ELECTROPHORETIC VARIABILITY IN DALL'S PORPOISE (*PHOCOENOIDES DALLI*) IN THE NORTH PACIFIC OCEAN AND BERING SEA

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ABSTRACT.—We describe electrophoretic variability at 26 loci in 360 specimens of Dall's porpoise (*Phocoenoides dalli*, Cetacea, Phocoenidae) collected from three locations in the Bering Sea and North Pacific Ocean. Nine of the 11 variable loci were polymorphic at the $P = 0.99$ level. Average heterozygosity for these specimens was 0.058, an above average value for a mammal. This may reflect a large, stable population size. Although genotypic proportions from each location generally agreed with Hardy-Weinberg expectations, significant heterozygote deficiencies were detected at two loci in a sample from the North Pacific Ocean. The result of subdividing this sample and rechecking the Hardy-Weinberg proportions suggested that a region of mixing is present at 50°N to 52°N. A pooled sample of Bering Sea and North Pacific Ocean specimens resulted in larger chi-square values—one-third of the loci were statistically significant—than with the individual treatments of the two samples. We, therefore, rejected the hypothesis that the two samples represent one interbreeding population.

In the last 20 years, surveys of electrophoretic variation have provided detailed information about amounts and patterns of genetic variation within and among populations of plants and animals (Nevo et al., 1984). Mammals have been generally well studied in this regard, with over 180 species investigated to date, but particular mammalian groups have been underrepresented primarily because of the difficulties of obtaining a sufficient number of specimens throughout the species' range. For example, only a few cetacean species have been examined electrophoretically (minke whales, *Balaenoptera acutorostrata*; Simonsen et al., 1982; Wada (1983*a*) and striped dolphins, *Stenella coeruleoalba*; Wada, 1983*b*). A large number of Dall's porpoise (*Phocoenoides dalli*) taken incidentally by international fisheries in the western North Pacific Ocean and Bering Sea were available to us for electrophoretic analysis.

Dall's porpoise occurs in the North Pacific Ocean in coastal and oceanic water from Baja California north in an arc across the Aleutian Islands and Bering Sea to the Sea of Japan and Sea of Okhotsk. They usually occur in small groups of two to five animals. Mean age at sexual maturity is approximately 3.5 years at an average body length of 1.8 m (±0.03); maximum lifespan is about 22 years, although most live less than 13 years (Newby, 1982). Their principal food in the western North Pacific is squid (Decapoda) and mesopelagic fish (Crawford, 1981).

The genus *Phocoenoides* generally is considered monospecific (Houck, 1976). However, Andrews (1911) recognized two species, *P. dalli* and *P. truei*, based on differences in color patterns. The more abundant color morph, the *dalli*-type, has a black body with a white lateral-ventral patch and occurs throughout the North Pacific Ocean, southern Bering Sea, Sea of Japan, and Okhotsk Sea. The *truei*-type has an anteriorly extended white patch and is confined to an area off the east coast of Japan. Mixed groups composed of both color types have been reported in the western North Pacific (Miyazaki et al., 1984). In addition to these two color morphs, infrequent occurrences of individuals that were all black (Morejohn, 1979; Nishiwaki, 1966), all white (Joyce et al., 1982), or striped (Morejohn, 1979) also have been reported.

In this study, we examined the amount and distribution of genetic variability within the *dalli*-type in the North Pacific Ocean and Bering Sea. We were particularly interested in these two

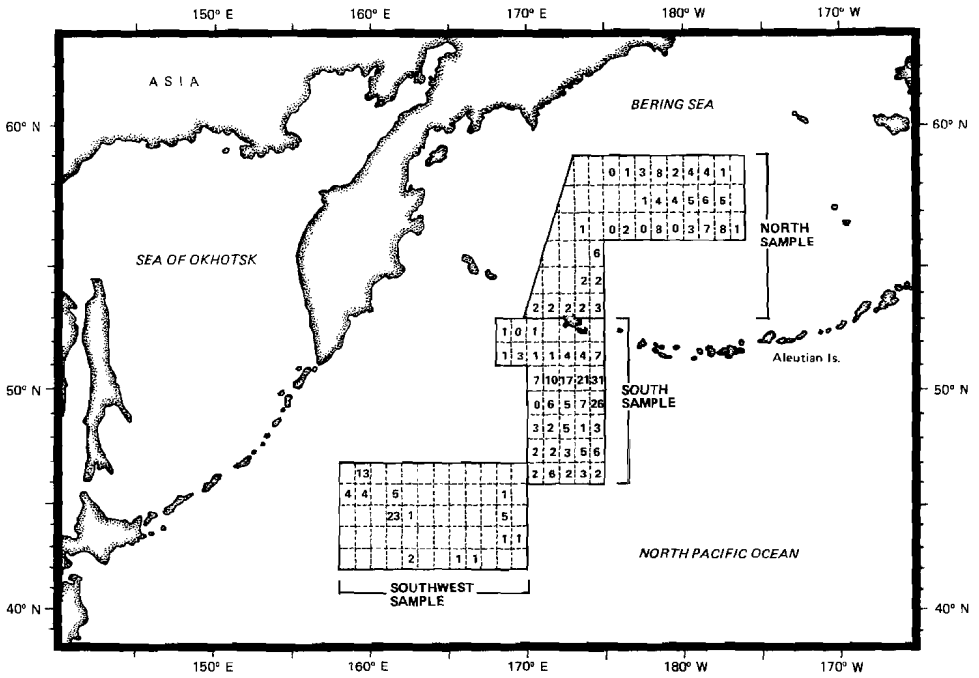

FIG. 1.—Number of Dall's porpoises captured in 1° latitude-longitude blocks. Specimens were pooled into three samples as indicated for analyses.

oceanographic regions because of the continued inadvertent pressure on Dall's porpoise incidentally captured by international gill-net fisheries for salmon (*Oncorhynchus* sp.) and squid. Using electrophoretic data, we tested the null hypothesis that there are no genetic differences between collections of individuals taken from these two regions. This study represents the most extensive electrophoretic investigation to date of a widely distributed marine mammal with respect to the number of loci and specimens examined.

METHODS

Tissues were collected in June and September 1982 from 360 incidentally caught Dall's porpoises. Specimens were grouped into three samples (Fig. 1): a northern (N) sample from the Bering Sea (n = 99), a southern (S) sample from below the Aleutian Islands (n = 200), and a sample (SW) from southwest of the Aleutian Islands collected in August–September (n = 61). Muscle, heart, liver, and kidney tissues, and approximately 5 ml of blood were collected from each specimen and stored frozen until electrophoretic analysis. Electrophoretic data from fetuses were compared with data from their respective mothers to check our genetic interpretation of electrophoretic variability at the polymorphic loci. Data from fetuses were not used in other analyses.

Tissues were subjected to electrophoretic analysis on horizontal starch gels using standard procedures. Enzymes were identified on the gels with specific histochemical-staining procedures described in Allendorf et al. (1977) or as described in Table 1. Assumptions for interpreting electrophoretic phenotypes are described in Utter et al. (1987).

We used a standard electrophoretic nomenclature (outlined in Allendorf and Utter, 1979) for loci and alleles. Multiple loci for an enzyme were designated with hyphenated numerals, with the locus encoding for the least anodal (i.e., closest to the origin) homomer (identical protein subunits) designated as one, the next as two, and so on. Alleles were referred to numerically with the most common allelle at a locus designated 100. Other alleles were assigned numbers representing the mobility of their homomeric protein relative to the migration distance of the homomeric protein of allele 100.

Over 50 enzyme systems were examined preliminarily, but only 14 enzymes—reflecting 26 loci—were

TABLE 1.—*Enzymes and electrophoretic conditions for Dall's porpoise.*

Enzyme (abbreviation and E.C. number)	Number of loci	Electrophoresis		Variable
		Tissues	Buffer[1]	
Adenosine deaminase (ADA, E.C. 3.5.4.4)	2	kidney	AC	no, no
Adenylate kinase (AK, E.C. 2.7.4.3)	1	kidney	AC	yes
Aspartate aminotransferase (AAT, E.C. 2.6.1.1)	2	liver	AC	no, no
Alcohol dehydrogenase (ADH, E.C. 1.1.1.1)[2]	3	kidney	AC	no, no, no
Esterase (EST, E.C. 3.1.1.1)[3]	2	liver	AC	yes, no
Glucosephosphate isomerase (GPI, E.C. 5.3.1.9)	2	heart	TC/LB	yes, no
Isocitrate dehydrogenase (IDH, E.C. 1.1.1.42)	2	liver	AC[2], TC/LB	yes, yes
Lactate dehydrogenase (LDH, E.C. 1.1.1.27)	3	heart	TC/LB	yes, no, no
Malate dehydrogenase (MDH, E.C. 1.1.1.37)	3	heart	AC	no, yes, no
Malate dehydrogenase (MDHp, E.C. 1.1.1.40)	1	heart	AC	yes
Mannosephosphate isomerase (MPI, E.C. 5.3.1.8)	1	heart	TC/LB	yes
Peptidase (TAPEP, E.C. 3.4.11-)[4]	2	liver	AC	no, no
Phosphogluconate dehydrogenase (PGDH, E.C. 1.1.1.44)	1	heart	AC	yes
Superoxide dismutase (SOD, E.C. 1.15.1.1)	1	liver	AC	yes

[1] Buffers: AC described by Clayton and Tretiak (1972). Gel: 0.002 M citrie acid, pH 6.0. Electrode: 0.04 M citric acid, pH 6.5. Both buffers are pH adjusted with N-(3-Amionpropyl)-morpholine. TC/LB described by Ridgeway et al. (1970). Gel: 0.03 M Tris-0.005 M citric acid, pH 8.5, Electrode: 0.06 M lithium hydroxide-0.3 M boric acid, pII 8.1. Gels were made using 99% gel buffer and 1% electrode buffer.
[2] Gel and cathodal electrode tray each contained 4 mg of $NADP^+$.
[3] Substrate was 4-methyl umbelliferal butyrate (viewed in ultraviolet light).
[4] Substrate was leucyl-glycyl-glycine.

clearly and reliably resolved for a complete screening of individuals. Electrophoretic conditions for the 14 enzymes are given in Table 1. Only kidney, liver, and heart tissues were necessary for these enzymes.

The amount of electrophoretic variability at a locus in a sample of individuals was measured as heterozygosity (h), defined as $h = 1 - \sum X_i^2$, where X_i is the frequency of the ith allele at the locus. The values of h also are the heterozygous proportions expected under Hardy-Weinberg equilibrium. The amount of variability in a sample over all loci was estimated as the average heterozygosity per locus ($\bar{H}$), where $\bar{H}$ is simply the mean h over all loci examined in the sample.

Differences between samples were tested in standard chi-square (χ^2) contingency tests using allelic and genotypic frequency data. Observed frequencies of genotypes for each polymorphic locus were compared to those expected under Hardy-Weinberg equilibrium by treating the N, S, and SW samples individually, and by treating the N and S samples together as a pooled sample. The latter Hardy-Weinberg tests were done to check the assumption that the N and S samples are not different, i.e., represent one interbreeding population. If the assumption is correct, pooling of N and S data into one sample would not alter the Hardy-Weinberg results (Turner and Grosse, 1980). In the Hardy-Weinberg tests, infrequent genotypes were pooled as described in Table 2. Analyses were done with the computer program BIOSYS-1 (Swofford and Selander, 1981), as adapted for a Burroughs 7800 computer.

Although it was not possible to use progeny-testing experiments to confirm the genetic interpretation of the electrophoretic banding patterns, electrophoretic differences were interpreted as reflecting allelic variation at individual genetic loci. The electrophoretic banding patterns agreed with the expected distribution of genotypes according to Hardy-Weinberg equilibrium, and with patterns predicted from information regarding the subunit composition of the enzyme studied. Most importantly, data from nine polymorphic loci for 12 mother-fetus pairs conformed to a genetic model of electrophoretic variability.

TABLE 2.—*Results of Hardy-Weinberg tests. Genotypic and allelic frequencies are presented for polymorphic loci (P = 0.99; h = heterozygosity) in three samples of Dall's porpoise taken north of the Aleutian Islands in the Bering Sea (N), south of the Aleutian Islands (S), and southwest of the Bering Sea (SW). Allele mobilities are presented in Table 4.*

Locus	Locale	Genotypes a/a	a/b	b/b	a/c	n	Allelic frequencies a	b	c	Hardy-Weinberg[1] Individual χ^2	Pooled (N + S) χ^2
Ak	N	80	17	2		99	0.894	0.106		0.88	
(h = 0.160)	S	171	26	2	1	200	0.923	0.075	0.003	0.61	1.59
	SW	50	11			61	0.910	0.090		0.60	
Est-1	N	95	4			99	0.980	0.020		0.04	
(h = 0.049)	S	187	13			200	0.968	0.032		0.23	0.26
	SW	60	1			61	0.992	0.008		0	
Gpi-1	N	92	5	1	1	99	0.960	0.035	0.005	4.72*	
(h = 0.075)	S	185	12	—	3	200	0.963	0.030	0.007	0.30	0.76
	SW	56	2	—	3	61	0.959	0.016	0.025	0.11	
Idh-2	N	50	45	4	—	99	0.732	0.268		2.51	
(h = 0.404)	S	99	87	12	1	199	0.719	0.279	0.002	1.74	3.92*
	SW	30	26	3	1	61	0.713	0.270	0.016	0.41	
Idh-1	N	72	20	1		93	0.882	0.118		0.09	
(h = 0.166)	S	169	23	5		197	0.916	0.084		11.28**	5.39*
	SW	53	7	1		61	0.926	0.074		1.60	
Mdh-2	N	96	3			99	0.985	0.015		0.02	
(h = 0.033)	S	195	5			200	0.988	0.012		0.04	0.15
	SW	58	2	1		61	0.967	0.033		14.20**	

[1] Hardy-Weinberg calculations are based on three genotypic classes: homozygotes for the most common allele, common allele/rare allele heterozygotes, and rare allele heterozygotes, and other heterozygotes ($d.f.$ = 1). * $P < 0.05$, ** $P < 0.01$.

RESULTS

Electrophoretic variation was detected at 11 of the 26 loci. Heterozygous phenotypes were two, three, and five bands depending on whether the protein was a monomer, dimer, or tetramer. The variation at Sod and Ldh-1 consisted of one and two heterozygous individuals, respectively. For the nine remaining polymorphic loci, the frequency of the common allele was less than 0.99. At four of these loci (Est-1, Pgdh, Gpi-1, and Mdh-1), the frequency of the common allele was between 0.95 and 0.99. At Idh-1, Mdhp, and Ak, the frequency of the common allele was approximately 0.90 (Table 2). For Idh-2 and Mpi, the common allele had a frequency of about 0.73 (Tables 2 and 3). Six alleles were detected at Mdhp and seven alleles were detected at Pgdh and Mpi. Electrophoretic mobilities of the homomeric proteins of the alleles are presented in Table 4.

The largest values of heterozygosity were h = 0.37 for Mpi and h = 0.40 for Idh-2 (Tables 2 and 3). Over all loci, $\bar{H}$ ranged from 0.059 in the N sample to 0.055 in the SW sample. Grand mean for heterozygosity over all samples was 0.058. The mean number of alleles per locus ranged from 1.62 in the N and SW samples to 1.96 in the S sample (grand mean = 1.73). At the 0.99 criterion for polymorphic loci, the percent polymorphic loci averaged 34 over the three samples.

The three samples were similar with regard to allele and genotype frequencies. For example, the largest allele-frequency difference among samples was only 6% [for Mpi^{100}]. Thus, it was not surprising that no statistically significant allelic or genotypic-frequency differences were detected among the three samples in chi-square contingency tests.

Twenty-seven "individual" χ^2 values (i.e., three samples by nine loci per sample = 27) were computed for Hardy-Weinberg equilibrium in the N, S, and SW samples (Tables 2 and 3). Four tests identified statistically significant heterozygote deficiencies. These included the Gpi-1 locus in the N sample (P = 0.03) and the Mdh-2 locus in the SW sample for which, in both cases, single individuals with a b/b genotype inflated χ^2 values. Heterozygote deficiencies were detected at two loci in the S sample: for Idh-1 (P = 0.001) and Mpi (P = 0.02). The total χ^2 values ($d.f.$ =

TABLE 3.—*Results of Hardy-Weinberg tests. Genotypic and allelic frequencies are presented for polymorphic loci (P = 0.99; h = heterozygosity) in three samples of Dall's porpoise taken north of the Aleutian Islands in the Bering Sea (N), south of the Aleutian Islands (S), and southwest of the Aleutian Islands (SW). Allele mobilities are presented in Table 4.*

		Genotypes											Allelic frequencies							Hardy-Weinberg[1]	
																				Individ.	Pooled (N + S)
Locus	Locale	a/a	a/b	b/b	a/c	b/c	a/d	a/e	a/f	a/g	b/f	*n*	a	b	c	d	e	f	g	χ^2	χ^2
Mdhp	N	86	10	1	—	—	2	—	—	—	—	99	0.929	0.061		0.010				0.60	
(*h* = 0.166)	S	162	28	4	2	—	2	2	—	—	—	200	0.895	0.090	0.005	0.005	0.005			1.82	2.62
	SW	52	8	—	—	—	—	—	1	—	—	61	0.926	0.066				0.008		0.39	
Mpi	N	61	22	8	7	1	—	—	—	—	—	99	0.763	0.197	0.040					3.61	
(*h* = 0.076)	S	120	55	14	3	2	1	1	—	1	1	198	0.758	0.220	0.013	0.003	0.003	0.003	0.003	5.15*	9.65*
	SW	40	14	2	3	—	—	—	—	—	—	59	0.822	0.152	0.025					0.14	
Pgdh	N	91	4	—	2	—	—	—	1	—	—	98	0.964	0.020	0.010			0.005		0.13	
(*h* = 0.366)	S	184	8	—	3	—	1	1	1	1	—	199	0.962	0.020	0.008	0.003	0.003	0.003	0.003	0.31	0.44
	SW	55	3	—	2	—	—	1	—	—	—	61	0.951	0.025	0.016		0.008			0.17	

[1] Hardy-Weinberg calculations are based on three genotypic classes: homozygotes for the most common allele, common allele/rare allele heterozygotes, and rare allele heterozygotes, and other heterozygotes (*d.f.* = 1). * $P <$ 0.05.

TABLE 4.—*Observed alleles. Mobility of homomeric proteins of alleles relative to the mobility of the homomer (identical protein subunits) of the common allele which is designated as 100. Cathodally migrating homomers are identified by negative values.*

	Allele designations						
Locus	a	b	c	d	e	f	g
Ak	100	80	42				
Est-1	100	70					
Gpi-1	100	400	800				
Idh-2	100	110	127				
Idh-1	−100	−150					
Mdh-2	100	83					
Mdhp	100	200	136	77	45	150	
Mpi	100	87	110	90	79	54	
Pgdh	100	46	77	30	17	0	90

9) were 12.61 for the N sample ($P = 0.18$), 22.38 for the S sample ($P = 0.01$), and 18.15 for SW ($P = 0.03$). The overall Hardy-Weinberg value in SW was not statistically significant when the data from Mdh-2 were removed.

Hardy-Weinberg tests were computed for "pooled" data for each of the nine polymorphic loci from the N and S samples. With the exception of Gpi-1 and Idh-1, the "pooled" χ^2 values were greater than either of their respective "individual" χ^2 values. Three of the nine tests using pooled data were statistically significant: Idh-1, Idh-2, and Mpi. For Idh-1 and Mpi, there was a deficiency of heterozygotes. The total χ^2 value over the nine loci ($d.f. = 9$) was 24.69, $P = 0.003$. Because the "pooled" N + S sample had higher χ^2 values and one-third of the loci were not in Hardy-Weinberg equilibrium, we rejected the null hypothesis that the N and S samples are one interbreeding population. Inclusion of the SW sample in the pooled analysis resulted in a total χ^2 of 32.4 ($P < 0.001$), indicating a further increase of heterogeneity.

There was a significant deficiency of heterozygotes at two loci in the S sample. Because heterozygote deficiency may result when two or more populations with differing allelic frequencies are treated as one population (Wahlund effect), we further explored genotypic distributions in the S sample by subdividing the sample. Because the focus of this study is orientated north and south (e.g., Bering Sea sample versus Pacific Ocean), we subdivided the S sample from south to north by degrees latitude. Subsets then were tested for Hardy-Weinberg equilibrium. We pooled specimens collected along a latitude, then along adjacent latitudes, until a sample size of approximately 50 was reached. Three subsamples were established: South: 46–48° ($n = 47$), South: 49° ($n = 44$), and South: 50–52° ($n = 109$). Further subdivision of South: 50–52° was not possible because of the sparse distribution of individuals along these latitudes (Fig. 1).

In general, allelic frequencies did not change as a result of subdividing the S sample. Only one significant change was seen in allelic frequency among the three new subsamples. The frequency of Ak^{100} was 0.94, 0.98, and 0.90 for the three subsamples, south to north, respectively ($\chi^2 = 11.6$, $P = 0.02$). When the three subsamples were tested for Hardy-Weinberg equilibrium, the two southerly subsamples, South: 46–48° and South: 49°, were in Hardy-Weinberg equilibrium: total $\chi^2 = 6.8$ ($P = 0.65$) and $\chi^2 = 5.6$ ($P = 0.59$), respectively. Only one locus approached statistical significance in these two subsamples: Idh-1 in South: 46–48° ($P = 0.05$). In contrast, subsample South: 50–52° had significant heterozygote deficiencies at Idh-1, Mpi, and Mdhp with total $\chi^2 = 23.9$ ($P = 0.004$). If the deviation from Hardy-Weinberg equilibrium in the S sample was caused by intermixing of populations, then it occurs between 50°N and 52°N.

DISCUSSION

The considerable electrophoretic variation observed in Dall's porpoises contrasts markedly with earlier work in biochemical genetics of marine mammals that indicated low levels of genetic variability in several species (Sharp, 1981). Eleven of 26 loci examined had detectable electrophoretic variation; and the common allele for five of these loci segregated at $P < 0.95$.

Previous electrophoretic studies indicate that mammals generally have less electrophoretic variability than other vertebrates. Nevo et al. (1984) computed an average heterozygosity ($\bar{H}$) for mammals of 0.041 for 184 species—a low value in comparison to other vertebrate classes like amphibians ($\bar{H} = 0.067$, $n = 61$), reptiles ($\bar{H} = 0.083$, $n = 75$), and fishes ($\bar{H} = 0.051$, $n = 183$). Two species of cetaceans have been studied electrophoretically. Wada (1983*a*) estimated average heterozygosity in 40 specimens of striped dolphins as 0.021 for 15 loci. In a study of minke whales, Wada (1983*b*) reported that average heterozygosity for 15 loci ranged from 0.023 in specimens from the Japanese coast ($n = 34$) to 0.112 in specimens from the Antarctic ($n = 8{,}900$). Thus, with 34% polymorphic loci (nine loci), and an average heterozygosity of 0.058, Dall's porpoises are well above the mean estimates of electrophoretic variability in mammals (but below that for minke whales in the Antarctic).

A variety of hypotheses have been advanced to explain levels and patterns of electrophoretically-detected protein variation in natural populations (Ayala, 1976). Depending on the relative role assigned to natural selection in effecting the observed variation, these hypotheses may be classified as either selectionist or neutralist. Selectionist hypotheses assume that the observed variability is primarily directed by natural selection, whereas the neutralist hypothesis is based on the assumption that observed patterns of protein polymorphisms are predominantly the result of gene flow, random genetic drift, and mutation rate. Because the neutral model requires fewer assumptions (Selander and Whittam, 1983), it has been employed as a null hypothesis in descriptions of electrophoretic variability in a variety of fishes (Allendorf and Utter, 1979; Shaklee and Salini, 1985; Winans, 1980).

Common to all theories of protein polymorphism is the idea that genetic drift in small populations reduces within-population heterozygosity. As Coyne (1984:727) stated: " . . . allozyme heterozygosity . . . may reflect the *historic* effective population size of a species, which includes bottlenecks and fluctuations in population size occurring during many generations" [the emphasis is ours]. Therefore, differences in heterozygosity among species may result mostly from differences in historical population size. For example, the northern elephant seal (*Mirounga angustirostris*) was almost extirpated by heavy exploitation along the west coast of North America in the late 1800s. The remnant population may have been as small as 20 individuals. After the population expanded to more than 30,000 animals, an electrophoretic survey failed to detect variability at 24 loci (Bonnell and Selander, 1974). For many species of cetaceans and terrestrial mammals, however, little is known about long-term population dynamics. We know that Dall's porpoise is one of the most abundant cetaceans in the Pacific Ocean, with population estimates ranging from 1 to 2.8 million for the species. Although Dall's porpoises are incidentally exploited in international fisheries, there is no evidence that they have undergone any population bottlenecks. Thus, the above-average estimate of genetic variation in Dall's porpoises may simply reflect a large, stable population size.

Detecting variability at nine loci permitted us to examine the genetic differences among the three samples. We wished to know if the northern sample from the Bering Sea differed from the southern sample in the North Pacific Ocean. Results of between-group analyses are equivocal. No differences in allelic or genotypic frequency were found between these two samples. Yet Hardy-Weinberg results indicated that the two samples are best treated separately: pooling the north and south samples produced greater deviations from the Hardy-Weinberg model than individual treatment of the samples. Two southern subsamples of the S sample were in agreement with the Hardy-Weinberg model. The apparent heterogeneity in the south sample—specifically, between 50° and 52°N—may be caused by mixing of genetically different populations in this area. If this is true, the source of immigration into this area is unknown. That the admixture is not caused by porpoises from the Bering Sea is indicated by significant deviations from Hardy-Weinberg in an analysis of samples N and S: 50–52° ($P < 0.001$). Are porpoises from the Bering Sea and the North Pacific Ocean one interbreeding population? Not according to our data. However, we believe this conclusion should be verified by testing the repeatability of these results, by examining protein variation in samples from Japan and North America, and by evaluating

the congruence of electrophoretic data with other characters such as morphological data. A more complete view of genetic population structure of the Dall's porpoise will result as our electrophoretic results are combined with existing information and studies in progress.

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