

## Review of the status of the western North Pacific gray whale; stock structure hypotheses, and recommendations for methods of future genetic studies.

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### ABSTRACT

The North Pacific Gray whales (*Eschrichtius robustus*) are considered to consist of a large (19,000) eastern population and a small (ca. 155) western population. Genetic comparisons between eastern and western gray whales indicate that the populations are distinct. However in recent years, satellite tagging and photographic and genetic matches have provided evidence of overlap of the migration routes of the eastern and western populations and raise questions as to whether these whales are distinct populations. This paper reviews the issue of stock structure of North Pacific gray whales and the status of the western gray whale population. We present a range of plausible stock structure hypotheses and a discussion of genetic methods needed to test them.

**Introduction.**—The gray whale (*Eschrichtius robustus*) was once common in the North Pacific and North Atlantic Oceans but was extirpated from the Atlantic by the early 1700s. The extant North Pacific population is considered to be comprised of two populations or stocks. An eastern North Pacific population (eastern gray whales) winters in the subtropical waters of Baja, Mexico and migrates along the continental shelf of western North America primarily to summer feeding grounds in the Bering, Chukchi and Beaufort Seas. A western North Pacific population (western gray whales), the subject of this paper, inhabits summer feeding grounds in the Sea of Okhotsk, off the northeast coast of Sakhalin Island and the southeastern coast of the Kamchatka Peninsula. However, its migratory and wintering habits are not well known. Information collected since the 1930s show the western gray whale to migrate in coastal waters of Japan and South Korea to wintering habitat somewhere in the South China Sea (Weller and Brownell, 2012). Recent genetic studies suggest that eastern and western gray whales are discrete (Lang et al., 2011a).

Both the Atlantic and Pacific populations were hunted extensively and over-hunting likely contributed to the extinction of the Atlantic population (Mead and Mitchell, 1984; Weller and Brownell, 2012). The Pacific populations were reduced to very low numbers as well. With regard to the level of depletion of the Pacific population, Alter et al. (2012) estimate the number of mature females at the bottleneck to be approximately 1,300. This estimate is based on genetic diversity of the extant North Pacific gray whale population and thus includes both stocks in its calculations. Pre-commercial whaling population size of the eastern Pacific gray whale population was estimated to be 15,000 to 20,000 based on an examination of whaling records (Henderson, 1984). However, little is known of the historical population size of the western North Pacific population. Berzin and Vladimirov (1981) estimated that the western North Pacific population numbered 1,000 to 1,500 individuals prior to 1910, and this number has been generally accepted. However, Alter et al. (2007, 2012a) used genetic methods to estimate historical population sizes and concluded that the Pacific population, including both eastern and western stocks, likely numbered approximately 100,000 individuals prior to whaling. The

relative sizes of the eastern and western populations were not estimated. Notwithstanding the uncertainty of the pre-exploitation size of the western North Pacific gray whale, it clearly had a much larger distribution than the population that now summers in the Sea of Okhotsk (Reeves et al., 2008) and it was reduced to a much smaller size than the eastern population.

Currently, the western population only numbers about 155 (IUCN 2012a) and is considered as critically endangered (IUCN, 2008). Only 32 reproductive females have been documented in this population (Burdin et al., 2011) and the loss of a single reproductive female annually could be sufficient to lead to the loss of the population (IWC, 2006, pp.10, 67). This contrasts markedly with the eastern population which was reduced to approximately 2,000 but has made a strong recovery and now numbers about 19,000 (Laake et al., 2009). Potential threats to the western population include accidental takes by fishermen (IWC 1994; Kato et al., 2006), poaching, ship strikes, pollution, and oil and gas development near their summer feeding sites.

The western North Pacific gray whale population is believed to have been comprised of two subpopulations; a small Japanese subpopulation that wintered in the straits between the islands of Honshu, Kyushu and Shikoku, and summered north of the island of Hokkaido (Andrews, 1914; Mizue, 1951) and the Okhotsk-Korean subpopulation that summered in the Sea of Okhotsk and wintered in Korea and China. Whales of the latter population were hunted near Sakhalin Island, the Kuril Islands, and Korea in the first half of the 20<sup>th</sup> Century (Brownell and Chun, 1977) but by 1966 the population was considered to be extinct (Bowen 1974; Weller et al., 2002; Cooke et al., 2008). However, in the late 1960s and the 1970s small numbers of whales in groups of one to three were sighted in the Sea of Okhotsk, South China Sea and the Sea of Japan (Ilyashenko, 2011). The population was estimated to be 100-200 individuals by Berzin and Yablokov (1978; cited in Ilyashenko, 2011). In the 1980s larger groups of whales began to be observed.

It is generally assumed that the small population of whales that summers off the northeastern coast of Sakhalin Island is the surviving remnant of the western North Pacific gray whale population (Weller et al., 1999, 2012). Occasional sightings or strandings of whales in Japan, Korea and China give credence to the belief that this population summered in the Sea of Okhotsk and migrated south to wintering sites in Asia which is thought to be the historical migration pattern of the western North Pacific gray whale. One ostensibly migrating whale killed in Japan was matched photographically to a whale photographed as a calf in the Sea of Okhotsk (Weller et al., 2008; Weller and Brownell, 2012) providing the first confirmation of this migratory corridor in recent times. Since 2002 photographic and biopsy data have been collected from the whales that summer in the Sea of Okhotsk on the northeastern coast of Sakhalin Island and southeast Kamchatka (Tyurneva et al., 2012). Genetic studies have compared these whales to various samples taken from the eastern North Pacific gray whale population using mitochondrial DNA (mtDNA) sequences which track maternal lineages, and a moderate number (8-13 depending on the study) of microsatellite loci which are biparentally inherited markers. Both the mtDNA and microsatellite loci show statistically significant differentiation of the eastern and western populations (Lang et al., 2010).

Taken together, the evidence appears to support the hypothesis that this small population is the remnant of the once presumed extinct western North Pacific gray whale population. However, in 2010 a satellite tag was placed on a 13-year old male western gray whale off the northeast coast

of Sakhalin Island (Mate et al., 2011). The whale, known as “Flex” began his migratory journey on December 12, 2010 by travelling eastward to the west coast of the Kamchatka Peninsula. He swam around the southern tip of Kamchatka and proceeded north along the coast to Kamchatka Bay. By January 3, 2011 Flex began to swim east across the Bering Sea towards the North American continent. He crossed the Gulf of Alaska and arrived at the coast of Washington, USA by February 2, 2011. The transmitter failed three days later on February 5 near the Oregon coast with Flex apparently heading south along the North American coast.

Better data were obtained from a transmitter placed on a female western North Pacific gray whale at Sakhalin named “Varvara” in 2011. That transmitter lasted for more than a year and Varvara was tracked from Sakhalin to the eastern North Pacific gray whale wintering areas off western Baja, Mexico, and then back again to Sakhalin (IUCN 2012b).

Flex’ surprising journey prompted examination of other possible records to determine if the whales that summer in the Sea of Okhotsk might generally migrate to and from North America rather than, or in addition to wintering habitats in Asia. Matches of photographs of whales taken at Sakhalin were made with photographs of whales from British Columbia (n = 6, Weller et al., 2011) and Mexico (n = 13, Urban et al., 2012) and genetic matches (n = 2, Lang et al., 2011a) of whales biopsied at Sakhalin and Southern California have now been reported as well as the whales with satellite tags (unpublished). Thus, a total of 23 whales have been identified that have travelled between the Sakhalin Island summering localities and North America. This represents approximately 15% of the western North Pacific gray whale population.

Clearly questions remain about the population biology of the whales that summer in the Sea of Okhotsk. Central to this is the finding of significant mtDNA and nuclear gene differences between this population and the eastern gray whales in the face of what appears to be a high level of mixing. This paper seeks to clarify the potential stock structure scenarios that are consistent with the data on genetics, distribution and movements of these whales and makes recommendations regarding genetic methods to help resolve the issue.

**Genetic differentiation of western and eastern North Pacific gray whales.**—The genetics of the western North Pacific gray whale population has been studied and compared to the eastern gray whale population using mtDNA (LeDuc et al., 2002; Kanda et al., 2010; Meschersky et al., 2012), nuclear microsatellites (Lang, 2010; Lang et al., 2010b), and both (Lang et al., 2011a). These studies consistently show evidence of genetic divergence between the populations expressed as statistically significant differences in mtDNA haplotype frequencies ( $F_{st}$ ) and microsatellite allele frequencies ( $F_{st}$ ). The level of genetic diversity (e.g., heterozygosity) is similar for microsatellites as is nucleotide diversity of mtDNA, but mtDNA haplotype diversity is substantially greater for the eastern population than for the western population (Lang et al., 2011a). The findings that two of the estimates of genetic diversity are similar and the values for these estimates are fairly high indicate that a substantial amount of genetic variation exists within the small western population, despite the severe population reduction caused by hunting. However, the distributional pattern of haplotypes is distinct between the two populations with two haplotypes being of very high frequency in the western population (haplotype A, 0.51 and B, 0.44) whereas the most common haplotype in the eastern gray whale population was 0.15

(haplotype A). The genetic results are consistent with the two populations being distinct, and of drastically different sizes especially with respect to the number of breeding females.

The question of genetic distinctness between the two populations, however, seems to be inconsistent with the observation of a substantial (but as yet unknown) proportion of western gray whales migrating to North America rather than to wintering habitats in Asia. And it must also be recognized that an apparently high level of (primarily) male mediated gene flow has been documented by Lang et al. (2011a) who report a significant  $F_{st}$  for microsatellites for females, but not for males between the eastern and western populations. (When the sexes are combined the analysis shows a significant  $F_{st}$ , but when sexes are analyzed separately only the female comparison is significant. Of course, statistical power is inevitably lost when the sample sizes are reduced for separate analyses of the sexes.). The fact that both males and females in approximately equal numbers (but from an admittedly small sample size) of the western population are known to migrate to North America (Urban et al., 2012), further questions the population structure of gray whales in the Pacific basin.

**Population structure hypotheses.**—In light of the uncertainty of the nature and history of the western population it is useful to consider stock structure hypotheses that could be consistent with current information on genetics, movements, and distribution of the eastern and western North Pacific gray whale populations.

- Hypothesis 1: a single panmictic population (the eastern gray whales, the western population is extinct; no population structure within the eastern population).
- Hypothesis 2: a single metapopulation (the eastern gray whales includes a genetically distinct subpopulation that summers in the Sea of Okhotsk, genetic differentiation could be due to familial structure or founder effect, or driven entirely by matrilineal fidelity).
- Hypothesis 3: A large eastern population that co-inhabits with the surviving remnant of the western population on the summering range in the Sea of Okhotsk, but the two populations do not interbreed (eastern animals migrate to NA, western animals to Asia).
- Hypothesis 4: A large eastern population that interbreeds with the surviving remnant of the western population (eastern animals migrate to NA, western animals to Asia).
- Hypothesis 5: Two surviving populations, one very large eastern population and a small western population (ca. 155 animals). The Sea of Okhotsk population consists entirely of western gray whales which migrate to both NA and Asia.

These five hypotheses are not exhaustive of stock-structure possibilities but will serve to frame a discussion of what is needed from genetics to resolve the issue. To begin, it must be stated that the well entrenched hypothesis of two geographically isolated and genetically distinct pre-depletion North Pacific gray whale populations consisting of an eastern population that migrated along the North American coast and a western population that migrated along the Asian coast might not be correct. There is very good evidence of the two migratory corridors, but there is no data available regarding genetic differentiation of Asian and North American wintering populations. The best way, and perhaps the only way, of determining the genetic makeup of the pre-depletion western gray whale is by genetic analysis of historical samples as was previously suggested by Brownell et al. (2009). While tissue samples that predate the depletion are not available, bones, baleen or other sub-fossil materials, and even cultural artifacts from the period might be used. Such material has been successfully used to help reconstruct the population

structure of bowhead whales (Alter et al., 2012b; Borge et al., 2007; Morin et al., 2012) and to investigate the impacts of whaling on eastern North Pacific gray whales (Alter et al., 2012a).

Hypothesis 1 considers a single panmictic population representing the extant eastern North Pacific gray whale population. The hypothesis implies both the absence of the (extinct) western gray whale, and a lack of substructure within the extant population. While the western gray whale might be extinct, clearly there is ample evidence of genetic differentiation of the Sea of Okhotsk population (Lang et al., 2011a) to reject the hypothesis of panmixia.

Hypothesis 2 considers the eastern population to be a metapopulation with subpopulations that can be somewhat genetically distinct but not necessarily completely isolated. There is already evidence that the eastern population is functioning as a metapopulation in that the Pacific Coast Feeding Group (PCFG) is genetically distinct in terms of mtDNA (Frasier et al., 2011) from the main population and the Sakhalin population might also be functioning as a “feeding group”. Under this hypothesis the western population would not be a remnant of the pre-depletion western gray whale population, but instead a small population founded by a group of eastern emigrants that have diverged genetically due to a strong founder effect and genetic drift. This is consistent with the observations of no signature of a bottleneck and a non-significant  $F_{st}$  for males (Lang et al., 2011a). Thus the population that summers in the Sea of Okhotsk would represent an expanding population established by a small number of founders and whose genetic differentiation is driven by female fidelity to the summer feeding area. It is also consistent with the observed migration data wherein Sea of Okhotsk whales migrate to the NA wintering lagoons in Mexico. Whales that have migrated south along the Asian coast and to Japan are explained as wanderers from the eastern population as discussed in previous studies (Nishiwaki and Kasuya, 1970; Bowen, 1974; Ilyashenko, 2011).

Hypothesis 3 considers the whales summering in the Sea of Okhotsk to include animals of eastern descent along with the surviving remnants of the pre-depletion western North Pacific gray whale population. The two populations do not interbreed as mating takes place during migration toward the respective wintering areas. This is consistent with the genetics data, as well as the observations of movements between the Sea of Okhotsk and both NA and Asia. However, a Wahlund effect would be expected to cause diploid loci to be out of HW equilibrium and to be maintained across generations. A Wahlund effect is a reduction of observed heterozygosity in a sample caused by subpopulation structure. It stems from the fact that when samples from two populations with different allele frequencies are inadvertently mixed and analyzed as a single population, there appears to be a deficit of heterozygosity. This occurs even when both populations are in Hardy-Weinberg equilibrium. The severity of the Wahlund effect is determined by the degree of genetic differentiation of the two populations.

Hypothesis 4 also considers the whales that summer in the Sea of Okhotsk to include animals of eastern descent along with the surviving remnants of the pre-depletion western North Pacific gray whale population but in this scenario the two populations interbreed. This is consistent with the genetics data, as well as the observations of movements between the Sea of Okhotsk and both NA and Asia. The Wahlund effect would be reduced in each generation at a rate depending on the level of interbreeding.

Hypothesis 5 considers the Sea of Okhotsk whales all to be descendants of the pre-depletion western North Pacific gray whale population but the population includes animals that migrate to NA as well as animals that migrate to Asia. The Sea of Okhotsk whales that migrate to North America maintain a degree of reproductive isolation from eastern gray whales because of temporal differences in the timing of the migrations of the respective populations, during which time mating occurs. Under this scenario, one would expect to have observed significant bottleneck test results, but those tests are not very sensitive. This hypothesis is consistent with the data on gray whale movements, and the genetics data showing overall mtDNA and microsatellite differentiation of the eastern and western populations.

Of the five stock structure hypotheses given above the most unlikely is hypothesis 1 as there is ample evidence of genetic subdivision. Hypothesis 5 also seems unlikely as 1) the population does not show a significant signature of a bottleneck, 2) paternity analysis revealed a high percentage of “missing fathers” within this population (Lang et al., 2010a), these likely are part of the eastern gray whale population, and 3) the population possesses a number of nuclear microsatellite loci that are out of Hardy-Weinberg equilibrium which could be evidence of a Wahlund effect (mixing of populations).

So the most likely scenarios are hypotheses 2, 3 and 4 which differ in their assumption of whether the genetic signatures of population differentiation between the Sea of Okhotsk whales and the eastern gray whale population is due to founder effect resulting from a small number of eastern gray whales establishing the population (2) or the existence of surviving western gray whales (3 and 4), and if there are surviving western gray whales do they interbreed with eastern whales (3) or not (4). It is not possible to prove one way or the other which of these is correct with the current data so we will make recommendations as to the methods and sample design that could be followed to better understand the history and makeup of these populations.

**Recommendations.**—To establish the genetic makeup of the pre-depletion western North Pacific gray whale population we must obtain adequate samples of sub-fossil or cultural artifacts as explained above. This could be done by visiting appropriate museums that might have skeletal material, and possibly historical whaling sites in Japan, Russia and Korea. In addition, a much more extensive assessment of the genetics of the eastern population should be undertaken. This could include analysis of the samples already collected from the Mexican wintering lagoons, but also samples taken from summer feeding sites in the Bering and Beaufort Seas.

Clearly a weakness in the current data is the high proportion sampled of the small Sea of Okhotsk population versus the very low proportion sampled of the eastern North Pacific gray whale population. Based on current data one can conclude that the Sea of Okhotsk population differs significantly from the eastern gray whale samples that have been analyzed, but our confidence in saying they differ significantly from the eastern North Pacific gray whale population is dependent upon how representative are the current samples of the very large eastern population.

The most recent study (Aimee Lang, Pers. Comm.) to address the issue of genetic stock structure within the eastern Pacific gray whale included 177 individuals taken from the summer feeding grounds in the Pacific Northwest (northern California to British Columbia), Chukotka (Russia),

and Barrow (Alaska). This latest study is an improvement over previous eastern gray whale genetic studies in that it included samples from animals from feeding sites, as opposed to only including samples from animals that stranded during migration. Nonetheless, the adequacy of sampling is still clearly not optimal as it fails to comprehensively cover the large summer range of the eastern gray whale and represents such a small fraction of the estimated 19,000 animals in the population.

The major point here is that our understanding of genetic diversity of the eastern North Pacific gray whale population is weak and will require analyses of large numbers of samples taken from feeding grounds and wintering grounds.

We must also improve upon the methods currently being used. The mtDNA control region is widely used in population and evolutionary studies of mammals including cetaceans. Nonetheless, it is known to have limitations especially due to homoplasmy caused by recurrent mutations at hyper-variable sites (Phillips et al., 2009, 2012). To get around this problem, additional protein coding genes, which are more conservative and less subject to recurrent mutations, should be sequenced for all of the animals in the existing database as well as in the future. Minimally this should include two genes such as cytochrome b and ND2. This has already been done by Meschersky et al. (2012) and Alter et al. (2007) examined cytochrome b in eastern North Pacific gray whales. But if next generation sequencing is performed it could be possible to sequence the entire 16,000 bases of the mtDNA molecule.

We should also change the methods used to analyze nuclear DNA genetic markers. Microsatellite loci have an advantage over almost any other nuclear markers in typically possessing very high rates of mutation and hence high levels of variability. But the disadvantages of this method include 1) they are markers of identity by state rather than identity by descent, 2) they cannot be used effectively in analytical methods that are based on phylogenetic analyses, and 3) they are not easily reproduced from lab to lab. Whereas mtDNA studies use sequence analyses and build upon data produced in previous studies deposited in GenBank, microsatellite data must be generated anew for each study.

The current suite of microsatellite loci being used (Lang et al., 2011a) have the additional drawback that they have all been identified and developed from other species of whales. This has been shown to lead to problems with scoring due to potential inexact matches between the primer sequences of the source species compared to that of the species being studied. And, whereas there is no cause for questioning the veracity of the data produced in previous studies, it is simply not the best analytical method available today.

Single Nucleotide Polymorphisms (SNPs) have been shown to be more reliable in scoring, can be used in phylogenetic methods, are reproducible from lab to lab, and the sequences can be deposited in GenBank and thus built upon study by study as is presently done for mtDNA. Moreover, they can be used to analyze ancient or historical samples whereas microsatellites cannot (Morin et al., 2012). The only remaining advantage of microsatellites is that the larger number of alleles per locus provides greater analytical power than for SNPs. But even this can be compensated for by increasing the number of SNP loci. By using genomics methods, it is

possible to identify and analyze thousands of SNP loci which provide the best possible resolution even in analyses requiring high analytical power such as kinship analyses.

With a large set of SNP loci available for analysis, studies can employ a wider variety of experimental designs depending upon the questions to be addressed. For example, markers can be selected for analysis from genes of the immune system, genes open to selection, neutral markers, DNA repair genes, etc. Since it is likely that in the future questions regarding gray whale genetics will expand beyond the current focus of gene diversity and population structure, a more robust tool kit for genetics is needed. Such studies might include examination of genes related to health (such as immune function), development, the sensory adaptations of gray whales (vision, hearing, and smell), longevity, detoxification systems, etc.

We propose that a gray whale genome program be initiated. Whereas the ultimate goal will be to sequence and annotate the genome of the species, the immediate goal of the program will be the development of a SNP panel for use in population genetics. Such a panel could be developed and the primers and methods published with data validation within two years. The methods of next-generation sequencing have advanced to the point where such a “reduced representation” genomic analysis can be done quickly and is less expensive than was possible just a few years ago.

**Concluding remarks.**—Because of the status of the western North Pacific gray whale as critically endangered according to the IUCN, the Scientific Committee of the International Whaling Commission has adopted a conservation plan and further recommended that a collaborative Pacific-wide study be developed under the auspices of the IWC (IWC 2011). The methods proposed in this paper, if developed and implemented, will provide data to better resolve issues, such as population structure and historical demography that are keys to the development of a sound conservation and monitoring program and will provide the opportunity for investigators to build upon databases developed in previous studies. Clarification of the demographic history of the extant North Pacific gray whale will also potentially impact the conservation status of the Sakhalin population. For example, if it is determined that this population is a subpopulation of the eastern gray whale (e.g., hypothesis 2) it might reduce the priority status of the population. However, if it is found that the Sakhalin population includes both eastern and western gray whales (hypotheses 3 and 4) the identification and protection of the small number of western gray whales would remain a high priority.

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