

# Killer Whale (*Orcinus orca*) Genetic Diversity

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## *Bibliography*

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## **Background & Scope**

This bibliography was prepared for a researcher with the National Marine Fisheries Service. The scope of this bibliography is limited to materials regarding specific genetic information in killer whales found worldwide since 1990.

These materials relate to genetic diversity in killer whales and include articles and reports featuring information about mitochondrial DNA, phylogenetic analysis, the D-loop sequence, and control region sequence.

## **Sources Reviewed**

The following sources were reviewed: BioOne Complete, Dimensions, Google Scholar, Lens.org, ProQuest Earth, Atmospheric, and Aquatic Science Collection, PubMed Central, Science.gov, ScienceDirect, Taylor & Francis Online, Web of Science, WorldWideScience.org, and the NOAA Institutional Repository.

## Bibliography

Árnason, Ú., Lammers, F., Kumar, V., Nilsson, M. A., & Janke, A. (2018). Whole-Genome Sequencing of the Blue Whale and Other Rorquals Finds Signatures for Introgressive Gene Flow. *Science Advances*, 4(4), eaap9873. <https://doi.org/10.1126/sciadv.aap9873>

Reconstructing the evolution of baleen whales (Mysticeti) has been problematic because morphological and genetic analyses have produced different scenarios. This might be caused by genomic admixture that may have taken place among some rorquals. We present the genomes of six whales, including the blue whale (*Balaenoptera musculus*), to reconstruct a species tree of baleen whales and to identify phylogenetic conflicts. Evolutionary multilocus analyses of 34,192 genome fragments reveal a fast radiation of rorquals at 10.5 to 7.5 million years ago coinciding with oceanic circulation shifts. The evolutionarily enigmatic gray whale (*Eschrichtius robustus*) is placed among rorquals, and the blue whale genome shows a high degree of heterozygosity. The nearly equal frequency of conflicting gene trees suggests that speciation of rorqual evolution occurred under gene flow, which is best depicted by evolutionary networks. Especially in marine environments, sympatric speciation might be common; our results raise questions about how genetic divergence can be established.

Baird, R. W., McSweeney, D. J., Bane, C., Barlow, J., Salden, D. R., Antoine, L. R. K., . . . Webster, D. L. (2006). Killer Whales in Hawaiian Waters: Information on Population Identity and Feeding Habits. *Pacific Science*, 60(4), 523-530. <https://doi.org/10.1353/psc.2006.0024>

Killer whales (*Orcinus orca*) have only infrequently been reported from Hawaiian waters, and most of what is known about killer whales worldwide comes from studies in coastal temperate waters. Here we present 21 records of killer whales from within the Hawaiian Exclusive Economic Zone between 1994 and 2004. Killer whales were recorded nine months of the year, most around the main Hawaiian Islands. Although there were more records than expected during the period when humpback whales are abundant around the Islands, there is likely an increase in sighting effort during that period. Killer whales were documented feeding on both a humpback whale and cephalopods, and two species of small cetaceans were observed fleeing from killer whales. Although it is possible that there are both marine mammal-eating and cephalopod-eating populations within Hawaiian waters, it seems more likely that Hawaiian killer whales may not exhibit foraging specializations as documented for coastal temperate populations. Saddle patch pigmentation patterns were generally fainter and narrower than those seen in killer whales from the temperate coastal North Pacific. Analysis of skin samples from two animals indicated two mitochondrial haplotypes, one identical to the "Gulf of Alaska transient 2" haplotype (a mammal-eating form), and the other a new haplotype one base different from haplotypes found for mammal-eating killer whales in coastal Alaskan waters.

Baker, C. S., Lento, G. M., Cipriano, F., & Palumbi, S. R. (2000). Predicted Decline of Protected Whales Based on Molecular Genetic Monitoring of Japanese and Korean Markets. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, 267(1449), 1191-1199. <https://doi.org/10.1098/rspb.2000.1128>

We present a two-tiered analysis of molecular genetic variation in order to determine the origins of 'whale' products purchased from retail markets in Japan and the Republic of (South) Korea during 1993-1999. This approach combined phylogenetic analysis of mitochondrial DNA sequences for identification

of protected species with a statistical comparison of intraspecific haplotype frequencies for distinguishing regional subpopulations or 'stocks' hunted for scientific research by the Japanese and killed incidentally in coastal fisheries by the Koreans. The phylogenetic identification of 655 products included eight species or subspecies of baleen whales, sperm whales, a pygmy sperm whale, two species of beaked whales, porpoises, killer whales and numerous species of dolphins as well as domestic sheep and horses. Six of the baleen whale species (the fin, sei, common-form and small-form Bryde's, blue or blue/fin hybrid, and humpback) and the sperm whale are protected by international agreements dating back to at least 1989 for all species and 1966 for some species. We compared the haplotype frequencies from the Japanese market sample to those reported from scientific hunting in the western North Pacific stock for products derived from the exploited North Pacific minke whale. The market sample differed significantly from the scientific catch ( $p < 0.001$ ), showing a greater than expected frequency of haplotypes characteristic of the protected Sea of Japan stock. We used a 'mixed-stock' analysis and maximum-likelihood methods to estimate that 31% (95% confidence interval 19-43%) of the market for this species originated from the Sea of Japan stock. The source of these products was assumed to be undocumented 'incidental takes' from fisheries' by-catch, although we cannot exclude the possibility of illegal hunting or smuggling. The demographic impact of this undocumented exploitation was evaluated using the model of population dynamics adopted by the Scientific Committee of the International Whaling Commission. For the range of exploitation consistent with the market sample, this protected stock was predicted to decline towards extinction over the next few decades. These results confirmed the power of molecular methods in monitoring retail markets and pointed to the inadequacy of the current moratorium for ensuring the recovery of protected species. More importantly, the integration of genetic evidence with a model of population dynamics identified an urgent need for actions to limit undocumented exploitation of a 'protected' stock of whales.

Barrett-Lennard, L. G. (2000). *Population Structure and Mating Patterns of Killer Whales (*Orcinus orca*) as Revealed by DNA Analysis*. (Doctor of Philosophy), University of British Columbia, Canada.  
<https://doi.org/10.14288/1.0099652>

This thesis reports a genetic investigation of population segregation, social organization, and mating patterns in killer whales (*Orcinus orca*) of the northeastern Pacific Ocean. Previous studies identified two sympatric, non-associating populations, fish-eating residents and mammal-eating transients, and described many aspects of their demography, ecology, and social behaviour. Less is known about a third offshore population. Here, I focused on two aspects of killer whale social organization that are unusual among wellstudied mammals: maintenance of complete segregation between residents and transients in sympatry, and lack of dispersal in individual residents of either sex. I began by developing and testing lightweight pressure-propelled biopsy darts. They were an efficient way of acquiring skin samples from free-ranging whales and caused only minor behavioural responses in sampled animals. Using these darts and sampling stranded carcasses, colleagues and I collected biopsies from 269 individually-identified killer whales in British Columbia and Alaska. I used DNA from the biopsies to sequence the mitochondrial D-loop of 111 matriline, and genotyped all individuals at 11 polymorphic microsatellite loci. I found that residents and transients are strongly differentiated genetically and that there is little or no gene flow between them. Both are divided into three genetically differentiated regional subpopulations. Each resident subpopulation is more closely related to other resident subpopulations than to any transient subpopulation and vice versa, implying that the differences between residents and transients stem from a single divergence. The offshore population is not closely related to either of the other populations. The propensity of killer whales to live in fixed groups of a few hundred individuals apparently allows sympatric or parapatric populations to diverge genetically and could eventually result in speciation. I

examined mating patterns in residents by conducting paternity tests and analysing fixation indices based on microsatellite genotypes. I found that residents rarely mate within their pods. Further, in the most thoroughly-sampled resident subpopulation, most matings were between rather than within acoustic clans (groups of pods with similar acoustic repertoires). Because pods within clans proved to be closely related, inter-clan mating appears to be an inbreeding avoidance mechanism. Most matings were between individuals from the same subpopulation. This pattern of population segregation coupled with inbreeding avoidance closely resembles marriage patterns in many human societies.

Barrett-Lennard, L. G., & Ellis, G. M. (2007). *Population Structure and Genetic Variability in Northeastern Pacific Killer Whales: Towards an Assessment of Population Viability*. (Research Document 2001/065). Nanaimo, B.C. Retrieved from [https://www.dfo-mpo.gc.ca/csas-sccs/publications/resdocs-docrech/2001/2001\\_065-eng.htm](https://www.dfo-mpo.gc.ca/csas-sccs/publications/resdocs-docrech/2001/2001_065-eng.htm)

Long term studies of killer whales (*Orcinus orca*) in the coastal waters of British Columbia have identified two sympatric non-associating populations: fish-eating residents and mammal-eating transients. A third group, the offshores, frequents the outer continental shelf. The resident population contains two regional subpopulations in British Columbia and is currently listed as threatened by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC). In Alaska one additional putative subpopulation of residents and two of transients have been reported. This complex of populations and subpopulations persisting in the absence of obvious dispersal barriers presents a problem to conservation managers who must decide whether subpopulations should be assessed separately or in combination. Clearly, the decisions should rest on an understanding of the discreteness of the subpopulations. Here, we report a molecular study designed to contribute to such an understanding. This study a) characterized each known subpopulation of killer whales genetically, b) compared genetic variability between the subpopulations and c) analysed mating patterns within the resident subpopulations to determine inbreeding levels.

Lightweight pneumatic darts were used to take biopsy samples from 269 individually-identified killer whales off British Columbia and Alaska. Nuclear DNA from the samples was typed at 11 polymorphic microsatellite loci, and the entire mitochondrial D-loop was sequenced. The results were used to construct population phylogenies, assess genetic diversity, calculate fixation indices (F-statistics), and conduct paternity analyses. The following findings were key: 1) resident and transient killer whales are reproductively isolated, 2) the division of each into three regional subpopulations is supported genetically, 3) offshores are genetically differentiated from all known resident and transient subpopulations, 4) residents have lower levels of genetic variation than transients, 5) the observation from field studies that residents remain in their natal groups for life is typical of the recent history of the population, 6) despite their lack of permanent dispersal, residents mate outside their natal groups.

One transient subpopulation (the critically endangered AT1 population of the northern Gulf of Alaska) appears to be genetically isolated from all other subpopulations. Permanent dispersal between the remaining two transient subpopulations is very rare or non-existent, but gene flow mediated by occasional intermatings could not be ruled out. In the resident population, occasional intermatings may occur between the northern resident subpopulation (which inhabits central and northern British Columbian waters) and the Alaska resident subpopulation (found off the panhandle region of southern Alaska and the Gulf of Alaska coast). Our findings are consistent with the complete genetic isolation of the southern resident subpopulation of southern British Columbia and northern Washington. The

southern resident subpopulation is of conservation concern because of its small size (less than 85 individuals), a recent decline, and high contaminant loads.

Paternity analysis showed that resident killer whales have strong (presumably behavioural) inbreeding avoidance mechanisms. In all but one instance, pod members were excluded as possible fathers of calves in the same pod. In the northern resident community, the majority of matings were between individuals from pods belonging to different "acoustic clans". No paternity matches were made between southern residents and members of the other two resident subpopulations, however, there were several possible matches between the latter two populations.

We recommend that three resident subpopulations, three transient subpopulations, and the offshore population should be recognized as separate stocks or management units for conservation purposes in British Columbia and Alaska.

Bolaños-Jiménez, J., Mignucci-Giannoni, A. A., Blumenthal, J., Bogomolni, A., Casas, J. J., Henríquez, A., . . . Luksenburg, J. A. (2014). Distribution, Feeding Habits and Morphology of Killer Whales *Orcinus orca* in the Caribbean Sea. *Mammal Review*, 44(3-4), 177-189.  
<https://doi.org/10.1111/mam.12021>

1. Killer whales *Orcinus orca* are found in all oceans of the world, but most of our knowledge on the species comes from studies conducted at higher latitudes. Studies on killer whales in the Caribbean have been scarce. 2. We compiled 176 records of killer whales from the Caribbean, including 95 previously unreported records and 81 records recovered from the literature, consisting of 27 capture or kill records, 4 stranding records and 145 sighting records. 3. Our results indicate that killer whales are widespread in the Caribbean Sea and can be found year-round in the region. Mean group size was 3.7 animals. A diversity of prey items was recorded, including sea turtles and marine mammals and possibly fish. We cannot exclude ecotype or morphotype-specific dietary specialization in the Caribbean population. A preliminary morphological analysis of 10 characters in 52 individuals from 21 different groups suggests that Caribbean killer whales do not represent any of the four Antarctic and subantarctic types, type 1 from the northwest Atlantic, or 'resident' and 'transient' killer whales from the northwest Pacific. Some Caribbean killer whales share a combination of characters typical of type 2 in the North Atlantic, whereas others share those typical of 'offshore' killer whales in the northwest Pacific. The significance of this is unclear. Comparison of Caribbean killer whales to previously described morphotypes and ecotypes is hampered by the lack of detailed, quantitative data on variation within other types, as well as by the lack of comparisons of genetic diversity. 4. Our study adds to the growing knowledge of the diversity of killer whales worldwide but underscores that additional research is warranted in the tropics.

Caballero, S., Jackson, J., Mignucci-Giannoni, A. A., Barrios-Garrido, H., Beltran-Pedrerros, S., Montiel-Villalobos, M. A., . . . Baker, C. S. (2008). Molecular Systematics of South American Dolphins *Sotalia*: Sister Taxa Determination and Phylogenetic Relationships, with Insights into a Multi-Locus Phylogeny of the Delphinidae. *Molecular Phylogenetics and Evolution*, 46(1), 252-268.  
<https://doi.org/10.1016/j.ympev.2007.10.015>

The evolutionary relationships among members of the cetacean family Delphinidae, the dolphins, pilot whales and killer whales, are still not well understood. The genus *Sotalia* (coastal and riverine South

American dolphins) is currently considered a member of the Stenoninae subfamily, along with the genera *Steno* (rough toothed dolphin) and *Sousa* (humpbacked dolphin). In recent years, a revision of this classification was proposed based on phylogenetic analysis of the mitochondrial gene cytochrome b, wherein *Sousa* was included in the Delphininae subfamily, keeping only *Steno* and *Sotalia* as members of the Stenoninae subfamily. Here we investigate the phylogenetic placement of *Sotalia* using two mitochondrial genes, six autosomal introns and four Y chromosome introns, providing a total of 5,196 base pairs (bp) for each taxon in the combined dataset. Sequences from these genomic regions were obtained for 17 delphinid species, including at least one species from each of five or six currently recognized subfamilies plus five odontocete outgroup species. Maximum Parsimony, Maximum Likelihood and Bayesian phylogenetic analysis of independent (each fragment) and combined datasets (mtDNA, nuDNA or mtDNA+nuDNA) showed that *Sotalia* and *Sousa* fall within a clade containing other members of Delphininae, exclusive of *Steno*. *Sousa* was resolved as the sister taxon to *Sotalia* according to analysis of the nuDNA dataset but not analysis of the mtDNA or combined mtDNA+nuDNA datasets. Based on the results from our multi-locus analysis, we offer several novel changes to the classification of Delphinidae, some of which are supported by previous morphological and molecular studies.

Duchêne, S., Archer, F. I., Vilstrup, J. T., Caballero, S., & Morin, P. A. (2011). Mitogenome Phylogenetics: The Impact of Using Single Regions and Partitioning Schemes on Topology, Substitution Rate and Divergence Time Estimation. *Plos One*, 6(11), e27138.  
<https://doi.org/10.1371/journal.pone.0027138>

The availability of mitochondrial genome sequences is growing as a result of recent technological advances in molecular biology. In phylogenetic analyses, the complete mitogenome is increasingly becoming the marker of choice, usually providing better phylogenetic resolution and precision relative to traditional markers such as cytochrome b (CYTB) and the control region (CR). In some cases, the differences in phylogenetic estimates between mitogenomic and single-gene markers have yielded incongruent conclusions. By comparing phylogenetic estimates made from different genes, we identified the most informative mitochondrial regions and evaluated the minimum amount of data necessary to reproduce the same results as the mitogenome. We compared results among individual genes and the mitogenome for recently published complete mitogenome datasets of selected delphinids (Delphinidae) and killer whales (genus *Orcinus*). Using Bayesian phylogenetic methods, we investigated differences in estimation of topologies, divergence dates, and clock-like behavior among genes for both datasets. Although the most informative regions were not the same for each taxonomic group (COX1, CYTB, ND3 and ATP6 for *Orcinus*, and ND1, COX1 and ND4 for Delphinidae), in both cases they were equivalent to less than a quarter of the complete mitogenome. This suggests that gene information content can vary among groups, but can be adequately represented by a portion of the complete sequence. Although our results indicate that complete mitogenomes provide the highest phylogenetic resolution and most precise date estimates, a minimum amount of data can be selected using our approach when the complete sequence is unavailable. Studies based on single genes can benefit from the addition of a few more mitochondrial markers, producing topologies and date estimates similar to those obtained using the entire mitogenome.

Ellendersen, A. C. J. (2020). *Phylogenetic Analysis of Killer Whale (Orcinus orca) and Humpback Whale (Megaptera Novaeangliae) Populations Along the Northern Norwegian Fjords and Adjacent Waters*. (Master Thesis), UiT The Arctic University of Norway, Retrieved from  
<https://hdl.handle.net/10037/19258>



Killer whales (*Orcinus orca*) and humpback whales (*Megaptera novaeangliae*) are two widely distributed cetacean species and both seasonally congregate in the waters off the fjords in Northern Norway to feast on the Norwegian Spring Spawning herring (*Clupea harengus*). With phylogenetic analysis of complete mitochondrial genomes, obtained by shotgun sequencing, from individuals sampled through four years, this study has attempted to shed light on the geographical origin and phylogenetic position of Norwegian killer whales and humpback whales in the global context of each species. In total, 19 haplotypes were identified among 134 killer whales, and 18 haplotypes were identified among 94 humpback whales. The killer whales sampled in Northern Norway showed structuring between individuals and cluster in a clade with other individuals from Eastern North Atlantic Ocean previously described in literature. The humpback whales showed less clear clustering within the global context but have revealed a potential connection of four individuals with haplotypes from the Southern Hemisphere. Overall, this study suggests that the feeding aggregations in Northern Norway gather killer whales mainly from Eastern North Atlantic Ocean, and humpback whales from the North Atlantic and possibly from the South Atlantic Ocean.

Esteban, R., Verborgh, P., Gauffier, P., Gimenez, J., Martin, V., Perez-Gil, M., . . . de Stephanis, R. (2016). Using a Multi-Disciplinary Approach to Identify a Critically Endangered Killer Whale Management Unit. *Ecological Indicators*, 66, 291-300.  
<https://doi.org/10.1016/j.ecolind.2016.01.043>

A key goal for wildlife managers is identifying discrete, demographically independent conservation units. Previous genetic work assigned killer whales that occur seasonally in the Strait of Gibraltar (SoG) and killer whales sampled off the Canary Islands (CI) to the same population: Here we present new analyses of photo-identification and individual genotypes to assess the level of contemporary gene flow and migration between study areas, and analyses of biomarkers to assess ecological differences. We identified 47 different individuals from 5 pods in the SoG and 16 individuals in the CI, with no matches found between the areas. Mitochondrial DNA control region haplotype was shared by all individuals sampled within each pod, suggesting that pods have a matrifocal social structure typical of this species, whilst the lack of shared mitogenome haplotypes between the CI and SoG individuals suggests that there was little or no female migration between groups. Kinship analysis detected no close kin between CI and SoG individuals, and low to zero contemporary gene flow. Isotopic values and organochlorine pollutant loads also suggest ecological differences between study areas. We further found that one individual from a pod within the SoG not seen in association with the other four pods and identified as belonging to a potential migrant lineage by genetic analyses, had intermediate isotopic values and contaminant between the two study areas. Overall our results suggest a complex pattern of social and genetic structuring correlated with ecological variation. Consequently at least CI and SoG should be considered as two different management units. Understanding this complexity appears to be an important consideration when monitoring and understanding the viability of these management units. Understand the viability will help the conservation of these threatened management units.

Filatova, O. A., Borisova, E. A., Meschersky, I. G., Logacheva, M. D., Kuzkina, N. V., Shpak, O. V., . . . Hoyt, E. (2018). Colonizing the Wild West: Low Diversity of Complete Mitochondrial Genomes in Western North Pacific Killer Whales Suggests a Founder Effect. *Journal of Heredity*, 109(7), 735-743. <https://doi.org/10.1093/jhered/esy037>

In the North Pacific, fish-eating R-type "resident" and mammal-eating T-type "transient" killer whales do not interbreed and differ in ecology and behavior. Full-length mitochondrial genomes (about 16.4 kbp) were sequenced and assembled for 12 R-type and 14 T-type killer whale samples from different areas of the western North Pacific. All R-type individuals had the same haplotype, previously described for R-type killer whales from both eastern and western North Pacific. However, haplotype diversity of R-type killer whales was much lower in the western North Pacific than in the Aleutian Islands and the eastern North Pacific. T-type whales had 3 different haplotypes, including one previously undescribed. Haplotype diversity of T-type killer whales in the Okhotsk Sea was also much lower than in the Aleutian Islands and the eastern North Pacific. The highest haplotype diversity for both R- and T-type killer whales was observed in the Aleutian Islands. We discuss how the environmental conditions during the last glacial period might have shaped the history of killer whale populations in the North Pacific. Our results suggest the recent colonization or re-colonization of the western North Pacific by small groups of killer whales originating from the central or eastern North Pacific, possibly due to favorable environmental changes after the Last Glacial Maximum.

Foote, A. D., Hooper, R., Alexander, A., Baird, R. W., Baker, C. S., Ballance, L., . . . Morin, P. A. (2021). Runs of Homozygosity in Killer Whale Genomes Provide a Global Record of Demographic Histories. *Molecular Ecology*, 1-16. <https://doi.org/10.1111/mec.16137>

Abstract Runs of homozygosity (ROH) occur when offspring inherit haplotypes that are identical by descent from each parent. Length distributions of ROH are informative about population history; specifically, the probability of inbreeding mediated by mating system and/or population demography. Here, we investigated whether variation in killer whale (*Orcinus orca*) demographic history is reflected in genome-wide heterozygosity and ROH length distributions, using a global data set of 26 genomes representative of geographic and ecotypic variation in this species, and two F1 admixed individuals with Pacific-Atlantic parentage. We first reconstructed demographic history for each population as changes in effective population size through time using the pairwise sequential Markovian coalescent (PSMC) method. We found a subset of populations declined in effective population size during the Late Pleistocene, while others had more stable demography. Genomes inferred to have undergone ancestral declines in effective population size, were autozygous at hundreds of short ROH (<1 Mb), reflecting high background relatedness due to coalescence of haplotypes deep within the pedigree. In contrast, longer and therefore younger ROH (>1.5 Mb) were found in low latitude populations, and populations of known conservation concern. These include a Scottish killer whale, for which 37.8% of the autosomes were comprised of ROH >1.5 Mb in length. The fate of this population, in which only two adult males have been sighted in the past five years, and zero fecundity over the last two decades, may be inextricably linked to its demographic history and consequential inbreeding depression.

Foote, A. D., Martin, M. D., Louis, M., Pacheco, G., Robertson, K. M., Sinding, M. S., . . . Morin, P. A. (2019). Killer Whale Genomes Reveal a Complex History of Recurrent Admixture and Vicariance. *Molecular Ecology*, 28(14), 3427-3444. <https://doi.org/10.1111/mec.15099>

Reconstruction of the demographic and evolutionary history of populations assuming a consensus tree-like relationship can mask more complex scenarios, which are prevalent in nature. An emerging genomic toolset, which has been most comprehensively harnessed in the reconstruction of human evolutionary history, enables molecular ecologists to elucidate complex population histories. Killer whales have limited extrinsic barriers to dispersal and have radiated globally, and are therefore a good candidate

model for the application of such tools. Here, we analyse a global data set of killer whale genomes in a rare attempt to elucidate global population structure in a nonhuman species. We identify a pattern of genetic homogenisation at lower latitudes and the greatest differentiation at high latitudes, even between currently sympatric lineages. The processes underlying the major axis of structure include high drift at the edge of species' range, likely associated with founder effects and allelic surfing during postglacial range expansion. Divergence between Antarctic and non-Antarctic lineages is further driven by ancestry segments with up to four-fold older coalescence time than the genome-wide average; relicts of a previous vicariance during an earlier glacial cycle. Our study further underpins that episodic gene flow is ubiquitous in natural populations, and can occur across great distances and after substantial periods of isolation between populations. Thus, understanding the evolutionary history of a species requires comprehensive geographic sampling and genome-wide data to sample the variation in ancestry within individuals.

Foote, A. D., & Morin, P. A. (2016). Genome-Wide Snp Data Suggest Complex Ancestry of Sympatric North Pacific Killer Whale Ecotypes. *Heredity*, 117(5), 316-325.  
<https://doi.org/10.1038/hdy.2016.54>

Three ecotypes of killer whale occur in partial sympatry in the North Pacific. Individuals assortatively mate within the same ecotype, resulting in correlated ecological and genetic differentiation. A key question is whether this pattern of evolutionary divergence is an example of incipient sympatric speciation from a single panmictic ancestral population, or whether sympatry could have resulted from multiple colonisations of the North Pacific and secondary contact between ecotypes. Here, we infer multilocus coalescent trees from >1000 nuclear single-nucleotide polymorphisms (SNPs) and find evidence of incomplete lineage sorting so that the genealogies of SNPs do not all conform to a single topology. To disentangle whether uncertainty in the phylogenetic inference of the relationships among ecotypes could also result from ancestral admixture events we reconstructed the relationship among the ecotypes as an admixture graph and estimated f<sub>4</sub>-statistics using TreeMix. The results were consistent with episodes of admixture between two of the North Pacific ecotypes and the two outgroups (populations from the Southern Ocean and the North Atlantic). Gene flow may have occurred via unsampled 'ghost' populations rather than directly between the populations sampled here. Our results indicate that because of ancestral admixture events and incomplete lineage sorting, a single bifurcating tree does not fully describe the relationship among these populations. The data are therefore most consistent with the genomic variation among North Pacific killer whale ecotypes resulting from multiple colonisation events, and secondary contact may have facilitated evolutionary divergence. Thus, the present-day populations of North Pacific killer whale ecotypes have a complex ancestry, confounding the tree-based inference of ancestral geography.

Foote, A. D., Morin, P. A., Durban, J. W., Pitman, R. L., Wade, P., Willerslev, E., . . . da Fonseca, R. R. (2011). Positive Selection on the Killer Whale Mitogenome. *Biology letters*, 7(1), 116-118.  
<https://doi.org/10.1098/rsbl.2010.0638>

Mitochondria produce up to 95 per cent of the eukaryotic cell's energy. The coding genes of the mitochondrial DNA may therefore evolve under selection owing to metabolic requirements. The killer whale, *Orcinus orca*, is polymorphic, has a global distribution and occupies a range of ecological niches. It is therefore a suitable organism for testing this hypothesis. We compared a global dataset of the complete mitochondrial genomes of 139 individuals for amino acid changes that were associated with

radical physico-chemical property changes and were influenced by positive selection. Two such selected non-synonymous amino acid changes were found; one in each of two ecotypes that inhabit the Antarctic pack ice. Both substitutions were associated with changes in local polarity, increased steric constraints and alpha-helical tendencies that could influence overall metabolic performance, suggesting a functional change.

Foote, A. D., Morin, P. A., Durban, J. W., Willerslev, E., Orlando, L., & Gilbert, M. T. P. (2011). Out of the Pacific and Back Again: Insights into the Matrilineal History of Pacific Killer Whale Ecotypes. *Plos One*, 6(9). <https://doi.org/10.1371/journal.pone.0024980>

Killer whales (*Orcinus orca*) are the most widely distributed marine mammals and have radiated to occupy a range of ecological niches. Disparate sympatric types are found in the North Atlantic, Antarctic and North Pacific oceans, however, little is known about the underlying mechanisms driving divergence. Previous phylogeographic analysis using complete mitogenomes yielded a bifurcating tree of clades corresponding to described ecotypes. However, there was low support at two nodes at which two Pacific and two Atlantic clades diverged. Here we apply further phylogenetic and coalescent analyses to partitioned mitochondrial genome sequences to better resolve the pattern of past radiations in this species. Our phylogenetic reconstructions indicate that in the North Pacific, sympatry between the maternal lineages that make up each ecotype arises from secondary contact. Both the phylogenetic reconstructions and a clinal decrease in diversity suggest a North Pacific to North Atlantic founding event, and the later return of killer whales to the North Pacific. Therefore, ecological divergence could have occurred during the allopatric phase through drift or selection and/or may have either commenced or have been consolidated upon secondary contact due to resource competition. The estimated timing of bidirectional migration between the North Pacific and North Atlantic coincided with the previous inter-glacial when the leakage of fauna from the Indo-Pacific into the Atlantic via the Agulhas current was particularly vigorous.

Foote, A. D., Morin, P. A., Pitman, R. L., Ávila-Arcos, M. C., Durban, J. W., van Helden, A., . . . Gilbert, M. T. P. (2013). Mitogenomic Insights into a Recently Described and Rarely Observed Killer Whale Morphotype. *Polar Biology*, 36(10), 1519-1523. <https://doi.org/10.1007/s00300-013-1354-0>

Identifying evolutionary divergent taxonomic units, e.g. species and subspecies, is important for conservation and evolutionary biology. The 'type D' killer whale, *Orcinus orca*, is a rarely observed morphotype with a pelagic, circumpolar subantarctic distribution, making dedicated research and therefore taxonomic study extremely difficult to date. In this study, we used DNA target enrichment hybridisation capture coupled to high throughput sequencing, to obtain the first DNA sequence from the only known museum specimen of this recently described morphotype. The high coverage, complete mitogenome sequence was compared to a previously published global dataset of 139 individuals, indicating that this type is highly divergent to all previously genetically sequenced killer whale forms. The estimated divergence time (390,000 years ago) from its most recent common ancestor with other extant killer whale lineages was the second oldest split within the killer whale phylogeny. This study provides the first genetic support of type D potentially being a distinct subspecies or species of killer whale, although further samples are needed to identify whether there is monophyly of mitogenome sequences and whether nuclear DNA also indicates reproductive isolation. These findings also highlight the value of natural history museum collections and new technologies to investigate the taxonomy of rare, cryptic or difficult to access species.

Foote, A. D., Newton, J., Avila-Arcos, M. C., Kampmann, M. L., Samaniego, J. A., Post, K., . . . Gilbert, M. T. (2013). Tracking Niche Variation over Millennial Timescales in Sympatric Killer Whale Lineages. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, 280(1768), 20131481. <https://doi.org/10.1098/rspb.2013.1481>

Niche variation owing to individual differences in ecology has been hypothesized to be an early stage of sympatric speciation. Yet to date, no study has tracked niche width over more than a few generations. In this study, we show the presence of isotopic niche variation over millennial timescales and investigate the evolutionary outcomes. Isotopic ratios were measured from tissue samples of sympatric killer whale *Orcinus orca* lineages from the North Sea, spanning over 10 000 years. Isotopic ratios spanned a range similar to the difference in isotopic values of two known prey items, herring *Clupea harengus* and harbour seal *Phoca vitulina*. Two proxies of the stage of speciation, lineage sorting of mitogenomes and genotypic clustering, were both weak to intermediate indicating that speciation has made little progress. Thus, our study confirms that even with the necessary ecological conditions, i.e. among-individual variation in ecology, it is difficult for sympatric speciation to progress in the face of gene flow. In contrast to some theoretical models, our empirical results suggest that sympatric speciation driven by among-individual differences in ecological niche is a slow process and may not reach completion. We argue that sympatric speciation is constrained in this system owing to the plastic nature of the behavioural traits under selection when hunting either mammals or fish.

Foote, A. D., Newton, J., Piertney, S. B., Willerslev, E., & Gilbert, M. T. (2009). Ecological, Morphological and Genetic Divergence of Sympatric North Atlantic Killer Whale Populations. *Molecular Ecology*, 18(24), 5207-5217. <https://doi.org/10.1111/j.1365-294x.2009.04407.x>

Ecological divergence has a central role in speciation and is therefore an important source of biodiversity. Studying the micro-evolutionary processes of ecological diversification at its early stages provides an opportunity for investigating the causative mechanisms and ecological conditions promoting divergence. Here we use morphological traits, nitrogen stable isotope ratios and tooth wear to characterize two disparate types of North Atlantic killer whale. We find a highly specialist type, which reaches up to 8.5 m in length and a generalist type which reaches up to 6.6 m in length. There is a single fixed genetic difference in the mtDNA control region between these types, indicating integrity of groupings and a shallow divergence. Phylogenetic analysis indicates this divergence is independent of similar ecological divergences in the Pacific and Antarctic. Niche-width in the generalist type is more strongly influenced by between-individual variation rather than within-individual variation in the composition of the diet. This first step to divergent specialization on different ecological resources provides a rare example of the ecological conditions at the early stages of adaptive radiation.

Foote, A. D., Vijay, N., Ávila-Arcos, M. C., Baird, R. W., Durban, J. W., Fumagalli, M., . . . Wolf, J. B. W. (2016). Genome-Culture Coevolution Promotes Rapid Divergence of Killer Whale Ecotypes. *Nature Communications*, 7. <https://doi.org/10.1038/ncomms11693>

Analysing population genomic data from killer whale ecotypes, which we estimate have globally radiated within less than 250,000 years, we show that genetic structuring including the segregation of potentially functional alleles is associated with socially inherited ecological niche. Reconstruction of

ancestral demographic history revealed bottlenecks during founder events, likely promoting ecological divergence and genetic drift resulting in a wide range of genome-wide differentiation between pairs of allopatric and sympatric ecotypes. Functional enrichment analyses provided evidence for regional genomic divergence associated with habitat, dietary preferences and post-zygotic reproductive isolation. Our findings are consistent with expansion of small founder groups into novel niches by an initial plastic behavioural response, perpetuated by social learning imposing an altered natural selection regime. The study constitutes an important step towards an understanding of the complex interaction between demographic history, culture, ecological adaptation and evolution at the genomic level.

Foote, A. D., Vilstrup, J. T., De Stephanis, R., Verborgh, P., Abel Nielsen, S. C., Deaville, R., . . . Piertney, S. B. (2011). Genetic Differentiation among North Atlantic Killer Whale Populations. *Molecular Ecology*, 20(3), 629-641. <https://doi.org/10.1111/j.1365-294X.2010.04957.x>

Population genetic structure of North Atlantic killer whale samples was resolved from differences in allele frequencies of 17 microsatellite loci, mtDNA control region haplotype frequencies and for a subset of samples, using complete mitogenome sequences. Three significantly differentiated populations were identified. Differentiation based on microsatellite allele frequencies was greater between the two allopatric populations than between the two pairs of partially sympatric populations. Spatial clustering of individuals within each of these populations overlaps with the distribution of particular prey resources: herring, mackerel and tuna, which each population has been seen predated. Phylogenetic analyses using complete mitogenomes suggested two populations could have resulted from single founding events and subsequent matrilineal expansion. The third population, which was sampled at lower latitudes and lower density, consisted of maternal lineages from three highly divergent clades. Pairwise population differentiation was greater for estimates based on mtDNA control region haplotype frequencies than for estimates based on microsatellite allele frequencies, and there were no mitogenome haplotypes shared among populations. This suggests low or no female migration and that gene flow was primarily male mediated when populations spatially and temporally overlap. These results demonstrate that genetic differentiation can arise through resource specialization in the absence of physical barriers to gene flow.

Ford, M. J., Parsons, K. M., Ward, E. J., Hempelmann, J. A., Emmons, C. K., Hanson, M. B., . . . Park, L. K. (2018). Inbreeding in an Endangered Killer Whale Population. *Animal Conservation*, 21(5), 423-432. <https://doi.org/10.1111/acv.12413>

There are genetic risks associated with small population sizes, including loss of genetic diversity and inbreeding depression. The southern resident killer whale *Orcinus orca* population is a group of similar to 80 whales listed as 'endangered' under the U.S. Endangered Species Act. Recovery efforts are focused on increasing prey and reducing impacts from environmental disturbance, but the population's small size and insularity suggest that inbreeding depression could also be important. We analyzed genotypes at 68-94 nuclear loci from 105 individuals to refine a population pedigree to evaluate inbreeding and the relationship between multi-locus heterozygosity and fitness. Our results expand upon an earlier study and shed new light on both inbreeding within this population and the mating patterns of killer whales. We found that only two adult males sired 52% of the sampled progeny born since 1990. Confirming earlier results, we found male reproductive success increased with age. Based on the pedigree, four sampled offspring were the result of inbred mating - two between a parent and offspring, one between paternal half-siblings, and one between uncle and half-niece. There is no evidence to date that the

survival or fecundity of these individuals is lower than normal. There was some evidence for inbreeding depression in the form of a weakly supported relationship between multi-locus heterozygosity and annual survival probability, but the power of our data to quantify this effect was low. We found no evidence of inbreeding avoidance in the population, but a late age of breeding success for males may indirectly limit the frequency of parent/offspring mating. The effective number of breeders in the population is currently similar to 26, and was estimated to have ranged from 12-53 over the past 40 years. The population that produced the oldest (pre-1970) sampled individuals was estimated to have 24 effective breeders. Overall, our results indicate that inbreeding is likely common in the population, but the fitness effects continue to be uncertain.

Herman, D. P., Burrows, D. G., Wade, P. R., Durban, J. W., Matkin, C. O., LeDuc, R. G., . . . Krahn, M. M. (2005). Feeding Ecology of Eastern North Pacific Killer Whales *Orcinus orca* from Fatty Acid, Stable Isotope, and Organochlorine Analyses of Blubber Biopsies. *Marine Ecology Progress Series*, 302, 275-291. <https://doi.org/10.3354/meps302275>

Blubber biopsy samples from eastern North Pacific killer whales *Orcinus orca* were analyzed for fatty acids, carbon and nitrogen stable isotopes and organochlorine contaminants. Fatty acid profiles were sufficiently distinct among the 3 reported ecotypes ('resident,' 'transient' or 'offshore') to enable individual animals to be correctly classified by ecotype and also by mitochondrial DNA (mtDNA) haplotype. Profiles of PCBs also enabled unambiguous classification of all 3 killer whale ecotypes, but stable isotope values lacked sufficient resolution. Fatty acid, stable isotope and PCB profiles of the resident and transient ecotypes were consistent with those expected for these whales based on their reported dietary preferences (fish for resident whales, marine mammals for transients). In addition, these ecotype profiles exhibited broad similarity across geographical regions, suggesting that the dietary specialization reported for resident and transient whales in the well-studied eastern North Pacific populations also extends to the less-studied killer whales in the western Gulf of Alaska and Aleutian Islands. Killer whales of the same ecotype were also grouped by region of sample collection. The mean stable isotope ratios of various regional groups differed considerably, suggesting that the prey preferences of these North Pacific killer whales may be both region and ecotype specific. Furthermore, 3 specific ecotypes of killer whales were found to have measured stable isotope values that were consistent with dietary preferences reported in the literature. Finally, although the offshore population had blubber fatty acid profiles implicating fish as its primary prey, contaminant and stable isotope results were equally congruent with predation on marine mammals.

Hoelzel, A. R. (1991). *Analysis of Regional Mitochondrial DNA Variation in the Killer Whale; Implications for Cetacean Conservation*. International Whaling Commission. Special issue, 18. Retrieved from <https://archive.iwc.int>

Three putative killer whale populations inhabiting the straits east of Vancouver Island, British Columbia were investigated for mitochondrial DNA variation. The whole mitochondrial genome was mapped using six-base-pair recognition site enzymes and the entire D-loop region was sequenced from one individual from each population. Two of these populations of killer whales forage on fish and were highly similar, while the third population of whales, which forages on marine mammals, was as distinct as allopatric populations (in Iceland and Argentina). These results are discussed in the context of killer whale conservation.

Hoelzel, A. R., Dahlheim, M., & Stern, S. J. (1998). Low Genetic Variation among Killer Whales (*Orcinus orca*) in the Eastern North Pacific and Genetic Differentiation between Foraging Specialists. *Journal of Heredity*, 89(2), 121-128. <https://doi.org/10.1093/jhered/89.2.121>

Killer whales from the coastal waters off California through Alaska were compared for genetic variation at three nuclear DNA markers and sequenced for a total of 520 bp from the mitochondrial control region. Two putative sympatric populations that range throughout this region were compared. They can be distinguished by social and foraging behavior and are known as “residents” and “transients.” We found low levels of variation within populations compared to other cetacean species. Comparisons between fish (resident) versus marine mammal (transient) foraging specialists indicated highly significant genetic differentiation at both nuclear and mitochondrial loci. This differentiation is at a level consistent with intraspecific variation. A comparison between two parapatric resident populations showed a small but fixed mtDNA haplotype difference. Together these data suggest low levels of genetic dispersal between foraging specialists and a pattern of genetic differentiation consistent with matrifocal population structure and small effective population size.

Hoelzel, A. R., & Dover, G. A. (1991). Genetic Differentiation between Sympatric Killer Whale Populations. *Heredity*, 66, 191-195. <https://doi.org/10.1038/hdy.1991.24>

The genetic variation within and between putative Killer whale (*Orcinus orca*) populations was examined by DNA fingerprinting nuclear genomes and sequencing the D-loop region of the mitochondrial genome. Mitochondrial DNA variation indicated that two sympatric populations in the northeastern Pacific were as genetically distinct as North Pacific populations from a South Atlantic population. The two sympatric populations are known to pursue different foraging strategies. DNA fingerprinting showed very low levels of variation within populations relative to comparisons between allopatric populations, suggesting inbreeding. These results are consistent with predictions about the genetic structure of Killer whale populations based on behavioural observations and variation in colour morphology.

Hoelzel, A. R., Hancock, J. M., & Dover, G. A. (1991). Evolution of the Cetacean Mitochondrial D-Loop Region. *Molecular Biology and Evolution*, 8(3), 475-493. <https://doi.org/10.1093/oxfordjournals.molbev.a040662>

We sequenced the mitochondrial DNA D-loop regions from two cetacean species and compared these with the published D-loop sequences of several other mammalian species, including one other cetacean. Nucleotide substitution rates, DNA sequence simplicity, possible open reading frames (ORFs), and potential RNA secondary structure were investigated. The substitution rate is an order of magnitude lower than would be expected on the basis of reports on human sequence variation in this region but are consistent with interspecific primate and rodent D-loop sequence variation and with estimates of substitution rates from whole mitochondrial genomes. Deletions/insertions are less common in the cetacean D-loop than in other vertebrate species. Areas of high sequence simplicity (clusters of short repetitive motifs) across the region correspond to areas of high sequence divergence. Three regions predicted to form secondary structures are homologous to such putative structures in other species; however, the presumptive structures most conserved in cetaceans are different from those reported for other taxa. While all three species have possible long ORFs, only a short sequence of seven amino acids is shared with other mammalian species, and those changes that had occurred within it are all



nonsynonymous. We conclude that DNA slippage, in addition to point mutation, contributes to the evolution of the D-loop and that regions of conserved secondary structure in cetaceans and an ORF are unlikely to contribute significantly to the conservation of the central region.

Hoelzel, A. R., Hey, J., Dahlheim, M. E., Nicholson, C., Burkanov, V., & Black, N. (2007). Evolution of Population Structure in a Highly Social Top Predator, the Killer Whale. *Molecular Biology and Evolution*, 24(6), 1407-1415. <https://doi.org/10.1093/molbev/msm063>

Intraspecific resource partitioning and social affiliations both have the potential to structure populations, though it is rarely possible to directly assess the impact of these mechanisms on genetic diversity and population divergence. Here, we address this for killer whales (*Orcinus orca*), which specialize on prey species and hunting strategy and have long-term social affiliations involving both males and females. We used genetic markers to assess the structure and demographic history of regional populations and test the hypothesis that known foraging specializations and matrifocal sociality contributed significantly to the evolution of population structure. We find genetic structure in sympatry between populations of foraging specialists (ecotypes) and evidence for isolation by distance within an ecotype. Fitting of an isolation with migration model suggested ongoing, low-level migration between regional populations (within and between ecotypes) and small effective sizes for extant local populations. The founding of local populations by matrifocal social groups was indicated by the pattern of fixed mtDNA haplotypes in regional populations. Simulations indicate that this occurred within the last 20,000 years (after the last glacial maximum). Our data indicate a key role for social and foraging behavior in the evolution of genetic structure among conspecific populations of the killer whale.

Hoelzel, A. R., Natoli, A., Dahlheim, M. E., Olavarria, C., Baird, R. W., & Black, N. A. (2002). Low Worldwide Genetic Diversity in the Killer Whale (*Orcinus orca*): Implications for Demographic History. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, 269(1499), 1467-1473. <https://doi.org/10.1098/rspb.2002.2033>

A low level of genetic variation in mammalian populations where the census population size is relatively large has been attributed to various factors, such as a naturally small effective population size, historical bottlenecks and social behaviour. The killer whale (*Orcinus orca*) is an abundant, highly social species with reduced genetic variation. We find no consistent geographical pattern of global diversity and no mtDNA variation within some regional populations. The regional lack of variation is likely to be due to the strict matrilineal expansion of local populations. The worldwide pattern and paucity of diversity may indicate a historical bottleneck as an additional factor.

Huijser, L. A. E., Bérubé, M., Cabrera, A. A., Prieto, R., Silva, M. A., Robbins, J., . . . Palsbøll, P. J. (2018). Population Structure of North Atlantic and North Pacific Sei Whales (*Balaenoptera borealis*) Inferred from Mitochondrial Control Region DNA Sequences and Microsatellite Genotypes. *Conservation Genetics*, 19(4), 1007-1024. <https://doi.org/10.1007/s10592-018-1076-5>

Currently, three stocks of sei whales (*Balaenoptera borealis*) are defined in the North Atlantic; the Nova Scotian, IcelandDenmark Strait and Eastern North Atlantic stocks, which are mainly based upon historical catch and sighting data. We analyzed mitochondrial control region DNA (mtDNA) sequences and genotypes from 7 to 11 microsatellite loci in 87 samples from three sites in the North Atlantic;

Iceland, the Gulf of Maine and the Azores, and compared against the North Pacific using 489 previously published samples. No statistically significant deviations from homogeneity were detected among the North Atlantic samples at mtDNA or microsatellite loci. The genealogy estimated from the mtDNA sequences revealed a clear division of the haplotypes into a North Atlantic and a North Pacific clade, with the exception of one haplotype detected in a single sample from the Azores, which was included in the North Pacific clade. Significant genetic divergence between the North Atlantic and North Pacific Oceans was detected (mtDNA  $\Phi_{ST} = 0.72$ , microsatellite Weir and Cockerham's  $\Theta = 0.20$ ;  $p < 0.001$ ). The coalescent-based estimate of the population divergence time between the North Atlantic and North Pacific populations from the sequence variation among the mtDNA sequences was at 163,000 years ago. However, the inference was limited by an absence of samples from the Southern Hemisphere and uncertainty regarding mutation rates and generation times. The estimates of inter-oceanic migration rates were low ( $Nm$  at 0.007 into the North Pacific and at 0.248 in the opposite direction). Although estimates of genetic divergence among the current North Atlantic stocks were low and consistent with the extensive range of movement observed in satellite tagged sei whales, the high uncertainty of the genetic divergence estimates precludes rejection of multiple stocks in the North Atlantic.

Jourdain, E., Ugarte, F., Víkingsson, G. A., Samarra, F. I. P., Ferguson, S. H., Lawson, J., . . . Desportes, G. (2019). North Atlantic Killer Whale *Orcinus orca* Populations: A Review of Current Knowledge and Threats to Conservation. *Mammal Review*, 49(4), 384-400.  
<https://doi.org/10.1111/mam.12168>

1. The first comprehensive review on North Atlantic killer whales *Orcinus orca* was published in 1988. Since then, a significant increase in published studies has substantially improved our understanding of occurrence patterns, major food sources, abundance and population structuring in the North-east Atlantic. Dedicated studies on killer whales in the Mid- and West Atlantic were undertaken beginning in 2006, mainly following an increase in their presence due to rapidly changing environmental conditions in the Arctic regions of Canada and Greenland. 2. Compiling 111 scientific articles and reports published from 1957 to date, this review assesses the current state of knowledge of North Atlantic killer whale populations. We reviewed distribution, abundance, movements, genetic structure, acoustics, population parameters, and threats, whilst highlighting the connection among regions from east to west. 3. Our results indicated that, while North Atlantic killer whales should be recovering following the end of the harvest, culling and live captures in the 1980s, new emerging threats including chemical pollution, anthropogenic noise and increasing unregulated subsistence harvest in Greenland could be hampering this rebound. 4. There is an urgent need to collect data on the abundance and population structure of killer whales in Greenland and Eastern Canada. A lack of information across most regions of the North Atlantic Ocean has prevented regional status assessments from being conducted. Ongoing and future studies should be aimed at collecting relevant data to undertake these assessments, particularly genetic samples and photo-identification.

LeDuc, R. G., Robertson, K. M., & Pitman, R. L. (2008). Mitochondrial Sequence Divergence among Antarctic Killer Whale Ecotypes Is Consistent with Multiple Species. *Biology letters*, 4(4), 426-429. <https://doi.org/10.1098/rsbl.2008.0168>

Recently, three visually distinct forms of killer whales (*Orcinus orca*) were described from Antarctic waters and designated as types A, B and C. Based on consistent differences in prey selection and habitat preferences, morphological divergence and apparent lack of interbreeding among these broadly

sympatric forms, it was suggested that they may represent separate species. To evaluate this hypothesis, we compared complete sequences of the mitochondrial control region from 81 Antarctic killer whale samples, including 9 type A, 18 type B, 47 type C and 7 type-undetermined individuals. We found three fixed differences that separated type A from B and C, and a single fixed difference that separated type C from A and B. These results are consistent with reproductive isolation among the different forms, although caution is needed in drawing further conclusions. Despite dramatic differences in morphology and ecology, the relatively low levels of sequence divergence in Antarctic killer whales indicate that these evolutionary changes occurred relatively rapidly and recently.

Mitani, Y., Kita, Y. F., Saino, S., Yoshioka, M., Ohizumi, H., & Nakahara, F. (2021). Mitochondrial DNA Haplotypes of Killer Whales around Hokkaido, Japan. *Mammal Study*, 46(3), 1-7. <https://doi.org/10.3106/ms2020-0072>

In this study, we examined a genetic variation of killer whales, *Orcinus orca*, from off the coast of Hokkaido, Japan, by sequencing the D-loop and cytochrome b (Cyt-b) regions of the mitochondrial genome. Three D-loop and two Cyt-b haplotypes were identified from eight skin biopsies. These five haplotypes had been previously deposited at GenBank and the International Nucleotide Sequence Database Collaboration (INSDC). Two D-loop and one Cyt-b haplotypes were consistent with the marine mammal-eating "Transient" ecotype previously reported in Japanese waters. One D-loop and one Cyt-b haplotypes were identified as the fish-eating "Resident" or "Offshore" ecotype that is the first record of this ecotype in Japanese waters. Our study showed that different ecotypes exist in Japanese waters, contributing to the conservation and management of killer whales.

Morin, P. A., Archer, F. I., Foote, A. D., Vilstrup, J., Allen, E. E., Wade, P., . . . Harkins, T. (2010). Complete Mitochondrial Genome Phylogeographic Analysis of Killer Whales (*Orcinus orca*) Indicates Multiple Species. *Genome research*, 20(7), 908-916. <https://doi.org/10.1101/gr.102954.109>

Killer whales (*Orcinus orca*) currently comprise a single, cosmopolitan species with a diverse diet. However, studies over the last 30 yr have revealed populations of sympatric "ecotypes" with discrete prey preferences, morphology, and behaviors. Although these ecotypes avoid social interactions and are not known to interbreed, genetic studies to date have found extremely low levels of diversity in the mitochondrial control region, and few clear phylogeographic patterns worldwide. This low level of diversity is likely due to low mitochondrial mutation rates that are common to cetaceans. Using killer whales as a case study, we have developed a method to readily sequence, assemble, and analyze complete mitochondrial genomes from large numbers of samples to more accurately assess phylogeography and estimate divergence times. This represents an important tool for wildlife management, not only for killer whales but for many marine taxa. We used high-throughput sequencing to survey whole mitochondrial genome variation of 139 samples from the North Pacific, North Atlantic, and southern oceans. Phylogenetic analysis indicated that each of the known ecotypes represents a strongly supported clade with divergence times ranging from approximately 150,000 to 700,000 yr ago. We recommend that three named ecotypes be elevated to full species, and that the remaining types be recognized as subspecies pending additional data. Establishing appropriate taxonomic designations will greatly aid in understanding the ecological impacts and conservation needs of these important marine predators. We predict that phylogeographic mitogenomics will become an important tool for improved statistical phylogeography and more precise estimates of divergence times.

Morin, P. A., LeDuc, R. G., Robertson, K. M., Hedrick, N. M., Perrin, W. F., Etnier, M., . . . Taylor, B. L. (2006). Genetic Analysis of Killer Whale (*Orcinus orca*) Historical Bone and Tooth Samples to Identify Western U.S. Ecotypes. *Marine Mammal Science*, 22(4), 897-909. <https://doi.org/10.1111/j.1748-7692.2006.00070.x>

Little is known about the historical range of killer whale ecotypes in the eastern North Pacific (ENP). It is possible that ranges have shifted in the last few decades because of changes in availability of food. In particular, the southern resident ecotype, currently found primarily in the inland waters of Washington State, is known to prey extensively on salmon, which have declined in recent decades along the outer coasts of Washington, Oregon, and California. To investigate historical distributions of this and the other ENP ecotypes, samples of teeth and bones were obtained from NMFS and museum collections. We amplified a short section of the mitochondrial DNA control region that contains four diagnostic sites that differentiate between haplotypes found in ecotypes of ENP killer whales. Results did not show any southern resident haplotypes in samples from south of the Washington State inland waterways. One whale genetically identified as a northern resident extends the known southernmost distribution of the population from Oregon to California. Items of diet identified from stomach contents of six of the whales genetically identified to ecotype conformed with what is known of the feeding habits of the various ecotypes.

Morin, P. A., Parsons, K. M., Archer, F. I., Avila-Arcos, M. C., Barrett-Lennard, L. G., Dalla Rosa, L., . . . Foote, A. D. (2015). Geographic and Temporal Dynamics of a Global Radiation and Diversification in the Killer Whale. *Molecular Ecology*, 24(15), 3964-3979. <https://doi.org/10.1111/mec.13284>

Global climate change during the Late Pleistocene periodically encroached and then released habitat during the glacial cycles, causing range expansions and contractions in some species. These dynamics have played a major role in geographic radiations, diversification and speciation. We investigate these dynamics in the most widely distributed of marine mammals, the killer whale (*Orcinus orca*), using a global data set of over 450 samples. This marine top predator inhabits coastal and pelagic ecosystems ranging from the ice edge to the tropics, often exhibiting ecological, behavioural and morphological variation suggestive of local adaptation accompanied by reproductive isolation. Results suggest a rapid global radiation occurred over the last 350,000 years. Based on habitat models, we estimated there was only a 15% global contraction of core suitable habitat during the last glacial maximum, and the resources appeared to sustain a constant global effective female population size throughout the Late Pleistocene. Reconstruction of the ancestral phylogeography highlighted the high mobility of this species, identifying 22 strongly supported long-range dispersal events including interoceanic and interhemispheric movement. Despite this propensity for geographic dispersal, the increased sampling of this study uncovered very few potential examples of ancestral dispersal among ecotypes. Concordance of nuclear and mitochondrial data further confirms genetic cohesiveness, with little or no current gene flow among sympatric ecotypes. Taken as a whole, our data suggest that the glacial cycles influenced local populations in different ways, with no clear global pattern, but with secondary contact among lineages following long-range dispersal as a potential mechanism driving ecological diversification.

Moura, A. E., Janse van Rensburg, C., Pilot, M., Tehrani, A., Best, P. B., Thornton, M., . . . Hoelzel, A. R. (2014). Killer Whale Nuclear Genome and Mtdna Reveal Widespread Population Bottleneck

During the Last Glacial Maximum. *Molecular Biology and Evolution*, 31(5), 1121-1131.  
<https://doi.org/10.1093/molbev/msu058>

Ecosystem function and resilience is determined by the interactions and independent contributions of individual species. Apex predators play a disproportionately determinant role through their influence and dependence on the dynamics of prey species. Their demographic fluctuations are thus likely to reflect changes in their respective ecological communities and habitat. Here, we investigate the historical population dynamics of the killer whale based on draft nuclear genome data for the Northern Hemisphere and mtDNA data worldwide. We infer a relatively stable population size throughout most of the Pleistocene, followed by an order of magnitude decline and bottleneck during the Weichselian glacial period. Global mtDNA data indicate that while most populations declined, at least one population retained diversity in a stable, productive ecosystem off southern Africa. We conclude that environmental changes during the last glacial period promoted the decline of a top ocean predator, that these events contributed to the pattern of diversity among extant populations, and that the relatively high diversity of a population currently in productive, stable habitat off South Africa suggests a role for ocean productivity in the widespread decline.

Moura, A. E., Kenny, J., Chaudhuri, R. R., Hughes, M., Welch, A. J., Reisinger, R. R., . . . Hoelzel, A. R. (2014). Population Genomics of the Killer Whale Indicates Ecotype Evolution in Sympatry Involving Both Selection and Drift. *Molecular Ecology*, 23(21), 5179-5192.  
<https://doi.org/10.1111/mec.12929>

The evolution of diversity in the marine ecosystem is poorly understood, given the relatively high potential for connectivity, especially for highly mobile species such as whales and dolphins. The killer whale (*Orcinus orca*) has a worldwide distribution, and individual social groups travel over a wide geographic range. Even so, regional populations have been shown to be genetically differentiated, including among different foraging specialists (ecotypes) in sympatry. Given the strong matrifocal social structure of this species together with strong resource specializations, understanding the process of differentiation will require an understanding of the relative importance of both genetic drift and local adaptation. Here we provide a high-resolution analysis based on nuclear single-nucleotide polymorphic markers and inference about differentiation at both neutral loci and those potentially under selection. We find that all population comparisons, within or among foraging ecotypes, show significant differentiation, including populations in parapatry and sympatry. Loci putatively under selection show a different pattern of structure compared to neutral loci and are associated with gene ontology terms reflecting physiologically relevant functions (e.g. related to digestion). The pattern of differentiation for one ecotype in the North Pacific suggests local adaptation and shows some fixed differences among sympatric ecotypes. We suggest that differential habitat use and resource specializations have promoted sufficient isolation to allow differential evolution at neutral and functional loci, but that the process is recent and dependent on both selection and drift.

Moura, A. E., Kenny, J. G., Chaudhuri, R. R., Hughes, M. A., Reisinger, R. R., de Bruyn, P. J. N., . . . Hoelzel, A. R. (2015). Phylogenomics of the Killer Whale Indicates Ecotype Divergence in Sympatry. *Heredity*, 114(1), 48-55. <https://doi.org/10.1038/hdy.2014.67>

For many highly mobile species, the marine environment presents few obvious barriers to gene flow. Even so, there is considerable diversity within and among species, referred to by some as the 'marine

speciation paradox'. The recent and diverse radiation of delphinid cetaceans (dolphins) represents a good example of this. Delphinids are capable of extensive dispersion and yet many show fine-scale genetic differentiation among populations. Proposed mechanisms include the division and isolation of populations based on habitat dependence and resource specializations, and habitat release or changing dispersal corridors during glacial cycles. Here we use a phylogenomic approach to investigate the origin of differentiated sympatric populations of killer whales (*Orcinus orca*). Killer whales show strong specialization on prey choice in populations of stable matrifocal social groups (ecotypes), associated with genetic and phenotypic differentiation. Our data suggest evolution in sympatry among populations of resource specialists.

O'Sullivan, S., & Mullin, K. D. (1997). Killer Whales (*Orcinus orca*) in the Northern Gulf of Mexico. *Marine Mammal Science*, 13(1), 141-147. <https://doi.org/10.1111/j.1748-7692.1997.tb00618.x>

No Abstract

Olavarría, C., Baker, C. S., & Tezanos-Pinto, G. (2013). Low Mtdna Genetic Diversity among Killer Whales around New Zealand. *New Zealand Journal of Marine and Freshwater Research*, 48(1), 147-153. <https://doi.org/10.1080/00288330.2013.844721>

We report here the genetic diversity of killer whales around New Zealand and compare samples collected in this region (n = 11) with larger geographic databases of mtDNA control region sequences to investigate the relationship of the New Zealand killer whales with more distant populations/ecotypes. Eight variable sites defined four haplotypes, revealing a low mtDNA genetic diversity when compared with other cetacean species and to that observed worldwide for killer whales. The geographic distribution and segregation of haplotypes within New Zealand suggested that this population could be geographically structured. Only one of the New Zealand haplotypes matched with those from other distant regions (the Eastern North Atlantic and Western South Atlantic populations).

Olsen, D. W., Matkin, C. O., Mueter, F. J., & Atkinson, S. (2020). Social Behavior Increases in Multipod Aggregations of Southern Alaska Resident Killer Whales (*Orcinus orca*). *Marine Mammal Science*, 36(4), 1150-1159. <https://doi.org/10.1111/mms.12715>

Killer whales (*Orcinus orca*) are highly social and occasionally gather in large aggregations that reach 150 individuals. During 338 encounters with Southern Alaska resident killer whales, we collected 1,352 hr of behavioral data to assess the probability of various behaviors based on season, number of pods present, presence of rarely sighted pods, and number of mitochondrial DNA haplotypes present. A binomial generalized linear model was used to estimate the role of these factors in the probability of four behaviors, foraging, resting, socializing, and traveling. The presence of "rarely sighted" pods (sighted in <5% of encounters) significantly increased probability of social behavior, and significantly decreased probability of resting. The number of pods present also significantly increased probability of increased social behavior. The presence of rarely sighted pods and the number of pods present did not have a significant interaction. Ordinal day and number of mitochondrial DNA haplotypes appears to not have changed the probability of any behavior. Foraging remained the predominant behavior throughout all factors. The concurrent increase in social behavior and decrease in resting behavior with rarely sighted

Pods present implies an unusually high importance of social behavior in the lives of resident killer whales.

Parsons, K. M., Durban, J. W., Burdin, A. M., Burkanov, V. N., Pitman, R. L., Barlow, J., . . . Wade, P. R. (2013). Geographic Patterns of Genetic Differentiation among Killer Whales in the Northern North Pacific. *Journal of Heredity*, 104(6), 737-754. <https://doi.org/10.1093/jhered/est037>

The difficulties associated with detecting population boundaries have long constrained the conservation and management of highly mobile, wide-ranging marine species, such as killer whales (*Orcinus orca*). In this study, we use data from 26 nuclear microsatellite loci and mitochondrial DNA sequences (988bp) to test a priori hypotheses about population subdivisions generated from a decade of killer whale surveys across the northern North Pacific. A total of 462 remote skin biopsies were collected from wild killer whales primarily between 2001 and 2010 from the northern Gulf of Alaska to the Sea of Okhotsk, representing both the piscivorous "resident" and the mammal-eating "transient" (or Bigg's) killer whales. Divergence of the 2 ecotypes was supported by both mtDNA and microsatellites. Geographic patterns of genetic differentiation were supported by significant regions of genetic discontinuity, providing evidence of population structuring within both ecotypes and corroborating direct observations of restricted movements of individual whales. In the Aleutian Islands (Alaska), subpopulations, or groups with significantly different mtDNA and microsatellite allele frequencies, were largely delimited by major oceanographic boundaries for resident killer whales. Although Amchitka Pass represented a major subdivision for transient killer whales between the central and western Aleutian Islands, several smaller subpopulations were evident throughout the eastern Aleutians and Bering Sea. Support for seasonally sympatric transient subpopulations around Unimak Island suggests isolating mechanisms other than geographic distance within this highly mobile top predator.

Pilot, M., Dahlheim, M. E., & Hoelzel, A. R. (2010). Social Cohesion among Kin, Gene Flow without Dispersal and the Evolution of Population Genetic Structure in the Killer Whale (*Orcinus orca*). *Journal of Evolutionary Biology*, 23(1), 20-31. <https://doi.org/10.1111/j.1420-9101.2009.01887.x>

In social species, breeding system and gregarious behavior are key factors influencing the evolution of large-scale population genetic structure. The killer whale is a highly social apex predator showing genetic differentiation in sympatry between populations of foraging specialists (ecotypes), and low levels of genetic diversity overall. Our comparative assessments of kinship, parentage and dispersal reveal high levels of kinship within local populations and ongoing male-mediated gene flow among them, including among ecotypes that are maximally divergent within the mtDNA phylogeny. Dispersal from natal populations was rare, implying that gene flow occurs without dispersal, as a result of reproduction during temporary interactions. Discordance between nuclear and mitochondrial phylogenies was consistent with earlier studies suggesting a stochastic basis for the magnitude of mtDNA differentiation between matrilineal groups. Taken together our results show how the killer whale breeding system, coupled with social, dispersal and foraging behaviour, contributes to the evolution of population genetic structure.

Pitman, R. L., & Ensor, P. (2003). Three Forms of Killer Whales (*Orcinus orca*) in Antarctic Waters. *Journal of Cetacean Research and Management*, 5(2), 131-139. Retrieved from <https://archive.iwc.int>

This paper provides field descriptions and biological observations of three different forms of killer whale (*Orcinus orca*) that occur in Antarctica based on field observations and a review of available photographs. Identifications were based on the relative size and orientation of the white eyepatch and the presence or absence of a dorsal cape. Type A (presumably the nominate form) has a medium-sized eyepatch oriented parallel to the body axis, no dorsal cape, it occurs mainly off-shore in ice-free water, has a circumpolar distribution and apparently preys mainly upon Antarctic minke whales (*Balaenoptera bonaerensis*). Type B also has an eyepatch oriented parallel to the body axis, but the eyepatch is at least twice as large as in Type A, it has a dorsal cape, mainly inhabits inshore waters, regularly occurs in pack-ice, is distributed around the continent and is regularly sighted in the Antarctic Peninsula area. Although it may also prey upon Antarctic minke whales and possibly humpback whales (*Megaptera novaeangliae*), seals seem to be the most important prey item. Type C has a small, forward-slanted eyepatch, a dorsal cape, inhabits inshore waters and lives mainly in the pack-ice; it occurs mostly off East Antarctica, and to date it has been recorded feeding only on Antarctic toothfish (*Dissostichus mawsoni*). Type C appears to be referable to *Orcinus glacialis* as described by Berzin and Vladimirov (1983). Although similar ecological specialisations have been reported for sympatric killer whale populations in the Northeast Pacific (i.e. an inshore mammal-eater, an inshore fish-eater and an offshore form), the extent of morphological divergence, habitat segregation and, perhaps, reproductive isolation, appears to be more pronounced among Antarctic populations. Although under a Biological Species Concept these forms appear to warrant separate species status, it will be important to show that this interpretation is consistent with results of molecular genetic analyses and additional morphological studies.

Reeves, I. M., Totterdell, J. A., Barceló, A., Sandoval-Castillo, J., Batley, K. C., Stockin, K. A., . . . Möller, L. M. (2021). Population Genomic Structure of Killer Whales (*Orcinus orca*) in Australian and New Zealand Waters. *Marine Mammal Science*, 1-24. <https://doi.org/10.1111/mms.12851>

Population genomic data sets have enhanced power to detect cryptic and complex population structure and generate valuable information for the conservation and management of wildlife species. Globally, killer whales (*Orcinus orca*) are considered to have a complex population structure due to their ability to specialize in a variety of ecological niches. In the Australasian region, they are found year round in New Zealand waters and are sighted in all Australian waters, with seasonal aggregations in the northwest (NWA) and southwest (SWA). Regionally, there is some knowledge regarding killer whale abundance, diet, acoustics, and social structure, but limited information about their population structure. Here, we present a population structure assessment of Australasian killer whales using 17,491 high quality genome-wide single nucleotide polymorphisms (SNPs), combined with sequences of the mitochondrial DNA control region. The results indicate a minimum of three populations: New Zealand, NWA, and SWA. These populations present moderate levels of genomic diversity, negligible levels of inbreeding, small effective population sizes, and low contemporary migration rates among them. Mitochondrial DNA analysis elucidated five closely related haplotypes, suggestive of matrilineal societies, consistent with killer whales elsewhere. This information will assist conservation management of killer whales in the Australasian region.

Service, N. M. F. (2004). *Endangered and Threatened Wildlife and Plants: Proposed Threatened Status for Southern Resident Killer Whales*. Federal Register Retrieved from <https://www.govinfo.gov/content/pkg/FR-2004-12-22/pdf/04-27929.pdf>



We, the NMFS, have completed an update on the status review of Southern Resident killer whales (*Orcinus orca*) under the Endangered Species Act (ESA). Based on the review of the best available scientific and commercial information, including new data, published papers, and workshop reports available since the review in 2002, we are proposing to list the Southern Resident killer whales as threatened because these killer whales constitute a distinct population segment (DPS) under the ESA and are likely to become endangered in the foreseeable future throughout all or a significant portion of their range. We are not proposing to designate critical habitat at this time, but are requesting public comments on the issues pertaining to this proposed rule.

Stokes, A. (2018). Genetic Insights into the Biogeography and Evolutionary History of the Killer Whale. *UC Davis: University Library*. Retrieved from <https://escholarship.org/uc/item/7gc0d2hg>

This paper reviews genetic studies undertaken to generate an accurate phylogeny of killer whale (*Orcinus orca*) lineages. Three phylogenies, distinct in branching order and timing of divergences, are discussed. Of the three phylogenies, two are based on mitochondrial DNA and show more ancient divergence times for killer whale lineages. The third phylogeny, based on nuclear DNA, indicates that killer whales diversified more recently. The differing phylogenies have differing implications for biogeographic inference and for species assessments. The nuclear based phylogeny suggests that killer whale lineages diverged in sympatry while the mitochondrial based phylogenies as well as an empirical study indicate that the divergences more likely occurred in allopatry. The mitochondrial based phylogenies also support revision of killer whale taxonomy as there is indication that killer whales constitute multiple species and subspecies instead of a single species. The types of research that would be helpful in confirming hypotheses based on the phylogenies are discussed.

Tavares, S. B., Samarra, F. I. P., Pascoal, S., Graves, J. A., & Miller, P. J. O. (2018). Killer Whales (*Orcinus orca*) in Iceland Show Weak Genetic Structure among Diverse Isotopic Signatures and Observed Movement Patterns. *Ecology and Evolution*, 8(23), 11900-11913. <https://doi.org/10.1002/ece3.4646>

Local adaption through ecological niche specialization can lead to genetic structure between and within populations. In the Northeast Pacific, killer whales (*Orcinus orca*) of the same population have uniform specialized diets that are non-overlapping with other sympatric, genetically divergent, and socially isolated killer whale ecotypes. However, killer whales in Iceland show intrapopulation variation of isotopic niches and observed movement patterns: some individuals appear to specialize on herring and follow it year-round while others feed upon herring only seasonally or opportunistically. We investigated genetic differentiation among Icelandic killer whales with different isotopic signatures and observed movement patterns. This information is key for management and conservation purposes but also for better understanding how niche specialization drives genetic differentiation. Photo-identified individuals (N = 61) were genotyped for 22 microsatellites and a 611 bp portion of the mitochondrial DNA (mtDNA) control region. Photo-identification of individuals allowed linkage of genetic data to existing data on individual isotopic niche, observed movement patterns, and social associations. Population subdivision into three genetic units was supported by a discriminant analysis of principal components (DAPC). Genetic clustering corresponded to the distribution of isotopic signatures, mtDNA haplotypes, and observed movement patterns, but genetic units were not socially segregated. Genetic differentiation was weak ( $F_{ST} < 0.1$ ), suggesting ongoing gene flow or recent separation of the genetic units. Our results show that killer whales in Iceland are not as genetically differentiated, ecologically discrete, or

socially isolated as the Northeast Pacific prey-specialized killer whales. If any process of ecological divergence and niche specialization is taking place among killer whales in Iceland, it is likely at a very early stage and has not led to the patterns observed in the Northeast Pacific.

Whitehead, H. (1998). Cultural Selection and Genetic Diversity in Matrilineal Whales. *Science*, 282(5391), 1708-1711. Retrieved from <https://www.jstor.org/stable/2896863>

Low diversities of mitochondrial DNA (mtDNA) have recently been found in four species of matrilineal whale. No satisfactory explanation for this apparent anomaly has been previously suggested. Culture seems to be an important part of the lives of matrilineal whales. The selection of matrilineally transmitted cultural traits, upon which neutral mtDNA alleles "hitchhike," has the potential to strongly reduce genetic variation. Thus, in contrast to other nonhuman mammals, culture may be an important evolutionary force for the matrilineal whales.

Whitehead, H. (2017). Gene-Culture Coevolution in Whales and Dolphins. *Proceedings of the National Academy of Sciences of the United States of America*, 114(30), 7814-7821. <https://doi.org/10.1073/pnas.1620736114>

Whales and dolphins (Cetacea) have excellent social learning skills as well as a long and strong mother-calf bond. These features produce stable cultures, and, in some species, sympatric groups with different cultures. There is evidence and speculation that this cultural transmission of behavior has affected gene distributions. Culture seems to have driven killer whales into distinct ecotypes, which may be incipient species or subspecies. There are ecotype-specific signals of selection in functional genes that correspond to cultural foraging behavior and habitat use by the different ecotypes. The five species of whale with matrilineal social systems have remarkably low diversity of mtDNA. Cultural hitchhiking, the transmission of functionally neutral genes in parallel with selective cultural traits, is a plausible hypothesis for this low diversity, especially in sperm whales. In killer whales the ecotype divisions, together with founding bottlenecks, selection, and cultural hitchhiking, likely explain the low mtDNA diversity. Several cetacean species show habitat-specific distributions of mtDNA haplotypes, probably the result of mother-offspring cultural transmission of migration routes or destinations. In bottlenose dolphins, remarkable small-scale differences in haplotype distribution result from maternal cultural transmission of foraging methods, and large-scale redistributions of sperm whale cultural clans in the Pacific have likely changed mitochondrial genetic geography. With the acceleration of genomics new results should come fast, but understanding gene-culture coevolution will be hampered by the measured pace of research on the socio-cultural side of cetacean biology.

Whitehead, H. (2020). Cultural Specialization and Genetic Diversity: Killer Whales and Beyond. *Journal of Theoretical Biology*, 490, 110164. <https://doi.org/10.1016/j.jtbi.2020.110164>

Culturally-transmitted ecological specialization can reduce niche breadths with demographic and ecological consequences. I use agent-based models, grounded in killer whale biology, to investigate the potential consequences of cultural specialization for genetic diversity. In these models, cultural specialization typically reduces the number of mitochondrial haplotypes, mitochondrial haplotype diversity, mitochondrial nucleotide diversity, and heterozygosity at nuclear loci. The causal route of this decline is mostly indirect, being ascribed to a reduction in absolute population size resulting from

cultural specialization. However, small group size exacerbates the decline in genetic diversity, presumably because of increased founder effects at the initiation of each cultural ecotype. These results are concordant with measures of low genetic diversity in the killer whale, although culturally-transmitted ecological specialization alone might not be sufficient to fully account for the species' very low mitochondrial diversity. The process may also operate in other species.

Yusmalinda, N. L. A., Anggoro, A. W., Suhendro, D. M., Ratha, I. M. J., Suprpti, D., Krebs, D., & Cahyani, N. K. D. (2018). Species Identification of Stranded Cetaceans in Indonesia Revealed by Molecular Technique. *Jurnal Ilmu dan Teknologi Kelautan Tropis*, 9(2), 465-474. <https://doi.org/10.29244/jitkt.v9i2.19283>

Stranding cases of cetaceans in Indonesia including whales, dolphins, and porpoises have recently increasingly become unfold and handled by many people. According to data from Whale Stranding Indonesia (WSI), there have been 40 stranding cases in different parts of Indonesia from early 2016 until February 2017. One of the major obstacles for the people who are handling strandings is to identify the species based on morphology alone when the body is in an advanced stadium of decomposition. WSI recorded that 21% of the species are unidentifiable. For that reason, this research aims to introduce a molecular genetics approach for identifying stranded cetaceans. Mitochondrial DNA of the gene control region was amplified using a Polymerase Chain Reaction (PCR) method. Sequence data were compared with data from the genebank through percentage overlap. From the 36 individuals, which have been used in this research, 26 amplified samples had base lengths varying between 445-490 base pairs. Molecular methods successfully identified 15 species and 13 genus of Cetacea from different localities in Indonesia. This study shows that molecular genetic techniques can be used as a method to identify species of cetaceans, in particular of stranded individual, which are hard to identify morphologically. The molecular data may complete the genetic database and become a reference for research on genetic diversity among marine mammal populations in Indonesia.

Zerbini, A. N., Waite, J. M., Durban, J. W., LeDuc, R., Dahlheim, M. E., & Wade, P. R. (2006). Estimating Abundance of Killer Whales in the Nearshore Waters of the Gulf of Alaska and Aleutian Islands Using Line-Transect Sampling. *Marine Biology*, 150, 1033-1045. <https://doi.org/10.1007/s00227-006-0347-8>

Killer whale (*Orcinus orca* Linnaeus, 1758) abundance in the North Pacific is known only for a few populations for which extensive longitudinal data are available, with little quantitative data from more remote regions. Line-transect ship surveys were conducted in July and August of 2001–2003 in coastal waters of the western Gulf of Alaska and the Aleutian Islands. Conventional and Multiple Covariate Distance Sampling methods were used to estimate the abundance of different killer whale ecotypes, which were distinguished based upon morphological and genetic data. Abundance was calculated separately for two data sets that differed in the method by which killer whale group size data were obtained. Initial group size (IGS) data corresponded to estimates of group size at the time of first sighting, and post-encounter group size (PEGS) corresponded to estimates made after closely approaching sighted groups. 'Resident'-type (fish-eating) killer whales were more abundant than the 'transient'-type (mammal-eating). Abundance estimates of resident killer whales (991 [95% CI = 379–2,585] [IGS] and 1,587 [95% CI = 608–4,140] [PEGS]), were at least four times greater than those of the transient killer whales (200 [95% CI = 81–488] [IGS] and 251 [95% CI = 97–644] whales [PEGS]). The IGS estimate of abundance is preferred for resident killer whales because the estimate based on PEGS data

may show an upward bias. The PEGS estimate of abundance is likely more accurate for transients. Residents were most abundant near Kodiak Island in the northern Gulf of Alaska, around Umnak and Unalaska Islands in the eastern Aleutians, and in Seguam Pass in the central Aleutians. This ecotype was not observed between 156 and 164°W, south of the Alaska Peninsula. In contrast, transient killer whale sightings were found at higher densities south of the Alaska Peninsula between the Shumagin Islands and the eastern Aleutians. Only two sightings of 'offshore'-type killer whales were recorded during the surveys, one northeast of Unalaska Island and the other south of Kodiak Island. These are the first estimates of abundance of killer whale ecotypes in the Aleutian Islands and Alaska Peninsula area and provide a baseline for quantifying the role of these top predators in their ecosystem.