

High proportion of protected minke whales sold on Japanese markets due to illegal, unreported or unregulated exploitation

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Keywords

IUU exploitation; IWC; fisheries bycatch; DNA profiling.

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Received 17 June 2009; accepted 25 June 2009

doi:10.1111/j.1469-1795.2009.00302.x

Abstract

Whale meat products sold on Japanese markets originate from two stocks of North Pacific (NP) minke whales *Balaenoptera acutorostrata scammoni*: the depleted J-stock, which has been protected since 1986 but continues to be killed as fisheries 'bycatch', and the more abundant O-stock, which is hunted under special permit (scientific whaling). We investigated the geographic distribution and temporal changes in stock composition of NP minke whale products sold on Japanese markets between December 1997 and June 2004. From nearly 1200 'whale meat' products purchased during this time, 250 were identified as NP minke whales by phylogenetic analysis of mitochondrial DNA (mtDNA) sequences. The 250 NP minke whale products were found to represent 201 unique 'market individuals' after exclusion of replicate products using microsatellite genotypes. Market individuals were further classified into four mtDNA haplogroups, three of which are characteristic of the J-stock (J-type) and one characteristic of the O-stock (O-type). There were moderate differences in the proportions of J-type individuals found in coastal prefectures, perhaps reflecting regional differences in the sale of local bycatch, but no significant difference across time. The absence of a change over time was inconsistent with the four- to fivefold increase in reported bycatch, from an average of 25–122 whales year⁻¹, following a 2001 regulation allowing commercial sale of whales taken as bycatch. Using a mixed-stock analysis based on haplogroup frequencies over the entire survey period, we estimated that 46.1% (SE, 4.2%) of all market individuals originated from the J-stock. This estimate of illegal, unreported or unregulated (IUU) exploitation is higher than expected from the officially reported bycatch, suggesting either large-scale under-reporting and/or unrecognized takes of J-stock minke whales from Pacific coastal waters by the scientific hunt. Our estimates of the true level of IUU exploitation have important implications for recovery of this depleted coastal stock.

Introduction

The North Pacific (NP) minke whale *Balaenoptera acutorostrata scammoni* is thought to comprise at least two genetically distinct stocks around Japan: the O-stock, found in offshore Pacific waters, and the J-stock, found primarily in the East Sea/Sea of Japan (Fig. 1) and perhaps, in near-shore waters along the Pacific coast (IWC, 2004). The O-stock is considered to be relatively abundant but the J-stock was depleted as the result of intense commercial exploitation by South Korea, and to a lesser extent Japan, between 1962 and 1986. During this 24-year period, 13 734 animals were taken from the J-stock (Kim, 1999). In 1983, the

Scientific Committee of the International Whaling Commission (IWC) recommended that the J-stock should be classified as a 'protection stock' (IWC, 1984). This classification came into effect in 1986, coinciding with the global moratorium on commercial whaling. Although there is no accepted estimate of current abundance for the J-stock, computer simulations used by the Scientific Committee of the IWC to model population dynamics of both O- and J-stocks, suggest that the J-stock remains depleted (IWC, 2004).

More than 20 years after the 1986 moratorium on commercial whaling, products from both stocks continue to be sold in Japanese domestic markets. These products come from two documented sources: whales killed by the Japanese

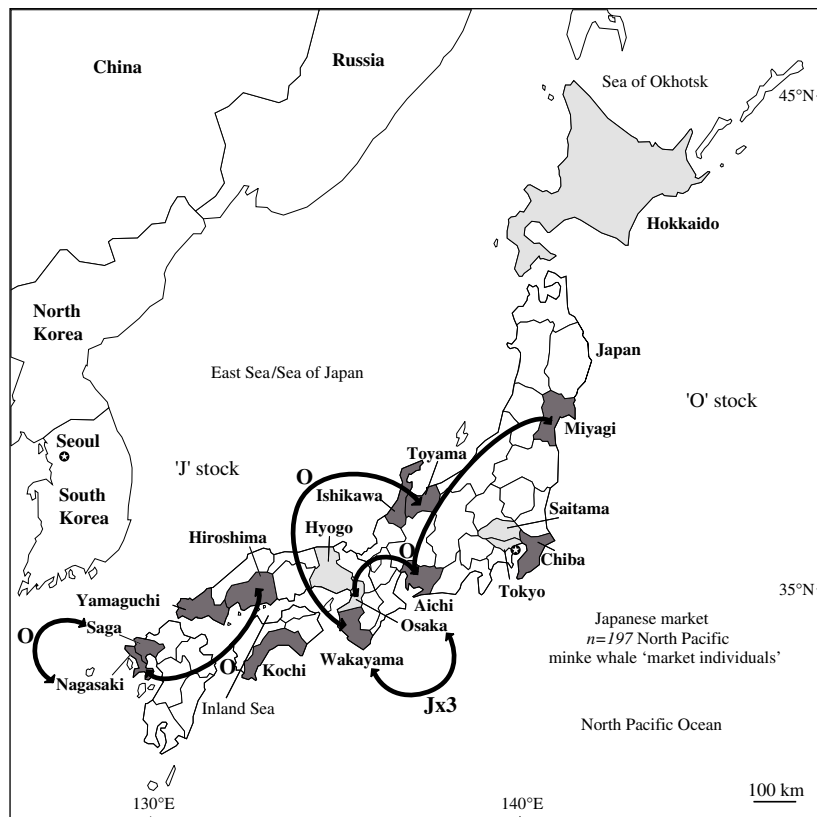


Figure 1 Japanese prefectures where North Pacific minke whale *Balaenoptera acutorostrata scammoni* products were purchased during market surveys conducted between December 1997 and June 2004. Eleven prefectures, shaded in darker grey, were used for regional coastal analyses. Five prefectures, shaded in light grey, were excluded from regional coastal analyses, either because they had no coastal borders, or could not reliably be assigned to one of three coastal regions: north-east, south-east and west coast. Arrows indicate matches between prefectures of replicate products from the same market individuals, determined by microsatellite profiling, mtDNA haplotype and genetic sex information. Letters adjacent to arrows (O or J) indicate the stocks that these products represent. Matches within prefectures are not shown (but see Table S1 for details). Reported numbers of whales killed as by catch and in scientific hunting are summarised from the annual Report of the Scientific Committee of the IWC, as published in the *Journal of Cetacean Research Management* (1999–2006).

Table 1 Japanese market sampling, reported bycatch and scientific hunting of North Pacific minke whales *Balaenoptera acutorostrata scammoni* (1997–2004)

Year	Market individuals	Sex ratio F:M (U)	Reported by-catch	JARPN or JARPNII	JARPN or JARPNII (F:M)	References
1997	Not included		27	100	13:87	IWC, 1999, Vol. 1 Suppl., p. 239
1998	38	N/A	24	100	11:89	IWC, 2000, Vol. 2 Suppl., p. 281
1999	46	2:0 (44)	19	100	29:71	IWC, 2001, Vol. 3 Suppl., p. 351
2000	20	6:13 (1)	29	40	5:35	IWC, 2002, Vol. 4 Suppl., p. 387
2001	11	7:4 (0)	89	100	7:93	IWC, 2003, Vol. 5 Suppl., p. 439
2002	31	17:13 (1)	116	150	33:117	IWC, 2004, Vol. 6 Suppl., p. 392
2003	24	10:12 (2)	137	150	36:114	IWC, 2005, Vol. 7 Suppl., p. 379
2004	27	11:14 (2)	113	159	22:137	IWC, 2006, Vol. 8 Suppl., p. 295

Sex ratios are provided for market surveys and JARPN or JARPNII.

N/A indicates that sex was not determined for any samples during that year.

JARPN, Japanese Whale Research Program under Special Permit for North Pacific Minke Whales.

scientific research programme (scientific whaling) and whales killed in the extensive set nets (bycatch) along the coast of Japan (Tobayama, Yanagisawa & Kasuya, 1992; Mills *et al.*, 1997). The scientific hunt of NP minke whales began in 1994 as the Japanese Whale Research Program under Special Permit for North Pacific Minke Whales (JARPN) and is directed primarily at the O-stock in off-shore waters. Between 1994 and 2002, the JARPN programme killed up to 100 whales year⁻¹ in pelagic waters off the Pacific coast of Japan (Table 1). This programme's successor, JARPNII, commenced in the summer of 2002

and expanded catch effort to include Japanese Pacific coastal waters. In 2004, the annual take was increased to 160 NP minke whales. The entanglement of whales in nets dates back to at least the 17th century in Japan, when it was the basis for an early form of commercial whaling (Kasuya, 2009). The history of 'incidental' bycatch of whales is less well documented but 'official records' have been included in Japan's national progress reports to the IWC since 1979 (Tobayama *et al.*, 1992). These records show that most minke whales are killed in coastal set nets ('trap net'); fixed fishing structures with a 'guide' up to 1 km in length,

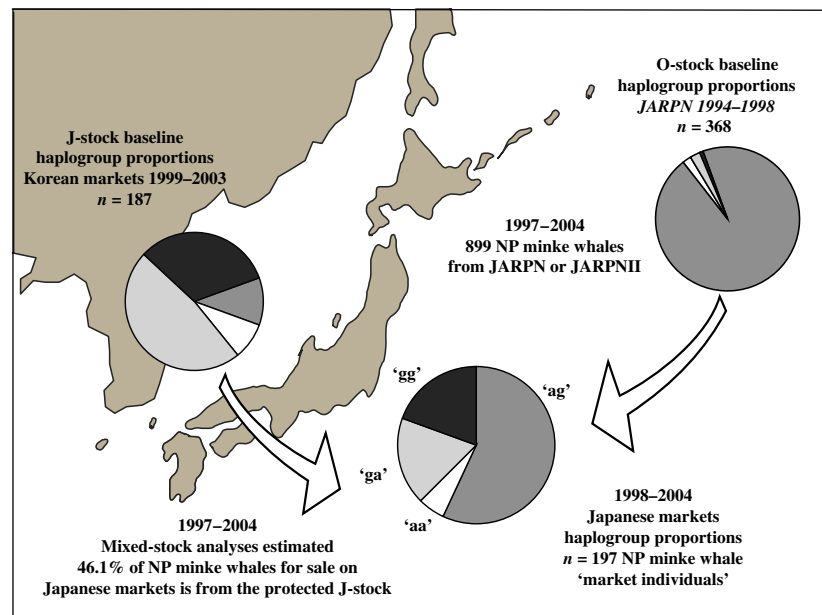
extending from shore to offshore and leading to a large 'box' to retain the trapped fish (or whales). There are about 20 000 trap nets operating in Japanese coastal waters, including both seasonal and year-round operations in almost all coastal prefectures (Kasuya, 2009). Based on extrapolation from set net effort, Tobayama *et al.* (1992) estimated that the true number of minke whales killed in nets was likely to be *c.* 100/year during much of the 1980s, a time when government progress reports to the IWC showed only an average of 7 whales year⁻¹. Considering the high value of minke whales (up to US\$40 200 per whale at that time, Kasuya, 2007), Tobayama *et al.* (1992) speculated that most of the bycatch was sold secretly rather than reported officially.

The reported bycatch of minke whales remained low through the 1990s until July 2001, when Japanese Ministerial Ordinance No. 92 came into effect, allowing fishers to legally kill, distribute and sell whales caught in coastal fishing set nets. Before this time, the distribution and sale of products from bycatch was ostensibly restricted by a previous government administrative order, permitting only the 'local use' of products (Mills *et al.*, 1997). The 2001 ordinance included a legal requirement that fishers report whales taken as bycatch and to submit a tissue sample from all bycaught whales to the Institute of Cetacean Research in Tokyo for genetic analysis (Anonymous, 2001). A substantial increase in the annual reported bycatch coincided with these changed regulations: from 19–29 whales year⁻¹ in the period 1997–2000, to 89–137 whales year⁻¹ in the period 2001–2004 (Table 1).

Molecular monitoring of commercial markets provides an important method for verifying reported bycatch and detecting other sources of illegal, unreported or unregulated (IUU) exploitation (Baker, 2008). Direct surveys of whale meat products for sale on Japanese markets have been conducted since 1993, using molecular taxonomy for species

identification (e.g. Baker & Palumbi, 1994) and molecular ecology to infer the stock origins of NP minke whales (Baker *et al.*, 2000; Dalebout *et al.*, 2002). For the latter, inference of stock origin is based on 'reference' data available from both scientific whaling (Goto & Pastene, 1997, M. Goto & L. A. Pastene, unpubl. data) and market surveys in Korea (Baker *et al.*, 2000). These data show that variation at two nucleotide positions of the control region define four haplogroups, which differentiate the O- and J-stocks with high confidence (see Fig. 2): more than 95% of O-stock whales taken in scientific whaling from 1994–1998 shared one haplogroup (M. Goto & L. A. Pastene, unpubl. data) and more than 92% of J-stock whales products purchased on Korean markets from 1999 to 2003 shared one of the other three haplogroups (Baker *et al.*, 2000; S. Lavery *et al.*, unpubl. data). Using this reference information, previous surveys of Japanese markets identified a larger than expected proportion of products originating from the protected J-stock (Baker *et al.*, 2000; Dalebout *et al.*, 2002). In particular, Baker *et al.* (2000) used mixed-stock analyses of Japanese market products (*n* = 81) to show that J-stock whales likely constituted 31% (95% CL, 19–43%) of the Japanese domestic whale meat market between 1993 and 1999. This proportional contribution was significantly higher than expected given the low reported bycatch at that time (average 25 whales year⁻¹) (Baker, 2002) and suggested that 'true' bycatch was, in fact, closer to 100 whales year⁻¹, comparable to the earlier estimate by Tobayama *et al.* (1992). Using the population dynamic model adopted by the Scientific Committee of the IWC, Baker *et al.* (2000) predicted that this level of unregulated exploitation was likely to result in a decline toward extinction of the depleted J-stock over the next few decades. The Scientific Committee of the IWC has also expressed its concern for the J-stock, given the high levels of reported bycatch in both Japan and

Figure 2 Mitochondrial DNA control region haplogroup proportions from North Pacific (NP) minke whales *Balaenoptera acutorostrata scammoni* for sale on Japanese commercial markets between 1998 and 2004. Also shown are the haplogroup proportions of: (1) O-stock NP minke whales inferred from the Japanese scientific hunt between 1994 and 1998; (2) J-stock NP minke whales from the East Sea/Sea of Japan inferred from products purchased in Korean markets between 1999 and 2003 (S. Lavery *et al.*, unpubl. data). Mixed-stock analysis estimated that 46.1% of NP minke whale 'market individuals' comes from the protected J-stock.



Korea and the recent 'suspicion of illegal catches' (IWC, 2009).

Here, we evaluate predicted changes in the proportion of J-stock minke whales available on Japanese markets before and after the 2001 regulatory change regarding the distribution and sale of fisheries bycatch. Assuming the veracity of official bycatch records, we predicted that our market surveys would detect an increase in the proportion of J-stock whales available on Japanese markets, corresponding to the roughly fourfold increase in reported bycatch since 2001, and perhaps an increase in the proportion of females, given the reported male sex bias of the scientific hunt (Table 1). Alternatively, a finding of similar proportions before and after the 2001 regulatory change (i.e. accepting the null hypothesis) would be consistent with high IUU takes before 2001, with an improved reporting after 2001. To improve on the previous methods of Baker *et al.* (2000), which relied on the proportion of total products rather than the proportion of individual whales represented in the products, we used DNA profiling [including microsatellite loci, mitochondrial DNA (mtDNA) haplotypes and sex] to identify replicate products originating from the same whale or 'market individuals' (e.g. Dalebout *et al.*, 2002). Contrary to expectations from the increase in official bycatch reports, we did not detect a significant increase in the proportion of J-type whales on the market after 2001, and contrary to the requirement of 'local use' before 2001, we found products from individual J-stock whales distributed in multiple prefectures. Given these findings, we revised the previous mixed-stock analysis of the 'true' J-stock proportions (Baker *et al.*, 2000), using the larger and more representative sample of market individuals for the entire survey period of 1998–2004. Our results suggest a higher overall level of IUU exploitation and a wider coastal distribution of the J-stock than assumed previously in IWC management procedures and modelling of population dynamics.

Methods

Market sampling

Whale products were purchased between December 1997 and June 2004 from speciality shops, fisheries markets, restaurants and department stores in a total of 16 prefectures throughout Japan (Fig. 1, Table 2). Eleven prefectures were distributed among three coastal regions as follows: (1) north-east coast (Pacific Ocean) – Chiba and Miyagi; (2) south-east coast (Pacific Ocean and Inland Sea) – Aichi, Hiroshima, Kochi and Wakayama; (3) west coast (East Sea/Sea of Japan) – Ishikawa, Nagasaki, Saga, Toyama and Yamaguchi (Fig. 1, Table 2). The remaining five prefectures could not be assigned specifically to a coastal region for the following reasons: Saitama does not have a coastal border; Hokkaido and Hyogo have multiple coastal borders (Fig. 1); and Tokyo and Osaka are large central cosmopolitan regions with high concentrations of whale meat markets that sell products from multiple sources around Japan.

Before 2002, products were purchased non-systematically from outlets in 13 prefectures (Table 2) over periods of several months each year. To evaluate the predicted effects of the 2001 regulatory change regarding the sale of fisheries bycatch (see 'Introduction'), and to sample more representatively from the three coastlines, an altered sampling strategy was implemented for the period June 2002–June 2004. During this time, we conducted five synoptic market surveys that focused on four Japanese prefectures, one from each of the three coastal regions: north-east coast – Miyagi; south-east coast – Wakayama; west coast – Ishikawa; and no assignable coast – Osaka, a central cosmopolitan prefecture with a small coast along the Inland Sea and little or no reported bycatch (Fig. 1, Table 2). In order to test our predictions about the temporal changes in proportions and distributions of J-stock minke products on Japanese markets, market samples were grouped as follows: products collected before July 2001 (referred to as 1998–2001) represented the market before the changed regulations while samples collected during the five synoptic surveys plus an additional 23 market products collected between October and December 2001 (referred to as 2002–2004) represented the market following the changed regulations. Additional details of market sampling are described in Dalebout *et al.* (2002). Characteristics of the inferred supply chain for the distribution and sale of whale meat products arising from scientific hunting and bycatch are described elsewhere (IWC, 2006; Baker, 2008) and discussed below in relation to our estimates of J:O proportions (see 'Discussion').

DNA extraction and portable polymerase chain reaction (PCR) protocols

As in previous surveys of commercial markets (Baker & Palumbi, 1994; Baker, Cipriano & Palumbi, 1996; Dalebout *et al.*, 2002), DNA extractions from whale tissue and subsequent PCR amplifications were conducted locally using 'portable' PCR protocols (Baker *et al.*, 1996). Tissue from each product was prepared for PCR amplification using Chelex resin (BioRad Laboratories, Hercules, CA, USA) as described in Baker *et al.* (1996). Amplified (synthetic) products were isolated either by agarose gel electrophoresis and band excision, or, since 2001, by biotin labelling and binding to streptavidin-coated plates. Isolated DNA products were washed free of 'native' DNA as required by CITES regulations (Bowen & Avise, 1994; Jones, 1994) before being transported to our home laboratory for further analysis. Field amplifications of an 800 base pair (bp) fragment from the 5'-end of the mitochondrial control region were performed using primers M13Dlp1.5-L and Dlp8G-H (G. M. Lento, N. J. Patenaude & C. S. Baker, unpubl. data). A 384 bp fragment of the mtDNA cytochrome *b* gene was also amplified from most products using the primers TGLUD-L and CYB2-H (Palumbi, 1996) to confirm species identity. These synthetic fragments were re-amplified in our home laboratory and sequenced on an ABI 377 or ABI 3100 Automated DNA Sequencer (Applied Biosystems Inc., Foster City, CA, USA) using Big Dye Chemistry™.

Table 2 Geographic and temporal distribution of North Pacific (NP) minke whale *Balaenoptera acutorostrata scammoni* market individuals ($n=201$) from the J-type (East Sea/Sea of Japan) and O-type (offshore Pacific) on the Japanese market by prefectures, regions and sampling periods

Coastal region	Prefecture	1998–2001			2002–2004			Total	
		O-type products	J-type products	Sex ratio F:M (U)	O-type products	J-type products	Sex ratio F:M (U)	O-type products	J-type products
North-east coast of Japan	Chiba	5	3	0:2 (6)	N/A	N/A	N/A	5	3
	Miyagi	16 ^a	6	3:4 (15)	10	6	6:8 (2)	26	12
	<i>Proportion (%)</i>	<i>70.0</i>	<i>30.0</i>		<i>62.5</i>	<i>37.5</i>		<i>67.4</i>	<i>32.6</i>
South-east coast of Japan	Aichi	2 ^a	0	1:0 (1)	N/A	N/A	N/A	2	0
	Hiroshima	1 ^b	0	0:0 (1)	N/A	N/A	N/A	1	0
	Kochi	4	0	0:0 (4)	N/A	N/A	N/A	4	0
	Wakayama	18	22 ^{c,d,e}	10:3 (26)	20 ^f	13	14:18 (1)	38	35
	<i>Proportion (%)</i>	<i>53.2</i>	<i>46.8</i>		<i>60.6</i>	<i>39.4</i>		<i>56.3</i>	<i>43.7</i>
West coast of Japan	Ishikawa	N/A	N/A	N/A	5	14	13:6	5	14
	Nagasaki	2 ^{b,g}	0	N/A	N/A	N/A	N/A	2	0
	Saga	3 ^a	4	0:0 (7)	N/A	N/A	N/A	3	4
	Toyama	N/A	N/A	N/A	3 ^g	4	2:4 (1)	3	4
	Yamaguchi	N/A	N/A	N/A	0	1	0:1 (0)	0	1
	<i>Proportion (%)</i>	<i>55.5</i>	<i>44.5</i>		<i>29.6</i>	<i>70.4</i>		<i>33.3</i>	<i>66.7</i>
No coast or coast of prefecture unassignable	Hokkaido	3	1	0:0 (4)	N/A	N/A	N/A	3	1
	Hyogo	2	1	1:0 (7)	N/A	N/A	N/A	2	1
Osaka	Osaka	12 ^a	10 ^{c,d,e}	3:8 (5)	3	4	2:5 (0)	15	14
	Saitama	1	0	1:0 (1)	N/A	N/A	N/A	1	0
	Tokyo	6	0	1:0 (6)	N/A	N/A	N/A	6	0
	<i>Proportion (%)</i>	<i>66.7</i>	<i>33.3</i>		<i>42.9</i>	<i>57.1</i>		<i>62.8</i>	<i>37.2</i>
Total numbers of market individuals		75	47	18:17 (83)	41	42	37:42 (4)	116	89

Replicate products of seven individuals sampled in more than one prefecture, are included in the totals of each prefecture where the replicates occurred (indicated below). Thus the total number of O- and J-type products is 205 rather than 197. Sex ratios are given corresponding to all 205 products and are, therefore, slightly different to those reported in the text for which the eight replicate products were removed.

^aJ99.52+JW99.A21+J00.25 Aichi/Osaka/Miyagi.

^bJ99.N1+JW99.H8 Nagasaki/Hiroshima.

^cJ99.35+J99.79 Osaka/Wakayama.

^dJ99.42+JW99.03 Osaka/Wakayama.

^eJ00.38+J01.32 Osaka/Wakayama.

^fJ02.008+J02.080 Toyama/Wakayama.

^gJ98C-21+J98D-81 Saga/Nagasaki.

Numbers of whale meat products and sex ratios (female:male:unknown) are given for prefectures and proportions (%) of O- and J-type products are given for each coastal region.

N/A indicates that prefecture was not sampled during the sampling period.

The control region was re-amplified using the primers M13Dlp1.5-L and Dlp5-H or Dlp4-H yielding products of ~550 or 450 bp, respectively (Dalebout *et al.*, 2005). The sex of most products collected between July 1999 and 2004 was determined in the field by multiplex PCR reaction using two primer pairs that amplify different sized fragments from the ZFX and SRY regions, located on the X and Y mammalian chromosomes, respectively (Gilson *et al.*, 1998). Products purchased before July 1999 were not typed for sex.

In order to identify replicate products from the same individuals, five microsatellite loci (three tetramers, GATA28, GATA417 and GATA98, from Palsbøll *et al.* (1997); and two dimers, GT23 and GT575, from Berube *et al.*, 2000) were amplified from all NP minke products (S. Lavery *et al.*, unpubl. data). Five additional dimeric microsatellite loci (GT211, GT310 and GT509 from Berube *et al.*, 2000; EV21 from Valsecchi & Amos, 1996; and rw31

from Waldick, Brown & White, 1999) were amplified from products in some surveys. All microsatellite loci were re-amplified using fluorescent-labelled primers for multiplex electrophoresis on an ABI 373A or 377 Automated Sequencer (Applied Biosystems, Foster City, CA, USA). Allele sizes were determined by using an internal size standard (Tamra 350) in each lane for all runs. Allele sizes were standardized using control individuals representing the most common alleles for each locus. These allelic standards were included on all gels. All samples were electrophoresed twice to confirm that allele sizes were consistent between runs.

Identification of haplotypes, haplogroups and replicate products

A standard length of up to 464 bp mtDNA control region was sequenced, depending on quality of DNA, to identify up

to 34 variable sites characterized in previous studies of NP minke whales (Baker *et al.*, 2000, 2007). Variation at these sites resolved up to 36 unique haplotypes, depending on the length of sequence. All haplotypes were further classified into one of four haplogroups based on two nucleotide substitutions known to be characteristic of the two stocks (A and G at positions 298 and 463). These two positions were initially identified as characteristic of the two stocks based on extensive mtDNA restriction fragment length polymorphisms and control region sequences reported from the scientific and earlier commercial catches, and supported by subsequent control region sequences from Korea market surveys (see 'Introduction' and 'Data analysis'). Because our inference of stock origins relies on these haplogroup classifications rather than known geographic origin, we refer to market individuals as either 'O-type' (having haplogroup AG) or 'J-type' (having haplogroups AA, GA or GG) NP minke whales. Replicate products were identified based on genetic matches between microsatellite loci, mitochondrial control region haplotype sequences and molecular sex information. Not all samples could be unambiguously typed for all loci so a conservative approach was used to identify replicate products: if two or more products could not be distinguished by genotyping of at least three microsatellite loci, and they shared the same mtDNA haplotype and sex, we assumed the products were derived from the same individual (Dalebout *et al.*, 2002; Baker *et al.*, 2007).

Data analysis

The proportion of market individuals representing each of the four haplogroups (AG, AA, GA and GG) and two stock types (O and J) were calculated for each prefecture and coastal region for the two temporal samples (1998–2001 and 2002–2004). Temporal changes in haplogroup and stock-type proportions and sex ratios between the periods 1998–2001 and 2002–2004 were investigated using χ^2 -tests of independence. In addition, geographic differences in the distribution of haplogroup and stock-type proportions between the three coastal regions were investigated between pairs of regions using χ^2 -tests. Mixed-stock analyses (Pella & Milner, 1987) of haplogroup frequencies were used to estimate the proportional contribution of O- and J-type whales to products available on Japanese markets using the Statistical Program for Analysing Mixtures (SPAM Version 3.7, Debevec *et al.*, 2000). This approach finds a maximum likelihood solution to explain the haplogroup frequencies of a mixed sample based on the proportional contribution of two or more source stocks with different but overlapping haplogroup frequencies. Confidence intervals were calculated from bootstrap simulations of the source and mixed-stock samples, as implemented in SPAM. The source stocks assumed to contribute to the Japanese market sample were the O- and J-stocks (although we cannot exclude the possible contribution of a third stock, see 'Discussion'). Baseline O-stock haplogroup frequencies were taken from those reported for the JARPN programme ($n = 368$ for

1994–1998; M. Goto & L. A. Pastene, unpubl. data) and assumed to consist almost entirely of O-stock. Baseline J-stock haplogroup frequencies were taken from products purchased in Korean market surveys ($n = 187$ for 1999–2004; S. Lavery *et al.*, unpubl. data) and assumed to originate entirely from coastal fisheries bycatch in the East Sea/Sea of Japan (J-stock).

Results

Census of NP minke whale 'market individuals' by microsatellite DNA profiling

A total of 1174 'whale meat' products were purchased in Japan from December 1997 to June 2004. Of these, 250 products were identified as NP minke whales through phylogenetic analyses of mitochondrial control region and cytochrome *b* sequences. The remaining 924 products were identified as representing at least 18 species of odontocetes (sperm whales, beaked whales, dolphins and porpoises), seven species of mysticete whales and a horse (e.g. Baker *et al.*, 2000). Microsatellite profiles, plus mtDNA haplotype and sex information (where available), indicated that the 250 minke whale products came from at least 201 unique individuals. Four market individuals could not be assigned a haplogroup because of missing information at position 463 (control region), thus 197 market individuals were available for further analyses. Thirty-three market individuals were represented by more than one product, including the 11 individuals reported previously by Dalebout *et al.* (2002). Seven market individuals had replicates sampled in multiple prefectures: one each from Toyama/Wakayama; Hiroshima/Nagasaki; Saga/Nagasaki; Aichi/Osaka/Miyagi; and three individuals sampled in Osaka/Wakayama (Fig. 1). Of the seven market individuals found in multiple prefectures, three were J-type and purchased before the 2001 regulatory change (Table 2). The remaining 26 market individuals were resampled within one of five prefectures, with most replicate samples ($n = 15$) found in the Wakayama prefecture. Some replicate samples were purchased on the same day in the same shop (considered pseudoreplicates) but others were purchased as much as 6 months apart (see supporting information, Table S1 and Dalebout *et al.*, 2002).

Spatial and temporal patterns of distribution of O- and J-type products

Products from O-type minke whales, assumed to originate primarily from the scientific hunt, were sampled in 15 of the 16 prefectures (Table 2). Products from J-type minke whales, assumed to originate primarily from bycatch, were sampled in 10 of the 16 prefectures and all three coastal regions (Table 2). Moderate differences in O- and J-type proportions were found among the three coastal regions. West coast markets had a significantly higher proportion of J-type individuals than markets in the north-east

($\chi^2_{d.f.1} = 9.63$, $P < 0.002$) and south-east ($\chi^2_{d.f.1} = 6.23$, $P < 0.013$), with J-type whales dominating the west coast (66.7%) and O-type whales more abundant in the north-east (67.4%) and south-east (56.3%) (Table 2). There were also significant differences in haplogroup proportions between the west coast and north-east ($\chi^2_{d.f.3} = 12.89$, $P < 0.005$) and west coast and south-east ($\chi^2_{d.f.3} = 9.31$, $P < 0.025$), with the most notable difference in the occurrence of the AA haplogroup (J-type): 16% of west coast samples had the AA haplogroup compared with c. 2 and 4% for the north-east and south-east coasts, respectively. There were no significant differences in market haplogroup or stock proportions between the north-east and south-east regions.

Although there was an overall increase in the proportion of J-type minke whales found the market surveys in the period following the changed regulations (38.3% in 1999–2001 vs. 51.2% in 2002–2004), this difference was not significant at either the four-haplogroup ($\chi^2_{d.f.3} = 4.67$, $P < 0.20$) or two-stock levels ($\chi^2_{d.f.1} = 2.76$, $P < 0.10$) (Table 3). Thus, we could not reject the null hypothesis that the two temporal samples represented the same underlying proportion of J:O stocks. Further, there was no significant difference between the two temporal sampling periods in the proportion of products from females compared with males, as would be expected given the highly male-biased catch from the scientific whaling [1998–2001, 1:1 (F:M) $n = 32$ cf. 2002–2004, 0.9:1 (F:M) $n = 78$, $\chi^2_{d.f.1} = 0.02$, $P < 0.90$] (Table 2, after removal of replicates among prefectures).

Table 3 Proportions of O- and J-type haplogroups of North Pacific minke whales *Balaenoptera acutorostrata scammoni* sampled in Japanese markets (reported here), Korean markets (Baker *et al.*, 2007) and the JARPN scientific hunt (from M. Goto & L. A. Pastene, unpubl. data)

	<i>n</i>	AG	AA	GA	GG
JARPN 1994–1998	368	350	7	9	2
Proportions (%)		95.1	1.9	2.4	0.5
Japanese Market					
1998–2004	197	111	13	35	38
Proportions (%)		56.3	6.6	17.8	19.3
Japanese Market					
1998–2001	115	71	5	20	19
Proportions (%)		61.7	4.3	17.4	16.5
Japanese Market					
2002–2004	82	40	8	15	19
Proportions (%)		48.8	9.8	18.3	23.3
Korean Market					
1999–2003	187	21	16	89	61
Proportions (%)		11.2	8.6	47.6	32.6
		AG = O-type	AA, GA, GG = J-type		

Proportions for Japanese markets are shown for before (1998–2001) and after (2002–2004) changes in by-catch regulations and for the entire study period. JARPN proportions are assumed to reflect haplogroups of the 'pure' O-stock, while Korean market proportions are assumed to reflect haplogroups of the 'pure' J-stock.

JARPN, Japanese Whale Research Program under Special Permit for North Pacific Minke Whales.

Mixed-stock analysis

A mixed-stock analysis was run for each of the two temporal samples (1998–2001 and 2002–2004) and the sum of the log-likelihood values was compared with the log likelihood for the analysis of the combined sample. The result of this test was not significant ($\chi^2_{d.f.1} = 1.17$, $P < 0.25$) and thus, as with the test of proportions, we could not reject the null hypothesis that the two temporal samples represented the same baseline mixture of the O- and J-stocks. Consequently, we used the entire sampling period to obtain an improved single estimate of market stock proportions. Based on the total sample of 197 individuals, the maximum likelihood estimate for stock contributions to the market was 46.1% J-stock (SE, 4.2%; 95% CL, 37.7–56.2%) and 53.9% O-stock (SE, 4.2%; 95% CL, 43.9–62.3%) (Fig. 2).

Discussion

Effects of changed regulations and market sampling

The changed Japanese domestic regulations in 2001, which allowed for the wider distribution and sale of whale meat from bycatch throughout Japanese domestic markets, did not result in the expected significant increase in the overall proportion of J-type whales detected by our market surveys (Tables 2 and 3). The lack of a significant increase, in combination with the larger than expected proportion of J-type whales available on Japanese markets overall, suggests large-scale under-reporting of incidental takes of NP minke whales before the 2001 administrative order and an improved reporting after the order. The observed marginal (non-significant) increase in proportion of J-type whales in the 2002–2004 surveys is more likely to be influenced by our increased sampling in west coast prefectures during this period. The higher proportion of J-type whales found on the markets in these prefectures (Table 2) presumably reflects some sale of local bycatch. However, we note the transport between prefectures of products from individual J-type whales before 2001, at a time when the regulation allowed only 'local use' of bycatch. This transport of products is consistent with speculation by Tobayama *et al.* (1992) that whales taken as bycatch were sold secretly and thus entered into the complex supply chain of commercial whale meat in Japan (Baker, 2008).

Given the absence of a significant temporal change in the proportion of J:O stock individuals represented in the markets, we sought to improve the previous estimate of J-stock proportions on Japanese markets (Baker *et al.*, 2000) using a revised mixed-stock analysis for the entire study period. The previous mixed stock estimate of 31% (95% CL, 19–43%) J-stock was based on 81 minke whale products and did not exclude possible replicates using DNA profiling (Baker *et al.*, 2000). Our current estimate, based on a much larger sample size of unique market individuals ($n = 197$) from a wider geographic sampling (16 prefectures) and a greater time period (7 years), indicated that J-stock minke

whales accounted for 46.1% (95% CL, 37.7–56.2%) of products sold on the Japanese market between 1998 and 2004.

However, given the challenges of sampling in such a large and complex market, we must consider two questions regarding our estimates: (1) Was our sampling of NP minke whales an unbiased representation of the national whale meat market? ; (2) Did the change in sampling after 2001 bias our analysis of the predicted temporal trend in J-stock market individuals? Our surveys sampled widely across Japan and included some purchases of NP minke whale products in 16 of the 47 prefectures of Japan. The total number of samples was large ($n = 1174$) and, given the poor quality of product labelling (IWC, 2006), presumably unbiased with respect to species composition. The total number of NP minke whale products was also large ($n = 250$) and given the poor quality of product labelling, presumably unbiased with respect to stock origin. The mixing of whale meat products in this nation-wide supply chain is likely to further reduce the potential for bias of purchases with respect to stock. However, our analysis of geographic variation did show a significantly higher proportion of J-stock in the west coast prefectures, suggesting that mixing in the supply chain does not completely randomize the distribution of local bycatch. Given this tendency, our earlier surveys almost certainly under-sampled J-stock products, given that west coast prefectures account for roughly half of the Japanese coastline but only accounted for ~6% of the market individuals for 1998–2001. After 2001, west coast prefectures accounted for 32.5% of the market individuals, still less than the 60% J-stock proportion in overall bycatch on Japanese markets assumed in the IWC population simulations. Thus, in regards to question 1, we consider that the large number of products purchased, the greater inclusion of west coast prefectures in the 2002–2004 surveys, and the genotyping to identify market individuals, provided an improved estimate of the proportion of J- and O-stock available on Japanese markets relative to previous estimates (i.e. Baker *et al.*, 2000). In regards to question 2, we note that the more representative sampling of the west coast in our post-2001 surveys should have contributed to the expected direction of the trend in the official reporting, that is, an increase in the proportion of J-type market individuals, thus, increasing the probability of rejecting the null hypothesis of ‘no change’. Instead, we found no significant difference in the proportion of J-stock individuals before and after the 2001 regulatory change, despite the reported four- to fivefold increase in reported bycatch.

An improved estimate of IUU exploitation

Our revised estimate of J-stock proportion of 46.1% is disturbingly large given the previous prediction (based on lower estimated rates of exploitation) that the J-stock is likely to become extinct in the next few decades under reported rates of bycatch (Baker *et al.*, 2000). Thus, our revised estimate provides critical information for revising the ‘total takes over time’ for inclusion in the IWC’s ongoing

in-depth assessment of J-stock minke whales (IWC, 1999a). For this, we followed Baker *et al.* (2000) in calculating an approximation of the true J-stock take using the estimated proportion of J-stock on the market, the known size of the scientific catch, and the known or assumed stock composition of the bycatch and scientific catch. Unfortunately, the Government of Japan has never reported on the genetic identity of bycatch and has not reported the genetic identity of the scientific catch since the 1994–1998 summary by M. Goto & L. A. Pastene (unpubl. data). To account for the uncertainties in O- and J-stock proportions from coastal bycatch and the scientific hunt, we calculated the potential J-stock takes for a range of alternative values. For the proportion of J-stock in the total Japanese bycatch, we considered two values: 60 and 100%. The lower value of 60% J-stock follows the RMP implementation simulation trials of the IWC (IWC, 1999b) and is based on the approximate ratio of bycatch from west coast to east coast prefectures. The upper value of 100% assumes all coastal minke whales are J-stock and, for the purposes of these calculations provides a ‘conservative’, if implausible, upper bound of total J-stock takes. For the proportion of J-stock in the scientific hunt before 2001, we used the available information from 1994 to 1998: 5% J-stock and 95% O-stock (M. Goto & L. A. Pastene, unpubl. data). After 2001, however, components of the scientific hunt moved closer to the Japanese coast, perhaps increasing the proportion of J-stock in the total catch. To allow for this change, we considered an alternate proportion of 20% J-stock and 80% O-stock in the scientific hunt.

For the years 1997–2000, the range of 60–100% for J-stock proportion in bycatch was not consistent with our estimated market proportions and the average official reported bycatch of 25 whales year⁻¹ (Table 4). As Baker *et al.* (2000) concluded, the observed market proportions in these years were only reconcilable with a two- to fourfold under-reporting in official records (i.e. a true bycatch of > 100 whales year⁻¹). For the years 2002–2004, our calculations suggest that some combination of a high proportion of J-stock in both bycatch and the scientific hunt would be consistent with the average official reported bycatch of 122 whales year⁻¹. However, the assumption of 100% J-stock bycatch seems unlikely given the reported O-stock distribution and abundance in Japanese Pacific coastal waters (IWC, 2004). Instead, it seems more plausible that, within the range of our assumptions, the proportion of J-stock is at some intermediate upper value (e.g. 80% J-stock) for overall bycatch, and at the higher end for the scientific catch (e.g. 20% J-stock). Although such a scenario is plausible and roughly consistent with the recent reported bycatch, it is not consistent with the current assumptions of the RMP implementation simulation trials used by the IWC to set nominal catch quotas for the O-stock (IWC, 2004). These simulation trials used the official reports of bycatch and the lower assumed level of J-stock proportions. More importantly, even in our most optimistic scenarios, the estimated true take of J-stock minke whales is more than 100 whales year⁻¹ from Japanese waters alone. This does

Table 4 Calculated total annual bycatch of North Pacific minke whales *Balaenoptera acutorostrata scammoni* based on 46.1% J-stock available for sale on Japanese markets, under various scenarios of assumed J-stock proportions from coastal bycatch (60 or 100%) and assumed O-stock proportions from the scientific hunts (95% for JARPN and 80% for JARPNII)

Years	NP minke whale bycatch				Scientific hunt – JARPN or JARPNII		Total bycatch and scientific hunt	Total J-stock from bycatch and scientific hunt	% J-stock
	Assumed proportion J-stock (%)	Average # J-stock	Average # O-stock	Total annual bycatch	Average take	Assumed proportion O-stock (%)			
1997–2001	100	67	0	67	88	95	155	72	46.5
	60	156	104	260	88	95	348	161	46.3
2002–2004	100	74	0	74	153	80	227	105	46.3
	60	168	112	280	153	80	433	199	46.0

Annual incidental takes were calculated separately for 1997–2001 (JARPN) and 2002–2004 (JARPNII) to factor in changes in average annual takes and assumed O-stock proportions for JARPN and JARPNII. See text for more details.

JARPN, Japanese Whale Research Program under Special Permit for North Pacific Minke Whales; NP, North Pacific.

not include the even larger number of J-stock minke whales taken as bycatch or by directed illegal hunting in Korea, which also allows the commercial sale of bycatch in local markets (Mills *et al.*, 1997). A capture–recapture analysis of Korean market products across the years 1999–2003 suggested that the true number of minke whales entering local trade was 827 (SE, 164), nearly twice the number in official reports of bycatch for this 5-year period (Baker *et al.*, 2007). Together, the combined estimates of IUU exploitation from market surveys in Japan, as presented here, and in Korea, as presented by Baker *et al.* (2007), are approximately twice as large as the Japanese scientific hunt for this species (Table 1).

Management implications

Market surveys conducted from 1997 to 2004 indicate higher proportions of J-type minke whales for sale on Japanese markets than expected from documented takes in the annual scientific hunt and reported bycatch. Our results provide an improved estimate of the numbers of protected J-stock whales taken over time and suggest that total bycatch was high throughout the survey period and, within the bounds of our confidence limits, could be equal to or greater than the scientific hunt of NP minke whales. Nonetheless, several alternative scenarios may also account for the higher than expected numbers of J-type whales sampled. Discounting the possibility of large-scale smuggling of J-stock whales from Korea to Japan (e.g. Dalebout *et al.*, 2002; S. Lavery *et al.*, unpubl. data), the remaining hypotheses centre on different proportional contributions of the O- and J-stock to bycatch and the scientific hunt. Critical information for evaluating these scenarios, including the haplogroup frequencies and distributions of the O- and J-stocks in Japanese coastal waters, is presumably collected by the Institute for Cetacean Research, Tokyo, as part of the national ‘DNA register’ of whales intended for commercial sale (Baker, 2008). However, this information has not been made available to the Scientific Committee of the IWC, despite the recent focus on in-depth assessments of these stocks (IWC, 2007). Thus, we urge greater transparency in

reporting data from both the scientific hunt and Japanese coastal bycatch, particularly the genetic data needed to determine the frequencies of O- and J-type minke whales from each source. In addition, a comprehensive genetic investigation of minke whales throughout Japanese coastal waters is needed, with particular emphasis on the Pacific coast. As Japanese coastal waters will likely include a large proportion of one or more depleted coastal stocks (including the J-stock), we recommend that such a genetic study be conducted using biopsy sampling, rather than the lethal methods used in the current scientific whaling programme. This is of particular importance given the high level of IUU takes in Korean waters and the proposal by Japan to initiate a ‘small-type’ coastal whaling programme (Cooke, Leaper & Papastavrou, 2009), both of which pose additional threats to coastal stocks.

Acknowledgements

Funding for market surveys and genetic analyses was provided by: the International Fund for Animal Welfare (to C.S.B. and N.F.); the Whale and Dolphin Conservation Society (to F.C.); and the University of Auckland (to C.S.B.). Paper preparation was supported by a grant from the Pacific Life Foundation (to C.S.B.). We thank two anonymous reviewers and the associate editor R. Williams for helpful comments on an earlier draft. The last author (C.S.B.) takes full responsibility for the primary information used in the analyses and for the inference of IUU whaling, as represented by Japanese market surveys.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Table S1. Sample information for 250 minke whale-meat products comprising 201 market individuals purchased on Japanese markets between December 1997 and June 2004. For each product the following information is given: market individual ID; sample ID; prefecture where product was purchased; haplogroup based on nucleotide bases as positions 298 and 463 of the mitochondrial DNA control region; stock type based on haplogroup; genetic sex information; date of purchase; the city and/or market/shop type

from which the product was purchased; and description of product by shop or restaurant owner. Market individual refers to the 201 unique minke whales sampled in the 250 whalemeat products. Market individuals represented by more than one product (replicates) are also shown.

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