Mitogenomic Phylogenetics of Fin Whales (*Balaenoptera physalus spp.): Genetic Evidence for Revision of Subspecies

Frederick I. Archer¹, Phillip A. Morin¹, Brittany L. Hancock-Hanser¹, Kelly M. Robertson¹, Matthew S. Leslie¹, Martine Bérubé³, Simone Panigada⁴, Barbara L. Taylor¹

¹Southwest Fisheries Science Center, National Marine Fisheries Service, La Jolla, California, United States of America, ²Scripps Institution of Oceanography, University of California San Diego, La Jolla, California, United States of America, ³Centre for Ecological and Evolutionary Studies, University of Groningen, Groningen, The Netherlands, ⁴Tethys Research Institute, Milano, Italy

Abstract

There are three described subspecies of fin whales (*Balaenoptera physalus*): *B. p. physalus* Linnaeus, 1758 in the Northern Hemisphere, *B. p. quoyi* Fischer, 1829 in the Southern Hemisphere, and a recently described pygmy form, *B. p. patachonica* Burmeister, 1865. The discrete distribution in the Northern Pacific and North Atlantic raises the question of whether a single Northern Hemisphere subspecies is valid. We assess phylogenetic patterns using ~16 K base pairs of the complete mitogenome for 154 fin whales from the North Pacific, North Atlantic - including the Mediterranean Sea - and Southern Hemisphere. A Bayesian tree of the resulting 136 haplotypes revealed several well-supported clades representing each ocean basin, with no haplotypes shared among ocean basins. The North Atlantic haplotypes (n = 12) form a sister clade to those from the Southern Hemisphere (n = 42). The estimated time to most recent common ancestor (TMRCA) for this Atlantic/Southern Hemisphere clade and 81 of the 97 samples from the North Pacific was approximately 2 Ma. 14 of the remaining North Pacific samples formed a well-supported clade within the Southern Hemisphere. The TMRCA for this node suggests that at least one female from the Southern Hemisphere immigrated to the North Pacific approximately 0.37 Ma. These results provide strong evidence that North Pacific and North Atlantic fin whales should not be considered the same subspecies, and suggest the need for revision of the global taxonomy of the species.

Introduction

Fin whales (*Balaenoptera physalus* Linnaeus, 1758) are distributed across the temperate to subpolar waters of the world. The Society of Marine Mammalogy currently recognizes three subspecies: *B. p. physalus* Linnaeus, 1758 in the Northern Hemisphere, *B. p. quoyi* Fischer, 1829 in the Southern Hemisphere, and the pygmy fin whale, *B. p. patachonica* Burmeister, 1865 [1]. The distinction between Northern and Southern Hemisphere fin whales was first proposed in a comparative study of the osteology of Bryde’s whales (*Balaenoptera edeni* Anderson, 1879) in which Lønberg [2] noted differences in the vertebral characteristics of fin whales in the two hemispheres, leading to the suggestion that Southern Hemisphere whales were a different subspecies, bearing the name *B. p. quoyi*. Tomilin [3] independently noted both the larger mean and maximum body sizes of Southern Hemisphere whales, also suggesting that subspecific status was warranted under the same name. These differences were later verified by morphological examinations of a larger series of specimens in a study of body measurements and organ weights of fin whales from the North Atlantic and Antarctica [4], which found that Antarctic fin whales have a greater percentage of blubber weight than those caught off of Iceland while having similar muscle weights, making the Icelandic whales appear leaner. The maximum body length of fin whales in the Antarctic (>23 m) was about 3–4 m greater than those in the Northern Hemisphere [4,5].

The establishment and recognition of the Southern Hemisphere *B. p. quoyi* automatically placed all Northern Hemisphere fin whales within the nominate subspecies *B. p. physalus*. Differentiation between the hemispheres is a pattern mirrored in many cetaceans [6,7] and is well supported. In contrast, the default condition that all Northern Hemisphere fin whales belong to the same subspecies (*B. p. physalus*) has not been evaluated and is unlikely given their disjunct distribution in the North Atlantic and North Pacific.

Recently, Clarke [8] has presented evidence that more than one form of fin whale may exist in the Southern Hemisphere in his description of the pygmy fin whale *B. p. patachonica* Burmeister, 1865 [8]. The form is described as small (approximately 18–24 m) and dark with black baleen [9–11]. The type specimen was collected from a stranding at the mouth of the Río de la Plata, Argentina [12] at approximately 36°S, and Clarke [8] suggests that they do not extend further south than approximately 55°S.

Recent genetic and acoustic studies on this species have focused on population-level differentiation within ocean basins in the Northern Hemisphere, although some limited comparisons...
between North Atlantic and North Pacific populations have been conducted. Bérubé et al [13] found no shared mitochondrial DNA (mtDNA) haplotypes between fin whales sampled in the Gulf of California and those sampled in the strata containing the North Atlantic and Mediterranean; the average $F_{ST}$ value for six microsatellite loci was 0.51 [14], which is several times larger than the mean $F_{ST}$ of 0.12 for comparisons between North Atlantic populations and the Mediterranean Sea. Hatch and Clark [15] found a significant correlation between measures of mtDNA and microsatellite differentiation and geographic distance among fin whales from various sites in the North Pacific and North Atlantic, but no correlation using paternally inherited DNA from the y-chromosome (yDNA), which the authors interpreted as suggesting some degree of male-mediated dispersal. However, because their analyses were not hierarchically stratified by geography, they did not address the question of yDNA differentiation between ocean basins. In other words, most of the correlation they present could be due to within-ocean-basin comparisons. Additionally, while not fully diagnostic, Hatch and Clark [15] also found that 92% of singing whales from the North Pacific, North Atlantic, and Mediterranean Sea could be correctly classified to the region within the ocean basin from which they were sampled based on components of their calls. Those that were misclassified were most often misclassified to a region within the same ocean basin, indicating ocean-basin-specific call components.

It is very unlikely that significant gene flow has occurred between North Pacific and North Atlantic fin whales at least since the closing of the Isthmus of Panama around 4 Ma [16,17]. During the feeding season, North Pacific fin whales are not known to extend past the Bering Sea into the Chukchi Sea farther north than approximately 70°N [18]. In the North Atlantic, they occur in the Norwegian Sea and have been detected up to 80°N in the Greenland Sea and approximately 75°N in the Barents Sea [19,20]. On the western side of Greenland, they have been detected to about 70°N in Davis Strait [21]. During research cruises in the eastern tropical Pacific from August to December, they are rarely encountered south of the Baja Peninsula, Mexico [22], and are extremely rare if not entirely absent in the western Caribbean Sea or Gulf of Mexico [23–25].

We present the first study of the phylogenetic relationship of fin whales from three of the primary ocean basins in which they occur: the North Atlantic, North Pacific, and Southern Ocean. Historically, phylogeographic analyses of large whales have proven to be a difficult endeavor. This is a result of their overall body sizes and widespread distribution, which makes it difficult to accumulate, archive, and examine a sufficient number of osteological specimens from across their range. The rapid development of new molecular techniques, such as Next Generation Sequencing (NGS) [26,27], as well as computer-intensive analytical methods, such as Bayesian phylogenetics [28] has offset some of those problems by extracting more information from the available soft tissue samples, thus improving our understanding of patterns of divergence at multiple taxonomic levels [29–31]. Here we examine the phylogenetic relationship as well as the degree and timing of divergence of fin whales between each ocean basin using the complete mitochondrial DNA sequence generated using NGS. We also examine the geographical distribution of clades based on mitogenome sequences within a larger dataset of control region sequences generated with standard Sanger sequencing methods.

### Methods

#### Ethics Statement

Procedures for ensuring animal welfare during biopsy sampling were approved as part of the Scientific Research permits issued by the National Marine Fisheries Service under the authority of the Marine Mammal Protection Act of 1972 (16 U.S.C. 1361 et seq.), the regulations governing the taking and importing of marine mammals (MMPA) (50 CFR part 216), the Endangered Species Act of 1973 (ESA) (16 U.S.C. 1531 et seq.), and the regulations governing endangered fish and wildlife permits (50 CFR parts 222–226). Biopsies were taken under NMFS permit numbers 779–1339, 779–1663, 14007, 774–1437, 774–1714, 1026/689424, and 873 issued to the National Marine Fisheries Service Southeast Fisheries Science Center and Southwest Fisheries Science Center. The samples originating from outside US jurisdiction were imported under CITES Import permit numbers US774223 and US689420, and under CITES Certificate of Scientific Exchange #690543. CITES permits are issued by the U.S. Fish & Wildlife Service. The Southwest Fisheries Science Center is a Registered Scientific Institution under CITES (US052).

#### Samples

A total of 435 fin whale samples were collected from the North Pacific, North Atlantic, Mediterranean Sea, and Southern Ocean (Figure 1). Samples from the North Pacific, North Atlantic, and Mediterranean Sea would currently be classified as Northern Hemisphere fin whales (*Balaenoptera physalus physalus*), while those from the Southern Ocean represent Southern Hemisphere fin whales (*B. p. patachonica*). We were unable to obtain any samples that could be positively identified as pygmy fin whales (*B. p. patachonica*) for this study. Most samples are from biopsies of living whales taken at sea, but a few North Pacific samples were from stranded individuals. To ensure that our mitogenome dataset represented the full range of mitochondrial diversity in each ocean basin, we selected a subset of these samples based on mitochondrial control region (CR) haplotypes previously generated for another project via Sanger-sequencing as described below.

#### Control Region Sanger-Sequencing

For 430 samples, we sequenced the first 412 base pairs of the hypervariable mtDNA control region (CR). Genomic DNA was extracted using several standard methods including a sodium chloride protein precipitation (modified from Miller et al [32]), a silica-based filter purification (DNaseq kit; Qiagen, Valencia, CA, 2011). We conducted a preliminary examination of the mitogenome sequences using the complete mitochondrial DNA sequence generated using NGS. We also examined the geographical distribution of clades based on mitogenome sequences within a larger dataset of control region sequences generated with standard Sanger sequencing methods.

### Figure 1. Location of fin whale mitogenome samples (n = 154).

Each small circle represents a single sample. Larger symbols are: red triangle = reference sequence from Arnsen et al (1998), red diamond = Mediterranean Sea samples (n = 5), blue diamond = stranded western Australia samples (n = 2).

doi:10.1371/journal.pone.0063396.g001
Mitogenome Assembly

Consensus sequences were generated from mitogenome sequence reads using a custom pipeline written by FIA (available at the Dryad data repository, http://dx.doi.org/doi:10.5016/dryad.cv35b). The mpileup module in SAMTOOLS [39] was used to convert the resulting BAM-format alignment file into a “pileup” text format that lists the base composition across reads at each site in the reference sequence. This text file was then parsed by custom R code to create the consensus sequence for each individual, using the following rules. If a given site had fewer than three reads, an “N” was placed in the consensus. If the coverage was between three and five, and all reads contained the same nucleotide, then that nucleotide was used in the consensus; otherwise, the consensus received an “N” for that site. If coverage was greater than five, then the nucleotide that occurred in 70% or more of the reads was used in the consensus. If no nucleotide frequency exceeded 70%, then an “N” was inserted. All mitogenome sequences (fin whale plus outgroup species) were initially aligned with MAFFT [40] followed by a refinement of alignments by eye.

We compared the first 412 base pairs of the control region in the NGS sequences with those from the Sanger-sequenced dataset for all but the five Mediterranean samples and the reference sequence. If the NGS sequence had an “N” at a site or was different from the base call in the Sanger-sequence, and the site had a strong, high-quality peak in the Sanger-sequence chromatogram, then it was replaced by the Sanger-sequence base pair. These Sanger-supplemented NGS sequences were then used in the phylogenetic analyses.

Mitogenomic Phylogenetics of Fin Whales

We compiled sequences from five humpback whales (*Megaptera novaeangliae*) as the outgroup to fin whales given their sister species relationships in several studies [41–43]. The full mitogenome sequence was available for one humpback sample (Genbank Accession # NC006927 [43]). The remaining four were partial sequences composed of only the coding genes (Genbank Accession #s JF90425, CEErath et al unpublished data; GQ535254–GQ43292 representing individual coding regions from samples GOM0949, GOM9084, and SEA07041 [41]). With these sequences, we compiled two datasets, one composed of the complete 16,423 base pairs of the mitogenome with just the single humpback outgroup, and the other composed of 11,406 base pairs of the protein coding genes, using all five humpback samples (referred to below as “mito” and “cds” datasets respectively).

We estimated phylogenetic relationships and divergence times for both datasets using BEAST v1.7 [28]. In both the *mito* and *cds* datasets, all fin whale sequences were constrained to be monophyletic. The five humpback whale sequences were also constrained to be monophyletic in the *cds* dataset. Based on the results of an analysis with jModelTest [44], we selected the HKY+G substitution model with 4 substitution categories for both datasets. Models were run using a strict molecular clock for which we set a prior distribution on the mean substitution rate to Uniform (1e-5, 1e-2) based on the results of preliminary runs and published estimates of substitution rates in Cetacea [30,41,43,45,46]. A Yule speciation tree model was used and initialized with an UPGMA tree. The prior on the tree root was set as Normal (15.8, 2.8), corresponding to the estimate of time since most recent common ancestor (TMRCA) between fin and humpback whales [43]. A total of 10,000,000 MCMC iterations were run, with every 1,000th iteration saved to create the posterior sample. Convergence and sufficient mixing of the posterior samples were evaluated by examination of the effective sample sizes (ESSs) and sampling traces for each parameter using Tracer v1.5 [47].

Supplemental material, including sample numbers, collection details, and GenBank accession numbers for each haplotype, parameters for mitogenome assembly, BEAST input files, full Bayesian posterior sample, and annotated trees are available at the Dryad data repository (http://dx.doi.org/doi:10.5061/dryad.084g8).

Results

There were a total of 103 CR haplotypes in the Sanger-sequenced data set (Table 1). Haplotypic diversity was high both within ocean basins as well as across all samples. The minimum diversity within an ocean basin was 0.828 for the North Atlantic, which also had the fewest samples. There were no shared haplotypes among ocean basins. There were two fixed differences between the North Atlantic and North Pacific (sites 181 and 198), and one between the North Atlantic and Southern Hemisphere sequences (site 198).
mito rates from both the full mitogenome (haplotypes were shared among ocean basins. The region sequences (Table 1). None of the 136 mitogenome in the mitogenome dataset was higher than in the Sanger control or within samples from a given ocean basin. As expected, diversity any particular region of the mitogenome, either across all samples bases. There was no significant clustering of missing data within one, with 94% of the sequences having fewer than ten missing bases. The median number of missing bases in a sequence was 36. After alignment and base calling, approximately 33% of the consensus sequences had no missing bases. The median number of missing bases in a sequence was one, with 94% of the sequences having fewer than ten missing bases. There was no significant clustering of missing data within any particular region of the mitogenome, either across all samples or within samples from a given ocean basin. As expected, diversity in the mitogenome dataset was higher than in the Sanger control region sequences (Table 1). None of the 136 mitogenome haplotypes were shared among ocean basins.

Bayesian estimates of the TMRCA and nucleotide substitution rates from both the full mitogenome (mito) and coding region (cds) datasets were very similar (Figure 2 and 3). Both analyses produced results with high ESSs and stable, well-mixed posterior samples after approximately 100,000 iterations. Thus, unless otherwise specified, we will only refer to results from the Sanger analysis. Mean substitution rate estimates (2.94e-3, 95% HPD = 1.79e-3–4.45e-3) agree well with estimates from Jackson et al [41] for mysticetes across the mitogenome (3.1e-3, 95% HPD = 2.6e-3–3.7e-3), and Sasaki et al [43] as reported in Nabholz et al [46] between humpback and fin whales (8e-3, 95% CI = 5e-3–2e-2), and between Bryde’s and sei whales (7e-3, 95% CI = 3e-3–1.2e-2) [41,43,46]. However our estimates are slightly less than those made by Dornburg et al [45] for within fin whales (1.1e-2, 95% HPD = 9e-3–1.2e-2), and within humpbacks (7.7e-3, 95% HPD = 5.6e-3–9.5e-3) [45].

The Bayesian phylogenetic tree shows a strong association of clades to the three ocean basins (Figure 2 and 3). Most of the North Pacific samples (n = 81) fall within one clade (NP clade A), which diverged from the other fin whales approximately 2 Ma (95% HPD = 1.1–2.8 Ma). All North Atlantic and Mediterranean samples diverged from the remaining Southern Hemisphere and North Pacific samples approximately 1 Ma (95% HPD = 0.6–1.5 Ma). Within this North Atlantic clade, the Mediterranean samples do not share haplotypes with samples from the rest of the North Atlantic, nor do they form a separate clade on their own. A striking feature in the remainder of the tree is the presence of two clades of North Pacific samples among the Southern Hemisphere samples. The outermost clade (North Pacific clade B) contains only two samples, one from Hawaii and the other from the Gulf of California. The posterior probability (PP) for the node joining this clade to the rest of the samples is relatively low (0.68) in both the mito and cds trees (0.68 and 0.73 respectively) indicating uncertain placement. This is also evidenced by its position internal to Southern Hemisphere clade A in the mito tree and external to it in the cds tree. However, the second, more recently diverged clade of 14 North Pacific samples (North Pacific clade C) is well supported (PP = 1) as closely related to Southern Hemisphere samples. This clade is estimated to have diverged approximately 0.37 Ma (95% HPD = 0.19–0.54 Ma). The TMRCA of all samples within this clade is more recent (approximately 0.06 Ma, 95% HPD = 0.06–0.21 Ma).

In order to examine the representation and distribution of North Pacific clades A and C in a larger sample of animals from the North Pacific (ignoring clade B due to its uncertain placement and small sample size), we conducted a simple assignment test of the North Pacific samples for which we had Sanger D-loop sequences that were not included in the NGS mitogenome data. We calculated the mean Jukes-Cantor distance between these samples and all samples in each of the two clades. Samples were then assigned to the clade to which they had the shortest mean pairwise distance.

The results of this analysis indicate that although both clades are represented in the larger sample from the North Pacific, there is a slight, but significant difference in the frequencies of geographic

| Table 1. Number of samples, haplotypes, and sequence diversity for each sequence dataset. |
|----------------------------------|-----------------|-----------------|-----------------|
| **Sanger CR**                   | **Samples**     | **Haplotypes**  | **Variable Sites** | **Haplotypic Diversity** |
| North Pacific                   | 346             | 50              | 36               | 0.935                      |
| North Atlantic                  | 28              | 12              | 16               | 0.828                      |
| Southern Hemisphere             | 48              | 41              | 36               | 0.993                      |
| Total                           | 422             | 103             | 55               | 0.955                      |

| **Mitogenome CR**               | **Samples**     | **Haplotypes**  | **Variable Sites** | **Haplotypic Diversity** |
| North Pacific                   | 97              | 49              | 36               | 0.980                      |
| North Atlantic                  | 8               | 8               | 14               | 1                          |
| Southern Hemisphere             | 43              | 41              | 36               | 0.997                      |
| Total                           | 148             | 98              | 54               | 0.991                      |

| **Mitogenome**                  | **Samples**     | **Haplotypes**  | **Variable Sites** | **Haplotypic Diversity** |
| North Pacific                   | 97              | 82              | 501              | 0.996                      |
| North Atlantic                  | 14              | 12              | 97               | 0.967                      |
| Southern Hemisphere             | 43              | 42              | 438              | 0.999                      |
| Total                           | 154             | 136             | 925              | 0.998                      |

“Sanger CR” is the 412 bp of the control region generated from Sanger sequences. “Mitogenome CR” is the corresponding 412 bp of the control region from the NGS mitogenome sequence, and “Mitogenome” is the 16.4 Kbp full mitochondrial sequence generated from NGS reads. Note that the North Atlantic Mitogenome CR set does not include the 5 Mediterranean samples and the reference sequence from Arnason et al. (1991) for which no comparable Sanger sequences were generated.

doi:10.1371/journal.pone.0063396.t001

Alignment of the mitogenome reads to the reference produced high quality consensus sequences 16,401 bp in length for most samples. The median number of reads aligning to the reference for each sample was 23,608. The median coverage (the number of reads aligning to a given site on the reference) per sample was 136. Of the 153 mitogenomes, 142 had at least one read covering every site. Of the remaining 11 sequences, the maximum number of sites with no coverage was 36. The results of this analysis indicate that although both clades are widely represented in the larger sample from the North Pacific, there is a slight, but significant difference in the frequencies of geographic
strata from which they were sampled. Figure 4 shows the distribution of the difference in mean pairwise distances to North Pacific clade A and C for the 249 North Pacific Sanger-sequenced control region samples. Of these, 237 were closer to the North Pacific clade A, while the remaining 12 were closer to clade C. We then combined these assignments with the 97 NGS samples and examined the frequency distribution of sampling strata by clade (Table 2). Although the overall sample size of clade C is considerably smaller, there is indication that the sampling strata are differentially represented in the clades ($\chi^2$ p-value = 0.014). Most notably, a higher proportion of North Pacific clade A is composed of samples from south of Pt. Conception, California (Gulf of California and Southern California Bight), while a higher proportion of clade C is composed of samples from north of Pt. Conception (California, Oregon, Washington and Gulf of Alaska).

Nevertheless, the presence of clade C in all regions examined does not suggest that this clade could represent a relatively isolated group of whales that would warrant separate management as a stock or perhaps subspecies. Samples from both clades A and C were collected together in four out of 15 sampling events where more than one sample was taken. We did not find any differences between the clades in the sex ratio of samples, sampling season, or year.

In the full mitogenome there were 27 fixed differences between all North Pacific and North Atlantic haplotypes, and 28 fixed differences between the North Atlantic and Southern Hemisphere (Table 3). Because of the polyphyletic relationship of the North Pacific and Southern Hemisphere, there were no fixed differences between haplotypes from those two ocean basins. However, when North Pacific clades A and C were examined separately, there

---

**Figure 2. Summary of Bayesian fin whale phylogenetic tree using full mitogenome sequences (mito dataset).** The root leads to divergence of fin whales from humpbacks. Branches with two or more samples in the same ocean basin have been collapsed. Numbers in parentheses are number of samples at each branch tip, except for the single Southern Hemisphere samples in clade 8 (SWFSC Lab ID 91296). Scale at bottom is node age in millions of years. Time to Most Recent Common Ancestor (TMRCA) estimates, 95% Highest Posterior Density (HPD), and posterior probabilities (PP) of each numbered node are given in the inset table. TMRCA values not reported for nodes with PP<0.9. The full annotated tree is available at the Dryad data repository, http://dx.doi.org/10.5061/dryad.084g8.

doi:10.1371/journal.pone.0063396.g002
were 64 and 13 fixed differences between each clade and the Southern Hemisphere, respectively. Interestingly, the two North Pacific clades were more different from one another than either was from the other two ocean basins, with 108 fixed differences between them. The second greatest difference was the 94 fixed differences between North Pacific clade A and the North Atlantic. The number of fixed differences within the more commonly sequenced cytochrome B gene and control region was proportionally similar to the full mitogenome relative to sequence length. The only comparison without at least one diagnostic site aside from the entire North Pacific and Southern Hemisphere was in the control region between North Pacific clade C and the Southern Hemisphere.

Discussion

The three currently described subspecies of fin whales (*Balaenoptera physalus physalus*, *B. p. quoyi*, *B. p. patachonica*) have been based on morphological differences found in a limited series of specimens from whaling in the North Atlantic and Southern Ocean [2,3,8]. Since then, although there have been genetic and acoustic studies examining population structure within ocean basins, as well as among populations between ocean basins [13,14,48], little work has been done to re-examine the taxonomy of this globally-distributed species.

The results of this study, the first to explicitly examine the divergence between North Pacific and North Atlantic fin whales in comparison to the Southern Hemisphere, show strong phylogeographic structuring among these three ocean basins. The North Atlantic (including samples from the Mediterranean Sea) formed the only monophyletic clade, diverging from other fin whales in either the North Pacific or Southern Hemisphere approximately 0.99 Ma (95% HPD = 0.56–1.46 Ma). The polyphyletic North Pacific was distributed in three clades in the tree, the largest of which diverged from all other fin whale haplotypes approximately 1.94 Ma (95% HPD = 1.09–2.81 Ma), and the other two associated with Southern Hemisphere whales. These estimates are congruent with those made by Bérubé et al [14] with North Pacific and North Atlantic/Mediterranean fin whales having diverged 1–3 Ma. These patterns in conjunction with the large number of fixed differences between North Atlantic fin whales and all other ocean basins strongly indicate that *Balaenoptera physalus physalus*, the

---

**Figure 3. Summary of Bayesian fin whale phylogenetic tree using protein coding mitogenome sequences (cds dataset).** The root leads to divergence of fin whales from humpbacks. Branches with two or more samples in the same ocean basin have been collapsed. Numbers in parentheses are number of samples at each branch tip. Time to Most Recent Common Ancestor (TMRCA) estimates, 95% Highest Posterior Density (HPD), and posterior probabilities (PP) of each numbered node are given in the inset table. TMRCA values not reported for nodes with PP<0.9. The full annotated tree is available at the Dryad data repository http://dx.doi.org/10.5061/dryad.084g8.

doi:10.1371/journal.pone.0063396.g003
Northern Hemisphere fin whale, is not composed of a single subspecies.

Among globally distributed mysticetes, like fin whales, the amount of divergence between closely related taxa in each hemisphere and ocean basin varies. It is believed that the generic migratory pattern of large whales (feeding in higher latitudes during the summer months, and travelling to lower latitudes to calve and breed in the winter) serves as a relatively effective barrier to trans-equatorial gene flow [6,7], leading towards reproductive isolation and ultimately speciation in each hemisphere. However, some species, like blue whales (*Balaenoptera musculus* Linnaeus, 1758) can be found near the equator either seasonally or year-round [49], and trans-equatorial migrations and movements between ocean basins have been observed in other species as well [50,51]. Changes in oceanographic conditions, such as cooling during Pleistocene glacial periods, could force anti-tropical forms closer together, increasing the likelihood of exchange [6]. These processes would be expected to produce a pattern in which anti-tropical pairs with a greater distributional hiatus near the equator are also more taxonomically divergent.

Right whales (*Eubalaena* spp. Gray, 1864), which are distributed in temperate to subpolar waters and are rarely encountered below approximately 15°–20° latitude in either hemisphere [52–54], represent one end of this spectrum. For this genus, there is a broad 30°–40° band that separates whales in the two hemispheres. Historically, two antitropical species of right whales were recognized: *Eubalaena glacialis* Müller, 1776 in the Northern Hemisphere, and *E. australis* Desmoulins, 1822 in the Southern Hemisphere [55]. Rosenbaum et al [7] demonstrated that within the mitochondrial control region, *E. glacialis* contained two reciprocally monophyletic matrilines [7]. The matriline containing haplotypes from the North Pacific was more closely related to the Southern Hemisphere *E. australis* than to *E. glacialis* in the North Atlantic, which were basal in the tree. The authors therefore suggested that North Pacific right whales should be elevated to full species status as *E. japonica* Lacépède, 1818, a designation later confirmed with a suite of nuclear loci [56]. Within the 292 bp examined by Rosenbaum et al [7], there were between 6 and 7 fixed differences between *Eubalaena* species. In comparison, in the same region in our fin whale sequences, there are only two fixed differences between North Atlantic and North Pacific samples, one fixed difference between North Atlantic and Southern Hemisphere samples and no fixed differences between North Pacific and Southern Ocean samples.

With a distribution more like that of fin whales, minke whales are represented both by antitropical species and subspecies pairs. The common minke whale (*Balaenoptera acutorostrata* Lacépède, 1804) can be found from subpolar waters during the summer feeding season, to more temperate to tropical waters in the winter breeding period [55,57–59]. Within this species, there are three recognized subspecies: *B. a. acutorostrata* in the north Atlantic, *B. a. scanmani* Deméré, 1986, in the North Pacific, and the dwarf minke (*B. a. subsp.*) in the Southern Hemisphere [55]. The sister species to the common minke whale, the Antarctic minke whale (*B. bonaerensis* Burmeister, 1867) is restricted to the Southern Hemisphere. The TMRCA between the two minke whale species has been estimated to be between 4.4 and 4.9 Ma, and the TMRCA of the three common minke whale (*B. acutorostrata*) subspecies was estimated at 1.2 Ma (95% CI = 0.3–2.2 Ma) [60], very similar to the TMRCA of all fin whale haplotypes in this study (1.9 Ma, 95% HPD = 1.1–2.9 Ma).

The taxonomy of blue whales (*Balaenoptera musculus*), which has yet to be fully elucidated, may represent the other end of this spectrum. In the Pacific, blue whales are found around the productive tropical Costa Rica Dome year round [49], and feeding has been documented off the equatorial Galapagos Islands [61]. It is likely that at least seasonally, waters from south of the Equator to northern Peru can contain blue whales from both the Northern and Southern Hemispheres [49,62]. The nominate subspecies (*B. m. musculus*) contains whales in the North Atlantic and North Pacific combined. Two additional subspecies are recognized, the subantarctic “pygmy” blue whales (*B. m. brevicea*

ichara, 1966), and the Antarctic “true” blue whales (*B. m. intermedia* Burmeister, 1871–72) [55]. Although they are morphologically diagnosable, the amount of genetic differentiation among subspecies described to date is low compared to that found for other recognized subspecies of whales, as well as that found between ocean basins in the fin whale data in this study [62,63].

Thus, with their temperate distributions, fin whales exhibit patterns of divergence intermediate to those of minke and blue whales.

Table 2. Distribution of North Pacific sampling strata in phylogenetic clades from assignment of control region sequences.

| Strata                      | NP Clade A | NP Clade C |
|-----------------------------|------------|------------|
| Bering Sea                  | 21 (0.06)  | 2 (0.07)   |
| Gulf of Alaska              | 111 (0.35) | 12 (0.43)  |
| California, Oregon, Washington | 38 (0.12) | 9 (0.32)   |
| Southern California Bight   | 114 (0.36) | 3 (0.11)   |
| Gulf of California          | 32 (0.10)  | 1 (0.04)   |
| Hawaii                      | 2 (0.01)   | 1 (0.04)   |

Values are number of samples with the proportion of samples in each stratum in parentheses. Samples include both those assigned from control region sequences and mitogenome sequences used to build the Bayesian tree. doi:10.1371/journal.pone.0063396.t002

Figure 4. Distribution of difference between mean distances to North Pacific clade A and North Pacific clade C for all mtDNA control region sequences. Values below 0 indicate that the sample is closer to clade A than clade C. doi:10.1371/journal.pone.0063396.g004
been recognized as a resident population based on both genetic studies of Alaska [71]; and the whales in the Sea of Cortez, which have been described [67]. Although population structure in the North Atlantic and Mediterranean fin whales have also been recognized [64,65]. However, given that the divergence of North Pacific clade A is approximately 1.52 Ma older than North Pacific clade C, we believe it is most likely that clade C represents a migration event. The estimated position of North Pacific clade B in the tree, basal to the Southern Hemisphere haplotypes, would be more consistent with incomplete lineage sorting, but the relatively weak PP of this clade (0.64) make any inferences about its origin tenuous at best.

While it is clear that the mitogenome can provide enhanced resolution for phylogenetic patterns [29–31], it is nonetheless still inherited as a single locus with multiple linked genes and as such may produce gene trees that are not the same as the "species" trees due to introgression or hybridization [64]. With the rapid growth of Next Generation Sequencing, we are likely to see an order-of-magnitude increase in the number of nuclear loci that can be applied to phylogenetic questions [66].

Berubé et al. [13,14] have shown significant population differentiation between Mediterranean and North Atlantic populations as well as evidence of structure between fin whales from the western and eastern North Atlantic [13,14]. Acoustic differences between North Atlantic and Mediterranean fin whales have also been described [67]. Although population structure in the North Pacific has not been fully elucidated, Mizroch et al [68] discussed five possible populations, or "feeding aggregations": the eastern and western groups that move along the Aleutians [69,70]; the East China Sea group; a group that moves north and south along the west coast of North America between California and the Gulf of Alaska [71]; and the whales in the Sea of Cortez, which have been recognized as a resident population based on both genetic and acoustic differences [13,15,72]. Multiple fin whale call types have been described for the eastern North Pacific (personal communication, E. Oleson, Pacific Island Fisheries Science Center, National Marine Fisheries Service) [15], suggesting that there may be further subdivision along the west coast of North America. In light of this, it is intriguing that although we did not see strong phylogeographic structure within ocean basins in our data, we did see differential representation of the North Pacific clades A and C on either side of Pt. Conception, CA. Whether or not population subdivision or diversity in the North Pacific is related to patterns of historical immigration will be better addressed by future analyses of nuclear and acoustic data.

The taxonomic status of North Pacific fin whales is unclear. If analyses of nuclear loci indicate current gene flow between the clade A and clade C mitochondrial matrilines, this would suggest that all eastern North Pacific fin whales are members of a single, new subspecies. On the other hand, if significant differentiation between these two clades is observed in nuclear markers, then further work should be conducted to further describe other differences between these two sympatric forms. Given its placement in the tree, clade C would likely fall within the current definition for B. p. quoyi, with the odd result of "Southern Hemisphere" fin whales residing in the North Pacific. The sympatric clade A would then become a new subspecies.

Future genetic studies would be greatly enhanced by the inclusion of more samples from regions in which fin whales are known to occur. All but two of the Southern Hemisphere samples came from a single region sampled over a two-year period [73,74] and did not encompass the full range of fin whales across the Southern Ocean [75]. The inclusion of samples from the South Atlantic and South Pacific would allow us to clarify the evolutionary relationship of the North Atlantic and North Pacific and help identify potential avenues of dispersal. Additionally, these samples would allow for the examination of further structuring within B. p. quoyi in the Southern Hemisphere. In particular, they would be valuable for examining the validity of the low- to mid-latitude pygmy fin whales, B. p. patachonica. The description presented by Clarke [8] is primarily based on an examination of whaling records, historical descriptions of external morphology, and the biological examination of one specimen. Thus, genetic samples of whales from this region will be necessary to fully

| Table 3. Number of fixed differences between ocean basins and phylogenetic clades in the full mitogenome, cytochrome B, and the control region. |
|-----------------------------------------------|----------------|----------------|----------------|----------------|
|                                           | North Pacific | North Pacific Clade A | North Pacific Clade C | North Atlantic |
| Full mitogenome (16,423 bp)                  |               |                 |                   |               |
| North Pacific Clade C                         | –             | 108             |                   |               |
| North Atlantic                                | 27            | 94              | 77               |               |
| Southern Hemisphere                           | 0             | 64              | 13               | 28            |
| Cytochrome B (1,139 bp)                       |               |                 |                   |               |
| North Pacific Clade C                         | –             | 11              |                   |               |
| North Atlantic                                | 3             | 11              | 6                |               |
| Southern Hemisphere                           | 0             | 7               | 1                | 2             |
| Control region (412 bp)                       |               |                 |                   |               |
| North Pacific Clade C                         | –             | 1               |                   |               |
| North Atlantic                                | 2             | 3               | 4                |               |
| Southern Hemisphere                           | 0             | 1               | 0                | 1             |

The first "North Pacific" column represents all North Pacific samples (clades A, B, and C).
doi:10.1371/journal.pone.0063396.t003

PLOS ONE | www.plosone.org 8 May 2013 | Volume 8 | Issue 5 | e63396
evaluate this proposed subspecies and its relationship to other Southern Hemisphere whales.

In all ocean basins, fin whale populations were greatly reduced by commercial whaling in the early 20th century [68,76]. As a result, fin whales in both the Atlantic and Pacific are listed as “Endangered” under the United States Endangered Species Act and by the International Union for the Conservation of Nature and Natural Resources (IUCN). In the North Pacific, North Atlantic, and Mediterranean Sea, fin whales appear to be particularly vulnerable to ship strikes [76–79]. In the eastern North Pacific, populations are increasing [80]. Their status is uncertain in the North Atlantic and Southern Ocean, regions where limited whaling is still occurring [76]. To effectively manage uncertain in the North Atlantic and Southern Ocean, regions particularly vulnerable to ship strikes [76–79]. In the eastern Atlantic, and Mediterranean Sea, fin whales appear to be

Acknowledgments

The authors would like to thank Patricia Rosel of the Southeast Fisheries Science Center, Jorge Urban, the Virginia Aquarium & Marine Science Center Foundation, the Riverhead Foundation for Marine Research and Preservation, the Marine Mammal Stranding Network of New Jersey, the University of North Carolina, Wilmington, Cascadia Research Collective, the National Marine Mammal Lab, and the International Whaling Commission for providing DNA and tissue samples for this study. We would also like to thank Jennifer Jackson for her insights into balaenopterid phylogeny, as well as Alexei Drummond and Greg Rouse for helpful analytical suggestions. We appreciate the work of the staff at The Scripps Research Institute for generating the NGS data, and Rich Cosgrove of the Southwest Fisheries Science Center for his scientific computing support. Thanks to William Perrin and Karen Martien for helpful comments on this manuscript.

Author Contributions

Conceived and designed the experiments: FIA PAM BLT. Performed the experiments: FIA PAM BLH KMR MSL. Analyzed the data: FIA. Contributed reagents/materials/analysis tools: FIA MB SP BLT. Wrote the paper: FIA BLT.

References

1. Committee on Taxonomy (2012) List of marine mammal species and subspecies. Society for Marine Mammalogy. University of Washington. 196 p.
2. Lüönd P (1931) The Skeleton of Balaenoptera physalus and Balaenoptera borealis. Arkiv f Zoologi 23.
3. Tomlin A (1946) Taxonomic differentiation and the geographical races of cetaceans (Cetacea: Suborder Mysticeti). Acta Zoologica Fennica 16: 465–472.
4. Lockyer C, Waters T (1986) Weights and anatomical measurements of northeastern Atlantic fin (Balaenoptera physalus, Linnaeus) and sei (B. borealis, Lesson) whales. Mar Mamm Sci 2: 169–193.
5. Lockyer C (1978) Body weights of some species of large whales. Conseil Permanent International pour l’Exploration de la Mer 36: 259–273.
6. Davies JL (1963) The antitropical factor in cetacean speciation. Evolution 17: 107–116.
7. Rosenbaum HC, Brownell RL, Brown MW, Schaeff C, Portway V, et al. (2000) World-wide genetic differentiation of Eschrichtius: questioning the number of right whale species. Mol Ecol 9: 1793–1802.
8. Clarke R (2004) Pygmy fin whales. Mar Mamm Sci 20: 329–334.
9. Bennett AG (1931) Whaling in the Antarctic. Edinburgh: Wm. Blackwood & Sons Ltd.
10. Lalibale F (1905) Las ballenas de nuestros mares. La Revista del Jardin Zoologico, Buenos Aires 1: 20–82.
11. Mackintosh NA (1942) The southern stocks of whalebone whales. Discovery Reports 22: 197–300.
12. Burmister H (1865) Letter on a new species of whale Balaenoptera patagonica from Argentina. Proc Zool Soc, London 13: 190–193.
13. Bérube M, Urban J, Diaz AE, Brownell RL, Palsbøll PJ (2002) Genetic identification of a small and highly isolated population of fin whales (Balaenoptera physalus) in the Sea of Cortez, Mexico. Conserv Genet 3: 183–190.
14. Bérube M, Aguilar A, Dendale D, Larsen F, Di Sciara GN, et al. (1998) Population genetic structure of North Atlantic, Mediterranean Sea and Sea of Cortez fin whales, Balaenoptera physalus (Linnaeus 1758): analysis of mitochondrial and nuclear loci. Mol Ecol 7: 585–599.
15. Hatch LT, Clark CW (2000) Acoustic differentiation between fin whales in both the North Atlantic and North Pacific Oceans, and integration with genetic estimates of divergence. International Whaling Commission Scientific Meeting.
16. Kiegwin LDJ (1978) Pliocene closing of the Isthmus of Panama, based on proxies. London: The Micropalaeontological Society, Special Publications, The Geological Society. 429–444.
17. Schmidt DN (2007) The closure history of the Central American seaway: FIA PAM BLH KMR MSL. Analyzed the data: FIA. Contributed reagents/materials/analysis tools: FIA MB SP BLT. Wrote the paper: FIA BLT.
18. Simon ML (2010) The sounds of whales and their food: Baleen whales, their foraging behaviour, ecology and habitat use in an arctic habitat. Aarhus University.
19. Hamilton TA, Redfern JV, Barlow J, Ballance LT, Gerrodette T, et al. (2009) Atlas of cetacean sightings for Southwest Fisheries Science Center cetacean and ecosytem surveys, 1986–2003. La Jolla, CA: U.S. Dept. of Commerce, National Oceanic and Atmospheric Administration, National Marine Fisheries Service, Southwest Fisheries Science Center. 70 p.
20. Jefferson TA, Lynn SK (1994) Marine mammal sightings in the Caribbean Sea and Gulf of Mexico, Summer 1991. Caribl J Sci 30: 85–89.
21. Maze-Foley K, Mullin KD (2006) Cetaceans of the oceanic northern Gulf of Mexico: Distributions, group sizes and interspecific associations. J Cetacean Res Manage 8: 203–213.
22. Reeves RR, Lund JN, Smith TD, Josephson EA (2011) Insights from whaling logbooks on whales, dolphins, and whaling in the Gulf of Mexico. Gulf Mex Sci 39: 46–67.
23. Mardis ER (2008) Next-generation DNA sequencing methods. Annu Rev Genomics Hum Genet 9: 307–402.
24. Mardis ER (2011) A decade’s perspective on DNA sequencing technology. Nature 478: 198–203.
25. Drummond AJ, Suchard MA, Xie D, Rambaut A (2012) Bayesian Phylogenetics with BEAUti and the BEAST 1.7. Mol Biol Evol 29: 1969–1973.
26. Duchene S, Archer FL, Vihtrup J, Caballero S, Morin PA (2011) Mitogenome Phylogenetics: The Impact of using Single Regions and Partitioning Schemes on Topology, Substitution Rate and Divergence Time Estimation. Plos One 6.
27. Morin PA, Archer FL, Foote AD, Vihtrup J, Allen EE, et al. (2010) Complete mitochondrial genome phylogenetic analysis of killer whales (Orcinus Orca) indicates multiple species. Genome Res 20: 590–596.
28. Vihtrup JT, Ho SY, Foote AD, Morin PA, Kreb D, et al. (2011) Mitogenomic phylogenetic analyses of the Delphinidae with an emphasis on the Globicephalinae. BMC Biol Evol 11: 65.
29. Miller SA, Dykes DD, Polesky HF (1988) A Simple Salting out Procedure for Extracting DNA from Human Nucleated Cells. Nucleic Acids Res 16: 1215–1215.
30. Rosel PE, Dixon AE, Heyning JE (1994) Genetic analysis of sympatric morphotypes of common dolphins (genus: Delphinus). Mar Biol 119: 159–167.
31. Naugel E, Rooks M, Xuan Z, Bhattacharjee A, Benjamin Gordon D, et al. (2009) Hybrid selection of discrete genomic intervals on custom-designed microarrays for massively parallel sequencing. Nat Prot 4: 960–974.
32. Hancock-Hanson BL, Frey A, Leslie MS, Dutton PH, Archer FL, et al. (2013) Targeted multiplex next-generation sequencing: advances in techniques of mitochondrial and nuclear DNA sequencing for population genetics. Molecular Ecology Resources 13: 254–268.
33. Arnason U, Gullberg A, Widgren B (1991) The complete nucleotide sequence of the mitochondrial and nuclear DNA. Nature 470: 198–203.
34. Mazurek KA, Leventhal D, Auerbach D, Mebane J, Hahn J, et al. (2011) Mitogenomic phylogenetic analyses of the Delphinidae with an emphasis on the Globicephalinae. BMC Biol Evol 11: 65.
35. Miller SA, Dykes DD, Polesky HF (1988) A Simple Salting out Procedure for Extracting DNA from Human Nucleated Cells. Nucleic Acids Res 16: 1215–1215.
36. Rosel PE, Dixon AE, Heyning JE (1994) Genetic analysis of sympatric morphotypes of common dolphins (genus: Delphinus). Mar Biol 119: 159–167.
37. Naugel E, Rooks M, Xuan Z, Bhattacharjee A, Benjamin Gordon D, et al. (2009) Hybrid selection of discrete genomic intervals on custom-designed microarrays for massively parallel sequencing. Nat Prot 4: 960–974.
38. Hancock-Hanson BL, Frey A, Leslie MS, Dutton PH, Archer FL, et al. (2013) Targeted multiplex next-generation sequencing: advances in techniques of mitochondrial and nuclear DNA sequencing for population genetics. Molecular Ecology Resources 13: 254–268.
39. Arnason U, Gullberg A, Widgren B (1991) The complete nucleotide sequence of the mitochondrial and nuclear DNA. Nature 470: 198–203.
40. Mitogenomic Phylogens of Fin Whales
40. Katoh K, Misawa K, Kuma K, Miyata T (2002) MAFFT: a novel method for rapid multiple sequence alignment based on fast Fourier transform. Nucleic Acids Res 30: 3059–3066.
41. Jackson JA, Baker CS, Vant M, Steel DJ, Medrano-Gonzalez L, et al. (2009) Big and small phylogenetic estimates of molecular evolution in baleen whales (suborder mysticeti). Mol Biol Evol 26: 2427–2440.
42. McGowen MR, Spaulding M, Gatesy J (2009) Divergence date estimation and a comprehensive molecular tree of extant cetaceans. Mol Phylogenet Evol 53: 189–206.
43. Sasaki T, Nikaido M, Hamilton H, Goto M, Kato H, et al. (2005) Mitochondrial phylogenetics and evolution of mysticete whales. Syst Biol 54: 77–90.
44. Posada D (2008) jModelTest: Phylogenetic model averaging. Mol Biol Evol 25: 1253–1256.
45. Domburg A, Brandley MC, McGowen MR, Near TJ (2012) Relaxed Clocks and Inferences of Heterogeneus Patterns of Nucleotide Substitution and Divergence Time Estimates across Whales and Dolphins (Mammalia: Cetacea). Mol Biol Evol 29: 721–736.
46. Nabholtz B, Glemm S, Gaitier N (2008) Strong variations of mitochondrial rate across mammals - the longevity hypothesis. Mol Biol Evol 25: 120–130.
47. Rambaut A, Drummond AJ (2009) Tracer: MCMC Trace Analysis Tool. http://tree.bio.ed.ac.uk/software/tracer/.
48. Hatch LT (2004) Male genes and male song: Integrating genetic and acoustic data in defining fin whale, Balaenoptera physalus, management units. Cornell University. 277 p.
49. Gilpatrick JW, Perryman WL (2008) Geographic variation in external morphology of North Pacific and Southern Hemisphere blue whales (Balaenoptera musculus). J Cetacean Res Manage 10: 9–21.
50. Glover KA, Kanda N, Haug T, Pastene LA, Oien N, et al. (2010) Movement of Antarctic minke whales to the Arctic. PLoS One 5: e15197.
51. Stone GS, Florez-Gonzalez L, Katona S (1990) Whale Migration Record. University of California, Davis.
52. Balaena glacialis
53. Scarff JE (1986) Historic and present distribution of the right whale (Eubalaena glacialis) in the southern North Atlantic. Report of the International Whaling Commission Report 10: 43–63.
54. Ensor P, Minami K, Morse L, Olson P, Sekiguchi K (2007) Report of the 2007–2008 International Whaling Commission-Southern Ocean Whale and Ecosystem Research (IWC-SOWER) Cruise. International Whaling Commission Report of the 2007–2008 International Whaling Commission-Southern Ocean Whale and Ecosystem Research (IWC-SOWER) Cruise. International Whaling Commission. 51 p.
55. Rice DW (1998) Marine mammals of the world: systematics and distribution. Lawrence, KS: Society for Marine Mammalogy.
56. Gaines CA, Hare MP, Beck SE, Rosenbaum HC (2003) Nuclear markers confirm taxonomic status and relationships among highly endangered and closely related right whale species. Proceedings of the Royal Society - Biological Sciences 272: 533–542.
57. Mitchell ED (1991) Winter records of the minke whale (Balaenoptera acutorostrata acutorostrata) in the northeastern part of the Pacific Ocean, Bering and Chukchi Seas. In: Panin KI, editor. Soviet Research on Marine Mammals of the Far East. 103–106.
58. Berzin AA, Rovnin AA (1966) Distribution and migration of whales in the northeastern part of the Pacific Ocean, Bering and Chukchi Seas. In: Panin KI, editor. Soviet Research on Marine Mammals of the Far East. 103–106.
59. Nasu K (1974) Movement of baleen whales in relation to hydrographic conditions in the northern part of the North Pacific Ocean and the Bering Sea. In: Hood DW, Kelley EJ, editors. Oceanography of the Bering Sea. Fairbanks: Institute of Marine Science, University of Alaska. 345–361.
60. Rice DW (1974) Whales and whale research in the eastern North Pacific. In: Schevill WE, editor. The whale problem: a status report. Cambridge, MA: Harvard University Press. 170–195.
61. Palacios DM (1999) Blue whale (Balaenoptera musculus) occurrence off the Galapagos Islands, 1978–1995. J Cetacean Res Manage 1: 41–51.
62. Conway CA (2005) Global population structure of blue whales, Balaenoptera musculus ssp., based on nuclear genetic variation: University of California, Davis.
63. LeDuc B, Dizon AE, Goto M, Pastene LA, Kato H, et al. (2007) Patterns of genetic variation in Southern Hemisphere blue whales and the use of assignment test to detect mixing on the feeding grounds. J Cetacean Res Manage 9: 73–80.
64. Funk DJ, Onland KE (2005) Species-level paraphyly and polyphyly: Frequency, causes, and consequences, with insights from animal mitochondrial DNA. Annu Rev Ecol Evol Syst 34: 397–423.
65. Holder MT, Anderson JA, Holloway AK (2001) Difficulties in detecting introgression. Syst Biol 50: 978–982.
66. Crossman JE, Bird SM, Zellmer AJ, Carestem IC, Burnfield RT (2012) Applications of next-generation sequencing to phylogeography and phylogenetics. Mol Phylogenet Evol 66: 526–538.
67. Castellote M, Clark CW, Lammers MO (2011) Fin whale (Balaenoptera physalus) population identity in the western Mediterranean Sea. Mar Mamm Sci 28: 329–344.
68. Miczka SA, Rice DW, Breivik JM (1984) The Fin Whale, Balaenoptera physalus. Mar Fish Rev 48: 20–24.
69. Berzin AA, Roovin AA (1966) Distribution and migration of whales in the northeastern part of the Pacific Ocean, Bering and Chukchi Seas. In: Panin KI, editor. Soviet Research on Marine Mammals of the Far East. 103–106.
70. Nasu K (1974) Movement of baleen whales in relation to hydrographic conditions in the northern part of the North Pacific Ocean and the Bering Sea. In: Hood DW, Kelley EJ, editors. Oceanography of the Bering Sea. Fairbanks: Institute of Marine Science, University of Alaska. 345–361.
71. Rice DW (1974) Whales and whale research in the eastern North Pacific. In: Schevill WE, editor. The whale problem: a status report. Cambridge, MA: Harvard University Press. 170–195.
72. Tershy BR, Urban-Ramirez J, Breese D, Rojas-Bracho L, Findley LT (1993) Are fin whales resident to the Gulf of California? Revista de Investigacion Cientifica 1: 69–72.
73. Ensor P, Komiyama H, Beasley I, Fukutome K, Olson P, et al. (2007) Report of the 2006–2007 International Whaling Commission-Southern Ocean Whale and Ecosystem Research (IWC-SOWER) Cruise. International Whaling Commission Report of the 2006–2007 International Whaling Commission-Southern Ocean Whale and Ecosystem Research (IWC-SOWER) Cruise. International Whaling Commission. 78 p.
74. Ensor P, Minami K, Morse L, Olson P, Sekiguchi K (2008) Report of the 2007–2008 International Whaling Commission-Southern Ocean Whale and Ecosystem Research (IWC-SOWER) Cruise. International Whaling Commission. 51 p.
75. Branch TA, Butterworth DS (2003) Estimates of abundance south of 60°S for cetacean species sighted frequently in the 1978/79 to 1997/98 IWC-IDCRS-SOWER sighting surveys. J Cetacean Res Manage 3: 251–270.
76. United States. National Marine Fisheries Service. Office of Protected Resources. (2010) Final recovery plan for the fin whale, Balaenoptera physalus. Silver Spring, MD: Office of Protected Resources, National Marine Fisheries Service, National Oceanic and Atmospheric Administration.
77. David L, Alleaume S, Guetet C (2011) Evaluation of the potential of collision between fin whales and maritime traffic in the northwestern Mediterranean Sea in summer, and mitigation solutions. J Mar Anim Ecol 4: 17–26.
78. Panigada S, Pesante G, Zanardelli M, Capoulade F, Gannier A, et al. (2006) Mediterranean fin whales at risk from fatal ship strikes. Mar Pollut Bull 52: 1287–1290.
79. Perry ML, Demaster DP, Silber GK (1999) The fin whale. Mar Fish Rev 61: 44–51.
80. Moore JE, Barlow J (2011) Bayesian state-space model of fin whale abundance trends from a 1991–2008 time series of line-transect surveys in the California Current. J Appl Ecol 48: 1195–1205.