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Geographic Variation in the Skull Morphology of the Finless Porpoise *Neophocaena phocaenoides* in Japanese Waters

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Geographic variation in the skull morphology of the finless porpoise was studied with special reference to identifying local populations in Japanese waters. Twenty-five skull characters were measured for 146 specimens. These specimens were divided into five samples on the basis of available distributional information: 1) from Sendai Bay to Tokyo Bay, 2) Ise Bay and Mikawa Bay, 3) Inland Sea and the adjacent waters, 4) Omura Bay, 5) Ariake Sound and Tachibana Bay. Morphological differences were examined by the analysis of covariance and canonical discriminant analysis. The skull morphology varied among the samples. The porpoises in Ise Bay and Mikawa Bay possessed rather narrow skulls. There was no evidence that skull morphology was more similar between geographically close areas. Such geographic variation suggests that porpoises in each area rarely intermingle. We considered that there are at least five local populations in Japanese waters.

Key words: finless porpoise, *Neophocaena phocaenoides*, skull morphology, geographic variation, population identification, Japanese waters

The finless porpoise *Neophocaena phocaenoides* is a small cetacean distributed in the coastal waters of tropical and temperate Asia.[1)] Geographic differences in its skull morphology have been pointed out among porpoises in the Indian Ocean, Chinese waters, and Japanese waters[2-6)] and among animals within Chinese waters.[7-9)] Geographic variation in this morphology may also be observed within Japanese waters. This variation provides evidence for the identification of local populations, which here possess the same meaning as stocks. However, no such study has previously been conducted.

Occurrence of the porpoise is confirmed widely in Japanese coastal waters, but frequent sightings are reported only from the several limited waters.[10)] A geographic difference in the parturition season was found in Japanese waters.[11)] These results suggest multiple populations.

This study aims to clarify the geographic variation in the skull morphology of the finless porpoise in Japanese waters and to identify local populations.

Materials and Methods

We examined skulls of 146 finless porpoises from Japanese coastal waters (Table 1). These skulls are deposited in aquariums, museums, and schools in Japan: Himeji City Aquarium (HCA), Kitakyushu Museum and Institute of Natural History (KMINH), Kamogawa Sea World (KSW), Matsushima Aquarium (MA), Minamichita Beachland Aquarium (MBA), Marine World Umino-Nakamichi (MWUN), Natural History Museum and Institute, Chiba (NHMIC), National Science Museum, Tokyo (NSMT), Nagasaki University (NU), Oarai Aquarium (OA), Toba Aquarium (TA), and Waji Elementary School (WES). For specimens at Nagasaki University, age

Table 1. List of the finless porpoise *Neophocaena phocaenoides* specimens examined

Localities	Specimen number
From Sendai Bay to Tokyo Bay (ST)	KSW*1 NP-001; NHMIC CBM-ZZ-250; NSMT 23751,*2 24660;*2 OA 5.*3
Ise Bay and Mikawa Bay (IM)	MA MN-01; MBA NP800524-1, 860809, 860912-3, 880802-26; NSMT 24963, 28371; TA 23,*8 27,*4 51;*8 WES NP860625-21.
Inland Sea and the adjacent waters (IS)	HCA 2, 3,*5 19,*6 20-23, 26, 27, 29, 32-34, 36, 38-40; KMINH VR100.005,*7 100.006, 100.007, 100.008, 100.009; MWUN 89-1226, 90-0320, 90-0406; NSMT 24850, 24908,*6 24910,*2 24911, 24945, 24946, 24950, 24953, 24954, 24955,*6 24956, 24957, 24964, 27885; NU 1055, 1078, 1081, 1084, 1085, 1086, 1098, 1100, 1104.
Omura Bay (OB)	NU 997, 1014, 1016, 1052, 1090, 1095, 1096, 1109.
Ariake Sound and Tachibana Bay (AT)	NU 994, 996, 1000, 1002-1010, 1012, 1013, 1015, 1018, 1021, 1022, 1024, 1027-1029, 1032, 1033, 1035, 1037, 1038, 1040-1042, 1046, 1047, 1050, 1051, 1053, 1054, 1056-1065, 1067, 1071-1076, 1088, 1091-1094, 1097, 1099, 1102, 1103, 1105-1108, 1110-1117.

*1 For abbreviations, see text.

*2-7 These were considered to be sexually or physically mature because they were pregnant, lactating, or showed complete fusion of all vertebral epiphyses with centra (2, Miyazaki;[12)] 3, Y. Yoshida: OA, pers. comm.; 4, O. Tsukada: TA, pers. comm.; 5, T. Tochimoto: HCA, pers. comm.; 6, Amano *et al.*;[6)] 7, KMINH, pers. comm.).

*8 These animals had been kept in TA for eight years (TA 23) and five years (TA 51; O. Tsukada: TA, pers. comm.).

as well as sexual or physical maturity had previously been examined.[11,13] Age had not been determined for the other specimens, while information on sexual or physical maturity was available for 10 animals and the period of captivity in Toba Aquarium was available for 2 animals (Table 1). The senior author measured 25 skull characters of all the specimens with calipers or rulers to the nearest 1 mm (Fig. 1).

For statistical analyses, the specimens were grouped into five samples: 1) from Sendai Bay to Tokyo Bay (hereinafter referred to as the ST sample, $n=5$), 2) Ise Bay and Mikawa Bay (IM, $n=11$), 3) Inland Sea and the adjacent waters (IS, $n=48$), 4) Omura Bay (OB, $n=8$), 5) Ariake Sound and Tachibana Bay (AT, $n=74$). This division was based on the following. Shirakihara *et al.*[10] reported that finless porpoises are mainly distributed in four coastal waters, *i.e.*, ST, IM, IS, and the coastal waters of western Kyushu (Fig. 2). In the coastal waters of western Kyushu, Shirakihara *et al.*[14] indicated that they are common in OB and AT, but rare in Sumo Nada. All the specimens used in this study were collected within these five areas.

Because of small sample sizes in the ST, IM, and OB samples, we did not conduct separate analyses for each sex. Thus, characters that showed sexual dimorphism by the analysis of covariance (explained below) were not used. These characters were Nos. 10 and 20 in the AT porpoises[13] and No. 19 in the IS sample.

Considering that many specimens were cranially immature, geographic differences were examined by two methods. The first was the analysis of covariance (ANCOVA) using the data for all the specimens. This is based on an assumption that the allometric relationship holds irrespective of age: $\log_{10}y = a\log_{10}x + \log_{10}b$, where a and b are constants, x is the condylobasal length and y is the measurement of one of remaining characters. Measurements of the following 6 characters were not used as y: two characters (Nos. 24 and 25) with no significant regression ($p>0.05$) and four characters (2, 3, 6, and 14) with significant differences ($p<0.05$) among the five samples in a. ANCOVA was carried out with the GLM procedure of SAS.[15]

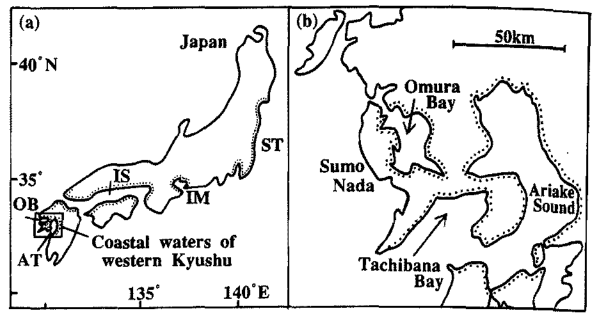

Fig. 2. (a) Coastal waters where the finless porpoise *Neophocaena phocaenoides* is mainly distributed.[10,14)]

ST, waters from Sendai Bay to Tokyo Bay; IM, Ise Bay and Mikawa Bay; IS, Inland Sea and the adjacent waters; OB, Omura Bay; AT, Ariake Sound and Tachibana Bay.

(b) Enlarged map of coastal waters of western Kyushu.

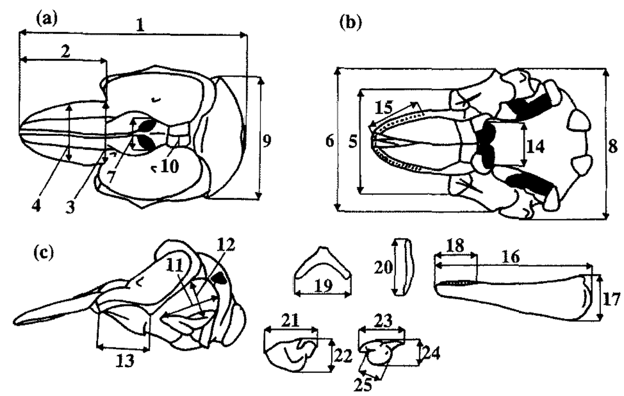

Fig. 1. Skull measurements of the finless porpoise *Neophocaena phocaenoides*.

(a) Dorsal, (b) ventral, and (c) lateral aspects of skull. No. 1, condylobasal length; 2, length of rostrum; 3, width of rostrum at base; 4, width of rostrum at midlength; 5, greatest preorbital width; 6, greatest postorbital width; 7, greatest width of external nares; 8, greatest width across zygomatic processes of squamosal; 9, width between parietals; 10, greatest width of left nasal; 11, greatest length of left posttemporal fossa; 12, greatest width of left posttemporal fossa at right angles to greatest length; 13, length of left orbit; 14, greatest width of internal nares; 15, length of upper left tooth row; 16, greatest length of left ramus; 17, greatest height of left ramus at right angles to greatest length; 18, length of lower left tooth row; 19, greatest width between tip of thyrohyals (measured only when fusion had already occurred between the basihyal and thyrohyals); 20, greatest length of left stylohyal; 21, greatest length of left tympanic bulla; 22, greatest width of left tympanic bulla; 23, greatest length of left periotic; 24, greatest width of left periotic; 25, diameter of cochlear portion of left periotic.

The second method was the canonical discriminant analysis (CDA) which was performed to visually interpret the differences in the skull morphology among the five samples using only the data for characters whose growth had ceased. On the basis of the skull development of the AT porpoises,[13] we selected data for five tympano-periotic characters (Nos. 21–25) for all the animals and data for 16 other characters (Nos. 1–9, 11–13, 15–18) for individuals whose ages were estimated to be 4 years or older. In cases where the age of a porpoise was not determined, we used only the data for individuals which were sexually or physically mature (Table 1). We also added measurements of two animals kept in Toba Aquarium for over 4 years. Of these data, 11 characters (Nos. 2, 4, 6, 8, 12, 13, 15–18, 22) were excluded from CDA because of missing values. We conducted CDA with the CANDISC procedure[16] using two data sets: data for four tympano-periotic characters (Nos. 21, 23–25) and data for six other characters (Nos. 1, 3, 5, 7, 9, 11).

Results

Geographic difference was found in $\mathrm{Log}_{10}b$ for 6 of 15 characters by ANCOVA ($p<0.01$, Table 2): width of rostrum at midlength (No. 4), greatest preorbital width (5), greatest width across zygomatic processes of squamosal (8), width between parietals (9), greatest length of left posttemporal fossa (11), and length of lower left tooth row (18). The adjusted means of three characters related to the skull width (Nos. 4, 5, 8) were lowest in the IM sample. Figure 3 shows that the IM sample possesses the narrower skull than other samples.

Table 2. Results of analyses of covariance on geographic differences in skull measurements of finless porpoises *Neophocaena phocaenoides* from five coastal waters in Japan

Character No.*2	ST*1		IM		IS		OB		AT	
	n	AD*3 (mm)	*n*	AD (mm)	*n*	AD (mm)	*n*	AD (mm)	*n*	AD (mm)
4	5	52.6^{a*4}	9	45.6^{abcd}	40	50.3^{b}	8	49.2^{c}	71	50.1^{d}
5	5	115.3^{a}	10	104.0^{abcd}	44	110.6^{be}	8	114.4^{c}	71	114.0^{de}
8	5	143.5^{a}	10	133.1^{abcd}	45	141.4^{b}	7	145.1^{ce}	70	140.2^{de}
9	5	120.2^{a}	10	114.4^{ab}	46	118.1^{bc}	8	117.3	72	115.7^{c}
11	5	56.7	9	53.6	44	54.1^{a}	8	54.5	71	56.5^{a}
18	3	72.4^{a}	8	69.7^{b}	41	67.8^{c}	8	70.5^{d}	66	65.9^{abcd}

*1 For abbreviations, see text.
*2 Only character with significant difference ($p<0.01$) are showed among all the 15 characters examined. Character numbers are defined in Fig. 1.
*3 Adjusted mean.
*4 Same superscript in each row indicates significant difference between the two ADs ($p<0.01$).

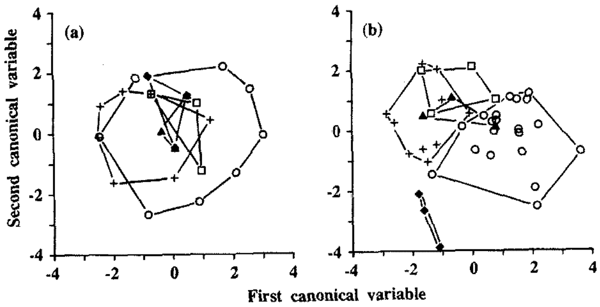

Fig. 4. Scatter plots of scores on the first and second canonical variables derived from (a) four tympano-periotic characters and (b) six other characters.

To avoid congestion, only marginal scores in each sample are plotted and connected with lines in (a), whereas scores of all the specimens are showed in (b). ▲, ST; ◆, IM; +, IS; □, OB; ○, AT.

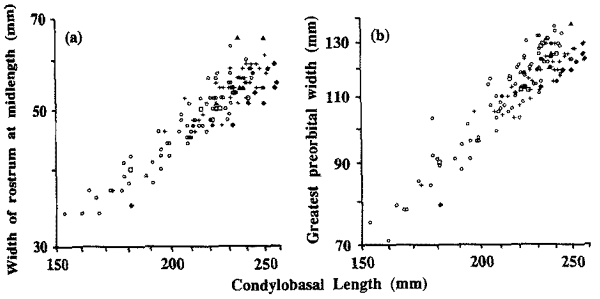

Fig. 3. (a) Relationship between condylobasal length and width of rostrum at midlength (No. 4).

(b) Relationship between condylobasal length and greatest preorbital width (No. 5).

▲, ST; ◆, IM; +, IS; □, OB; ○, AT.

Scores on the first and second canonical variables derived by CDA are plotted in Fig. 4. The cumulative proportion of both variables was 0.97 for four tympano-periotic characters and 0.89 for the remaining six characters. Among the five samples, scores for the tympano-periotic characters overlapped each other (Fig. 4a). On the other hand, the AT sample separated visually from three other samples (IM, IS, and OB) with respect to scores for the other six characters (Fig. 4b). The IM sample specimens were also visually distinct from the others.

Discussion

The skull morphology of the finless porpoise varied noticeably within Japanese waters. The IM porpoises possessed rather narrow skulls (Table 2, Fig. 3). It should be noted that there was no evidence that skull morphology was more similar between geographically close areas: for example, differences were detected between ST and IM, between IM and IS, and between OB and AT, whereas there was some similarity between the more distantly located AT and ST (Table 2, Fig. 4b). The morphology of the OB porpoises seemed more similar to those in IS than those in AT (Fig. 4b). Such geographic variation suggests that finless porpoises from four areas, ST, IM, IS+OB, and AT, rarely intermingle. In support of this, during the period 1973-82, many animals were captured alive in IM and IS, whereas only one porpoise was captured in the waters between them.[17]

Morphological differences were not detectable in the skulls of porpoises from IS and OB. No difference in the parturition season has been confirmed between these two waters because only one specimen was available for estimating this season in OB (M. Shirakihara, pers. comm.). But coastal waters between IS and OB do not possess the geographical conditions (dominance of non-rocky bottoms and offshore extension of areas with depth less than 50 m) that are commonly observed in waters where the porpoise is distributed.[10] In these waters, sightings are rare.[10,14]

On the basis of morphological differences reported here and ecological studies,[10,11,14] we considered that there are at least five local populations of the finless porpoise in Japan. Genetic studies will be required for more detailed analyses of this population separation.

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