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A new interpretation of the stock identity in the Antarctic minke whale based on analyses of genetics and non-genetics markers

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ABSTRACT

Stock identity in the Antarctic minke whales was investigated by means of different analytical approaches using samples obtained during JARPA surveys from 1987/88 to 2003/04 austral summer seasons in Areas IIIE, IV, V and VIW. Analytical approaches used were genetics (mtDNA RFLP and microsatellite) and non-genetics (mean body length of physically matured whales, morphometrics and distribution of parasite *Anisakis simplex*). The different analyses were conducted on same geographical/temporal strata. Samples were grouped into six longitudinal strata used by JARPA surveys: IIIE (35°-70°E); IVW (70°-100°E) (north and south); IVE (100°-130°E); VW (130°-165°E); VE (165°E-170°W) (north and south) and VIW (170°W-145°W). Overall, all the analytical approaches showed substantial spatial heterogeneity. The general pattern of spatial variation was concordant among most of the approaches: a) Whales in Area IIIE were similar to those in Areas IVW and IVE in the characteristics of the biological markers, b) Whales in Area VIW were similar to those in Area VE and c) Whales in Areas IIIE, IVW, IVE were different in the characteristics of the biological markers to whales in Areas VE, VIW. Therefore results are consistent with the hypothesis of two stocks, possibly related to the proposed breeding areas in the eastern Indian and western South Pacific Oceans, respectively. The pattern of spatial differentiation found provides little support for IWC stock boundaries among III, IV, V and VI. Names proposed for these stocks are 'Eastern Indian Ocean Stock' (I-stock) and 'Western South Pacific Stock' (P-stock). A fine-scale mtDNA analysis was conducted to investigate boundary between stocks. Based on this analysis, a 'soft' boundary is proposed near longitude 165°E.

KEY WORDS: ANTARCTIC MINKE WHALE, STOCK IDENTITY, GENETICS, BIOLOGICAL PARAMETERS, MORPHOMETRY, ECOLOGICAL MARKERS

INTRODUCTION

The study on stock identity in Antarctic minke whale is conducted under the JARPA research objective titled 'elucidation of the stock structure of the Southern Hemisphere minke whales to improve stock management'. Information on stock identity is important for a) the estimation of biological parameters, which should ideally be carried out on the basis of biologically identified stock units and b) the application of RMP on this resource.

Hoelzel and Dover (1989) defined three categories of stocks: 'dynamic stock' is the fundamental unit described by a population model or assessment procedure, 'management stock' is the group of whales occurring within a specific geographical boundary which is actively or potentially exploited and 'genetic stock' is a genetically differentiated population within a species. The aim of JARPA is the identification of management units that match as much as possible the geographical and temporal boundaries of genetic stocks.

Stock structure scenarios

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The minke whale like all the other balaenopterids (except the Bryde's whale) are believed to undertake seasonal migrations between feeding grounds in the Antarctic waters in summer and breeding grounds in the tropical or temperate regions in winter. For this species, however, there is only a single evidence of such linkage, based on mark-recapture data. Two whales that had been marked in the Antarctic were recovered off Brazil (Buckland and Duff, 1989). There are also a few indirect evidences on this linkage based on ecological markers (Nemoto *et al*., 1980; Ohsumi, 1973).

Only one of the breeding grounds has been identified in Brazil based on Discovery mark recovery analysis (Buckland and Duff, 1989). Of interest for the stock identity studies of JARPA in Antarctic Areas IV and V, however, is the information on location of possible breeding grounds in low latitudes of the Indian and western South Pacific Oceans. Kasamatsu *et al*. (1995) examined Japanese sighting data obtained during 1976 to 1987. Based on spatial distribution in tropical and sub-tropical waters during the latter half of the conception period of the species, they suggested that there were two breeding grounds in the eastern and western South Pacific and two others in the eastern and western Indian Ocean. The breeding grounds that could be related to JARPA research areas in the Antarctic feeding grounds are the eastern Indian Ocean and the western South Pacific. Very little is known about the pattern of movement of this species between low latitude breeding grounds and high latitude feeding grounds.

The simplest stock scenario in the feeding grounds is that whales in Areas IIIE, IV, V and VIW belong to one stock (single stock scenario). Whales in these areas would migrate indistinctly to different wintering grounds in low latitudes. The alternative is that whales in these Areas belong to two stocks (two stock- scenario). In this case whales would present site fidelity to specific wintering grounds in low latitudes. Under this second scenario several sub-scenarios can be postulated with the extreme options being: a) whales from different breeding stocks fully segregate in the Antarctic feeding ground so that they can be identified in both breeding and feeding grounds, and b) whales from different breeding stocks fully mix in the Antarctic feeding grounds so that they can be identified in the breeding grounds but not in the feeding grounds.

The analyses conducted in the present study are focused to test these two main scenarios of stock structure in the Antarctic minke whale.

Results presented to the 1997 review meeting and posterior developments

During the JARPA midterm review meeting conducted in 1997 (IWC, 1998), the information presented on stock structure of the Antarctic minke whale was based mainly on analyses of mtDNA on samples taken by JARPA between 1987/88 and 1994/95. The statistical analyses were based on AMOVA PHIstatistics (Excoffier *et al*., 1992) and the main results were summarized in the review meeting report as follows (IWC, 1998):

a) A high degree of heterogeneity (as measured by mtDNA) exists with the ordinary form of the minke whale (Antarctic minke whale) within Areas IV and V.
b) The heterogeneity observed in Areas IV and V is attributable to both longitudinal and temporal components in distribution.
c) The observed pattern of genetic heterogeneity is not consistent with current stock boundaries (i.e. between Areas IV and V).
d) There are at least two distinct 'genetic stocks' in Areas IV and V.

The meeting recognized that the available mtDNA data were consistent with the occurrence of more than one stock in the JARPA research area. However no boundaries were proposed or discussed at that opportunity.

Based mainly on results of mtDNA RFLP analysis (Pastene *et al*. 1996) presented to the 1997 JARPA review meeting, a working hypothesis on stock structure was presented, which suggested a main stock ('core') distributed in Areas IV and V and an additional stock ('western') distributed in western part of Area IV and a temporal component to their distribution. The term 'core stock' implied the concept of a large stock occupying all (or most of) Areas IV and V.

To investigate eastern and western distribution of the hypothesized 'core stock' the JARPA surveys have covered the eastern part of Area III and western part of Area VI since the austral summer season 1995/96. MtDNA analysis on the new samples obtained from Area IIIE failed to detect any boundary

of the 'core stock' to the west as the pattern of mtDNA heterogeneity found in the western part of Area IV early in the 1989/90 survey (attributed to a hypothetical 'western stock') (Pastene *et al*, 1996) was not found in samples from Area IIIE (Pastene and Goto, 1997; Pastene *et al*. 2001). The detailed grouping of samples of the present study in IVW and the use of additional analytical approaches, are useful to investigate further the apparent mtDNA heterogeneity in that sector.

Importance of multi-approach analysis in the study of stock structure

In reviewing the results on stock structure derived from JARPA, the Scientific Committee has noted that only preliminary conclusions can be drawn at this stage and that more concrete conclusions will be able to be made following the completion of different analyses. It further supported the suggestion that additional analyses using alternative groupings and analytical methods should be conducted (IWC, 2004). On this regard the 1997 JARPA review meeting recommended that other analyses be conducted (in addition to mtDNA) and the possibility of further structure in the 'core stock' was not discarded (IWC, 1998).

As mentioned above previous results on stock identity have derived from a single approach: mtDNA RFLP analysis. However, the most effective way to address questions on stock identity is to consider results from several techniques, genetics and non-genetics (Donovan, 1991; Pastene *et al*., 2000; Perrin, 2001; Rugh *et al*., 2003). A good example of this was the comprehensive results on stock identity on North Pacific minke whale presented during the JARPN review meeting (IWC, 2001). In the case of the Antarctic minke whale the application of multi-approaches to investigate stock identity is particularly desirable because previous genetic analysis suggested that the effect size in this species is low and then, results obtained by a single marker should be checked using independent markers.

In response to those suggestions, the study on stock structure under the JARPA was extended by the use of several biological markers, both genetics and non-genetics and more detailed grouping of samples. These approaches were used for examining samples of the JARPA from 1987/88 to 2003/04. Results found are discussed in the context of the stock structure scenarios listed above.

MATERIALS AND METHOD

Samples

Minke whales sampled by JARPA surveys in Areas IIIE (35°-70°E), IV (70°-130°E), V (130°E-170°W) and VIW (170°-145°W) between 1987/88 and 2003/04, were used in the analysis. All samples were taken randomly along pre-defined track-lines.

Grouping of samples

The same geographical sectors used by JARPA surveys were used in the analysis: IIIE (35°-70°E), IVW (70°-100°E) north and south (IVWN, IVWS including the Pridz Bay), IVE (100°-130°E), VW (130°-165°E), VE (165°E-170°W) north and south (VEN, VES) and VIW (170°-145°W). Because IVW and VE involve a considerable wider latitudinal range, only in these two cases the JARPA's north/south division was considered. Then a total of eight primary geographical strata were used in the analysis (Figure. 1).

In each stratum samples were further divided on a monthly basis. This temporal analysis enabled us to check for the possibility of a temporal component in the distribution of stocks. In general analyses followed a stepwise fashion. First, each stratum was tested for monthly variation. Next, north and south strata were tested in IVW and VE. Finally pairwise comparisons were conducted among the longitudinal strata. Depending of the kind of analytical approach, analyses were conducted for each sex as well as for the total samples (F+M).

Samples from several years were pooled in each stratum. This required the assumptions that the pattern of seasonal movement are the same for a given breeding stock in different years; that lateral movement on feeding ground and pattern of mixing are similar between years and that sampling effort was not biased from one year to the next.

In the 1998/99 survey, the Ross Sea was not accessible and samples in VE were taken only in the northern part. Samples of stratum 'VES' in 1998/99 were included into stratum VEN.

Analytical approaches

MtDNA

Crude mtDNA were treated with six polymorphic restriction enzymes (*Acc*I, *Ban*I, *Hinc*II, *Hpa*I and *Ssp*I). Haplotypes were defined on the basis of the combination of the restriction pattern of these enzymes. Details of the laboratory work can be found in Pastene *et al*. (1993) and Pastene *et al*. (1996). Differences in the frequency of haplotypes among strata were tested by the randomized chi-square test (Roff and Bentzen, 1989), as recommended by the Scientific Committee. A total of 10,000 simulations were made in each test. The level of significance obtained by this method is called the P-value. A P-value smaller than 5% was used as a criterion to reject the null hypothesis of panmixia. Analyses were conducted for male and female separately as well for both sample combined. Sequential Bonferroni corrections were made in case of multiple tests.

A total of 5,838 minke whale samples (JARPA 1987/88-2003/04) were used for this analysis (2,643 females and 3,195 males) (Table 1).

Microsatellite

Genotypes were scored at 6 microsatellite loci: EV1, EV104, GT023, GT195, GT211 and DlrFCB14. Details of laboratory work can be found in Abe *et al*. (1999) with some modifications. All the statistical tests were conducted using the computer program GENEPOP (Raymond and Rousset, 1995). Tests for genetic heterogeneity were based on Fisher's exact probability test. Tests for deviation from the Hardy-Weinberg equilibrium were also conducted. Analyses were conducted for male and female separately as well for both sample combined. Decision of statistically significance on hypothesis testing was made using the Fisher Exact value obtained from summing the negative logarithm of P-values over the total loci (Fisher, 1950). A P-value smaller than 5% was used as a criterion to reject the null hypothesis of panmixia.

A total of 5,808 minke whale samples (JARPA 1989/90-2003/04) were used for this analysis (2,606 females and 3,202 males) (Table 1).

Biological parameters

The mean body length of physically matured whales (MBLM) was compared among whales from different temporal and geographical strata. Physically matured individuals were defined as those with epiphysis fusion occurring in the 6th thoracic vertebrae. The t-test and ANOVA were used for testing differences in mean body length among strata. A P-value smaller than 5% was used as a criterion to reject the null hypothesis of panmixia. Sequential Bonferroni corrections were made in case of multiple tests. Analyses were conducted for males and females separately.

A total of 2,323 minke whales (JARPA 1987/88-2003/04) (892 females and 1,431 males) were examined (Table 1).

Morphometrics

In order to eliminate the effect of bias due to difference among researchers, the measurements that were less susceptible to such differences were selected for the analysis. Selection of these measurements took into consideration the opinion of experienced researchers. The 10 external measurements used in this study are shown in Figure. 2.

Analysis of covariance (ANCOV) (using body length as a covariate) was used to compare whales from different geographical strata. Sequential Bonferroni corrections were made in case of multiple comparisons. A P-value smaller than 5% was used as a criterion to reject the null hypothesis of panmixia. A Discriminant Analysis was used to corroborate or otherwise the results from ANCOV. Analyses were conducted for male and female separately.

A total of 5,549 samples (JARPA 1987/88-2003/04) were used in this analysis (2,502 females and 3,047 males) (Table 1).

Parasite distribution

Parasites have been used as biological indicators of host stocks and feeding habits. *Anisakis simplex*, which is a well known gastric nematode, is often used as a biological indicator because of its wide range of distribution. The minke whale is known to be the most important final host of *A. simplex* in the northern North Pacific (Kuramochi, 1996). The prevalence (percentage of infected individuals per host examined) of *A. simplex* was examined in the JARPA research area in the context of stock identity.

Combined female and male samples were used for the analysis.

A total of 6,338 minke whales were examined in this study (JARPA 1987/88-2003/04) (Table 1).

RESULTS

mtDNA

Monthly variation

Table 2 shows the results of the heterogeneity test for monthly variation in each stratum for female, male and both sexes combined. None of the P-values obtained was smaller than 0.05.

Latitudinal variation in IVW and VE

Table 3 shows the results of the heterogeneity test for latitudinal mtDNA variation in IVW and VE. None of the P-values obtained was smaller that 0.05. Because no significant differences were found between IWWN and IVWS and between VEN and VES, the total sample for IVW and VE were used in the subsequent analyses.

Longitudinal variation

Tables 4a and 4b show the results of pair-wise statistical comparisons among six longitudinal strata for females and males, respectively. In both cases the total P-value was non significant, notwithstanding several pair-wise comparisons resulted in P-values below 0.05. In the case of females two of these P-values remain significant after Bonferroni correction. Most of these cases occur in comparisons between strata in IIIE, IV and strata in VW, VE. Although some differences occur, the general pattern of variation between females and males are similar.

To investigate further whether or not differences occur between females and males, mtDNA haplotype frequencies were compared between sexes in each of the longitudinal strata. None of the comparisons resulted in P-values below 0.05 (IIIE: F218, M311 P=0.2469; IVW: F622, M799 P=0.4145; IVE: F601, M633 P=0.8901; VW: F409, M608 P=0.3845; VE: F664, M602 P=0.1207; VIW: F129, M242 P=0.7886).

Table 4c shows the results of the pair-wise statistical comparisons among six longitudinal strata for female and male samples combined. The total P-value was significant and several pair-wise comparisons resulted in P-values below 0.05. Four of them remained significant after Bonferroni correction (IIIE-VE, IVW-VE and IVE-VE). Comparisons between IVW, IVE and VIW resulted in P-values below 0.05 but these were not significant after Bonferroni corrections. This result is probably due to the sample size of VIW, which is the smallest of all strata.

Results of pair-wise comparisons suggest a) no significant differences among IIIE, IVW and IVE, b) no significant differences between VIW, VE and VW, c) significant differences between IIIE, IVW, IVE and VE.

Microsatellites

Monthly variation in the strata

Tables 5a, 5b and 5c show the results of statistical test for microsatellite allele frequencies monthly variation in female, male and total sample (female+male), respectively. No significant heterogeneity due to this temporal stratification was found.

Latitudinal variation

Tables 6a, 6b and 6c shows the results of the statistical test for microsatellite allele frequencies latitudinal variation in female, male and total sample (female+male), respectively. Only in the case of females a significant P-value was found in the comparison IVWN and IVWS, which is attributed to locus EV1. In subsequent analyses IVWN and IVWS was treated separately in the case of females.

Test for HardyWeinberg equilibrium

Tables 7a, 7b and 7c show the results of the test for Hardy-Weinberg equilibrium in female, male and total sample (female+male), respectively. None of the tests resulted in significant departure from equilibrium.

Longitudinal variation

Results of the statistical pairwise comparisons among longitudinal strata are shown in Table 8a, 8b and 8c for females, males and total samples (females + males), respectively. The total P-value was significant in the case of females and total samples. No significant heterogeneity was found in the case of males.

In the case of females, several pairwise comparisons resulted in significant P-values. Notably, strata IVWN and IVWS differed significantly from strata VE and VIW.

Biological parameters-mean body length of physically matured whales

Monthly variation

Table 9 shows the results of the statistical test for monthly variation. None of the comparisons showed a P-value smaller than 0.05.

Latitudinal variation

Table 10 shows the results of the statistical test for latitudinal variation in IVW and VE. In the case of males, P-values smaller than 0.05 were obtained in VE. None of the other comparisons resulted in significant P-value. In subsequent analyses males are considered separately for VEN and VES.

Longitudinal variation

Tables 11 and 12 shows the results of the statistical test for longitudinal variation. The total P-values were highly significant for both females and males (Table 11). Results of pairwise comparisons were similar for females and males (Table 12). No significant differences were found among IIIE, IVW, IVE and VW. Also no significant differences were found between VIW and VE. These two strata differed significantly among them. Although VEN and VES differed in the case of males, both of these strata showed a similar pattern of variation in the comparison to other strata.

Morphometrics

Monthly variation

Several instances of 'significant' P-values were found in the comparison among months in the strata. However, these results are considered suspicious because no consistency in differences was observed among strata and sex. Furthermore the discriminant variables of the Discriminant Analysis were not significant for the same temporal sub-divisions. Such results could be due to the small sample sizes used in this analysis. In subsequent analyses, samples from several months were combined in the geographical strata.

Latitudinal variation

Table 13 shows the results of the statistical test for latitudinal variation in morphometric characters in Strata IVW and VE. In the case of males a significant P-value was found for three measurements in stratum VE. However this result was not supported by the Discriminant Analysis, as the discriminant variables in these three cases were not significant. None of the other measurements differed significantly between north and south in Strata IVW and VE. In subsequent analyses north and south samples were combined in IVW and VE.

Longitudinal variation

Tables 14a and 14b show the results of the pairwise comparison among longitudinal strata using ANCOV for females and males, respectively. There are significant differences in all measurements used. Pattern of variation was similar between males and females. After Bonferroni correction, results can be summarized as follow: a) there is no significant difference among IIIE, IVW b) there is no significant difference among VE and VIW, c) there are significant differences in all measurements between IIIE, IVW and VE, VIW and d) no clear pattern of differentiation was found in Strata IVE and VW.

Although the Discriminant Analysis suggested that only 23.3% and 22.7% of the samples classified correctly into the six longitudinal strata for females and males, respectively, the discriminant variables were significant.

Parasite distribution

Table 15 shows the prevalence of *Anisakis simplex* by geographical strata and sex. Prevalence is similar between female and males host. Results indicate that prevalence is higher in strata V, VIW than IIIE, IV.

Figure 3 shows the infection rate of the parasite *Anisakis simplex* in Antarctic minke whales (female and male combined), by 5° longitude slices. The higher rates are observed from longitude 155°E to 170°W, with a peak in sector 165°-170°E.

DISCUSSION

Temporal variation

The analytical approaches used in this study showed no monthly variation in the geographical strata. A previous mtDNA studies showed mtDNA temporal heterogeneity in IVW (Pastene *et al*., 1996). These authors attributed such heterogeneity to additional stock structure and speculated that a different stock could be distributed in Area IIIE. However subsequent analysis in contiguous Area IIIE showed no evidence of additional structure (Pastene and Goto, 1997; Pastene *et al*. 2001). Furthermore none of the approaches used in the present study showed evidences of substantial temporal variation in IVW. Some degree of intra-stock variation is possible given the large sample sizes used in the analyses and wide distribution.

Latitudinal variation

Little latitudinal variation was evident from our analysis in Strata IVW and VE. Microsatellite analysis, however, showed some degree of differentiation between north and south in IVW for females. The analysis of mean body length of physically matured whales showed some degree of differentiation between north and south in VE for male samples. The analyses of other biological markers do not support the latitudinal sub-division in these strata. Again, such latitudinal variation do not necessarily reflects additional structure but some degree of intra-stock variation

Longitudinal variation

The results of the different analytical approaches in this case were consistent and they showed substantial longitudinal heterogeneity.

The general pattern of differentiation was well correlated with geography with the most distant strata being differentiated from each other, e.g. IIIE+IVW was different from VIW+VE. This pattern was evident from the results of all approaches used.

Table 16 summarizes the results of the different analytical approaches with regard longitudinal variation.

mtDNA

Pattern of mtDNA longitudinal variation was similar between sexes. The analysis conducted for the combined female and male samples showed substantial longitudinal heterogeneity. Results suggested that whales in IIIE, IVW and IVE are similar in haplotype frequencies; whales in VE and VIW are similar; whales in IIIE, IVW, IVE are different from whales in VE, VIW.

Microsatellites

Females showed more differentiation among longitudinal strata than males. In the comparison among strata, allele frequencies among female samples of IVWN and IVWS differed significantly from those of VE and VIW. In the case of total samples whales in IIIE, IVW differed significantly from VW; whales in IVW differed from whales in VE.

The present microsatellite analysis was thought more informative than the allozyme analysis conducted in the past (Wada and Numachi, 1991).

Mean body length of physically matured whales

Pattern of longitudinal variation was similar between sexes. No significant heterogeneity was found among samples from IIIE, IVW, IVE and VW. No significant heterogeneity was observed between VIW and VE (for females, VEN or VES for males) but these two strata differed significantly from IIIE, IVW, IVE and VW.

Body length at physical maturity might differ depending on nutritional condition (Kato, 1987), so observed difference might reflect feeding site fidelity, instead of stock differentiation. However, results

found for this biological parameter are similar to those found by genetics markers so little weight is attributed to this possibility.

Morphometry
The pattern of longitudinal morphometric differentiation was similar between sexes. Differences among longitudinal strata were more sensitive than other markers. However, the general pattern of discrimination was similar to other markers.

Parasite analysis
The prevalence of *Anisakis simplex* varied considerably among Areas being higher in Areas V and VIW than IIIE and IV. Estimates of prevalence should be seen with caution as data were not weighted by the effort spent in each Area or sector. Furthermore interpretation of results in the context of stock identity is difficult due to a lack of paucity of information about the biology of this parasite. No information is available on when and where this nematode infect minke whales and how long they stay in their stomachs. However results in this study suggest that whales in Areas V and VIW (or VE and VIW) do not migrate in large number to the west (Areas IIIE and IV) because if they move in large number to these Areas the infection rate should not be so different.

Evaluation of stock structure scenarios
Based on the results of the different approaches summarized in Table 16, it is reasonable to conclude that the single stock scenario can not be applied to Antarctic minke whales in the Antarctic feeding grounds of Areas IIIE-VIW. The pattern of structure is consistent with a two-stock scenario. Probably these stocks are related to the breeding areas in the eastern Indian Ocean and western South Pacific suggested by Kasamatsu *et al*. (1995). The following names are proposed for these stocks: Eastern Indian Ocean Stock (I-Stock) and Western South Pacific Ocean Stock (P-Stock).

Because the different analytical approaches were able to differentiate whales from different longitudinal sector, the extreme sub-scenario of full mixing of stocks in the Antarctic can be discarded because different stocks can not be discriminated under such scenario. The remaining question is whether these stocks are fully segregated in the feeding ground or if they partially mix. The possibility of mixing can not be discarded but such possibility can not be corroborated without analysis of samples from the breeding grounds. Sampling and analysis of whales from the breeding grounds will be very useful for a better interpretation of the pattern of variation in the Antarctic.

Management requires that stock boundaries be identified. While the analysis of microsatellites and morphometrics were not clear to indicate any boundary, the analysis of mtDNA (Table 4c) and mean body length of physically matured whales (Table 12) suggested a possible stock separation around longitude 165°E, between strata VW and VE. This was investigated further using mtDNA, which was more informative than microsatellites, in a fine-scale longitudinal analysis.

The first step in this exercise was to define a baseline sample to be compared to smaller sectors in the research area. Table 4 showed a large P-value in the mtDNA comparison between western and eastern part of Area IV, which suggest that haplotype frequencies are very similar between these two sectors. Further no significant yearly differences were found in Area IVW (8 years involved; P=0.8431, P=0.3636 and P=0.3537 for females, males and total sample, respectively). Similarly no significant yearly differences were found in Area IVE (9 years involved; P=0.0646, P=0.1137 and P=0.2088 for females, males and total sample, respectively). Area IVW was used to make comparisons to 10°-sectors to the east (e.g. Area IVE, VW and VE) (Table 17a). Area IVE was used to make comparisons to 10°-sectors to the west (e.g. Area IVW and IIIE) (Table 17b).

As shown in Table 17a, for total samples, large P-values are obtained until sector 150-160°E. From sector 150-160°E probabilities become smaller and statistically significant with the exception of sector 170°E-180°. In the case of females P-values become smaller after sector 150°-160°E. In the case of males significant differences are observed from sector 180°-170°W. None comparison made to the west (Table 17b) showed a P-value smaller than 0.05.

Although there is not a clear longitudinal 'cut', it is reasonable to conclude that the western part of Area V is more related to I-stock than P-stock. Therefore a boundary between I and P Stocks at 165°E is proposed for management purpose. Such boundary is consistent with geography and oceanographic conditions, which change around that longitude (Figure 4). That longitude coincides with the aperture

of the Ross Sea and from the oceanographic point of view this sector is influenced by the Ross Sea Gyre. Many of the circulation and water mass features vary markedly with longitude. Therefore a boundary line around 165°E should be interpreted as a 'soft boundary' rather than a `fix boundary`. It is probable that the two stocks mix to each other across that 'soft' boundary, which could changes with years and with oceanographic and ice-conditions (Figure 4). This interpretation will fix better with the results of different biological markers. The distribution of Antarctic krill concentrations has been related to bottom topography, sea-ice and hydrographic features (Ichii, 1990). Yearly variability in these features in the sector around 165°E could have some effect on annual fluctuation on the distribution of krill concentrations and this, in turn, could affect the distribution of minke whale around that longitudinal sector.

Consistency with results from mark-recapture

Results on mark-recapture analysis conducted during the time of commercial whaling in the areas surveyed by JARPA could assist greatly in the interpretation of results on stock structure found in this study.

Kato *et al* (1993) used information from marks both released and recovered within the Antarctic i.e. 110 marks or 101 recaptured individuals. All but one mark were recovered during commercial whaling operations. One mark in his analysis was recovered during a JARPA survey (3 Feb. 1992). The authors noted that a) more whales appear to move west than east, b) patterns of longitudinal movement are very similar between sexes, c) although some individuals moved great distances (over 100° longitude), most whales appear to return to relatively close to the sector in which they were marked (30°-40° longitude apart), d) the longitudinal distance between marking and recovery for the 1 year-group (animals recaptured one year after marking) seems to be wider than in either subsequent seasons or 'in-season recoveries'. The range up to 120° to the west (average, 42.10°) and 60 to the east (average, 25.10°) while the majority of subsequent year groups remain within 40°.

With regard to stock structure Kato *et al*. (1993) noted that the absence of marks crossing 80°E and 160°E (Figure 5) suggests the possibility of separate feeding stocks but, as suggested by Buckland and Duff (1989) and Best (1990), this should be compared with the catch and marking effort distribution before reaching any general conclusion. After an analysis of catch and marking effort, Kato *et al*. (1993) concluded that both marking and catching effort were almost evenly allocated among sectors between 50°E and 140°E. Based on the results of such analysis they suggested that a possible boundary at 80°E is not an artifact of geographical bias in marking or catching effort.

Two other marks recovered during JARPA surveys were not available for the Kato *et al*. (1993)'s analysis. One of them (elapsed time of 12 years) was marked in the eastern part of Area V and recovered in the western part of this Area. The other one (elapsed time of 21 years) was marked western part of Area V and recovered in the eastern part of Area IV.

Mark-recapture results are partially consistent with the boundary suggested for management purpose in this study. According to this approach, a lot of minke whales move through IWC boundary between Areas IV and V at 130°E. Mark-recapture results suggest boundaries at 80°E and 160°E. While the boundary at 160°E is consistent with our proposal of 165°E, boundary at 80°E proposed by mark-recapture analysis is not consistent with the results of our study, which suggested that Area IIIE is similar to Area IV.

Further research needs

The following topics are recommended for future studies on stock identity:

a) Stock boundary in the Antarctic feeding grounds should be considered as 'soft' instead of 'hard'. Yearly changes in stocks distribution and boundaries should be investigated in the future.
b) Western boundary of the I-stock and eastern boundary of the P-stock should be investigated in the future.
c) To elucidate the possibility of mixing in the feeding ground, samples and genetic analysis of whales from the breeding grounds are necessary. Experiments of satellite tracking would be very useful to examine lateral movement and possible mixing in the feeding grounds as well movement between feeding grounds and lower latitudes wintering grounds.

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Table 1: Number of samples examined by geographical strata, analytical approach and sex.

Areas IIIE and IV

	IIIE		IVWN		IVWS		IVW		IVE	
	F	M	F	M	F	M	F	M	F	M
mtDNA	218	311	160	302	462	497	622	799	601	633
Microsatellites*	227	322	163	320	484	532	647	852	524	556
MBLM	53	94	31	139	141	210	172	349	161	276
Morphometric	199	281	140	281	435	486	575	767	564	641
Parasite	227	322	165	321	488	534	653	855	645	711

Areas V and VIW

	VW		VEN		VES		VE		VIW	
	F	M	F	M	F	M	F	M	F	M
mtDNA	409	608	184	467	480	135	664	602	129	242
Microsatellites*	442	639	162	450	467	131	629	581	137	252
MBLM	178	314	45	220	252	76	297	296	31	102
Morphometric	371	555	173	437	507	155	680	592	113	211
Parasite	442	641	198	497	586	171	784	668	137	253

* Sample size changes among loci. Figures shown are the maximal sample size used among the loci.

Table 2: Results of the heterogeneity test for monthly mtDNA variation in each geographic stratum, by sex.

Strata	Sex	Dec.	Jan.	Feb.	March	P-value
IIIE	F	191	0	6	21	0.4271
	M	257	0	8	46	0.5026
	Total	448	0	14	67	0.2740
IVWN	F	42	80	36	2	0.3521
	M	70	150	80	2	0.5791
	Total	112	230	116	4	0.0720
IVWS	F	38	78	314	32	0.6142
	M	116	123	205	53	0.2023
	Total	154	201	519	85	0.0528
IVE	F	53	265	254	29	0.1514
	M	52	320	226	35	0.3043
	Total	105	585	480	64	0.1926
VW	F	48	128	165	68	0.9732
	M	96	152	208	152	0.4394
	Total	144	280	373	220	0.3876
VEN	F	8	139	14	23	0.6734
	M	10	318	59	80	0.4741
	Total	18	457	73	103	0.5767
VES	F	0	60	286	134	0.2243
	M	0	33	83	19	0.9787
	Total	0	93	369	153	0.6118
VIW	F	101	3	0	25	0.5031
	M	189	6	0	47	0.7057
	Total	290	9	0	72	0.4875

Table 3: Results of the heterogeneity test for latitudinal mtDNA variation in IVW and VE strata.

		North	South	P-value
IVW	F	160	462	0.9158
	M	302	497	0.3956
	Total	462	959	0.5000
VE	F	184	480	0.0985
	M	467	135	0.5701
	Total	651	615	0.1201

Table 4a: Results of the heterogeneity test for longitudinal mtDNA variation in female samples. The total P-value was 0.1057. P-values smaller than 0.05 are underlined. Bold show those P-values that remain significant after Bonferroni corrections.

	IIIE (218)	IVW (622)	IVE (601)	VW (409)	VE (664)	VIW (129)
IIIE	-	0.4799	0.1149	<u>0.0052</u>	**0.0003**	0.7390
IVW		-	0.3574	0.1554	**0.0034**	0.4436
IVE			-	0.5172	0.1512	0.7229
VW				-	0.0844	0.4947
5E					-	0.4506
6W						-

Table 4b: Results of the heterogeneity test for longitudinal mtDNA variation in male samples. The total P-value was 0.1439. P-vales smaller than 0.05 are underlined.

	IIIE (311)	IVW (799)	IVE (633)	VW (608)	VE (602)	VIW (242)
IIIE	-	0.5843	0.7554	0.2773	0.1445	<u>0.0140</u>
IVW		-	0.8852	0.3421	<u>0.0037</u>	0.0799
IVE			-	0.6264	<u>0.0089</u>	<u>0.0203</u>
VW				-	0.5111	0.5970
5E					-	0.5072
6W						-

Table 4c: Results of the heterogeneity test for longitudinal mtDNA variation in total samples (F+M). The total P-value was 0.0024. P-values smaller than 0.05 are underlined. Bold show those P-values that remain significant after Bonferroni corrections.

	IIIE (529)	IVW (1,421)	IVE (1,234)	VW (1,017)	VE (1,266)	VIW (371)
IIIE	-	0.7812	0.0475	0.0074	**0.0009**	**0.0028**
IVW		-	0.9375	0.0086	**0.0001**	0.0273
IVE			-	0.5238	**0.0041**	0.0116
VW				-	0.1054	0.4793
VE					-	0.6143
VIW						-

Table 5a: Results of the heterogeneity test for monthly microsatellite variation in female, in each geographic stratum.

Strata	Microsatellite locus						
	EV1	EV104	GT211	DlrFCB14	GT195	GT23	All loci
IIIE	0.218	0.532	0.458	0.204	0.512	0.658	0.510
IVWN	0.194	0.246	0.851	0.606	0.854	0.966	0.801
IVWS	0.725	0.224	0.722	0.170	0.882	0.583	0.689
IVE	0.374	0.910	0.611	0.170	0.221	0.710	0.583
VW	0.959	0.779	0.516	0.035	0.344	0.551	0.449
VEN	0.008	0.864	0.316	0.580	0.881	0.566	0.255
VES	0.858	0.333	0.887	0.688	0.531	0.388	0.880
VIW	0.076	0.486	0.849	0.635	0.815	0.321	0.572

Table 5b: Results of the heterogeneity test for monthly microsatellite variation in male, in each geographic stratum.

Strata	Microsatellite locus						
	EV1	EV104	GT211	DlrFCB14	GT195	GT23	All loci
IIIE	0.105	0.408	0.580	0.835	0.779	0.266	0.538
IVWN	0.008	0.716	0.549	0.827	0.292	0.514	0.207
IVWS	0.758	0.258	0.985	0.108	0.564	0.967	0.707
IVE	0.628	0.559	0.291	0.900	0.419	0.641	0.830
VW	0.747	0.408	0.265	0.386	0.895	0.934	0.838
VEN	0.738	0.622	0.907	0.661	0.677	0.288	0.924
VES	0.890	0.811	0.850	0.443	0.549	0.245	0.882
VIW	0.617	0.535	0.240	0.099	0.501	0.701	0.462

Table 5c: Results of the heterogeneity test for monthly microsatellite variation in total sample (female+male), in each geographic stratum.

Strata	Microsatellite locus						
	EV1	EV104	GT211	DlrFCB14	GT195	GT23	All loci
IIIE	0.088	0.436	0.391	0.521	0.733	0.358	0.415
IVWN	0.325	0.531	0.695	0.550	0.514	0.729	0.830
IVWS	0.679	0.202	0.963	0.023	0.654	0.602	0.338
IVE	0.574	0.993	0.228	0.917	0.434	0.874	0.906
VW	0.916	0.379	0.052	0.232	0.879	0.982	0.508
VEN	0.423	0.548	0.659	0.790	0.787	0.109	0.691
VES	0.870	0.516	0.713	0.617	0.579	0.602	0.945
VIW	0.238	0.392	0.490	0.301	0.738	0.864	0.662

Table 6a: Results of the heterogeneity test for latitudinal microsatellite variation in females, in strata IVW and VE.

Strata	Microsatellite locus						
	EV1	EV104	GT211	DlrFCB14	GT195	GT23	All loci
IVW-NxS	0.001	0.100	0.562	0.042	0.475	0.117	**0.002**
VE-NxS	0.951	0.324	0.860	0.145	0.628	0.816	0.796

Table 6b: Results of the heterogeneity test for latitudinal microsatellite variation in males, in strata IVW and VE.

Strata	Microsatellite locus						
	EV1	EV104	GT211	DlrFCB14	GT195	GT23	All loci
IVW-NxS	0.819	0.697	0.476	0.827	0.140	0.156	0.560
VE-NxS	0.164	0.550	0.468	0.199	0.092	0.656	0.232

Table 6c: Results of the heterogeneity test for latitudinal microsatellite variation in total samples (female+male), in strata IVW and VE.

Strata	Microsatellite locus						
	EV1	EV104	GT211	DlrFCB14	GT195	GT23	All loci
IVW-NxS	0.497	0.498	0.790	0.452	0.111	0.150	0.367
VE-NxS	0.894	0.843	0.785	0.326	0.667	0.446	0.930

Table 7a: Result of the test for Hardy-Weinberg equilibrium in females, in each geographical stratum.

Strata	Microsatellite locus						
	EV1	EV104	GT211	DlrFCB14	GT195	GT23	All loci
IIIE	0.570	0.225	0.265	0.411	0.792	0.490	0.577
IVWN	0.546	0.836	0.117	0.022	0.169	0.995	0.147
IVWS	0.095	0.278	0.349	0.730	0.351	0.142	0.191
IVE	0.968	0.397	0.206	0.883	0.272	0.614	0.711
VW	0.746	0.142	0.719	0.351	0.733	0.725	0.744
VE	0.201	0.597	0.624	0.191	0.262	0.665	0.447
VIW	0.799	0.719	0.369	0.194	0.944	0.106	0.529

Table 7b: Result of the test for Hardy-Weinberg equilibrium in males, in each geographical stratum.

Strata	Microsatellite locus						
	EV1	EV104	GT211	DlrFCB14	GT195	GT23	All loci
IIIE	0.979	0.255	0.200	0.988	0.491	0.453	0.701
IVW	0.463	0.542	0.772	0.170	0.744	0.569	0.741
IVE	0.670	0.613	0.598	0.784	0.569	0.205	0.816
VW	0.536	0.896	0.833	0.170	0.397	0.521	0.743
VE	0.736	0.380	0.847	0.473	0.416	0.583	0.844
VIW	0.041	0.638	0.580	0.140	0.386	0.096	0.090

Table 7c: Result of the test for Hardy-Weinberg equilibrium in total samples (female+male), in each geographical stratum.

Strata	Microsatellite locus						
	EV1	EV104	GT211	DlrFCB14	GT195	GT23	All loci
IIIE	0.740	0.286	0.055	0.903	0.169	0.135	0.162
IVW	0.094	0.846	0.022	0.300	0.330	0.350	0.078
IVE	0.799	0.829	0.305	0.991	0.213	0.729	0.861
VW	0.454	0.934	0.926	0.217	0.846	0.203	0.750
VE	0.108	0.160	0.797	0.092	0.162	0.918	0.144
VIW	0.242	0.967	0.292	0.026	0.925	0.126	0.149
All strata	0.447	0.302	0.057	0.520	0.808	0.196	0.257

Table 8a: Results of the heterogeneity test for longitudinal microsatellite variation in females.

Strata	Microsatellite locus						
	EV1	EV104	GT211	DlrFCB14	GT195	GT23	All loci
All strata	0.039	0.166	0.559	0.005	0.562	0.171	**0.010**
IIIE x IVWN	0.861	0.044	0.428	0.770	0.394	0.417	0.416
IIIE x IVWS	0.000	0.364	0.241	0.496	0.071	0.922	**0.008**
IIIE X IVE	0.044	0.437	0.260	0.658	0.607	0.966	0.405
IIIE x VW	0.094	0.574	0.091	0.555	0.389	0.983	0.317
IIIE x VE	0.370	0.791	0.246	0.267	0.380	0.940	0.620
IIIE x VIW	0.254	0.483	0.406	0.012	0.190	0.885	0.101
IVWN x IVE	0.079	0.034	0.786	0.260	0.914	0.047	**0.046**
IVWN x VW	0.189	0.120	0.533	0.105	0.467	0.160	0.101
IVWN x VE	0.200	0.001	0.568	0.054	0.386	0.038	**0.001**
IVWN x VIW	0.287	0.006	0.710	0.002	0.917	0.267	**0.004**
IVW-S x IVE	0.125	0.985	0.700	0.169	0.512	0.117	0.295
IVW-S x VW	0.311	0.774	0.771	0.543	0.028	0.305	0.295
IVWS x VE	0.094	0.482	0.424	0.053	0.005	0.003	**0.000**
IVWS x VIW	0.320	0.274	0.627	0.000	0.613	0.176	**0.004**
IVE x VW	0.811	0.314	0.114	0.506	0.937	0.090	0.342
IVE x VE	0.484	0.429	0.476	0.744	0.778	0.337	0.793
IVE x VIW	0.558	0.581	0.914	0.013	0.966	0.600	0.426
VW x VE	0.353	0.148	0.208	0.203	0.998	0.347	0.279
VW x VIW	0.811	0.486	0.505	0.006	0.755	0.686	0.259
VE x VIW	0.320	0.344	0.750	0.001	0.768	0.807	0.052

Table 8b: Results of the heterogeneity test for longitudinal microsatellite variation in males.

Strata	Microsatellite locus						
	EV1	EV104	GT211	DlrFCB14	GT195	GT23	All loci
All strata	0.393	0.387	0.544	0.320	0.023	0.711	0.217

Table 8c: Results of the heterogeneity test for longitudinal microsatellite variation in total samples (female+male).

Strata	Microsatellite locus						
	EV1	EV104	GT211	DlrFCB14	GT195	GT23	All loci
All strata	0.128	0.220	0.250	0.152	0.044	0.382	**0.039**
IIIE x IVW	0.048	0.335	0.399	0.313	0.313	0.499	0.186
IIIE X IVE	0.301	0.372	0.291	0.193	0.587	0.598	0.427
IIIE x VW	0.039	0.308	0.132	0.335	0.051	0.680	**0.040**
IIIE x VE	0.386	0.551	0.314	0.202	0.194	0.491	0.347
IIIE x VIW	0.092	0.288	0.275	0.263	0.094	0.489	0.097
IVW x IVE	0.798	0.632	0.804	0.710	0.912	0.195	0.919
IVW x VW	0.429	0.751	0.518	0.650	0.000	0.324	**0.012**
IVW x VE	0.181	0.043	0.571	0.037	0.158	0.004	**0.001**
IVW x VIW	0.109	0.047	0.322	0.132	0.848	0.612	0.110
IVE x VW	0.504	0.766	0.155	0.547	0.010	0.347	0.109
IVE x VE	0.681	0.433	0.256	0.445	0.639	0.656	0.743
IVE x VIW	0.391	0.194	0.657	0.443	0.708	0.415	0.609
VW x VE	0.218	0.181	0.090	0.331	0.263	0.409	0.117
VW x VIW	0.211	0.405	0.349	0.322	0.413	0.977	0.520
VE x VIW	0.308	0.664	0.259	0.138	0.715	0.427	0.429

Table 9: Results of the statistical comparison for monthly variation in mean body length of physically matured whales.

	Male									Female								
	Nov.+Dec.		Jan.		Feb.		Mar.		p-value	Nov.+Dec.		Jan.		Feb.		Mar.		p-value
	mean	n	mean	n	mean	n	mean	n		mean	n	mean	n	mean	n	mean	n	
IIIE	8.59	73	-	0	8.73	2	8.62	19	0.762	9.15	44	-	0	-	0	9.09	9	0.710
IVWN	8.58	34	8.58	68	8.48	36	8.75	1	0.330	9.23	4	9.09	20	9.14	7	-	0	0.768
IVWS	8.57	58	8.48	52	8.50	81	8.62	19	0.174	9.26	7	9.10	23	9.10	103	9.03	8	0.572
IVE	8.57	17	8.59	129	8.56	106	8.59	24	0.936	8.90	11	9.13	62	9.12	80	9.27	8	0.129
VW	8.55	47	8.52	84	8.52	95	8.58	88	0.473	9.09	25	9.03	68	9.19	63	9.10	22	0.095
VEN	8.51	6	8.42	147	8.49	24	8.39	4	0.741	-	0	8.93	38	8.72	2	-	0	0.350
VEN(+98/99VES)	8.51	6	8.42	147	8.45	27	8.48	40	0.686	-	0	8.93	38	8.72	2	9.24	5	0.066
VES(-98/99)	-	0	8.43	13	8.31	50	8.30	13	0.415	-	0	9.02	22	8.90	151	8.86	79	0.143
VIW	8.40	84	8.47	2	-	0	8.43	16	0.878	8.90	25	8.56	1	-	0	8.79	5	0.447

Table 10: Results of the statistical comparison for latitudinal variation in mean body length of physically matured whales in IVW and VE

	Male					Female				
	North		South		p-value	North		South		p-value
	mean	n	mean	n		mean	n	mean	n	
IVW	8.56	139	8.53	210	0.342	9.12	31	9.10	141	0.775
VE (98/99VES→VEN)	8.44	220	8.33	76	**0.011**	8.96	45	8.90	252	0.283
VE (-98/99VES)	8.43	181	8.33	76	**0.018**	8.92	40	8.90	252	0.672

Table 11: Statistical comparison of mean body length of physically matured whales among geographical strata

	Area																			
	IIIE		IVW		IVE		VW		VE		VEN		VEN (+98/99VE		VES (-98/99)		VIW		p-value
	mean	n	mean	n	mean	n	mean	n	mean	n	mean	n	mean	n	mean	n	mean	n	p-value
Male (-9899VES)	8.60	94	8.54	349	8.58	276	8.54	314			8.43	181			8.33	76	8.40	102	<0.01
Male (9899VES→VEN	8.60	94	8.54	349	8.58	276	8.54	314					8.44	220	8.33	76	8.40	102	<0.01
Female	9.14	53	9.11	172	9.12	161	9.10	178	8.91	297							8.87	31	<0.01

Table 12: Statistical comparison of mean body length of physically matured whales among geographical strata (multiple comparison)

Male	n	mean	IIIE	IVW	IVE	VW	VEN (+98/99VES)	VES (-98/99)	VIW
IIIE	94	8.60	-	0.092	0.583	0.111	**0.000**	**0.000**	**0.000**
IVW	349	8.54		-	0.105	0.912	**0.000**	**0.000**	**0.000**
IVE	276	8.58			-	0.140	**0.000**	**0.000**	**0.000**
VW	314	8.54				-	**0.000**	**0.000**	**0.000**
VEN (+98/99VES)	220	8.44					-	**0.007**	0.337
VES (-98/99)	76	8.33						-	0.104
VIW	102	8.40							-

Male	n	mean	IIIE	IVW	IVE	VW	VEN	VES (-98/99)	VIW
IIIE	94	8.60	-	0.090	0.580	0.108	**0.000**	**0.000**	**0.000**
IVW	349	8.54			0.103	0.912	**0.000**	**0.000**	**0.000**
IVE	276	8.58				0.137	**0.000**	**0.000**	**0.000**
VW	314	8.54					**0.000**	**0.000**	**0.000**
VEN	181	8.43						**0.012**	0.446
VES (-98/99)	76	8.33							0.102
VIW	102	8.40							-

Female	n	mean	IIIE	IVW	IVE	VW	VE	VIW
IIIE	53	9.14	-	0.569	0.727	0.511	**0.000**	**0.001**
IVW	172	9.11		-	0.754	0.900	**0.000**	**0.001**
IVE	161	9.12			-	0.661	**0.000**	**0.000**
VW	178	9.10				-	**0.000**	**0.001**
VE	297	8.91					-	0.618
VIW	31	8.87						-

Table 13: Results of the statistical comparison for latitudinal variation in morphometric characters in strata IVW and VE.

Female

	IVW	VE
V3	ns	ns
V4	ns	ns
V5	ns	ns
V6	ns	ns
V7	ns	ns
V8	ns	ns
V9	ns	ns
V19	ns	ns
V20	ns	ns

Male

	IVW	VE
V3	ns	$p<0.05$
V4	ns	ns
V5	ns	ns
V6	ns	ns
V7	ns	ns
V8	ns	ns
V9	ns	ns
V19	ns	$p<0.05$
V20	ns	$p<0.05$

Table 14a: Results of the statistical comparison for longitudinal variation in morphometric characters in female samples.

V3

	IIIE	IVW	IVE	VW	VE	VIW
IIIE (199)	-	ns	**0.003**	**p<0.001**	**p<0.001**	**p<0.001**
IVW (575)		-	**0.003**	**p<0.001**	**p<0.001**	**p<0.001**
IVE (564)			-	ns	**p<0.001**	**p<0.001**
VW (371)				-	**p<0.001**	**0.015**
VE (680)					-	ns
VIW (113)						-

V4

	IIIE	IVW	IVE	VW	VE	VIW
IIIE	-	ns	**0.001**	**p<0.001**	**p<0.001**	**p<0.001**
IVW		-	**0.015**	**p<0.001**	**p<0.001**	**p<0.001**
IVE			-	**0.023**	**p<0.001**	**p<0.001**
VW				-	**p<0.001**	**0.012**
VE					-	ns
VIW						-

V5

	IIIE	IVW	IVE	VW	VE	VIW
IIIE	-	ns	ns	**p<0.001**	**p<0.001**	**p<0.001**
IVW		-	ns	**p<0.001**	**p<0.001**	**p<0.001**
IVE			-	**0.002**	**p<0.001**	**p<0.001**
VW				-	**p<0.001**	ns
VE					-	ns
VIW						-

V6

	IIIE	IVW	IVE	VW	VE	VIW
IIIE	-	ns	ns	**p<0.001**	**p<0.001**	**p<0.001**
IVW		-	ns	**p<0.001**	**p<0.001**	**p<0.001**
IVE			-	**p<0.001**	**p<0.001**	**p<0.001**
VW				-	**p<0.001**	ns
VE					-	ns
VIW						-

V7

	IIIE	IVW	IVE	VW	VE	VIW
IIIE	-	ns	**0.001**	**p<0.001**	**p<0.001**	**p<0.001**
IVW		-	**0.031**	**p<0.001**	**p<0.001**	**p<0.001**
IVE			-	ns	**p<0.001**	**p<0.001**
VW				-	**p<0.001**	**0.028**
VE					-	ns
VIW						-

Table 14a (cont.)

V8

	IIIE	IVW	IVE	VW	VE	VIW
IIIE	-	ns	ns	**p<0.001**	**p<0.001**	**0.003**
IVW		-	ns	**p<0.001**	**p<0.001**	**p<0.001**
IVE			-	ns	**p<0.001**	ns
VW				-	**0.027**	ns
VE					-	ns
VIW						-

V9

	IIIE	IVW	IVE	VW	VE	VIW
IIIE	-	ns	ns	**p<0.001**	**p<0.001**	**0.002**
IVW		-	**0.026**	**p<0.001**	**p<0.001**	**p<0.001**
IVE			-	ns	**p<0.001**	ns
VW				-	**p<0.001**	ns
VE					-	ns
VIW						-

V19

	IIIE	IVW	IVE	VW	VE	VIW
IIIE	-	**0.036**	**p<0.001**	**p<0.001**	**p<0.001**	**p<0.001**
IVW		-	ns	**p<0.001**	**p<0.001**	**p<0.001**
IVE			-	ns	**p<0.001**	ns
VW				-	**p<0.001**	ns
VE					-	ns
VIW						-

V20

	IIIE	IVW	IVE	VW	VE	VIW
IIIE	-	ns	ns	**p<0.001**	**p<0.001**	**0.003**
IVW		-	**0.020**	**p<0.001**	**p<0.001**	**p<0.001**
IVE			-	**p<0.001**	**p<0.001**	ns
VW				-	**p<0.001**	ns
VE					-	**0.021**
VIW						-

Table 14b: Results of the statistical comparison for longitudinal variation in morphometric characters in male samples.

V3

	IIIE	IVW	IVE	VW	VE	VIW
IIIE (281)	-	ns	**p<0.001**	**p<0.001**	**p<0.001**	**p<0.001**
IVW (767)		-	**0.037**	**p<0.001**	**p<0.001**	**p<0.001**
IVE (641)			-	**p<0.001**	**p<0.001**	**p<0.001**
VW (555)				-	**p<0.001**	**0.012**
VE (592)					-	ns
VIW (211)						-

V4

	IIIE	IVW	IVE	VW	VE	VIW
IIIE	-	ns	**p<0.001**	**p<0.001**	**p<0.001**	**p<0.001**
IVW		-	**0.015**	**p<0.001**	**p<0.001**	**p<0.001**
IVE			-	**p<0.001**	**p<0.001**	**p<0.001**
VW				-	**p<0.001**	ns
VE					-	ns
VIW						-

V5

	IIIE	IVW	IVE	VW	VE	VIW
IIIE	-	ns	ns	**p<0.001**	**p<0.001**	**p<0.001**
IVW		-	ns	**p<0.001**	**p<0.001**	**p<0.001**
IVE			-	**p<0.001**	**p<0.001**	**p<0.001**
VW				-	**p<0.001**	ns
VE					-	ns
VIW						-

V6

	IIIE	IVW	IVE	VW	VE	VIW
IIIE	-	ns	ns	**p<0.001**	**p<0.001**	**p<0.001**
IVW		-	ns	**p<0.001**	**p<0.001**	**p<0.001**
IVE			-	**p<0.001**	**p<0.001**	**p<0.001**
VW				-	ns	ns
VE					-	ns
VIW						-

V7

	IIIE	IVW	IVE	VW	VE	VIW
IIIE	-	ns	**0.001**	**p<0.001**	**p<0.001**	**p<0.001**
IVW		-	**0.007**	**p<0.001**	**p<0.001**	**p<0.001**
IVE			-	**0.008**	**p<0.001**	**0.035**
VW				-	ns	ns
VE					-	ns
VIW						-

Table 14b (cont.)

V8

	IIIE	IVW	IVE	VW	VE	VIW
IIIE	-	ns	ns	**p<0.001**	**p<0.001**	**p<0.001**
IVW		-	ns	**p<0.001**	**p<0.001**	**p<0.001**
IVE			-	**0.008**	**0.038**	**p<0.001**
VW				-	ns	ns
VE					-	ns
VIW						-

V9

	IIIE	IVW	IVE	VW	VE	VIW
IIIE	-	ns	**p<0.001**	**p<0.001**	**p<0.001**	**p<0.001**
IVW		-	ns	**p<0.001**	**p<0.001**	**p<0.001**
IVE			-	**0.047**	ns	ns
VW				-	ns	ns
VE					-	ns
VIW						-

V19

	IIIE	IVW	IVE	VW	VE	VIW
IIIE	-	ns	**p<0.001**	**p<0.001**	**p<0.001**	**p<0.001**
IVW		-	ns	**p<0.001**	**p<0.001**	**0.006**
IVE			-	**0.015**	**p<0.001**	ns
VW				-	**0.026**	ns
VE					-	ns
VIW						-

V20

	IIIE	IVW	IVE	VW	VE	VIW
IIIE	-	ns	ns	**p<0.001**	**p<0.001**	ns
IVW		-	ns	**p<0.001**	**p<0.001**	ns
IVE			-	**p<0.001**	**p<0.001**	ns
VW				-	ns	ns
VE					-	**0.006**
VIW						-

Table 15: Prevalence of *Anisakis simplex* in Antarctic minke whales, by longitudinal strata and sex. In parenthesis is the number of animals examined.

IIIE			IVW			IVE		
F	M	T	F	M	T	F	M	T
0.00 (227)	0.31 (322)	0.18 (549)	0.00 (653)	0.06 (855)	0.03 (1,508)	0.62 (645)	0.98 (711)	0.81 (1,356)

VW			VE			VIW		
F	M	T	F	M	T	F	M	T
4.07 (442)	6.55 (641)	5.54 (1,083)	8.04 (784)	15.42 (668)	11.91 (1,452)	7.30 (137)	9.49 (253)	8.72 (390)

Table 16: Summary of the results on stock structure found by different approaches. MBLM= Mean body length of physically matured whales.

Method	Sex	JARPA samples	Pattern of Geographical variation
mtDNA	F+M	1987/88-2003/04	IIIE=IVW=IVE VIW=VE IIIE,IVW,IVE≠VE,VIW
Microsatellites	F	1987/88-2003/04	IVWN,IVWS ≠VE,VIW
	M	1987/88-2003/04	
	F+M	1987/88-2003/04	IIIE,IVW≠ VW IVW≠ VE
MBLM	F	1987/88-2003/04	IIIE=IVW=IVE=VW VIW=VE IIIE,IVW,IVE,VW≠VE,VIW
	M	1987/88-2003/04	VEN≠VES IIIE=IVW=IVE=VW VIW=VEN,VES IIIE,IVW,IVE,VW≠VEN,VES,VIW
Morphometrics	F	1987/88-2003/04	IIIE=IVW VIW=VE IIIE,IVW≠VE,VIW
	M	1987/88-2003/04	IIIE=IVW VIW=VE IIIE,IVW≠VE,VIW
Parasites	F	1987/88-2003/04	IIIE=IVW=IVE VE=VIW IIIE,IVW,IVE≠VE,VIW
	M	1987/88-2003/04	IIIE=IVW=IVE VW=VE IIIE,IVW,IVE≠VE,VIW

Table 17a: Results of the comparison of mtDNA haplotype frequencies between Area IVW and 10°-sectors in IVE, VW and VE, by sex (F, M) and for both samples combined (T: female+male). P-values smaller than 0.05 are underlined. In bold are those P-values that remain significant after Bonferroni correction.

Sectors	T(1,421)	F(622)	M(799)
(IVE) 100-110E (T394, F193, M201)	0.9903	0.8686	0.8981
(IVE) 110-120E (T443, F214, M229)	0.7616	0.2503	0.7903
(IVE) 120-130E (T397, F194, M203)	0.6005	0.0520	0.8279
(VW) 130-140E (T232, F107, M125)	0.5827	0.4305	0.8050
(VW) 140-150E (T280, F112, M168)	0.3046	0.6877	0.4183
(VW) 150-160E (T418, F153, M265)	**0.0011**	0.0615	0.1933
(VW-E) 160-170E (T216, F81, M135)	0.0568	0.0189	0.1619
(VE) 170E-180 (T511, F304, M207)	0.2092	0.0849	0.6074
(VE) 180-170W (T517, F215, M302)	**0.0007**	0.0532	**0.0054**

Table 17b: Results of the comparison of mtDNA haplotype frequencies between Area IVE and 10°-sectors in IVW and IIIE, by sex(F, M) and for both samples combined (T: female+male).

Sectors	T(1,234)	F(601)	M(633)
(IVW) 90-100E (T440, F200, M240)	0.4355	0.4806	0.3535
(IVW) 80-90E (T401, F155, M246)	0.8874	0.7122	0.8144
(IVW) 70-80E (T580, F267, M313)	0.6682	0.3831	0.3262
(IIIE) 60-70E (T224, F91, M133)	0.0529	0.0855	0.6765
(IIIE) 50-60E (T150, F52, M98)	0.4166	0.5581	0.6374
(IIIE) 35-50E (T155, F75, M80)	0.2036	0.4987	0.5728

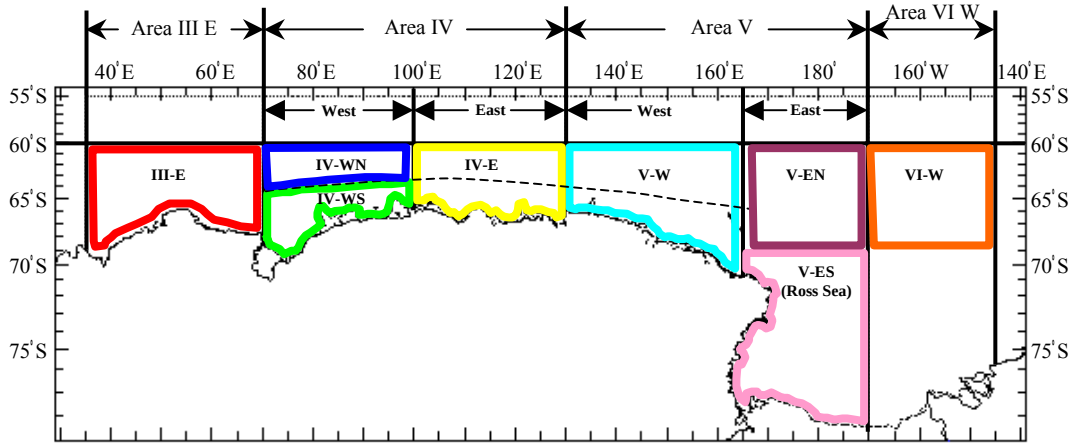

Figure 1: Primary geographic strata used in the analyses of stock identity.

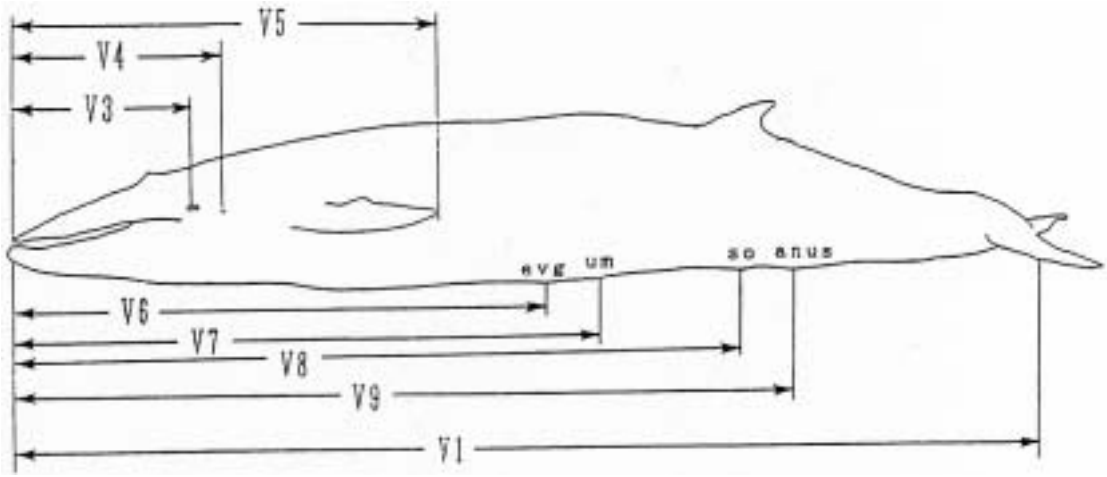

Figure 2: Body proportion measurements used in the morphometric analysis:

V1: Body length
V3: from the tip of snout to center of eye
V4: from the tip of snout to ear
V5: from the tip of snout to tip of flipper
V6: from the tip of snout to end of ventral gloves
V7: from the tip of snout to center of umbilicus
V8: from the tip of snout to sexual apparatus
V9: from the tip of snout to anus
V19: length of skull
V20: width of skull

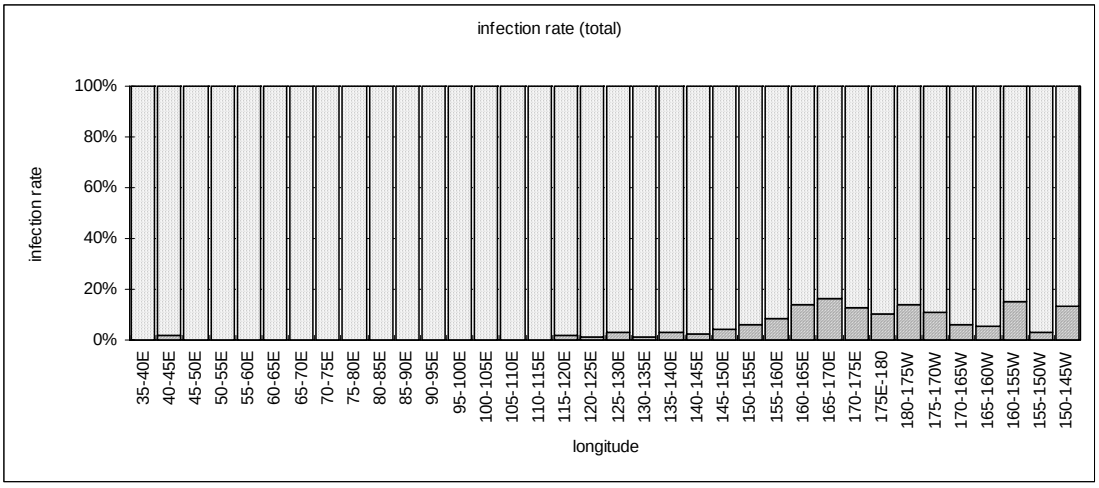

Figure 3: Infection rate of the parasite *Anisakis simplex* in Antarctic minke whales (female and male combined), by 5° longitude slice.

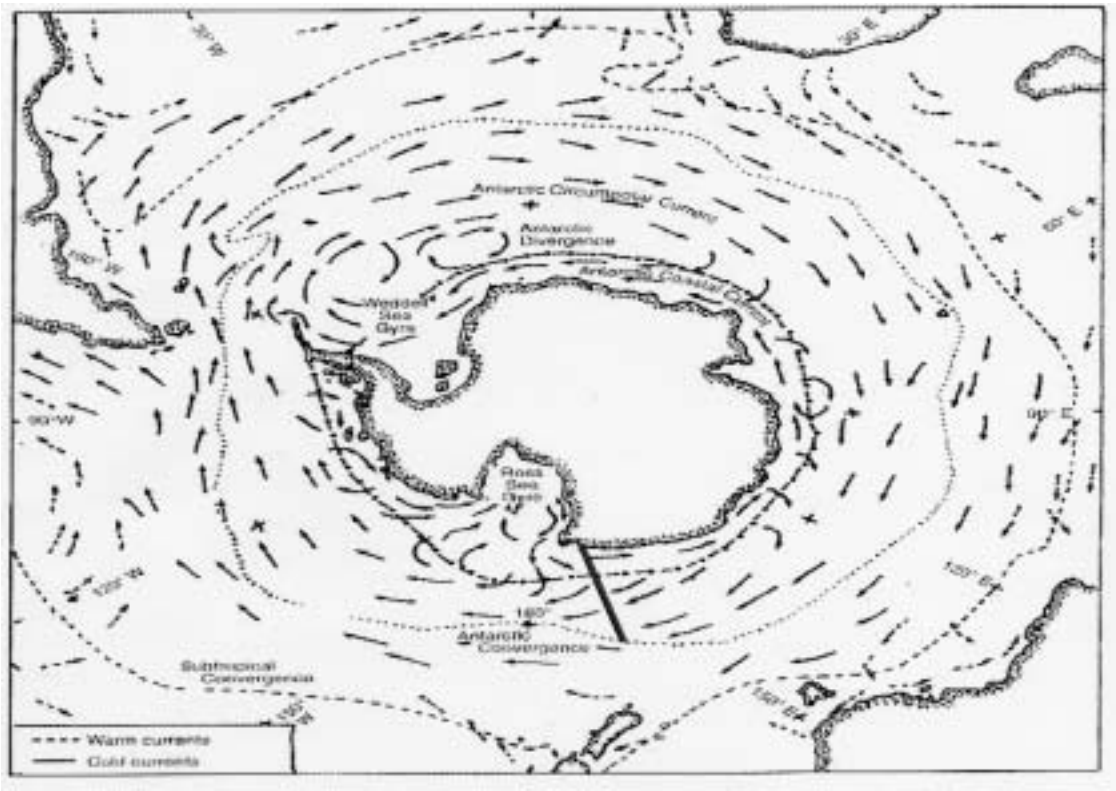

Figure 4: Surface currents in the Southern Ocean and the mean positions of the principal frontal zones. After Tchernia (1980) and Knox (1983). The line shows the division at 165°E.

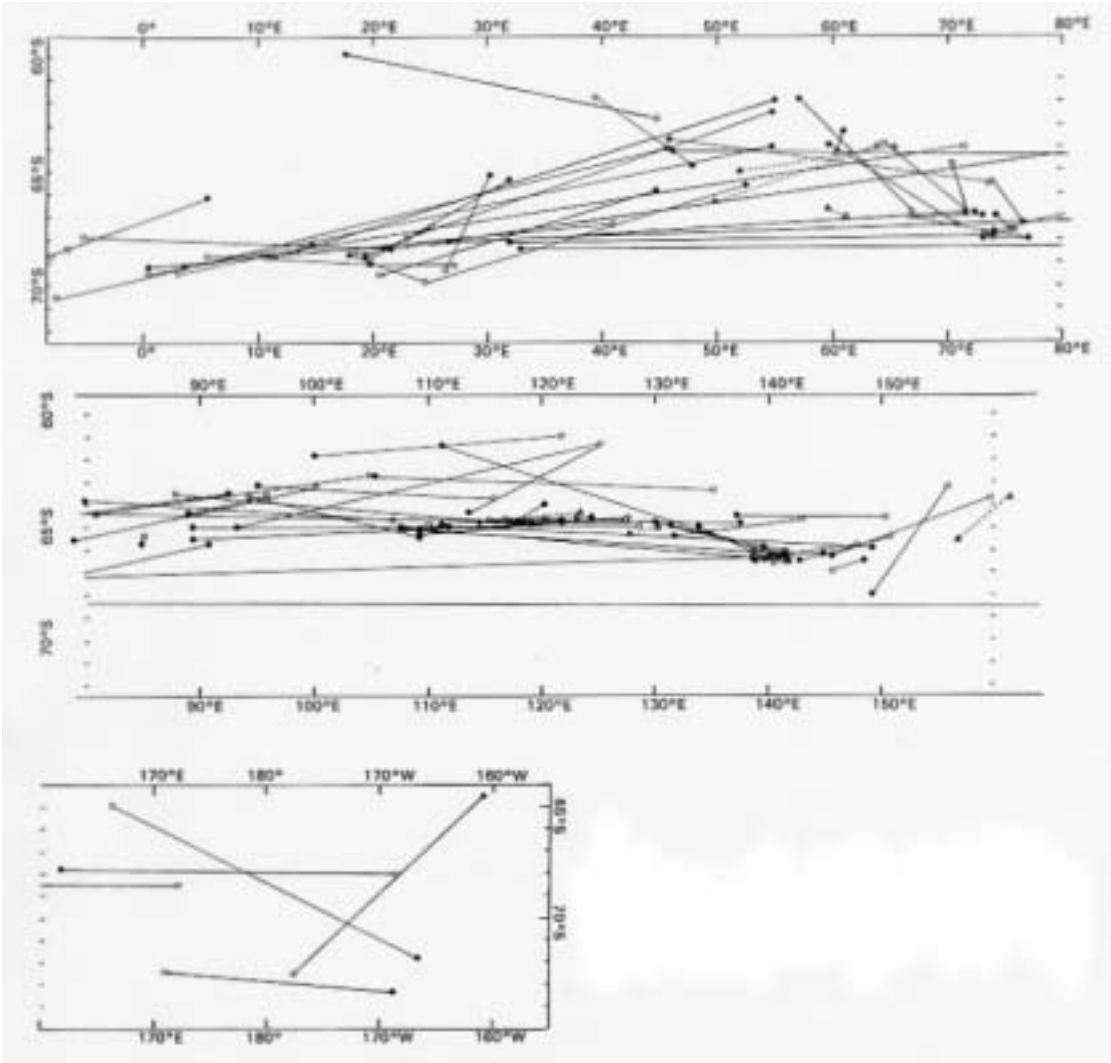

Figure 5: Position of marking and recovery of 101 Antarctic minke whales which were both marked and recaptured in the Antarctic. Open and closed circles indicate the positions marked and recaptured for animals recovered more than one year after marking, and triangles the in-season recoveries (From Kato *et al*. 1993).