MITOCHONDRIAL DNA VARIATION IN THE CRITICALLY ENDANGERED VAQUITA

PHOCOENA SINUS NORRIS AND MACFARLAND, 1958

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ABSTRACT

The vaquita, Phocoena sinus, is one of two critically endangered cetacean species, and is listed as an endangered species in both the United States and Mexico. These listings result from a small population size, estimated to be 224 animals, and a rapid decline in abundance (18% per annum) thought to be caused by human activities. To characterize the genetic composition of the vaquita, we have sequenced a portion of the mitochondrial DNA control region from 43 individuals collected between 1985 and 1993. All animals had identical sequences. While low genetic variability has been reported for cetacean species, this complete lack of polymorphism in the control region is unique. This result is concordant with the hypothesis that the evolutionary
The vaquita, *Phocoena sinus*, is one of the rarest and most endangered of all cetacean species. This small porpoise, endemic to the upper Gulf of California, Mexico, has the most restricted range of any marine cetacean species. Most records of this species come from the western and northern perimeter of the Gulf of California near San Felipe, Baja California, Rocos Consag, and El Golfo de Santa Clara, Sonora (Fig. 1), all in the shallow northernmost reaches of the Gulf of California (Silber 1990, Silber and Norris 1991, Gerrodette et al. 1995). In addition to its highly limited distribution, the vaquita is not very abundant and probably has not been throughout recent historical times. The species was not discovered and described until well into this century (Norris and McFarland 1958), with full descriptions of external morphology not available until 1987 (Brownell et al. 1987), despite the fact that other small cetacean species were known from the Gulf of California. Presently, vaquita abundance is estimated to be 567 (95% CI 177, 1,073) animals for the entire species (Jaramillo-Legorreta et al., this issue). Barlow et al. (1997) indicated that the vaquita population is declining at 17.7% per year (95% CI -43.2%, 19.3%). The extremely low abundance and high rate of decline may be explained by the high rates of incidental mortality the vaquita experiences due to mortalities in the gillnet and shrimp trawl fisheries (D’Agrosa et al. 1995, D’Agrosa 1995, Vidal 1995).

The vaquita is in perilous condition and the full extent of our knowledge should be applied towards reducing their risk of extinction. Mitochondrial DNA (mtDNA) data have proven invaluable in addressing questions of population structure, an integral part of management and conservation for many species, and evolutionary history. It is often the first genetic marker examined in the study of the genetics of rare or endangered species (Baker et al. 1993, Hoelzel et al. 1993, Schaef et al. 1993, Avise and Hamrick 1996). Here we examined mtDNA control-region sequence variation in the vaquita to gain insight into the level of genetic variability in the species. If the level of variability found is equivalent to (or higher than) that in other porpoise species, it could suggest the species has not lost genetic variability through bottleneck effects or through the rapid decline in abundance attributed to fishery-related mortality. A significantly lower level of genetic diversity might suggest the species has gone through a bottleneck, thereby providing information on the evolutionary history of the species. Alternatively, it could raise the question of whether the low variability could have been caused by the rapid decline in abundance due to incidental mortality (but see Amos 1996; Taylor and Rojas-Bracho, this issue). Further, a low level of mtDNA variability could be indicative of lowered levels of genetic variability overall in the species, raising
Figure 1. Range of vaquita in the northern Gulf of Mexico, and sampling sites (cross-hatch) and sample sizes from each site used in this study.

concerns about the degree of evolutionary flexibility in the species. Such information can be used to augment discussions of conservation and recovery of this rare species.

**Methods**

Skin samples were collected from fisheries-caught or stranded animals (Table 1, and Vidal 1995) between 1985 and 1993 and were preserved in a solution of 20% DMSO and saturated sodium chloride or frozen. The majority of the animals were collected from the area of El Golfo de Santa Clara, but samples representative of the entire range of the species, i.e., San Felipe to El Golfo de Santa Clara and south were also collected (Fig. 1). DNA was extracted following the methods of Rosel et al. (1995), or through two-hour 2% CTAB extractions (2% cetyl trimethyl ammonium bromide, 0.5% NaCl, 20Mm EDTA, 100mM Tris pH 9.0) at 55°C followed by three chloroform-isoamyl alcohol extractions and ethanol precipitation.3

The polymerase chain reaction (PCR; Saiki et al. 1985) was used to amplify a 450–600 base pair (bp) portion of the 5’ end of the hyper-variable control region of the mitochondrial DNA (mtDNA) molecule and flanking transfer RNA genes. The samples were amplified and sequenced as they were collected over a five-year period. As a result, amplification conditions, primers, and

3 Personal communication from J. Smith, Rhodes University, South Africa.
Table 1. Collection dates and locations of vaquita specimens. See also Vidal (1995).

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<th>Collection location</th>
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<td>UABC6-7693</td>
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Sequencing methods were varied. Amplification of the first twelve samples (Table 1) followed conditions of Rosel et al. (1995) and were sequenced manually using the solid-phase sequencing procedure and primers as described in Rosel et al. (1994). Nine samples were sequenced using an Applied Biosystems
373A automated DNA sequencer (ABI, Foster City, CA) as described in Rosel and Block (1996), using new amplification and sequencing primers—L15824 5' - CCTCUCTCTCCCTAAAGACT-3' and H16265 5' - GCCCGGTGGCA- GAAGGGG-3', numbered according to the fin whale sequence of Árnason et al. (1991). The remaining samples were amplified using a new primer L15780 5' - AGTCTTTGTAGTATAAAATACCTTGG-3' paired with H00034 of Rosel et al. (1995) following standard protocols. Some of these samples did not yield bright bands and were reamplified using an internal primer, L15817 5' - GAAAAGGAGGACTACACTCTCCTCC-3', paired with H16498 (Rosel et al. 1995). These PCR products were sequenced on an ABI 373 automated DNA sequencer according to the manufacturer's instructions. Sequences were obtained in both directions for all samples sequenced automatically. The resultant sequences were aligned by eye using the software provided by ABI or the software SeqPup (Gilbert 1994).

**RESULTS**

Due to the different-sized amplification products obtained using the different methodologies, total sequence length varied among some of the samples. All of the sequences were truncated to the shortest sequence obtained. Thus, DNA sequence from the first 322 base pairs of the mtDNA control region was obtained from each of 43 vaquitas, representing about 8% of the entire estimated abundance of the species in 1997. We found no variability across any of the samples. All sequences, despite being generated independently in three different laboratories over a period of five years, were identical. We obtained 380 base pairs of sequence from seven of these individuals, and even in these additional 58 base pairs no variability was seen. The sequence submitted to GenBank (Accession U09703) represents one of the longest sequences obtained.

Differences in sequencing protocols, particularly manual versus automated sequencing, necessitated the design of new oligonucleotide primers. Some primers that worked well for manual sequencing did not produce acceptable sequence under automated sequencing conditions. However, the new primer pairs L15824, H16265 and L15817, H16498 produced excellent sequence under the latter conditions.

**DISCUSSION**

Four of the top five critical conservation issues in cetacean biology involve small cetaceans and all involve small isolated populations (Table 2). The conservation status of the baiji, *Lipotes vexillifer*, is critical, and continued survival of this species is now dependent on capture and translocation of animals to a semi-natural reserve (Reeves and Leatherwood 1995). The vaquita, *Phocoena sinus*, is the second-most critically endangered cetacean species. The Indus river dolphin, *Platanista gangetica minor*, exists in the Indus river of Pakistan in four to six small (less than 150) subpopulations isolated from each other by dams.
Table 2. Population status of highly endangered cetacean species.

<table>
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<th>Species</th>
<th>Abundance estimate</th>
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<tr>
<td>Baiji</td>
<td>Lipotes vexillifer</td>
<td>≤ 200</td>
<td>1993 Ellis et al. 1993 as cited in</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Reeves and Leatherwood 1994</td>
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<tr>
<td>Vaquita</td>
<td>Phocoena sinus</td>
<td>224</td>
<td>1993 Barlow et al. 1997</td>
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<tr>
<td>Indus river dolphin (bhulan)</td>
<td>Platanista gangetica minor</td>
<td>&lt;500&lt;sup&gt;a&lt;/sup&gt;</td>
<td>1991 Reeves and Chaudhry 1998</td>
</tr>
<tr>
<td>Northern right whale</td>
<td>Balaena g. glacialis</td>
<td>295</td>
<td>1992 Knowlton and Kraus 1992</td>
</tr>
<tr>
<td>Ganges river dolphin (susu)</td>
<td>Platanista gangetica</td>
<td>3000–3500&lt;sup&gt;b&lt;/sup&gt;</td>
<td>1993 Reeves et al. 1993</td>
</tr>
</tbody>
</table>

<sup>a</sup> Subdivided among five or six populations.
<sup>b</sup> Subdivided among several river basins.
or barrages (Reeves et al. 1991, Reeves and Leatherwood 1994, Reeves and Chaudhry 1998). Similar circumstances exist for the Ganges river dolphin, *Platanista gangetica gangetica*, although a larger aggregate population size spread over a larger geographic range diminishes the critical status of the subspecies somewhat (Reeves and Leatherwood 1994). The situation facing the northern right whale is unclear. Although protected from hunting since the middle of the century, the North Atlantic population has shown no evidence of increasing abundance, remaining at an estimated 300 animals (Knowlton and Kraus 1994). All five species or subspecies suffer from habitat loss or degradation and incidental mortality, and have declining or at best stable population sizes. To date, genetic information has been published only for the right whale (Schaeff et al. 1993).

In this study, no variability was found in the control region sequences among the 43 vaquita sampled. This lack of variability contrasts sharply with what has been found for other porpoise and cetacean species (Baker et al. 1993, Rosel et al. 1994, O’Corry-Crowe et al. 1997). Even in cases where sample sizes were quite small, as for Dall’s porpoise, *Phocoenoides dalli*, and Burmeister’s porpoise, *Phocoena spinipinnis*, genetic variability and multiple haplotypes were found in the same portion of the control region (Rosel et al. 1995). It should be noted, however, that all of these species have larger population sizes. Thus, although genetic variability is generally thought to be lower overall in cetaceans (Shimura and Numachi 1987, Schlotterer et al. 1991), this result for the vaquita is unique.

Genetic variation within a population can be influenced by a variety of non-mutually exclusive factors, including small effective population size, the biogeographic history of the population, and a decrease in population size due to human-mediated effects. Which of these might best account for low variability in the vaquita mtDNA genome?

It is difficult to evaluate whether the vaquita has always had a small population size. However, the fact that *P. sinus* was not discovered until the middle of this century, despite knowledge of the presence of other small cetacean species in the Gulf of California, suggests that it has not been an abundant species during recent historical times. Furthermore, since long-term effective population size is generally equal to or lower than current population size (Nei and Graur 1984), *P. sinus* may have had a small long-term effective population size for most of its history, although probably historically larger than at present. Studies on American eels (Avise et al. 1986), red-winged blackbirds (Ball et al. 1988), and hardhead catfish (Avise et al. 1987) have all uncovered unexpectedly low levels of genetic variability; this has been attributed to small effective population sizes in these species (Avise et al. 1988). Thus, low genetic variability in the vaquita may be a historical feature of the species.

The evolutionary history of the species may explain the small population size. It has been suggested that *P. sinus* represents a relict population of an ancestral species that crossed the equator from the Southern Hemisphere during one of many periods of Pleistocene cooling and became trapped in the Gulf of California as water temperatures later rose (Norris and McFarland...
1958, Barnes 1985). During glacial maxima (e.g., 18,000 years ago), global cooling, compression of subtropical and tropical zones, and increased upwelling intensities along the eastern Pacific may have provided opportunities for interchange of more temperate species across the tropics (Lindberg 1991). Given this biogeographic history for the vaquita, if the founding isolated population was quite small and persisted as such for many generations, the decrease in genetic variability may have been significant (Barton 1984). Since the effective number of mtDNA genes is one quarter that of nuclear genes, mtDNA sequences have a much shorter time to fixation than do those of nuclear genes (Birky et al. 1983, 1989), and the loss of mtDNA variability during population bottlenecks is relatively more pronounced (Harrison 1989). Therefore, the lack of genetic variability in the vaquita control region may be due to a founder event or population bottleneck at the species' conception, followed by persistent small effective population size and the accompanying effects of genetic drift in small populations, rather than resulting from a recent, rapid decrease in abundance due to mortality in fishing gear, as has previously been suggested. Taylor and Rojas-Bracho (this volume) simulated vaquita population dynamics and found support for the lack of mtDNA diversity resulting from either a historical rarity or because the population was founded by few individuals. They found no support for the hypothesis that low diversity results from the recent decline in abundance.

The persistent small population size, and hence limited number of potential breeding adults, in the vaquita may have resulted in inbreeding in the species. The genetic consequences of inbreeding should not be ignored. With a census population estimate of only 567 animals, the effective population size for the species is lower still (Frankham 1995) making the vaquita vulnerable to genetic problems associated with inbreeding depression and amplifying the risk of extinction (Lynch 1996). The discovery that all 43 vaquita samples carry the same mtDNA control region haplotype raised the concern that the species was inbred and led to the study of Taylor and Rojas-Bracho (this issue). They modeled the risk of inbreeding depression in the vaquita using the genetic data presented here, and concluded that currently the species is not doomed to extinction due to inbreeding depression.

It should be noted that a lack of variability in the control region does not necessarily translate into low overall levels of heterozygosity in the nuclear genome, although most studies have indicated a direct relationship between levels of genetic variability in the mitochondrial genome and heterozygosity in the nuclear genome (Bonnell and Selander 1974, Hoelzel et al. 1993, Gotelli et al. 1994). However, if a population has always been small, there is the chance that recessive lethal mutations have been purged by selection when they become homozygous (Lande 1995). This could lead to the lowering of the genetic load on the population (or species), with the species becoming adapted to low genetic variability and inbreeding (Templeton 1987, Pope 1996). There are a number of examples of populations which exhibit low levels of genetic variability yet persist (Allendorf et al. 1979, Larsen et al. 1983, O'Brien et al. 1989, Reeve et al. 1990, Gilbert et al. 1991, Rave et al. 1994).
including the northern elephant seal, *Mirounga angustirostris*. Reduced to fewer than 100 individuals in the late 1800s due to hunting (Stewart *et al.* 1994), the species has recovered with full protection to an abundance of more than 100,000, increasing at a annual rate of 6% (Hoelzel *et al.* 1993, Stewart *et al.* 1994) despite a lack of any detectable allozyme polymorphism at 24 loci (Bonnell and Selander 1974) and limited variability in the mtDNA control region (Hoelzel *et al.* 1993) and nuclear genome (Lehman *et al.* 1993).

Given the low abundance and apparent recent rapid decline of the population, current discussions for vaquita conservation focusing on eliminating incidental mortality should take precedence over concerns related to the possible negative consequences of low mtDNA genetic variability. If incidental mortality of the species can be completely eliminated, the species could exhibit positive population growth (Hohn *et al.* 1996). Moreover, if the population regains moderate or large numbers, genetic variation may potentially be reintroduced through mutation (Lande and Barrowclough 1987). Such a recovery cannot occur unless incidental mortality is eliminated immediately.

However, genetic variability is crucial to the long-term survival of a species, through its role in allowing a species to adapt to environmental changes. If we infer that a low level of genetic variability in the vaquita mtDNA control region indicates that heterozygosity in the nuclear genome is also reduced, then this result may have significant bearing on further prioritization of conservation efforts. The Upper Gulf of California has experienced significant environmental changes over the last century and will face more in the future. Diversion of water from the Colorado River for irrigation in the United States has reduced water flow into the Gulf to negligible levels (Cisneros-Mata *et al.* 1995, Glenn *et al.* 1996). Certainly this has had an impact on the hydrodynamics and chemistry of the upper Gulf, which in turn may directly effect fish stocks and other prey foods of the vaquita (see Rojas-Bracho and Taylor, this issue). For the vaquita, with the potential for having a decreased degree of genetic flexibility in adapting to such changes, this aspect of conservation should not be overlooked. In the long-term, recovery and persistence also requires a healthy environment.

Further work on the vaquita should examine variability in the nuclear genome. Information on relatedness, breeding structure and social structure might better advance conservation efforts. Hypervariable simple repeat loci, or microsatellites, exhibit properties which make them a powerful tool for addressing issues of inbreeding, kinship, and breeding structure (Morin and Woodruff 1992, Amos *et al.* 1993, Bruford and Wayne 1993, Queller *et al.* 1993), as well as for studying population structure and genetic exchange (Gottelli *et al.* 1994, Paetkau and Strobeck 1994, Roy *et al.* 1994). We have begun examining microsatellite variability in the vaquita using loci isolated from the congeneric harbor porpoise, *Phocoena phocoena* (Rosel *et. al.* 1999) and have begun screening for vaquita microsatellites as well (Rojas-Bracho, unpublished). Preliminary examination using two loci of seven individuals has revealed multiple alleles at each locus. Most animals are heterozygous. It will be instructive to see how the microsatellite heterozygosity in the vaquita com-
pares to the harbor porpoise, a species that has not suffered a severe depletion in abundance. An estimate of effective population size from these data might usefully be compared to the recent abundance estimate to provide information on breeding success in the species (Frankham 1995).

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LITERATURE CITED


Ball, R. M., S. Freeman, F. C. James, E. Bermingham and J. C. Avise. 1988. Phylogeographic population structure of red-winged blackbirds assessed by mito-
chondrial DNA. Proceedings of the National Academy of Sciences, USA 85:1558–1562.


Gilbert, D. G. 1994. SeqPup, a biological sequence editor and analysis program for multiple computer systems. Version 0.5, Published electronically on the Internet at ftp://iubio.bio.indiana.edu/molbio/seqpup/.


ROSEL AND ROJAS-BRACHO: VAQUITA GENETIC VARIATION


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