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EVALUATION OF A PATERNITY METHOD BASED ON MICROSATELLITE DNA GENOTYPES FOR ESTIMATING THE ABUNDANCE OF ANTARCTIC MINKE WHALES (*BALAENOPTERA BONAERENSIS*) IN THE INDO-PACIFIC REGION OF THE ANTARCTIC

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Abstract

This study describes a paternity method based on microsatellite DNA genotypes to estimate the abundance of mature male Antarctic minke whales (*Balaenoptera bonaerensis*) in the Indo-Pacific region of the Antarctic using a maximum likelihood approach. The analyses were based on biological and genetic (microsatellite DNA at 12 loci) data from Antarctic minke whales collected by surveys of the Japanese Whale Research Program under Special Permit in the Antarctic-Phase II (JARPAII) in the Indo-Pacific region of the Antarctic. A total of 2,126 Antarctic minke whales taken in the austral summer seasons 2006/07, 2008/09, 2009/10, 2010/11 and 2011/12 from locations 35°E to 145°W were used in the analyses. The abundance of mature males estimated by this method was then extrapolated to estimate total abundance for comparison with results for abundance obtained using conventional line transect methods in the research area. The total abundance derived from the paternity method (ca. 210,000–220,000) was generally lower than that obtained by the line-transect method (ca. 260,000–410,000), although the figure from the line-transect method was within the 90% confidence interval of the estimates by the paternity method, and the area covered by both methods was slightly different. Additionally, the geographical locations of mother/fetus–father pairs provided the opportunity to evaluate the current hypothesis on population structure of this species in the Indo-Pacific region. Results for the geographical distribution of mother/fetus–father pairs were generally consistent with the hypothesis of separate Eastern Indian Ocean and Western South Pacific Ocean populations, because 8 of 10 pairs were found in the expected areas of distribution of either populations. However, two pairs were found in distant areas. As a whole, the results from the present study demonstrated the utility of the paternity method for estimating the abundance of Antarctic minke whales and for assisting the interpretation of population structure hypotheses.

Key words: Antarctic minke whale, paternity analysis, population structure, microsatellite DNA.

Introduction

Population abundance and trajectories provide key information required for effective conservation and management of wildlife. In the case of whaling, the International Whaling Commission (IWC) developed and adopted the Revised Management Procedure (RMP), a single-species management procedure[1] for calculating commercial catch limits for whaling of baleen whales (Anon, 1994; Punt and Donovan, 2007). The RMP consists of a series of rules to manage whaling (including multi-stock scenarios), based largely upon catches determined by a simple generic *Catch Limit Algorithm* (*CLA*), that requires two kinds of information: a time series of abundance estimates and catch-history data. The key to the approach is that the *CLA* was rigorously tested by simulation to ensure that it is robust to inevitable scientific uncertainty, while the implementation of the RMP in specific multi-stock situations is also tested by simulation to ensure robustness to evaluate uncertainty in key parameters (known as *Implementation Simulation Trials*, *ISTs*). The catch limits set by the *CLA* take into account the uncertainty in the abundance estimates and thus it is important to obtain abundance estimates with good precision. Abundance information about whales is also required for the development of ecosystem models and multi-species management procedures.

In recent decades, visual surveys using 'Distance sampling' approaches (e.g., Buckland *et al.*, 2001) have been the most common method for estimating the abundance of cetacean species. Amongst other assumptions, this approach depends upon an assumption that all animals on the trackline are seen (or can be corrected for the actual detection probability on the trackline—the so-called g(0) value). It is also assumed that, for estimating trends in a population (rather than trends within a geographical area), the full population is surveyed each time (difficult for wide-ranging species such as cetaceans). A good example of the complexity in the use of the line-transect method was the assessment of Antarctic minke whales by the IWC Scientific Committee (SC), based on three Antarctic circumpolar surveys conducted under the International Decade of Cetacean Research and Southern Ocean Whale and Ecosystem Research (IDCR/SOWER) programs. Obtaining robust abundance estimates from these surveys and then interpreting the results triggered a decade-long discussion in the IWC SC about the method of estimating g(0) and possible distributional shifts of whales over time e.g. to unsurveyed areas beyond the ice-edge of the survey region that prevents vessels entering (IWC, 2013).

Mark–recapture methods based on internal marks (Discovery type, e.g., see Buckland and Duff, 1989) or individual identification by photographic matching (e.g., Hammond *et al.*, 1990) can be used to estimate some marine mammal population sizes (Sobtzick, 2010). However, in the case of Antarctic minke whales the former method is not possible because there are no current catches of this species. Obtaining sufficient photographs for photographic identification and then matching them is considerably more difficult for Antarctic minke whales than say, humpback, right and blue whales.

Given the limitations mentioned above, alternative methods are being investigated for estimating the abundance of whales. Mark–recapture approaches based on genetic individual identification from biopsy samples have been used to estimate population abundance and to examine the migration patterns of whales (e.g., Palsbøll, 1999). Whilst valuable for smaller populations, the logistics of obtaining a sufficiently large sample size make it often impractical for large populations.

The most promising recent technique involves paternity testing. For paternity analyses, DNA profiles of mother/fetus, usually from a set of microsatellite loci, are used to look for potential fathers of the fetuses within the sample population. If their fathers are found, the number of matches can be used in traditional mark–recapture analyses (e.g., see Skaug and Øien, 2004). Paternity analysis and close-kin mark–recapture methods based on genetic data have been used to estimate the abundance of North Atlantic humpback whales (Palsbøll *et al.*, 1997; Nielsen *et al.*, 2001).

This study describes a paternity method based on microsatellite DNA genotypes to estimate the abun-

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[1] Sometimes in fisheries the term 'management strategy' is used.

dance of mature male Antarctic minke whales in the Indo-Pacific region of the Antarctic using a maximum likelihood approach. Mature male abundance is extrapolated to total abundance and the estimates compared with those obtained from conventional line-transect methods in the same research area. The paper also identifies additional research required to improve the precision of the paternity method for abundance estimate purposes. Finally, the geographical locations of mother/fetus–father pairs are used to evaluate the current hypothesis on population structure of this species in the Indo-Pacific region of the Antarctic.

Materials and methods

Samples

Samples from a total of 2,126 Antarctic minke whales were available from the surveys of the Japanese Whale Research Program under Special Permit in the Antarctic-Phase II (JARPAII) in the austral summer seasons 2006/07, 2008/09, 2009/10, 2010/11 and 2011/12. The surveys were conducted in the Indo-Pacific region of the Antarctic, in the IWC Management Areas (see Donovan, 1991) IIIE (35°–70°E), IV (70°–130°E), V (130°E–170°W) and VIW (170°–145°W) (Fig. 1). For each sampled whale, the following information was available: sample ID, sampling date, sampling location (latitude and longitude), sex and maturity, occurrence of fetus, age and the quality of the age estimation.

The details of the samples used in the analyses are presented in Table 1.

Microsatellite DNA

Each sample (including fetuses) was genotyped using 12 microsatellite DNA loci: EV1, EV104, GT211, DlrFB14, GT195, GT23, AC045, AC082, AC087, AC137, CA234 and GT129. The details of the laboratory work for DNA extraction and microsatellite DNA genotyping were reported by Pastene and Goto (2016). Loci CA234 and GT129 were excluded from the present analyses because of the existence of null alleles and genotyping errors. Individuals with missing allele data on some loci (576 animals) and some mother/fetus pairs that had mismatching alleles (37 animals) were also excluded from the statistical analysis.

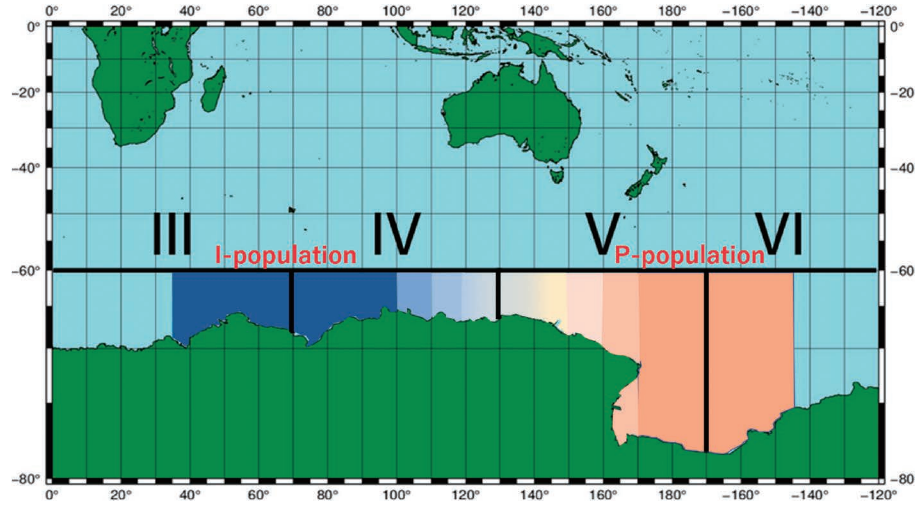

Fig. 1. IWC management Areas IIIE, IV, V and VIW where the study was conducted. The figure also shows a schematic representation of the hypothesis of population structure of Antarctic minke whale in the Indo-Pacific region of the Antarctic. At least two populations occur in this region, the Eastern Indian Ocean Population (I) and the Western South Pacific Ocean Population (P), which overlap in a transition area.

Table 1. Number of sampled individuals used in the analysis. Individuals which had missing data for one or more loci were excluded from the analysis.

		Area	2006/07	2008/09	2009/10	2010/11	2011/12
Female	With fetus (Mother/fetus pair)	IIIE–VW	0	0	156	0	12
		VE–VIW	242	43	0	78	79
	Immature or mature but without fetus	IIIE–VW	0	3	71	0	38
		VE–VIW	106	63	0	30	38
Male	Mature male	IIIE–VW	133[1]				
		VE–VIW	265[1]				
		IIIE–VW		150[2]			
		VE–VIW		145[2]			
		IIIE–VW			151[3]		
		VE–VIW			79[3]		
		IIIE–VW				33[4]	
		VE–VIW				83[4]	
		IIIE–VW	0	5	120	0	36
		VE–VIW	128	71	0	46	37
	Immature male	IIIE–VW	0	5	46	0	13
		VE–VIW	24	31	0	16	13

[1] The total number of mature males aged ≥6 years in 2006/07; [2] The total number of mature males aged ≥6 years in 2008/09; [3] The total number of mature males aged ≥6 years in 2009/10; [4] The total number of mature males aged ≥6 years in 2010/11.

Assumptions on population structure

Abundance estimates developed using the paternity method are presented here under two assumptions: (i) no population structure; and (ii) population structure based on the hypothesis proposed by Pastene and Goto (2016). Regarding (ii), the IWC SC (IWC, 2008) has agreed that there are at least two genetically distinct populations in this region, one in the east (Pacific or P-population) and the other in the west (Indian or I-population) with a ‘soft’ boundary between these populations in Areas IVE and VW, which changed by year and sex. For practical purposes, the present study assumes that the I-population is distributed from Area IIIE to Area VW, and the P-population from Area VE to Area VIW. Fig. 1 shows a schematic representation of the population structure of Antarctic minke whales in the Indo-Pacific region, and its relation with IWC Management Areas.

Identification of father from mother/fetus genotype profiles

The first step in the process of using the paternity method to estimate abundance is to examine the microsatellite DNA profiles of the mother/fetus pairs to look for potential fathers within the total sample. The probability of the fetus’s genotype at each locus, given the mother’s and potential father’s genotype, was calculated following Marshall *et al.* (1998). Table 2 shows the conditional probabilities for all compatible mother/fetus–potential father pairs. The possibility of a male being the true father is rejected when the probability of the fetus’s genotype is 0. In this study, 10 loci were used for the estimation, and the 10 probabilities for the fetus’s genotype multiplied. When the results are greater than 0, the potential father is considered the true father.

To aid interpretation, the sexual maturity of the males was considered. Males aged six years old or older were defined as mature males (Tamura and Konishi, 2014; Murase *et al.*, 2020) and the sensitivity of the results to using definitions of seven and eight years old was also examined.

The geographical positions of mother/fetus and true father pairs were mapped using Generic Map-

Table 2. Conditional probabilities for all compatible mother/fetus–potential father pairs.

Fetus's genotype (g_o)	Potential father's genotype (g_p)	Mother's genotype (g_m)	$\Pr(g_o \mid g_m, g_p)$	$\Pr(g_o \mid g_m)$
BB	BB	BB	1	b
BB	BX	BB	1/2	b
BB	BB	BX	1/2	$b/2$
BB	BX	BX	1/4	$b/2$
BC	BB	CC	1	b
BC	BX	CC	1/2	b
BC	BB	CY	1/2	$b/2$
BC	BX	CY	1/4	$b/2$
BC	BB	BC	1/2	$(b+c)/2$
BC	BY	BC	1/4	$(b+c)/2$
BC	BC	BC	1/2	$(b+c)/2$

X represents any allele other than B; Y represents any allele that is neither B nor C. The frequencies of alleles B and C are denoted b and c. $\Pr(g_o \mid g_m, g_p)$ is the probability of the fetus's genotype given the mother's and alleged father's genotypes and $\Pr(g_o \mid g_m)$ is the probability of the fetus's genotype given the mother's genotype (Marshall *et al.*, 1998).

ping Tools (GMT[2]) (Fig. 2).

Likelihood function for estimating the number of mature males

The likelihood function for the abundance of mature males was obtained as described by Nielsen *et al.* (2001). Assuming $I_j\,(i)$ is the event that the jth potential father is the true father of the ith fetus, $I_0\,(i)$ is the event that the potential father is not in the samples, $\boldsymbol{M_i}$ is the ith maternal genotype, $\boldsymbol{O_i}$ is ith associated genotype of the fetus, $\boldsymbol{F_j}$ is the genotype of the jth potential father, $\boldsymbol{A}$ is the matrix of allelic frequencies for all loci, N is the abundance of mature males in the area and n is the number of sampled mature males, then the likelihood function for N is expressed as:

$$
\begin{aligned}
L(N) &\propto \prod_i \Pr(\boldsymbol{O_i} \mid \boldsymbol{M_i}, \boldsymbol{F}, \boldsymbol{A}, N) \\
&= \prod_i \left(\frac{(N-n)}{N} \Pr(\boldsymbol{O_i} \mid \boldsymbol{M_i}, \boldsymbol{A}) + \frac{1}{N} \sum_{j=1}^{n} \Pr(\boldsymbol{O_i} \mid \boldsymbol{M_i}, \boldsymbol{F_j}) \right) \\
&= \prod_i \left(\frac{(N-n)}{N} \Pr\big(\boldsymbol{O_i} \mid \boldsymbol{M_i}, \boldsymbol{A}, I_0(i)\big) + \frac{1}{N} \sum_{j=1}^{n} \Pr\big(\boldsymbol{O_i} \mid \boldsymbol{M_i}, \boldsymbol{F_j}, I_j(i), \boldsymbol{A}, N\big) \right) \text{ for } N > n. \qquad (1)
\end{aligned}
$$

Here, $\Sigma_{j=1}^{n} \Pr(\boldsymbol{O_i} \mid \boldsymbol{M_i}, \boldsymbol{F_j})$ refers to the sum of the probabilities that the father of the ith fetus is the jth potential father when the ith maternal genotype and the jth potential father are given, and $\Pr(\boldsymbol{O_i} \mid \boldsymbol{M_i}, \boldsymbol{A})$ refers to the probability of the ith fetus's genotype given the ith mother's genotype. The point estimate of N was computed by maximizing the logarithm of $L(N)$, and the 90% confidence interval of N was calculated by the likelihood profile as $\{N;\ \log L(N) \geq \log L(\hat{N}) - 0.5\chi^2\ (0.10)\}$, where $\chi^2\ (0.10)$ is the 10th upper percentile of chi-square distribution with the degree of freedom 1.

To estimate the total abundance of Antarctic minke whales, the total was prorated based upon the proportions of males and females, and immature and mature whales, from the sampled data, under the assumption that the sample was representative of the true population (by assuming an equal selectivity from the population(s)). The proportion of male whales was 0.436 for the case of a single population, and 0.491 and 0.407 for I- and P-populations, respectively. Also, the proportion of immature whales

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[2] https://www.generic-mapping-tools.org/

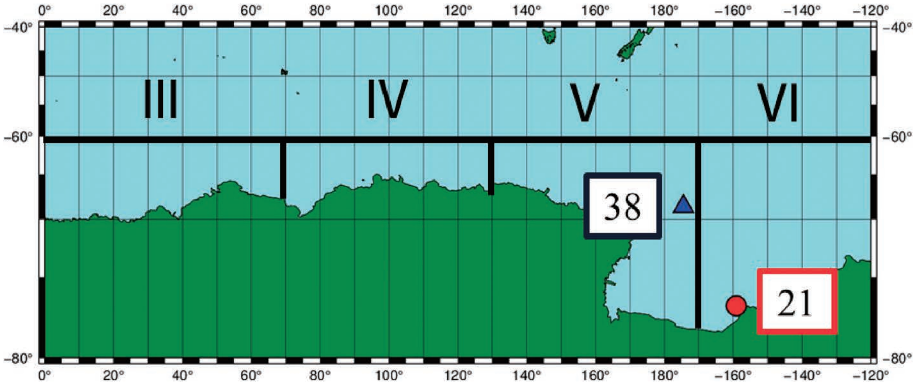

Fig. 2A. Positions of a mother-fetus pair and its true father. The circle indicates a female caught in 2006/07 and the triangle indicates a male caught in 2006/07. The red and blue boxed numbers are the ages of female and male, respectively.

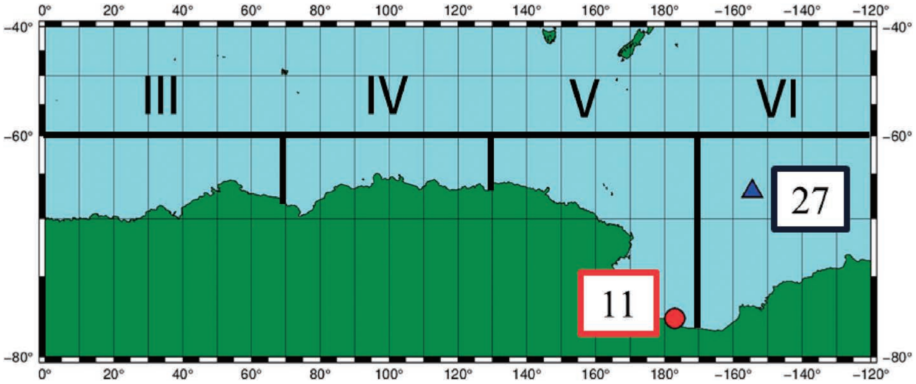

Fig. 2B. Positions of a mother-fetus pair and its true father. The circle indicates a female caught in 2006/07 and the triangle a male caught in 2008/09.

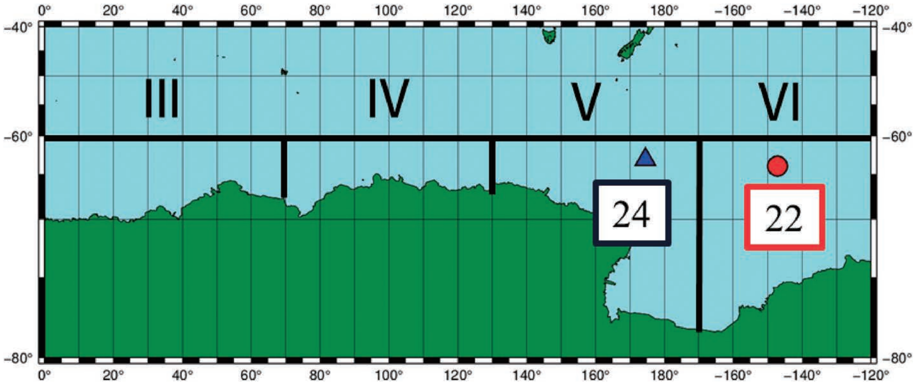

Fig. 2C. Positions of a mother-fetus pair and its true father. The circle indicates a female caught in 2006/07 and the triangle a male caught in 2010/11.

under the assumption of knife-edge maturity-at-age six years old was 0.254 for a single population, and 0.299 and 0.225 for I- and P-populations, respectively. For a sensitivity test, eight years old was used as the maturity age. In this case the immature proportion was 0.317 for a single population, and 0.366 and 0.286 for I- and P-populations, respectively.

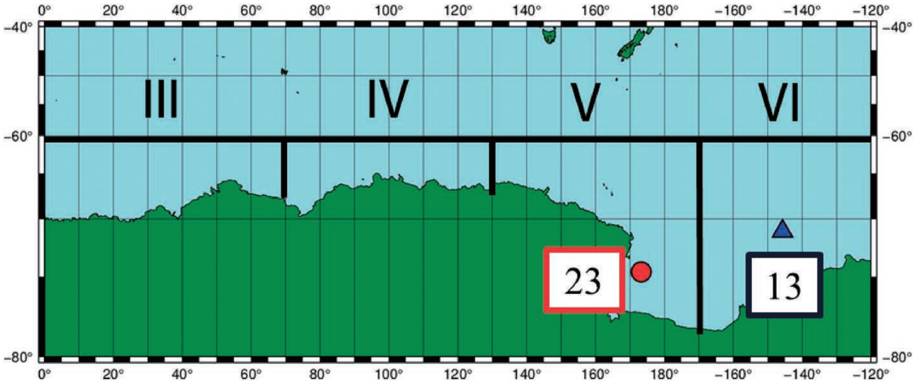

Fig. 2D. Positions of a mother-fetus pair and its true father. The circle indicates a female caught in 2006/07 and the triangle a male caught in 2011/12.

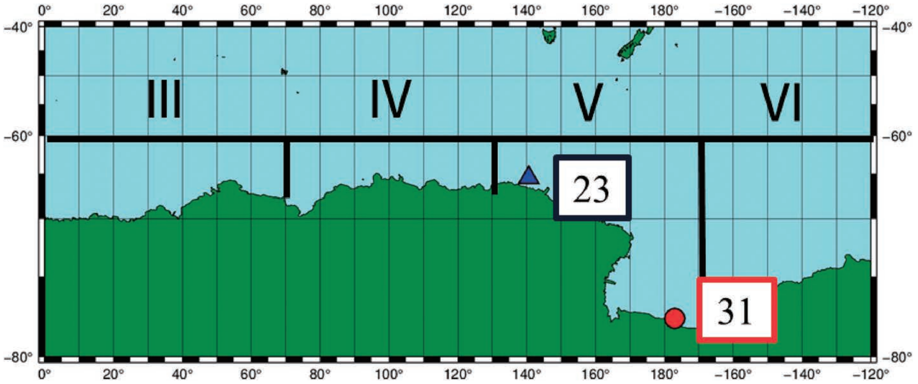

Fig. 2E. Positions of a mother-fetus pair and its true father. The circle indicates a female caught in 2006/07 and the triangle a male caught in 2011/12.

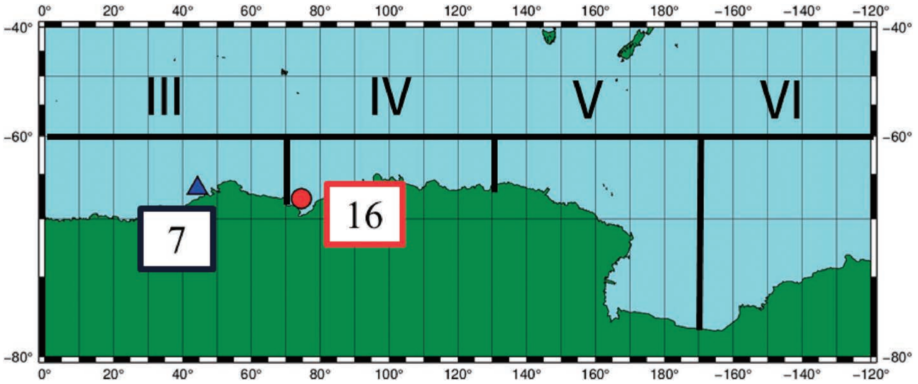

Fig. 2F. Positions of a mother-fetus pair and its true father. The circle indicates a female caught in 2009/10 and the triangle a male caught in 2009/10.

Results

Mother/fetus and mature male pairs

A total of 10 mother/fetus–father pairs were identified under the assumption of a maturity age of six years old. There were no cases of multiple fathers for one fetus. True fathers were found for five mothers/fetuses caught in 2006/07 and five mothers/fetuses caught in 2009/10.

The location of the matching pairs is shown in Figs. 2A–J. Eight pairs occurred in nearby geographical locations (Figs. 2A–H) while two pairs occurred in distant locations (Figs. 2I, J).

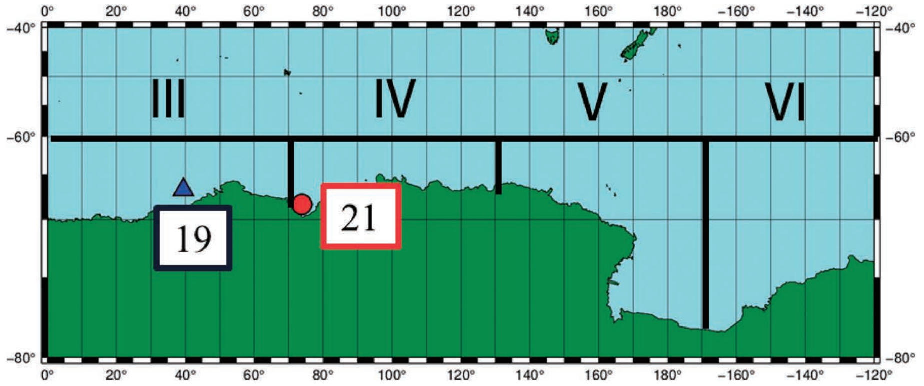

Fig. 2G. Positions of a mother-fetus pair and its true father. The circle indicates a female caught in 2009/10 and the triangle a male caught in 2009/10.

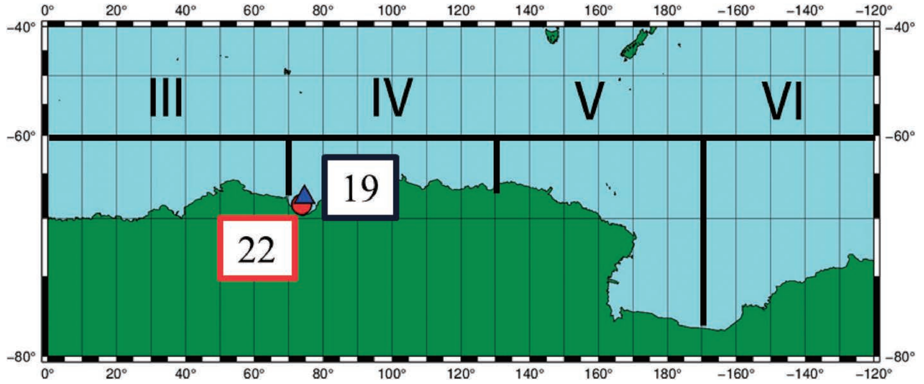

Fig. 2H. Positions of a mother-fetus pair and its true father. The circle indicates a female caught in 2009/10 and the triangle a male caught in 2009/10.

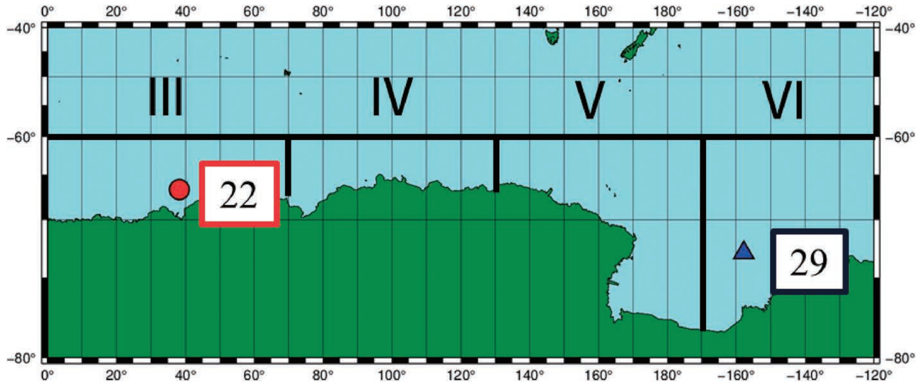

Fig. 2I. Positions of a mother-fetus pair and its true father. The circle indicates a female caught in 2009/10 and the triangle a male caught in 2011/12.

The abundance of mature males (population structure information not considered)

Combining data for all years, $\hat{N}_{\text{mature male}}$ was estimated to be 68,874 (90%CI=42,625–122,779). The likelihood profile is shown in Fig. 3. Using the ratios of males to females and immature to mature whales to estimate the total population, the total population size, $\hat{N}$, was estimated as 211,600 (90%CI=130,954–377,210).

The abundance of mature males (population structure information considered)

For the I-population and using data from the two relevant years (2009/10 and 2011/12), the estimat-

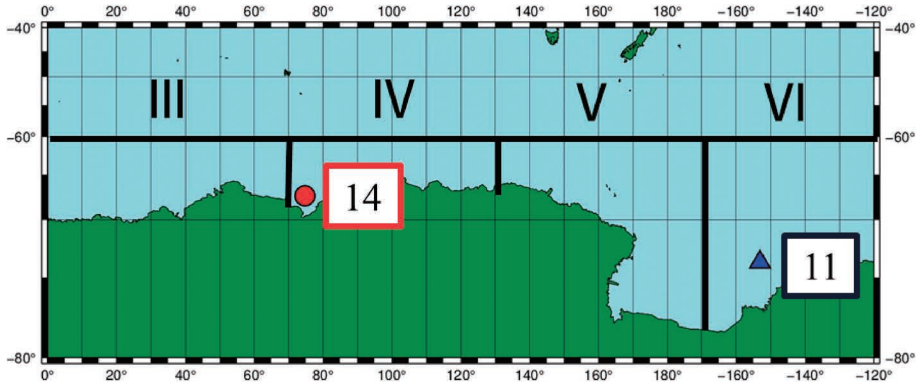

Fig. 2J. Positions of a mother-fetus pair and its true father. The circle indicates a female caught in 2009/10 and the triangle a male caught in 2011/12.

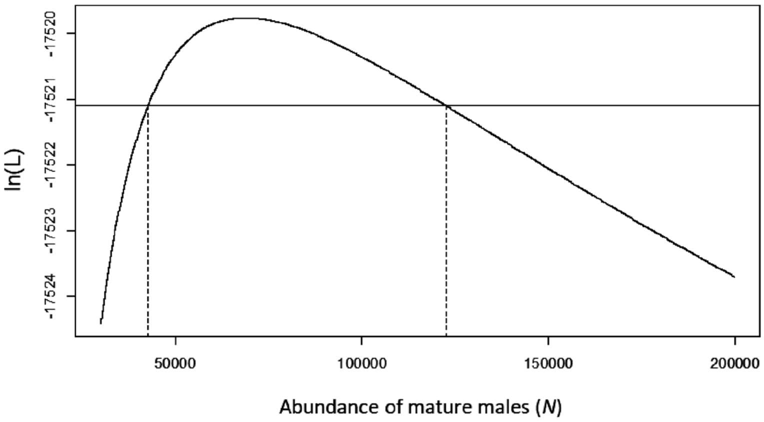

Fig. 3. The likelihood profile for $\hat{N}_{\text{mature male}}$ using 10 loci and five years of mother-fetus pairs and mature males for analysis without considering population structure (assumption of single population).

ed abundance of mature males $\hat{N}_{\text{mature male}}$ was 10,478 (90%CI=4,662–32,212), and the total population $\hat{N}$ was 30,432 (90%CI=13,540–93,556). The likelihood profile is shown in Fig. 4A.

For the P-population (2006/07, 2008/09, 2010/11 and 2011/12), the estimated abundance of mature males $\hat{N}_{\text{mature male}}$ was 59,961 (90%CI=28,853–161,155), and $\hat{N}$ was 189,946 (90%CI=91,401–510,506). The likelihood profile is shown in Fig. 4B.

There were 9 pairs when the age of sexual maturity in males was changed from six to eight years old. Therefore, six years old was used for the subsequent analysis of abundance. Comparison of abundance estimates are summarized in Table 3.

Discussion

The main objective of this study was to apply a new paternity method based on maximum likelihood to estimate the abundance of the Antarctic minke whale in the Indo-Pacific region of the Antarctic, and to evaluate this method by comparing the results with those obtained by line-transect methods in the same region.

Estimates from the paternity methods

There are some technical issues that need to be considered with respect to the paternity method estimates presented here. A key factor relates to the issues that resulted in the exclusion of a considerable amount of data due to the following reasons:

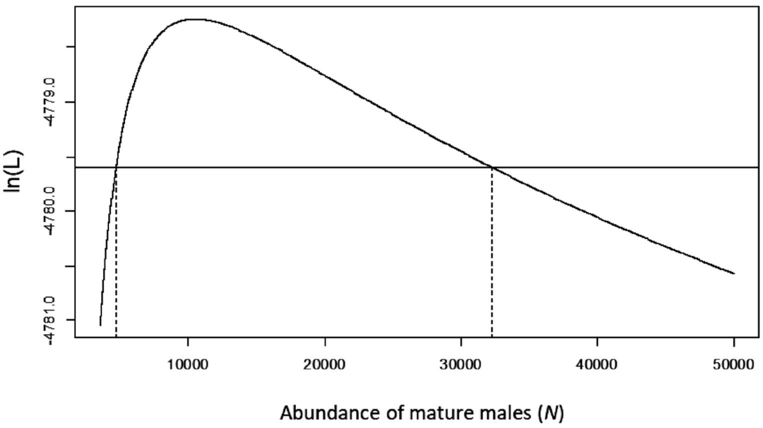

Fig. 4A. The likelihood profile for $\hat{N}_{\text{mature male}}$ using 10 loci in Areas IIIE, IV and VW using five years of mother-fetus pairs and mature males for analysis (I-population under the assumption of two populations).

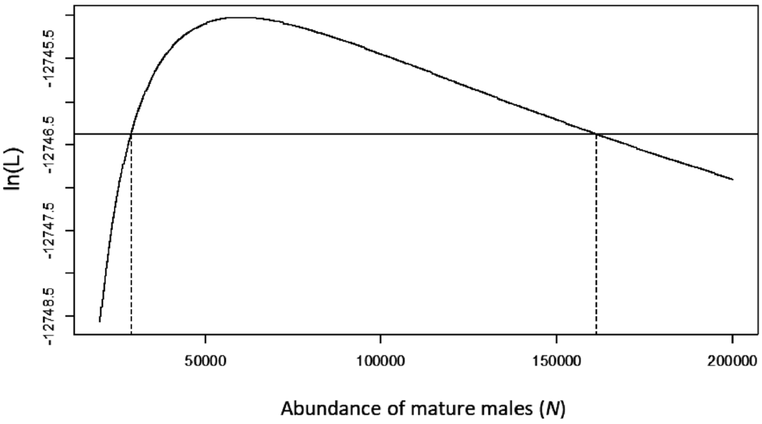

Fig. 4B. The likelihood profile for $\hat{N}_{\text{mature male}}$ using 10 loci in Areas VE and VIW using five years of mother-fetus pairs and mature males for analysis (P-population under the assumption of two populations).

(1) genotyping errors indicated by mother/fetus pairs with clearly different genotypes (37 pairs);
(2) missing allele information for some loci (576 individuals), indicating a genotyping error; and
(3) two loci with a high null allele frequency.

Presence of such genotyping errors and null alleles could cause reduction of matching cases, and therefore the estimated abundance tends to be positively biased. Such errors and allelic dropout can be considered in statistical models. However, such technical drawbacks in the DNA experiment should also be examined and, where possible, corrected so that updated data can be used in future analyses. Data collected after the 2011/12 austral summer season should be also used.

For practical reasons, the assumption of population structure considered a hard boundary between the I and P-populations. Refined analyses should consider the probability of assignment of each individual to each population in the overlap area.

Finally, this method considered only the relationship between mother/fetus and father. If other relative categories such as siblings are incorporated into the analyses, then the estimation performance (precision and accuracy) could be improved (Bravington *et al.*, 2016a; b).

Comparison with estimates from line-transect surveys

The preliminary results on abundance can be summarized as follows: i) there were no substantial differences in abundance under the two assumptions on population structure; ii) there was a slight difference in I-population estimate depending on the assumption for maturity age used, which gave an impact on the candidate fathers and successful pairs; and iii) the abundance derived from the paternity

Table 3. Results of abundance estimates for the Antarctic minke whales derived from the paternity analysis (in this paper) and a comparison with the estimates obtained using the line-transect method from the IWC SOWER programme (IWC, 2013, p.27) and JARPA/JARPAII (Hakamada and Matsuoka, 2014).

Method	Assumption/Data	IWC Management Area							Remarks
		Area III		Area IV	Area V		Area IV		
		III–W	III–E		V–W	V–E	VI–W	VI–E	
Paternity analysis with single population	Base case		211,600 (90%CI=130,954–377,210)						Maturity age=6 yrs old
	Sensitivity case		228,478 (90%CI=137,936–422,368)						Maturity age=8 yrs old
Paternity analysis with I- and P-populations	Base case			30,432 (90%CI=13,540–93,556)	189,946 (90%CI=91,401–510,506)				Maturity age=6 yrs old
	Sensitivity case			45,637 (90%CI=17,359–192,539)	182,458 (90%CI=87,924–488,166)				Maturity age=8 yrs old
Line transect method	IDCR/SOWER (1992/93–2003/04, IWC 2013)	93,215 (CV=0.35)		55,237 (CV=0.49)	183,915 (CV=0.36)		80,835 (CV=0.37)		All the estimates were corrected by g(0) estimates. The CVs include the additional variance.
	JARPA/JARPAII (1989/90–2008/09, Hakamada and Matsuoka 2014)			56,699* (30,585–95,725)	207,012* (132,431–299,433)				All the estimates were corrected by g(0)estimates. The interval in brackets is a range of time series estimates.

*An average (and the range in brackets) of a series of abundance estimates in Hakamada and Matsuoka (2014).

method was similar or somewhat lower than that obtained by the line-transect method (Table 3). It should be noted that this comparison was not straightforward because the research areas covered by the two methods are not identical (for example, the western part of Area III and eastern part of Area VI were not covered by the paternity method). The figure from the line-transect method, however, tends to be within the 90% confidence interval of the estimates by the paternity method.

Possible advantage of the paternity analysis over the line transect method is a less demanding requirement of the coverage of the habitat area. In the line transect method, the survey is assumed to cover the whole habitat area while the genetic tagging does not require this condition strongly as far as the sampling is randomly conducted. However, in the paternity analysis, false positive and/or false negative in matching between mother/fetus and father is crucial, and therefore the method is subject to over- or under-estimation depending on the quality of matching. Also, if the number of matching is quite low and the population size is large, "recapture probability" and "actual number of recapture" might be so low and it could cause a large extent of uncertainty in the abundance estimation. In fact, in our analyses, the matching occurred only in 10 pairs for hundreds of thousands of population size, and hence the 90% CI tends to be wide. To increase the recapture probability, other kinship definitions such as half-sibling can be used for improving estimation performance. This warrants further extension of methods to simultaneously account for different kinship types and population structure.

Inference of results for population structure hypotheses

The study offered the opportunity to compare the information obtained from this study with the current population structure hypotheses for the Indo-Pacific region. The geographical positions of mother/fetus–true father pairs are broadly consistent with the hypothesis of separate I- and P-populations. A total of 8/10 pairs was found in the expected areas of distribution of either I- or P-population. For example, five pairs were found in the expected area of distribution of the P-population while three pairs were found in the expected area of distribution of the I-population. In two cases, however, mother/fetus–true father pairs were found in quite different feeding areas. In the first case, the mother/fetus was caught in the expected area of I population while the true father was found in the expected area of the P-population. In the second case, the mother/fetus was caught in the expected feeding area of the I-population while the true father was found in the expected area of the P-population. These two examples are not inconsistent with the hypothesis of I- and P-populations, because it is expected that some whales move longitudinally within the feeding grounds, wherever they breed, and that such movements are more marked in males (Kitakado *et al.*, 2014; Murase *et al.*, 2020).

Conclusion

The results from this study have demonstrated the utility of the paternity method for obtaining abundance estimates of the Antarctic minke whale because the estimates are compatible with those obtained using the line-transect method. A number of ways to improve the estimates have been identified.

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