Some concerns for stock definition in minke whales

Naohisa Kanda, Mutsuo Goto, and Luis A. Pastene

The Institute of Cetacean Research, 4 —18, Toyomi —cho, Chuo —ku, Tokyo 104-0055, JAPAN

ABSTRACT

Examination of population structure (stock structure in fisheries) is essential for conducting effective management of minke whales.   Biochemical and molecular genetics analysis have been used to attempt to distinguish reproductively isolated populations of minke whales for evaluating the IWC stock divisions.   It is important to know, however, that the genetic data may not fully compatible to demographic distinction of the populations due to the characteristics of genetic data and the biology of minke whales.   For instance, their capability of long-distance dispersal obscures population boundaries detectable by using genetic markers due to high mixing rate between the populations.   In this report, we address our thoughts and concerns for interpretation of genetic data in defining population structure of minke whales.

INTRODUCTION

Genetic population structure is examined by quantifying the amount and distribution of genetic diversity in a taxon within a geographic area.   Genetic diversity can be partitioned into components of genetic variation within populations and genetic differences among populations.   Loss of genetic variation within populations can be associated with a reduction in a variety of fitness attributes (Mitton and Grant, 1984; Allendorf and Leary, 1986) and is expected to reduce the chances of them being able to make adaptive responses to future changing conditions through the process of natural selection (Fisher, 1930; Ayala, 1965, 1969; Frankham, 1980).   Genetic differences among populations may be also important for population persistence.   Some of this differentiation among populations may have evolved as adaptations to their local environments (Fox, 1993; Phillipp and Clausen, 1995).   These local adaptations can be disrupted or broken down by a loss of genetic variation due to a reduction in population size.   Genetic variation within populations and genetic differences among populations, therefore, can be important for both short and long term population viability.

'Population' is referred to genetically isolated breeding units.   In the area of fisheries sciences, however, reproductively isolated populations are commonly designated as 'stock' and genetic population structure as stock structure for management purpose.   In this report, we use the term 'population' in most cases because we think it is genetics-oriented.   We may use the term 'stock' when we deal with fisheries management.

Both geneticists and managers have long recognized the usefulness of the genetic information to identify reproductively isolated populations.   However, a major and recurrent problem in defining populations is to determine how much differences are enough to be significant.   The best strategy in defining populations (or stocks) is to use all available information for or against reproductive isolation.

THE CASE OF MINKE WHALES

Population structure of minke whales

Minke whales are capable of migrating long distance in both west to east and north to south. This suggests that population differentiation in minke whales tend to be very weak due to high mixing between populations.

Minke whales migrate between breeding and feeding grounds. Their breeding grounds, however, have not yet been found. This is partially because no aggregation of minke whale females has been found during their breeding season (Kasamatsu, 2000), suggesting they might not have specific breeding grounds as other whales, such as humpback whales, have. They probably distribute widely at low and middle latitude.

Around the Japanese coast, at least two different populations are known to exist: one population distributes in the North Pacific and the other in the Sea of Japan (Omura and Sakiura, 1956; Ohsumi, 1977; Kato, 1992; Wada and Numachi, 1991; Goto and Pastene, 1997; Pastene *et al.*, 1999). These two populations differ each other in body size, conception dates, allozyme allele frequencies, and mitochondrial DNA (mtDNA) haplotype frequencies, suggesting their reproductive isolation. Whales in both areas migrate to the southern part of the Okhotsk Sea in spring, and then stay there till the end of summer (Omura and Sakiura, 1956; Hatanaka and Miyashita, 1997). Although they share feeding ground in the southern part of the Okhotsk Sea, their temporal distribution there appears not to overlap completely (Omura and Sakiura, 1956; Goto and Pastene, 1997).

Contrary to the case between the North Pacific and Sea of Japan populations, data from studies of genetics, morphometry, and conception date showed the lack of clear population differentiation among samples within the western North Pacific (reviewed by Hatanaka, 1997 and Pastene *et al.*, 1999). The samples were collected from a very wide geographic area in the western North Pacific from 1994 to 1999 on the basis of stock boundaries set by the International Whaling Commission, i.e., sub-areas 7, 8, and 9 (IWC, 1994). Both biochemical and molecular genetics analysis detected no genetic differences among these samples except the ones collected from the western part of the sub-area 9 in 1995 and 2000 that showed a weak genetic heterogeneity in mitochondrial DNA haplotype frequencies (i.e., Goto *et al.*, 2001). This suggests that these samples came from a genetically same group of minke whales (but see next section).

As in the western North Pacific, population differentiation of minke whales seems to be very weak in the Southern Hemisphere (reviewed by Pastene and Goto, 1999). Data from the studies of genetics, morphology/morphometry, tagging pollutant burden, and catch and sighting distribution detected some degrees of population differentiation. Observed differences, however, were very small, and the population boundaries indicated by these studies were inconsistent from each other even though some of these studies used same samples.

Because of the above observations, unless there are any physical or geographic obvious barriers that separate different groups of whales from others (i.e., Japanese Archipelago separating the Sea of Japan population and North Pacific population of minke whales), minke whales tend not to build up strong population differentiation among them.

Thoughts and concerns for examining minke whale populations using genetic markers

The Stock Identification Working Group was established to develop stock definitions for the purpose of effective management of whales (IWC, 1999). At the 51st meeting of the Scientific Committee, summaries of all of the

studies conducted on minke whales from the both North Pacific and Southern Hemisphere were introduced and discussed (IWC, 2000a). It seems, however, that a consensus view on stock definition has not been developed yet probably due to the lack of agreement within the Working Group on identifying management unit to be conserved (IWC, 2000a). That includes the interpretation of genetic data.

Biochemical and molecular genetic markers have been extensively used in order to describe population genetic structure of minke whales (Wada and Numachi, 1991; Wada *et al.*, 1991; Goto and Pastene, 1997). We should, however, carefully interpret the genetic data and apply these to separation and management of minke whale populations.

Gene flow vs dispersal rate
Population genetics, on the one hand, deals with maintenance of genetic variability in a population, and then it looks at the value of gene flow. Fisheries management, on the other hand, focuses on replenishment of the population by recruitment after human exploitation, and thus it looks at the value of dispersal rate. Gene flow estimates the number of migrants per generation that successfully genetically contributed to a population, while dispersal rate estimates the number of migrants per year that physically move to a population. The level of gene flow, therefore, is generally much less than that of dispersal rate.

Selectively neutral genetic markers mainly show counter-relationship between gene flow and genetic drift in describing population structure. Genetic drift is random changes in the gene frequencies of small isolated populations. In theory, one migrant per local population per generation is sufficient to obscure any disruptive effects of genetic drift (Lewontin, 1974; Mills and Allendorf, 1996). Although such small contribution can maintain current genetic diversity and divergence, it is obvious that one migrant per generation is too low to be an appreciable factor in rapidly rebuilding a depleted population. In another word, no evidence of genetic differences among populations that examined by genetic markers may be attributable to a few migrants per generation between independent populations.

No obvious physical or geographic features and their capability of long-distance dispersal decrease opportunities for isolation and differentiation of minke whale populations in the western North Pacific. Furthermore, their large population size allows only a few migrants to compensate the effects of genetic drift. Intra-oceanic genetic divergence among populations of minke whales, if existed, can be thus very small.

The most common method for estimating gene flow is to estimate fixation index Fst and use this estimated value to estimate the migration parameter mNe (m is migration rate and Ne is effective population size) from the equation $Fst = 1/(1+4mNe)$ with assuming an island model (Hartl and Clark, 1989). Fst represents the level of population differentiation and mNE the number of migrants. The equation, however, indicates that the inverse relationship between Fst and mNe make the equation not reliable for precise estimation of the rate of migration for high gene flow species due to the low limits of confidence interval (Waples, 1998). Assumptions of the island model are also often violated in natural populations.

Increasing sample sizes or the number of genetic markers analyzed could increase the power of detecting such small genetic differences. Although these options may detect small genetic differences, the differences may be so small that ignoring them may be trivia for defining populations or stocks. The differences are not necessarily biologically meaningful. We, therefore, need to determine how small differences are enough to be different populations, e.g., the IWC's stock definition. The IWC thus recognizes the dispersal rate as the key

3

parameter for stock definition. Once the dispersal rate is defined, we can in theory convert it to the rate of gene flow with some assumptions. It should be emphasize again, however, that the proposed dispersal rate may be much higher than we can detect using genetic markers. Defining the level of dispersal rate and separating stocks, therefore, should be taken into account both non-genetic and genetic data.

Sampling scheme

The region where minke whales breed are still unknown. Our samples were collected from migratory corridor and feeding grounds. Sampling of specimens outside breeding grounds violates the assumption of random sampling in testing the null hypothesis that minke whale adults randomly return to the breeding grounds (Waples, 1998). Strictly speaking, therefore, the result we obtained only indicates how minke whales distribute within their feeding ground, but do not indicate how many breeding populations exist. It is danger, therefore, to rely too much on the results obtained from these samples to define the structure of breeding units. Making strong conclusions from these samples may mislead our understanding of minke whale population structure.

We do not mean that the examination of minke whales collected from their feeding grounds is useless. Combined use of the results from both feeding and breeding grounds are the best option (e.g., Pastene and Baker, 1997). Exploring genetic structure in the feeding grounds are thus still important for a better understanding of minke whale life history. We may be also able to detect evidence of the existence of multiple breeding populations with conducting multiple-year samplings in feeding grounds by looking for consistent temporal and spatial genetic differences among samples (e.g., temporal difference of the distribution of individuals from the Sea of Japan and North Pacific populations in the southern part of the Okhotsk Sea. see Goto and Pastene, 1997).

Application of models

We recognize the usefulness of the population genetics models to understand the population structure of minke whales (e.g., Taylor *et al.,* 2000). Two migration models in population genetics have been well used to examine population structure: Wright's Island model and Kimura's stepping stone model (Hartl and Clark, 1989). Any of these models can be applied to minke whales. If individuals from same populations move between breeding and feeding ground together and migration may occur occasionally only between adjacent populations, they would be under the stepping stone model. If individuals from different breeding grounds utilize same, one large feeding ground, mix, and then randomly migrate down to breeding grounds, they would be under the island model. Using only one model (e.g., Taylor *et al.,* 2000 using only stepping stone model), therefore, is not appropriate to identify population structure. We still do not know even what kinds of the models better fit to minke whale population structure. In general, our approach should be to test which models the observed pattern of population structure better fit to.

Metapopulation structure

Recently, IWC working group on stock definition recognized the potential utility of metapopulation analysis for whale management (IWC, 2000b). A metapopulation structure is defined as a network of semi-isolated populations with some level of regular or intermittent migration and gene flow among them, in which individual populations may go extinct but then be recolonized soon from other populations (Meffe and Carrol, 1994).

We can test whether the minke whale populations constitute the metapopulation structure by simply comparing genetic diversity observed from mtDNA to nuclear DNA markers. Under the metapopulation structure, loss of genetic variability is expected to be much greater in mtDNA than in nuclear DNA because mtDNA has small effective population size due to its haploidy and maternally inheritance (Birky *et al.,* 1983). Results from the

4

nuclear DNA and mtDNA studies (reviewed by Pastene and Goto, 1999; Pastene *et al.,* 1999) showed that all of the different classes of genetic markers exhibited exceptionally high polymorphism in the same samples of minke whales and that the genetic diversity of mtDNA was comparable to that of nuclear DNA. These results indicate that the metapopulation structure characterized by frequent recolonization and local extinctions of isolated populations are probably not characteristic of minke whale populations.

Retention of high polymorphism at different kinds of genetic markers indicates historically large effective population size of minke whales. Broad overlap of common alleles with few numbers of unique alleles in any of these markers rather suggest that genetic differences among minke whale populations are small in most cases. For whale management especially from genetics perspective, it is reasonable for us to treat minke whales as consisting of a single or a few large populations than as of many small isolated populations unless there are any evidence of apparent population differentiation detected.

CONCLUSION

Genetic analysis is powerful. It depicts the genetic consequences of migration, which allows us to estimate the level of reproductive isolation among different populations. Genetic data alone, however, may not provide sufficient information on identifying population differentiation especially for highly mobile whales. The key for sound management is, therefore, to spend our every effort to gain understandings of genetics, biology, and ecology of the species. Although we need to recognize limitations of each, we should take advantages of the often complementary nature of the different types of information (see Waples, 1998).

ACKNOWLEDGEMENTS

We thank H. Hatanaka for helpful comments on an earlier version of this manuscript.

LITERATURE CITED

Allendorf, F.W., and Leary, R. F. 1986. Heterozygosity and fitness in natural populations of animals. Pages 57-76 in M. E. Soulé, editor. *Conservation biology: the science of scarcity and diversity.* Sinauer Associates, Inc, Sunderland, Massachusetts.

Ayala, F. J. 1965. Evolution of fitness in experimental populations of *Drosophila serrata. Science* 50:903-905

Ayala, F. J. 1969. Evolution of fitness. V. Rate of evolution in irradiated *Drosophila. Proc. Natl. Acad. Sci. USA* 63:790-793.

Birky, C. W. Jr., Maruyama, T., and Fuerst, P. 1983. An approach to population and evolutionary genetic theory for genes in mitochondria and chloroplasts, and some results. *Genetics* 103:513-527.

Fisher, R. A. 1930. *The genetic theory of natural selection.* Oxford University Press, Oxford.

Fox, M. G. 1993. A comparison of zygote survival of native and non-native walleye stocks in two Georgian Bay rivers. *Environ. Biol. Fishes* 38:379-383.

Frankham, R. 1980. The founder effect and response to artificial selection in *Drosophila.* Pages 87-90 *in* A. Robertson, editor. *Selection experiments in laboratory and domestic animals.* Farnham Royal, Commonwealth Agricultural Bureaux, Slough.

Goto, M. and Pastene, L. A. 1997. Population structure of the western North Pacific minke whale based on an RFLP analysis of the mtDNA control region. *Rep. Intl. Whal. Commn.* 47:531-537.

Goto, M., Kanda, N., and Pastene, L. A. 2001. Genetic examination of western North Pacific minke whales

including samples from JARPN II. Paper SC/53/RMP11 presented to the IWC Scientific Committee, July 2001 (unpublished).

Hartle, D. L. and Clark, A. G. 1989. *Principles of population genetics, 2nd ed.* Sinauer Associates Inc., Sunderland, Massachusetts. pp.306-323.

Hatanaka, H. 1997. A short review of hypotheses on minke whale stock structure in the western part if the North Pacific. *Rep. Intl. Whal. Commn.* 47:553-555.

Hatanaka, H., and Miyashita, T. 1997. On the feeding migration of the Okhotsk Sea-West Pacific stock of minke whales, estimates based on length composition data. *Rep. Intl. Whal. Commn.* 47:557-564.

International Whaling Commission. 1994. Report of the Scientific Committee, Annex G. Report of the Working Group on North Pacific Mink Whale Management Trials. *Rep. Intl. Whal. Commn.* 44:120-144.

International Whaling Commission. 1999. Report of the Scientific Committee, Annex D. Appendix 4. A recommendation by the RMP Working Group on Stock Identification to establish a working group of the Scientific Committee in stock definition. *J. Cetacean Res. Mgmt.* 1(Suppl.):82-83.

International Whaling Commission. 2000a. Report of the Scientific Committee, Annex M. Report of the Working Group on Stock Definition. *J. Cetacean Res. Mgmt.* 2(Supple.):290-294.

International Whaling Commission. 2000b. Report of the Scientific Committee, Annexes I. Report of the Working Group on Stock Definition. 52nd meeting of the International Whaling Commision, Adelaide, Australia, 2000.

Kasamastu, F. 2000. *Ecology of Whales.* Kouseihsa-Kouseikaku, Tokyo Japan (in Japanese).

Kato, H. 1992. Body length, reproduction and stock separation of minke whales off northern Japan. *Rep. Intl. Whal. Commn.* 42:443-453.

Lewontin, R. C. 1974. *The genetic basis of evolutionary change.* Columbia University Press, New York.

Meffe, G. K., and Carroll, C. R. 1994. *Principles of Conservation Biology.* Sinauer Associates Inc., Sunderland, Massachusetts. pp.562

Mills, S. L., and Allendorf, F. W. 1996. The one-migration-per-generation rule in conservation and management. *Cons. Biol.* 10:1509-1518.

Mitton, J. B. and Grant, M. C. 1984. Associations among protein heterozygosity, growth rate, and developmental homeostasis. *Annu. Rev. Ecol. Syst.* 17:391-421.

Ohsumi, S. 1977. Minke whales in the coastal waters of Japan. *Rep. Intl. Whal. Commn.* 27:164-166.

Omura, H. and Sakiura, H. 1956. Studies on the little piked whale from the coast of Japan. *Sci. Rep. Whal. Res. Inst. Tokyo* 11:1-37.

Pastene, L. A., and Baker, C. S. 1997. Diversity and distribution of mtDNA lineages from humpback whales on the feeding and wintering grounds of the Southern Hemisphere. Paper SC/49/SH26 presented to the IWC Scientific Committee, October 1997 (unpublished).

Pastene, L. A., and Goto, M. 1999. Review of the studies on stock identity in the minke whales *Balaenoptera acutorostrata* from the Southern Hemisphere. Paper SC/51/CAS30 presented to the IWC Scientific Committee, May 1999 (unpublished).

Pastene, L. A., Goto, M., and Fujise, Y. 1999. Review of the studies on stock identity in the minke whales *Balaenoptera acutorostrata* from the North Pacific. Paper SC/51/RMP15 presented to the IWC Scientific Committee, May 1999 (unpublished).

Phillipp, D. P. and Clausen, J. E. 1995. Fitness and performance differences between two stocks of largemouth bass from different river drainages within Illinois. *American Fisheries Society Symposium* 15:236-243.

Taylor, B. L., Chivers, S. J., and Dizon, A. E. 2000. Estimating the statistical power to detect population subdivision using mitochondrial DNA. Paper SC/F2K/J4 presented to the IWC Scientific Committee Workshop to Review the Japanese Whale Research Programme under Special Permit for North

Pacific Minke Whales (JARPN), Tokyo, 7-10 February 2000 (unpublished).

Wada, S. and K. Numachi. 1991. Allozyme analyses of genetic differentiation among the populations and species of the *Balaenoptera*. *Rep. Intl. Whal. Commn. Special Issue* 13:125-154.

Wada, S., Kobayashi, T., and Numachi, K. 1991. Genetic variability and differentiation of mitochondrial DNA in minke whales. *Rep. Intl. Whal. Commn. Special Issue* 13:203-214.

Waples, R. S. 1998. Separating the wheat from the chaff: Patterns of genetic differentiation in high gene flow species. *J. Hered.* 89:438-450.