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Genetic evidence for migration of males between schools of the long-finned pilot whale *Globicephala melas*

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ABSTRACT: The genetic variation at 3 polymorphic allozyme loci was investigated in a population sample comprising approximately 650 individuals of the long-finned pilot whale *Globicephala melas* caught in the Faroe Islands. The sample consisted of pregnant females (carrying foetuses), non-pregnant females and males. The genetic variation was analyzed with a selection component analysis. At 2 of the loci the hypothesis of no male reproductive selection was rejected. It was concluded that the fathers of the foetuses differed genotypically from the males found in the schools, indicating that males migrate between schools to mate.

KEY WORDS: Selection component analysis · *Globicephala melas* · Migration · Allozyme data

INTRODUCTION

Allozyme studies of the genetic variation and population structure of the long-finned pilot whale *Globicephala melas* (Andersen 1988, 1993) have revealed significant differences in allele frequencies among a number of the 31 schools analyzed. This heterogeneity was not influenced by the age structure in the total sample nor could it be explained by a geographically segregated population structure. The question is, how can we explain this observation, and how do we interpret the population structure of the long-finned pilot whale? The following results from earlier studies provide some possible, but inconclusive answers: (1) allele frequency differences were most frequent among females from different schools, implying that females within schools are more closely related to each other than to females in different schools; (2) significant deviations from Hardy-Weinberg proportions reflected by males in several schools could imply a migration of males between schools, although the effect of natural selection cannot be excluded; (3) the detected linkage disequilibrium could also be maintained by migration of mature males between schools.

The school size for 10 schools of the long-finned pilot whale caught at the Faroe Islands between 1976 and 1986 ranged from 24 to 316 individuals. It is known from observations that the long-finned pilot whale forms herds containing up to 2000 individuals (Brown 1961). This suggests that long-finned pilot whale schools fuse, but it is not known whether the herds reform into the original schools or whether new schools are produced. Furthermore, in a DNA-fingerprinting study Amos et al. (1991) have found that for a large fraction of the foetuses, the accompanying males could not be the fathers. This led to the suggestion that the observed heterogeneity arises from combinations of school fusions and fissions, migration of mature males between the schools, and a strong maternal family structure within the schools consisting of several female lineages.

In the present study we apply the selection component analysis of Christiansen & Frydenberg (1973) using allozyme data from mother-offspring combinations from earlier studies to test the hypothesis of a sex-specific migration between the schools.

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MATERIAL AND METHODS

Material. *Globicephala melas* is a relatively small whale; females and males may reach lengths of 5 and 6 m, respectively. Females become sexually mature at the age of 6 yr, whereas males reach maturity at 12 yr (Desportes 1985). The current estimate of the population size around the Faroe Islands is 778000 (CV = 0.295) (Buckland et al. 1993).

In connection with an international research program on the biology of the long-finned pilot whales off the Faroe Islands, which ran from 1986 to 1988, tissue samples were collected from 31 schools and used in allozyme studies (Andersen 1988, in press). The nature of the Faroese drive fishery for pilot whales is such that whole schools are caught in an opportunistic catch, which means that the sample is unbiased. ('Schools' is the ordinary term used for pilot whales and refers to the group of individuals caught in the drive fishery.)

Methods. Three polymorphic allozyme loci were used: *Est-1*, esterase, E.C. 3.1.1.1; *Mpi*, mannose phosphate isomerase, E.C. 5.3.1.8; and *Sod-1*, superoxide dismutase, E.C. 1.15.1.1 (Andersen 1988).

Analysis of the population structure revealed that the population of long-finned pilot whale schools off the Faroe Islands was heterogeneous. In the present study we have therefore chosen to restrict the total sample of 31 schools to only the largest homogeneous group of schools containing foetuses. The largest homogeneous group of schools was found by means of a G_H-test of independence in an R×C contingency table performed on total number of alleles in each school (Sokal & Rohlf 1981). The largest number of schools providing sufficient material for examination of each of the 3 loci was then chosen to represent the sample. The total sample for the loci *Mpi* and *Sod-1* consisted of the following 19 schools: 860712, 860911, 860915, 860925, 861025, 861101, 861111, 861115, 861128, 861223, 870122, 870207, 870323, 870410, 870516, 870722, 870724, 870802, 870829. The total sample for the *Est-1* locus included 13 of these schools, where 861025, 870122, 870207, 870323, 870410, 870516 were excluded due to lack of liver samples (Andersen 1993).

The allozyme data from these schools consist of a population sample that includes mother-offspring combinations, non-pregnant females and males. The format of the data set is well suited for analysis with the selection component method of Christiansen & Frydenberg (1973). This analysis formulates a sequence of increasingly restrictive hypotheses about the data, and tests for the action of several components of natural selection: gametic selection, sexual selection and zygotic selection. In addition, it tests for random mating. We have chosen to use the terms 'mothers' (or 'pregnant females') and 'non-pregnant females' instead of 'fertile' and 'sterile' females, in accordance with the use in later applications of selection component analysis (see e.g. Christiansen et al. 1973). The use of 'pregnant' and 'non-pregnant' emphasizes that females in 1 of these 2 groups of iteroparous organisms may have been in the other group at other stages in their life history. Some of the hypotheses of selection component analysis may seem crude from a biological point of view, but they are probably the best that can be tested statistically with a population sample such as the present one. The titles of the hypotheses (see 'Results') are as in Christiansen & Frydenberg (1973). In the original analysis, the hypotheses were tested by comparison of expected and observed distributions with χ^2 goodness-of-fit tests. We have chosen to use likelihood-ratio tests, a procedure that was adopted in later extensions of the selection component analysis (Østergaard & Christiansen 1981, Siegismund & Christiansen 1985). The differences between these test statistics and the goodness-of-fit test statistics were always small. Estimates of the genotypic distributions of males that fathered offspring were established using the gene counting procedure outlined by Christiansen et al. (1977). Williams et al. (1990) have presented an alternative, but we have chosen to adhere to the original procedures.

RESULTS

The genotypic distributions at the 3 studied loci, *Est-1*, *Mpi*, and *Sod-1*, are given in Tables 1 to 3 for the population sample. All 3 loci are polymorphic with 2 common alleles, denoted A_1 and A_2. The sample size

Table 1 *Globicephala melas*. *Est-1* locus: observed genotypic distributions, and expected (in *italic* type) distributions under Hypothesis 6. The expected numbers of offspring are conditional on the observed numbers of mothers

Mother	Offspring			Sum of mothers	Non-breeding females	Males
	A_1A_1	A_1A_2	A_2A_2			
A_1A_1	19	8		27	80	28
	19.6	*7.4*		*24.2*	*75.3*	*36.9*
A_1A_2	8	10	1	19	53	33
	6.9	*9.5*	*2.6*	*18.3*	*56.9*	*27.9*
A_2A_2		0	0	0	10	9
				3.5	*10.8*	*5.3*
Sum	27	18	1	46	143	70

Table 2. *Globicephala melas*. *Mpi* locus: observed genotypic distributions, and expected distributions (in *italic* type) of offspring and males under Hypothesis 3 and of females under Hypothesis 4. The expected numbers of offspring are conditional on the observed numbers of mothers

Mother	Offspring			Sum of mothers	Non-breeding females	Males
	A_1A_1	A_1A_2	A_2A_2			
A_1A_1	14	10		24	77	26
	10.3	*13.7*		*27.3*	*73.7*	*30.5*
A_1A_2	19	29	18	66	178	67
	14.1	*33*	*18.9*	*65.9*	*178.1*	*68.3*
A_2A_2		22	23	45	110	58
		19.3	*25.7*	*41.9*	*113.2*	*52.2*
Sum	33	61	41	135	365	151

Table 3. *Globicephala melas*. *Sod-1* locus: observed genotypic distributions, and expected distributions (in *italic* type) of offspring and males under Hypothesis 3 and of females under Hypothesis 4. The expected numbers of offspring are conditional on the observed numbers of mothers

Mother	Offspring			Sum of mothers	Non-breeding females	Males
	A_1A_1	A_1A_2	A_2A_2			
A_1A_1	7	6		13	61	33
	6.7	*7.3*		*19.1*	*54.9*	*44.7*
A_1A_2	24	32	9	65	173	63
	16.7	*32.5*	*15.8*	*61.4*	*176.6*	*62.6*
A_2A_2		35	9	44	117	52
		22.6	*21.4*	*41.5*	*119.5*	*40.8*
Sum	31	73	18	122	351	148

for the *Est-1* locus was smaller because, as mentioned earlier, no liver samples existed from 6 schools. Below, we present the different hypotheses of the selection component analysis.

Hypothesis 1, Female gametic selection. In the absence of gametic selection, heterozygous females segregate the alleles A_1 and A_2 at a ratio of 1:1. Therefore, half of their offspring are expected to be heterozygotes, irrespective of the allele frequency of the male gametes, which is indicated in the expected distributions in Table 1 to 3. The hypothesis is tested with a single degree of freedom. None of the tests show significant differences (see Table 4). Thus, we conclude that heterozygous females segregate in the expected way.

Hypothesis 2, Random mating. If males mate with females irrespective of the female genotype, we expect that the transmitted male gametes have the same frequencies for all 3 female genotypes. Instead of the 3 allele frequencies necessary to describe the transmitted male gametes in the different female genotypes, a single allele frequency is sufficient, and the hypothesis can be tested with 2 degrees of freedom. Because there were no A_2A_2 homozygotes at the *Est-1* locus, random mating could only be tested among the A_1A_1 and A_1A_2 genotypes. In this case, the test has only 1 degree of freedom. For all 3 loci this hypothesis is accepted (Table 4), so we conclude that there is evidence of random mating with respect to the variation at these loci.

Hypothesis 3, Male reproductive selection. In Hypothesis 1 it was shown that females segregate at a ratio of 1:1 at all 3 loci. If males also do this, and if the collected males are the fathers of the collected off-

Table 4. *Globicephala melas*. Tests of the hypotheses in the selection component analysis

Hypothesis	df	*Est-1*		*Mpi*		*Sod-1*	
		χ^2	p	χ^2	p	χ^2	p
(1) Mendelian segregation	1	0.05	0.82	0.97	0.32	0.02	0.90
(2) Random mating	2[a]	1.39	0.24	0.57	0.75	3.18	0.20
(3) Male reproductive selection	1	1.74	0.19	4.87	0.03	24.43	0.00
(4) Female sexual selection	2	5.79	0.06	0.87	0.65	3.32	0.19
(5) Sex-specific zygotic selection	2	5.80	0.06				
(6) Zygotic selection	1	0.05	0.82				
Sum	8	14.82	0.06				

[a]At the *Est-1* locus the df = 1; see text

spring, the allele frequencies of transmitted male gametes should reflect the genotypic distribution of males. At the *Est-1* locus this hypothesis is accepted, but it is rejected at the 5% level at the other 2 loci (Table 4). A look at Tables 2 & 3 reveals the reason. At the *Mpi* locus, the frequency of transmitted A_1 alleles is 0.519, whereas the frequency of this allele among the sampled males is 0.394. The expected distribution of males under Hypothesis 3 in Table 2 yields the following frequencies of the 3 genotypes: A_1A_1 0.202, A_1A_2 0.452, and A_2A_2 0.346, where A_1 has a frequency of 0.428. The frequency of the transmitted A_1 alleles is too high to be accounted for by the observed distribution of males. At the *Sod-1* locus, the difference in allele frequencies of the transmitted male gametes and of the observed males is even higher. The offspring have received A_1 male gametes at a frequency of 0.733, whereas the males carry this allele at a frequency of 0.436. The expected distribution under Hypothesis 3 is: A_1A_1 0.302, A_1A_2 0.423, and A_2A_2 0.276, where allele A_1 has a frequency of 0.514. As at the *Mpi* locus, the expected distribution under Hypothesis 3 cannot account for both the distribution of the observed males and the frequencies of the transmitted alleles. The fathers of the sampled offspring must have transmitted allele A_1 at a higher frequency.

Hypothesis 4, Female sexual selection. If females mate irrespective of their own genotype at the studied loci, we expect the genotypic distributions of pregnant and non-pregnant females to be the same. This hypothesis is not dependent on any of the previous hypotheses and can be tested with a standard test for homogeneity between the 2 classes. This test has 2 degrees of freedom. The genotypic distributions of these 2 female classes do not differ at any of the 3 loci, so the selection component analysis does not detect an effect of any of the alleles on reproductive success. This indicates that the chance that a female will become a mother is independent of the genotype she carries at the studied loci.

Hypothesis 5, Differential zygotic selection between the sexes. If natural selection acts on the studied polymorphisms in the form of zygotic (or viability) selection, one may ask whether it has the same effect in both sexes. This is done in the selection component analysis by estimating a common genotypic distribution for the 2 female classes and the males, under the assumption that this group carries alleles with the same frequencies as transmitted to the offspring. This hypothesis is dependent on the previous hypotheses and therefore *cannot* be applied to the polymorphisms at the *Mpi* and the *Sod-1* loci. The test for this hypothesis is not significant for the *Est-1* locus, so we conclude that there is no detectable zygotic selection at this locus. If natural selection is operative, it has the same impact on the 2 sexes.

At the other 2 loci we can make a hypothesis about zygotic selection by comparing the genotypic distribution of all the females – which is homogeneous within this sex, as shown in Hypothesis 3 – with the genotypic distribution of the males. This hypothesis does not depend on any of the previous hypotheses, since it does not include the distributions of the offspring. It can be tested with a standard test for homogeneity, which has 2 degrees of freedom. The test statistics and the probabilities of observing more extreme values at the *Mpi* and the *Sod-1* loci are $\chi^2 = 2.90$, $p = 0.23$ and $\chi^2 = 4.21$, $p = 0.12$, respectively. So, there is no indication in the present sample that natural selection acts on the variation at these 2 loci via a different zygotic survival among the sexes.

Hypothesis 6, Zygotic selection. If natural selection acts through differential zygotic survival of the different genotypes, and it is assumed that (1) there is no fecundity selection and (2) polymorphism is at equilibrium with respect to selection, genotypic distributions would deviate from the expected Hardy-Weinberg distribution, where allele frequencies are estimated from the total adult group and alleles transmitted to the offspring group. This hypothesis is dependent on the previous hypotheses and is only open to reasonable interpretation if the previous hypotheses have been accepted. Therefore, this hypothesis was not tested for the *Mpi* and *Sod-1* loci.

Hypothesis 6 is accepted for the *Est-1* locus. Thus, we accept that there is no evidence that natural selection acts on this polymorphism and that there is random mating with respect to the variation at this locus. The polymorphism can therefore be described with a single parameter: the frequency of A_1 is 0.726.

We can apply a weaker test for zygotic selection at the *Mpi* and *Sod-1* loci. Under Hypothesis 5, we accepted a homogeneous genotypic distribution of the observed adult classes. We can now ask whether these distributions are in accordance with the expected Hardy-Weinberg distributions, where allele frequencies have been estimated from the observed genotypes of the adults. This is a standard test for Hardy-Weinberg proportions and is given in Table 5. There is no

Table 5. *Globicephala melas*. Observed and expected (in *italic* type) Hardy-Weinberg distributions of the sum of all 3 adult groups at the *Mpi* and the *Sod-1* loci

Locus	A_1A_1	A_1A_2	A_2A_2	n	χ^2	p
Mpi	127	311	213	651	0.49	0.48
	122.6	*319.8*	*208.6*			
Sod-1	107	301	213	621	0.00	1.00
	106.8	*301.5*	*212.8*			

evidence of any deviation from the expected distributions at the *Mpi* and *Sod-1* loci. It seems unlikely that zygotic selection acts on these 2 polymorphisms.

DISCUSSION

At the *Est-1* locus all hypotheses of the selection component analysis were accepted, indicating that there was no evidence that natural selection acted on this polymorphism. At the other 2 loci, *Mpi* and *Sod-1*, Hypothesis 3 (no male reproductive selection) was rejected in both cases. Apart from this rejection, there was no evidence that other components of natural selection affected these 2 polymorphisms.

We interpret the rejection of no male reproductive selection as being a result of the migration of males between the schools, based on either of the following 2 possible explanations: (1) segregation in heterozygous males is *not* Mendelian, or (2) the genotypic distribution of males that have fathered offspring differs from the observed genotypic distribution of the males that have been collected. Thus, the rejection of Hypothesis 3 could be caused either by gametic or by sexual selection in males, or by many other factors which might also skew male reproductive success. Such an example of a relation between fitness components and specific genotypes has been found in female red deer (Pemberton et al. 1991).

The selection component analysis assumes that a single population has been sampled. The rejection of Hypothesis 3 can, in this case, be produced by either of the causes mentioned above. We pooled several schools of the long-finned pilot whale, chosen to represent the largest homogeneous sample of this species. This procedure probably reduces the noise arising from the significant genetic differences found between the different schools. This genetic differentiation could cause a rejection of a hypothesis in the selection component analysis. The pooling procedure allows for an additional explanation of the observed male reproductive selection. If males have a tendency to migrate between different schools of whales, the male group included in the present sample might have come from schools with different allele frequencies. This could explain why the genotypic distribution of males differs from that of fathers that transmitted gametes to the offspring. At the *Est-1* locus the difference in allele frequencies between males and transmitted male gametes is 0.11, which is of the same order as at the *Mpi* locus (0.13). Despite this, Hypothesis 3 was accepted, which might be a Type II error because of the lower sample size for the *Est-1* locus. The observed phenomenon might therefore be quite general for different loci. The allele frequencies of mature males in the excluded schools were 0.500 at the *Mpi* locus, 0.417 at the *Sod-1* locus and 0.724 at the *Est-1* locus, which for the *Est-1* and the *Mpi* loci is sufficient to explain the difference between the observed and transmitted gametes (*Est-1*, 0.750; *Mpi*, 0.519) in the present sample. For the *Sod-1* locus the difference is too large (transmitted, 0.733; observed, 0.436) to be accounted for by the allele frequency of excluded males (0.417), which could be explained by selection or by the possibility that gametes could come from other, non-observed schools and still be in the meta-population.

The way we selected the data has a 'homogenizing' effect that acts in the opposite direction of our explanation for rejection of Hypothesis 3. We believe, therefore, that the discovered rejection is caused by a real phenomenon and that male migration or gene flow between the schools is a reasonable explanation. The greatest discrepancy in allele frequency difference between males and offspring was found at the *Sod-1* locus. In this case, the difference between allele frequencies of fathers and those of mothers must also have been relatively large. With an allele frequency of $p_{♀}$ in females and $p_{♂}$ in males, the offspring are expected to show a heterozygote excess of $(p_{♀} - p_{♂})^2/2$ relative to the Hardy-Weinberg proportions based on the average gene frequencies of the 2 sexes. Table 3 shows that the genotypic distribution of the offspring contains an excess of heterozygotes that is significantly different from the Hardy-Weinberg distribution ($\chi^2 = 5.47$, df = 1, $p = 0.02$). This deviation is probably due to the above-mentioned factor.

Our results are in accordance with the findings of Amos et al. (1991), who studied 5 Faroese long-finned pilot whale schools consisting of 34 mother-offspring combinations. They showed that for 88% of the foetuses, the fathers were not among the accompanying mature males. Analysis of the paternal alleles also indicated that the males are polygynous and that the male contribution changes from year to year. In addition, previously known facts about the social structure of *Globicephala melas* indicate that the schools are composed of an excess of mature females relative to males (Sergeant 1962, Martin et al. 1987). One explanation for the difference in numbers of females and males could be that males have a total higher mortality rate than females, as shown for the short-finned pilot whale *Globicephala macrorhynchus* by Kasuya & Marsh (1984). Males of this species are also polygynous. The social structure of the short-finned pilot whale school is formed by a breeding unit composed of adult males and females of different reproductive stages, and by immature and pubertal individuals. Adult males may migrate between the schools and form schools dominated by adult males. Female associations probably persist for a longer period and females

and juveniles in the schools are presumably related (Kasuya & Marsh 1984). This social structure resembles the social structure of the long-finned pilot whale. Another odontocete with a related social structure is the sperm whale *Physeter macrocephalus* (Whitehead 1987). Here the basic social entity consists of adult females with offspring and immature males. In sperm whales, old mature males observed off the Galápagos Islands exhibited a searching strategy, moving from one school to the next during the mating season (Whitehead 1987). At other times of the year they occurred in small groups or as solitary individuals, while the young mature males occurred in bachelor groups (Gaskin 1985). Yet no bachelor groups have been observed for the long-finned pilot whale, which indicates that the males should be found within the schools. Amos et al. (1991) also suggest that the school structure is basically matrilineal and that males do not mate within their school. This supports our interpretation of the rejection of Hypothesis 3.

One explanation for the genetic differences found between schools of the long-finned pilot whale in the North Atlantic could be that the population structure comprises an assemblage of schools, each consisting of a number of female family groups. The schools are genetically connected through migration of males and, occasionally, through fusions and fissions of a number of schools. The males that enter a school may be genetically differentiated from the females in the school, which increases heterozygosity among the offspring. The difference in allele frequencies between males and females could be increased by a low effective number of males that mate. Counteracting the increased heterozygosity in the offspring is the fact that the schools are relatively small and that genetic drift produces different allele frequencies in the schools, which, due to the Wahlund effect, results in an excess of homozygotes for the total assemblage of schools. The combination of these forces causes an overall agreement of the genotypic distributions with Hardy-Weinberg proportions at the 3 studied loci.

Recent observations of mitochondrial genetic differences between sympatric populations or subpopulations and several distinct seasonal subpopulations suggest that different behavioral strategies (different foraging strategy and different maternal migratory destinations) may explain other findings similar to those in the present study (Baker et al. 1990, Bigg et al. 1990, Hoelzel & Dover 1991).

The selection component analysis of Christiansen & Frydenberg (1973) was developed for an organism with non-overlapping generations. Some of the individuals that have been grouped into a specific category in this study could in previous years have belonged to other groups. It is known from an analysis of ovaries in the 19 schools (G. Desportes pers. comm.) that the group of non-pregnant females included some that had bred in previous years. Some of the females that had not yet bred would probably have bred in later years, had they not been caught. A possible means of including such phenomena in the analysis would be to use an extension of the selection component method for populations with overlapping generations described by Christiansen & Frydenberg (1976); this aproach was applied by Christiansen et al. (1977) in a population of the live-bearing marine teleost *Zoarces viviparous*. However, due to the relatively small sample of long-finned pilot whales, the use of this extension of selection component analysis would probably be of limited value.

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