWHI populations is stronger than between any of the social clusters within the MHI. It is harder to say how different the NWHI population is from other strata simply because of sampling issues (a relatively low sample size with most samples likely from one social cluster). Table 3B suggests that the NWHI population is differentiated from the other strata (including the MHI population) at about the same level.

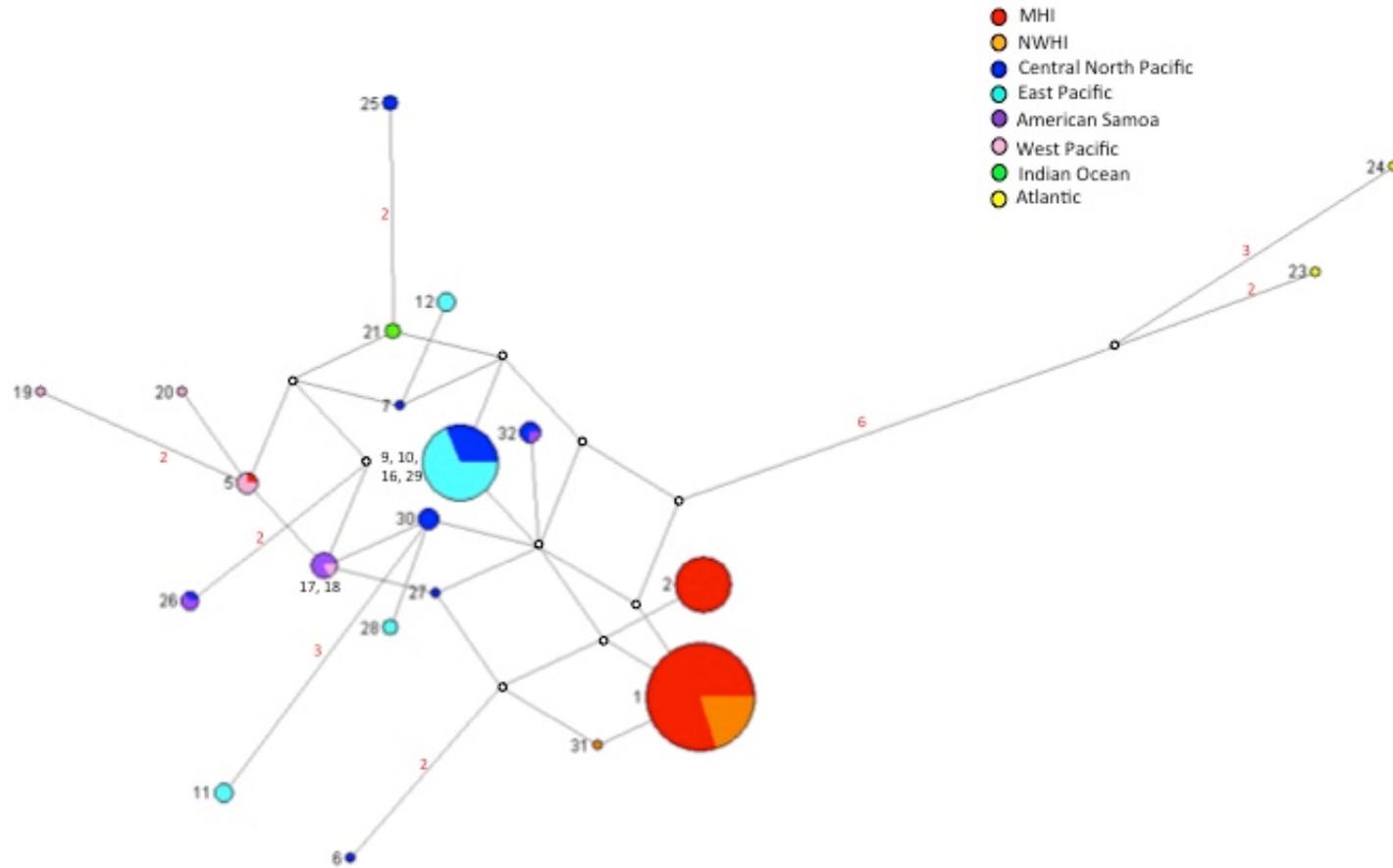


Figure 6. Median joining network for false killer whales where the strata are shown in Figure 7 below. Numbers next to the nodes correspond to haplotype number and the sizes of the nodes are proportional to the frequencies of the haplotype. Each node is shaded to indicate the fraction of false killer whales with that haplotype that comes from each geographic location (see key). This figure is a 2-dimensional representation of a 3-dimensional configuration. Intersections of lines with small clear circles represent unsampled haplotypes whereas unmarked intersections result from one line crossing behind another line, but not actually intersecting it). For example, haplotype 2 differs from haplotype 1 by 2 mutations and haplotype 31 differs from haplotype 1 by a single mutation. Haplotype 2 differs from haplotype 31 by 3 base pairs.

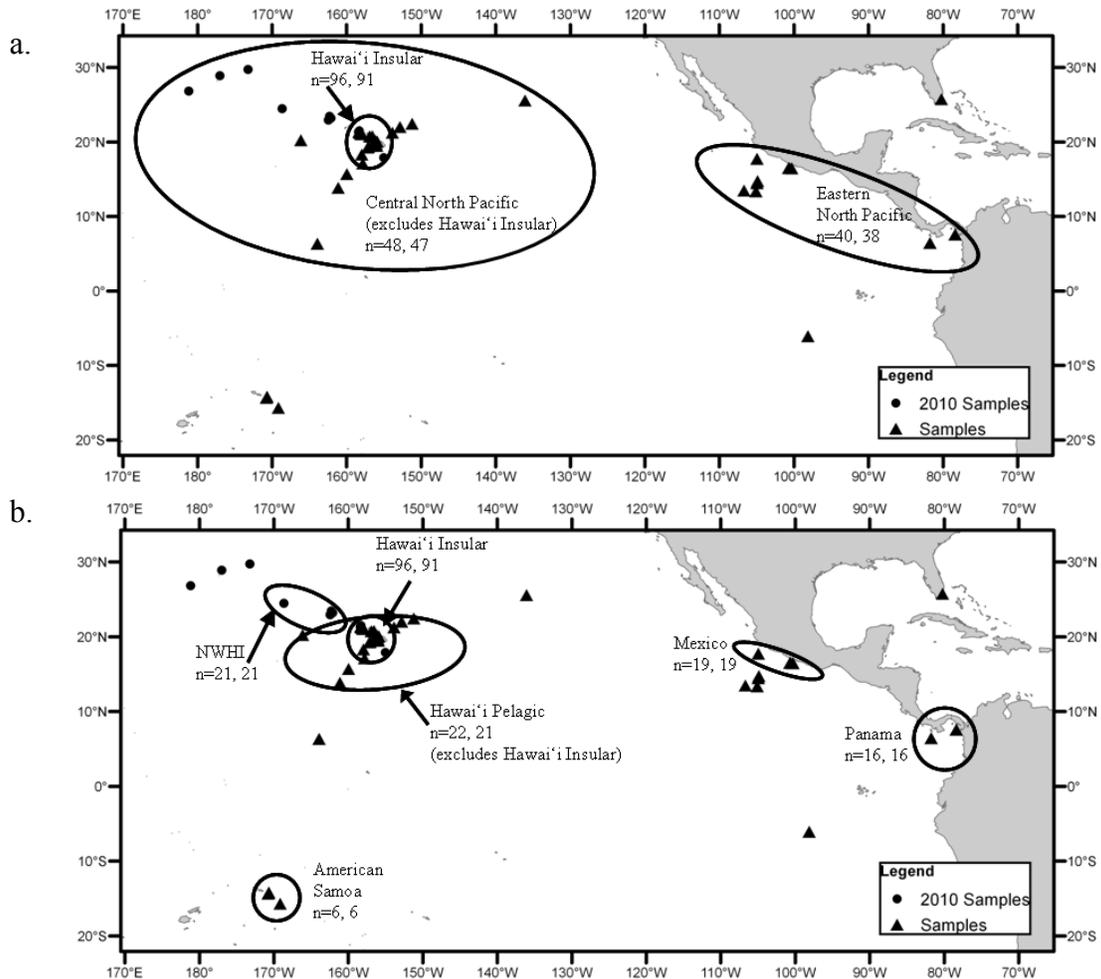


Figure 7. False killer whale mtDNA and nucDNA data sets were analyzed for two broad-scale stratifications shown in (a), and the fine-scale stratification shown in (b). Sample sizes for the mtDNA and nucDNA data sets are presented, respectively.

The utility of different metrics for estimating genetic differentiation is currently the subject of considerable debate among geneticists (e.g., Hedrick 2005; Jost 2008; Ryman and Leimar 2009, Leng and Zhang 2011, Meirmans and Hedrick 2011). F_{ST} is the most commonly used measure of genetic differentiation. It is inversely proportional to the effective number of individuals moving between populations per generation ($N_e m$) (Wright 1965), and can therefore be used to make inferences regarding the level of gene flow between populations (Meirmans and Hedrick 2011). However, F_{ST} has several shortcomings. It is strongly correlated with mutation rate and, therefore, within population diversity. Consequently, F_{ST} is negatively biased when calculated using highly polymorphic loci, such as microsatellites. Several F_{ST} analogs, including F'_{ST} (Meirmans 2006), use normalization to attempt to correct for this bias. However, normalization breaks the connection to Wright's formulae. Consequently, the normalized estimators do not

exhibit the expected relationship to gene flow (Kronholm et al. 2010). Jost (2008) developed a new metric, D , which he claims estimates ‘true allelic differentiation’, unlike F_{ST} and its analogs. However, D is not appropriate for examining the level of gene flow between populations (Jost 2009). Consequently, in their recent review of F statistics Meirmans and Hedricks (2011) recommended the use of F_{ST} and F'_{ST} in demographic studies like those of Chivers et al. (2011) and Martien et al. (2011). None of these measures (F_{ST} , F'_{ST} and D) can be meaningfully compared across data sets that use different genetic loci due to their dependence on mutation rate (Leng and Zhang 2011; Meirmans and Hedrick 2012). However, because all of the samples used by Chivers et al. (2011) and Martien et al. (2011) were genotyped for the same loci and all strata had comparable levels of diversity in the nucDNA data set, comparisons of F_{ST} and F'_{ST} values within and between Chivers et al. (2011) and Martien et al. (2011) strata are valid.

This results of Tables 2 and 3 differ somewhat from an analysis of false killer whale population structure (Chivers et al. 2011) that used a Bayesian clustering program STRUCTURE 2.3.1 (Pritchard et al. 2000, Falush et al. 2003, Hubisz et al. 2009) to cluster the samples on the basis of their microsatellite genotypes (i.e., the nucDNA data set). This program clusters samples into a named number of groups to maximize Hardy-Weinberg equilibrium. Chivers et al. (2011) used an admixture model with correlated frequencies to cluster the samples into $k = 1-5$ groups and ran STRUCTURE 3 times for each value of k . They compared estimates of likelihood and ancestry across runs to confirm convergence. They evaluated support for different values of k by comparing the mean log-likelihood of model runs. They used a burn-in of 50,000 and a run length of 500,000, and all other parameters were left at program defaults.

Table 2. Pairwise comparisons using mtDNA data, with sample sizes in parentheses. (A) comparisons between MHI social clusters with χ^2 p -values below the diagonal and F_{ST} above the diagonal. (B) comparisons between the different geographic strata. The χ^2 test is the most powerful statistic to detect differentiation (see full explanation in Chivers et al. 2010).

(A)	<table border="1"> <thead> <tr> <th>Social group</th> <th>1</th> <th>2</th> <th>3</th> </tr> </thead> <tbody> <tr> <td>1 (30)</td> <td>NA</td> <td>-0.04988</td> <td>0.3795</td> </tr> <tr> <td>2 (12)</td> <td>0.4028</td> <td>NA</td> <td>0.4940</td> </tr> <tr> <td>3 (23)</td> <td>0.0003</td> <td>0.0005</td> <td>NA</td> </tr> </tbody> </table>						Social group	1	2	3	1 (30)	NA	-0.04988	0.3795	2 (12)	0.4028	NA	0.4940	3 (23)	0.0003	0.0005	NA																																	
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MHI Insular	--	0.1009	0.6066	0.6394	0.5138	0.6343																																																	
NWHI	0.0110	--	0.7372	0.8034	0.5883	0.8486																																																	
Mexico	< 0.0001	< 0.0001	--	0.5756	0.0765	0.5899																																																	
Panama	< 0.0001	< 0.0001	< 0.0001	--	0.4612	0.6734																																																	
Hawaii Pelagic	< 0.0001	< 0.0001	< 0.0001	< 0.0001	--	0.4069																																																	
American Samoa	< 0.0001	< 0.0001	< 0.0001	< 0.0001	< 0.0001	--																																																	

The STRUCTURE results reveal the genetic distinctness of the MHI insular population of false killer whales, and the limited gene flow between that population and the other putative populations sampled in the CNP and ENP (Table 4, Figure 8). The STRUCTURE analysis uses only the nucDNA data set, and the results indicated that the nuclear genome of the NWHI animals is more similar to that of the other sampled CNP animals than to that of the MHI insular population. One must keep in mind, however, that sample size for the NWHI remains small and, therefore, inferences about how this population relates to others are consequently somewhat weak.

Table 3. Pairwise comparisons using nucDNA data with sample sizes in parentheses. (A) comparisons between MHI social clusters with χ^2 p-values below the diagonal and F'_{ST} above the diagonal. (B) comparisons between the different geographic strata with χ^2 p-values below the diagonal and F'_{ST} above the diagonal.

(A)		Social group		
		1	2	3
1 (30)		NA	0.0356	0.0413
2 (11)		0.1718	NA	0.0726
3 (23)		0.0010	0.0090	NA

Putative population	Hawaii		Mexico (n = 19)	Panama (n = 14)	Hawaii	American
	Insular (n = 91)	NWHI (n = 21)			Pelagic (n = 21)	Samoa (n = 6)
MHI insular	--	0.1209	0.1117	0.1533	0.0347	0.1453
NWHI	< 0.0001	--	0.1466	0.1907	0.0716	0.2120
Mexico	< 0.0001	< 0.0001	--	0.1367	0.0710	0.1287
Panama	< 0.0001	< 0.0001	< 0.0001	--	0.1271	0.2346
Hawaii Pelagic	< 0.0001	0.0002	0.0005	0.0002	--	0.1040
American Samoa	< 0.0001	< 0.0001	0.0004	< 0.0001	0.0007	--

However, nearly all the NWHI animals had the most common haplotype of the MHI insular population. This incongruence between the nucDNA and mtDNA data sets suggests that (1) the NWHI and MHI insular populations were likely founded by closely related false killer whales, leading them to share a common mtDNA haplotype, and (2) the NWHI population may have, in recent evolutionary time, experienced higher rates of gene flow with pelagic animals than with the MHI insular population, leading them to have more nucDNA similarities to pelagic animals. What is most clear is that the MHI insular population is clearly separable from all other strata (including the NWHI). The actual likelihood values for the STRUCTURE runs are highest for 3 populations ($k = 3$), but the third 'population' is considered noise. False killer whales from all areas, including MHI insular and NWHI, get a small and variable percentage of their ancestry assigned to group 3, but there is no rhyme or reason to it. It is a common and well-known

behavior of STRUCTURE that the likelihood often jumps dramatically when the 'correct' number of groups is reached and then continues to gradually increase as the number of groups increases.

Table 4. Summary of log-likelihood values from STRUCTURE runs. The number of groups (k) defined by STRUCTURE varied from 1 to 5. Three replicate analyses were run for each value of k . The model with the highest mean log-likelihood across replicate runs is shown in bold.

k	Replicate 1	Replicate 2	Replicate 3	Mean
1	-9314.2	-9313.5	-9314	-9313.9
2	-9151.2	-9149.2	-9150.6	-9150.3
3	-9110.6	-9117.5	-9115.6	-9114.6
4	-9298.2	-9759.5	-9741.9	-9599.9
5	-9480.3	-9662.5	-9465.1	-9536.0

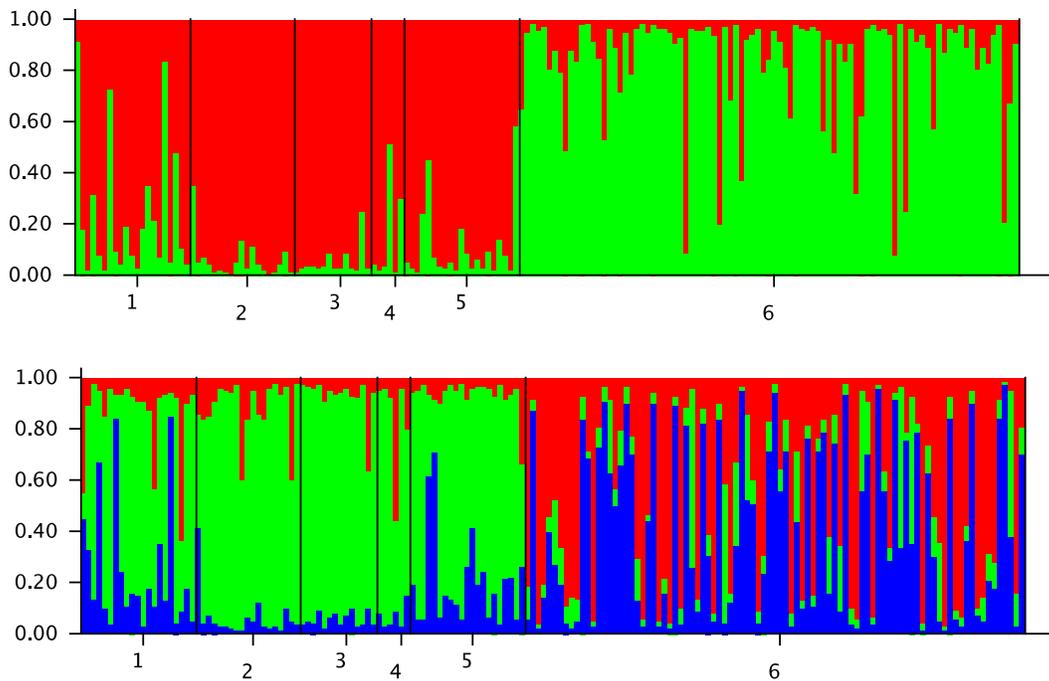


Figure 8. Graphical representation of the results of the STRUCTURE analysis for the models with (upper) $k = 2$ and (lower) $k = 3$. Bars are shaded as to the proportion of the individual's ancestry that is attributable to each of the groups defined by STRUCTURE. Numbers along the bottom of each graph identify the stratum where a sample was collected: 1 = Hawaii pelagic, 2 = Mexico, 3 = Panama, 4 = American Samoa, 5 = NWHI and 6 = MHI insular. The numbers are shown in the middle of their respective sample set, and a black vertical line delineates the sample set for each stratum.

Conclusions from the New Genetics Information

Recent genetic analyses have strengthened the evidence for differentiation of the MHI insular population from all other false killer whale strata including the NWHI population. However, some important factors need to be kept in mind when considering the implications of these data. First, the sampling in the NWHI is more limited than within the MHI, which leaves considerable uncertainty about the relationship between this population and others, including the MHI. The fact that the most common mtDNA haplotype in both strata is haplotype 1 and that this haplotype is found nowhere else speaks strongly to one of these strata originating through colonization by the other. Finding a new haplotype in the NWHI that is closely related to haplotype 1 is consistent with a population that has been separated long enough to have developed its own unique haplotype (not found in the MHI). The lack of haplotype 2 in the NWHI results in the strong differentiation between this stratum and the MHI, although limited sampling that likely comes from one social cluster in the NWHI and the absence of haplotype 2 in one of the MHI social clusters weaken this inference. In contrast, the nuclear data support stronger differentiation between the NWHI and MHI populations than the differentiation found among MHI social clusters. In addition, the MHI population is as different from the NWHI population as it is from the other more distant strata (supported by both F_{st} and STRUCTURE results). These data are consistent with the notion of two insular Hawaiian populations that now have little gene flow and that represent a mtDNA lineage that has been separated from all other false killer whale populations for a substantial period of time.

Because the strength of inferences from the genetic data depend on sampling, it is helpful to consider the sampling in some detail. False killer whales in the main Hawaiian Islands have been more intensely observed and sampled in the wild than any other group in the world for a number of reasons: 1) the multi-purpose surveys conducted by Baird and colleagues over the past 13 years have given more opportunity to encounter false killer whales than elsewhere, 2) the high profile of the Hawaiian Islands provide a lee conducive to study cetaceans from a small vessel, 3) the density of false killer whales in the near-shore island habitat is higher than in the pelagic habitat. Even so, encounters occur at the rate of once every 17.4 days in the MHI. Obtaining data from the nearby pelagic habitat and the NWHI is more difficult and obtaining samples will necessitate both time and considerable resources. Obtaining the 21 samples from the NWHI resulted from a cruise using a large research vessel that spent 39 days surveying the NWHI, with 15 of those days in very good sighting conditions (less than Beaufort 3). To obtain samples from more social clusters will likely require at least this level of effort and potentially take several years to have both good weather and an adequate survey platform. Obtaining more samples from the nearby pelagic waters requires a large research vessel with the ability to launch small sampling boats similar to what was used for the 2002 and 2010 HICEAS cruises. On average, each ~175-day cruise added 5.5 pelagic false killer whale samples. These cruises happened 8 years apart, so doubling the number of samples in this stratum could take another 16 years. On average, less than 1 sample per year is added from fisheries interactions near Hawaii. Thus, although sampling limits inferences from the genetic data, the MHI are extremely well sampled, their mtDNA haplotypes have not been found anywhere else in the world outside of Hawaii and obtaining more pelagic samples in a timely manner is unlikely.

Ecology of the Hawaiian Archipelago

The oceanography and ecology of the Hawaiian Islands were reviewed as part of the 2010 Status Review; however, differences or similarities between the southern and northern portions of the archipelago were not evaluated. To evaluate whether MHI insular and NWHI false killer whales may be ecologically discrete or significantly separate based on ecological factors, a literature review was conducted.

The Hawaiian Archipelago is a relatively unusual tract of terrestrial habitat in the CNP, being a long chain of islands in a gradient of sizes stretching diagonally across the center of the basin. This island chain strongly influences basin-wide oceanographic and atmospheric processes (e.g. the North Pacific gyre) resulting in many small-scale processes of relevance to terrestrial and aquatic organisms living in and around the archipelago. The geography and oceanography of the two regions of the archipelago, the MHI and the NWHI, can be markedly different from that of the surrounding oceanic regions and from each other, yet the ecological significance of these differences is not well described.

The oceanic region surrounding Hawaiian Archipelago is a part of the large CNP pelagic province (Spalding et al. 2012). This area is bounded by major ocean currents and is characterized by a general clockwise circulation pattern. Lower-latitude regions are primarily oligotrophic with productivity tending to increase with increasing latitude. Peaks in productivity are seen in latitudes 30-45° N as a result of the subtropical frontal zone along the northward boundary and the adjacent transition zone chlorophyll front (Polovina et al. 2001). These regions of high productivity alternately migrate approximately 1000 km north or south seasonally, and during their southward shift they impinge on the northern extent of the Hawaiian Archipelago; hence, the NWHI can experience large fluctuations in productivity during the north/south movements of these features. Seasonal variability in temperature also separates the NWHI and the MHI. For example, the largest seasonal fluctuations in sea surface temperature can occur in the northernmost portion of the NWHI, which can receive both the coolest temperatures as well as the warmest temperatures despite the northerly latitudes. Seasonality is much reduced in the MHI with only moderate changes between a warmer period of consistent trade winds and a cooler period of slightly more variable winds. These differences in temperature and productivity as well as the large differences in the variation of temperature and productivity serve as key areas of distinctiveness between the NWHI and the MHI for organisms residing there and depending on the local food web. Additionally, ocean current and trade wind impingement upon the archipelago also have differential effects based on the sizes of the land masses in the archipelago.

The MHI in the southern portion of the archipelago are made up of the largest islands in the archipelago, with the island of Hawaii having 428 km of coastline with quasi-continental conditions in some areas as a result of broad shelf regions along long stretches of coastline. The high-elevation volcanic features in the MHI (e.g., Mauna Kea, Mauna Loa, Kilauea, Haleakala) contribute to the large expanses of emergent land and also have a large impact on the prevailing currents and trade wind flow patterns around the MHI. The impacts of ocean currents on the archipelagic bathymetry and the wind funneling between islands have resulted in uniquely different spatial patterns of habitat in the leeward areas, channel areas, and windward areas of

each island ecosystem. In the MHI, windward areas are characterized by moderate to heavy rainfall, cooler temperatures, windy conditions, and rougher sea conditions (e.g., swell, breaking waves, currents), whereas leeward areas are characterized by dryness, warmer temperatures, low winds, and calmer sea conditions. Eddies (both cyclonic and anticyclonic) often form in the leeward areas of the larger islands, which can then be quasi-stationary or slowly move downstream generally to the west. These eddies are important circulation features and can be very important biologically due to patterns of productivity, thermal regimes, and organism transport. While rainfall does occur in the NWHI, the amount and patterns of variability in NWHI rainfall more closely mimic those in leeward areas of the MHI than the windward MHI regions. The enhanced amount of freshwater runoff in the MHI contributes significantly to coastal productivity in the MHI nearshore regions (Friedlander and DeMartini 2002). This increased productivity, coupled with the increased turbulent mixing caused by the island impingement on the flow field, is thought to be a large component of productivity gradients called the “island mass effect” (Doty and Oguri 1956, Gilmartin and Revelante 1974). This island effect can extend many hundreds or even thousands of kilometers to the west in some instances (Xie et al. 2001). Such effects are absent or negligible in and around the small features comprising the NWHI. The large bathymetric features of the MHI also interact strongly with the underlying tidal patterns, giving rise to a variety of enhanced tidal currents, fronts, and features that are absent in the NWHI and other oceanic environments with minimal tidal impacts. Shoreline complexity and the large bays and harbors in the MHI create a complicated oceanographic system that is absent for the most part in the NWHI.

Climate variability in the CNP, consisting principally of El Niño, La Niña, and the longer-term Pacific Decadal Oscillation, can impart differential effects to the Hawaiian Archipelago, depending on location. Due to the geographic extent of the archipelago and the patterns of wind and temperature variability, the NWHI and MHI often encounter opposing endpoints of climate variability. For example, during La Niña the NWHI may experience warmer conditions than average, while at the same time the MHI may experience cooler conditions than average. Since temperature has a fundamental impact on metabolic rates, productivity, ocean currents, etc., the contrast in ecological setting can be striking.

Geomorphologically, the NWHI and MHI are also quite different from the perspective of aquatic organisms. The absolute amount of shallow habitat and the relative amount of shallow habitat in comparison to overall aquatic habitat are both much greater in the MHI due to the presence of shelf features around the higher islands. These shallow regions, often in the protective lee of higher islands (e.g., Penguin Bank, Kohala Shelf), offer very unique habitats not found elsewhere in the archipelago.

Despite clear differences in the oceanographic and climatic forcing within the archipelago, there are also striking similarities between the NWHI and the MHI. Most islands, atolls, and submerged banks within the archipelago are only separated by tens of kilometers or less, providing linkages for reef and pelagic fish and other organisms all along the archipelago. Both regions are part of the larger CNP province (Spalding et al. 2012), so defined because of the strong biogeographic affinities shared by spatial components of this region. For example, many species of aquatic organisms that are endemic to Hawaii will freely range up and down the Hawaiian Archipelago, including both the NWHI and the MHI. Similarly, the non-endemic fish

fauna of the archipelago is not separable into biogeographic units; most of the observed archipelagic patterns of abundance are related to differences in anthropogenic stress or simply related to differences in latitude and/or water temperature with no clear breakpoints of ecological clustering aside from species with very particular habitat or dietary requirements. While the near-island habitat is disjunct and a mixture of emergent and submerged features, the surrounding aquatic habitat in contrast is continuous, fluid, and in constant motion, including a significant amount of turbulent motion which tends to homogenize the aquatic environment. Oceanographically, water masses of the world oceans are often identified by their unique combination of temperature and salinity. There is no evidence of such structuring of these characteristics over the span of the Hawaiian Archipelago (Pickard and Emory, 1982), suggesting that over this geographic scale there is no physical separation of the aquatic habitat.

The known prey of false killer whales include tunas, billfishes, mahimahi, lustrous pomfret, scrawled filefish, and threadfin jack (Baird et al. 2008, Oleson et al. 2010), all of which have very widespread Pacific populations and are found throughout the Hawaiian Archipelago. Abundance of the tunas and billfishes varies with latitude. Prey species like swordfish and albacore are generally more abundant at higher latitudes (such as the latitudes of the NWHI) whereas other prey species like yellowfin tuna and blue marlin are more abundant at lower latitudes (such as the latitudes of the MHI.) However, abundance also tends to vary seasonally by latitude, and to vary differently by species (Hyder 2009). There are no observations of differential prey exploitation patterns by MHI insular and NWHI false killer whales, nor are there enough observations within the MHI insular population to evaluate differences by latitude or by season. Large pelagic fish, such as bigeye tuna appear to show affiliation with points of attraction in a mid-ocean habitat, not restricted to floating objects and seamounts, such that larger features, such as islands, also act as points of attraction for bigeye tuna (Sibert et al. 2003). This suggests differences in availability of bigeye tuna, and probably other fish species, to false killer whales at different locations throughout the archipelago. However, the fine-scale distribution of large pelagic fish relative to false killer whale foraging has not been evaluated.

In summary, there are both differences and similarities between the NWHI and the MHI, but there are insufficient data to evaluate exactly how false killer whales fit within the ecosystem or to help identify which oceanographic or ecologic features are most important for maintaining or promoting separation of MHI insular and NWHI populations. The physical and biological settings can be quite different yet there are compelling arguments to support the notion that the archipelago represents a single continuous habitat. The nature and degree of adaptation by an organism would be key determinants of how these differences and similarities can result in an ecologically structured region over the span of the archipelago.

Determination of the DPS

As in the 2010 Status Review, in evaluating discreteness and significance the BRT considered a number of factors related to MHI insular false killer whale behavior, ecology, and genetics. Some discreteness and significance factors as defined by the DPS guidance were not considered in detail, as the team determined there was still no evidence to suggest that those factors were

applicable to MHI insular false killer whales. In particular, there is no new evidence to suggest that MHI insular false killer whales are discrete from other false killer whale populations based on marked physical or physiological separation, nor is the population delimited by international jurisdictional boundaries, as it occurs entirely within U.S. waters. The BRT again dismissed significance criteria based on loss of the discrete segment resulting in a significant gap in the range of the taxon, because MHI insular false killer whales already overlap in range with the Hawaii pelagic stock and the NWHI stock, and the remaining nearshore area that would be vacated if the insular population were lost is geographically very small compared to the overall species range. The team also again dismissed significance criteria based on the discrete segment representing the only surviving natural occurrence within its historical range, as false killer whales are known to occur throughout tropical and subtropical waters of all oceans. Each remaining discreteness and significance criterion relevant to MHI insular false killer whales was discussed separately, and the original arguments for and against each factor were updated and reevaluated given new information available since the 2010 Status Review.

As in the 2010 Status Review, the BRT used the plausibility point method to evaluate each discreteness and significance factor potentially relevant to MHI insular false killer whales, with each team member asked to allocate 10 points among the arguments for and against each factor. Allocating points in this manner allowed individual team members to express their level of certainty on each of the factors, such that placement of all 10 points either for or against a particular factor would indicate certainty in the arguments or evidence presented. Point allocations from all team members were combined to produce a measure of percentage plausibility, where a factor score greater than 50% indicates that the arguments in favor of that factor carry more weight than the arguments against it, and where higher percentages indicate greater confidence in the supporting arguments than do lower values. Determinations of discreteness and significance were based on overall assignment of at least 50% of the total plausibility points in favor of the DPS factor, and assignment of at least 6 of 10 points to arguments in favor of a factor by at least 5 team members. For example, if the total point allocation to arguments in favor of a factor exceeded 50%, but 4 or fewer members voted in support of that factor (defined as more than 5 of their 10 points), then the factor was not considered by the Team to support the DPS designation. Higher aggregated plausibility point totals were considered to provide stronger evidence in support of a factor than lower point totals. Revised individual arguments for and against each factor and individual point-allocation are listed in Appendix A.

Determination of ESA discreteness

The BRT continued to find strong support for a finding that MHI insular false killer whales are discrete from other false killer whales. The team found that MHI insular false killer whales are markedly separated from other false killer whales based on behavioral factors. In particular, MHI insular false killer whales form a tight social network, with most identified false killer whales linked to all others through at least two distinct associations and with none of the identified false killer whales linking to animals outside of the nearshore areas of the MHI. These association data are strong and relate directly to the mating patterns and the resulting genetic patterns that have been observed. One BRT member noted that during the 2010 deliberations they had placed

more weight on the unknown identity of animals seen near Kauai, and that knowledge of the association of those animals with the NWHI population has made the behavioral discreteness more clear. Further, phylogeographic analysis indicates that the MHI insular population is nearly isolated with little, if any, emigration of females between adjacent island-associated populations. Additionally, significant differences occur in nucDNA between the main Hawaiian Islands insular population and the other populations, indicating there is little male-mediated gene flow. Finally, telemetry studies show all 27 satellite-tagged Hawaiian insular false killer whales have remained within the main Hawaiian Islands (Baird et al. 2012), and consist of three primary social clusters with different primary habitats. More than one BRT member noted that there is still uncertainty about false killer whale behavior and the association of the MHI insular and NWHI population; however, the BRT concluded that the weight of the evidence continues to strongly support recognition of MHI insular false killer whales as behaviorally discrete from other false killer whales in the taxon.

In the 2010 Status Review, the BRT indicated that the MHI insular population was also ecologically discrete from other populations. During this reevaluation, the Team did not find sufficient evidence to maintain its earlier support for discreteness based on ecological factors. Although movement data continue to indicate that MHI insular false killer whales have adapted to a different ecological habitat than their pelagic conspecifics, it is less certain that they inhabit a unique ecological setting given the existence of an island-associated population with the NWHI. Twenty-seven MHI insular false killer whales instrumented with satellite tags, whose locations have been evaluated in detail, show close association with the MHI in waters with a median depth of 623 m, which is substantially shallower than global oceanic habitat for the species and the median depth for a satellite-tagged Hawaiian pelagic false killer whale and three tagged NWHI false killer whales (Baird et al. 2009, Baird et al. accepted). Oceanographic differences between the MHI and NWHI are clear, and can be linked to differences in local productivity. However, a lack of information on false killer whale foraging patterns in the two regions together with lack of evidence for meaningful differences in the ecology of upper trophic-level predators, led the BRT to dismiss ecological discreteness as a basis for judging DPS discreteness.

Determination of ESA significance

The BRT continued to find support for its earlier conclusion that MHI insular false killer whales are significant to the taxon to which they belong. Significance to the taxon was based primarily on marked genetic differences, although weaker support for existence in a unique ecological setting and maintenance of cultural diversity was also evident. Further, the BRT continued to find slightly stronger support for significance based on all factors taken together. The BRT found very strong support that MHI insular false killer whales differ markedly from other populations of the species in their genetic characteristics. The magnitude of mtDNA differentiation is large enough to infer that time has been sufficient and gene flow low enough to allow adaptation to MHI insular habitat and that the area would not be readily repopulated by pelagic whales without such adaptation. MHI insular false killer whales exhibit strong phylogeographic patterns that are consistent with a founding event for island-associated false killer whales, followed by local evolution of a mitochondrial haplotype unique to the MHI

insular population. Although NWHI false killer whales share one haplotype with MHI insular false killer whales, each population is also characterized by its own unique daughter haplotype. Occurrence of a unique daughter haplotype (31) within a relatively small sample from the NWHI population is significant as nearly two-thirds of individuals in the MHI insular population have been sampled without any evidence of this haplotype in that population. The nuclear data also continue to suggest strong differentiation of the MHI insular population, perhaps even stronger than in the initial evaluation because of new information on whales in the NWHI. A Bayesian analysis (STRUCTURE) using all sampled false killer whale populations (Chivers et al. 2011) indicated separation into two populations—the MHI insular population and all others, including the NWHI island-associated animals. The same STRUCTURE analysis indicates that male-mediated gene flow into the MHI insular population from false killer whales in other areas, including island-associated animals in the NWHI, is at a very low level. The nucDNA results suggest very low gene flow from other populations, such that individually sampled MHI insular false killer whales can be genetically assigned to the MHI insular population with high likelihood.

The BRT acknowledged that uncertainty remains in the genetic comparisons of the MHI insular population to other Pacific false killer whales. Although the MHI insular population is very well sampled with roughly two-thirds of the false killer whales represented, pelagic false killer whale genetics are poorly sampled with large sampling gaps to both the west and east of Hawaii, and uncertainty remains about the structure of the NWHI population. Low levels of male-mediated gene flow were identified based on the genetics results. Despite these uncertainties, the available sample size from Hawaiian false killer whales (MHI, NWHI, and pelagic) is substantial and overall the Team felt that significant differences based on multiple measures was noteworthy and that it is unlikely that new samples will significantly alter the overall story toward more similarity between these groups. Therefore, the weight of the evidence supported a finding of marked differentiation in genetic characteristics between the discrete MHI insular false killer whale population and other populations of the species, thus making the MHI population significant to the taxon.

In the 2010 Status Review, the BRT found reasonably strong support for significance based on persistence in a unique ecological setting and for significance of cultural uniqueness. Both of these factors still provide support for the significance determination; however, the support is weaker than in the initial evaluation, primarily because of uncertainties raised with the existence of another island-associated population in the NWHI. Team members finding support of ecological significance noted primarily the influence of different oceanographic factors, such as leeward eddies and freshwater input, which result in localized higher productivity in the MHI but which do not occur in the NWHI. Habitat analyses indicate that clusters of false killer whales preferentially use the northern coast of Molokai and Maui, the north end of the Big Island, and a small region southwest of Lanai. This behavior suggests the whales may seek out areas where prey are concentrated by local oceanographic conditions. MHI insular false killer whales appear to generally occur closer to land and in shallower water than whales in the NWHI population, which may be related to differences in oceanographic conditions in the two locations. The BRT noted significant uncertainty with regard to the relationship between these seemingly unique MHI oceanographic processes and the ecology of a pelagic predator such as false killer whales.

The BRT assigned plausibility points in favor of significance based on ecological setting, but noted the greater uncertainty about this factor than in the original DPS evaluation.

As in the original evaluation of significance, the BRT still found that culture (knowledge passed through learning from one generation to the next) is likely to play an important role in the evolutionary potential of false killer whales because transmitted knowledge may help whales adapt to changes in local habitats. However, the finding was weaker than in the previous evaluation due to the lack of information on cultural differences between the MHI insular and NWHI populations. While some Team members noted that cultural transmission is a strong force in social odontocetes, playing a significant role in population structure and persistence, others thought that there was little evidence for specific differences in cultural aspects of the MHI and NWHI populations. Significant uncertainty was represented in the BRT's evaluation of culture; however, the Team found weak support for cultural significance.

The BRT discussed the relative weakness of the ecological and cultural factors for significance and concluded that these factors taken alone do not provide strong support for significance of the DPS. However, the combination of ecological and cultural factors, taken together with the stronger genetic evidence, provided slightly greater support for significance of the DPS than the genetics alone by increasing the Team's confidence that the population is unique. As in the 2010 Status Review, the BRT separately evaluated the significance criteria based on all of the factors taken together and found that the particular combination of qualities makes this population unique; the MHI insular population has adapted to this particular environment in a way that likely has not and cannot occur with this species anywhere else in the world. The BRT emphasizes that, even without considering ecological and cultural factors, the significance factor is met because MHI insular false killer whales differ markedly from other populations of the species in their genetic characteristics.

Dissenting Views

The panel's consensus view that MHI insular false killer whales are a discrete and significant population was based on a strong vote in 2 of the 5 areas of evidence considered: 1) marked separation as a consequence of behavioral factors (including genetic evidence of reproductive separation); and 2) marked genetic differentiation.

The dissenting opinion was that a recommendation for a DPS finding would give too much weight to genetic evidence, and that the genetic evidence was not sufficiently convincing due to substantial uncertainties. Although the genetics of these whales suggests their being a DPS is very plausible, this finding is far from certain. The lack of convincing evidence from other aspects of biology and ecology in the current review, and the substantial change in the panel's views on these aspects in comparison to the 2010 review, strongly influenced the dissent. In the 2010 review, the BRT recommendation was based on many factors besides genetics, but that was before the discovery of the NWHI population. The possibility of finding other archipelago-associated groups of whales with further research was outlined in arguments against a finding of marked behavioral and ecological discreteness and significance in the 2010 review. When more research was conducted, such an example was found. Congress instructed that the exercise of authority with regard to DPS findings be used "...sparingly and only when the biological

evidence indicates that such action is warranted." (Senate Report 151, 96th Congress, 1st Session). The dissenting opinion reflects reservations about the current DPS finding given the dependence of the finding on genetic evidence alone.

The dissenting opinion is not expressed by an expert on genetics, and so it is based on arguments provided by more expert members of the panel in their attempt to fairly consider any weak aspects of the genetic evidence. In summary, false killer whales from only four NWHI false killer whale encounters have been genetically sampled to date, which could be considered an insufficient sample to establish whether the difference in mtDNA frequencies is representative of a true separation of the NWHI population from the MHI insular population. Pelagic false killer whale genetics are also poorly sampled with large sampling gaps to both the west and east of Hawaii. It is possible that mtDNA haplotypes found in the MHI insular population could be found elsewhere in these inadequately sampled areas.

The MHI insular false killer whales were most likely founded by haplotype 1 false killer whales, which have since split into two groups, one in the NWHI and one in the MHI (or else one of these groups may have been founded by the other), followed by further differentiation. The presence of the newly documented haplotype 1 false killer whales in the NWHI argues against the view that MHI animals have unique abilities to adapt to local conditions and could not be replaced by false killer whales from the NWHI. And one of the three social clusters within the MHI insular population has only haplotype 1 even though haplotype 2 is common in the other two social clusters. The primary difference in mtDNA between the NWHI and the MHI insular groups is the lack of haplotype 2, the difference would be more certain if greater sampling of the NWHI were to find that the apparent difference is not a result of undersampling of social clusters.

Lastly, the failure of existing genetic data to detect male-mediated gene flow between MHI insular false killer whales and other populations may be due to biases resulting from inadequate sampling of nearby pelagic false killer whales. If male-mediated gene flow is occurring, the genetic differences between MHI insular false killer whales and other populations would not be as large as they appear to be from the mtDNA evidence. If the level of male-mediated gene flow was high enough, then genetic adaptation to local habitat would be unlikely and MHI insular animals could be replaced by pelagic or NWHI animals if the habitat became available as a result of the extirpation of MHI insular false killer whales.

The dissenting opinion is that these uncertainties with the genetic evidence are reason not to recommend a DPS finding and because of Congress's instruction to make DPS findings "sparingly", a higher level of certainty is required.

Conclusions

Table 5. Summary of BRT evaluation of discreteness and significance based on point allocations to arguments in support of or against each factor considered in detail by the team (see Appendix A for a complete list of point allocations by team member). The first set of columns (% Points) represent the aggregate of all 80 total points (10 per each of 8 members) represented as a percent. The last column (# Team Members) represents the number of members who placed more than 5 of their 10 points in favor of the supporting arguments for a given factor.

Criteria	Percentage (%) Points supporting each factor	Percentage (%) Points against each factor	# Team Members in favor of supporting arguments
<i>Discreteness</i>			
Behavioral discreteness	79	21	7
Ecological discreteness	56	44	4
<i>Significance</i>			
Ecological significance	55	45	5
Genetic significance	69	31	7
Other factors (i.e. Cultural significance).	53	47	5
Ecological, genetic, and cultural factors taken together	70	30	7

The BRT has determined through consensus that MHI insular false killer whales are a DPS of the global false killer whale taxon. The BRT found strong support for discreteness and significance based on behavioral factors and marked genetic differences, respectively, between MHI insular false killer whales and their conspecifics in other areas. The overall determination involves various levels of uncertainty in all of the factors used to judge discreteness and significance. Remaining uncertainty, as measured by the minority of points assigned (less than 50% of the aggregate plausibility points for each factor) to arguments against individual discreteness and significance factors was primarily a result of the lack of information about the biology and ecology of NWHI false killer whales, the specific role that MHI insular and NWHI false killer whales play within the ecosystem and how those roles are maintained. However, lack of information on the NWHI population does not negate the information that is presently available and the application of the best-available science standard supports designation of the MHI insular population as a DPS.

Literature Cited

- Baird, R.W., A.M. Gorgone, D.J. McSweeney, D.L. Webster, D.R. Salden, M.H. Deakos, A.D. Ligon, G.S. Schorr, J. Barlow and S.D. Mahaffy. 2008. False killer whales (*Pseudorca crassidens*) around the main Hawaiian Islands: long-term site fidelity, inter-island movements, and association patterns. *Marine Mammal Science* 24:591-612.
- Baird, R.W., M.B. Hanson, G.S. Schorr, D.L. Webster, D.J. McSweeney, A.M. Gorgone, S.D. Mahaffy, D. Holzer, E.M. Oleson and R.D. Andrews. 2012. Assessment of range and primary habitats of Hawaiian insular false killer whales: a scientific basis for determination of "critical habitat". *Endangered Species Research* 18(1): 47-61
- Baird, R.W., E.M. Oleson, J. Barlow, A.D. Ligon, A.M. Gorgone, and S.D. Mahaffy. Accepted. Photo-identification and satellite tagging of false killer whales provides evidence of an island-associated population in the Northwestern Hawaiian Islands. *Pacific Science*.
- Baird, R.W. 2012. Preliminary results from photo-identification and satellite-tagging of false killer whales off the island of Kauai in June 2012. CRC Report to PIFSC.
- Bradford, A.L., K.A. Forney, E.M. Oleson, and J. Barlow. 2012. Line-transect abundance estimates for false killer whales in the pelagic region of the Hawaiian Exclusive Economic Zone and in the insular waters of the Northwestern Hawaiian Islands. PIFSC Admin Report H-12-02.
- Carretta, J.V., E.M. Oleson, D.W. Weller, A.R. Lang, K.A. Forney, J. Baker, B. Hanson, K. Martien, M.M. Muto, M.S. Lowery, J. Barlow, D. Lynch, L. Carswell, R.L. Brownell, D.K. Matilla, and M.C. Hill. 2012. U.S. Pacific Marine Mammal Stock Assessments: 2012 (Draft). NOAA-TM-NMFS-SWFSC-XXX. In public comment.
- Chivers, S.J., R.W. Baird, K.M. Martien, B.L. Taylor, F.I. Archer, A.M. Gorgone, B.L. Hancock, N.M. Hedrick, D K. Mattila, D.J. McSweeney, E.M. Oleson, C.L. Palmer, V. Pease, K.M. Robertson, J. Robbins, J.C. Salinas, G.S. Schorr, M. Schultz, J.L. Theileking and D.L. Webster. 2010. Evidence of genetic differentiation for Hawai'i insular false killer whales (*Pseudorca crassidens*). 44p. NOAA Technical Memorandum, NOAA-TM-NMFS-SWFSC-458.
- Chivers, S.J., R.W. Baird, K.M. Martien, B.L. Taylor, F.I. Archer, V. Pease, K.M. Robertson, B.L. Hancock-Hanser, J. Robbins, D K. Mattila, C.L. Palmer, A.M. Gorgone, D.J. McSweeney, G.S. Schorr, and D.L. Webster. 2011. Genetic differentiation of Hawaii insular false killer whales: analyses updated with new samples from the northwest Hawaiian Islands. PSRG Report PSRG-2011-15.
- Doty, M.S. and M. Oguri. 1956. The island mass effect. *Journal du Conseil* 33-37.
- Falush, D., M. Stephens and J. K. Pritchard. 2003. Inference of population structure using multilocus genotype data: Linked loci and correlated allele frequencies. *Genetics* 164:1567–1587.

- Friedlander, A.M. and E.E. DeMartini. 2002. Contrasts in density, size, and biomass of reef fishes between the northwestern and the main Hawaiian Islands: the effects of fishing down apex predators. *Marine Ecology Progress Series* 230: 254-264.
- Gilmartin, M. and N. Revelante. 1974. The 'island mass' effect on the phytoplankton and primary production of the Hawaiian Islands. *Journal of Experimental Marine Biology and Ecology* 16: 181-204.
- Hedrick P.W. 2005. A standardized genetic differentiation measure. *Evolution* 59:1633-1638.
- Hubisz, M. J., D. Falush, M. Stephens and J. K. Pritchard. 2009. Inferring weak population structure with the assistance of sample group information. *Molecular Ecology Resources* 9:1322–1332.
- Hyder. P., K. Bigelow, R. Brainard, M. Seki, and J. Firing. 2009. Migration and abundance of bigeye tuna (*Thunnus obesus*), and other pelagic species, inferred from catch rates and their relation to variations in the ocean environment. SOEST 09-02 JIMAR Contribution 09-37. 60p.
- Jost L. 2008. *GST* and its relatives do not measure differentiation. *Molecular Ecology* 17:4015-4026.
- Jost L. 2009. *D* vs. *GST*: Response to Heller and Siegismund (2009) and Ryman and Leimar (2009). *Molecular Ecology* 18:2088-2091.
- Kronholm I., O. Loudet, and J. de Meaux. 2010. Influence of mutation rate on estimators of genetic differentiation- lessons from *Arabidopsis thaliana*. *BMC Genetics* 11:33.
- Leng L. and D.-X. Zhang. 2011. Measuring population differentiation using *GST* or *D*? A simulation study with microsatellite DNA markers under a finite island model and nonequilibrium conditions. *Molecular Ecology* 20:2494-2509.
- Martien, K.K., R.W. Baird, S.J. Chivers, E.M. Oleson, and B.L. Taylor. 2011. Population structure and mechanisms of gene flow within island-associated false killer whales around the Hawaiian Archipelago. PSRG Report PSRG-2011-14
- Meirmans P.G. 2006. Using the AMOVA framework to estimate a standardized genetic differentiation measure. *Evolution* 60:2399-2402.
- Meirmans P.G. and P.W. Hedrick. 2011. Measuring genetic differentiation: F_{ST} and related measures. *Molecular Ecology Resources* 11:5-18.
- Newman M.E.J. 2006. Modularity and community structure in networks. *Proceedings of the National Academy of Sciences* 103: 8577–8582.
- Pickard, G. L. and W. J. Emery. 1982. Descriptive Physical Oceanography: An Introduction. Pergamon Press. 249 pp.

- Oleson, E.M., C.H. Boggs, K.A. Forney, M.B. Hanson, D.R. Kobayashi, B.L. Taylor, P.R. Wade, and G.M. Ylitalo. 2010. Status Review of Hawaiian Insular False Killer Whales (*Pseudorca crassidens*) under the Endangered Species Act. U.S Dep. Commerc. NOAA Tech Memo., NOAA-TM-NMFS-PIFSC-22. 140 p. + Appendices.
- Polovina, J.J., E. Howell, D.R. Kobayashi, and M.P. Seki. 2001. The transition zone chlorophyll front, a dynamic global feature defining migration and forage habitat for marine resources. *Progress in Oceanography* 49: 469-483.
- Pritchard, J. K., M. Stephens and P. Donnelly. 2000. Inference of population structure using multilocus genotype data. *Genetics* 155:945–959.
- Ryman N. and O. Leimar. 2009. *GST* is still a useful measure of genetic differentiation- a comment on Jost's *D*. *Molecular Ecology* 18:2084-2087.
- Sibert, J.R., M.K. Musyl, and R.W. Brill. 2003. Horizontal movements of bigeye tuna (*Thunnus obesus*) near Hawaii determined by Kalman filter analysis of archival tagging data. *Fisheries Oceanography* 12(3): 141-151.
- Spalding, M.D. V.N. Agostini, J. Rice, and S.M. Grant M. 2012. Pelagic provinces of the world: A biogeographic classification of the world's surface pelagic waters. *Ocean & Coastal Management*, 60. 19-30.
- Whitehead, H. 2008. Analyzing animal societies: quantitative methods for vertebrate social analysis. University of Chicago Press, Chicago, IL.
- Wright S. 1965. The interpretation of population structure by F-statistics with special regard to systems of mating. *Evolution* 19:395-420.
- Xie, S. P., W.T. Liu, Q. Liu, and M. Nonaka. 2001. Far-reaching effects of the Hawaiian Islands on the Pacific Ocean-Atmosphere system. *Science* 292:2057-2060.

Appendix A. DPS Evaluation & Scores

As in the 2010 Status Review, the reevaluation of the DPS used a structured decision-making system based on assignment of plausibility points to detailed arguments for and against each discreteness and significance factor. BRT members independently allocated plausibility points on the discreteness and significance criteria by distributing 10 points between the arguments for and against each factor. Allocating points in this manner allowed individual team members to express their level of certainty on each of the factors, such that placement of all 10 points either for or against a particular factor would indicate certainty in the arguments or evidence presented. The detailed arguments and the resulting distribution of scores are provided to fully document the team's decisions as outlined in the text of this report. Anonymized individual final team member scores are shown below.

Determination of discreteness

1. Evaluation of DPS Discreteness Criteria—Are Main Hawaiian Islands (MHI) insular false killer whales markedly separated from other populations of the same taxon as a consequence of behavioral factors?

Arguments in favor of marked separation as a consequence of behavioral factors

Throughout their distribution, false killer whales are considered a wide-ranging pelagic species not typically associated with coastal or island habitats. In addition to the MHI insular population, an island-associated population of false killer whales is now known to occur in the Northwestern Hawaiian Islands (NWHI), and other populations may occur around other island areas. However, behavioral separation of the MHI insular population is supported by the following lines of evidence:

- MHI insular false killer whales are linked through a tight social network, comprising three primary social clusters, without any linkages to animals outside of the main Hawaiian Islands.
 - All but 4 identified false killer whales encountered within 40 km of shore near the islands of Oahu, Maui, Lanai, and Hawaii are linked to all others through at least 2 distinct associations and often many more if they have been frequently sighted (Baird et al. 2005, Baird 2009). None of these animals has ever been linked to any other false killer whales photographed in the North Pacific.
 - Three separate, but associated social clusters preferentially use different portions of the MHI ecosystem (Baird et al 2012). This social clustering is analogous to Southern Resident killer whale social structure, where mating occurs both within and between social clusters (Ford et al. 2011), and where these different social units seasonally use different portions of the California Current ecosystem.
- Telemetry data show that all 27 satellite-linked telemetry-tagged MHI insular false killer whales remained within the main Hawaiian Islands (Baird et al. 2010, Baird et al. 2012), in contrast with a single tagged pelagic false killer whale, which ranged far from shore

and 5 tagged NWHI false killer whales, which ranged from Kauai to Gardner Pinnacles and out to 125 km from shore (Baird et al. accepted, Baird et al. unpublished data).

- MHI insular and NWHI island-associated animals have little overlap in range and have not been seen in the same area at the same time. Similar to Northern and Southern Resident killer whales, this is likely related to preferential use of different portions of the ecosystem, likely a function of the cultural traditions that have developed in each community.
- Genetic analyses indicate an isolated population in the main Hawaiian Islands.
 - Genetic data corroborate and strengthen evidence on the magnitude of the separation indicated by photo-ID and telemetry data. There is strong differentiation in maternally inherited mtDNA between the MHI insular population and the other, adjacent populations, namely the NWHI whales and pelagic false killer whales (Chivers et al. 2010, Chivers et al. 2011). This indicates there is little, if any, emigration of females between these populations. Additionally, there are significant differences in nuclear DNA between the MHI insular and the other populations, indicating there is little male-mediated gene flow (either emigration or mating) from any other population including island-associated NWHI animals. The photo-ID and telemetry data indicate separation, but on only a short time-scale, whereas the genetic data indicate that this separation is on a longer time-scale and hence is more ‘marked’.

Arguments against marked separation as a consequence of behavioral factors

An apparent island-associated population of false killer whales also occurs within the NWHI suggesting that NWHI animals with island-associated behavior could colonize the main Hawaiian Islands and that the MHI insular separation should not be considered ‘marked’.

Arguments against behavioral separation are:

- Although limited, available data suggest that another population of island-associated false killer whales occurs within the NWHI with range overlapping that of the MHI insular population near Kauai (Baird et al. accepted).
 - Five false killer whales satellite tagged near Nihoa and Kauai displayed island-associated movements ranging between Gardner Pinnacles and Kauai, generally remaining over shelf waters and near the small islands and atolls over periods up to 52 days (Baird et al. accepted, Baird 2012).
- The sample size and distribution are inadequate to characterize genetic separation.
 - NWHI false killer whales share 1 of 2 mtDNA haplotypes with MHI insular false killer whales. False killer whales from only 4 NWHI encounters have been sampled to date, which could be considered an insufficient sample to establish whether the difference in mtDNA frequencies is representative of a true separation of these populations. For example, one social cluster within the MHI insular population has only haplotype 1 even though haplotype 2 is common in the other 2 social clusters. The primary difference in mtDNA between the NWHI and the MHI insular populations is the lack of haplotype 2. Accordingly, the argument for a difference in mtDNA frequencies would carry

- more weight with a larger sampling of the NWHI false killer whales to assure that the difference is not a result of undersampling of social clusters.
- Although the MHI insular population is very well sampled with nearly two-thirds of the false killer whales represented, pelagic false killer whale genetics are poorly sampled with large sampling gaps to both the west and east of Hawaii. It is possible that mtDNA haplotypes found in Hawaii could be found elsewhere in these inadequately sampled areas.

2. Evaluation of DPS Discreteness Criteria—Are main Hawaiian Islands insular false killer whales markedly separated from other populations of the same taxon as a consequence of ecological factors?

Arguments in favor of marked separation based on ecological discreteness:

False killer whales are generally reported to inhabit deep oceanic habitats, and are not typically associated with shallow waters near coastlines and islands. Main Hawaiian insular false killer whales inhabit an unusual ecological setting because they, along with NWHI false killer whales are found primarily in island-associated waters that are relatively shallow and productive compared to surrounding oligotrophic oceanic waters. Evidence supporting marked separation based on ecological discreteness includes:

- Movement data show that MHI insular false killer whales have adapted to a different ecological habitat than their pelagic conspecifics.
 - Twenty-seven MHI insular false killer whales instrumented with satellite-linked telemetry tags remained closely associated with the main Hawaiian Islands, with most commonly visited areas characterized by a median depth of 623 m (Baird et al. 2012). This is substantially shallower than the global oceanic habitat, and it contrasts with one pelagic false killer whale satellite-tagged about 42 km from the Hawaiian Islands that was tracked through waters with a median depth of 3844 m. This shallower near-island habitat supports enhanced productivity, and the tight association of MHI insular false killer whales suggests they have adapted to a different ecological habitat than their oceanic conspecifics even when foraging on pelagic prey species.
- False killer whale habitat in the MHI differs from that of their NWHI conspecifics.
 - The distribution of the three NWHI false killer whales that have been tracked is characterized by being much farther offshore (38.6–55 km) and generally in water deeper (697–2506 m) (Baird 2012) than waters occupied by the MHI insular population. The larger land mass and steep slopes of the main Hawaiian Islands yield higher precipitation, vegetation, and nutrient input from land than the low-lying primarily submerged islands and atolls of the NWHI. Mountainous areas of the MHI disrupt westward wind and current flows, generating persistent leeward eddies that may increase productivity and attract higher-trophic-level predators even closer to the MHI than in the NWHI. Nearshore productivity within the NWHI declines from north to south, with the primary influx in productivity associated with the seasonal southbound movement of the

Subtropical Front and the South Subtropical Front over the northern reaches of the NWHI.

- Concentrations of persistent organic pollutants have been determined for approximately 35 MHI false killer whales and the data suggest that MHI insular false killer whales may forage on island-associated prey.
 - MHI insular false killer whales have elevated levels of fire retardants (PBDEs), a contaminant primarily associated with urban environments. These elevated levels suggest that both MHI insular false killer whales and their prey may be associated with the urban island environment.

Arguments against marked separation based on ecological discreteness:

The ecological setting in which false killer whales are found around the main Hawaiian Islands is not unique. Arguments against marked separation based on ecological discreteness include:

- An island-associated population of false killer whales is known to occur in the NWHI, indicating that the island association of false killer whales in the MHI, although unusual, has at least one other analog. Differences in the ecology and oceanography of the separate portions of the archipelago are not significant, and all of the prey that false killer whales are known to exploit occur within the entirety of this insular habitat.
- We lack data from other similar coastal or island habitats where undocumented discrete false killer whale populations may occur.
- Prey species of false killer whales range widely in open-ocean habitats and areas near oceanic islands such as the Hawaiian Islands, such that false killer whale occurrence around Hawaii is not ecologically unique.

Discreteness: MHI insular false killer whales are markedly separated from other populations of the same

Factor 1: Are Main Hawaiian Islands insular false killer whales markedly separated from other populations of the same taxon as a consequence of behavioral factors?			
	Yes	No	Total
A	8	2	10
B	7	3	10
C	5	5	10
D	8	2	10
E	9	1	10
F	10	0	10
G	8	2	10
H	8	2	10
TOTAL	63	17	80
	79%	21%	100%

Factor 2: Are Main Hawaiian Islands insular false killer whales markedly separated from other populations of the same taxon as a consequence of ecological factors?			
	Yes	No	Total
A	5	5	10
B	3	7	10
C	7	3	10
D	4	6	10
E	4	6	10
F	8	2	10
G	7	3	10
H	7	3	10
TOTAL	45	35	80
	56%	44%	100%

The BRT expressed strong support for a finding of marked separation based on behavioral factors.

Determination of significance

1. Evaluation of DPS Significance Criteria—Do Main Hawaiian Islands insular false killer whales persist in an ecological setting unusual or unique for the taxon?

Arguments in favor of persistence in a significant ecological setting

Main Hawaiian Islands insular false killer whales persist in an ecological setting unusual or unique from other false killer whale populations. Lines of evidence in support of this significant ecological setting include:

- MHI insular false killer whales' use of prey associated with island habitat may require specialized knowledge of locations and seasonal conditions that aggregate prey or make them more vulnerable to predation. In an insular habitat, such foraging grounds may occur more regularly or in more predictable locations than on the high seas.
- The shelf and slope waters surrounding the main Hawaiian Islands that are occupied by MHI insular false killer whales differ from the surrounding oligotrophic oceanic waters by being relatively shallow and productive.
 - The mesopelagic boundary community supports a local food chain that may support insular false killer whales;
 - The insular habitat is influenced by the island mass effect, or regions of higher productivity attributed to land-based inputs such as nutrients and freshwater, and wake effects;
 - MHI insular false killer whales have been observed to consume threadfin jack and filefish, two species that are primarily found in coral reef habitats near the coast.
 - Contaminant levels have been determined for approximately 35 MHI false killer whales and the data are consistent with consuming nearshore prey contaminated by local urban runoff.
- Although another false killer whale population occurs in the NWHI, the MHI habitat is influenced by different oceanographic factors, such as leeward eddies and freshwater input, which result in localized higher productivity, which the NWHI likely does not have.
 - Habitat analyses indicate that clusters of false killer whales preferentially use the northern coast of Molokai and Maui, the north end of the Big Island, and a small region southwest of Lanai. This behavior may be a response to locations where local oceanographic effects concentrate prey, although prey concentration has not been documented. Similar behavior has not been observed in the NWHI but this may be related to small sample size.
 - MHI insular false killer whales appear to generally occur closer to land and in shallower water than members of the NWHI population and this may be related to differences in oceanographic conditions in the two locations. A similar situation exists within resident-type killer whales, where the southern and southeastern Alaska communities generally occur in different ecosystems (California Current and Gulf of Alaska, respectively) with occurrence patterns unique to those systems.

- Movement and photographic resighting data suggest MHI insular false killer whales employ an unusual foraging strategy compared to most other false killer whales.
 - The home range of this population appears to be extremely small compared to that of other medium body-sized, piscivorous odontocetes, such as resident-type killer whales, which maintain larger home ranges in more productive habitats.
 - Pelagic false killer whales are at a lower population density in a lower productivity environment, suggesting that they must occupy a larger home range to find sufficient prey.

Arguments against persistence in a significant ecological setting

MHI insular false killer whales do not occupy an ecological setting unusual or unique from other false killer whale populations. Arguments against ecological significance include:

- There are insufficient data to conclude that the MHI are a unique ecological setting for false killer whales.
- Existence of another island-associated population just north of the MHI and with overlapping range suggests the ecological setting for the MHI insular population is not unique.
- There is insufficient evidence to conclude that MHI insular false killer whales have a unique foraging strategy.
 - False killer whales are socially complex, adaptable animals, such that pelagic animals may be able to alter their foraging strategies to colonize insular Hawaiian waters. Another island-associated population in the NWHI appears already to have adapted to local island habitat.
 - Evidence for a unique foraging strategy by insular false killer whales is largely inferential and based on limited data on movements, habitat preferences, and prey selection. Data are lacking to indicate a different foraging strategy by NWHI false killer whales
 - Home range is a poor indicator of foraging strategy because it can be influenced by other factors, such as social behavior.
- There are insufficient data to conclude specialization on localized resources.
 - There are too few observations of foraging by insular false killer whales to adequately quantify the use of island-associated prey.
 - Inferences from contaminant data are based on samples from approximately 35 MHI insular false killer whales and 3 pelagic false killer whales, such that comparisons of contaminant levels and ratios with other populations are very limited.
 - Contaminant sources are unknown and may not be based solely on local prey.

2. Evaluation of DPS Significance Criteria—Is there evidence that Main Hawaiian Islands insular false killer whales differ markedly from other populations of the species in their genetic characteristics?

Arguments in favor of marked genetic differentiation

Main Hawaiian Islands insular false killer whales differ markedly from other populations of the species in their genetic characteristics. Evidence supporting marked differences includes:

- MHI insular false killer whales are significantly differentiated from pelagic whales in mtDNA and nuclear DNA.
- MHI insular false killer whales exhibit strong phylogeographic patterns that are consistent with a founding event for island-associated false killer whales, followed by local evolution of a mitochondrial haplotype unique to the MHI insular population.
- The magnitude of mtDNA differentiation is large enough to infer that time has been sufficient and gene flow low enough to allow adaptation to MHI insular habitat and that the area would not be readily repopulated by pelagic whales without such adaptation.
 - The MHI insular false killer whales have two haplotypes that differ by one genetic change. Because these haplotypes are found nowhere outside the Hawaiian Islands, it is likely that one haplotype originated by two mutations from the other haplotype and has now become fairly common, which is consistent with isolation from other false killer whales for a long time. The NWHI insular false killer whales share one of these haplotypes but not the other, although sampling of the NWHI population remains limited. In addition, NWHI insular false killer whales have another haplotype that differs by one mutation that is found only in the NWHI, suggesting maternal isolation of this group for a long time. The fact that this haplotype (31) was not found in the MHI despite very strong sampling provides strong evidence for the MHI having very low interchange of females with the NWHI.
 - Geneticists use one effective migrant per generation a rule of thumb to indicate the level of gene flow below which adaptation to local habitat is likely. Comparisons using mtDNA of MHI insular false killer whales to those in all other geographic strata, excluding the NWHI, indicate there is less than one migrant per generation.
- Nuclear data (microsatellites) are consistent with little gene flow between the MHI insular false killer whales and all other false killer whales, including the island-associated animals in the NWHI.
 - Nuclear data from this marker strongly suggest discreteness. Microsatellite data, in general, are not as useful as mtDNA for answering the question of whether genetic differentiation has taken place on a long time-scale because of the high mutation rate and mode of mutation that allows alleles of the same length to have different evolutionary histories.
 - A Bayesian analysis (STRUCTURE) using all sampled false killer whale populations indicates separation into two populations—the MHI insular population and all others, including the NWHI island-associated animals. Evaluation of the nucDNA suggests that NWHI are likely more closely related to pelagic false killer whales than to the MHI insular population.
 - The same STRUCTURE analysis indicates that male-mediated gene flow to the MHI insular population from any other area including the NWHI island-associated animals is at a very low level.

- Both genetic markers are consistent with marked genetic differentiation.
 - Considering all the genetic evidence, the most parsimonious explanation for the patterns found in mtDNA and nuclear DNA is that the Hawaiian Islands were founded by a social cluster with haplotype 1. The main and NWHI island insular groups have been separated long enough to have their own unique “daughter” mtDNA haplotypes. The MHI insular population shows further evidence of significance because, unlike the NWHI, nuclear DNA suggests very low gene flow from other populations such that false killer whales can be genetically identified as belonging to their group with high likelihood.

Arguments against marked genetic differentiation

Main Hawaiian Islands insular false killer whales might not differ markedly from other populations of the species in their genetic characteristics. Arguments against marked differentiation are:

- Populations of false killer whales associated with the Hawaiian Islands were most likely founded by haplotype 1 false killer whales, which subsequently split into two groups (or one area was founded by whales in the other area) and further differentiated. The presence of the newly documented haplotype 1 false killer whales in the NWHI argues against the idea that false killer whales adapted to local conditions within the main Hawaiian Islands that could not be replaced by false killer whales from the NWHI.
- The sample distribution is inadequate to characterize marked genetic separation.
 - Although the MHI insular population is very well sampled with approximately two-thirds of the false killer whales represented, pelagic false killer whale genetics are poorly sampled with large sampling gaps to both the west and east of Hawaii.
 - NWHI false killer whales share one of two mtDNA haplotypes with MHI insular false killer whales. False killer whales from only four NWHI encounters have been sampled to date, which could be considered to be an insufficient sample to establish whether the difference in mtDNA frequencies is representative of a deep separation of these populations. For example, one social cluster within the MHI insular population has only haplotype 1 even though haplotype 2 is common in the other two social clusters. The primary difference in mtDNA between the NWHI and the MHI insular populations is the lack of haplotype 2. The difference would be more convincing if it were based on a larger sampling of the NWHI to assure that the difference is not a result of undersampling of social clusters.
 - STRUCTURE results on the relationship of NWHI false killer whales to whales in other populations are weak because the sample size for the NWHI is small. The inference that NWHI animals are more closely related to non-MHI animals than to the MHI insular animals drawn from STRUCTURE is contradicted by some comparisons of genotype frequencies using F_{st} (Table 9b in Chivers et al. 2011)
- The existing genetic data may have failed to detect ongoing male-mediated gene flow between MHI insular false killer whales and other populations because of potential biases as a result of inadequate sampling of nearby pelagic false killer whales.

- It is plausible that sampling of nearby pelagic and NWHI whales is insufficient to allow inferences about gene flow from nearby males that conceivably could mate with insular females. If such mating is occurring, offspring would have the mtDNA of their mothers but half of their nuclear DNA would be from their pelagic or NWHI fathers. Under this scenario, the genetic differences between MHI insular false killer whales and other populations would not be as large.
- If the level of male-mediated gene flow was high enough, then adaptation of MHI insular false killer whales to their local habitat would be less significant because if animals in this population were extirpated they could be replaced by pelagic or NWHI animals as the MHI insular habitat became available.
- There is one likely case of male-mediated gene flow into the MHI insular population from the pelagic population
 - A male with a non-MHI insular haplotype was biopsied and photographed with other MHI insular animals off the Island of Hawaii. Although this male was never seen again, a whale was later biopsied that relatedness analysis indicated was likely to be his son (Martien et al. 2011).

3. Evaluation of DPS Significance Criteria—Do Main Hawaiian Islands insular false killer whales exhibit *other* factors that are significant for the taxon? Significance of cultural diversity:

Arguments in favor of significant cultural diversity

Culture (knowledge passed through learning from one generation to the next) is likely to play an important role in the evolutionary potential of false killer whales. The MHI insular population contributes to cultural diversity that may enhance the ability of false killer whales to adapt to environmental change. Evidence in support of the significance of cultural diversity includes:

- MHI insular and NWHI false killer whales may each possess unique knowledge of nearshore foraging areas that is transmitted through learning. Learning is a common feature of other social odontocetes. The movements of each group of island-associated false killer whales demonstrate a clear preference for particular areas of the inshore waters. However, there is little overlap in their ranges and, as such, neither group would be familiar with other's areas of primary foraging importance.
- MHI insular false killer whale social clusters use distinct habitat areas.
- False killer whales are highly social mammals with long interbirth intervals and reproductive senescence suggesting transfer of knowledge is important to successful persistence in this unique Hawaiian habitat.
- Learning to persist in this unique habitat may take many generations.

Arguments against significant cultural diversity

The cultural diversity of the insular population is not significant to the persistence of false killer whales. Arguments against the significance of cultural diversity include:

- There is little direct evidence that cultural transmission is important to the evolutionary potential of false killer whales.

- There is little evidence that learning is important to persistence in Hawaiian waters. Observations of movements and genetic discreteness could result from territorial behavior alone.
- The existence of another island-associated population of false killer whales in the Northwestern Hawaiian Islands makes any cultural attributes of the MHI insular population less unique.

Significance Factors

Factor 1: Do Main Hawaiian Islands insular false killer whales persist in an ecological setting unusual or unique for the taxon?

	Yes	No	Total
A	2	8	10
B	8	2	10
C	4	6	10
D	3	7	10
E	8	2	10
F	7	3	10
G	6	4	10
H	6	4	10
TOTAL	44	36	80
	55%	45%	100%

Factor 2: Do Main Hawaiian Islands insular false killer whales differ markedly from other populations of the species in their genetic characteristics?

	Yes	No	Total
A	8	2	10
B	8	2	10
C	7	3	10
D	8	2	10
E	7	3	10
F	7	3	10
G	7	3	10
H	3	7	10
TOTAL	55	25	80
	69%	31%	100%

Factor 3: Do Main Hawaiian Islands insular false killer whales exhibit cultural diversity that is significant for the taxon?

	Yes	No	Total
A	6	4	10
B	5	5	10
C	7	3	10
D	6	4	10
E	6	4	10
F	3	7	10
G	1	9	10
H	8	2	10
TOTAL	42	38	80
	53%	48%	100%

Factor 4: Are Main Hawaiian insular false killer whales significant to the taxon because of genetic, ecological, and cultural factors taken together?

	Yes	No	Total
A	7	3	10
B	8	2	10
C	8	2	10
D	7	3	10
E	7	3	10
F	3	7	10
G	8	2	10
H	8	2	10
TOTAL	56	24	80
	70%	30%	100%

The BRT found MHI insular false killer whales to be significant to the taxon in which the population belongs. There was strong support for a finding of marked genetic differences, with weaker support for ecological and cultural significance. The BRT found slightly stronger support for significance to the taxon based on all factors taken together.