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POPULATION STRUCTURE OF FINLESS PORPOISES (*NEOPHOCAENA PHOCAENOIDES*) IN COASTAL WATERS OF JAPAN

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ABSTRACT. – To clarify population structure of finless porpoises (*Neophocaena phocaenoides*) in Japan, a sequence of studies have been conducted: a questionnaire survey and aerial sighting surveys to obtain information on porpoise distribution, and analyses of skull morphology and mitochondrial DNA control region sequences to examine their geographic variation. The first two surveys indicated that finless porpoises are mainly distributed in five coastal regions in Japan (Sendai Bay—Tokyo Bay, Ise—Mikawa Bays, Inland Sea—Hibiki Nada, Omura Bay, and Ariake Sound—Tachibana Bay) and that occurrence of animals is rare in the other areas. The latter two analyses revealed geographic differences in the morphology and sequences among the five areas. Finless porpoises in each of the five regions are considered to belong to distinct populations.

KEY WORDS. – Finless porpoise, *Neophocaena phocaenoides,* Japan, population structure, distribution, geographic variation.

INTRODUCTION

The finless porpoise (*Neophocaena phocaenoides*) is a small toothed cetacean inhabiting coastal waters of tropical and temperate Asia (Kasuya, 1999). In eastern Asia, the finless porpoise is distributed along the Chinese coast, the western and southern coasts of the Korean Peninsula, and throughout much of the Japanese Archipelago.

In Japan, occurrence of the porpoises had been reported from several areas, e.g., Sendai Bay, Tokyo Bay, Ise Bay, Inland Sea, and coastal waters of western Kyushu (Mizue et al., 1965; Nishiwaki, 1965; Ogawa, 1973; see Fig 1). However, because extensive systematic surveys have not been conducted, the distribution of this species in Japanese waters is poorly understood. The existence of three populations of finless porpoises has been proposed in coastal waters of China (Gao & Zhou, 1993), and it seems likely that similar population subdivision exists in Japan. Indeed, geographic variation has been reported in the timing of parturition between animals in coastal waters of western Kyushu and other Japanese waters (Shirakihara et al., 1993).

In Japan, although the porpoises are not a target for commercial fisheries, animals have been taken incidentally by fishing nets (Shirakihara et al., 1993). Other types of human activities may also threaten the existence of this species. Detailed information on its distribution and population structure is necessary for the conservation of the porpoise. In order to accumulate the information, I have conducted a sequence of studies in collaboration with K. Shirakihara, M. Shirakihara, H. Kishino, M. Yoshioka, S. Chow, and A. Takemura. These studies consist of a questionnaire survey and aerial sighting surveys to obtain information on porpoise distribution in Japan, and examination of geographic variation in the skull morphology and mitochondrial DNA control region sequences to clarify population structure of finless porpoises. The present report summarizes results from the studies.

QUESTIONNAIRE SURVEY

In order to obtain information on distribution of finless porpoises in Japan, we conducted a questionnaire survey of fisheries cooperative associations (Shirakihara et al., 1992). The associations covered most of the Japanese coast (see Fig. 1a) and each association is composed of fishermen engaged in various types of fisheries (e.g., line and net fishing and cultural fishery). Distinctive features of the porpoise, i.e., lack of beak and dorsal fin, reduce the possibility of confusion with other small cetaceans. Thus, we considered that fishermen probably notice and identify finless porpoises if the animals are distributed in their fishing grounds. Questions were 'Have you sighted finless porpoises?', 'How often have you sighted finless porpoises?', 'Have you seen finless porpoises taken incidentally or found beachcast?', 'Do you know a local name for the finless porpoise?', etc. Three photographs and an explanatory note on distinctive features on the porpoise were also enclosed with the questionnaire. The questionnaire was sent to all the 2,053 associations in Japan, except those in Hokkaido. This is because past studies

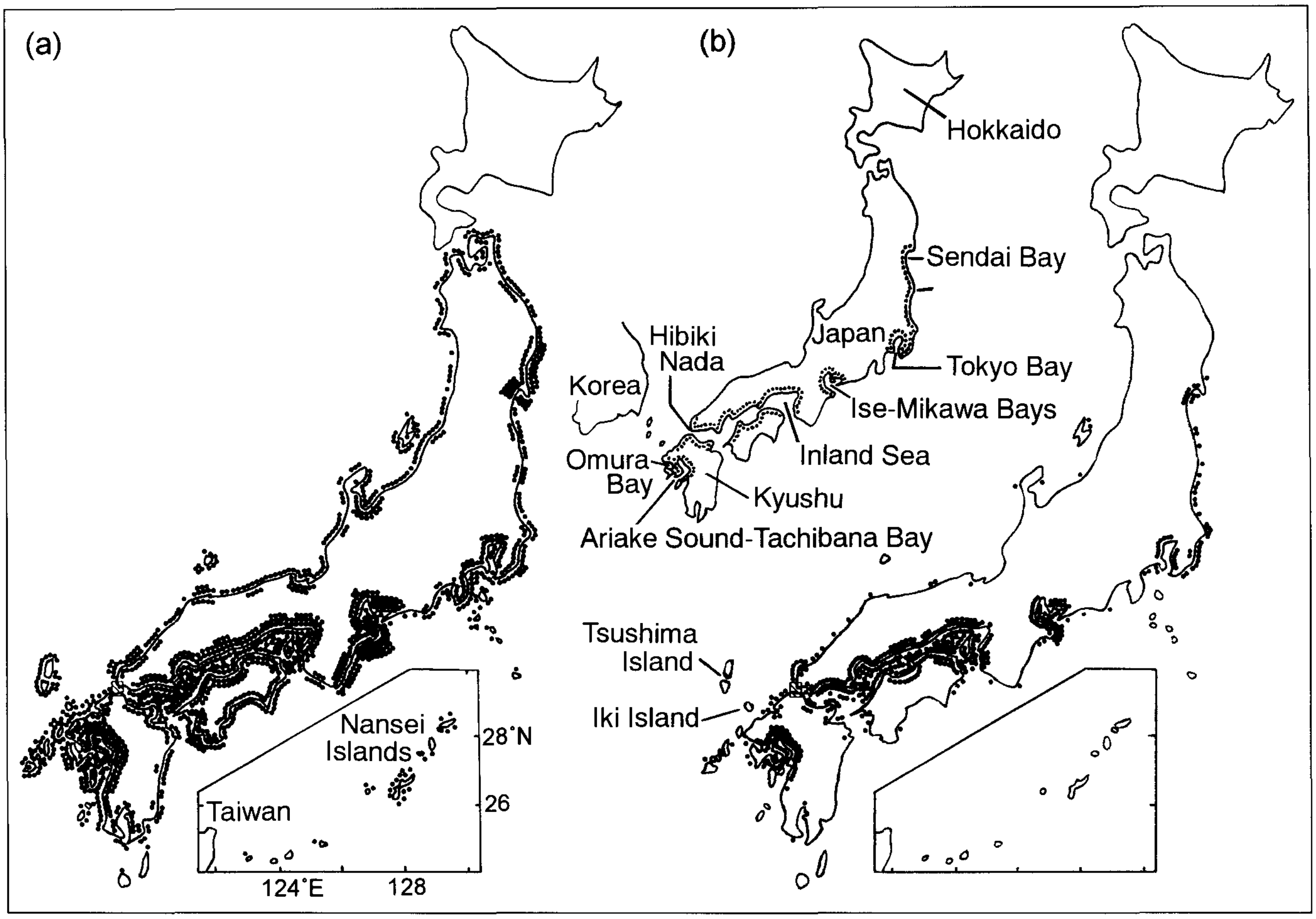

Fig. 1. Location of fisheries cooperative associations which replied to the questionnaire survey (a), and which reported sightings of finless porpoises (b). The coastal waters with dotted lines are considered to be main distributional area of finless porpoises in Japan.

indicated that coastal waters of Hokkaido are far beyond the northern limit of finless porpoise distribution in Japan (Kasuya et al., 1984; Kawamura et al., 1983; Kawamura, 1986). Of the 2,053 questionnaires, 1,382 (67%) were returned. Locations of fisheries cooperative associations which replied to the questionnaires are shown in Figure 1a.

The questionnaires were returned from all over Japan, i.e., not only from the mainland but also from isolated small islands. Figure 1b shows locations of associations reporting that they had sighted finless porpoises. Such associations were concentrated in five coastal waters: Sendai Bay—Tokyo Bay, Ise—Mikawa Bays, Inland Sea—Hibiki Nada, Omura Bay, and Ariake Sound—Tachibana Bay. In those areas, many fishermen had sighted porpoises once or more per year. Animals were frequently taken incidentally or found stranded. Furthermore, fishermen in every area knew unique local names for the finless porpoise. These results suggest that finless porpoises are familiar in the waters. On the other hand, few sighting reports were obtained from the other areas, e.g., coastal waters between Tokyo Bay and Ise—Mikawa Bays and between Hibiki Nada and Omura Bay. In these waters, frequency of porpoise sightings, including animals taken incidentally or stranded, was very low, e.g., 'a dead animal had been sighted only once'. There are no local names for the finless porpoise there; fishermen in the areas called the porpoises as 'dolphin' or 'whale'. The results indicate that finless porpoises are rare in these waters.

It is obvious that there is some unreliability in reports from fishermen, because we can not confirm who returned answers. They may possibly confuse the finless porpoise with the other cetacean species. However, if answers from many neighboring associations coincide with each other, reliability of the answers becomes more certain. Indeed, sighting reports were close together in Figure 1b. Thus, we considered that results from the questionnaire survey reasonably reflect the distribution of finless porpoises in Japan. The results indicate that finless porpoises are mainly distributed in the five areas with frequent sighting reports and that animals seldom occur in other areas. This geographically discrete distribution suggests that Japanese finless porpoises are subdivided into small populations.

AERIAL SIGHTING SURVEYS

To confirm reliability of porpoise distribution from the questionnaire survey, we analyzed sighting data from aerial sighting surveys conducted for abundance estimation of finless porpoises in coastal waters of western Kyushu (Yoshida et al., 1997, 1998). In those waters, the questionnaire survey suggests that finless porpoises are mainly distributed in Omura Bay and Ariake Sound—Tachibana Bay.

The 88 east-west transect lines were placed at intervals of

1.85 km (1 nautical mile) in Omura Bay (12 lines), Ariake Sound (42), Tachibana Bay (16), and Yatsushiro Sound (18; Fig. 2a). In past ship sighting surveys for finless porpoises conducted in coastal waters of western Kyushu, no sightings were obtained with naked eye over 500m perpendicular distance from the transect line (Shirakihara et al., 1994). Thus, we considered that the same animals/groups are not sighted multiple times from lines neighboring at intervals of 1.85 km. In addition to the east-west lines, a north-south line was drawn in Sumo Nada and Tachibana Bay each. Of the east-west lines, one-third in Ariake Sound (14 lines) and Yatsushiro Sound (six) and one-half in Tachibana Bay (eight) were selected and flown at each survey.

A single-propeller, high-wing, four-seater aircraft (Cessna 172) flew above the transect lines at the lowest practical speed and altitude in order to enhance detection of porpoises: 167 km/hour (90 knots) and 152 m (500 ft). Two observers with extensive experience in sighting surveys for finless porpoises always sat in the rear seats and searched the area perpendicular to the transect line without optical aids. When the observers detected porpoise groups, they counted the number of individuals in each group (group size) and a recorder sitting in the copilot seat noted time, aircraft location measured by GPS, and group size.

Because detectability of porpoises was low in poor sea conditions with white caps, surveys were carried out on days with good sea conditions (Beaufort wind scale of 2 or less). All the 17 surveys were conducted during January 1993 and May 1994, though four surveys were discontinued because sea conditions turned bad (Table 1). Ariake Sound and Tachibana Bay were searched on separate days, owing to the limit of the flying time of the airplane. Transect lines in Yatsushiro Sound were flown with lines in Ariake Sound or Tachibana Bay. The north-south lines were searched during flights between the airport in Omura Bay and Ariake Sound or Tachibana Bay. Each set of lines was surveyed 4-10 times at intervals of 1-3 months.

A total of 399 porpoise groups (882 animals) were sighted during the flights totaling 4077.1 km (Table1; Fig. 2b). In Omura Bay, four surveys covered 621.5 km of transect lines and resulted in 55 sightings (88 animals). In Ariake Sound, the observers detected 278 porpoise groups (471 animals) during 10 flights (distance searched = 2072.1 km). In Tachibana Bay, 44 porpoise groups (290 animals) were recorded during four flights of the east-west line (856.2 km) and 22 groups (33 animals) during six flights of the north-south line (170.2 km). In these waters, observers detected porpoises in every season. However, no porpoises were sighted during four surveys in Yatsushiro Sound (208.4 km) and five surveys in Sumo Nada (148.7 km). Moreover, at the mouth of Tachibana Bay, no sightings were recorded (Fig. 2b). These results suggest that, in western Kyushu, finless porpoises are mainly distributed in Omura Bay and Ariake Sound—Tachibana Bay and that the animals seldom move to the neighboring waters, i.e., Yatsushiro Sound and Sumo Nada. This distributional pattern conforms to results from the questionnaire survey. Thus, we considered that Figure 1, derived from the questionnaire survey, reflects the actual distribution of finless porpoises in Japan.

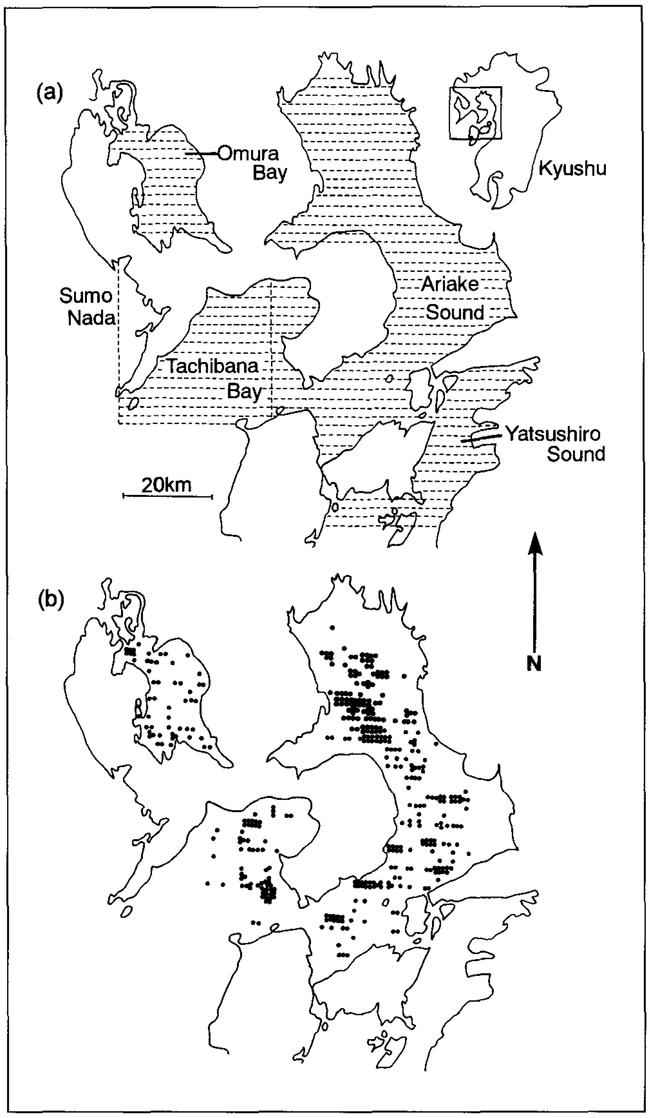

Fig. 2. Transect lines for aerial sighting surveys of finless porpoise distribution in coastal waters of western Kyushu (a) and sighting locations of finless porpoise groups made during aerial sighting surveys in 1993-1994 (b).

MORPHOMETRIC ANALYSIS OF THE SKULL

Geographic differences have been reported in skull morphology among finless porpoises in the Indian Ocean, Chinese waters, and Japanese waters (Amano et al., 1992; Jefferson, 2002) and furthermore within Chinese waters (Wang, 1992a, b; Zhou et al., 1993). If finless porpoises in Japan are subdivided into small populations, the differences may also be detected among the Japanese animals. In this study, geographic differences in skull morphology of Japanese finless porpoises were examined to obtain information on their population structure (Yoshida et al., 1995).

For skulls of 146 animals, most of which were caught incidentally or found on the beach, 25 skull characters were measured with calipers or rulers to the nearest 1 mm by the

Table 1. A summary of aerial sighting surveys for finless porpoises in coastal waters of western Kyushu, Japan. Values in parentheses were collected at Beaufort wind scale of 2 or less.

Area	Date	Weather	Distance Searched (km)	Animals/Groups
Omura Bay	28 Aug 1993	Fair	158.0 (158.0)	18/14 (18/14)
	20 Nov 1993	Cloudy	152.0 (152.0)	20/10 (20/10)
	4 Feb 1994	Cloudy	153.4 (153.4)	10/7 (10/7)
	31 May 1994	Cloudy	158.1 (158.1)	40/24 (40/24)
	Pooled		621.5 (621.5)	88/55 (88/ 55)
Ariake Sound	26 Jan 1993	Fair	102.0 (102.0)	42/ 17 (42/17)
	25 Feb 1993	Fair	275.7 (245.3)	38/ 19 (33/16)
	5 May 1993	Fair	282.2 (249.9)	129/68 (128/67)
	17 Jun 1993 [a]	Fair	116.0 (26.1)	2/2 (0/0)
	20 Jun 1993 [b]	Fair	258.3 (139.6)	9/8 (9/8)
	22 Jul 1993	Fair	260.2 (249.0)	51/37 (51/37)
	31 Aug 1993	Fair	256.1 (256.1)	77/52 (77/52)
	20 Nov 1993 [a]	Cloudy	85.0 (82.3)	12/7 (12/7)
	12 Dec 1993 [a]	Fair	168.6 (146.9)	37/ 21 (35/19)
	25 Jan 1994	Fair	268.0 (261.5)	74/ 47 (74/47)
	Pooled		2072.1 (1758.7)	471/278 (461/270)
Tachibana Bay	28 Aug 1993	Fair	217.2 (217.2)	27/13 (27/13)
	5 Nov 1993	Fair	213.4 (186.7)	24/11 (24/11)
	5 Feb 1994 [c]	Fair	212.3 (212.3)	239/20 (239/20)
	20 May 1994 [b]	Fair	213.3 (122.5)	0/0 (0/0)
	Pooled		856.2 (738.7)	290/ 44 (290/ 44)
Tachibana Bay [d]	25 Feb 1993	Fair	28.6 (26.8)	10/6 (10/6)
	5 May 1993	Fair	28.6 (28.6)	3/3 (3/3)
	20 Jun 1993	Cloudy	28.7 (24.1)	0/0 (0/0)
	22 Jul 1993	Cloudy	27.5 (27.5)	15/9 (15/9)
	31 Aug 1993	Fair	28.5 (28.5)	5/4 (54)
	25 Jan 1994	Fair	28.3 (24.5)	0/0 (0/0)
	Pooled		170.2 (160.0)	33/ 22 (33/22)
Yatsushiro Sound	25 Jan 1994	Fair	22.2 (22.2)	0/0 (0/0)
	5 Feb 1994	Fair	72.8 (72.8)	0/0 (0/0)
	8 May 1994 [a]	Fair	28.3 (16.2)	0/0 (0/0)
	20 May 1994	Fair	85.1 (85.1)	0/0 (0/0)
	Pooled		208.4 (196.3)	0/0 (0/0)
Sumo Nada [d]	28 Aug 1993	Fair	31.2 (31.2)	0/0 (0/0)
	5 Nov 1993	Fair	29.4 (29.4)	0/0 (0/0)
	5 Feb 1994	Fair	30.9 (30.9)	0/0 (0/0)
	8 May 1994	Fair	25.9 (25.9)	0/0 (0/0)
	20 May 1994	Fair	31.3 (31.3)	0/0 (0/0)
	Pooled		148.7 (148.7)	0/0 (0/0)
Total			4077.1 (3623.9)	882/399 (872/391)

a Not all of the scheduled lines were surveyed because of deterioration of sea conditions.

b All the lines were flown, whereas Beaufort wind scale of 3 or more was recorded over about half of the distance searched.

c Two large groups with sizes of 82 and 117 individuals were detected.

d A transect line parallel to the longitudinal line was flown.

author. These skulls are deposited in aquaria, museums, universities, and an elementary school in Japan. All individuals were collected within the five main distributional areas from the questionnaire survey: five animals in Sendai Bay—Tokyo Bay, 11 in Ise—Mikawa Bays, 48 in Inland Sea--Hibiki Nada, eight in Omura Bay, and 74 in Ariake Sound—Tachibana Bay. We, thus, conducted pairwise comparisons of skull morphology among the areas.

Since many specimens were cranially immature, geographic differences were examined using two methods. The first method was the analysis of covariance (ANCOVA) using measurements from all specimens. This method is based on an assumption that the allometric relationship between condylobasal length (from tip of rostrum to hindmost margin of occipital condyles) and the other characters holds irrespective of age. In order to avoid a Type I error due to multiple comparisons, a 1% significant level was selected in the ANCOVA. The second method was the canonical discriminant analysis (CANDISC) which was performed to visually interpret the differences in the skull morphology among the five areas, using data from skulls of animals aged four years or older. This is because Yoshida et al. (1994) indicated that skulls of finless porpoises in Ariake Sound—Tachibana Bay ceased growing by four years old. In both methods, measurements of characters showing sexual dimorphism (Yoshida et al., 1994) were not used for combining data of both sexes. Finally, we analyzed measurements of 15 and six characters for ANCOVA and CANDISC, respectively.

The ANCOVA revealed geographic differences ($p < 0.01$) in six of the 15 characters among the five areas, except for a comparison between Inland Sea—Hibiki Nada and Omura Bay. The relationship between condylobasal length and width of rostrum at midlength is shown in Fig. 3a. The figure indicates that specimens from Ise—Mikawa Bays possess relatively narrower rostrums. The other two characters related to the skull width, i.e., greatest preorbital width and greatest width across zygomatic processes of squamosal, also showed the lowest values in the Ise—Mikawa specimens. Animals in Ise—Mikawa Bays appear to possess a narrower skull than porpoises in the other areas. This result suggests that porpoises in Ise—Mikawa Bays belong to different populations from animals in the other areas.

Scores on the first and second canonical variables derived by CANDISC are plotted in Fig. 3b. The figure indicates that animals in Ariake Sound—Tachibana Bay separated visually from individuals in three other areas, i.e., Ise—Mikawa Bays, Inland Sea—Hibiki Nada, and Omura Bay. Specimens from Ise—Mikawa Bays were also visually distinct from the others. The skull morphology of Omura Bay animals seemed more similar to those of porpoises in the Inland Sea—Hibiki Nada than those from Ariake Sound—Tachibana Bay. These results indicate that skull morphology is different between neighboring waters, except for between Inland Sea—Hibiki Nada and Omura Bay. From the geographic variation found in skull morphology, we considered that finless porpoises are subdivided into at least four populations in Japan: Sendai Bay—Tokyo Bay, Ise—Mikawa Bays, Inland Sea—Hibiki Nada and Omura Bay, and Ariake Sound—Tachibana Bay populations.

ANALYSIS OF MITOCHONDRIAL DNA SEQUENCES

In order to obtain further information on the population structure of finless porpoises in Japan, we examined geographic differences in mitochondrial DNA (mtDNA) control region sequences of the porpoises (Yoshida et al., 2001). Tissue samples were collected from 173 animals. Muscle, liver, or skin was obtained from 160 dead animals

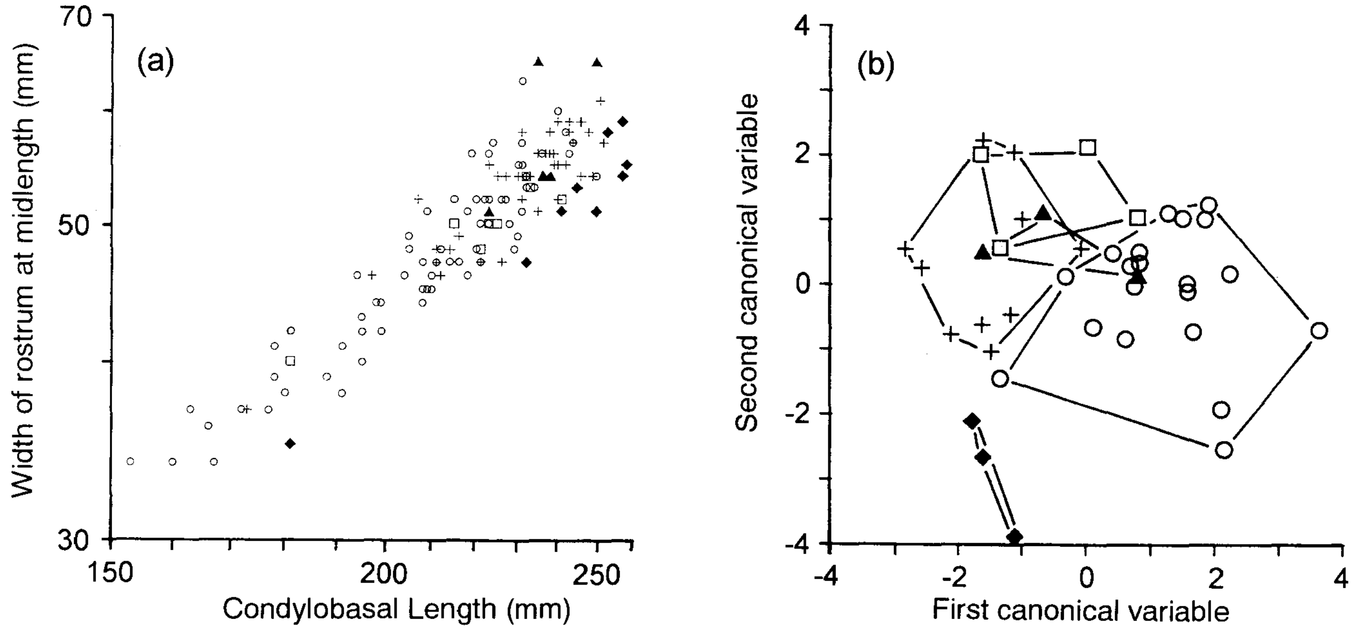

Fig. 3. Relationship between condylobasal length and width of rostrum at midlength (a) and scatter plots of scores on the first and second canonical variables derived from six skull characters of Japanese finless porpoises (b). ▲ Sendai Bay—Tokyo Bay; ◆ Ise-Mikawa Bays; + Inland Sea—Hibiki Nada; □ Omura Bay; ○ Ariake Sound—Tachibana Bay.

Table 2. Frequency distribution of mitochondrial DNA control region haplotypes (a-j) of finless porpoises in five coastal regions where animals are mainly distributed in Japan.

Area	Haplotypes										Total
	a	b	c	d	e	f	g	h	i	j	
Sendai Bay—Tokyo Bay	7 (7, 0)[a]	7 (3, 4)	0	0	0	0	0	0	0	0	14 (10, 4)
Ise—Mikawa Bays	0	4 (4, 0)	52 (28, 21)[b]	0	0	0	0	0	0	0	56 (32, 21)[b]
Inland Sea—Hibiki Nada	0	0	0	27 (10, 17)	3 (1, 2)	0	0	0	0	0	30 (11, 19)
Omura Bay	0	0	0	8 (6, 2)	0	0	0	0	0	0	8 (6, 2)
Ariake Sound—Tachibana Bay	0	0	0	9 (5, 4)	0	46 (28, 18)	6 (3, 3)	2 (0, 2)	1 (1, 0)	1 (0, 1)	65 (37, 28)

a Male, female.
b Sex was unknown for 3 animals.

and two live individuals from skin biopsies. Blood was collected from 11 live animals kept in aquaria. All the individuals were obtained from the five main distributional areas (see Table 2).

Total cellular DNA was extracted from the tissues by standard phenol—chloroform procedure (for details, see Yoshida et al., 2001). The control region was amplified using primers "t-PRO" (5'-CCTCCCTAAGACTCAAGGAA-3') and "Primer-2" (5'-GAAGAGGGATCCCTGCCA AGCGG-3') with the following temperature conditions (0.5 min at 96°C, 0.5 min at 60°C and 1.5 min at 72°C for 30 cycles) and sequenced. Then, we aligned the sequences to detect haplotypes, using the program Clustal W 1.7 (Thompson et al., 1994). Geographic heterogeneity in frequency distribution of haplotypes was examined from the randomized chi-square test (Roff & Bentzen, 1989) using the program ROFF (Matsuishi 1992) followed by the sequential Bonferroni method (Rice, 1989). The population genetic structure was quantified from Wright's *F*-statistics (F_{ST}; Wright, 1951) using the program Arlequin (Schneider et al., 1997). Significance of the observed pairwise F_{ST}-values were determined by comparison with 1,000 random permutation tests. Gene flow (*Nm*) was evaluated from pairwise F_{ST}; i.e., $Nm = (1/F_{ST} - 1)/2$ (Slatkin, 1985).

A total of 345 base pairs of the mtDNA control region were sequenced for all the animals and 10 unique haplotypes were found (types a-j). Number of nucleotide substitutions between them ranged from one to six and all substitutions were transitional changes. No insertions or deletions were detected. Sequences of the 10 haplotypes have been deposited in GenBank under accession numbers AF193543-193552.

The frequency distribution of haplotypes found in each of the five areas is shown in Table 2. The geographic heterogeneity in the distribution was analyzed by pooling both sexes, because of no sexual heterogeneity ($p > 0.05$). Of the 10 haplotypes, two types (b and d) were shared by animals from more than one area, whereas the other eight types were each found only in one area. Such haplotypes were most common in two waters: type c in Ise—Mikawa Bays and type f in Ariake Sound—Tachibana Bay. The frequency distribution of haplotypes differed (χ^2 = 22.00-121.00, $p < 0.05$) among the 5 locations, except for a comparison between Inland Sea—Hibiki Nada and Omura Bay ($\chi^2 = 0.87$, $p = 0.10$).

The estimated F_{ST}-values ranged from -0.013 between Inland Sea—Hibiki Nada and Omura Bay to 0.893 between Ise—Mikawa Bays and Omura Bay (Table 3). Among the five areas, observed values were positive and different ($p < 0.05$) from those calculated with 1,000 randomizations, except for a comparison between Inland Sea—Hibiki Nada and Omura Bay. The estimate of gene flow was infinity between Inland Sea—Hibiki Nada and Omura Bay, while the estimates were extremely low among all other areas (Table 3). The genetic analysis indicates limited dispersal of animals among the four areas, i.e., Sendai Bay—Tokyo Bay, Ise—Mikawa Bays, Inland Sea—Hibiki Nada and Omura Bay, and Ariake Sound—Tachibana Bay. This result suggests that Japanese finless porpoises are subdivided into at least four small populations.

DISCUSSION

The questionnaire survey and aerial sighting surveys indicated that finless porpoises are mainly distributed in five coastal waters in Japan and that occurrence of the porpoises is rare in the other waters. This geographically discrete distribution suggests that Japanese porpoises are subdivided into five small populations, i.e., Sendai Bay—Tokyo Bay,

Table 3. *F*-statistics (above the diagonal) and gene flow (*Nm*; below the diagonal) evaluated among finless porpoises in five coastal areas of Japan.

	Sendai Bay —Tokyo Bay	Ise —Mikawa Bays	Inland Sea —Hibiki Nada	Omura Bay	Ariake Sound —Tachibana Bay
Sendai Bay—Tokyo Bay		0.571*	0.763*	0.672*	0.563*
Ise—Mikawa Bays	0.376		0.869*	0.893*	0.723*
Inland Sea—Hibiki Nada	0.155	0.076		-0.013	0.734*
Omura Bay	0.245	0.060	∞		0.685*
Ariake Sound—Tachibana Bay	0.388	0.191	0.181	0.230	

* Significant difference of observed *F*-statistics ($P < 0.05$) with the sequential Bonferroni correction (Rice 1989).

Ise—Mikawa Bays, Inland Sea—Hibiki Nada, Omura Bay, and Ariake Sound—Tachibana Bay populations. Our morphological and genetic studies support existence of the populations. The studies revealed geographic differences in skull morphology and mtDNA sequences among the five waters, whereas no differentiation was revealed between animals from Inland Sea—Hibiki Nada and Omura Bay. This result was possibly caused by low statistical power from the small sample size of Omura Bay. Indeed, past distributional study indicates that movements of porpoises between Hibiki Nada and Omura Bay are probably rare; there are no reports of porpoise occurrence in coastal areas between the two waters (Shirakihara et al., 1994). For animals in Omura Bay, their estimated abundance is much lower (187 individuals; Yoshida et al., 1998) than estimates in the other waters: 1,952 in Ise—Mikawa Bays (Miyashita et al., 1994), 4,900 in Inland Sea (Kasuya & Kureha, 1979), and 3,093 in Ariake Sound—Tachibana Bay (Yoshida et al., 1997). For conservation purposes, porpoises in Omura Bay should be treated separately from animals in Inland Sea—Hibiki Nada until sufficient information on population structure is accumulated. Thus, we conclude that Japanese finless porpoises are subdivided into five small populations.

Our studies reveal strong philopatry of the finless porpoise. There is little evidence of frequent movements of animals between Omura Bay and Ariake Sound—Tachibana Bay, which are only 60 km apart. Coastal waters between Omura Bay and Ariake Sound—Tachibana Bay possess rocky and steep bottom topography. Habitats of finless porpoises in Japan consist of a dominance of sandy or muddy bottoms and offshore extension of shallow regions with depth of less than 50m, while rocky or steep waters are not occupied by the porpoises (Shirakihara et al., 1992). Possibly these geographical environments restrict animal movement between neighboring ranges. Population structure of finless porpoises should be examined in detail throughout the species' range.

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