



Genetic structure of the beaked whale genus *Berardius* in the North Pacific, with genetic evidence for a new species

PHILLIP A. MORIN¹, Marine Mammal and Turtle Division, Southwest Fisheries Science Center, National Marine Fisheries Service, NOAA, 8901 La Jolla Shores Drive, La Jolla, California 92037, U.S.A. and Scripps Institution of Oceanography, UCSD, 9500 Gilman Drive, La Jolla, California 92037, U.S.A.; **C. SCOTT BAKER** Marine Mammal Institute and Department of Fisheries and Wildlife, Oregon State University, 2030 SE Marine Science Drive, Newport, Oregon 07365, U.S.A.; **REID S. BREWER** Fisheries Technology, University of Alaska Southeast, 1332 Seward Avenue, Sitka, Alaska 99835, U.S.A.; **ALEXANDER M. BURDIN** Kamchatka Branch of the Pacific Geographical Institute, Partizanskaya Str. 6, Petropavlovsk-Kamchatsky, 683000 Russia; **MEREL L. DALEBOUT** School of Biological, Earth, and Environmental Sciences, University of New South Wales, Sydney, New South Wales 2052, Australia; **JAMES P. DINES** Natural History Museum of Los Angeles County, 900 Exposition Boulevard, Los Angeles, California 90007, U.S.A.; **IVAN D. FEDUTIN AND OLGA A. FILATOVA** Faculty of Biology, Moscow State University, Moscow 119992, Russia; **ERICH HOYT** Whale and Dolphin Conservation, Park House, Allington Park, Bridport, Dorset DT6 5DD, United Kingdom; **JEAN-LUC JUNG** Laboratoire BioGEMME, Université de Bretagne Occidentale, Brest, France; **MORGANE LAUF** Marine Mammal and Turtle Division, Southwest Fisheries Science Center, National Marine Fisheries Service, NOAA, 8901 La Jolla Shores Drive, La Jolla, California 92037, U.S.A.; **CHARLES W. POTTER** U.S. National Museum of Natural History, PO Box 37012 Smithsonian Institution, Washington, DC 20013, U.S.A.; **GAETAN RICHARD** Laboratoire BioGEMME, Université de Bretagne Occidentale, Brest, France and Département de Biologie, Ecole Normale Supérieure de Lyon, 46 Allée d'Italie, 69007 Lyon, France; **MICHELE RIDGWAY** Oceanus Alaska, Auke Bay Ocean Center, Suite 355, PO Box 211470, Auke Bay, Alaska 99821, U.S.A.; **KELLY M. ROBERTSON** Marine Mammal and Turtle Division, Southwest Fisheries Science Center, National Marine Fisheries Service, NOAA, 8901 La Jolla Shores Drive, La Jolla, California 92037, U.S.A.; **PAUL R. WADE** Alaska Fisheries Science Center, National Marine Fisheries Service, NOAA, 7600 Sand Point Way NE, Seattle, Washington 98115, U.S.A.

ABSTRACT

There are two recognized species in the genus *Berardius*, Baird's and Arnoux's beaked whales. In Japan, whalers have traditionally recognized two forms of Baird's beaked whales, the common "slate-gray" form and a smaller, rare "black" form. Previous comparison of mtDNA control region sequences from three black specimens to gray specimens around Japan indicated that the two forms comprise different stocks and potentially different species. We have expanded sampling to include control region haplotypes of 178 Baird's beaked whales from across their range in the

¹Corresponding author (e-mail: phillip.morin@noaa.gov).

North Pacific. We identified five additional specimens of the black form from the Aleutian Islands and Bering Sea, for a total of eight “black” specimens. The divergence between mtDNA haplotypes of the black and gray forms of Baird’s beaked whale was greater than their divergence from the congeneric Arnoux’s beaked whale found in the Southern Ocean, and similar to that observed among other congeneric beaked whale species. Taken together, genetic evidence from specimens in Japan and across the North Pacific, combined with evidence of smaller adult body size, indicate presence of an unnamed species of *Berardius* in the North Pacific.

Key words: Baird’s beaked whale, Arnoux’s beaked whale, Ziphiidae, mitochondrial DNA, phylogenetics, population structure, cetacean.

Beaked whales are the second most speciose family of cetaceans but remain poorly understood. There are currently 22 recognized species (Committee on Taxonomy 2016), comprising 24% of all cetacean species, and nine of them have been described in the last century, including one since the millennium (Dalebout *et al.* 2002, van Helden *et al.* 2002). A few species (*e.g.*, Perrin’s beaked whale, *Mesoplodon perrini*; Dalebout *et al.* 2002) are known only from remains of a few stranded animals. These diverse and unusual whales are typically found at very low density and in deep off-shore or deep basin waters, and observing them is complicated by their medium-to-small size (3–13 m), deep diving behavior that keeps them below the surface for up to an hour (Mead 2009), and low surface profile that makes them difficult to spot in rougher sea-state conditions (*e.g.*, higher Beaufort level or swell) (Barlow *et al.* 2001).

The largest and one of the most common beaked whale species is Baird’s beaked whale, *Berardius bairdii*, of the cold-temperate North Pacific. It is typically found along the continental slope between 1,000 and 3,000 m (though sometimes on the shelf-edge as well; Fedutin *et al.* 2015) north of 35° latitude in the western Pacific (Omura *et al.* 1955, Kasuya 1986) and north of ~24° latitude in the eastern Pacific, ranging as far north as the north Bering Sea (~62°N) (Kasuya and Ohsumi 1984, Kasuya 2009). Winter distribution is not known, and it is presumed that they move to deeper waters, with at least some time spent in the tropics, as evidenced by the presence of cookie-cutter shark bite scars (Nakano and Tabuchi 1990, Kasuya 2011, Fedutin *et al.* 2015). Its abundance has earned it the dubious honor of being one of only two beaked whale species targeted by commercial hunting historically, and it remains a species targeted by the Japanese whaling industry. Whalers have traditionally recognized a black and a slate-gray form of Baird’s beaked whales around Japan (Omura *et al.* 1955). In his book on small cetaceans in the vicinity of Japan, Kasuya (2011) reviewed whaler observations that indicated the presence of at least two types of Baird’s beaked whales in Japanese waters: the more common slate-gray form, and a smaller, darkly pigmented form found near the northern tip of Hokkaido in the Sea of Okhotsk. This smaller form was called by the fishermen *kuro-tsuchi* [black Baird’s beaked whale] or *karasu* [crow or raven] (Kasuya 2011), and T. Yamada proposed that these represented a form distinct from Baird’s and Cuvier’s beaked whales (*Ziphius cavirostris*) found in the area, based on morphological examination of three stranded animals (Yamada and Tajima 2010, as reported in Kasuya 2011). Groups of the smaller whales were repeatedly observed in the Nemuro Strait off the northeast corner of Hokkaido and were characterized as being similar in body shape but only 60%–70% of the adult body size of Baird’s beaked whales, and had fewer or less “intense” tooth marks on their bodies. They also exhibited scarring from cookie-cutter sharks similar to those seen regularly on Baird’s beaked whales (Kasuya 2011), and indicative of at

least some time spent in tropical waters. Hershkovitz (1966) reviewed all of the nominal names proposed for cetaceans and he only found that one other nominal species had been described for *Berardius* in the North Pacific. A portion of a skull from Bering Island, Commander Islands was described as *B. vegae* (Malm 1883). We have not examined the morphology or the genetics of this specimen, which was deposited in the Stockholm Museum of Natural History.

Genetic analysis of the two types of Baird's beaked whale around Japan was presented by Kitamura *et al.* (2013), in which they identified three specimens that had "features characteristic of the black group." These three specimens had significantly different mitochondrial control region haplotypes and differed at 1–2 nucleotide positions in the nuclear α -2-actin intron one (ACTA2I) from 64 specimens assigned to the "gray" form based on morphology and the season in which they were collected. Beaked whale species are characterized by having high interspecific control region divergence (average 8.57%; range 3.37%–20.49%) and low intraspecific diversity (0.85%; 0%–1.15%) (Dalebout *et al.* 2004, Dalebout *et al.* 2007), conforming to the "bar-coding gap" that is the basis of species identification with DNA bar codes in many well-characterized species groups (Meyer and Paulay 2005, Alfonsi *et al.* 2013). The divergence between the three black form mtDNA haplotypes identified by Kitamura *et al.* (2013) and the seven haplotypes found in the common "gray" form was 4.4%–5.1%, while the intratype distances ranged from 0.2% to 0.9% (excluding indels, calculated from sequences presented in Kitamura *et al.* 2013). Based on genetic differences and the positioning of the divergent haplotypes in a phylogenetic tree of the Ziphiidae, Kitamura *et al.* (2013) suggested that there were two "stocks" of Baird's beaked whales around Japan, and that their data supported the occurrence of cryptic species in the genus *Berardius*.

Here we present genetic analysis of 178 samples from across the North Pacific, spanning the known range (in spring/summer/fall) of Baird's beaked whales, to further characterize the genetic diversity of the genus beyond waters surrounding Japan. We identify several recently stranded and museum specimens of the "black" form based on mtDNA sequences being identical to or very similar (differing by 1–2 bp) to previously identified black form specimens (Kitamura *et al.* 2013). Addition of these specimens allows us to evaluate genetic, morphological and distributional data supporting the presence of a second species of *Berardius* in the North Pacific. Specifically, we evaluate the net DNA sequence divergence as a line of evidence supporting species-level divergence between the two forms of *Berardius* in the North Pacific, and their relationships to the other recognized congener, Arnoux's beaked whale (*Berardius arnuxii*), found only in the Southern Ocean. We also evaluate the limited evidence (suggested from traditional knowledge; Kasuya 2011) for size differences between the two forms based on external morphology of two adult black form specimens compared to published size distributions of Baird's beaked whales, and for differences in distribution or habitat use that could provide additional lines of evidence for two species of *Berardius* in the North Pacific.

MATERIALS AND METHODS

Samples, DNA Extraction and Sequencing

Samples were obtained by biopsy sampling of live whales, and from stranded animals, market samples in Japan and Korea, and museum specimens (Table S1). All

field-collected samples were identified as Baird's beaked whales, though one (sample 144310) was suspected to be the black form based on size and other external morphology. Two museum specimens were also identified initially as putative black form *Berardius* based on size information (see Table S1). Field-collected samples were stored either frozen at -80°C without preservative, or frozen at -20°C and preserved in 20% DMSO saturated with NaCl or in 100% ethanol. DNA was extracted from tissue samples using a silica-membrane method (DNeasy blood and tissue kit or Qiaextractor DX reagents, Qiagen, Valencia, CA). Historical bone and tooth samples were obtained from museum and private collections and DNA was extracted in a separate "ancient DNA" laboratory as described in Morin *et al.* (2006). Market samples were extracted and DNA amplified as described in Baker *et al.* (1996).

Amplification and sequencing was performed as described in Martien *et al.* (2014) using primers H16498 (Rosel *et al.* 1994), L15829, H497 (Martien *et al.* 2014) and primer DL3c (GTGAAACCAGCAACCCGC, aka L16252, developed at SWFSC). Sequences were assembled using Sequence Scanner (v1.0, Applied Biosystems, Grand Island, NY) or Sequencher v 5.2 sequence analysis software (Gene Codes Corporation, Ann Arbor, MI) and aligned using the MUSCLE alignment program (Edgar 2004) with default settings and eight iterations in Geneious (v6.1.6, Biomatters, Ltd., Auckland, New Zealand), and checked by eye. Unique variant sites were verified after alignment by rechecking the electropherogram alignments (confirming unique sites in both directions), and the new unique haplotype b4 was sequenced twice from separate DNA extractions. Unique 920–976 bp haplotypes have been submitted to GenBank (accession numbers KT936578–KT936586).

Resulting sequences were truncated to 431 bp (432 bp aligned) to match published sequences of *B. arnuxii* and the haplotypes of the sequences reported by Kitamura *et al.* (2013). We obtained haplotype sequences from Genbank for the seven gray form haplotypes and three black form haplotypes representing 64 sequence from Kitamura *et al.* (2013) from around Japan, and from all other recognized Ziphiidae species and from the two species of *Kogia* used as an outgroup. Accession numbers for all sequences used in this study are presented in Table S2.

Analytical Methods

Phylogenetic analysis of the Ziphiidae, including *Kogia sima* and *K. breviceps* as outgroups, was performed using Bayesian analysis in the program BEAST (v1.8; Drummond and Rambaut 2007). Sequences used for the phylogenetic analysis were as in Kitamura *et al.* (2013), except that we added four haplotype sequences of *Mesoplodon botaula*, one additional haplotype sequence of *M. densirostris*, and the two new *Berardius* sp. haplotypes from this study (Table S2). We used the program jModelTest (v2.1; Durriba *et al.* 2012) to select the optimal mutation model (HKY) based on the Bayesian Information Criteria (BIC), with kappa and frequencies estimated by BEAST. We used the relaxed log-normal clock and a Yule speciation process. We performed 10 million Markov Chain Monte Carlo (MCMC) chains and verified convergence and tree likelihood ESS > 200 using the program Tracer (v1.5.0; Drummond and Rambaut 2007). The maximum clade credibility tree was generated using TreeAnnotator (v1.7.4) (Drummond and Rambaut 2007) with a burn-in of 1,000 trees. The input and output xml files are available from the authors on request.

A haplotype median joining network (Bandelt *et al.* 1999) was generated from the truncated 432 bp alignment of unique *Berardius* sp. haplotypes using the program PopArt (<http://popart.otago.ac.nz>), with epsilon set to zero. Additional mtDNA

haplotypes of *B. bairdii* obtained from Japanese market sampling (Endo *et al.* 2005, 2010) were included for estimation of haplotype frequencies. Haplotype frequencies for each geographic region are in Table S3.

Analyses of net nucleotide divergence, d_A (Nei and Li 1979, Nei and Kumar 2000) was calculated using the *strataG* package (v1.0; Archer 2016) for R (R Development Core Team 2011) based on the best nucleotide model (K80) for just the *Berardius* sequences as determined with the program jModelTest (Darriba *et al.* 2012). Diagnostic sites (nucleotide positions fixed for different nucleotides between groups) were determined by visual inspection of the aligned *Berardius* haplotype sequences. Haplotype diversity and population divergence measures F_{ST} , Φ_{ST} , and χ^2 (within the gray form) were also calculated using the *StrataG* package in R (with model K80 for Φ_{ST}). Strata used for analyses are in Table S4. A Mantel test for isolation by distance (IBD) was conducted in GenAlix (v6.5; Peakall and Smouse 2006, 2012) based on pairwise Φ_{ST} genetic distances and approximate straight-line distances between geographic regions shown in Figure 1.

RESULTS

Our samples were distributed throughout the coastal range of the species, from Japan to Mexico (Fig. 1), but few samples were taken outside of the continental shelf due to both low encounter rate and lower sampling effort (Kasuya and Ohsumi 1984, Hamilton *et al.* 2009). Haplotypes were designated as being from the black or gray form based on being identical to, or 1–2 bp different from,

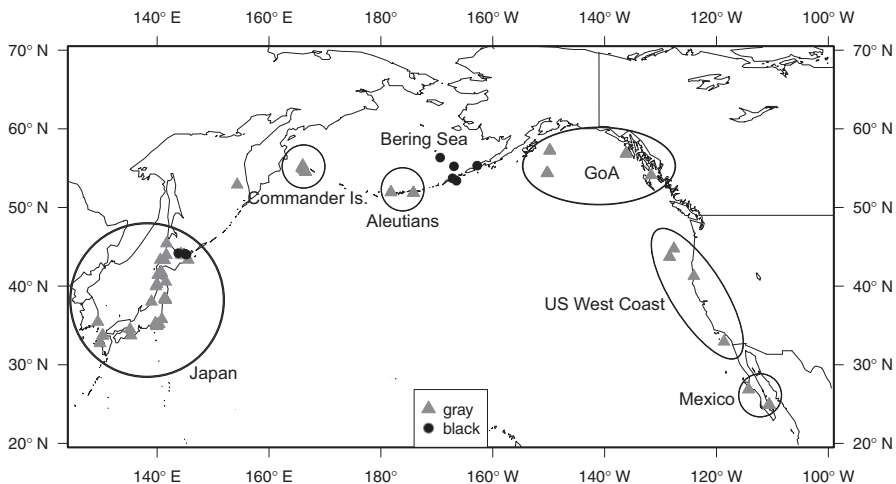


Figure 1. Distribution of samples used in this study. Sample locations around Japan were inferred from shore-based whaling stations described in Kitamura *et al.* (2013) or market samples, and do not necessarily reflect the region where the animal was collected. Some sampling locations represent multiple samples, and/or samples that yielded sequence data to identify form but not haplotype (and therefore not used in further analyses of diversity or population structure). Individual sample location details are in Table S2. Strata used for population analyses are encircled and described in Tables 3 and S4.

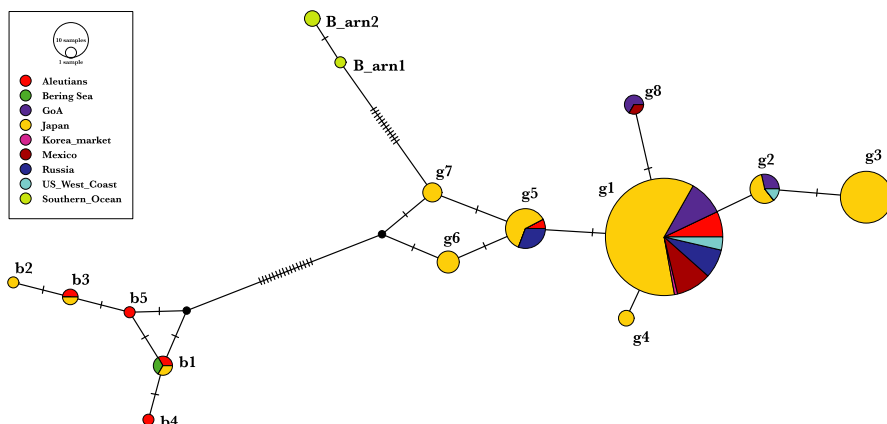


Figure 2. Haplotype network of gray and black form haplotypes. Haplotype sequences were truncated to 431 bp for alignment to published *Berardius arnuxii* sequences. Haplotypes g1–g7 and b1–b3 were described by Kitamura *et al.* (2013). Haplotypes g8, b4, and b5 are from this study. Circle sizes are proportional to sample number. Small black circles represent inferred haplotypes (not sampled). Haplotypes are colored according to geographic region as in Figure 1 for the gray form, except that “Russia” includes the Commander Islands and northern Sea of Okhotsk samples. Slash marks along the lines connecting haplotypes indicate the number of DNA sequence differences.

haplotypes associated with morphologically identified individuals from Kitamura *et al.* (2013), and being part of a monophyletic clade for each type (Fig. 2, 3). Specimens identified as the black form were clustered around northern Japan ($n = 3$; Kitamura *et al.* 2013) and in the Bering Sea and eastern Aleutians ($n = 5$; Fig. 1). One stranded specimen (SWFSC ID 144310) and two museum specimens that were identified based on external or skull morphology as likely black form were confirmed to also have mtDNA haplotypes that were identical or very similar (1–2 bp) to known black form haplotypes. Of the two additional samples identified genetically as black form, one (41749) was extensively photographed and the skeleton rearticulated for display at a high school on Unalaska Island. The other (7969) had no associated photographs or morphological data. Of the gray specimens ($n = 169$), length data of adult stranded animals were available from the Commander Islands ($n = 1$; Fedutin *et al.* 2012), northern California ($n = 1$; ID = 17152), and the Gulf of California ($n = 10$; Urban *et al.* 2007), and all were at least 9.8 m and had one of the eight gray-form haplotypes. Although length data were provided for many of Kitamura *et al.*'s (2013) specimens, maturity status was not provided except for one of the black form specimens.

We generated control region sequences from 64 *Berardius* samples, added 49 sequences from previously generated Japanese market sampling and combined the data with previously published haplotype data ($n = 65$, Dalebout *et al.* 2004, Kitamura *et al.* 2013) for a total of 178 sequenced individuals of *Berardius* (Fig. 1, Table S1). We identified two new haplotypes (b4, b5; Fig. 2) that were within 1bp of previously published haplotypes found in the black form of *Berardius*, and one new haplotype (g8) differing by 1 bp from the most common haplotype in the gray form (Fig. 2). All other sequences were identical over the 431 bp truncated sequence to previously published haplotype sequences (Kitamura *et al.* 2013). Two of the three

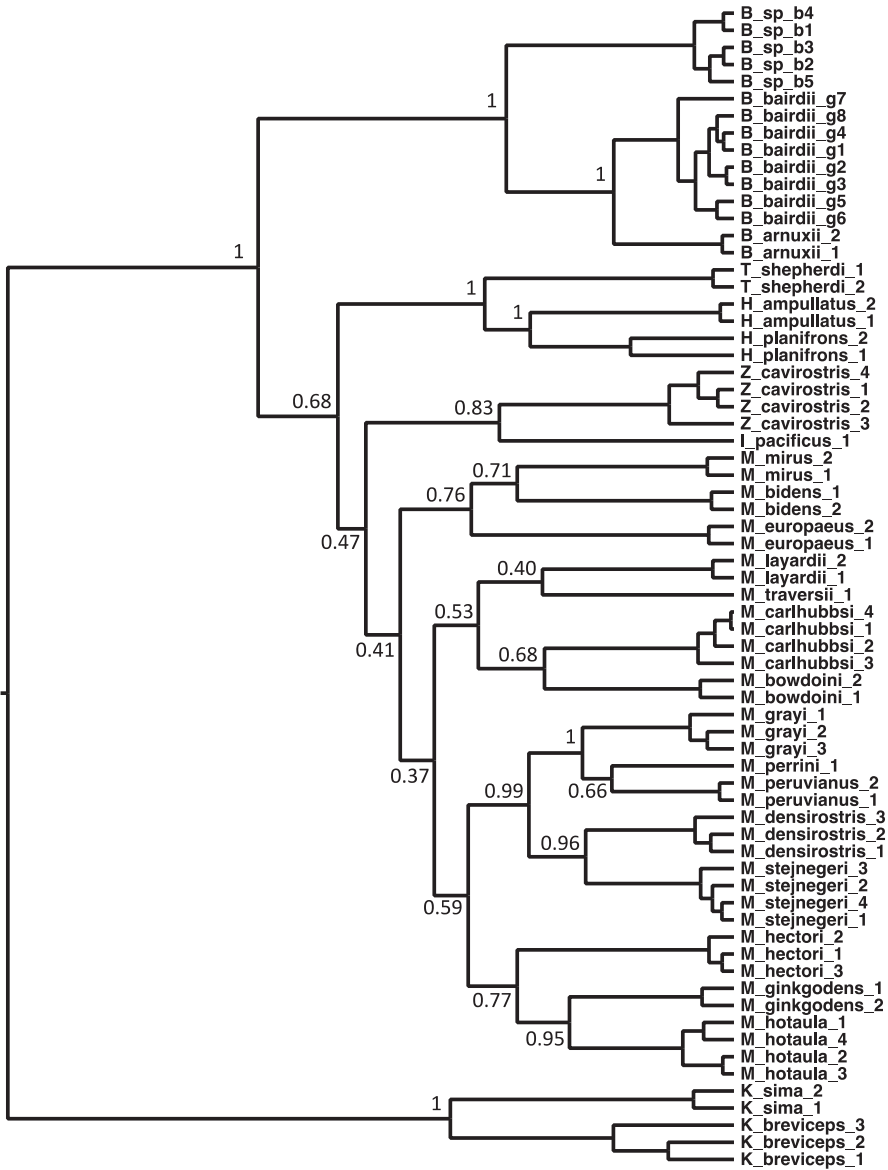


Figure 3. Phylogeny of Ziphiidae and outgroup *Kogia* samples based on mitochondrial control region sequences (481 bp alignment), including all haplotypes identified in *Berardius Bairdii* samples. Gray form haplotypes are labeled g1–8. Black form haplotypes are labeled b1–5. Numbers at nodes between species are posterior probabilities.

black form haplotypes from Japan were found in samples near the Aleutians, and three of the seven gray form haplotypes (g1, g2, g5) from Japan were found in other sampling locations (Fig. 2). The new gray form haplotype (g8) was only found in three samples from the eastern Pacific.

Phylogenetic analysis of the Ziphiidae based on the short control region sequence (481 bp when aligned to *Kogia sima* and *K. breviceps*) clustered all haplotypes of the black form of Baird's beaked whale as a monophyletic group sister to both Baird's and Arnoux's beaked whales, and the three together form a monophyletic group with high support (HPD = 1, Fig. 3). Maximum likelihood (Dalebout *et al.* 2004) and Bayesian phylogenies (this study) based on the control region have produced monophyletic species groups for most ziphiid species.

The haplotype network (Fig. 2) of *Berardius* haplotypes illustrates the relative frequencies and diversity of haplotypes across the range of the genus. Tick-marks in the figure indicate the number of nucleotide differences between haplotypes and show that diversity within each of the three types is significantly less than divergence between them. Within the gray form of Baird's whales, one haplotype (g1) was the most common throughout the North Pacific, and all but one of the haplotypes have been found in the western Pacific near Japan, with only one haplotype found just in samples from the eastern Pacific (haplotype g8). Within the black form, two of the five haplotypes were shared between Japan and the Aleutians/Bering Sea (Fig. 2).

Previous analyses of genetic differences among beaked whale species have relied on various metrics, including percent divergence and diagnostic sites (Dalebout *et al.* 2002, 2004) and net nucleotide divergence (d_A) (Dalebout *et al.* 2007, 2014; Kitamura *et al.* 2013). The net nucleotide divergence between the three *Berardius* clades ranged from 0.032 to 0.064, and there were 12–26 diagnostic sites among them (Table 1). These measures of divergence are affected by within-group diversity, so are likely to be slight overestimates due to the small number of samples available for the black form and *B. arnuxii*.

Treating the two forms of *Berardius* in the North Pacific as genetically distinct, we calculated haplotype diversity within each type and, for the gray form, in different geographic regions. Sample sizes differed widely among regions, with Japan having more than an order of magnitude more samples than any other region and including seven of the eight haplotypes found within the gray form. However, some of the strata in the eastern Pacific had similar haplotype diversity despite relatively small sample sizes (Table 2), and a unique haplotype (haplotype g8, Fig. 2). There were too few samples of the black form to look at regional differences in haplotype diversity, but overall haplotype diversity was high.

Genetic divergence among regional strata of the gray form indicates some potential population structure, especially between Japan and other strata (Table 3). However, little is known about genetic relatedness of individuals within groups, and sampling could be biased by capture or stranding of related individuals in some groups. To control for potential nonrandom sampling of related individuals, we removed all but one individual from groups of samples with the same mtDNA haplotype collected together (same date and location) and also all market samples, as they were of unknown provenance. Each successive removal of samples to control for relatedness

Table 1. Net divergence (d_A) and number of diagnostic sites (including indels) among the three *Berardius* forms.

Strata	Net divergence (d_A)	Diagnostic sites
Baird's, Arnoux's	0.032	12
Black, Baird's	0.044	16
Black, Arnoux's	0.064	26

Table 2. Summary statistics for mtDNA of the two forms of *Berardius* in the North Pacific. GoA = Gulf of Alaska. One sample from the Sea of Okhotsk (ID = 23629) had an unresolved gray-form haplotype (g1 or g4), so is not included in summary statistics).

Population	Number of samples	Number of haplotypes	Haplotype diversity
Black form (all)	8	5	0.86
Gray form			
Japan	113	7	0.57
Commander Is.	13	2	0.46
Aleutians	9	2	0.22
GoA	16	3	0.43
US West Coast	5	2	0.40
Mexico	12	2	0.17

reduced the number of significant divergence values, so that in the most conservative analysis, only one pairwise comparison among strata (Commander Island *vs.* Gulf of Alaska) showed a significant difference. In the reduced data set, at least one sample size in each pairwise comparison was <12, so conclusions from the subsampled data set about population structure of the gray form across the North Pacific are limited. A Mantel test for isolation by distance was not significant.

DISCUSSION

Cetacean species have been described under a number of species concepts in recent years. Here, we consider a pattern of reciprocal monophyly and concordance with morphological distinctiveness (for at least some specimens used in the analysis) to be strong initial evidence of species-level distinctiveness. This satisfies the phylogenetic species concept, as interpreted by Rosenbaum *et al.* (2000) for right whales, and at least the minimum requirement of two lines of evidence required by the Lineage Concordance Species Concept, as interpreted by Dalebout *et al.* (2004), and as recommended by Reeves *et al.* (2004). We consider that additional evidences of divergence or distinctiveness from nuclear DNA loci is desirable but not necessary for our initial proposal to recognize these two forms as species. A formal description is pending a full description of a holotype for the black form and a review of the holotype for the nominate Baird's species at museums in the United States and Japan.

The topology of the Bayesian tree suggests that the Northern and Southern Hemisphere species (*B. bairdii* and *B. arnuxii*) share a common ancestor more recently than they do with the black form. Although the control region can be a poor sequence to use for phylogenetic studies, especially for inference of divergence times (Duchene *et al.* 2011), in the case of beaked whales it has been demonstrated to provide unambiguous support for species identification (Dalebout *et al.* 2004, 2007). At the genus level, the closer relationship in the phylogenetic tree between Baird's and Arnoux's beaked whales could indicate an initial species divergence between the northern and southern hemispheres, resulting in the black form in the north and the ancestor of Arnoux's and Baird's beaked whales in the south, followed by a dispersal from the Southern to the Northern Hemisphere and secondary contact between the two currently sympatric forms. Although it appears that the two forms have remained genetically isolated based on mtDNA, analysis of nuclear DNA will have to be conducted to determine whether gene flow occurred initially or is ongoing; preliminary data

Table 3. Gray-form strata divergence estimates for three pairwise estimators: F_{ST} , Φ_{ST} , and χ^2 (P -value only), with sample sizes. Pairwise comparisons were done with all samples and with samples removed to reduce the chance of nonrandom sampling of closely related individuals in some strata. The third comparison was conducted with all of the Japanese market samples removed since nothing is known about date and locations of catch. Shading indicates significance at $P < 0.05$ (dark gray) or $P \leq 0.1$ (light gray).

Strata 1	Strata 2	All samples						Samples reduced to 1 per date/location						Samples reduced to 1 per date/location, Japan market samples removed					
		n (s1/s2)	F_{ST}	Φ_{ST}	P -value	χ^2		n (s1/s2)	F_{ST}	Φ_{ST}	P -value	χ^2		n (s1/s2)	F_{ST}	Φ_{ST}	P -value	χ^2	
Aleutians	GoA	9/16	0.00	0.03	0.300		3/7	-0.11	0.02	0.335		3/7	-0.11	0.02	0.361				
Aleutians	Japan	9/113	0.04	0.03	0.644		3/103	-0.08	-0.04	0.558		3/54	-0.12	-0.10	0.859				
Aleutians	Mexico	9/12	-0.05	0.00	0.680		3/3	-0.20	0.00	1.000		3/3	-0.20	0.00	1.000				
Aleutians	Commander Is.	9/13	0.01	0.01	0.348		3/12	-0.26	-0.26	1.000		3/12	-0.26	-0.26	1.000				
Aleutians	U.S. West Coast	9/5	-0.05	0.03	0.345		3/4	-0.15	0.02	1.000		3/4	-0.15	0.02	1.000				
GoA	Japan	16/113	0.04	0.05	0.014		7/103	0.00	0.01	0.047		7/54	-0.02	0.00	0.201				
GoA	Mexico	16/12	0.00	-0.02	0.600		7/3	-0.23	-0.17	1.000		7/3	-0.23	-0.17	1.000				
GoA	Commander Is.	16/13	0.07	0.17	0.023		7/12	0.04	0.15	0.085		7/12	0.04	0.15	0.081				
GoA	U.S. West Coast	16/5	-0.12	-0.09	1.000		7/4	-0.20	-0.16	1.000		7/4	-0.20	-0.16	1.000				
Japan	Mexico	113/12	0.08	0.07	0.065		103/3	-0.03	0.04	0.029		54/3	-0.05	0.02	0.123				
Japan	Commander Is.	113/13	0.05	0.07	0.100		103/12	0.05	0.08	0.104		54/12	0.02	0.04	0.346				
Japan	U.S. West Coast	113/5	-0.01	-0.05	0.490		103/4	-0.03	-0.08	0.397		54/4	-0.06	-0.08	0.558				
Mexico	Commander Is.	12/13	0.14	0.19	0.094		3/12	0.01	0.18	0.120		3/12	0.01	0.18	0.122				
Mexico	U.S. West Coast	12/5	-0.01	0.06	0.537		3/4	-0.15	0.02	1.000		3/4	-0.15	0.02	1.000				
Commander_Is.	U.S. West Coast	13/5	0.02	0.14	0.173		12/4	0.02	0.16	0.155		12/4	0.02	0.16	0.161				

based on a single locus and samples from only around Japan indicated that the two types in the North Pacific are genetically distinct in the nuclear genome as well (Kitamura *et al.* 2013).

Sample size is heavily biased towards Japan due to sampling of commercially hunted whales, which is likely to be the reason why so many haplotypes are found in Japan compared to other locations, though it cannot be ruled out that the area around Japan harbors more genetic diversity than other areas (*e.g.*, as seen in stocks of pilot whales; Oremus *et al.* 2009, Van Cise *et al.* 2016). Most of the gray form haplotypes were shared among regions across the known range of Baird's beaked whales, but it is not clear at this point whether significant divergence among populations is a result of population structuring or IBD. Significant divergence of the Commander Islands stratum may also be due to sampling of a subpopulation that has been observed to return repeatedly to that region and may represent a local breeding stock (Fedutin *et al.* 2015). Use of nuclear markers and additional sampling to fill gaps between regions and increase sample sizes are needed to clarify population structure further.

Distribution of black form specimens was surprisingly clumped, with three samples from the Sea of Okhotsk at the northern tip of Hokkaido (Kitamura *et al.* 2013), and five samples clustered in the Bering Sea and eastern Aleutians. Although Baird's beaked whales are known to occur also in the Okhotsk and Bering Seas (Tomilin 1957; Kasuya and Ohsumi 1984; Kasuya 1986, 2011), they are relatively rare and there have been reports of a different species in the Okhotsk Sea, attributed to northern bottlenose (*Hyperoodon ampullatus*), Cuvier's (*Ziphius cavirostris*) and the black or dwarf Baird's beaked whale (Kasuya 1986, 2011). All of our Bering Sea samples of the black form were obtained north of 53° latitude (Aleutians and Bering Sea) and between 162°W and 170°W (Fig. 1), while gray form specimens were sampled to the east and west in the Aleutians, Commander Islands, and Gulf of Alaska. Sample sizes in this region remain small, but the distribution of black and gray forms suggests different distribution or habitat use.

Inference of subspecies and species based on genetic data is increasingly common but remains controversial (Hebert *et al.* 2003, Tautz *et al.* 2003, Astrin *et al.* 2006, Dupuis *et al.* 2012). For many cetaceans, where taxonomy is hindered by the dearth of skeletal materials representing the diversity within and between widely distributed species, genetic approaches may be the only way to identify new species or subspecies in the foreseeable future. At a workshop on taxonomy of cetaceans in 2004 (Reeves *et al.* 2004), participants concluded that a single "line of evidence" (*e.g.*, morphology or mtDNA sequence) was sufficient for delineating new subspecies, and two lines of evidence were needed to delineate species. Taylor *et al.*² have compiled a set of quantitative and qualitative guidelines to aid in consistently applying multiple lines of evidence to support subspecies and species status in cetaceans when genetic data are the primary evidence. The strength of criteria is dependent on species variables, but Taylor *et al.*² determined that net divergence (d_A) from mtDNA control region sequences provide a particularly good divergence metric for taxonomic delineation, with values between 0.004 and 0.02 typically found among cetacean subspecies, and values greater than 0.02 representative of species. In addition, if male-mediated gene flow cannot be ruled out (*e.g.*, only mtDNA data are available), then other evidence such as morphological differentiation or ecological or geographical separation can be used to support species status.

²Personal communication from Barbara Taylor, NOAA NMFS, Southwest Fisheries Science Center, 8901 La Jolla Shores Drive, La Jolla, California 92120, U.S.A., May 2016.

Based on those guidelines, we have evaluated several aspects of the mtDNA data, combined with broad geographic sampling and morphological data to determine whether the data support elevation of the black form of Baird's beaked whale to a new species within the genus *Berardius*. All of the pairwise comparisons between the three mtDNA clades in the *Berardius* phylogeny resulted in a large number of diagnostic sites and $d_A > 0.02$, strongly supporting divergence at the species level. In analyses of the control region sequences of beaked whales, Dalebout *et al.* (2002, 2004, 2007) characterized ziphiid species as generally having <2% intraspecific variation and >4% interspecific divergence. Dalebout *et al.* (2007) tested the ability to identify species based on this "barcoding gap" with a broad sampling of species within the most speciose beaked whale genus (*Mesoplodon*) and inclusion of geographically diverse samples within species, and concluded that mtDNA control region and cytochrome *b* sequences enabled "unambiguous species identifications in this group under the phylogenetic species concept." The *Berardius* clades followed this pattern as well, with <1% intraclade variation and 3.5%–6.7% divergence among the three clades. The smaller (<4%) divergence was between the two currently recognized species in different ocean basins, while the proposed new species differed from both of the recognized species by greater than 4%.

Six of the eight black form specimens were initially identified based on size and morphological differences as putative black form specimens prior to genetic ID (three from Kitamura *et al.* 2013, three from this study). Comparable morphological data in the form of external measurements of adults are only available from two of the black form specimens, but extensive external measurements from Baird's beaked whales around Japan have been previously published (Omura *et al.* 1955, Kishiro 2007). The measurements reported by Kishiro (2007) from 47 male and 31 female Baird's beaked whales from the Pacific coast of Japan most likely represent only the gray form (Kasuya 2011, Kitamura *et al.* 2013) and correspond closely to measurements routinely taken for stranding reports in the United States. The two genetically identified adult black specimens were both male and measured 733 cm (specimen z144310, Table S1) and 660 cm (specimen SNH08019; Kitamura *et al.* 2013), whereas the average adult male size from Kishiro (2007) was 998.9 cm (range 886–1,090 cm). Interestingly, although Kishiro (2007) does not recognize the possibility of two types of *Berardius* in his samples, the mean size from his Sea of Okhotsk specimens ($n = 34$) is similar, but the range is larger than in the other two regions (700–1,080 cm). Omura *et al.* (1955) also noted a bi-modal distribution of *Berardius* specimens in the Sea of Okhotsk, with several specimens of both sexes in the range of 23–25 ft (~700–760 cm). Both of these studies may reflect the inclusion of a few of the black form in the Okhotsk groups, but since the samples were not verified to be adults, it could also reflect inclusion of subadult specimens.

Based on mtDNA alone, we cannot rule out recent or ongoing male-mediated gene flow across the range, but the morphological evidence and nuclear genetic data from Japan suggest this is not the case. Evidence from nuclear DNA currently only exists for the three Japanese specimens of the black form, which all shared a single fixed difference in the α -2-actin intron one (ACTA2I) relative to 50 of the gray form from around Japan (Kitamura *et al.* 2013). Given the limited genetic signal and difficulty of obtaining DNA sequences from museum specimens, we have not attempted to expand the ACTA2I sequence data set to the range-wide *Berardius* samples.

The data presented here from multiple lines of evidence (genetics, morphology, distribution) suggest that the black form is a previously unnamed species in the

genus *Berardius* that probably has a more limited range in the North Pacific or uses different habitat than Baird's beaked whale. The few specimens identified to date, despite extensive surveys of specimens around Japan and a more limited number of stranded or biopsied live animals from other regions of the North Pacific, suggest that this unnamed species is relatively rare or a less frequent visitor to continental slopes and canyons where they may be observed, caught by predominantly shore-based whalers, or drift to shore when dead. Geographic clumping of the black form in the Okhotsk and Bering Seas, while preliminary and not indicative of species-level divergence in itself, may indicate differential distributions or use of habitats by the gray and black forms. Morphological data from the black form remain scarce, and as such do not constitute a strong line of evidence for species-level difference, but the association between size, color, and/or other external morphology that is outside of the norm for Baird's beaked whales have been consistently associated with the genetically distinct group of mtDNA haplotypes, and provide further evidence by which additional specimens that may have been classified as Baird's beaked whale may be looked at more closely, especially once type specimens in Japan and the US have been characterized.

ACKNOWLEDGMENTS

We are grateful to those who provided samples to the SWFSC Marine Mammal and Turtle Tissue Collection: Robin Baird and John Calambokidis, Cascadia Research Collective; T. Holms, Humboldt State University; Dee Allen, Kim Parsons, and Oswaldo Vasquez, NMML; Kate Wynne, University of Alaska Fairbanks Sea Grant Program; Barbara Mahoney, NMFS Alaska Regional Office and The Alaska Marine Mammal Stranding Network; Jorge Urban, Universidad Autónoma de Baja California Sur; St. George Traditional Council Island Sentinel Hertha Kashaverof; Kathy Bureck-Huntington and Dylan Peterson, Alaska Veterinary Pathology Services; Bob Pitman, John Durban, Lisa Ballance, Jay Barlow, and Karen Forney, SWFSC. Naoko Funahashi assisted with access to Japanese market samples with support from the International Fund for Animal Welfare. Tadasu Yamada suggested the specimen in the Smithsonian Marine Mammal collection for genetic identification; We thank Eric Archer, James Mead, Lee Post, Patricia Rosel, and three anonymous reviewers for helpful discussion.

LITERATURE CITED

- Alfonsi, E., E. Meheust and S. Fuchs, *et al.* 2013. The use of DNA barcoding to monitor the marine mammal biodiversity along the French Atlantic coast. *Zookeys* 365:5–24.
- Archer, E., F. I. Archer, P. E. Adams and B. B. Schneiders, 2016. strataG: An R package for manipulating, summarizing, and analyzing population genetic data. *Molecular Ecology Resources*, doi:10.1111/1755-0998.12559.
- Astrin, J. J., B. A. Huber, B. Misof and C. F. C. Klütsch. 2006. Molecular taxonomy in pholcid spiders (Pholcidae, Araneae): Evaluation of species identification methods using CO1 and 16S rRNA. *Zoologica Scripta* 35:441–457.
- Baker, C. S., F. Cipriano and S. R. Palumbi. 1996. Molecular genetic identification of whale and dolphin products from commercial markets in Korea and Japan. *Molecular Ecology* 5:671–685.
- Bandelt, H. J., P. Forster and A. Rohl. 1999. Median-joining networks for inferring intraspecific phylogenies. *Molecular Biology and Evolution* 16:37–48.

- Barlow, J., T. Gerrodette and J. Forcada. 2001. Factors affecting perpendicular sighting distances on shipboard line-transect surveys for cetaceans. *Journal of Cetacean Research and Management* 3:201–212.
- Committee on Taxonomy. 2016. List of marine mammal species and subspecies. Society for Marine Mammalogy. Available at <http://www.marinemammalscience.org> (consulted on 18 May 2016).
- Dalebout, M. L., J. G. Mead, C. S. Baker, A. N. Baker and A. L. Van Helden. 2002. A new species of beaked whale *Mesoplodon perrini* sp. N. (Cetacea: Ziphiidae) discovered through phylogenetic analyses of mitochondrial DNA sequences. *Marine Mammal Science* 18:577–608.
- Dalebout, M. L., C. S. Baker, J. G. Mead, V. G. Cockcroft and T. K. Yamada. 2004. A comprehensive and validated molecular taxonomy of beaked whales, family Ziphiidae. *Journal of Heredity* 95:459–473.
- Dalebout, M. L., C. S. Baker, D. Steel, *et al.* 2007. A divergent mtDNA lineage among *Mesoplodon* beaked whales: Molecular evidence for a new species in the tropical Pacific? *Marine Mammal Science* 23:954–966.
- Dalebout, M. L., C. S. Baker, D. Steel, *et al.* 2014. Resurrection of *Mesoplodon hotaula* Deraniyagala 1963: A new species of beaked whale in the tropical Indo-Pacific. *Marine Mammal Science* 30:1081–1108.
- Darriba, D., G. L. Taboada, R. Doallo and D. Posada. 2012. jModelTest 2: More models, new heuristics and parallel computing. *Nature Methods* 9:772.
- Drummond, A. J., and A. Rambaut. 2007. BEAST: Bayesian evolutionary analysis by sampling trees. *BMC Evolutionary Biology* 7:214.
- Duchene, S., F. I. Archer, J. Vilstrup, S. Caballero and P. A. Morin. 2011. Mitogenome phylogenetics: The impact of using single regions and partitioning schemes on topology, substitution rate and divergence time estimation. *PLOS ONE* 6:e27138.
- Dupuis, J. R., A. D. Roe and F. a. H. Sperling. 2012. Multi-locus species delimitation in closely related animals and fungi: One marker is not enough. *Molecular Ecology* 21:4422–4436.
- Edgar, R. C. 2004. MUSCLE: A multiple sequence alignment method with reduced time and space complexity. *BMC Bioinformatics* 5:113.
- Endo, T., K. Haraguchi, Y. Hotta, Y. Hisamichi, S. Lavery, M. L. Dalebout and C. S. Baker. 2005. Total mercury, methyl mercury, and selenium levels in the red meat of small cetaceans sold for human consumption in Japan. *Environmental Science & Technology* 39:5703–5708.
- Endo, T., Y. Hisamichi, O. Kimura, *et al.* 2010. Stable isotope ratios of carbon and nitrogen and mercury concentrations in thirteen toothed whale species taken from the Western Pacific Ocean off Japan. *Environmental Science & Technology* 44:2675–2681.
- Fedutin, I. D., O. A. Filatova, E. G. Mamaev, E. I. Chekalski, A. M. Burdin and E. Hoyt. 2012. The results of long-term monitoring and first evidence of stable social associations in Baird's beaked whales (*Berardius bairdii*) in the waters of the Commander Islands, Russian Far East. *International Whaling Commission, SC/64/SM5*.
- Fedutin, I. D., O. A. Filatova, E. G. Mamaev, A. M. Burdin and E. Hoyt. 2015. Occurrence and social structure of Baird's beaked whales, *Berardius bairdii*, in the Commander Islands, Russia. *Marine Mammal Science* 31:853–865.
- Hamilton, T. A., J. V. Redfern and J. Barlow, *et al.* 2009. Atlas of cetacean sightings for Southwest Fisheries Science Center cetacean and ecosystem surveys: 1986–2005. U.S. Department of Commerce, NOAA Technical Memorandum, NOAA-TM-NMFS-SWFSC-440. 70 pp.
- Hebert, P. D. N., A. Cywinska, S. L. Ball and J. R. Dewaard. 2003. Biological identification through DNA barcodes. *Proceedings of the Royal Society B-Biological Sciences* 270:313–321.
- Hershkovitz, P. 1966. Catalog of living whales. *Bulletin of the United States National Museum* 246:1–259.

- Kasuya, T. 1986. Distribution and behavior of Baird's beaked whales off the Pacific coast of Japan. *Scientific Reports of the Whales Research Institute, Tokyo* 37:61–83.
- Kasuya, T. 2009. Giant beaked whales: *Berardius bairdii* and *B. arnuxii*. Pages 498–500 in W. F. Perrin, B. Würsig and J. G. M. Thewissen, eds. *Encyclopedia of marine mammals*. Second edition. Academic Press, San Diego, CA.
- Kasuya, T. 2011. Conservation biology of small cetaceans around Japan [In Japanese]. University of Tokyo Press, Tokyo, Japan.
- Kasuya, T., and S. Ohsumi. 1984. Further analysis of the Baird's beaked whale stock in the western North Pacific. *International Whaling Commission, SC/35/SM25*.
- Kishiro, T. 2007. Geographical variations in the external body proportions of Baird's beaked whales (*Berardius bairdii*) off Japan. *Journal of Cetacean Research and Management* 9:89–93.
- Kitamura, S., T. Matsuishi, T. K. Yamada, *et al.* 2013. Two genetically distinct stocks in Baird's beaked whale (Cetacea: Ziphiidae). *Marine Mammal Science* 29:755–766.
- Malm, A. W. 1883. Skelettdelar af hval, insamlade under expeditionen med Vega 1878–1880. Bihang till Kongliga Svenska Vetenskapsakademien Handlingar 8:1–114.
- Martín, K. K., S. J. Chivers, R. W. Baird, *et al.* 2014. Nuclear and mitochondrial patterns of population structure in North Pacific false killer whales (*Pseudorca crassidens*). *Journal of Heredity* 105:611–626.
- Mead, J. G. 2009. Beaked whales, overview *Ziphiidae*. Pages 94–97 in W. F. Perrin, B. Würsig and J. G. M. Thewissen, eds. *Encyclopedia of marine mammals*. Second edition. Academic Press, San Diego, CA.
- Meyer, C. P., and G. Paulay. 2005. DNA barcoding: Error rates based on comprehensive sampling. *PLoS Biology* 3(12):e422.
- Morin, P. A., R. G. Leduc, K. M. Robertson, *et al.* 2006. Genetic analysis of killer whale (*Orcinus orca*) historical bone and tooth samples to identify western U.S. ecotypes. *Marine Mammal Science* 22:897–909.
- Nakano, H., and M. Tabuchi. 1990. Occurrence of the cookiecutter shark *Isistius brasiliensis* in surface waters of the North Pacific Ocean. *Japanese Journal of Ichthyology* 37:60–63.
- Nei, M., and S. Kumar. 2000. *Molecular evolution and phylogenetics*. Oxford University Press, New York, NY.
- Nei, M., and W. H. Li. 1979. Mathematical model for studying genetic variation in terms of restriction endonucleases. *Proceedings of the National Academy of Sciences of the United States of America* 76:5269–5273.
- Omura, H., K. Fujino and S. Kimura. 1955. Beaked whale *Berardius bairdii* of Japan, with notes on *Ziphius cavirostris*. *Scientific Reports of the Whales Research Institute, Tokyo* 10:89–132.
- Oremus, M., R. Gales, M. L. Dalebout, *et al.* 2009. Worldwide mitochondrial DNA diversity and phylogeography of pilot whales (*Globicephala* spp.). *Biological Journal of the Linnean Society* 98:729–744.
- Peakall, R., and P. E. Smouse. 2006. GenAlEx 6: Genetic analysis in Excel. Population genetic software for teaching and research. *Molecular Ecology Notes* 6:288–295.
- Peakall, R., and P. E. Smouse. 2012. GenAlEx 6.5: Genetic analysis in Excel. Population genetic software for teaching and research—an update. *Bioinformatics* 28:2537–2539.
- R Development Core Team. 2011. *R: A language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria.
- Reeves, R. R., W. F. Perrin, B. L. Taylor, C. S. Baker and S. L. Mesnick. 2004. Report of the workshop on shortcomings of cetacean taxonomy in relation to needs of conservation and management. U.S. Department of Commerce, NOAA Technical Memorandum NMFS-SWFSC-363. 94 pp.
- Rosel, P. E., A. E. Dizon and J. E. Heyning. 1994. Genetic-analysis of sympatric morphotypes of common dolphins (Genus *Delphinus*). *Marine Biology* 119:159–167.

- Rosenbaum, H. C., R. L. Brownell, Jr., M. W. Brown, *et al.* 2000. World-wide genetic differentiation of *Eubalaena*: Questioning the number of right whale species. *Molecular Ecology* 9:1793–1802.
- Tautz, D., P. Arctander, A. Minelli, R. H. Thomas and A. P. Vogler. 2003. A plea for DNA taxonomy. *Trends in Ecology & Evolution* 18:70–74.
- Tomilin, A. G. 1957. Mammals of the U.S.S.R. and adjacent countries. Pages 407–426 in V. G. Heptner, ed. *Mammals of Eastern Europe and adjacent countries*. Izdatel'stvo Akademi Nauk SSSR, Moscow, Russia.
- Urban, J. R., G. Cárdenas-Hinojosa, A. U. Gómez-Gallardo, Ú. González-Peral, W. Del Toro-Orazco and R. L. Brownell, Jr. 2007. Mass stranding of Baird's beaked whales at San Jose Island, Gulf of California, Mexico. *Latin American Journal of Aquatic Mammals* 6:83–88.
- Van Cise, A., P. A. Morin and R. W. Baird, *et al.* 2016. Redrawing the map: mtDNA provides new insights into the distribution and diversity of short-finned pilot whales in the Pacific Ocean. *Marine Mammal Science* doi: 10.1111/mms.12315.
- van Helden, A. L., A. N. Baker, M. L. Dalebout, J. C. Reyes, K. Van Waerebeek and C. S. Baker. 2002. Resurrection of *Mesoplodon traversii* (Gray, 1874) senior synonym of *M. babamondi* Reyes, Van Waerebeek, Cardenas and Yanez, 1995 (Cetacea: Ziphiidae). *Marine Mammal Science* 18:609–621.
- Yamada, T., and Y. Tajima. 2010. Exhibition of the giant mammals: Our friends in the sea [In Japanese]. Asahi Shinbunsha Press, Tokyo, Japan.

Received: 23 October 2015

Accepted: 21 May 2016

SUPPORTING INFORMATION

The following supporting information is available for this article online at <http://onlinelibrary.wiley.com/doi/10.1111/mms.12345/supinfo>.

Table S1. Sample information for samples used in this study (excluding previously published data), including the National Marine Fisheries Service (NMFS) SWFSC Marine Mammal and Marine Turtle Research (MMASTR) collection ID's (LABID), the haplotype ID's for both the short (431bp) and long (922bp) sequences, original collection ID (Field ID), collection year (Year), collection latitude and longitude and geographic region (Locality, when known), collection method (biopsy, stranding, market), tissue type, and comments on specific samples, including sex, length, and age class when known. Samples with a black-form haplotype are shaded in gray.

Table S2. Sequences used for *Berardius* and Ziphiidae analysis. New sequences generated for this study are highlighted in gray (in some cases, longer sequences of the same haplotype were generated, and submitted to GenBank with new accession numbers). Data on samples from Kitamura *et al.* 2013 are from supplementary table 1 of that publication.

Table S3. Count of haplotypes in each stratum. Haplotypes g1–g7 and b1–b3 were described by Kitamura *et al.* (2013). Haplotypes g8, b4, and b5 are from this study. Black form haplotypes (b1–b5) were not included in population analysis of Baird's beaked whales.

Table S4. Strata used for population analyses.

Table S1. Sample information for samples used in this study (excluding previously published data), including the National Marine Fisheries Service (NMFS) SWFSC Marine Mammal and Marine Turtle Research (MMASTR) collection ID's (LABID), the haplotype ID's for both the short (431bp) and long (922bp) sequences, original collection ID (Field ID), collection year (Year), collection latitude and longitude and geographic region (Locality, when known), collection method (biopsy, stranding, market), tissue type, and comments on specific samples, including sex, length, and age class when known. Samples with a black-form haplotype are shaded in gray.

LABID	431 bp haplotype	922 bp haplotype	Field ID	Year	Latitude	Longitude	Locality	Collection method	Tissue type	Comments
4963	g1	g1	WADA90-15/ LACM86029	1990	35.00	140.00	Japan	unknown	skin and blubber	
4964	g2	g2	WADA90-17/ LACM86030	1990	35.00	140.00	Japan	unknown	skin and blubber	
5283	g1 ^a	unknown	SWDP-92-20	1992	54.10	-131.67	Canada, British Columbia, Graham Is., Fife Pt.	stranding	muscle	12s failed ^a
7969	b3	b3	MFR970728.01	1997	55.23	-166.93	Bering Sea	biopsy	skin and blubber	biopsy of dead whale at sea
13878	g1	g1	SK-99-31	1999			Bangajin, East Coast, Korean Market, Brownell	market	muscle	
17152	g2	g2	VM2405	2000	41.28	-124.05	U.S.A., CA, Humboldt Co., Orick, Redwood Creek	stranding	skin and blubber	32ft (9.8m), male
17984	g1	g1	DSJ000801.15	2000	26.87	-114.25	Mexico	biopsy	skin and blubber	
17985	g1	g1	DSJ000801.16	2000	26.87	-114.25	Mexico	biopsy	skin and blubber	
23639	g1/g4	unknown	RUS#9-0007	2000	52.90	154.32	Russia, Sakhalin Is.	stranding	skin	Cannot distinguish between haplotypes g1 and g4 with short sequence (12s failed ^a)
28394	g1	g1	MAC020707.01	2002	57.25	-149.80	U.S.A., AK, North Pacific, Gulf of Alaska	biopsy	skin and blubber	
28395	g1	g1	MAC020707.02	2002	57.25	-149.80	U.S.A., AK, North Pacific, Gulf of Alaska	biopsy	skin and blubber	
28396	g1	g1	MAC020707.03	2002	57.25	-149.80	U.S.A., AK, North Pacific, Gulf of Alaska	biopsy	skin and blubber	
28397	g1	g1	MAC020707.04	2002	57.25	-149.80	U.S.A., AK, North Pacific, Gulf of Alaska	biopsy	skin and blubber	
35282	g1	g1	CP030713.01	2003	51.93	-178.20	U.S.A., AK, Aleutian Is., N. Tanaga Is.	biopsy	skin and blubber	
35283	g1	g1	CP030716.01	2003	51.83	-174.18	U.S.A., AK, Aleutian Is., SW of Amlia Is.	biopsy	skin and blubber	
35284	g1	g1	CP030716.02	2003	51.83	-174.18	U.S.A., AK, Aleutian Is., SW of Amlia is.	biopsy	skin and blubber	
35285	g5	g5	CP030716.03	2003	51.83	-174.18	U.S.A., AK, Aleutian Is., SW of Amlia Is.	biopsy	skin and blubber	
35286	g1	g1	CP030716.04	2003	51.83	-174.18	U.S.A., AK, Aleutian Is., SW of Amlia Is.	biopsy	skin and blubber	

35287	g1	g1	CP030716.05	2003	51.83	-174.18	U.S.A., AK, Aleutian Is., SW of Amlia Is.	biopsy	skin and blubber	
35288	g1	g1	CP030716.06	2003	51.83	-174.18	U.S.A., AK, Aleutian Is., SW of Amlia Is.	biopsy	skin	
35289	g1	g1	CP030716.07	2003	51.83	-174.18	U.S.A., AK, Aleutian Is., SW of Amlia Is.	biopsy	skin and blubber	
35974	g1	g1	CP030713.02	2003	51.93	-178.20	U.S.A., AK, Aleutian Is., N. Tanaga Is.	biopsy	skin	
41749	b4	b4	0704-BW-DM-01	2004	53.40	-166.48	U.S.A., AK, Unalaska, Summer & Bay Rd., near 2nd Priest Rock	stranding	skin	subadult female, skeleton rearticulated for display; 5.3m
43596	g1	g1	MAC040719.04	2004	54.37	-150.28	IFS	biopsy	skin and blubber	
43597	g1	g1	MAC040719.05	2004	54.37	-150.28	IFS	biopsy	skin and blubber	
43598	g1	g1	MAC040719.06	2004	54.37	-150.28	IFS	biopsy	skin and blubber	
44036	g1	g1	MAC041020.01	2004	56.85	-136.17	U.S.A., AK	biopsy	skin and blubber	
44037	g2	g2	MAC041020.02	2004	56.85	-136.17	U.S.A., AK	biopsy	skin and blubber	
44038	g2	g2	MAC041020.03	2004	56.85	-136.17	U.S.A., AK	biopsy	skin and blubber	
51131	g1	g1	DSJ050823.01	2005	43.72	-128.38	U.S.A., West Coast	biopsy	skin	
51132	g1	g1	DSJ050823.02	2005	43.72	-128.38	U.S.A., West Coast	biopsy	skin and blubber	
62941	g1	g1	OD050812-01	2005	54.37	-150.23	NGOA-offshore, Patton Seamounts	biopsy	skin	
62942	g8	g8	OD050812-02	2005	54.37	-150.23	NGOA-offshore, Patton Seamounts	biopsy	skin	
62943	g8	g8	OD050812-03	2005	54.37	-150.23	NGOA-offshore, Patton Seamounts	biopsy	skin	
62944	g1	g1	OD050812-04	2005	54.37	-150.23	NGOA-offshore, Patton Seamounts	biopsy	skin	
62945	g1	g1	OD050812-05	2005	54.37	-150.23	NGOA-offshore, Patton Seamounts	biopsy	skin	
64650	g1	g1	CRC20070417-01	2007	32.93	-118.65	U.S.A., CA, San Clemente Is.	biopsy	skin and blubber	
68608	g1	g1	B. bairdii 01	2006	24.89	-110.59	Mexico, California Gulf, Isla San Jose; Urban <i>et al.</i> 2007	stranding	skin and blubber	adult male, 10.62 m
68609	g1	g1	B. bairdii 02	2006	24.89	-110.59	Mexico, California Gulf, Isla San Jose; Urban <i>et al.</i> 2007	stranding	skin and blubber	adult male, 10.60 m
68610	g1	g1	B. bairdii 03	2006	24.89	-110.59	Mexico, California Gulf, Isla San Jose; Urban <i>et al.</i> 2007	stranding	skin and blubber	adult male, 10.03 m, 17 yr

68611	g8	g8	B. bairdii 04	2006	24.89	-110.59	Mexico, California Gulf, Isla San Jose; Urban <i>et al.</i> 2007	stranding	skin and blubber	adult male, 10.30 m, 42 yr
68612	g1	g1	B. bairdii 05	2006	24.89	-110.59	Mexico, California Gulf, Isla San Jose; Urban <i>et al.</i> 2007	stranding	skin and blubber	adult male, 10.10 m
68613	g1	g1b	B. bairdii 06	2006	24.89	-110.59	Mexico, California Gulf, Isla San Jose; Urban <i>et al.</i> 2007	stranding	skin and blubber	adult male, 10.19 m, 30 yr
68614	g1	g1	B. bairdii 07	2006	24.89	-110.59	Mexico, California Gulf, Isla San Jose; Urban <i>et al.</i> 2007	stranding	skin and blubber	adult male, 10.83 m, 17 yr
68615	g1	g1	B. bairdii 08	2006	24.89	-110.59	Mexico, California Gulf, Isla San Jose; Urban <i>et al.</i> 2007E	stranding	skin and blubber	adult male, 9.97 m, 31 yr
68616	g1	g1	B. bairdii 09	2006	24.89	-110.59	Mexico, California Gulf, Isla San Jose; Urban <i>et al.</i> 2007	stranding	skin and blubber	adult male, 10.60 m, 15 yr
68617	g1	g1	B. bairdii 10	2006	24.91	-110.60	Mexico, California Gulf, Isla San Jose; Urban <i>et al.</i> 2007	stranding	skin and blubber	adult male, 11.05 m, 9 yr
76728	g1	g1	MAC080807.01	2008	44.77	-127.60	U.S.A., West Coast	biopsy	skin and blubber	
144207	b5	b5	BDM294/ USNM276366	1948	53.72	-167.18	Unalaska Island	unknown	muscle	Subadult, putative black form ID based on skull size (T. Yamada)
144310	b1	b1	2014069	2014	56.34	-169.40	St George Is. stranding 2014	stranding	muscle	Adult male (2 sets of erupted teeth; (putative black type based on size (7.3 m), external morphology)
144515	b1		LACM91786	1993	55.32	-162.79	Izembek Lagoon, east Aleutians	unknown	bone	subadult male (putative black form based on total length (6.2 m); 12s failed ^a)
	g1	g1	Bering_2011.1	2011	55.05	165.83	Bering Is. (Commander Islands)	biopsy	skin	Adult male, ID = Co065
	g1	g1	Bering_2012.1	2012	55.35	166.04	Bering Is. (Commander Islands)	stranding	skin	Stranded whale, adult female, 10.7 m, No ID
	g5	g5	Bering_2013.1	2013	54.52	166.51	Bering Is. (Commander Islands)	biopsy	skin	adult female, ID = Co025
	g5	g5	Bering_2013.2	2013	54.52	166.51	Bering Is. (Commander Islands)	biopsy	skin	adult female, ID = Co059
	g1	g1	Bering_2013.3	2013	54.52	166.52	Bering Is. (Commander Islands)	biopsy	skin	adult female, ID = Co014
	g1	g1	Bering_2013.4	2013	54.51	166.52	Bering Is. (Commander Islands)	biopsy	skin	adult female, ID = Co068
	g1	g1	Bering_2014.1	2014	54.89	166.19	Bering Is. (Commander Islands)	biopsy	skin	Ad., ID = Co035
	g1	g1	Bering_2014.2	2014	54.97	166.07	Bering Is. (Commander Islands)	biopsy	skin	Juv., ID = Co130

						Islands)			
g1	g1	Bering_2014.3	2014	54.97	166.04	Bering Is. (Commander Islands)	biopsy	skin	Probably mother of Co130, ID = Co017
g1	g1	Bering_2014.4	2014	54.98	166.03	Bering Is. (Commander Islands)	biopsy	skin	Ad., ID = Co022
g5	g5	Bering_2014.5	2014	54.80	166.26	Bering Is. (Commander Islands)	biopsy	skin	Ad., ID = Co062
g5	g5	Bering_2014.6	2014	54.79	166.27	Bering Is. (Commander Islands)	biopsy	skin	Ad., No ID
g1	g1	Bering_2014.7	2014	55.01	165.96	Bering Is. (Commander Islands)	biopsy	skin	Ad., No ID
g3		BbaJW99-O16	17 February 1999	34.51	135.16	Japanese market	market	unknown	latitude/longitude inferred from locality
g1		BbaJE9518	9 July 1995			Japanese market	market	unknown	
g1		BbaJa9899	2 November 1998			Japanese market	market	unknown	
g1		BbaJa98100	2 November 1998			Japanese market	market	unknown	
g1		BbaJ98D52	14 February 1999			Japanese market	market	unknown	
g1		BbaJW99-A20	21 February 1999			Japanese market	market	unknown	
g3		BbaJa98D54	14 February 1999			Japanese market	market	unknown	
g6		BbaJ98D36	8 February 1999			Japanese market	market	unknown	
g1		BbaJ98D37	9 February 1999			Japanese market	market	unknown	
g1		JE02-HK05				Abashiri, Hokkaido (Sea of Okhotsk)	market	unknown	
g1		JE02-HK06				Abashiri, Hokkaido (Sea of Okhotsk)	market	unknown	
g1		JE02-HK07				Abashiri, Hokkaido (Sea of Okhotsk)	market	unknown	
g1		JE03-HK01				Abashiri, Hokkaido (Sea of Okhotsk)	market	unknown	
g1		JE02-C11				Chiba, Honshu (Pacific Ocean)	market	unknown	
g1		JE00-H01				Hakodate, Hokkaido (Sea of Japan)	market	unknown	
g1		JE01-H01				Hakodate, Hokkaido (Sea of Japan)	market	unknown	
g1		JE01-H05				Hakodate, Hokkaido (Sea of Japan)	market	unknown	
g1		JE01-H06				Hakodate, Hokkaido (Sea of Japan)	market	unknown	

g1	JE02-H01		Hakodate, Hokkaido (Sea of Japan)	market	unknown
g1	JE02-H05		Hakodate, Hokkaido (Sea of Japan)	market	unknown
g1	JE02-H07		Hakodate, Hokkaido (Sea of Japan)	market	unknown
g1	JE03-H01		Hakodate, Hokkaido (Sea of Japan)	market	unknown
g1	JE03-H02		Hakodate, Hokkaido (Sea of Japan)	market	unknown
g1	JE03-H03		Hakodate, Hokkaido (Sea of Japan)	market	unknown
g3	JE01-A01		Abashiri, Hokkaido (Sea of Okhotsk)	market	unknown
g3	JE01-A02		Abashiri, Hokkaido (Sea of Okhotsk)	market	unknown
g5	JE02-C20		Chiba, Honshu (Pacific Ocean)	market	unknown
g1	BbaJa9888	2 July 1998	Japanese market	market	unknown
g3	BbaJE9523	15 July 1995	Japanese market	market	unknown
g3	BbaJE9525	15 July 1995	Japanese market	market	unknown
g1	BbaJ98D13	7 July 1998	Japanese market	market	unknown
g1	BbaJa9838	16 April 1997	Japanese market	market	unknown
g1	BbaJW99-A2	21 February 1999	Japanese market	market	unknown
g3	BbaJ00-16	18 May 2000	Japanese market	market	unknown
g2	BbaJ98C18	28 February 1999	Japanese market	market	unknown
g1	BbaJE9520	11 July 1995	Japanese market	market	unknown
g4	BbaJE9695	2 December 1996	Japanese market	market	unknown
g1	BbaJW99-T44	22 February 1999	Japanese market	market	unknown
g3	BbaJW99-T41	22 February 1999	Japanese market	market	unknown
g1	BbaJ02-021		Japanese market	market	unknown
g1	BbaJ02-H1		Japanese market	market	unknown
g1	BbaJ02-H2		Japanese market	market	unknown
g3	BbaJ02-A1		Japanese market	market	unknown

g3	BbaJ02-A2	Japanese market	market	unknown
g3	BbaJ02-S4	Japanese market	market	unknown
g3	BbaJ02-S6	Japanese market	market	unknown
g3	BbaJ02-S7	Japanese market	market	unknown
g5	BbaJ02-018	Japanese market	market	unknown
g6	BbaJ02-T1	Japanese market	market	unknown

^a12s refers to the PCR product and/or sequencing from primers H497 and DL3c.

Table S2. Sequences used for *Berardius* and Ziphiidae analysis. New sequences generated for this study are highlighted in gray (in some cases, longer sequences of the same haplotype were generated, and submitted to GenBank with new accession numbers). Data on samples from Kitamura *et al.* 2013 are from supplementary table 1 of that publication.

Code	Family	Scientific name	Date found	Sampling region	Sex	Body length (cm)	Specimen number	CR haplotype (accession no.)	References
	Kogiidae	<i>Kogia breviceps</i>							
K. breviceps 1			17 November 2002	Oarai, Ibaraki	♂	144.5	EW00535	1 (AB571996)	Kitamura <i>et al.</i> 2013
K. breviceps 2			30 March 2002	Mikurajima, Tokyo	♂	200	EW00534	2 (AB571995)	Kitamura <i>et al.</i> 2013
K. breviceps 3								3 (AJ554055)	Arnason <i>et al.</i> 2004
		<i>Kogia sima</i>							
K. sima 1			13 July 2001	Kanoya, Kagoshima	♂	188	EW00066	1 (AB571997)	Kitamura <i>et al.</i> 2013
K. sima 2			11 August 2003	Ichinomiya, Chiba	♂	231.2	EW00063	2 (AB571998)	Kitamura <i>et al.</i> 2013
	Ziphiidae	<i>Berardius bairdii</i> (slate-gray)							
B. bairdii g1			2 August 1985	Wadoura, Chiba	♂	1,000	EW01000	Bba_g1 (AB571999, KT936582-3)	Kitamura <i>et al.</i> 2013, This study
B. bairdii g2			4 August 1985	Wadoura, Chiba	♂	965	EW01005	Bba_g2 (AB572000, KT936584)	Kitamura <i>et al.</i> 2013, This study
B. bairdii g3			31 July 1985	Wadoura, Chiba	♂	1,043	EW00997	Bba_g3 (AB572001)	Kitamura <i>et al.</i> 2013
B. bairdii g4			10 August 1985	Wadoura, Chiba	♂	1,065	EW01015	Bba_g4 (AB572002)	Kitamura <i>et al.</i> 2013
B. bairdii g5			4 August 1985	Wadoura, Chiba	♀	930	EW01007	Bba_g5 (AB572003, KT936585)	Kitamura <i>et al.</i> 2013, This study
B. bairdii g6			1 August 1985	Wadoura, Chiba	♀	978	EW00999	Bba_g6 (AB572004)	Kitamura <i>et al.</i> 2013
B. bairdii g7			3 August 1985	Wadoura, Chiba	♀	970	EW01004	Bba_g7 (AB572005)	Kitamura <i>et al.</i> 2013
B. bairdii g8				Gulf of Alaska, Gulf of California				Bba_g8 (KT936586)	This study
		<i>Berardius bairdii</i> (black)							
B. sp. 1			4 June 2008	Tokoro, Hokkaido, Bering Sea, Aleutians	♂	660	SNH08019	Bba_b1 (AB572006, KT936578)	Kitamura <i>et al.</i> 2013, This study
B. sp. 2			21 May 2009	Sea of Okhotsk, Hokkaido	♀	N.D.	SNH09009	Bba_b2 (AB572007)	Kitamura <i>et al.</i> 2013
B. sp. 3			22 June 2009	Utoro, Hokkaido, Aleutians	♀	N.D.	SNH09016	Bba_b3 (AB572008, KT936579)	Kitamura <i>et al.</i> 2013, This study
B. sp. 4			2004	Aleutians	♀		z41749	Bba_b4 (KT936580)	This study

B. sp. 5		1948	Aleutians			z144207	Bba_b5 (KT936581)	This study
	<i>Berardius arnuxii</i>							
B. arnuxii 1		3 January 1997	New Zealand	♂		Bar02	Bar_1 (AF036229)	Dalebout <i>et al.</i> 2004
B. arnuxii 2		31 December 1962	South Africa	♂		BarPEM28	Bar_2 (AY579532)	Dalebout <i>et al.</i> 2004
	<i>Tasmacetus shepherdi</i>							
T. shepherdi 1		1 August 1994	New Zealand	♂		Tsh01	1 (AF036226)	Dalebout <i>et al.</i> 2004
T. shepherdi 2		23 April 1994	New Zealand	♂		Tsh02	2 (AF036227)	Dalebout <i>et al.</i> 2004
	<i>Mesoplodon bidens</i>							
M. bidens 1		15 June 1992	United Kingdom	♀		MbiSAC1309--3	1 (AY579507)	Dalebout <i>et al.</i> 2004
M. bidens 2		19 August 1992	United Kingdom	♀		MbiSAC1880	2 (AY579508)	Dalebout <i>et al.</i> 2004
	<i>Mesoplodon densirostris</i>							
M. densirostris 1		21 September 2000	Mauritius	♂	400	EW00522	1 (AB610396)	Kitamura <i>et al.</i> 2013
M. densirostris 2		16 October 1998	New Zealand	♂		MdeNZ01	2 (AY579513)	Dalebout <i>et al.</i> 2004
M. densirostris 3		18 July 1993	United Kingdom	♀		MdeNHM-UK-1993/78	3 (AY579514)	Dalebout <i>et al.</i> 2004
	<i>Mesoplodon europaeus</i>							
M. europaeus 1		19 May 1994	U.S.A.	♂		MeuSW4120	1 (AY579515)	Dalebout <i>et al.</i> 2004
M. europaeus 2		16 January 1995	U.S.A.	♀		MeuSW3853	2 (AY579516)	Dalebout <i>et al.</i> 2004
	<i>Mesoplodon layardii</i>							
M. layardii 1		18 January 1996	Australia	♀		MlaySAM18078	1 (AY579523)	Dalebout <i>et al.</i> 2004
M. layardii 2		19 April 1997	Australia	♀		MlaySAM9788	2 (AY579524)	Dalebout <i>et al.</i> 2004
	<i>Mesoplodon hectori</i>							
M. hectori 1			Australia	♂		WA99-2	3 (AY028313)	Gales <i>et al.</i> 2002
M. hectori 2		19 February 1999	New Zealand	♀		MheNZ02	1 (AY579521)	Dalebout <i>et al.</i> 2004
M. hectori 3		29 September 1992	New Zealand	♂		MheNMNZ2173	2 (AY579522)	Dalebout <i>et al.</i> 2004
	<i>Mesoplodon grayi</i>							
M. grayi 1		22 August 1995	New Zealand	♂		Mgr05	1 (AY579519)	Dalebout <i>et al.</i> 2004
M. grayi 2		6 February 1996	New Zealand	♀		Mgr11	2 (AY579520)	Dalebout <i>et al.</i> 2004

M. grayi 3			Australia	♂		WA99-1	3 (AY028312)	Gales <i>et al.</i> 2002
	<i>Mesoplodon stejnegeri</i>							
M. stejnegeri 1		8 May 2008	Shosanbetsu, Hokkaido	♀	500	SNH08013	1 (AB610398)	Kitamura <i>et al.</i> 2013
M. stejnegeri 2		13 October 2008	Rausu, Hokkaido	N.D.	400	SNH08055	2 (AB610399)	Kitamura <i>et al.</i> 2013
M. stejnegeri 3		9 July 1996	U.S.A.	♂		MstSW9491	3 (AY579528)	Dalebout <i>et al.</i> 2004
M. stejnegeri 4		14 July 1998	U.S.A.			MstSW10402	4 (AY579527)	Dalebout <i>et al.</i> 2004
	<i>Mesoplodon bowdoini</i>							
M. bowdoini 1		19 November 1998	Australia	♂		MbowTMAG1593	1 (AY579509)	Dalebout <i>et al.</i> 2004
M. bowdoini 2		28 September 1937	New Zealand	♀		MbowNMNZ619	2 (AY579510)	Dalebout <i>et al.</i> 2004
	<i>Mesoplodon mirus</i>							
M. mirus 1		3 November 1977	U.S.A.	♂		MmiSW4968	1 (U70465)	Dalebout <i>et al.</i> 2004
M. mirus 2		13 August 1977	U.S.A.	♀		MmiSW4972	2 (AY579525)	Dalebout <i>et al.</i> 2004
	<i>Mesoplodon ginkgodens</i>							
M. ginkgodens 1		1994	Taiwan	♀		Mgin01	1 (AY579517)	Dalebout <i>et al.</i> 2004
M. ginkgodens 2							2 (KF027302)	Dalebout <i>et al.</i> 2014
	<i>Mesoplodon hotaula</i>							
M. hotaula 1							1 (KF027298)	Dalebout <i>et al.</i> 2014
M. hotaula 2							2 (KF027299)	Dalebout <i>et al.</i> 2015
M. hotaula 3							3 (KF027300)	Dalebout <i>et al.</i> 2016
M. hotaula 4							4 (KF027301)	Dalebout <i>et al.</i> 2017
	<i>Mesoplodon carlhubbsi</i>							
M. carlhubbsi 1		18 June 1998	Iwate, Japan	♀	233	EW01192	1 (AB572009)	Kitamura <i>et al.</i> 2013
M. carlhubbsi 2		19 June 08	Shinhidaka, Hokkaido	♀	473	SNH08031	2 (AB572010)	Kitamura <i>et al.</i> 2013
M. carlhubbsi 3		9 August 2009	Nemuro, Hokkaido	♀	510	SNH09023	3 (AB572011)	Kitamura <i>et al.</i> 2013
M. carlhubbsi 4		4 November 1992	U.S.A.	♀		McaSW1154	1 (AY579512)	Dalebout <i>et al.</i> 2004
	<i>Mesoplodon perrini</i>							
M. perrini 1		18 September 1997	U.S.A.	♂	224	TMMC-C75	1 (AF441258)	Dalebout <i>et al.</i> 2004
	<i>Mesoplodon peruvianus</i>							

M. peruvianus 1		19 February 1998	U.S.A.	♂		MpeLAM95654	1 (AY579526)	Dalebout <i>et al.</i> 2004
M. peruvianus 2			Peru			MpeJCR1926	2 (AF492413)	Dalebout <i>et al.</i> 2004
	<i>Mesoplodon traversii</i>							
M. traversii 1		1872	New Zealand	♂		NMNZ546	1 (AF439992)	Dalebout <i>et al.</i> 2004
	<i>Ziphius cavirostris</i>							
Z. cavirostris 1		4 February 2001	Taiyo, Ibaraki	♀	530	EW00004	1 (AB610403)	Kitamura <i>et al.</i> 2013
Z. cavirostris 2		8 May 2004	Shiraoi, Hokkaido	♀	N.D.	EW04598	2 (AB610404)	Kitamura <i>et al.</i> 2013
Z. cavirostris 3		1 April 1999	New Zealand	♂		Zca11	3 (AY579530)	Dalebout <i>et al.</i> 2004
Z. cavirostris 4		29 April 1993	United Kingdom	♂		ZcaSAC0356	4 (AY579531)	Dalebout <i>et al.</i> 2004
	<i>Hyperoodon ampullatus</i>							
H. ampullatus 1			Canada			HamSH9601	1 (AF350437)	Dalebout <i>et al.</i> 2004
H. ampullatus 2			Canada			HamSH9711	2 (AF350440)	Dalebout <i>et al.</i> 2004
	<i>Hyperoodon planifrons</i>							
H. planifrons 1		7 December 1994	New Zealand	♀		Hpl01	1 (AF036224)	Dalebout <i>et al.</i> 2004
H. planifrons 2		1 January 1997	New Zealand			Hpl04	2 (AY579529)	Dalebout <i>et al.</i> 2004
	<i>Indopacetus pacificus</i>							
I. pacificus 1		3 August 2002	Sendai, Kagoshima	♀	650	M33006/ EW00977	1 (AB572012)	Kitamura <i>et al.</i> 2013

Table S3. Count of haplotypes in each stratum. Haplotypes g1–g7 and b1–b3 were described by Kitamura *et al.* (2013). Haplotypes g8, b4, b5 are from this study. Black form haplotypes (b1–b5) were not included in population analysis of Baird’s beaked whales.

Haplotypes	Aleutians	GoA	Japan	Mexico	U.S. West Coast	Ohotsk Sea	Commander Is.
b1	2	—	1	—	—	—	—
b2	—	—	1	—	—	—	—
b3	1	—	1	—	—	—	—
b4	1	—	—	—	—	—	—
b5	1	—	—	—	—	—	—
g1	8	11	69	11	4	—	9
g2	—	2	4	—	1	—	—
g3	—	—	22	—	—	—	—
g4	—	—	2	—	—	—	—
g5	1	—	8	—	—	—	4
g6	—	—	4	—	—	—	—
g7	—	—	3	—	—	—	—
g8	—	2	—	1	—	—	—

Supplementary Table S4:
Strata used for population analyses.

LABID	id	population	Geographic_Area	Geog_gray	seq_source	haplotype	Geog_gray 1 per group	Geog_gray 1 per group woBaker
NA	B_arn1	B_arn			Dalebout2004	barn1		
NA	B_arn2	B_arn			Dalebout2004	barn2		
144310	2014069	black	Aleutians		SWFSC	b1		
41749	0704-BW-DM-01	black	Aleutians		SWFSC	b4		
NA	B_sp_1	black	Japan		Kitamura2014	b1		
NA	B_sp_2	black	Japan		Kitamura2014	b2		
NA	B_sp_3	black	Japan		Kitamura2014	b3		
	BDM294/USNM2763							
144207	66	black	Aleutians		SWFSC-USNM	b5		
144515	LACM91786	black	Aleutians		SWFSC-LACM	b1		
7969	MFR970728.01	black	Aleutians		SWFSC	b3		
35282	CP030713.01	gray	Aleutians	Aleutians	SWFSC	g1	Aleutians	Aleutians
35974	CP030713.02	gray	Aleutians	Aleutians	SWFSC	g1		
35283	CP030716.01	gray	Aleutians	Aleutians	SWFSC	g1	Aleutians	Aleutians
35284	CP030716.02	gray	Aleutians	Aleutians	SWFSC	g1		
35285	CP030716.03	gray	Aleutians	Aleutians	SWFSC	g5	Aleutians	Aleutians
35286	CP030716.04	gray	Aleutians	Aleutians	SWFSC	g1		
35287	CP030716.05	gray	Aleutians	Aleutians	SWFSC	g1		
35288	CP030716.06	gray	Aleutians	Aleutians	SWFSC	g1		
35289	CP030716.07	gray	Aleutians	Aleutians	SWFSC	g1		
NA	Bering_2011.1	gray	Commander_Is	Commander_Is	Jung-Filatova	g1	Commander_Is	Commander_Is
NA	Bering_2012.1	gray	Commander_Is	Commander_Is	Jung-Filatova	g1	Commander_Is	Commander_Is
NA	Bering_2013.1	gray	Commander_Is	Commander_Is	Jung-Filatova	g5	Commander_Is	Commander_Is
NA	Bering_2013.2	gray	Commander_Is	Commander_Is	Jung-Filatova	g5	Commander_Is	Commander_Is
NA	Bering_2013.3	gray	Commander_Is	Commander_Is	Jung-Filatova	g1	Commander_Is	Commander_Is
NA	Bering_2013.4	gray	Commander_Is	Commander_Is	Jung-Filatova	g1	Commander_Is	Commander_Is
NA	Bering_2014.1	gray	Commander_Is	Commander_Is	Jung-Filatova	g1	Commander_Is	Commander_Is
NA	Bering_2014.2	gray	Commander_Is	Commander_Is	Jung-Filatova	g1		
NA	Bering_2014.3	gray	Commander_Is	Commander_Is	Jung-Filatova	g1	Commander_Is	Commander_Is
NA	Bering_2014.4	gray	Commander_Is	Commander_Is	Jung-Filatova	g1	Commander_Is	Commander_Is
NA	Bering_2014.5	gray	Commander_Is	Commander_Is	Jung-Filatova	g5	Commander_Is	Commander_Is
NA	Bering_2014.6	gray	Commander_Is	Commander_Is	Jung-Filatova	g5	Commander_Is	Commander_Is
NA	Bering_2014.7	gray	Commander_Is	Commander_Is	Jung-Filatova	g1	Commander_Is	Commander_Is
28394	MAC020707.01	gray	GoA	GoA	SWFSC	g1	GoA	GoA
28395	MAC020707.02	gray	GoA	GoA	SWFSC	g1		
28396	MAC020707.03	gray	GoA	GoA	SWFSC	g1		
28397	MAC020707.04	gray	GoA	GoA	SWFSC	g1		
43596	MAC040719.04	gray	GoA	GoA	SWFSC	g1	GoA	GoA
43597	MAC040719.05	gray	GoA	GoA	SWFSC	g1		
43598	MAC040719.06	gray	GoA	GoA	SWFSC	g1		

44036	MAC041020.01	gray	GoA	GoA	SWFSC	g1	GoA	GoA
44037	MAC041020.02	gray	GoA	GoA	SWFSC	g2	GoA	GoA
44038	MAC041020.03	gray	GoA	GoA	SWFSC	g2		
62941	OD050812-01	gray	GoA	GoA	SWFSC	g1	GoA	GoA
62942	OD050812-02	gray	GoA	GoA	SWFSC	g8	GoA	GoA
62943	OD050812-03	gray	GoA	GoA	SWFSC	g8		
62944	OD050812-04	gray	GoA	GoA	SWFSC	g1		
62945	OD050812-05	gray	GoA	GoA	SWFSC	g1		
5283	SWDP-92-20	gray	GoA	GoA	SWFSC, Dalebout et al. 2004	g1	GoA	GoA
1	B_bairdii_1	gray	Japan	Japan	Kitamura2014	g1	Japan	Japan
10	B_bairdii_10	gray	Japan	Japan	Kitamura2014	g7	Japan	Japan
11	B_bairdii_11	gray	Japan	Japan	Kitamura2014	g7		
12	B_bairdii_12	gray	Japan	Japan	Kitamura2014	g2	Japan	Japan
13	B_bairdii_13	gray	Japan	Japan	Kitamura2014	g1	Japan	Japan
14	B_bairdii_14	gray	Japan	Japan	Kitamura2014	g3	Japan	Japan
15	B_bairdii_15	gray	Japan	Japan	Kitamura2014	g1	Japan	Japan
16	B_bairdii_16	gray	Japan	Japan	Kitamura2014	g1		
17	B_bairdii_17	gray	Japan	Japan	Kitamura2014	g1	Japan	Japan
18	B_bairdii_18	gray	Japan	Japan	Kitamura2014	g5	Japan	Japan
19	B_bairdii_19	gray	Japan	Japan	Kitamura2014	g3	Japan	Japan
2	B_bairdii_2	gray	Japan	Japan	Kitamura2014	g3	Japan	Japan
20	B_bairdii_20	gray	Japan	Japan	Kitamura2014	g5	Japan	Japan
21	B_bairdii_21	gray	Japan	Japan	Kitamura2014	g6	Japan	Japan
22	B_bairdii_22	gray	Japan	Japan	Kitamura2014	g1	Japan	Japan
23	B_bairdii_23	gray	Japan	Japan	Kitamura2014	g5	Japan	Japan
24	B_bairdii_24	gray	Japan	Japan	Kitamura2014	g1	Japan	Japan
25	B_bairdii_25	gray	Japan	Japan	Kitamura2014	g6	Japan	Japan
26	B_bairdii_26	gray	Japan	Japan	Kitamura2014	g7	Japan	Japan
27	B_bairdii_27	gray	Japan	Japan	Kitamura2014	g2	Japan	Japan
28	B_bairdii_28	gray	Japan	Japan	Kitamura2014	g3	Japan	Japan
29	B_bairdii_29	gray	Japan	Japan	Kitamura2014	g5	Japan	Japan
3	B_bairdii_3	gray	Japan	Japan	Kitamura2014	g3		
30	B_bairdii_30	gray	Japan	Japan	Kitamura2014	g1	Japan	Japan
31	B_bairdii_31	gray	Japan	Japan	Kitamura2014	g1		
32	B_bairdii_32	gray	Japan	Japan	Kitamura2014	g3	Japan	Japan
33	B_bairdii_33	gray	Japan	Japan	Kitamura2014	g1	Japan	Japan
34	B_bairdii_34	gray	Japan	Japan	Kitamura2014	g5	Japan	Japan
35	B_bairdii_35	gray	Japan	Japan	Kitamura2014	g1	Japan	Japan
36	B_bairdii_36	gray	Japan	Japan	Kitamura2014	g1	Japan	Japan
37	B_bairdii_37	gray	Japan	Japan	Kitamura2014	g4	Japan	Japan
38	B_bairdii_38	gray	Japan	Japan	Kitamura2014	g1	Japan	Japan
39	B_bairdii_39	gray	Japan	Japan	Kitamura2014	g5	Japan	Japan
4	B_bairdii_4	gray	Japan	Japan	Kitamura2014	g1	Japan	Japan
40	B_bairdii_40	gray	Japan	Japan	Kitamura2014	g1		
41	B_bairdii_41	gray	Japan	Japan	Kitamura2014	g1		

42	B_bairdii_42	gray	Japan	Japan	Kitamura2014	g1	Japan	Japan
43	B_bairdii_43	gray	Japan	Japan	Kitamura2014	g1	Japan	Japan
44	B_bairdii_44	gray	Japan	Japan	Kitamura2014	g1	Japan	Japan
45	B_bairdii_45	gray	Japan	Japan	Kitamura2014	g1	Japan	Japan
46	B_bairdii_46	gray	Japan	Japan	Kitamura2014	g3	Japan	Japan
47	B_bairdii_47	gray	Japan	Japan	Kitamura2014	g3	Japan	Japan
48	B_bairdii_48	gray	Japan	Japan	Kitamura2014	g1	Japan	Japan
49	B_bairdii_49	gray	Japan	Japan	Kitamura2014	g1	Japan	Japan
5	B_bairdii_5	gray	Japan	Japan	Kitamura2014	g3	Japan	Japan
50	B_bairdii_50	gray	Japan	Japan	Kitamura2014	g1	Japan	Japan
51	B_bairdii_51	gray	Japan	Japan	Kitamura2014	g1	Japan	Japan
52	B_bairdii_52	gray	Japan	Japan	Kitamura2014	g1	Japan	Japan
53	B_bairdii_53	gray	Japan	Japan	Kitamura2014	g1	Japan	Japan
54	B_bairdii_54	gray	Japan	Japan	Kitamura2014	g1	Japan	Japan
55	B_bairdii_55	gray	Japan	Japan	Kitamura2014	g1	Japan	Japan
56	B_bairdii_56	gray	Japan	Japan	Kitamura2014	g1		
57	B_bairdii_57	gray	Japan	Japan	Kitamura2014	g1	Japan	Japan
58	B_bairdii_58	gray	Japan	Japan	Kitamura2014	g1	Japan	Japan
59	B_bairdii_59	gray	Japan	Japan	Kitamura2014	g1	Japan	Japan
6	B_bairdii_6	gray	Japan	Japan	Kitamura2014	g1		
60	B_bairdii_60	gray	Japan	Japan	Kitamura2014	g1	Japan	Japan
61	B_bairdii_61	gray	Japan	Japan	Kitamura2014	g1	Japan	Japan
7	B_bairdii_7	gray	Japan	Japan	Kitamura2014	g1	Japan	Japan
8	B_bairdii_8	gray	Japan	Japan	Kitamura2014	g1		
9	B_bairdii_9	gray	Japan	Japan	Kitamura2014	g1		
NA	BbaJ00-16	gray	Japan	Japan	Baker	g3	Japan	
NA	BbaJ02-018	gray	Japan	Japan	Baker	g5	Japan	
NA	BbaJ02-021	gray	Japan	Japan	Baker	g1	Japan	
NA	BbaJ02-A1	gray	Japan	Japan	Baker	g3	Japan	
NA	BbaJ02-A2	gray	Japan	Japan	Baker	g3	Japan	
NA	BbaJ02-H1	gray	Japan	Japan	Baker	g1	Japan	
NA	BbaJ02-H2	gray	Japan	Japan	Baker	g1	Japan	
NA	BbaJ02-S4	gray	Japan	Japan	Baker	g3	Japan	
NA	BbaJ02-S6	gray	Japan	Japan	Baker	g3	Japan	
NA	BbaJ02-S7	gray	Japan	Japan	Baker	g3	Japan	
NA	BbaJ02-T1	gray	Japan	Japan	Baker	g6	Japan	
NA	BbaJ98C18	gray	Japan	Japan	Baker	g2	Japan	
NA	BbaJ98D13	gray	Japan	Japan	Baker	g1	Japan	
NA	BbaJ98D36	gray	Japan	Japan	Baker	g6	Japan	
NA	BbaJ98D37	gray	Japan	Japan	Baker	g1	Japan	
NA	BbaJ98D52	gray	Japan	Japan	Baker	g1	Japan	
NA	BbaJa98100	gray	Japan	Japan	Baker	g1	Japan	
NA	BbaJa9838	gray	Japan	Japan	Baker	g1	Japan	
NA	BbaJa9888	gray	Japan	Japan	Baker	g1	Japan	
NA	BbaJa9899	gray	Japan	Japan	Baker	g1	Japan	
NA	BbaJa98D54	gray	Japan	Japan	Baker	g3	Japan	

NA	BbaJE9518	gray	Japan	Japan	Baker	g1	Japan	
NA	BbaJE9520	gray	Japan	Japan	Baker	g1	Japan	
NA	BbaJE9523	gray	Japan	Japan	Baker	g3	Japan	
NA	BbaJE9525	gray	Japan	Japan	Baker	g3	Japan	
NA	BbaJE9695	gray	Japan	Japan	Baker	g4	Japan	
NA	BbaJW99-A2	gray	Japan	Japan	Baker	g1	Japan	
NA	BbaJW99-A20	gray	Japan	Japan	Baker	g1	Japan	
NA	BbaJW99-O16	gray	Japan	Japan	Baker	g3	Japan	
NA	BbaJW99-T41	gray	Japan	Japan	Baker	g3	Japan	
NA	BbaJW99-T44	gray	Japan	Japan	Baker	g1	Japan	
NA	JE00-H01	gray	Japan	Japan	Baker	g1	Japan	
NA	JE01-A01	gray	Japan	Japan	Baker	g3	Japan	
NA	JE01-A02	gray	Japan	Japan	Baker	g3	Japan	
NA	JE01-H01	gray	Japan	Japan	Baker	g1	Japan	
NA	JE01-H05	gray	Japan	Japan	Baker	g1	Japan	
NA	JE01-H06	gray	Japan	Japan	Baker	g1	Japan	
NA	JE02-C11	gray	Japan	Japan	Baker	g1	Japan	
NA	JE02-C20	gray	Japan	Japan	Baker	g5	Japan	
NA	JE02-H01	gray	Japan	Japan	Baker	g1	Japan	
NA	JE02-H05	gray	Japan	Japan	Baker	g1	Japan	
NA	JE02-H07	gray	Japan	Japan	Baker	g1	Japan	
NA	JE02-HK05	gray	Japan	Japan	Baker	g1	Japan	
NA	JE02-HK06	gray	Japan	Japan	Baker	g1	Japan	
NA	JE02-HK07	gray	Japan	Japan	Baker	g1	Japan	
NA	JE03-H01	gray	Japan	Japan	Baker	g1	Japan	
NA	JE03-H02	gray	Japan	Japan	Baker	g1	Japan	
NA	JE03-H03	gray	Japan	Japan	Baker	g1	Japan	
NA	JE03-HK01	gray	Japan	Japan	Baker	g1	Japan	
13878	SK-99-31	gray	Japan	Japan	SWFSC	g1	Japan	Japan
	WADA90-							
4963	15/LACM86029	gray	Japan	Japan	SWFSC	g1	Japan	Japan
	WADA90-							
4964	17/LACM86030	gray	Japan	Japan	SWFSC	g2	Japan	Japan
68608	B. bairdii 01	gray	Mexico	Mexico	SWFSC	g1	Mexico	Mexico
68609	B. bairdii 02	gray	Mexico	Mexico	SWFSC	g1		
68610	B. bairdii 03	gray	Mexico	Mexico	SWFSC	g1		
68611	B. bairdii 04	gray	Mexico	Mexico	SWFSC	g8	Mexico	Mexico
68612	B. bairdii 05	gray	Mexico	Mexico	SWFSC	g1		
68613	B. bairdii 06	gray	Mexico	Mexico	SWFSC	g1		
68614	B. bairdii 07	gray	Mexico	Mexico	SWFSC	g1		
68615	B. bairdii 08	gray	Mexico	Mexico	SWFSC	g1		
68616	B. bairdii 09	gray	Mexico	Mexico	SWFSC	g1		
68617	B. bairdii 10	gray	Mexico	Mexico	SWFSC	g1		
17984	DSJ000801.15	gray	Mexico	Mexico	SWFSC	g1	Mexico	Mexico
17985	DSJ000801.16	gray	Mexico	Mexico	SWFSC	g1		
64650	CRC20070417-01	gray	US_West_Coast	US_West_Coast	SWFSC	g1	US_West_Coast	US_West_Coast

51131	DSJ050823.01	gray	US_West_Coast	US_West_Coast	SWFSC	g1	US_West_Coast	US_West_Coast
51132	DSJ050823.02	gray	US_West_Coast	US_West_Coast	SWFSC	g1		
76728	MAC080807.01	gray	US_West_Coast	US_West_Coast	SWFSC	g1	US_West_Coast	US_West_Coast
17152	VM2405	gray	US_West_Coast	US_West_Coast	SWFSC	g2	US_West_Coast	US_West_Coast
NA	B_bairdii_62	gray			Arnason et al. 2004	g1		
NA	B_bairdii_64	gray			Dalebout et al. 2004	g1		
23169	RUS#9-0007	Gray			SWFSC	g1 or g4		