On the use of allele frequency data within a Bayesian framework: evaluation of the relative probabilities of alternative stock structure hypotheses for North Pacific minke whales

André E. Punt*, Douglas S. Butterworth+ and Shiro Wada†

Contact e-mail: punt@marine.csiro.au

ABSTRACT

Genotype frequency information for one or more loci is used within a Bayesian modelling framework to assign relative probabilities to alternative stock-structure hypotheses using the Bayes factor approach. This framework has advantages over maximum-likelihood estimation as it provides the information needed to select amongst hypotheses. For primarily illustrative purposes, the approach is applied to the data for the *Adh-1* and *Gpi* loci for sub-areas 6, 7, 8, 9 and 11 for North Pacific minke whales. The results confirm those of previous studies that there are (at least) two stocks to the east and west of Japan. In contrast, the results support the hypothesis of a single stock in sub-areas 7, 8 and 9 unless *a priori* the allele frequencies for stocks that are adjacent spatially are likely to be similar. This last result needs to be interpreted with caution as the mutation rate of allozymes is slow and so this caveat might apply in this case.

KEYWORDS: GENETICS; STOCK IDENTITY; NORTHERN HEMISPHERE; NORTH PACIFIC OCEAN; COMMON MINKE WHALE

INTRODUCTION

Some authors (Punt *et al.*, 1995; Butterworth *et al.*, 1996) have used maximum-likelihood methods to estimate mixing proportions for the J and O minke whale stocks in sub-area 7 of the North Pacific by analysing *Adh-1* and *Gpi* locus data. A disadvantage of a such methods is that while rejection of the null hypothesis of a single stock can be used to identify the presence of multiple stocks, an inability to reject the null hypothesis does not imply necessary acceptance of the hypothesis of a single stock. There are two reasons for this. The first is the sample size effect – if the sample sizes are too low, the null hypothesis may not be rejected even if there are two stocks present and there appear to be marked differences between the samples (i.e. the power of the test is too low). The second reason is that the underlying allele frequencies for two stocks that are found close to each other spatially may be very similar (in part because of occasional genetic exchange between the two stocks). In such circumstances, there may be inadequate power to distinguish the difference in frequencies, even given relatively large sample sizes.

Although most analyses of genetic data conducted worldwide are based on classical (frequentist) statistical methods, there have been calls for Bayesian methods to be applied (e.g. Shoemaker *et al.*, 1999). Bayesian methods can be used to calculate the relative probability of alternative hypotheses by means of the posterior odds ratio (Jeffreys, 1961). For example, Wade and DeMaster (1996) contrasted alternative models for the dynamics of the Eastern North Pacific stock of gray whales using this framework.

The present paper develops single- and two-stock models for allele-frequency data based on allozymes, where these models are then fitted using a Bayesian approach. This overall framework is then used to examine stock-structure hypotheses for minke whales in sub-areas 6, 7, 8, 9 and 11 of the North Pacific (see Fig. 1). These hypotheses have been developed in the context of developing *Implementation Simulation Trials* as part of the International Whaling Commission's Revised Management Procedure (IWC, 1999b). The choice of which sub-areas to group when developing alternative hypotheses about stock structure is a general management problem. However, for the purposes of this primarily illustrative study, the hypotheses are based on the assumptions that underlie most of the *Implementation Simulation Trials* for North Pacific minke whales (IWC, 2000) i.e. O and J stocks to the east and west of Japan, and O and W stocks to the east of Japan separated at 157°E (the boundary between sub-areas 8 and 9).

The analyses of this paper are restricted to use of allozyme data. Given the relative simplicity of the models for these data, they provide an ideal basis for illustrating the potential of the use of Bayesian methods for examining alternative stock-structure hypotheses. It should be noted, however, that because allozymes mutate at a slower rate than mtDNA and nuclear DNA such as microsatellites, they have lower power to detect genetic differences (Bossart and Pashley Powell, 1998). Notwithstanding this, allozymes are still used extensively in studies of stock structure, both for marine fish (e.g. Gardner and Ward, 1998) and cetaceans (e.g. Punt *et al.*, 1995 and Butterworth *et al.*, 1996), and allozymes and other genetic markers often produce similar results (Bossart and Pashley Powell, 1998). Nevertheless, as allozyme data can fail to detect differences when these exist, the results given here should be considered to be primarily illustrative. It is not intended that they should form the sole basis for evaluating the relative plausibility of different stock-structure hypotheses for North Pacific minke whales.

* *CSIRO Marine Research, GPO Box 1538, Hobart, TAS 7001, Australia.*
+ *MARAM (Marine Resource Assessment and Management Group), Dept of Mathematics and Applied Mathematics, University of Cape Town, Rondebosch 7701, South Africa.*
† *National Research Institute of Fisheries Science, Fukuura 2-12-4, Kanazawa-ku, Yokohama-shi, Kanagawa 236-8648, Japan.*

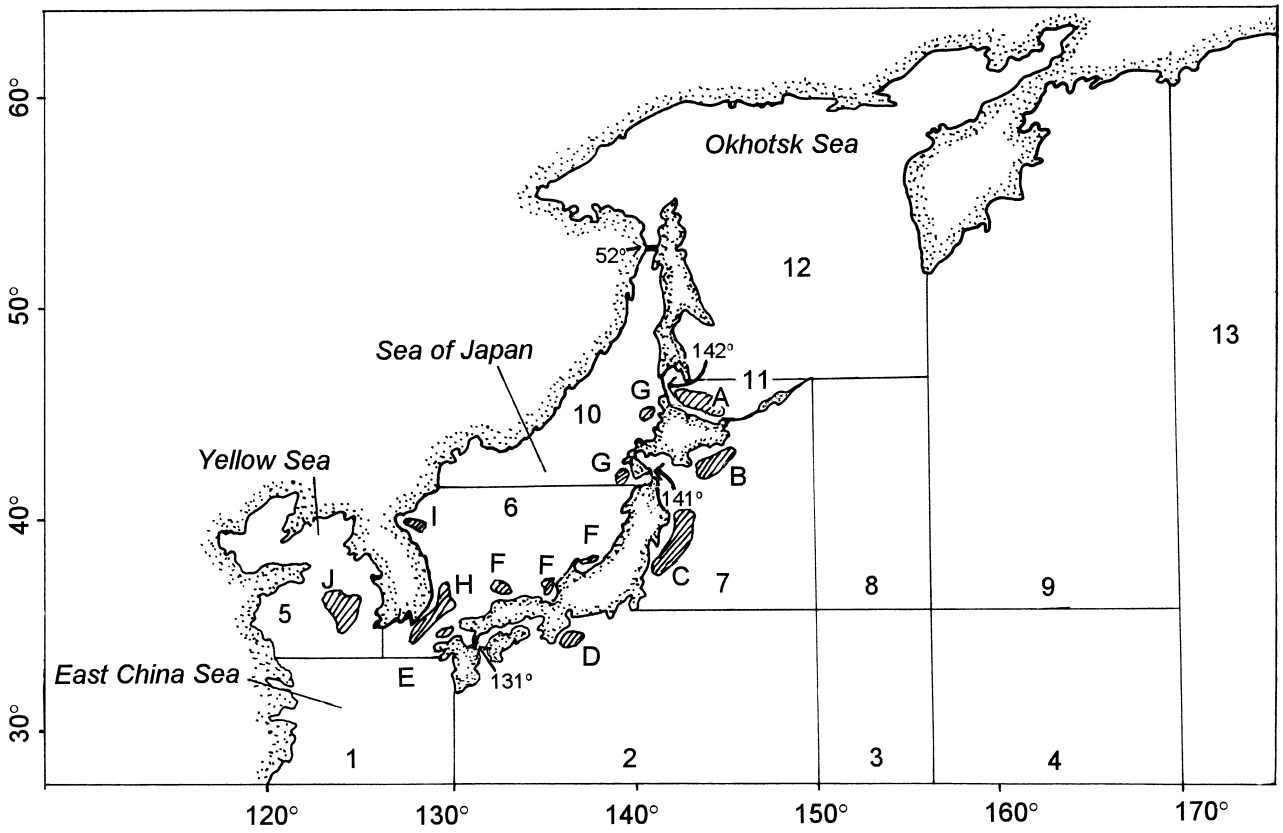

Fig. 1. Sub-areas of the North Pacific (from IWC, 2000).

MATERIALS AND METHODS

The basic data

Electrophoresis and enzyme staining from small (*ca* 20g) liver samples were performed following the procedures described by Wada and Numachi (1991). Samples were collected from animals sampled during the JARPN programme (IWC, 2001) and earlier commercial operations. All JARPN samples were stored at –70°C on board and –30°C in laboratory. The breakdown of the 497 JARPN samples is 21, 100, 77, 100, 100 and 99 over the years 1994-99. Samples from JARPN were collected from sub-areas 7, 8, 9 and 11 of the North Pacific while samples from commercial operations are available for sub-areas 6, 7 and 11.

The allele frequency data available for the analyses are listed in Table 1. They have been aggregated over years into three bi-monthly periods (April-May, June-July and August-September) and are presented for five of the thirteen sub-areas for North Pacific minke whales. Data for genotypes that constitute a very small fraction of the total (i.e. *dg*, *di*, *gg*, *gh*, and *hi* for the *Adh-1* locus) are omitted from Table 1 and the calculations of this paper. Fig. 2 shows the data aggregated over bi-monthly period (ignoring the data for sub-area 11 in April-May). Data for sub-areas 7 and 11 collected during commercial and JARPN operations are shown separately in Table 1.

Modelling gene-frequency information

Under the assumption of Hardy-Weinberg equilibrium, the fractions of the three major genotypes for each locus (for example, *hh*, *dh*, and *hh* for the *Adh-1* locus) in a homogenous stock are expected to be: $f_{hh} = p^2$, $f_{dh} = 2p(1\text{-}p)$ and $f_{dd} = (1\text{-}p)^2$ where p is the *Adh-1*^{h} proportion (Punt *et al.*, 1995). If it can be assumed that only a single (homogeneous) stock is found in a given sub-area *A*, the value for p^A_{Adh}, the *Adh-1*^{h} proportion for sub-area *A*, can be estimated by maximising the following multinomial log-likelihood (ignoring constant terms):

$$\ell \mathrm{n}L = n^A_{hh}\,\ell \mathrm{n}(f^A_{hh}) + n^A_{dh}\,\ell \mathrm{n}(f^A_{dh}) + n^A_{dd}\,\ell \mathrm{n}(f^A_{dd}) \qquad (1)$$

where:

n^A_{hh} is the number of samples from sub-area *A* with genotype *hh*;
n^A_{dh} is the number of samples from sub-area *A* with genotype *dh*; and
n^A_{dd} is the number of samples from sub-area *A* with genotype *dd*.

If similar data then become available for another sub-area *B*, a straightforward extension of this maximum-likelihood approach (Ratkowsky, 1981) can be used to test the assumption that there is only one stock in the two sub-areas.

Extending the standard approach

For the reasons given above, failure to show a significant lack of fit for a single-stock model to gene-frequency data does not provide conclusive evidence of a single stock only in both sub-areas. Even so, it is not acceptance/rejection of various stock structure hypotheses that is essential for the interpretation of the results of the *Implementation Simulation Trials* for the North Pacific minke whales (IWC, 1999a; 2000), but rather the assignment of relative

Table 1

Genotype frequencies for the *Adh-1* and *Gpi* loci for North Pacific minke whales (but omitting very rare *Adh-1* alleles). Due to the well-established fact of mixing of J and O stock animals in sub-area 11 during April-May, the data indicated by the asterisk are ignored in the calculations of this paper. The JARPN data include animals sampled between 1994 and 1999.

			Adh-1 locus			*Gpi* locus		
Sub-area	Period	Data source	*hh*	*dh*	*dd*	*bb*	*ab*	*aa*
6	Sep. - Oct.	Commercial	1	4	40	19	19	4
7	Apr. - May	JARPN	29	19	8	52	4	0
7	Jun. - Jul.	JARPN	23	24	5	52	1	0
7	Aug. - Sep.	JARPN	15	12	3	29	1	0
7	Apr. - May	Commercial	142	127	25	174	5	0
7	Jun. - Jul.	Commercial	93	90	18	132	7	0
7	Aug. - Sep.	Commercial	38	54	13	99	4	0
8	Apr. - May	JARPN	2	4	2	8	0	0
8	Jun. - Jul.	JARPN	31	35	10	73	5	0
8	Aug. - Sep.	JARPN	3	2	0	5	0	0
9	Apr. - May	JARPN	15	7	2	27	0	0
9	Jun. - Jul.	JARPN	55	55	7	117	6	0
9	Aug. - Sep.	JARPN	15	17	5	34	4	0
11	Jun. - Jul.	JARPN	8	27	12	45	4	0
11	Aug. - Sep.	JARPN	10	10	9	27	3	0
11*	Apr. - May	Commercial	64	72	64	112	13	2
11	Jun. - Jul.	Commercial	35	25	9	59	5	1
11	Aug. - Sep.	Commercial	11	7	1	14	0	0

probabilities to such hypotheses. This necessitates changing from maximum-likelihood to Bayesian methods. The posterior odds of two models is the product of the prior odds and the Bayes factor. The Bayes factor is given by the ratio:

$$P_1 / P_2 = \int\int_1 L(D \mid \underline{\phi}_1)\, p_1(\underline{\phi}_1)\, d\underline{\phi}_1 \Big/ \int\int_2 L(D \mid \underline{\phi}_2)\, p_2(\underline{\phi}_2)\, d\underline{\phi}_2 \quad (2)$$

where:

P_1 is the probability of model 1;

P_2 is the probability of model 2;

$L(D|\underline{\phi})$ is the likelihood of the data given the vector of parameters $\underline{\phi}$;

$\underline{\phi}_1$ is the parameter vector for model 1;

$\underline{\phi}_2$ is the parameter vector for model 2;

$p_1(\underline{\phi}_1)$ is the prior probability distribution for model 1; and

$p_2(\underline{\phi}_2)$ is the prior probability distribution for model 2.

The value of the Bayes factor, P_1/P_2, provides a quantitative measure of the relative weight of evidence in favour of models 1 and 2 (the posterior odds ratio) under the

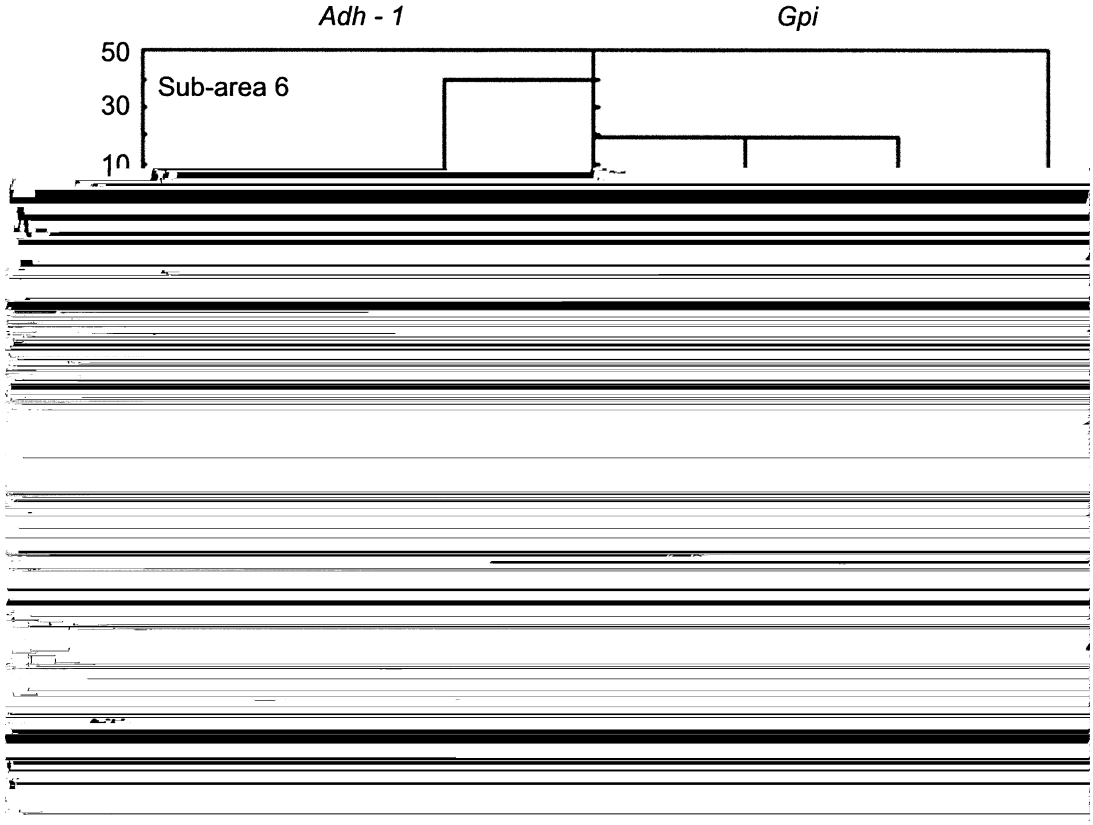

Fig. 2. The *Adh-1* and *Gpi* allele frequency data used for the analyses of this paper.

assumption that the models are equally likely *a priori* (i.e. prior odds of 1). For example, the value of Equation (2) in the limit of no informative data is 1, which indicates no preference for either model. Equation (2) involves multiple integration when there are multiple loci and for models in which the value of p_{Adh} is assumed to differ among sub-areas. Jeffreys (1961) and Kass and Raftery (1995) provide the following guidelines for the interpretation of values for the Bayes factor (Table 2).

The evidence for model 2 compared to model 1 can be determined by the ratio P_2/P_1 (i.e. by basing conclusions on the ratio P_1/P_2 but using the inverses of the values in the tables above).

Consider a situation where the Bayes factor is to be used to compare a single-stock model (model 1) with a two-stock model (model 2), and where data are available for two sub-areas A and B based on the *Adh-1* locus. Model 1 has a single parameter $p^A_{Adh} = p^B_{Adh}$, while model 2 has two parameters $p^A_{Adh} = p^B_{Adh}$ which may (or may not) be the same. A reasonable prior for p^A_{Adh} (and hence also p^B_{Adh} for model 1) is U[0, 1], because *a priori* there is no reason to favour any one value over another for this proportion. However, this is not a reasonable prior for p^B_{Adh} for model 2, as there is some *a priori* chance that p^B_{Adh} is positively correlated to p^A_{Adh}. This is because the *Adh-1* proportion for stocks that are adjacent in space may be similar as a result of limited genetic interchange (and/or common ancestry). The particular formalism chosen in this paper to model this *a priori* correlation is to assume a mixture distribution for the prior for p^B_{Adh}. This prior is U[0,1] with probability x and a distribution proportional to a symmetric triangular function centred on p^B_{Adh} of width $2e$ with probability $1-x$. This shape is illustrated in Fig. 3 – in cases where one or both sides of the triangle intersect the possibilities of 0 and/or 1 for p^B_{Adh}, the normalisation of the prior is adjusted appropriately. Other forms for the distribution centred at p^A_{Adh} could have been considered (e.g. normal), but this simple function is sufficient for the purposes of this paper which considers wide ranges of possible values for x and e. This mixture distribution therefore captures the range from a pure uniform prior ($x = 1$) to a delta-function prior at p^A_{Adh} ($x = 0; e = 0$). Naturally, the Bayes factor for an analysis based on this last prior would be 1.

Table 2

Guidelines for the interpretation of values for the Bayes factor as provided by (a) Jeffreys (1961) and (b) Kass and Raftery (1995).

Bayes Factor	Interpretation
(a) Jeffreys (1961)	
1 to 3.2	Not worth more than a bare mention
3.2 to 10	Substantial
10 to 100	Strong
>100	Decisive
(b) Kass and Raftery (1995)	
1 to 3	Not worth more than a bare mention
3 to 20	Positive
20 to 150	Strong
>150	Very strong

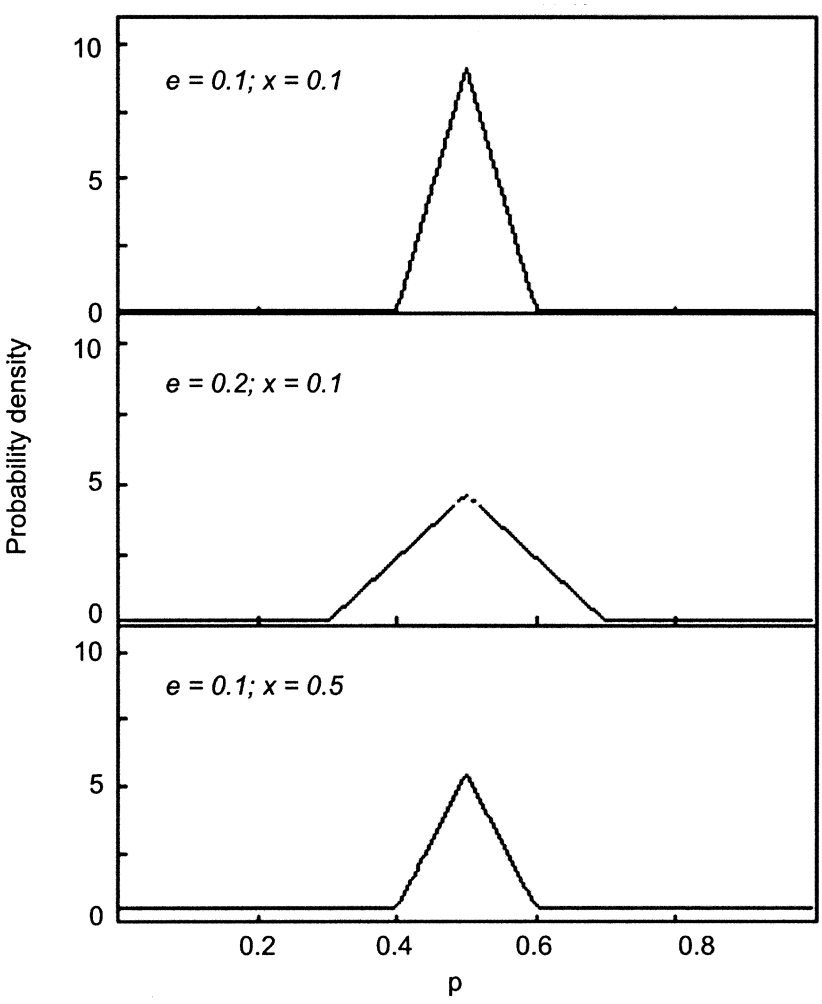

Fig. 3. The form of the prior distribution for p^B_{Adh} for various choices for e and x.

Either genetic mutation rate models, empirical evidence from adjacent stocks of the same species (through some form of meta-analysis of the results of stock structure examinations), or some combination of the two could form the basis for developing a prior for p^B_{Adh}, i.e. choosing values for e and x for the context considered here. Such considerations are beyond the scope of this paper, which is why the results of computations of Bayes factors are shown across wide ranges of values for these parameters. These computations were effected by integrating Equation (2) numerically using a simple (and therefore somewhat inefficient) variant of the Sample-Importance-Resample algorithm (Rubin, 1987).

RESULTS

J versus O stock comparisons

There is substantial evidence from allele frequency (Wada, 1984; Wada, 1991; Punt *et al.*, 1995; Butterworth *et al.*, 1996), conception date (Best and Kato, 1992), mtDNA (Goto and Pastene, 1997) and morphological (Kato *et al.*, 1992) information, that two minke whale stocks (J and O) are present in North Pacific sub-areas 6 (J stock) and 7+11 (primarily O). There is certainly mixing in sub-area 11 in April-May, and there may also be some J animals present in this sub-area in other months, and in sub-area 7 in August-September. A first test of the framework described above is therefore to apply it to the data for sub-areas 6, 7 and 11 to determine whether it provides a result that is consistent with those of previous investigations.

Table 3 lists the value of the Bayes factor (i.e. P_1/P_2) and the fraction of the total percentage probability assigned to the single-stock model, model 1 (i.e. $100P_1/(P_1+P_2)$) for a range of values for e and x. Results are shown in this Table for analyses based on each of the *Adh-1* and *Gpi* loci. The analyses in question compare the allele frequencies for sub-area 6 with those for sub-area 7, and also with those for sub-areas 7 and 11 combined. For this last dataset, the samples for the April-May period for sub-area 11 are omitted because it is known that substantial mixing between J and O stock animals occurs in sub-area 11 during this period (Punt *et al.*, 1995; Butterworth *et al.*, 1996).

The results in Table 3 conform exactly to expectations. Except for the case in which p^B_{Adh} is virtually perfectly correlated *a priori* with p^A_{Adh} ($e = 0.01$, $x = 0.00$), the single-stock model is accorded virtually no probability relative to that of the two-stock model. In all but this case, use of the Jeffreys/Kass and Raftery guidelines would lead to the conclusion that evidence in favour of two stocks is 'decisive'/'very strong'.

O versus W stock comparisons

For the purposes of these comparisons, it is assumed that the O stock is restricted to sub-areas 7, 8 and 11 (the data for sub-area 11 in April-May are ignored for the reason given above), and consideration is given to the possibility that sub-area 9 may contain a separate (W) stock. This hypothesis is based on the analysis of mtDNA data by Taylor (2000). Table 4 lists the values for the Bayes factor and the fraction of the total probability assigned to the single-stock model for the *Adh-1* and *Gpi* loci separately, while Table 5 lists these values when the data for the two loci are analysed together (the Scientific Committee has previously accepted that it is legitimate to treat these two sources of data as independent - IWC (1997). Results are shown in Tables 4 and 5 for the same factors as Table 3, except that, additionally, the sensitivity to excluding the data collected from commercial operations is examined.

Considering the results for each locus separately first, the Bayes factor indicates a preference for a single-stock model (i.e. $P_1/P_2 > 1$) for all choices for the factors examined, except when the analysis is based on the JARPN and commercial data for the *Adh-1* locus and the O stock is assumed to be in sub-areas 7+8 only. This option for the O stock is considered because of the possibility that some J stock animals may have been included in the commercial samples taken from sub-area 11. The extent of preference for the single-stock model increases with the values chosen for e and x. However, the results based on JARPN and commercial data indicate a lower preference for the single-stock model than those based solely on the JARPN

Table 3

Use of the Bayes factor to compare a single-stock with a two-stock model for North Pacific minke whales (models 1 and 2 respectively) for sub-areas 6, 7 and 11. P_1 is the probability of model 1 and P_2 is the probability of model 2. The column P_1/P_2 is, therefore, the Bayes factor, while the column $100\ P_1/(P_1+P_2)$ provides the percentage of the total probability assigned to the single-stock model. Results are shown for the *Adh-1* and *Gpi* loci separately, for analyses that either use or ignore the data for sub-area 1. (J) = J stock and (O) = O stock.

		Adh-1 locus				*Gpi* locus			
		Sub-areas 6 (J) and 11 (O)		Sub-areas 6 (J) and 7 (O)		Sub-areas 6 (J) and 7+11 (O)		Sub-areas 6 (J) and 7 (0)	
e	x	P_1/P_2	$\frac{100\,P_1}{P_1+P_2}$	P_1/P_2	$\frac{100\,P_1}{P_1+P_2}$	P_1/P_2	$\frac{100\,P_1}{P_1+P_2}$	P_1/P_2	$\frac{100\,P_1}{P_1+P_2}$
0.01	0	0.68	40.48	0.67	40.04	0.12	10.74	0.11	9.76
0.01	0.01	10^{-26}	10^{-24}	10^{-28}	10^{-26}	10^{-14}	10^{-12}	10^{-15}	10^{-13}
0.05	0.01	0	0	0	0	0	0	0	0
0.10	0.01	0	0	0	0	0	0	0	0
0.20	0.01	0	0	0	0	0	0	0	0
0.01	0.1	0	0	0	0	0	0	0	0
0.05	0.1	0	0	0	0	0	0	0	0
0.10	0.1	0	0	0	0	0	0	0	0
0.20	0.1	0	0	0	0	0	0	0	0
0.01	0.5	0	0	0	0	0	0	0	0
0.05	0.5	0	0	0	0	0	0	0	0
0.10	0.5	0	0	0	0	0	0	0	0
0.20	0.5	0	0	0	0	0	0	0	0
N/A	1	0	0	0	0	0	0	0	0

Table 4

Use of the Bayes factor to compare a single-stock with a two-stock model (models 1 and 2 respectively) for sub-areas 7, 8, 9 and 11. P_1 is the probability of model 1 and P_2 is the probability of model 2. The column P_1/P_2 is, therefore, the Bayes factor, while the column $100\ P_1/(P_1+P_2)$ provides the percentage of the total probability assigned to the single-stock model. Results are shown for data for the *Adh-1* and *Gpi* loci separately for analyses that either use or ignore the data for sub-area 11. An asterisk denotes a value for the Bayes factor that is 'positive', and two asterisks a value that is 'strong', based on the Kass and Raftery (1995) guidelines. (W) = W stock and (O) = O stock.

		Adh-1 locus				*Gpi* locus			
		Sub-areas 9 (W) and 7+8+11 (O)		Sub-areas 9 (W) and 7+8 (O)		Sub-areas 9 (W) and 7+8+11 (O)		Sub-areas 9 (W) and 7+8 (O)	
e	x	P_1/P_2	$\frac{100\,P_1}{P_1+P_2}$	P_1/P_2	$\frac{100\,P_1}{P_1+P_2}$	P_1/P_2	$\frac{100\,P_1}{P_1+P_2}$	P_1/P_2	$\frac{100\,P_1}{P_1+P_2}$
(a) JARPN and Commercial data									
0.01	0	1.00	49.9	0.98	49.5	1.11	52.6	0.95	48.8
0.01	0.01	1.00	50.0	0.98	49.5	1.11	52.7	0.97	49.2
0.05	0.01	0.91	47.6	0.64	39.1	2.29	69.6	1.07	51.8
0.10	0.01	1.02	50.5	0.49	33.0	3.42*	77.4	1.50	60.0
0.20	0.01	1.56	60.9	0.64	39.1	5.57*	84.8	2.32	69.9
0.01	0.1	1.09	52.2	1.04	51.0	1.22	55.0	1.05	51.2
0.05	0.1	1.00	49.9	0.70	41.2	2.50	71.5	1.18	54.0
0.10	0.1	1.11	52.5	0.53	34.7	3.74*	78.9	1.64	62.1
0.20	0.1	1.69	62.8	0.70	41.1	6.16*	86.0	2.58	72.0
0.01	0.5	1.71	63.1	1.37	57.8	2.16	68.3	1.80	64.3
0.05	0.5	1.59	61.3	1.01	50.2	4.34*	81.3	2.00	66.7
0.10	0.5	1.71	63.2	0.80	44.5	6.33*	86.4	2.76	73.4
0.20	0.5	2.47	71.1	0.99	49.6	10.11*	91.0	4.20*	80.8
N/A	1	6.27*	86.2	2.34	70.0	42.92**	97.7	18.42**	94.8
(b) JARPN data only									
0.01	0	1.02	50.4	1.01	50.4	1.09	52.2	1.05	51.2
0.01	0.01	1.02	50.5	1.02	50.5	1.09	52.2	1.05	51.1
0.05	0.01	1.27	55.9	1.25	55.6	2.10	67.7	1.66	62.4
0.10	0.01	1.86	65.0	1.82	64.6	3.13*	75.8	2.44	71.0
0.20	0.01	3.28*	76.6	3.19*	76.1	5.09*	83.6	3.98*	79.9
0.01	0.1	1.12	52.8	1.12	52.8	1.21	54.7	1.17	53.8
0.05	0.1	1.38	57.9	1.36	57.7	2.30	69.7	1.84	64.8
0.10	0.1	2.01	66.8	1.97	66.4	3.42*	77.4	2.67	72.8
0.20	0.1	3.50*	77.8	3.41*	77.3	5.58*	84.8	4.34*	81.3
0.01	0.5	1.88	65.3	1.87	65.2	2.12	68.0	2.02	66.9
0.05	0.5	2.27	69.4	2.24	69.2	3.98*	79.9	3.14*	75.9
0.10	0.5	3.24*	76.4	3.16*	76.0	5.73*	85.1	4.42*	81.6
0.20	0.5	5.30*	84.1	5.14*	83.7	9.10*	90.1	6.94*	87.4
N/A	1	14.71**	93.6	14.22**	93.4	39.64**	97.5	30.77**	96.9

data. The support for the single-stock model for the analyses based on *Adh-1* locus increases if the data for sub-area 11 are included. The possibility of preference for the two-stock model when only JARPN and commercial *Adh-1* data are considered disappears in such circumstances.

When x is 0.01, or when $x = 0.1$ and $e = 0.1$ or lower, the bulk of the values for the Bayes factor would rate as 'barely worth a mention' indicating that the data cannot conclusively select between the single- and two-stock hypotheses in those circumstances. However, these values for x and e correspond to giving very high *a priori* weight to the assumption that the two stocks may have similar allele frequencies. When the data for the two loci are analysed together (Table 5), discriminatory power is greatly enhanced and the preference for the single-stock model is considerably increased. A rating of positive (75% or more of the total probability) is assigned to the single-stock model for most of the values for e and x when all of the data (commercial and JARPN, sub-areas 7, 8, 9 and 11) are analysed simultaneously. The results in Tables 4 and 5 therefore support the hypothesis of a single stock in sub-areas 7, 8 and 9 unless *a priori* the allele frequencies for stocks that are adjacent spatially are likely to be similar. This last result needs to be interpreted with caution as the mutation rate of allozymes is slow so one might expect *a priori* similarity in allele frequencies even over quite wide spatial differences. The ability to select prior distributions that are consistent with this *a priori* expectation is one the benefits of the use of a Bayesian approach.

DISCUSSION

Interpreting the results

The results for the O-J and O-W comparisons behave differently as the prior assumed for the difference between the allele proportions for the two stocks is modified from one that gives high weight to this difference being low ($e = 0.01$, $x = 0$) to one that assumes that the two allele proportions are uncorrelated ($x = 1$). The reasons for this are explored in Fig. 4, which shows a numerical representation of the joint posterior distribution for the two allele proportions for these two extreme assumptions about the difference and for one of each of the O-J and O-W comparisons.

The posterior for the J and O stock allele frequencies differs depending on the choice of prior (Fig. 4 upper panels). The maximum-likelihood estimates for these proportions differ markedly (see, for example, table 3 of Punt *et al.*, 1995) so the prior that allows for these proportions to differ (i.e. the case $x = 1$) leads to a posterior that has high support where the likelihood has high support. As a result of this, priors that ignore the possibility of high

Table 5

Use of the Bayes factor based on data for both the *Adh-1* and *Gpi* loci to compare a single-stock with a two-stock model (models 1 and 2 respectively) for sub-areas 7, 8, 9 and 11. P_1 is the probability of model 1 and P_2 is the probability of model 2. The column P_1/P_2 is, therefore, the Bayes factor, while the column $100\ P_1/(P_1+P_2)$ provides the percentage of the total probability assigned to the single-stock model. Results are shown for analyses that either use or ignore the data for sub-area 11. An asterisk denotes a value for the Bayes factor that is 'positive', two asterisks a value that is 'strong', and three one that is 'very strong', based on the Kass and Raftery (1995) guidelines. (W) = W stock and (O) = O stock.

		JARPN and Commercial data				JARPN data only			
		Sub-areas 9 (W) and 7+8+11 (O)		Sub-areas 9 (W) and 7+8 (O)		Sub-areas 9 (W) and 7+8+11 (O)		Sub-areas 9 (W) and 7+8 (O)	
e	x	P_1/P_2	$\frac{100\,P_1}{P_1+P_2}$	P_1/P_2	$\frac{100\,P_1}{P_1+P_2}$	P_1/P_2	$\frac{100\,P_1}{P_1+P_2}$	P_1/P_2	$\frac{100\,P_1}{P_1+P_2}$
0.01	0	1.10	52.5	0.93	48.3	1.11	52.6	1.07	51.6
0.01	0.01	1.12	52.7	0.95	48.7	1.11	52.7	1.06	51.6
0.05	0.01	2.08	67.5	0.69	40.8	2.65	72.6	2.08	67.5
0.10	0.01	3.48*	77.7	0.74	42.6	5.82*	85.3	4.45*	81.7
0.20	0.01	8.69*	89.7	1.49	59.8	16.69*	94.3	12.69*	92.7
0.01	0.1	1.34	57.2	1.09	52.2	1.35	57.4	1.30	56.6
0.05	0.1	2.49	71.4	0.82	45.2	3.17*	76.0	2.51	71.5
0.10	0.1	4.14*	80.5	0.87	46.6	6.88*	87.3	5.27*	84.1
0.20	0.1	10.40*	91.2	1.80	64.2	19.51*	95.1	14.78*	93.7
0.01	0.5	3.69	78.7	2.47	71.2	3.99*	80.0	3.79*	79.1
0.05	0.5	6.89	87.3	2.02	66.9	9.03*	90.0	7.05*	87.6
0.10	0.5	10.85*	91.6	2.21	68.8	18.55*	94.9	14.00*	93.3
0.20	0.5	24.92**	96.1	4.14*	80.5	48.19**	98.0	35.69**	97.3
N/A	1	268.91***	99.6	43.05**	97.7	583.29***	99.8	437.61***	99.8

correlation between the allele proportions lead to higher values for the probability of the two-stock model ($=\iint L(D)|\underline{\phi})p_1(\underline{\phi})d(\underline{\phi})$). In contrast to the case for the O-J comparison, the posteriors for O-W allele proportions for the two extreme priors achieve their maxima at virtually the same point (Fig. 4 lower panels) although the posterior for the dispersed prior ($x = 1$) is less tight than that for the ($e = 0.01$, $x = 0$) prior. The impact of giving less *a priori* weight to the assumption that the two allele proportions are highly correlated (i.e. moving from the ($e = 0.01$, $x = 0$) to the ($x = 1$) prior) consequently reduces the *a priori* weight assigned to the region where the likelihood is high and hence leads to a lower value for the posterior probability of the two-stock model.

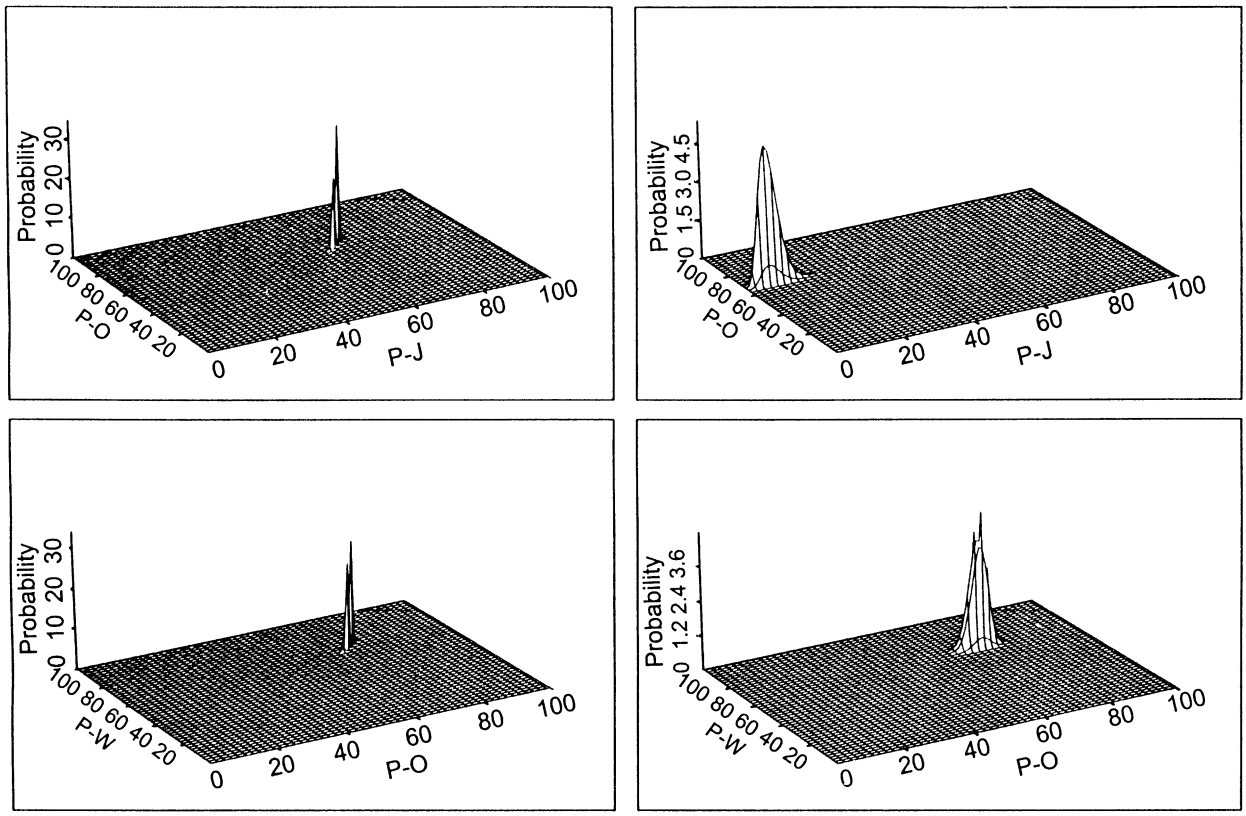

Fig. 4. Joint posterior distributions for the allele proportions based on models fitted to the *Adh-1* genotype frequency data. The results in the upper panels pertain to the comparison of sub-areas 6 and 7+11 while those in the lower panels pertain to the comparisons of sub-areas 7+8+11 and 9. The left panels are based on the ($e = 0.01$, $x = 0$) prior while the right panels are based on the ($x = 1$) prior.

The choice of prior distributions

The framework developed in this paper provides a basis to discriminate between single-stock and two-stock hypotheses. The results confirm the expectation from previous analyses that there is more than one stock of minke whales in sub-areas 6 and 7 of the North Pacific, but there is support for a single stock only in sub-areas 7, 8, and 9 for most choices for the parameters that define the prior for the two-stock model. However, for some choices for this prior (those that imply a high *a priori* correlation between the allele proportions for the two stocks), there is little basis to choose between a single-stock and a two-stock model. The appropriate choice of parameter values for a prior distribution for p, is therefore important.

Prior distributions can be 'informative' (as is the case in Tables 3, 4 and 5) and therefore based on information on differences in gene frequency for stocks of whales that are adjacent spatially and on genetic mutation theory. An alternative approach is to select a 'non-informative' prior distribution, although what constitutes 'non-information' in this case is not entirely clear. Kass and Raftery (1995) suggest that prior distributions could be chosen so that the parameter values corresponding to the maximum of the likelihood function under each model have similar prior probability. The priors considered in this paper were examined in this way and for the O-J comparison, the two-stock model was found to have been given lesser *a priori* weight than the single-stock model while the opposite effect occurred for the O-W comparison. Therefore, had the priors been chosen to given effect to Kass-Raftery approach, the magnitude of the preference for the two-stock model in the O-J case would have been stronger as would have the preference for the one-stock model in the O-W case.

A form of 'prior' that is only implicit in the analysis is the choice of boundary between putative stocks. Selection of a boundary between putative stocks is seldom based on a thorough analysis of existing data (and in fact the approach for conducting such an analysis is unclear anyway) and error in the choice of the boundary can have profound implications for the ability to correctly identify stock-structure when it is present. The problem of the appropriate choice of boundaries for stock-structure analyses is, however, not restricted to the use of Bayesian methods and also applies to traditional frequentist methods.

Extension to other data types and situations

The analyses of this paper are restricted to the use of allozyme data and the assumption that each sub-area included in the analysis contains a single homogeneous stock. In principle, it is possible to extend the methodology to other sources of data (e.g. mtDNA information) and for cases where there is mixing. However, this would increase the number of estimable parameters substantially, complicating both the design of the prior and the numerical process for the evaluation of the Bayes factor through Equation (2).

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