Annex S

Estimating Pre-whaling Abundance

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INTRODUCTION

A recent study by Roman and Palumbi (2003; SC/56/O21) used the degree of genetic diversity at the mitochondrial (mt) control region to infer historical levels of abundance of 240,000 humpback, 360,000 fin and 265,000 minke whales in the North Atlantic. The estimates reported by Roman and Palumbi greatly exceeded other previously reported estimates of current and pre-whaling abundance of these species in the North Atlantic. Table 1 lists issues which may explain the observed discrepancy between the genetically-based estimates reported by Roman and Palumbi, and other lower estimates. The Working Group also assessed the relevance of estimates of historic whale abundance to RMP-based management, and identified key research questions.

RECOMMENDATIONS

In order to assess if genetically-based estimates of abundance can inform the management of cetaceans, the Working Group recommends that the following aspects be investigated or undertaken.

To estimate:

• the ratio of effective to census population size in baleen whales:

- the mode and rate of the baleen whale mitochondrial control region at a scale relevant for translating intraspecific estimates of genetic diversity to effective population size;
- the genetic diversity at multiple unlinked nuclear loci in addition to mitochondrial loci;
- the degree of bias in the estimate of genetic diversity due to deviations from mutation-drift equilibrium as observed in North Atlantic minke and fin whales:
- the effect of un-sampled ghost populations upon the estimates of genetic diversity reported by Roman and Palumbi:
- the overall variance of the final abundance estimate derived from genetic diversity;
- the statistical reliability of catch estimates based upon whaling records; and
- the maximum abundance possible given the available habitat and prey resources.

REFERENCES

Roman, J. and Palumbi, S.R. 2003. Whales before whaling in the north Atlantic. *Science* 301: 508-510.

Table 1

Issues explaining the observed discrepancy between genetically-based abundance estimates (SC/56/O21) and estimates from other sources.

Issue/variable	Comments	Source
Genetics		
Single mtDNA marker/locus	Imprecise and inaccurate estimate of population diversity and divergence.	9
Mutation rate	Direct estimation of mutation rates from \sim 2,800 transmission events in humans revealed up to ten times higher rates than those obtained by phylogenetic estimation. If this is the case in baleen whales then genetic estimates of abundance should likely be adjusted downward, perhaps by as much as a factor of ten.	6
Un-sampled populations	Un-sampled (ghost) populations contribute different levels of genetic diversity to target population through immigration. <i>The presence of ghost populations can bias estimates of genetic diversity; the degree of bias will depend upon the migration rate and size of each population.</i>	3
Changing population size	North Atlantic fin and minke whale mt control region DNA sequences show strong signs of significant deviations from mutation-drift equilibrium in a manner consistent with exponential growth over evolutionary time. This aspect would negatively bias genetic estimates of abundance (in the case of North Atlantic fin and minke whales) to an unknown extent.	2,4
The estimate of genetic diversity is a harmonic mean over evolutionary time	Genetic diversity estimates are harmonic means strongly influenced by low effective population sizes. <i>Implies that historic abundance inferred from genetic diversity is likely negatively biased.</i>	
Catch data		
Approach	Total catches are estimated as the sum of known catches plus estimates of unknown catches derived from other information. A 'notional' upper bound of pre-whaling abundance is the current abundance plus total of known and estimated (extrapolated) catches. For North Atlantic humpback whales, the upper bound is 11,000 (current abundance) plus 29,000 (known and extrapolated catches) = 40,000 whales. For North Atlantic fin whales, upper bound is 56,000 (current abundance) plus 99,000 (known and extrapolated catches, which includes 25,000 unspecified whales) = 155,000. These notional upper bounds cannot be reconciled with Roman and Palumbi's genetic estimates of 240,000 and 360,000 humpback and fin whales, respectively.	5,12,13,1
Under-reporting	Absence of catch limits meant there was no incentive for underreporting prior to the 1930s; and the catch record after this time is largely complete.	12
Gaps in catch record	Known catch records (and other economic data) are employed to estimate catches for voyages/areas where catch records are poor.	12
Ecology		
Constraints driven by habitat and prey availability	Availability of sufficient suitable habitat and prey base to support the number of animals suggested by Roman and Palumbi's genetic estimates of abundance seems implausible.	
	For instance, Roman and Palumbi's genetic estimate implies approx 25,000 humpbacks and 36,000 fin whales occupying the Gulf of Maine.	
Management		
Relevance	Pre-whaling abundance is not an input parameter in the RMP, but is rather implicitly estimated from the catch history estimates.	7, 10, 11
Time frame	Roman and Palumbi's genetic estimates (even if correct) cannot be assigned to a sufficiently narrow historical time period; thus, their relevance to current management of whale populations cannot be assessed. Additional analyses of mitochondrial and nuclear loci suggest that western North Atlantic humpback whale population was unlikely (p<.05) to have undergone a 95% reduction (from 240,000 to the current 12,000), less than 600 years ago (nuclear DNA) or more than 2,000 years ago (mtDNA).	8

SOURCES

- 1. Allison, C. and Smith, T. In prep. 20th Century catches. To be submitted to Journal of Cetacean Research and Management.
- 2. Andersen, L.W., Born, E.W., Dietz, R., Haug, T., Øien, N. and Bendixen, C. 2003. Genetic population structure of minke whales (*Balaenoptera acutorostrata*) from Greenland, the North East Atlantic and the North Sea probably reflects different ecological regions. *Mar. Ecol. Prog. Ser.* 247: 263-280
- 3. Beerli, P. 2004. Effect of unsampled populations on the estimation of population sizes and migration rates between sampled populations. *Mol. Ecol.* 13:827-836.
- 4. Bérubé, M., Aguilar, A., Dendanto, D., Larsen, F., Notarbartolo di Sciara, G., Sears, R., Sigurjónsson, J., Urban-R, J. and Palsbøll, P.J. 1998. Population genetic structure of North Atlantic, Mediterranean Sea and Sea of Cortez fin whales, *Balaenoptera physalus* (Linnaeus, 1758): analysis of mitochondrial and nuclear loci. *Mol. Ecol.* 7: 585-600.
- 5. Holt, S.J. 2004. Counting whales in the North Atlantic letter to Editor. Science 303: 39.
- 6. Howell, N., Smejkal, C.B., Mackey, D.A., Chinnery, P.F., Turnbull, D.M. and Herrnstadt, C. 2003. The pedigree rate of sequence divergence in the human mitochondrial genome: There is a difference between phylogenetic and pedigree rates. *Am. J. Hum. Genet.* 72: 659-670.
- 7. Palsbøll, P.J., Bérubé, M., Robbins, J., Nettel-Hernanz, A., Clapham, P.J. and Matilla, D. 2004. Whales before whaling in the North Atlantic: nuclear DNA markers. Paper SC/56/O25.
- 8. Palsbøll, P.J. Unpublished results.
- Palumbi, S.R. and Baker, C.S. 1994. Contrasting population structure from nuclear intron sequences and mtDNA of humpback whales. Mol. Biol. Evol. 11: 426-435
- 10. Roman, J. and Palumbi, S.R. 2003. Whales before whaling in the North Atlantic. Science 301: 508-510.
- 11. Palumbi, S.R. and Roman, J. 2004. Pre-exploitation abundance of whales: Reading ecological history from population variation in DNA. Paper SC/56/O21.
- 12. Smith, T. D. and Reeves, R.R. 2004. Estimating whaling catch history. Paper SC/56/O22.
- 13. Walløe, L. 2004. Whales before whaling in the North Atlantic What about fin whales? Paper SC/56/O26.