THE ROYAL SOCIETY

Predicted decline of protected whales based on molecular genetic monitoring of Japanese and Korean markets

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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.

Keywords: molecular genetic monitoring; minke whales; population decline; protected stock; mitochondrial DNA; International Whaling Commission

1. INTRODUCTION

Following decades of mismanagement resulting in the commercial extinction of many whale populations and the depletion of most others, in 1982 the International Whaling Commission (IWC) voted to impose a moratorium on all commercial whaling. The moratorium was intended to provide time for the assessment of depleted populations ('stocks') of whales and for the development of a management procedure that would prevent over-exploitation in the case of any future commercial whaling. This Revised Management Procedure (RMP) is a formula for determining the level of allowable commercial catches for a stock based on its current abundance, history of exploitation, levels of incidental takes and overlap with adjacent stocks having differing catch histories (International Whaling Commission 1999*a*). Although accepted in principle by the IWC, the RMP cannot be implemented effectively without a larger management scheme that includes provisions for observation and monitoring in order to verify catch and trade records. Otherwise, regulated hunting of abundant oceanic populations or regional stocks under the RMP could act as a cover for illegal or unregulated exploitation of depleted stocks. The revelations of extensive illegal whaling by the former Soviet Union following the Second World War is compelling evidence of the critical importance of such an independent system of verification (Yablokov 1994).

Molecular genetic methods provide powerful new tools for the identification of the species origins of whale, dolphin and porpoise products from retail markets (Dizon *et al.* 2000)—the end-points of legal and illegal exploitation of wildlife. With the advent of the polymerase chain reaction (Saiki *et al.* 1988), DNA can be recovered from almost any biological source, even products that have been preserved, cooked or canned. Although the species origins of these products may be impossible to

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Received 10 February 2000 *Accepted* 9 March 2000

determine on the basis of appearance, they contain DNA, which can be sequenced and compared to known 'type' or 'reference' specimens. Species of whales, dolphins and porpoises can be distinguished by nucleotide substitutions in the sequences of loci such as the mitochondrial (mt) DNA control region or cytochrome *b* genes (Árnason *et al.* 1993; Rosel *et al.* 1995; Henshaw *et al.* 1997; Dalebout *et al.* 1998; LeDuc *et al.* 1999). In a phylogenetic framework, these substitutions represent fixed differences in character states and will group 'test' sequences from unknown products with reference sequences, to the exclusion of other reference sequences (Baker *et al.* 1996). The consistency of a phylogenetic identification can be evaluated statistically by bootstrap resampling of test sequences and reference sequences.

However, molecular genetic identification of stock origins is a more difficult problem. Stocks of whales are more likely to be distinguished by differences in the frequencies of their alleles rather than fixed differences at a locus (Baker & Palumbi 1997). This limits the use of a strictly phylogenetic approach (as noted by Dizon *et al.* 1992) and is more likely to require an estimation of assignment probability, which depends on the degree of genetic differences between putative source populations and chance attributes of particular individuals within a source population (e.g. the inheritance of a common or rare allele). In many cases it may not be possible to determine the stock origin of a single product with much confidence. However, attributing a sample collection of products to a particular stock is amenable to statistical tests and, in some cases, the maximum-likelihood estimation of the proportion of the sample attributable to alternative stocks (Bowen *et al.* 1996; Pella & Milner 1987).

The importance of distinguishing and conserving stocks or comparable population units is a well-recognized problem of current conservation biology and management (Donovan 1991; Waples 1991). There is a growing awareness that unique evolutionary histories and, perhaps, independent evolutionary trajectories are harboured below the systematic level generally recognized as defining species (Ryder 1986; Moritz 1994; Vogler & Desalle 1994). In general, it is stocks or subpopulations and not species that are the fundamental unit for setting catch or hunting limits of exploited species and for establishing critical habitats and evaluating the recovery of protected species.

Here we present a two-tiered analysis of molecular genetic variation in order to determine the origins of whale products purchased in retail markets in Japan and the Republic of (South) Korea. We first summarize published and unpublished results of market surveys conducted from 1993 to early 1999 using phylogenetic methods for identifying the species origins of commercial products. We then extend this phylogenetic approach with a 'population aggregation analysis' (Davis & Nixon 1992) of oceanic populations and a statistical comparison of mtDNA haplotype frequencies distinguishing regional stocks. Our intent was to assess the effectiveness of the current moratorium for protecting depleted species and stocks and to develop a system for monitoring retail markets should commercial whaling resume under the RMP. We considered that such a system should be capable

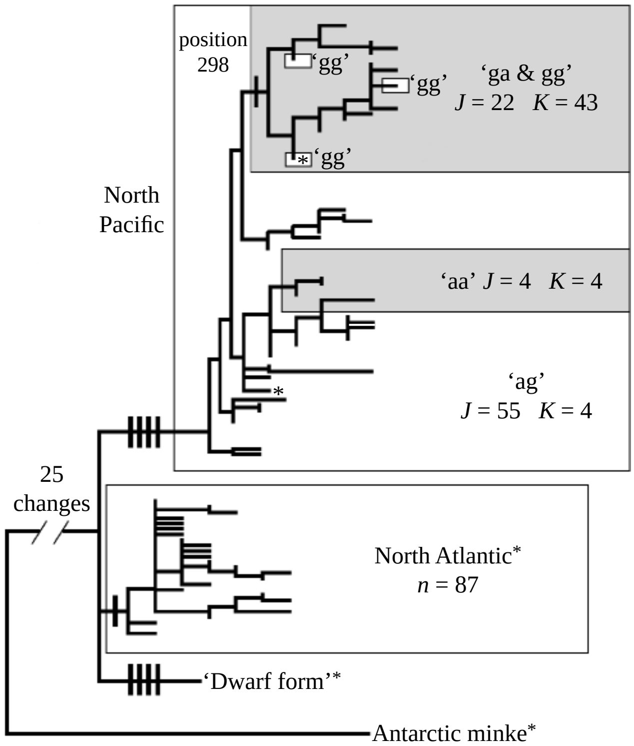

Figure 1. Phylogenetic reconstruction of the reference sequences from the mtDNA control region sequences of North Atlantic, southern dwarf and North Pacific minke whales shown in relation to commercial products from the Japanese and Korean retail markets ($n = 132$ products with full sequence length). The North Atlantic reference sequences were derived from a sample of the central and eastern North Atlantic stock hunted by Iceland and Norway ($n = 87$ individual whales). The neighbour-joining reconstruction (with Kimura two-parameter corrections) was based on the first 350 bp of the control region available for the central and eastern North Atlantic whales (Bakke *et al.* 1996). Fixed differences in nucleotide sequences distinguishing the North Pacific, North Atlantic and dwarf form are shown as vertical bars along the internal branches uniting these groups. The number of fixed differences distinguishing the Antarctic minke whale is shown above the broken branch. Branch termini of reference sequences, as summarized in Baker *et al.* (1996), are indicated by an asterisk. The position of haplotypes distinguishing the J and O stock and the frequencies of market products from Japan (J) and Korea (K) are shown adjacent to the branch termini (see figure 2). The A > G transition at position 298 occurs only once in the tree. The G > A transition at position 463 occurs several times, presumably as a result of multiple substitutions (homoplasy).

of verifying products from legitimate hunting and, if necessary, provide information on the likely origins of illegitimate products. We also considered that the system should provide information for incorporation into the accepted population model of the RMP to allow an estimation of the demographic impact or threat of any unregulated whaling. The need for such a system is not limited to whaling. Molecular monitoring of markets for other wildlife products, including sturgeon caviar (DeSalle & Birstein 1996), turtle meat (Roman & Bowen 2000) and sea lion penises (Malik *et al.* 1997) has found protected species and misrepresented products. This unregulated exploitation threatens the continued survival

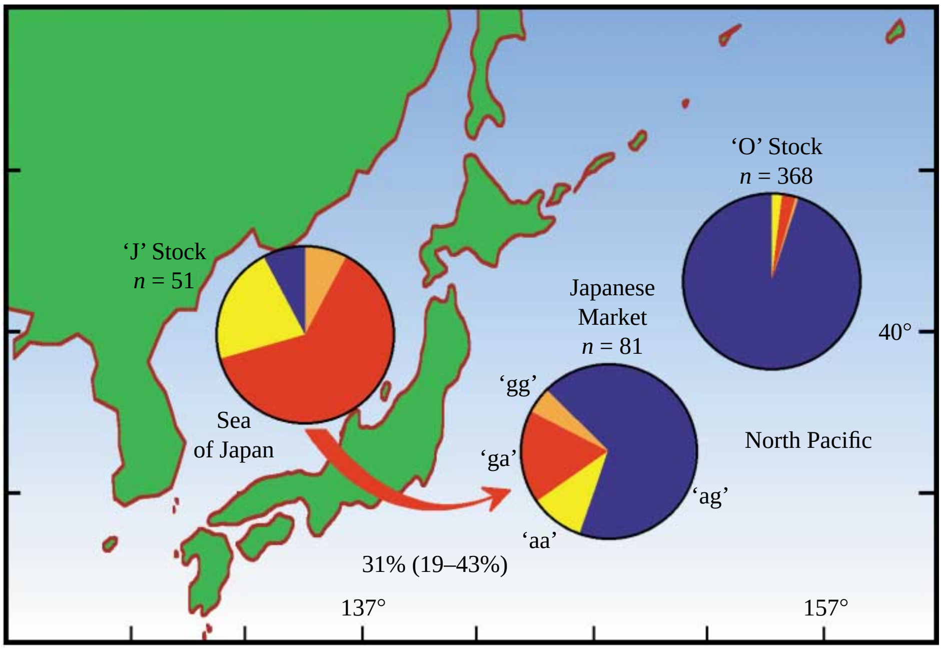

Figure 2. The frequencies of the mtDNA haplotypes of North Pacific minke whales obtained from three sources: (i) Japanese scientific whaling of the O stock during 1994–1998 (M. Goto and L. A. Pastene, unpublished report), (ii) by-catch of the J stock as represented by products purchased in Korean markets during 1994–1997, and (iii) products purchased in Japanese commercial markets during 1993–1999. The arrow and label indicate the source and proportion (with 95% bootstrap CIs) of undocumented J-stock products sold on the Japanese market as estimated by maximum likelihood, using a mixed-stock analysis as implemented in the computer program CONSQRT (Masuda *et al.* 1991). The sequences of the mtDNA haplotypes were classified into haplotypes defined by variable nucleotides at positions 298 and 463 relative to the 5′-end of the control region (see figure 1 and the text for details). The aligned sequences from the market samples are available from the first author's Internet home page (http://www.sbs.auckland.ac.nz/people/university_staff/baker_scott).

of rare species and undermines legitimate programmes for the sustainable use of abundant wildlife species.

2. IDENTIFICATION OF PRODUCTS FROM PROTECTED SPECIES AND STOCKS

Since the moratorium on commercial whaling took effect in 1986, the only documented and regulated source of whale products in Japan has been programmes for scientific research on minke whales. As part of this programme, Japan has killed up to 440 minke whales a year in the Antarctic since 1986 and another 100 minke whales a year in the western North Pacific since 1994. An alternative source of minke whale products could be Norway (Mulvaney 1993), which continues to hunt minke whales in the North Atlantic under an objection to the moratorium. However, the last legal export of these products was in 1986 and current Norwegian domestic policy prohibits further export (Larson 1994). South Korea has no programme of scientific whaling but reports that minke whales killed incidentally by coastal fisheries are the source of products sold openly in the commercial markets of some provinces (Mills *et al.* 1997). A national requirement to document these 'incidental takes' has been in effect since 1996 and a summary of takes is reported annually to the IWC (Kim 1999). Japan also allows the local distribution of products from whales taken incidentally by coastal fisheries but the reported number of these takes is small compared to the scientific hunt (see § 3). In both Japan and Korea, there is no official programme for the mitigation of incidental takes and the market for these products is entirely unregulated. Both countries also allow the sale of products from small cetaceans (e.g. beaked whales, dolphins and porpoises) taken incidentally by coastal fisheries and, in Japan, by directed hunts. There is no consensus on the management of small cetaceans by the IWC and the international moratorium on hunting applies only to baleen whales and the sperm whale.

To test whether commercial products are derived exclusively from this limited documented whaling, we purchased whale products from retail outlets throughout the main islands of Japan from 1993 to early 1999 and in coastal cities along the south-east coast of Korea from 1994 to 1997. In most cases, the products were labelled or verbally described only as 'kujira', the common name for whale in Japanese, or 'gorae', the common name for whale in Korean. In a few cases, the products were labelled or referred to by the common name for whale species, such as 'blue', 'fin', 'minke', etc., although these often proved to be inaccurate. Products labelled or referred to by common names for dolphin, porpoise or other cetaceans were avoided. An exception was made for a small number of dolphin products purchased intentionally in 1998 for pollutant analysis (M. P. Simmonds, K. Hanly and S. J. Dolman, unpublished report). The methods for the market surveys and molecular genetic and phylogenetic analyses are presented in detail elsewhere (Baker & Palumbi 1994; Baker *et al.* 1996; C. S. Baker, F. Cipriano, G. M. Lento and S. R. Palumbi, unpublished report; F. Cipriano and S. R. Palumbi, unpublished report; G. M. Lento, N. J. Patenaude and C. S. Baker, unpublished report).

Table 1. *Species origins of whale, dolphin and porpoise products purchased in the commercial markets of Japan and the Republic of (South) Korea during 1993–1999 as determined by phylogenetic reconstruction of the sequences from the mtDNA control region*

(All identifications of species, genera or family were supported by high bootstrap values (> 90%) using the methods described previously (Baker & Palumbi 1994; Baker *et al.* 1996). The sample sizes indicate the number of products identified to species and not necessarily the number of unique individuals represented by the products (see § 2). Sources: Baker & Palumbi (1994), Baker *et al.* (1996), Cipriano & Palumbi (1999), C. S. Baker, M. L. Dalebout, B. C. Congdon and G. M. Lento (unpublished report), F. Cipriano and S. R. Palumbi (unpublished report), G. M. Lento, M. J. Dalebout and C. S. Baker (unpublished report), G. M. Lento, N. J. Patenaude and C. S. Baker (unpublished report). Full references for unpublished reports are available from the first author's Internet home page (see figure 2).)

species	Japan 1993–1999	Korea 1994–1997	last legal source or year of genus' international protection
Mysticeti			
Northern Pacific minke, *Balaenoptera acutorostrata*	98	54	Japanese scientific whaling ongoing since 1994
Antarctic minke, *Balaenoptera bonaerensis*	293	2	Japanese scientific whaling ongoing since 1986
Bryde's, *Balaenoptera brydei/edeni*	6	2	1986 moratorium or 1987 by Japan under objection
pygmy Bryde's (unrecognized species) (Baker *et al.* 1996)	—	2	1986 moratorium or 1987 by Japan under objection
sei, *Balaenoptera borealis*	5	—	1986 moratorium or 1988 for Iceland scientific whaling
fin, *Balaenoptera physalus*	24	—	1986 moratorium or 1989 for Iceland scientific whaling
blue, *Balaenoptera musculus*	1	—	1966 for blue and 1989 Iceland or blue/fin hybrid scientific whaling for hybrid
blue/fin hybrid	1	—	1989, Iceland scientific whaling (Cipriano & Palumbi 1999)
humpback, *Megaptera novaeangliae*	4	—	1966
Odontoceti			
sperm whale, *Physeter macrocephalus*	3	—	1986 moratorium or 1987 by Japan under objection
pygmy sperm, *Kogia breviceps*	1	—	none
beaked whales, *Berardius bairdii* and *Ziphius cavirostris*	44	1	none
killer whales, *Orcinus orca*	1	1	none
dolphins (more than six species)	78	19	none
Dall's porpoise, *Phocoenoides dalli*	12	—	none
other mammals			
sheep	2	—	none
horse	1	—	none
total	574	81	—

Based on the phylogenetic analysis of sequences from the mtDNA control region, we identified the species origins of 655 'whale' products (table 1). This total included eight species or subspecies of baleen whales, two species of sperm whales, two species of beaked whales, porpoises, killer whales and numerous species of dolphins as well as domestic sheep and horses. As expected from the documented scientific hunting and incidental takes, the most common species found in the retail markets of both Japan and Korea were minke whales, accounting for 447 products or *ca.* 68% of the total products (including the unregulated products from small cetaceans). Contrary to expectation, however, was the continued availability of sperm whale and six baleen whale species. These seven species are protected with few exceptions by the moratorium or earlier IWC agreements (table 1). The sperm and common-form Bryde's whales have not been hunted legally since Japan withdrew its objection to the moratorium in 1987. The formal taxonomy of the pygmy or small-form Bryde's whale remains unresolved, but this species or subspecies would be considered protected under the moratorium. The sei whale was hunted until 1988 and the fin until 1989 under scientific permit by Iceland. Products from this hunt were exported to Japan for commercial sale until 1991. Blue and humpback whales have been protected worldwide since 1966. Analysis of nuclear genes from one of the two products identified by mtDNA as blue whale (purchased in 1993) showed that it originated from a blue/fin hybrid killed during scientific hunting by Iceland in 1989 (Cipriano & Palumbi 1999). Analysis of nuclear genes has not been conducted for the second blue whale product purchased in 1995.

Variation in the mtDNA sequences and preliminary microsatellite profiling established the individual identities of most of the products from protected species, e.g. the five sei whale and four humpback whale products each originated from unique individuals (C. S. Baker, M. L. Dalebout, B. C. Congdon and G. M. Lento, unpublished report; F. Cipriano and S. R. Palumbi, unpublished report). However, the microsatellite profiling was not exhaustive and the market surveys probably included duplicate products from the same individual (G. M. Lento, N. J. Patenaude and C. S. Baker, unpublished report). This should not affect the statistical comparison of the market proportions as a relative index of species composition (Dizon *et al.* 2000).

Although the geographical origins of the products from protected species could be identified in some cases by comparison to extensive data sets of reference sequences (e.g. the humpback products were found to be derived from the North Pacific) (F. Cipriano and S. R. Palumbi, unpublished report; G. M. Lento, N. J. Patenaude and C. S. Baker, unpublished report), this information is not relevant to verification of the current worldwide moratorium. Only the scientific and commercial hunting of minke whales is based on putative stock divisions, although undertaken under objection to the moratorium or by special permit and therefore outside the control of the IWC. For this reason, we used both phylogenetic and population aggregation analyses to determine the oceanic origins of the products from minke whales. Four forms of minke whales have been described from morphological differences or geographical distributions (Dizon *et al.* 1992): a North Atlantic, a North Pacific and two Southern Hemisphere forms (a common and a dwarf form). Genetic evidence supports the recognition of the common Southern Hemisphere form as a distinct species, the 'Antarctic' minke whale (Rice 1998). Based on this classification, our phylogenetic reconstruction identified 293 of the Japanese products and two of the Korean products as Antarctic minke whales, the sole target of scientific hunting by Japan in the Southern Hemisphere.

As yet, there has been no comprehensive analysis of the phylogenetic relationships between the two northern populations and southern dwarf forms or formal agreement on their taxonomic status. To evaluate the likely oceanic origin of the remaining 152 minke whale products from markets in Japan and Korea, sequences from these products were compared to available reference sequences from the North Pacific, North Atlantic and southern dwarf forms and to a population data set from 87 minke whales killed in the central and eastern North Atlantic by Iceland and Norway (Bakke *et al.* 1996). A population aggregation analysis revealed fixed or 'diagnostic' differences at five nucleotide positions between the Japanese/Korean products and North Atlantic minke whales (figure 1). The phylogenetic analyses were consistent with the population analysis, showing strong bootstrap support ($>95\%$) for uniting the Japanese/Korean products together with the North Pacific reference sequences against the North Atlantic population and southern dwarf form. Together these analyses confirmed the expectation that the Japanese/Korean market samples were derived from the North Pacific and, further, showed that this oceanic population is phylogenetically distinct from the North Atlantic population and southern dwarf form minke whales.

The Antarctic minke whales are divided into six stocks based on broad latitudinal divisions of the Southern Hemisphere. The scientific hunting of Antarctic minke whales is geographically widespread and none of the six recognized stocks in the Southern Hemisphere is classified as protected by the IWC. For these reasons, we did not attempt to estimate stock origins for this species. In the western North Pacific, two stocks are recognized by the IWC. Scientific hunting by Japan is limited to the pelagic waters to the east of Japan, an area occupied primarily by the 'O' stock (so-called because it is thought to migrate north into the Okhotsk Sea during part of the year). The reported incidental takes in Korea are limited to the coastal waters of the Sea of Japan and perhaps the Yellow Sea, areas occupied by the so-called 'J' stock. Although the O stock is reported to be relatively abundant, the J stock was depleted by commercial hunting prior to 1986 and is now classified as a protected stock (International Whaling Commission 1997). A biological distinction between these stocks was initially proposed based on seasonal measurements of foetal length (Omura & Sakiura 1956). Extrapolation of conceptions to date indicates a six-month difference in the breeding cycle of the stocks despite an apparent overlap in migratory range during part of the year. A degree of reproductive isolation between the O and J stocks is also indicated by recent surveys of mtDNA showing nearly fixed differences in a small number of mtDNA haplotypes as defined by restriction fragment length polymorphism (RFLP) analysis (Goto & Pastene 1997).

The large differences in the haplotype frequencies between the stocks allowed a simple test of the expectation that all Japanese market samples came from scientific whaling of the O stock. The comprehensive genetic information from the scientific whaling programme (Goto & Pastene 1997; M. Goto and L. A. Pastene, unpublished reports) was used to identify two variable nucleotide positions corresponding to four haplotypes with markedly different frequencies in the two stocks (figure 1) (B. C. Congdon, G. M. Lento and C. S. Baker, unpublished report). An A at position 298 of the control region and a G at position 463 defined the dominant haplotype of the O stock. Combinations of AA, GA or GG at these positions defined the dominant haplotypes in the J stock. For categorical statistical comparison, sequences from the scientific catch for the 1994–1998 seasons ($n=368$) (M. Goto and L. A. Pastene, unpublished report), the Korean market products ($n=51$) and the Japanese market products ($n=81$ sequences with sufficient length) were classified into these four haplotypes (figure 2). More than 95% of the whales killed in the scientific hunt were AG haplotypes while more than 92% of the Korean market products were AA, GA or GG haplotypes. Contrary to expectation, the haplotype frequencies of the Japanese market sample differed significantly from the scientific catch ($p<0.001$). More than 32% of the Japanese products were found to have one of the three haplotypes dominant in the J stock compared to less than 5% of these haplotypes observed in the scientific catch.

To verify that the Korean market products were representative of the J stock, we compared their haplotype frequencies to a sample of whales taken by Korean coastal whaling operations in September and October 1982 ($n=28$) (M. Goto and L. A. Pastene, unpublished

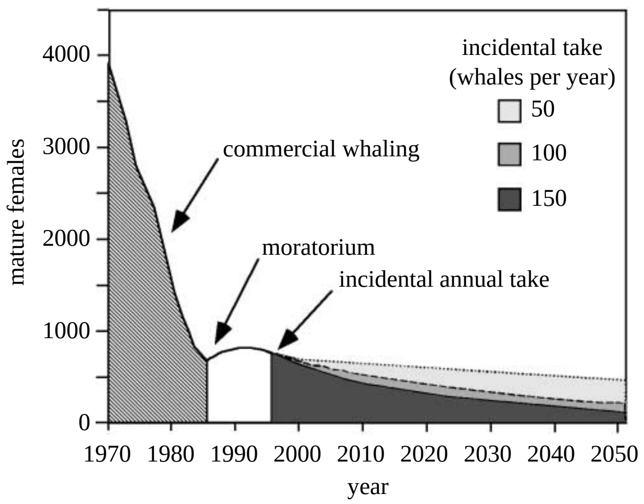

Figure 3. The estimated history and predicted future decline in the abundance of J-stock minke whales (mature females) under three assumed levels of incidental takes (50, 100 and 150 whales per year) for the period of 1998 onwards. Each alternative for the 1998 level of takes was assumed to vary in the future in proportion to the total abundance. The history and projections were based on median values from 100 computer simulations of the population model developed by the IWC Scientific Committee for the implementation of future commercial whaling under the RMP. With the exception of the estimated incidental takes for 1998 onwards, all conditions for the model followed the assumptions of the base case used by the IWC's assessment of the North Pacific minke whale (International Whaling Commission 1999*b*).

report). This small sample was the basis for the genetic analysis of the stock differences used in the current IWC assessment of the North Pacific population (International Whaling Commission 1999*b*). The frequencies of the Korean market products differed significantly from the historical commercial catch ($p < 0.0179$), showing a higher frequency of the AG haplotypes dominant in the O stock. These differences could result from the sale of products from undocumented exploitation of O-stock minke whales in Korean markets. However, the range of O-stock whales is outside the Korean Exclusive Economic Zone and delivery of products from this stock would be a violation of the Convention on International Trade in Endangered Species regulations governing importation from the sea. We know of no direct evidence for such illegal activity. Instead, we suggest the limited geographical and temporal coverage of the historical Korean whaling sample does not represent the full genetic diversity of the J stock. The market products reportedly derived from local by-catch (Kim 1999) and purchased throughout the south-eastern region of Korea across several years should provide a better estimate of J-stock diversity.

Having rejected the expectation that all North Pacific minke whale products in Japan originated from scientific hunting, we considered an alternative source of the products to be undocumented exploitation of the J stock. To estimate the proportion of this undocumented contribution to the market for this species, we used a 'mixed-stock' analysis of the haplotype frequencies developed for fisheries management (Pella & Milner 1987). In this approach, a maximum-likelihood solution is found to explain the haplotype frequencies of a mixed sample based on a proportional contribution of two or more 'source' stocks with differing but overlapping haplotype frequencies. The confidence limits for this estimate are based on bootstrap simulations of the source and mixed-stock samples. For our analysis, the two source stocks contributing to the mixed Japanese market sample were assumed to be the O stock, as represented by the Japanese scientific catch and the J stock, as represented by the Korean market sample. Based on the relative haplotype frequencies of these two sources' stocks, the maximum-likelihood estimate of the J-stock contribution to the Japanese retail market was found to be 31% with a 95% bootstrap confidence interval (CI) of 19–43% (1000 simulations).

3. PREDICTED DECLINE OF THE PROTECTED J STOCK

Prior to its classification as a protected stock by the IWC in 1986, the J stock was subject to exploitation from whaling operations based in the Republic of Korea and, to a lesser extent, Japan. The total recorded catch of this stock from 1962 to 1986 was 13 734 animals (Kim 1999) with annual catches by Korea reaching a peak of 1033 in 1977 (International Whaling Statistics 1988). In 1983, on the basis of declining catches per unit effort the IWC Scientific Committee concluded that the stock was depleted and recommended that it be classified as a protected stock (International Whaling Commission 1984). To allow for an orderly phase-out of whaling operations, the IWC delayed the imposition of the protected stock classification until 1986 when the general moratorium on commercial whaling also came into effect.

Given the depleted status of the J stock, the genetic evidence of continuing unregulated takes are of concern for the recovery prospects and perhaps survival of this population. To investigate the demographic implications of various levels of incidental takes of J-stock animals, we used the model and historical data set developed by the IWC Scientific Committee for the purpose of simulating the implementation of the RMP for commercial whaling. These 'implementation simulation trials' incorporate the assumed dynamics of the stocks and a range of assumptions about the extent of overlap or mixing of the stocks in time and space, in particular as these relate to the expected timing and location of future catches. The IWC Scientific Committee has recently conducted preliminary implementation simulation trials for future commercial exploitation of the O stock (International Whaling Commission 1999*b*). Because of the overlap in the seasonal distribution of the two stocks, the trials have also involved modelling the population dynamics of the J stock.

We modified the conditions for the simulation trials used by the IWC Scientific Committee to include two estimates of undocumented takes from the J stock. All other assumptions were according to the 'base case' adopted by the IWC Scientific Committee and reported in detail elsewhere (International Whaling Commission 1999*b*). These estimates arose from two lines of evidence: (i) documented incidental catches in Korean and Japanese waters, as reported by the Korean Ministry of Marine Affairs and Fisheries, and Japanese Ministries of Fisheries, and

(ii) undocumented catches in western Japanese waters as evidenced by the high proportion of J-stock animals on the Japanese market. Although it is probable that minke whales have been caught incidentally in Korean coastal fisheries since 1989, a requirement to report such catches has only been in effect since 1996. During 1996–1998, a total of 252 animals were reported caught for an average incidental take of 84 whales per year (Kim 1999). During 1995–1998, the Fisheries Agency of Japan reported an average nationwide incidental take (including stranded and beachcast specimens) of 25 minke whales per year (Anonymous 1995, 1996, 1997, 1998). No genetic information is collected from incidental takes but approximately 60% of these whales are reported to be from the west coast of Japan and, therefore, we assume will be of J-stock origin. Combining these reported sources from both Japan and Korea provided a minimum estimated incidental take of around 100 whales per year from the J stock.

The small number of documented incidental takes from Japanese waters was not sufficient to explain the observed market proportion of J-stock animals. If added directly to the scientific catch, the reported incidental take would provide an expected market proportion of *ca*. 16.5% J-stock products. This proportion fell below the 95% bootstrap CIs of the maximum-likelihood estimate. Possible sources of the additional catches include unreported incidental takes, undocumented importation (i.e. smuggling) of products from the Korean incidental takes and directed hunting in the Sea of Japan. Smuggling or hunting would be a direct violation of international agreements. For the purposes of the simulation we assumed that the additional catches arose only from undocumented incidental takes by Japan. To calculate the 'true' size of this incidental take, we solved for the value required to explain the market proportion of J-stock products using the known size of the scientific catch from the O stock (94 whales per year) and the coastal distribution of reported incidental takes (60% J stock). For the 31% proportion of J-stock products estimated by maximum likelihood, the required total incidental take was 100 whales per year, of which 60 would be of J-stock origin. This was surprisingly close to an independent estimate of the undocumented incidental takes based on extrapolation from reported takes and the efforts of coastal fisheries (Tobayama *et al*. 1992). Combining this estimate of Japanese incidental takes with the documented Korea takes suggested a total incidental take of close to 150 whales per year from the J stock.

We ran the simulation trials with our two estimates of incidental takes (100 or 150 total) for the period of 1998 onwards (figure 3). Presumed incidental takes prior to 1998 were set in the base case used for the IWC assessment and, in most years, were considerably lower than our estimates. Because the model used for the simulation trials accounted for the stochastic uncertainty of the current and future status of the stock, it was run 100 times for each of the two estimated levels of incidental takes. In accordance with IWC practice, the population projections were expressed in terms of the estimated number of mature females in the population although incidental takes were assumed to include both sexes. The median projection from the 100 replicates showed the J stock declining sharply during the period of directed commercial exploitation prior to the moratorium. After 1986, the stock increased for several years until the reported incidental takes from Korea initiated a second decline in about 1994. Under the estimated current additional takes of 100–150 animals per year, the decline was predicted to continue to dangerously low levels over the next few decades. Because the model assumed that future incidental takes were scaled in proportion to the abundance of the J stock, the rate of decline slowed after 1998. If this assumption were violated by a compensatory increase in fisheries' effort, the projected decline would be more rapid. We did not consider the higher estimate of incidental takes required to account for the upper confidence limit of the estimated proportion of J-stock products. Obviously, the projected declines under this level of take would also be more rapid.

To investigate the sensitivity of the J stock to reduced levels of incidental takes, should a programme of mitigation be implemented in the future, we also ran the simulation model under an assumed take of 50 animals per year. Even under this lower level, the population is predicted to continue to decline, although at a slower rate.

4. CONCLUSIONS

The results of our six-year survey of whale markets allowed us to answer three basic questions concerning the effectiveness of the current moratorium and management of limited scientific hunting and incidental takes. First, are the whale products sold in the commercial markets of Japan and Korea derived exclusively from the species taken by regulated scientific hunting? No, the products from the Japanese market included seven species protected by the moratorium. This finding is consistent with initial molecular monitoring based on previous market surveys (Baker & Palumbi 1994; Baker *et al*. 1996), as well as independent surveys by others (Phipps *et al*. 1998; Grohman *et al*. 1999; Fisheries Agency, Government of Japan, unpublished report). In total, the species protected by IWC agreements accounted for *ca*. 10% of the whale products from the Japanese markets excluding the unregulated products from small cetaceans. We are aware that meat and blubber from species hunted prior to the 1986 moratorium are reported to be kept in long-term frozen storage in Japan (Anonymous 1994). This could account for some of the products from protected species. A resolution on improved monitoring of whale products, which was passed by the IWC in 1997, encouraged member nations to report on the size and species of origin of the meat remaining in these stockpiles. However, to our knowledge no surveys using molecular methods have been undertaken in order to verify the species origins of stockpiles and no estimates are available for their contribution to the market. The Korean commercial market in whale products is apparently sustained by a level of incidental takes from coastal fisheries that approaches the level of commercial takes for some years prior to the moratorium. Although an effort has been made to document these takes, there has been no reported effort towards mitigation or regulation of this exploitation. Second, are products from the species taken by regulated scientific hunting (i.e. minke whales) derived exclusively from abundant stocks? No, the frequency of the Japanese market products with characteristic haplotypes of the protected J stock was approximately sixfold greater than that found in the catch from scientific hunting of the O stock. These differences allowed the first statistical estimation of the undocumented component of the whale market. Accounting for the potential distribution or sale of the reported incidental takes from Japanese coastal fisheries was not sufficient to explain this difference. Third, what is the relative extent or market proportion of undocumented whale products in Japanese retail markets? In addition to the 10% of the Japanese market (excluding small cetaceans) found to be from protected species, we used a maximum-likelihood approach to estimate that 31% of the products from exploited North Pacific minke whales originated from the protected J stock. Adjusting this estimate by the relative proportion of this species indicated that an additional 7% of the overall market in whale products originated from a protected stock. Together, therefore, the products from protected species and protected stocks accounted for *ca*. 17% of the total Japanese market.

The continued sale of protected species or stocks, as detected in our market surveys, points to a failing in the system for monitoring and verification of the limited levels of current whaling. However, the threat to the survival or recovery of the protected species from this otherwise undocumented exploitation is difficult to evaluate. The IWC has not completed a comprehensive assessment, which would allow modelling of the population impact of undocumented takes for these species; estimating the level of takes would be difficult given the low frequency of products from any one species. There is no such uncertainty in the conservation implications of our results for the J stock of North Pacific minke whales. The IWC assessment of this stock highlights its unique life-history parameters and genetic isolation as well as its severe depletion as a result of past commercial hunting. Our simulations of the population impact of continuing undocumented exploitation highlight the current threat to survival of this stock and the need for urgent action to address this management failure. For levels of incidental takes consistent with the market proportion of J-stock products (150 whales per year), the stock is predicted to decline towards extinction over the next several decades. Several assumptions used in the model and in our calculations could lead to an underestimation of the true takes. More importantly, we assumed that all undocumented products originate only from incidental takes rather than directed illegal hunting of these whales. If these assumptions were violated, the decline in the J stock could be precipitous.

For the J stock to avoid further depletion or extinction, every effort must be made to reduce the total take in Japanese and Korean waters to less than 50 animals per year. For this stock to recover, incidental or illegal directed takes must be reduced to levels approaching zero. Full protection for the J stock and other whale species, as intended by the moratorium, cannot be assured until scientific whaling and the sale and distribution of incidental takes are brought under full and transparent accountability.

Note added in proof. Our analysis did not include 32 minke whales killed in coastal waters north of Hokkaido during scientific hunting in 1996 because the mtDNA sequences of this catch have not been reported. The area north of Hokkaido is thought to include seasonal or migratory habitat for both the O and J stocks. Compared to the scientific catches from pelagic waters east of Japan, whales from the Hokkaido coast have a higher frequency of the common J-stock haplotypes, as defined by RFLPs (Goto & Pastene 1997). Based on the reported RFLP haplotypes, we estimated that six to nine of the 32 whales from the 1996 catch would be classified into the common J-stock haplotypes, using our sequence-based definition. The addition of this range of values to our analysis of the O-stock scientific catch (figure 2) does not affect the statistical significance or the interpretation of the test and maximum-likelihood estimation of market proportions.

We thank N. Funahashi for collection of the whale products from the retail markets and logistic support in Japan. We thank the Korean Federation of Environmental Movement and John Frizell, Greenpeace International, for collection of the whale products from the retail markets and logistic support in Korea. The simulation implementation trials of the J stock were provided by J. Cooke. We thank B. Congdon, M. Dalebout, N. Patenaude, J. Roman, Ye-Yong Choi and Tae Young Moon for assistance in the laboratory or the field. The analysis and interpretation of genetic evidence and population models benefited from discussions or assistance from N. Funahashi, B. Bowen, R. Brownell Jr, J. Cooke, A. E. Dizon, M. Donoghue, M. Masuda, V. Papastavrou, J. Pella and B. Taylor. MJ Research Inc. donated portable MiniCyclers for use in the field. Funding for the collection or analysis of the market products or reference samples was provided in part by Earthtrust, the International Fund for Animal Welfare, the Whale and Dolphin Conservation Society, Greenpeace International, the Pew Charitable Trust, the New Zealand Lottery Board, the New Zealand Marsden Fund and the University of Auckland. The funding for the analysis presented here was provided by the International Fund for Animal Welfare. The manuscript benefited from comments by H. Whitehead and an anonymous reviewer.

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