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Geographic variation in external morphology of Dall's porpoise, *Phocoenoides dalli*

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Abstract

We examined geographic variation in external measurements of Dall's porpoises, using 269 sexually mature specimens from throughout their range, excluding coastal waters off North America and the northern Okhotsk Sea. The lateral white patch is more caudad in *dalli*-type porpoises from the Sea of Japan than in those from other areas. This is a distinguishing character of the Sea of Japan–Okhotsk Sea population, and it indicates its independence along with genetic, morphological and ecological differences previously reported. Morphological and genetic differentiation suggests an older origin for this population. Sexual dimorphism is less developed in mature males from the eastern North Pacific than from other areas.

Introduction

Dall's porpoise (*Phocoenoides dalli*, True 1885) has two major color morphs, *truei*- and *dalli*-types (Houck, 1976; Kasuya, 1978). The former has a large lateral white patch extending as far anterior as the flipper and is distributed off the Pacific coast of northern Japan through the Kuril Islands to the central Okhotsk Sea (Kasuya, 1978, 1982; Miyashita & Doroshenko, 1990; Miyashita, 1991). The latter, in which the anterior border of the lateral patch is at the dorsal fin level, occupies the northern North Pacific, Sea of Japan, Okhotsk Sea and Bering Sea (Kasuya, 1978, 1982). The existence of eight breeding grounds, i.e. one in the central Okhotsk Sea for *truei*-type and one each in the southern and northern Okhotsk Sea, and Bering Sea, and four in the northern North Pacific for *dalli*-type, was suggested mainly from the distribution of mother and calf pairs (Kasuya & Ogi, 1987; Yoshioka *et al*., 1990). These breeding grounds are considered to be utilized by the discrete stocks (International Whaling Commission, 1991; Miyashita, 1991).

Geographic variation of Dall's porpoise was closely examined in terms of skull morphology (Walker & Sinclair, 1990; Amano & Miyazaki, 1992), genetic variability (Winans & Jones, 1988; Shimura, 1989), and life history parameters (Yoshioka *et al*., 1990; Amano & Kuramochi, 1992). However, there has been no quantitative analysis of geographic variation in external characteristics of Dall's porpoise. In this paper we examine geographic variation in external morphometrics and give some suggestion on differentiation of population and sexual dimorphism of this species.

Materials and methods

We used 174 males and 95 females, all of which were sexually mature. The male animals with a left testis weight of 40 g or heavier (Kasuya & Jones, 1984; Yoshioka *et al*., 1990; Amano & Kuramochi, 1992) and females with at least one corpus in the ovaries were regarded as sexually mature. Since reproductive data were not available for some of the Sea of Japan samples (17 males and 12 females), we inferred their sexual maturity from body length. Male porpoises over 192 cm and females over 187 cm, at which 50% of animals become mature for this population (Amano & Kuramochi, 1992), were estimated to be sexually mature.

Measurements data were obtained from animals taken by scientific research vessels using harpoon or drift gillnet, those taken incidentally by the salmon and squid drift gillnet fisheries, and those harpooned by the porpoise fisheries of Japan. Since the measurements of all the Sea of Japan samples and 11 of *truei*-type samples were obtained from the porpoises harpooned by porpoise fisheries and landed at Otsuchi Fish Market in Sanriku district of northern Japan, we were not able to record the locality of each specimen but only the fishing ground. The authors and four other scientists collected measurement data.

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Table 1. External measurements of Dall's purpose. Abbreviations are in parentheses

1. Body length, from tip of upper jaw to notch of flukes (BL).
2. Tip of upper jaw to angle of gape (T–G).
3. Tip of upper jaw to blowhole (T–B).
4. Tip of upper jaw to center of eye (T–EY).
5. Tip of upper jaw to ear (T–EA).
6. Tip of upper jaw to flipper (T–F).
7. Tip of upper jaw to foremost point of white patch (T–AW).
8. Tip of upper jaw to hindmost point of white patch (T–PW).
9. Tip of upper jaw to anterior insertion of dorsal fin (T–DF).
10. Tip of upper jaw to umbilicus (T–UM).
11. Tip of upper jaw to center of genital aperture (T–GA).
12. Tip of upper jaw to anus (T–AN).
13. Length of gape (LGP).
14. Angle of gape to center of eye (G–EY).
15. Center of eye to ear (EY–EA).
16. Anterior length of flipper, from anterior insertion to tip (FAL).
17. Posterior length of flipper, from posterior insertion to tip (FPL).
18. Flipper width at base (FBW).
19. Maximum flipper width (FMW).
20. Anterior length of dorsal fin, from anterior insertion to tip (DAL).
21. Posterior length of dorsal fin, from posterior insertion to tip (DPL).
22. Basal length of dorsal fin (DBL).
23. Height of dorsal fin (DH).
24. Anterior length of white patch of dorsal fin (DAW).
25. Posterior length of white patch of dorsal fin (DPW).
26. Span of flukes, from tip to tip (FKS).
27. Anterior length of fluke, from anterior insertion to tip (FKAL).
28. Posterior length of fluke, from notch to tip (FKPL).
29. Medial length of flukes, from anterior insertion to notch (FKL).
30. Length of white patch of fluke (FKW).
31. Girth at anterior insertion of flipper (GAF).
32. Girth at axilla (GAX).
33. Girth at anterior insertion of dorsal fin (GADF).
34. Girth at genital aperture (GGA).
35. Girth at anus (GAN).

Thirty-five measurements and their abbreviations are listed in Table 1 (Amano & Miyazaki, 1993). Indices of sexual dimorphism, or canting index (CI) and fluke shape index (FSI) were also analyzed (Jefferson, 1990; Amano & Miyazaki, 1993). Canting index was calculated with the formula: $CI=(DPL^2 - DH^2)^{1/2}/DBL$. Fluke shape index was a distance from the line connecting the tips of the flukes to the base of the notch. This index was recorded in a negative value when the notch was behind the line. We excluded measurements of FAL, FMW, DAL, DPW, and GGA from the analyses, because of possible interobserver error (Amano & Miyazaki, 1993).

We divided the samples into six geographic/color type groups, *truei*-type animals (33 males, 9 females), *dalli*-type animals from the Sea of Japan (25 males, 15 females), the Bering Sea (8 males, 9 females), and three areas of the North Pacific: between 154°E and 165°E (western area of the western North Pacific; 44 males, 24 females), between 165°E and 180° (eastern area of the western North Pacific; 42 males, 24 females), and east of 180° (offshore area of the eastern North Pacific; 22 males, 14 females) (Fig. 1). These divisions were similar to the stocks presently proposed, but did not include stocks in the northern Okhotsk Sea and off the coast of North America (International Whaling Commission, 1991; Miyashita, 1991).

Analyses of covariance, with body length and measurer as covariates, were performed using the GLM procedure (SAS Institute Inc., 1985). Measurement data were transformed into log scale. Homogeneity of slopes on BL was found to be violated in GADF ($P<0.05$) and this measurement was eliminated from the analyses. We excluded *truei*-type specimens in the comparison of T–AW, which is distinct between two color types. Since we could not ignore interobserver error, we added measurer as as covariate in ANCOVAs. In fact, we found significant effects of the measurer in 14 (males) and 11 (females) measurements in ANCOVAs ($P<0.05$). ANCOVAs with measurer as a covariate were also performed on two indices of sexual dimorphism. In ANCOVAs, the 1% significance level was selected to avoid Type I errors.

The CANDISC Procedure (SAS Institute Inc., 1985) was used to carry out canonical discriminant analyses for both sexes of *dalli*-type Dall's porpoises, using 10 log-transformed measurements (BL, T–F, T–AW, T–PW, T–DF, T–AN, FPL, FBW, DBL, FKS). These variables were selected after consideration of the results of ANCOVAs and sample size. In order to diminish interobserver error, data were adjusted previously, with the adjusted means for each measurer calculated by ANCOVAs with geographic area and body length a covariates. Multivariate analyses of covariance revealed significant effects of the measurer (Wilks' $\Lambda=0.44$ for males and 0.36 for females, $P<0.01$).

Results

Mean body length of mature Dall's porpoises was largest in the Sea of Japan and decreased from west to east in the North Pacific (Tables 2 and 3).

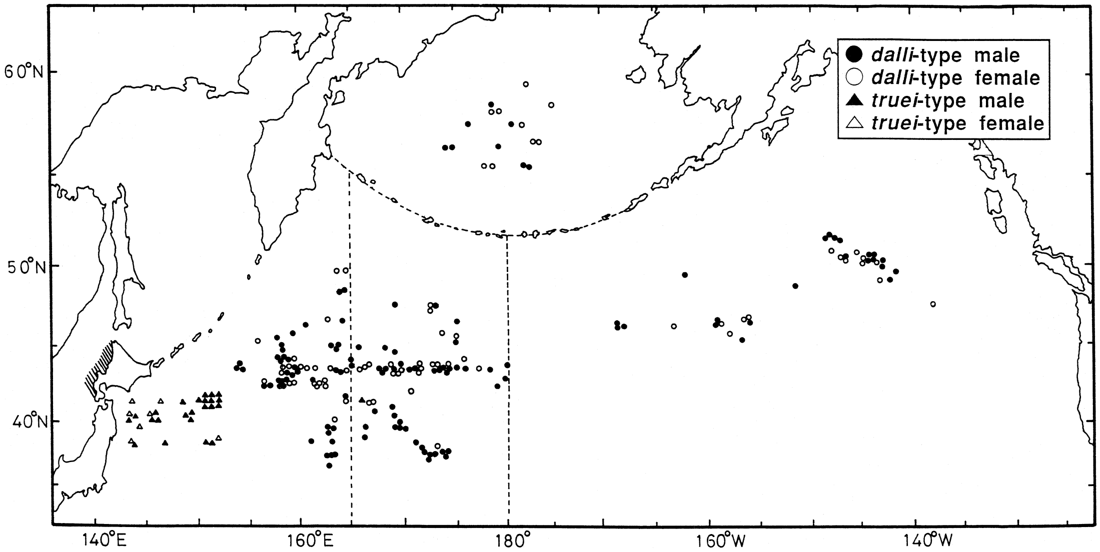

Figure 1. Sampling positions of sexually mature Dall's porpoises used in the present study. Shaded area indicates fishing ground in which the Sea of Japan samples were taken. Dotted lines are boundaries of geographical groups.

The distance from the tip of upper jaw to the foremost point of the lateral white patch (T–AW) was found to differ geographically in both sexes (Tables 2 and 3). The white patch was more posterior in the Sea of Japan *dalli*-type specimens than other *dalli*-types. Figure 2 shows that the lateral white patches of the Sea of Japan porpoises are posterior to the anterior insertion of dorsal fin, without exception.

Male specimens from the Bering Sea showed large distances from the tip of upper jaw to posterior parts of body (T–PW, T–UM, T–GA) and a large girth (GAN) in comparison with those from other areas. Mean fluke shape index of males from the offshore area of the eastern North Pacific was larger than those of males from other areas. The eastern North Pacific males also showed smaller mean values in other sexually dimorphic characters (GAN, canting index, Amano & Miyazaki, 1993). Females from the Sea of Japan had greater measurements from tip of upper jaw to anterior parts of the body (T–G, T–EA, T–F).

Figure 3 shows scatter plots of the first and second canonical variates. The Sea of Japan samples were clearly separated from others. This was attributed to the large distance from tip of upper jaw to white patch on the first axis (Table 4).

Discussion

Dall's porpoises from the Sea of Japan, which represent the Sea of Japan–Okhotsk Sea population, demonstrate a distinctive position among *dalli*-types of the lateral white patch. Because postnatal relative growth pattern of the distance from tip of upper jaw to the foremost point of the white patch was found to have a slightly negative allometry (Amano & Miyazaki, 1993), the anterior border of white patch does not move posteriorly with the body length. Therefore, the caudad white patches of Sea of Japan Dall's porpoises are not attributed to their large body length. Houck (1976) reported some variation in size of the white patch of *dalli*-type porpoises but he neither examined the specimens from the Sea of Japan, nor alluded to geographical correlation of this variation.

Many facts suggest genetic and ecological independence of the Sea of Japan–Okhotsk Sea population. Amano & Miyazaki (1992) showed that the Sea of Japan–Okhotsk Sea Dall's porpoises differ in skull morphometrics from porpoises of the North Pacific Ocean and Bering Sea. The Sea of Japan–Okhotsk Sea Dall's porpoises are the most divergent in the composition of genotypes of mt-DNA among the populations in the North Pacific and adjacent seas (Shimura, 1989). The mean body length at which sexual maturity is attained in this population is larger than those of other *dalli*-type populations, except for the population off the coast of North America (Yoshioka *et al.*, 1990; Amano & Kuramochi, 1992). Moreover, it was reported that the breeding season of the Sea of Japan–Okhotsk Sea population is earlier than those of the *truei*-type and western North Pacific *dalli*-type populations (Yoshioka *et al.*, 1990; Amano & Kuramochi, 1992). Finally, Walker (1990) discovered that the

Table 2. Results of analyses of covariance with measurer and body length as covariates. Comparisons of body length (cm), adjusted means of log-transformed measurements (cm), and indices of sexual dimorphism of male Dall's porpoises among areas. Only the measurements with significant differences are indicated. Untransformed equivalents of means are in parentheses

			Western North Pacific									
					Dalli-type							
	Sea of Japan		Truei-type		Western area		Eastern area		Eastern North Pacific		Bering Sea	
Measurement	*n*	Mean	*n*	Mean	*n*	Mean	*n*	Mean	*n*	Mean	*n*	Mean
BL	25	204.8^{abc}	33	201.5^{def}	44	194.2^{adg}	42	193.2^{beh}	22	180.7^{cfghi}	8	200.5^{i}
T–F	25	1.424 (28.6)	33	1.440^{a} (27.5)	44	1.417^{a} (26.1)	42	1.423 (26.5)	22	1.420 (26.3)	8	1.438 (27.4)
T–AW*	25	1.957^{abcd} (90.6)			43	1.819^{a} (65.9)	42	1.813^{b} (65.0)	20	1.802^{c} (63.4)	8	1.838^{d} (68.9)
T-PW	25	2.170^{a} (147.9)	26	2.166^{b} (146.6)	42	2.166^{c} (146.6)	40	2.166^{d} (146.6)	22	2.170^{e} (147.9)	7	2.188^{abcde} (154.2)
T–UM	20	1.932^{a} (85.5)	33	1.936^{b} (86.3)	44	1.935^{c} (86.1)	42	1.937^{d} (86.5)	22	1.941 (87.3)	8	1.953^{abcd} (89.7)
T–GA	25	2.061^{a} (115.1)	33	2.066^{b} (116.4)	44	2.067^{c} (116.7)	42	2.069^{d} (117.2)	22	2.072 (118.0)	8	2.086^{abcd} (121.9)
T–AN	25	2.126^{a} (133.7)	33	2.131 (135.2)	44	2.132 (135.5)	42	2.132 (135.5)	22	2.136 (136.8)	7	2.141^{a} (138.4)
FPL	25	1.215^{abc} (16.4)	32	1.194 (15.6)	44	1.192 (15.6)	41	1.185^{a} (15.3)	22	1.174^{b} (14.9)	7	1.176^{c} (15.0)
FBW	25	1.002 (10.0)	33	0.992 (9.8)	44	0.996^{a} (9.9)	42	0.981^{a} (9.6)	22	0.986 (9.7)	7	0.973 (9.4)
DBL	24	1.598 (39.6)	32	1.609 (40.6)	44	1.634^{a} (43.1)	42	1.609^{a} (40.6)	22	1.617 (41.4)	8	1.624 (42.1)
FKS	25	1.742 (55.2)	33	1.748^{a} (56.0)	43	1.743 (55.3)	41	1.726^{a} (53.2)	22	1.719 (52.4)	8	1.752 (56.5)
GAX	0	—	4	2.000 (100.0)	24	2.008 (101.9)	17	1.993^{a} (98.4)	22	1.996 (99.1)	6	2.020^{a} (104.7)
GAN	0	—	3	1.906^{a} (80.5)	25	1.919 (83.0)	18	1.918 (82.8)	22	1.906^{b} (80.5)	6	1.954^{ab} (90.0)
CI**	24	0.625	31	0.627	42	0.606	40	0.630^{a}	22	0.562^{ab}	8	0.684^{b}
FSI**	25	− 1.83^{a}	10	− 1.90^{b}	12	− 0.49^{c}	14	0.66^{d}	22	3.69^{abcd}	5	0.20

Significantly different (P<0.01) pairs of means are indicated with same superscript letters.
**Truei*-type was not included.
**Only measurer was included as a covariate for these variables.

infestation rates of *Phyllobothrium* of Dall's porpoise are different between the southern Okhotsk Sea and other areas.

The results of the morphological studies on geographic variation of Dall's porpoises (Amano & Miyazaki, 1992; present study) agree well with the results of analysis of mt-DNA that showed *truei*-type Dall's porpoises have a closer relationship with offshore North Pacific *dalli*-type populations than with the Sea of Japan–Okhotsk *dalli*-type population (Shimura, 1989). The fact that genetic and morphological divergence is emphasized in the Sea of Japan–Okhotsk Sea population, even though overall differentiation is not advanced so much in Dall's porpoises, suggests an older origin for this population and relatively recent dispersal of porpoises into the North Pacific and Bering Sea (Walker & Sinclair, 1990). These porpoises are considered to be now in the process of differentiation into several populations, which are recognised as stocks, and accumulating their characteristic genotypes in mt-DNA (Shimura, 1989).

It is interesting that the extremes of Dall's porpoise pigmentation, i.e. the largest (*truei*-type) and the smallest (*dalli*-type of the Sea of Japan–Okhotsk Sea population) lateral white patch, are distributed off the east and west coast of Japan, respectively. The calving grounds of both the Sea of Japan–Okhotsk Sea *dalli*-type and *truei*-type populations adjoin in the Sea of Okhotsk (Miyashita & Doroshenko, 1990; Miyashita, 1991). If mixing of animals occurs in the Okhotsk Sea, the very

Table 3. Results of analyses of covariance with measurer and body length as covariates. Comparisons of body length (cm) and adjusted means of log-transformed measurements (cm) of female Dall's porpoises among areas. Only the measurements with significant differences are indicated. Untransformed equivalents of means are in parentheses

			Western North Pacific									
					Dalli-type							
	Sea of Japan		Truei-type		Western area		Eastern area		Eastern North Pacific		Bering Sea	
Measurement	*n*	Mean	*n*	Mean	*n*	Mean	*n*	Mean	*n*	Mean	*n*	Mean
BL	15	195.4^{abcd}	9	189.4^{e}	24	184.9^{af}	23	180.2^{b}	14	175.8^{cef}	9	181.9^{d}
T–G	15	1.030^{ab} (10.7)	9	0.953^{a} (9.0)	24	0.955 (9.0)	23	0.953 (9.0)	14	0.915^{b} (8.2)	9	0.955 (9.0)
T–EA	15	1.424^{abc} (26.5)	9	1.382^{a} (24.1)	23	1.380^{b} (24.0)	22	1.376^{c} (23.8)	14	1.360 (22.9)	9	1.246 (17.6)
T–F	15	1.472^{ab} (29.6)	9	1.435 (27.2)	23	1.432 (27.0)	22	1.424^{a} (26.5)	14	1.412^{b} (25.8)	9	1.425 (26.6)
T-AW*	15	1.896^{abc}			24	1.816^{a} (65.5)	23	1.816^{b} (65.5)	14	1.828 (67.3)	9	1.807^{c} (64.1)
LGP	15	1.063 (11.6)	8	1.036^{a} (10.9)	14	1.052 (11.3)	12	1.070^{a} (11.7)	0	—	2	1.076 (11.9)
FKPL	15	1.425^{a} (26.6)	8	1.400 (25.1)	21	1.399 (25.1)	22	1.377^{a} (23.8)	14	1.387 (24.4)	9	1.383 (24.2)
GAN	0	—	6	1.831^{a} (67.8)	17	1.862^{a} (72.8)	16	1.852 (71.1)	14	1.849 (70.6)	9	1.853 (71.3)

Significantly different ($P<0.01$) pairs of means are indicated with same superscript letters.
**Truei*-type was not included.

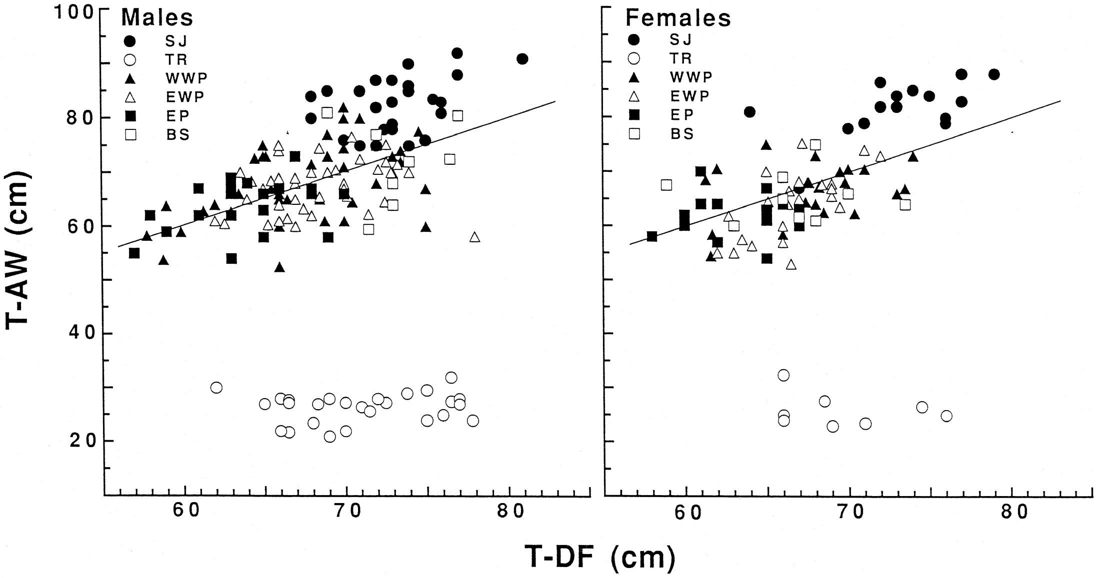

Figure 2. Relationships between distance from tip of upper jaw to anterior insertion of dorsal fin (T–DF) and to the foremost point of lateral white patch (T–AW). SJ indicates *dalli*-type Dall's porpoises from the Sea of Japan, TR *truei*-type, WWP *dalli*-type from western area of the western North Pacific, EWP eastern area of the western North Pacific, EP offshore area of the eastern North Pacific, BS the Bering Sea, lines T–AW=T–DF.

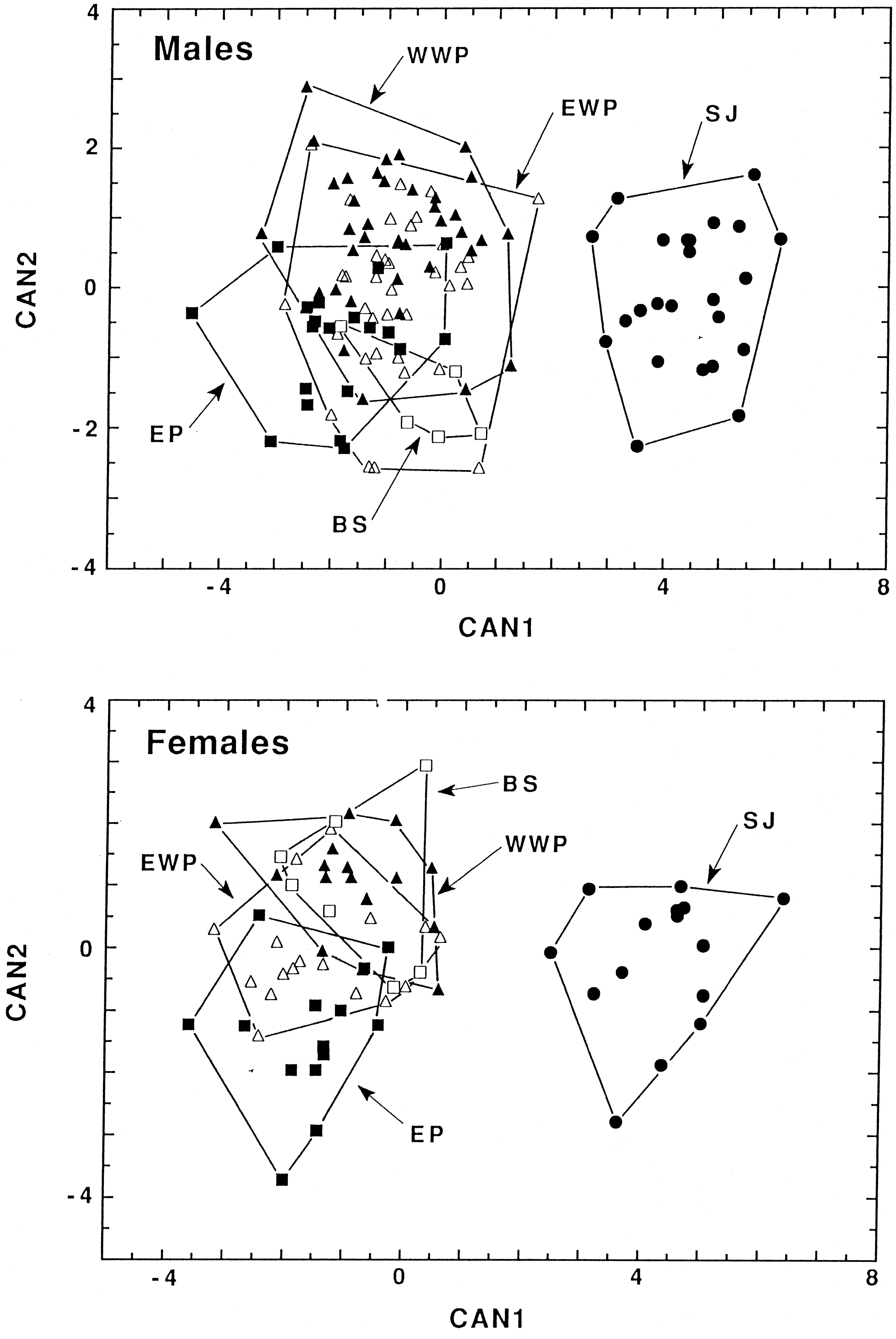

Figure 3. Scatter plots of the first and second canonical variates, based on 10 external measurements of *dalli*-type Dall's porpoises. For symbols see Fig. 2.

Table 4. Standardized canonical coefficients of the first and second canonical axes

Measurement	Males		Females	
	CAN1	CAN2	CAN1	CAN2
Proportion	0.869	0.068	0.828	0.117
BL	0.778	1.886	− 0.139	1.493
T–F	0.158	− 0.154	1.176	− 0.121
T–AW	1.897	− 0.202	1.258	− 1.133
T–PW	1.074	− 1.858	0.340	− 1.373
T–DF	− 0.475	− 0.575	0.078	1.353
T–AN	− 1.584	0.404	− 1.156	− 0.090
FPL	0.191	0.560	0.025	− 0.107
FBW	− 0.323	0.456	− 0.075	0.107
DBL	− 0.221	0.153	0.465	0.128
FKS	0.298	− 0.052	0.727	0.305

different pigmentation may act as an effective marker in the recognition of individuals of different populations to prevent interbreeding and enhance differentiation between the populations.

Differences in the position of the white patch are also useful for researchers to recognize the origin of free ranging or stranded *dalli*-type Dall's porpoises. When this marker is distinguished in sighting surveys, the data can provide important information on the migratory route of the Sea of Japan–Okhotsk population. *Dalli*-type Dall's porpoises occasionally stray further south from their normal range along the Pacific coast of Japan. We can tell whether these animals come from the Sea of Japan or offshore Pacific with a high probability.

We found that male Dall's porpoises from the offshore eastern North Pacific showed less sexual dimorphism than males from other areas. Lighter testis weights of the eastern North Pacific porpoises may partly explain this, if the development of sexually dimorphic characters correlates with that of testis. Mean testis weight of the eastern North Pacific porpoises is 100 g, lighter than mean weights of other areas; 133–140 g for other parts of the North Pacific and Sea of Japan, and 240 g for the Bering Sea.

Some factor may restrict development of dimorphic characters in the offshore eastern Pacific. Amano & Miyazaki (1992) found that Dall's porpoise skulls from coastal waters off Japan and North America are larger than those from other areas, and skulls from the offshore area of the eastern North Pacific are the smallest. They suggested that skull size is a reflection of food availability, because of the correlation between skull size and productivity of the ocean. Dall's porpoises from the offshore area of the eastern North Pacific showed less sexual dimorphism also in body size. Mean body length of males was larger than that of females by 9.4 cm in porpoises from the Sea of Japan, while by only 4.9 cm in those from the offshore eastern North Pacific (Tables 1 and 2). Development of dimorphic characters, as well as body size, must require extra energy, and an inferior nutritional condition may hinder the development of sexual dimorphism in the eastern North Pacific porpoises. Correlation between sexual dimorphism and environmental condition has been noted in several mammalian species. Ralls & Harvey (1985) suggested that geographic variation in sexual dimorphism of two species of North American weasels (*Mustela erminea* and *M. frenata*) was caused by geographic differences in abundance of prey. Patton & Smith (1990) considered that habitat quality affects variation in sexual dimorphism of the pocket gopher (*Thomomys bottae*), because size of males correlates with degree of sexual dimorphism and male size may be influenced by nutritional quality of food. Kaji *et al.* (1988) reported that limitation of food resources brought about decreases of antler size and points in male sika deer (*Cervus nippon*). More detailed studies on development and geographic variation of sexually dimorphic characters are required to test this possibility.

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