Geographic and temporal comparison of skulls of striped dolphins off the Pacific coast of Japan

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ABSTRACT

Skulls of striped dolphins taken by the drive fishery off the Pacific coast of Japan in 1958-79 and 1992, and those taken by research vessels in offshore waters of the northwestern North Pacific in 1992 were examined to study the geographic and temporal differences that are expected to suggest the identity of stocks exploited by the fishery. Coastal specimens collected in 1958-79 showed distinct sexual dimorphism in rostral width, while no dimorphism was found in recent (1992) coastal specimens. Females showed more obvious variation among samples, and recent coastal specimens were distinct from others. The present results provide some support for the view that the drive fishery has exploited dolphins from plural coastal stocks, and that coastal dolphins currently taken by the Taiji fishery and offshore dolphins ranging east of 145°E do not belong to the same stock. The need to obtain larger sample sizes is stressed.

KEYWORDS: STRIPED DOLPHIN; DIRECT CAPTURE; MORPHOMETRICS; STOCK IDENTITY; NORTH PACIFIC

INTRODUCTION

Striped dolphins (*Stenella coeruleoalba*) have a long history of exploitation along the Pacific coast of Japan (e.g. Miyazaki, 1983; Kishiro and Kasuya, 1993). They were taken in large numbers by a drive fishery at the Izu Peninsula (Shizuoka Prefecture) during the 1960s, with over 10,000 animals killed each year (Kasuya, 1999). The catch had declined drastically by the 1980s and it is thought that the fishery may have depleted the population to below 10% of its size in the 1950s (IWC, 1993; Kishiro and Kasuya, 1993). The drive fishery at Taiji, which began in 1973 and which had been taking a few thousand striped dolphins each year, has also shown a recent decline (Kishiro and Kasuya, 1993).

At least three stocks of striped dolphins in the western North Pacific have been proposed from sightings surveys (Kasuya and Miyashita, 1989; Miyashita, 1993; 1997): (1) south of 30°N; (2) from 145°E to at least 180° and north of 30°N; and (3) in Japanese coastal waters between 30° and 42°N. Kasuya and Miyashita (1989) suggested that the latter two stocks are distinct, since a drastic decline in catch would not have occurred if the two had been a single stock. The International Whaling Commission's Scientific Committee agreed that the available data supported the existence of a coastal stock (IWC, 1993).

This paper compares the skull morphology of animals taken from inshore and offshore areas to determine whether there are morphological differences that support the stock differentiation proposed by Kasuya and Miyashita (1989) and Miyashita (1993). In addition, specimens taken by the Japanese drive fishery from 1958-1979 (i.e. from the peak of the catch to its decline) were examined to see whether there is any temporal variation in skull morphology that may indicate historical changes in exploited stocks.

MATERIALS AND METHODS

Samples

Recent (1982) specimens from the drive fishery were collected by researchers from the National Research Institute of Far Seas Fisheries (NRIFSF) (Iwasaki and Kasuya, 1993). Sixteen offshore specimens were obtained from dolphins harpooned during the research cruise of the *Shinhoyo-maru* from July to September 1992 (Fig. 1). Twenty-four coastal specimens were collected under scientific supervision from the dolphins driven at Taiji (Iwasaki and Kasuya, 1993). Skulls were selectively taken from larger dolphins (body length 216-257cm). All of these specimens were prepared and deposited at the National Science Museum, Tokyo (NSMT).

Fifty-six striped dolphin skull specimens stored in the NSMT and the Museum of Comparative Zoology, Harvard University (MCZ) were also examined. Five of these were collected in the offshore area of the northwestern North Pacific between 1982 and 1984. Assuming there was no temporal variation in the proposed offshore group, these animals were added to that group. The other skulls were collected at the Izu Peninsula between 1958 and 1970, and at Taiji between 1969 and 1979, from when the drive fishery was at its peak through to the decline in captures.

For the coastal 1958-79 group, a comparison of measurements between localities (i.e. Izu *vs.* Taiji) and between year groups yielded no significant heterogeneity among them, apart from the fact that sexual dimorphism in rostrum width was more distinct in the 1978-79 Taiji sample. No significant sexual dimorphism was found in the other samples, but it is possible that the small sample sizes affected the analyses. In this study, all the 1958-79 coastal samples have been pooled into a single group.

A total of 74 specimens had teeth and the age of these animals was obtained following the method given in Kasuya (1976). Ito and Miyazaki (1990) stated that skull growth of this species ceases around three years of age, and therefore only specimens older than three years were used in the analyses. Fifteen specimens whose teeth were not available were included as they had obviously reached adult size and exhibited distal fusion of premaxilla and maxilla.

The age composition of each of the three groups (coastal 1958-79; coastal 1992; offshore) was comparable in females but not in males. The coastal 1958-79 males were older than those in the offshore sample (Kruskal-Wallis test, $p < 0.05$).

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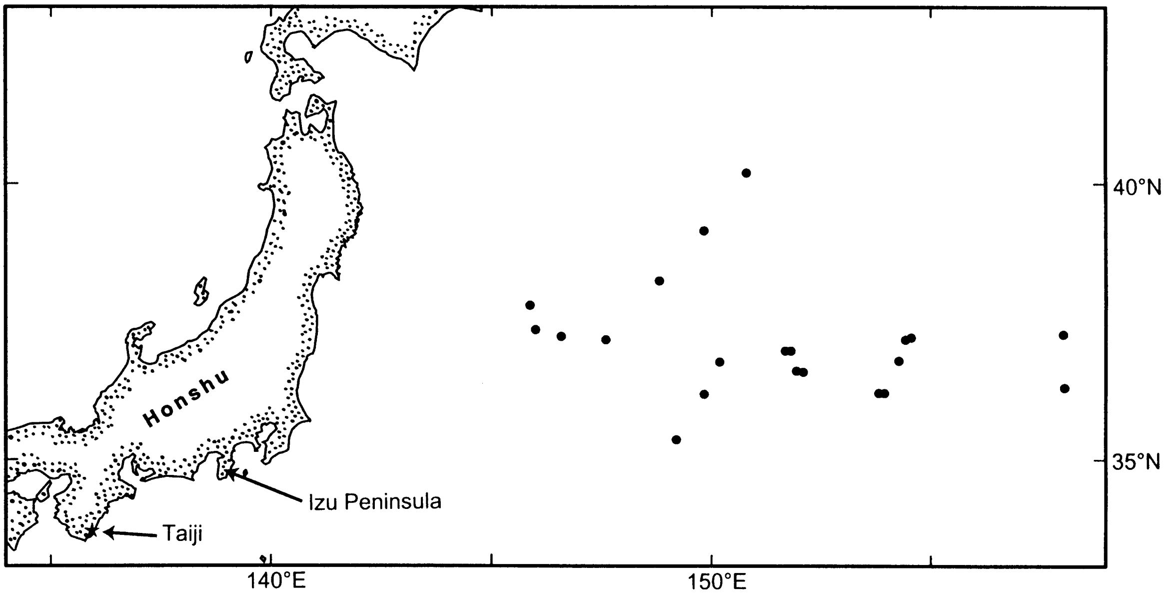

Fig. 1. Sampling localities of striped dolphins.

Twenty-five specimens lacked gender data. This was determined using sexual differences in the supraoccipital crest (Ito and Miyazaki, 1990); the supraoccipital protrudes forward over the frontal and its upper surface is smooth in adult females, whereas in adult males the surface of the vertex is rough and the overhang of the supraoccipital appears fused and indistinct. This approach was tested with 64 known-sex specimens and all specimens were correctly identified to sex.

All specimens examined are listed in Appendix Table 1. The available sample sizes by sex for each group are summarised in Table 1.

Table 1

Sample sizes used in this study. Note: not all skull characters could be measured in each specimen.

Group	Females	Males	Total
Coastal, 1958-79	19	25	44
Coastal, 1992	10	14	24
Offshore	8	13	21

Characters

A total of 39 characters were measured (Table 2). The rostra of most specimens were more or less separated distally, and although the measurements were taken with the rostrum laterally compressed, the distal measurement (WRT) did not seem to be appropriately corrected. Under these circumstances, the width of the gap on the palatal surface at one third of the length of the rostral length was measured, and a corrected WRT obtained by subtraction of this width.

Analyses

Skull measurements of the three groups (coastal 1958-79; coastal 1992; offshore) were compared using the non-parametric Mann-Whitney test and Kruskal-Wallis test with Tukey-type multiple comparison methods (Zar, 1996), in order to reduce the effect of small sample sizes. Analysis of covariance (ANCOVA) with the condylobasal length as a covariate was also carried out with *post hoc* comparisons utilising non-parametric methods. Canonical discriminant analysis after stepwise character selection was carried out for each sex using the STEPDISC and CANDISC procedures (SAS Inst. Inc., 1989).

RESULTS

Sexual dimorphism

Sexual dimorphism was found in a number of characters, although this varied among the three samples (Table 3, Appendix Table 2). Distinct sex-related differences in the distal width of the rostrum were found in the coastal 1958-79 group by both univariate tests and ANCOVAs. No significant correlations between any rostral width measurements and age were found in any individual group or in all groups combined (Kendall's rank correlation, $p > 0.05$; Fig. 2).

Temporal and geographic variation

Significant differences among groups were found in the rostrum of females in both absolute and relative comparisons (Tables 4 and 5). Animals in the 1958-79 coastal group have narrower rostra than those in the 1992 coastal group. The width of the rostrum at half-length differed absolutely and relatively in both sexes, being wider in the coastal 1992 group than the coastal 1958-79 group.

Although the sample size was small, 1992 coastal females were almost completely separate on the first canonical variate axes (Fig. 3). Animals from the 1958-79 coastal and offshore groups could not be distinguished. The overlap was greater for males, although each group showed some degree of dispersion from each other (Fig. 3). No canonical discriminant scores showed significant correlations with age (Kendall's rank correlation, $p > 0.05$).

DISCUSSION

Distinct sexual dimorphism in the width of the rostrum was found in the 1958-79 coastal group, supporting the finding of Ito and Miyazaki (1990). Geographical/temporal comparisons revealing a narrower rostral width in the 1958-79 coastal females suggested that sexual dimorphism

Table 2

Skull measurements of striped dolphins.

1	Condylobasal length - from tip of rostrum to hindmost margin of occipital condyles (CBL)
2	Length of rostrum - from tip to line across hindmost limits of antorbital notches (LR)
3	Width of rostrum at base - along line across hindmost limits of antorbital notches (WRB)
4	Width of rostrum at 60mm anterior to line across hindmost limits of antorbital notches (WR6)
5	Width of rostrum at mid-length (WRH)
6	Width of premaxillaries at mid-length of rostrum (WPH)
7	Width of rostrum at ¾ length, measured from posterior end (WRT)
8	Distance from tip of rostrum to external nares - to mesial end of anterior transverse margin of right nares (TE)
9	Distance from tip of rostrum to internal nares - to mesial end of posterior margin of right pterygoid (TI)
10	Greatest pre-orbital width (PROW)
11	Greatest post-orbital width (POOW)
12	Least supra-orbital width (SOW)
13	Greatest width of external nares (WEN)
14	Greatest width across zygomatic processes of squamosal (ZW)
15	Greatest width of premaxillaries (GWP)
16	Greatest parietal width, within post-temporal fossae (PW)
17	Internal length of braincase from hindmost limit of occipital condyles to foremost limit of cranial cavity along midline (LBC)
18	Greatest length of post-temporal fossa, measured to external margin of raised suture (LPTF)
19	Greatest width of post-temporal fossa at right angles to greatest length (WPTF)
20	Length of left orbit - from apex of preorbital process of frontal to apex of post-orbital process (LOB)
21	Length of antorbital process of left lacrimal (LLA)
22	Greatest width of internal nares (WIN)
23	Greatest length of bulla of left tympanoperiotic (LB)
24	Greatest length of periotic of left tympanoperiotic (LP)
25	Length of upper left tooth row - from hindmost margin of hindmost alveolus to tip of rostrum (LUTR)
26	Number of teeth - upper left (NTUL)
27	Number of teeth - upper right (NTUR)
28	Number of teeth - lower left (NTLL)
29	Number of teeth - lower right (NTLR)
30	Length of lower left tooth row - from hindmost margin of hindmost alveolus to tip of mandible (LLTR)
31	Greatest length of left ramus (LRAM)
32	Greatest height of left ramus at right angles to greatest length (HRAM)
33	Length of left mandibular fossa, measured to mesial rim of internal surface of condyle (LMF)
34	Length of basihyal along midline (LBH)
35	Greatest width of basihyal (WBH)
36	Greatest width of left thyrohyal proximally (WTH)
37	Greatest length of left thyrohyal (LTH)
38	Greatest width of left stylohyal (WSH)
39	Greatest length of left stylohyal (LSH)

Table 3

Significantly different skull measurements (mm, log-transformed; $p<0.05$) between sexes of striped dolphins from the western North Pacific revealed by analysis of covariance with Mann-Whitney test using condylobasal length as a covariate.

	Coastal, 1958-79					Coastal, 1992					Offshore, 1992				
	Female		Male			Female		Male			Female		Male		
Measurements	N	Mean	N	Mean	*p*	N	Mean	N	Mean	*p*	N	Mean	N	Mean	*p*
4 WR6	19	1.870	24	1.887	0.017	-	-	-	-	-	8	1.881	13	1.903	0.023
5 WRH	19	1.780	24	1.797	0.009	-	-	-	-	-	-	-	-	-	-
6 WPH	19	1.468	24	1.508	0.001	-	-	-	-	-	8	1.490	13	1.530	0.008
7 WRT	17	1.647	23	1.672	0.046	-	-	-	-	-	-	-	-	-	-
8 TE	19	2.508	24	2.504	0.046	-	-	-	-	-	-	-	-	-	-
19 WPTF	18	1.632	24	1.659	0.029	-	-	-	-	-	-	-	-	-	-
22 WIN	-	-	-	-	-	-	-	-	-	-	8	1.793	13	1.808	0.046
34 LBH	15	1.647	13	1.683	0.048	10	1.666	12	1.703	0.006	-	-	-	-	-
36 WTH	-	-	-	-	-	10	1.369	13	1.389	0.032	-	-	-	-	-

in the 1958-79 coastal group was a result of a narrower rostrum in females, rather than a wider rostrum in males. Although the 1992 offshore group showed significant differences in two of the rostral width measurements (WRH and WPH), all of the measurements had smaller means for females, and it is possible that additional significant differences would be detected if the sample size was larger. The 1992 coastal group showed no sexual differences in the rostrum (Table 3).

It is possible that ontogenetic variation affected the above difference in females, since the recent specimens were taken selectively from larger dolphins. However, the ages of recent coastal specimens were not significantly greater than earlier animals. In addition, no significant correlations were found between rostral measurements and age. It seems reasonable to conclude that sexual dimorphism in the rostrum was present in the striped dolphins taken off the Pacific coast of Japan between the 1950s and 1970s, but appeared to be absent in those taken in 1992. However, the possibility that the small recent sample size was responsible for this cannot be completely ruled out. Why such a difference may have occurred is an interesting question.

Archer (1996) reported clear sexual dimorphism in the rostrum width of striped dolphins from the eastern Pacific and the western Pacific. He also found statistically significant sexual differences between the eastern Atlantic and Mediterranean striped dolphins. In the eastern tropical Pacific, *Stenella attenuatata* and *S. longirostris* are also sexually dimorphic (Perrin, 1975; Schnell *et al.*, 1985; Douglas *et al.*, 1986; 1992). Females of both species were reported to possess attenuated rostra. This suggests a similar selective pressure in these species, which may be related to partitioning of feeding habits or male-male competition.

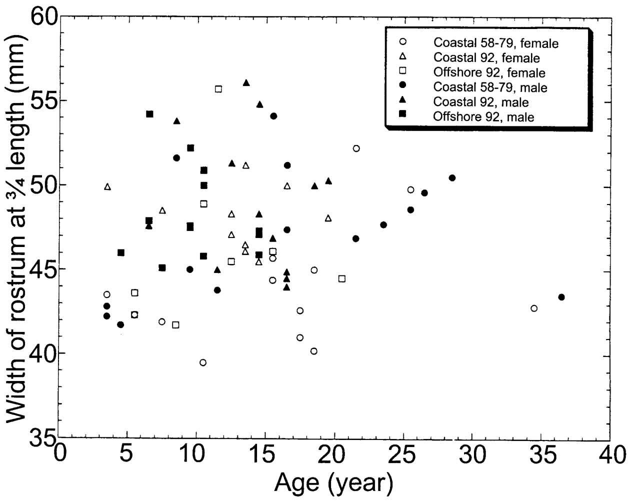

Fig. 2. Relationships between age and width of rostrum at 3/4 length of striped dolphins from the northwestern North Pacific.

Geographic/temporal differences were more obvious in females than males. This is illustrated on the scatterplots of canonical variates, in which most of the 1992 female coastal specimens could be identified from the others on the first axis that had a large WPH and WIN component (Fig. 3, Table 6). By contrast, males showed less variation and considerable overlap. However, even in males the measurements of rostral width were larger in the 1992 coastal group than in the 1958-79 group (Tables 2, 4, 5).

Clear differences were found between the 1958-79 and 1992 coastal groups, particularly for females. At least two potential explanations present themselves: (1) that the populations exploited by the drive fishery off the Pacific coast of Japan differed at the peak of the catch and in recent years; (2) that the same population has been exploited over time, but its morphology has changed with the decline in the population. For striped dolphins from the Izu Peninsula, the age at sexual maturity in females in the catch declined and the calving interval shortened between the 1950s and 1970s; it has been suggested that this was a density-dependent effect caused by improvement in nutritional condition with population depletion (Kasuya, 1985). There were insufficient specimens in the present sample to examine for temporal trends over the 1958-79 period. However, it seems unlikely that the widening of the rostrum in females, which would require strong selective pressure, could occur over such a short period. It is more plausible that the drive fishery has exploited more than one population over the last four decades. This is consistent with the view of Kasuya (1999),

Table 4

Significantly different skull measurements (mm, $p<0.05$) among three groups of striped dolphins from the western North Pacific revealed by Kruskal-Wallis test.

Measurements	Coastal, 1958-79		Coastal, 1992		Offshore, 1992		p	Direction of difference*
	N	Mean	N	Mean	N	Mean		
Females								
4 WR6	19	74.2	10	79.7	8	75.8	0.007	CR>CO
5 WRH	19	60.3	10	66.6	8	62.1	<0.001	CR>CO
6 WPH	19	29.5	10	34.1	8	30.9	<0.001	CR>CO, O
7 WRT	17	44.5	10	48.1	8	46.0	0.016	CR>CO
22 WIN	19	61.5	10	65.3	8	61.9	0.028	CR>CO
27 NTUR	15	46.1	8	45.3	7	48.6	0.018	O>CR
35 WBH	15	49.2	10	52.5	8	47.9	0.026	CR>O
Males								
6 WRH	24	62.8	14	66.9	13	65.3	0.008	CR>CO
21 LLA	25	57.5	14	61.1	13	58.8	0.033	CR>CO

* CO, coastal 1958-79; CR, coastal 1992; O, offshore samples.

Table 5

Significantly different skull measurements (mm, log-transformed; $p<0.05$) among three groups of striped dolphins from the western North Pacific revealed by analysis of covariance with Kruskal-Wallis test using condylobasal length as a covariate.

Measurements	Coasta1, 1958-79		Coastal, 1992		Offshore, 1992		p	Direction of difference*
	N	Mean	N	Mean	N	Mean		
Females								
4 WR6	19	1.872	10	1.899	8	1.877	0.011	CR>CO
5 WRH	19	1.781	10	1.822	8	1.791	<0.001	CR>CO
6 WPH	19	1.468	10	1.531	8	1.488	<0.001	CR>CO, O
7 WRT	17	1.648	10	1.681	8	1.661	0.031	CR>CO
35 WBH	15	1.691	10	1.718	8	1.680	0.020	CR>O
Males								
5 WRH	24	1.800	14	1.822	13	1.813	0.035	CR>CO
8 TE	24	2.510	14	2.512	13	2.517	0.018	O>CO
17 LBC	24	2.063	14	2.064	13	2.053	0.003	CR>O

*CO, coastal 1958-79; CR, coastal 1992; O, offshore samples.

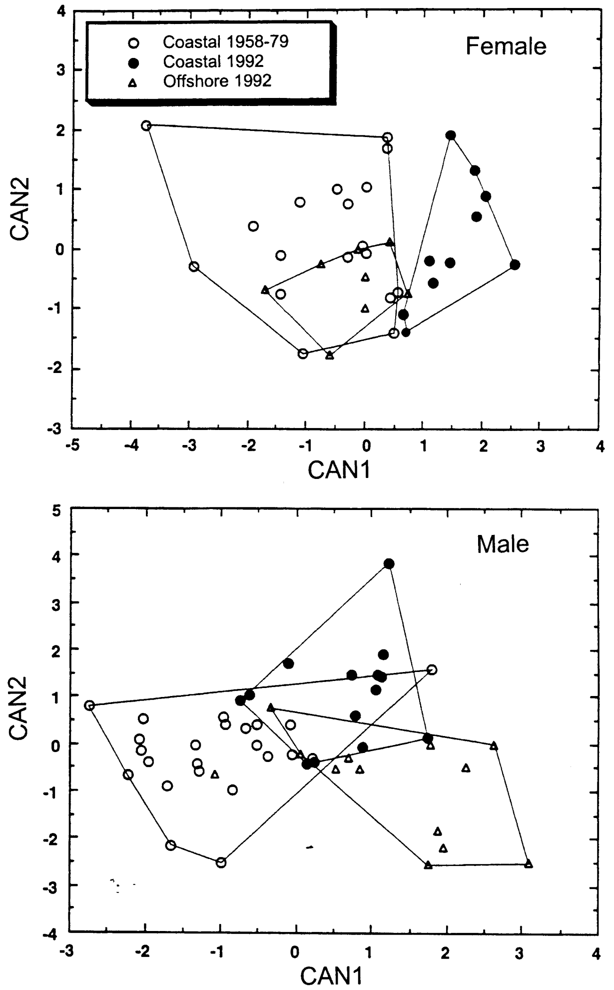

Fig. 3. Scatter plots of the first and second canonical variates for the three samples of striped dolphins off the Pacific coast of Japan.

Table 6

Standardised canonical coefficients for the first and second canonical axes.

Measurements	CAN1	CAN2
Females		
6 WPH	0.917	-0.355
17 LBC	-0.114	0.979
22 WIN	0.817	0.313
32 HRAM	-0.584	-0.663
Males		
2 LR	-2.103	1.535
5 WRH	0.449	0.626
8 TE	2.596	-2.035
14 ZW	0.769	0.065
16 PW	-0.945	0.212
17 LBC	-0.697	0.334
20 LOB	-0.038	0.586
21 LLA	0.550	0.606
22 WIN	-0.115	-0.819

who reviewed the available information and suggested that at least two coastal populations were taken in the drive fishery at Taiji. Loganathan *et al.* (1990) compared the organochlorine residue levels between animals taken in the drive fishery in 1978-79 and 1986 and found that the PCB and DDT levels remained similar while HCHs and HCB declined significantly. Although this may reflect a decline of HCHs and HCB in the environment, HCHs are thought to be removed slowly from the open ocean (Tanabe and Tatsukawa, 1983), and the differences in the levels of HCHs and HCB may indicate inter-population differences and not temporal trends.

The stock identity of the dolphins taken in the present Taiji fishery is of particular importance for management (IWC, 1993). Two genetic studies using the same sample sets as the present study failed to find a significant difference between offshore and Taiji dolphins in the mitochondrial DNA control region (RFLP, Sasaki and Numachi, 1997; sequence analysis, Yoshida and Iwasaki, 1997). This may reflect small sample sizes compared to the number of haplotypes found and, whilst significant differences in genetic data reveal different populations, the absence of detected differences cannot be assumed to imply a single stock. Although the present study implies that the striped dolphins taken recently at Taiji do not belong to the same stock as dolphins sighted in offshore waters east of 145°E, the small sample size precludes firm conclusions being drawn. The present results are not in conflict with the hypothesis that they may be members of the southern stock normally found south of 30°N (Kasuya and Miyashita, 1989; Miyashita, 1993) that is expanding northwards due to the decline of northern coastal stocks as suggested by Kasuya (1999).

Based on sightings data, Miyashita (1997) suggested that the offshore stock may move southwestwards into the Izu fishing ground from autumn to winter. This could not be investigated here as all recent specimens were from Taiji. If Kasuya and Miyashita (1989) are correct in suggesting that the catch in Izu decreased too drastically for the coastal stock to range far offshore, the offshore stock must not have been involved in the coastal drive fisheries. Further studies using genetic as well as morphological comparisons with larger sample sizes are required to answer the question of the stock identity of dolphins taken in the drive fishery.

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Appendix 1

Table 1

Specimens examined.

NSMT - National Science Museum, Tokyo; MCZ - Museum of Comparative Zoology, Harvard University.

Coastal 1958-79	
NSMT	M19774, M19775, M19776, M19777, M19778, M19779, M19780, M19781, M19782, M19785, M19786, M19787, M19789, M19790, M19791, M21389, M21392, M21393, M24620, M24621, M24622, M24640, M24644, M24645, M24650, M24700, M24704, M24705, M24706, M24744, M24833, M24834, M24838, M24839, M24844, M24916, TK326(not registered)
MCZ	52310, 52311, 52312, 52313, 52314, 52315, 52316, 52319
Coastal 1992	
NSMT	M29739, M29740, M29741, M29742, M29743, M29744, M29745, M29746, M29747, M29748, M29749, M29750, M29751, M29752, M29753, M29754, M29755, M29756, M29757, M29758, M29759, M29760, M29761, M29762
Offshore 1992	
NSMT	M25187, M26235, M26236, M26237, M26239, M29721, M29722, M29723, M29724, M29725, M29727, M29729, M29730, M29731, M29732, M29733, M29734, M29735, M29736, M29737, M29738

Table 2

Measurement values for skull morphology of three samples of striped dolphins from the northwestern North Pacific, with sexually dimorphic characters (Mann-Whitney test, $p<0.05$) indicated.

	Female				Male				
Measurements	N	Mean	SD	Range	N	Mean	SD	Range	Difference *p*
Coastal, 1958-79									
1. CBL	19	456.6	16.08	422.7-486.8	24	458.1	17.05	429.6-504.4	
2. LR	19	267.8	11.57	239.9-292.4	24	266.8	12.40	239.3-293.2	
3. WRB	19	113.4	5.97	103.4-124.3	25	114.7	5.70	102.0-124.4	
4. WR6	19	74.2	3.88	67.3-82.9	25	77.3	3.46	72.0-82.9	0.013
5. WRH	19	60.3	3.18	56.0-68.8	24	62.8	2.84	58.2-68.5	0.007
6. WPH	19	29.5	3.24	20.4-34.5	24	32.3	1.67	29.0-35.9	0.001
7. WRT	17	44.5	3.61	39.5-52.2	23	47.1	3.67	41.7-54.1	0.033
8. TE	19	321.3	13.51	289.5-347.2	24	320.2	14.74	289.7-353.2	
9. TI	19	328.3	12.76	300.6-354.0	22	327.1	16.00	291.2-361.9	
10. PROW	19	201.5	9.11	186.0-221.0	25	203.1	8.46	189.5-218.0	
11. POOW	19	221.4	8.84	205.7-237.5	25	224.4	9.63	208.2-249.9	
12. SOW	19	198.5	8.45	183.4-214.6	25	201.0	7.98	189.5-217.0	
13. WEN	19	48.8	2.64	44.8-53.6	25	48.3	2.02	42.7-50.7	
14. ZW	19	217.0	8.09	202.5-232.8	25	219.5	9.72	202.7-243.2	
15. GWP	19	86.4	4.38	78.5-96.4	25	86.4	3.68	79.1-93.3	
16. PW	18	189.1	7.58	171.4-199.0	24	189.3	7.41	176.8-207.9	
17. LBC	19	114.6	4.48	107.8-124.7	25	115.1	3.28	109.2-122.6	
18. LPTF	18	67.1	5.68	57.9-79.5	25	70.5	4.80	63.2-81.7	0.042
19. WPTF	18	43.0	4.15	36.1-54.4	25	45.6	4.65	38.9-56.5	
20. LOB	19	58.6	3.42	52.5-64.4	25	58.8	3.73	53.6-66.6	
21. LLA	19	57.4	4.84	48.5-64.4	25	57.5	3.39	51.1-65.0	
22. WIN	19	61.5	3.03	56.6-66.6	25	63.1	3.17	57.0-70.5	
23. LB	13	32.1	1.14	29.8-33.7	14	32.0	1.63	29.9-36.1	
24. LP	13	29.6	1.17	27.6-31.6	14	30.3	1.34	28.8-33.2	
25. LUTR	18	234.4	11.68	207.4-255.3	24	232.8	10.76	206.9-257.0	
26. NTUL	16	46.6	1.93	43-50	18	49.2	2.65	45-56	$0.005>p>0.002$
27. NTUR	15	46.1	2.10	43-50	18	48.9	2.40	45-54	$0.005>p>0.002$
28. NTLL	17	45.4	1.67	43-49	20	48.0	2.58	43-52	$0.005>p>0.002$
29. NTLR	18	45.8	1.77	42-49	21	48.1	2.59	44-53	0.006
30. LLTR	17	232.5	7.66	216.4-245.0	23	231.8	12.78	210.5-253.0	
31. LRAM	18	393.3	14.02	357.9-419.5	23	391.7	17.17	365.8-426.8	
32. HRAM	18	70.2	2.87	63.4-75.0	23	70.9	3.68	65.0-80.3	
33. LMF	18	129.9	6.37	118-144.4	23	130.2	7.85	115.7-145.1	
34. LBH	15	44.5	4.35	38.0-52.7	13	48.5	4.89	39.4-54.5	$0.05>p>0.02$
35. WBH	15	49.2	4.91	42.0-58.5	13	50.4	6.24	41.8-63.4	
36. WTH	15	23.3	2.37	20.0-28.6	13	23.4	2.64	19.0-28.0	
37. LTH	15	69.3	6.14	55.0-80.4	13	69.2	6.51	61.0-81.0	
38. WSH	13	17.5	1.75	15.8-21.4	13	17.4	1.77	15.0-20.4	
39. LSH	13	88.1	6.66	77.3-100.1	13	86.1	5.31	78.0-96.2	
Coastal, 1992									
1. CBL	10	462.2	17.73	425.0-488.1	14	467.2	9.27	451.0-485.0	
2. LR	10	271.0	11.48	246.8-287.3	14	272.7	8.93	256.9-292.9	
3. WRB	10	117.3	3.88	112.1-123.8	14	115.7	4.57	107.3-122.5	
4. WR6	10	79.7	3.18	74.0-84.4	14	80.1	4.42	73.9-91.2	
5. WRH	10	66.6	2.18	63.6-70.8	14	66.9	4.70	57.7-75.4	
6. WPH	10	34.1	1.62	32.0-37.0	14	34.2	3.10	29.6-40.0	
7. WRT	10	48.1	1.86	45.5-52.1	13	49.0	4.08	44.0-56.1	
8. TE	10	325.9	14.73	292.7-343.7	14	329.0	11.51	306.8-354.1	
9. TI	10	328.4	16.57	293.3-351.6	14	330.0	8.53	311.0-343.9	
10. PROW	10	208.3	5.83	196.9-214.7	14	207.7	5.45	197.1-218.9	
11. POOW	10	228.1	6.58	214.9-235.1	14	227.6	5.87	219.3-244.4	
12. SOW	10	205.1	6.59	191.9-211.9	14	204.0	5.84	195.8-220.1	
13. WEN	10	50.3	2.03	47.0-53.2	14	50.1	2.57	46.4-54.0	
14. ZW	10	223.4	6.84	210.1-230.5	14	225.8	6.84	216.8-241.4	
15. GWP	10	87.4	3.97	82.5-94.1	14	89.1	2.92	84.3-96.0	
16. PW	10	192.6	6.21	184.0-202.3	14	189.3	7.62	176.2-207.0	
17. LBC	10	114.7	4.08	110.5-121.7	14	116.7	3.66	110.0-121.4	
18. LPTF	10	69.2	4.43	61.2-75.8	14	69.3	5.04	61.8-80.9	
19. WPTF	10	45.0	3.73	39.5-51.4	14	44.3	3.74	37.9-50.4	
20. LOB	10	59.5	2.71	56.0-63.2	14	60.2	2.77	55.9-66.0	
21. LLA	10	60.0	6.05	51.1-70.1	14	61.1	4.26	54.2-69.1	
22. WIN	10	65.3	3.57	60.4-71.4	14	63.3	2.53	59.0-68.8	
23. LB	10	32.1	1.53	30.2-35.0	13	31.9	1.35	29.5-35.2	

continued

Table 2 cont.

Measurements	Female				Male				Difference p
	N	Mean	SD	Range	N	Mean	SD	Range	
24. LP	10	29.7	1.04	28.5-32.0	14	30.0	1.24	28.3-32.4	
25. LUTR	10	233.7	10.41	212.7-245.2	14	238.1	7.72	225.0-251.1	
26. NTUL	8	45.8	2.38	42-50	14	48.7	2.73	44-54	$0.05>p>0.02$
27. NTUR	8	45.3	2.49	43-50	14	48.0	2.80	43-53	
28. NTLL	10	44.9	2.81	42-49	14	46.9	2.73	41-52	
29. NTLR	10	44.6	2.95	41-50	14	47.0	2.75	42-51	
30. LLTR	10	234.0	14.22	207.7-256.1	14	235.4	8.67	215.8-249.9	
31. LRAM	10	398.0	16.37	363.2-419.3	14	399.9	9.07	382.2-415.1	
32. HRAM	10	69.8	3.26	64.5-74.2	14	72.1	2.62	67.0-76.1	
33. LMF	10	132.2	5.45	121.5-138.9	14	132.8	8.94	120.0-149.6	
34. LBH	10	46.5	3.14	41.3-50.3	12	50.5	2.90	43.0-53.8	$0.005>p>0.002$
35. WBH	10	52.5	3.32	49.0-60.0	12	51.0	4.52	42.7-57.8	
36. WTH	10	23.3	1.76	20.6-26.7	13	24.6	1.31	22.0-27.6	$0.05>p>0.02$
37. LTH	10	71.3	4.85	63.2-77.9	13	72.3	4.41	65.8-81.2	
38. WSH	10	17.9	1.24	16.1-20.0	14	17.3	1.30	15.6-19.8	
39. LSH	10	89.2	4.86	82.2-94.9	14	91.0	6.17	81.1-101.0	
Offshore, 1992									
1. CBL	8	461.1	11.8	446.8-481.4	13	465.2	15.85	442.0-510.9	
2. LR	8	272.3	11.64	257.9-293.3	13	273.5	10.27	261.4-302.0	
3. WRB	8		5.87	105.8-122.0	13	116.0	6.45	108.1-127.7	
4. WR6	8	75.8	5.67	71.1-88.2	13	80.5	4.71	75.7-89.0	$0.05>p>0.02$
5. WRH	8	62.1	4.76	55.8-71.0	13	65.3	3.11	60.5-70.8	
6. WPH	8	30.9	1.88	27.2-33.7	13	34.1	2.38	30.2-37.5	$0.005>p>0.002$
7. WRT	8	46.0	4.52	41.7-55.7	13	48.3	2.75	45.1-54.2	
8. TE	8	327.7	10.85	314.6-345.6	13	331.2	12.25	317.7-366.0	
9. TI	8	332.1	10.41	318.6-353.1	13	332.2	12.54	314.9-368.0	
10. PROW	7	203.4	7.33	193.0-213.8	13	206.6	6.88	197.0-221.2	
11. POOW	8	222.4	5.08	214.4-231.2	13	227.2	9.41	209.6-244.1	
12. SOW	8	199.0	6.66	188.8-208.7	13	203.6	8.36	190.0-220.8	
13. WEN	8	48.7	1.11	46.5-50.0	13	49.4	2.86	45.0-53.8	
14. ZW	8	218.6	5.35	212.0-226.9	13	224.1	8.43	209.0-237.7	
15. GWP	8	84.8	4.92	77.7-90.7	13	88.8	4.34	81.3-96.1	
16. PW	8	186.5	7.48	174.4-196.3	13	186.4	5.33	175.9-192.1	
17. LBC	8	112.5	3.33	106.0-117.3	13	113.4	3.98	104.9-119.7	
18. LPTF	8	69.5	3.12	66.3-74.0	13	71.6	3.45	65.7-76.5	
19. WPTF	8	44.6	2.74	40.0-48.6	13	45.0	3.86	37.6-51.5	
20. LOB	8	56.7	2.14	53.3-60.5	13	58.2	2.89	52.2-62.1	
21. LLA	8	57.3	1.87	54.6-61.0	13	58.8	2.61	54.9-62.1	
22. WIN	8	61.9	2.55	57.9-65.0	13	64.5	2.07	61.6-68.3	
23. LB	8	32.0	1.01	30.5-33.7	13	32.8	1.48	29.4-35.9	
24. LP	8	29.9	1.42	28.7-32.9	13	30.4	1.55	27.2-32.7	
25. LUTR	8	238.4	8.87	228.7-255.9	13	238.3	9.44	228.0-266.2	
26. NTUL	7	48.1	2.12	46-52	13	47.7	2.50	43-52	
27. NTUR	7	48.6	1.27	47-51	13	48.0	2.48	43-53	
28. NTLL	7	48.0	2.31	45-51	13	46.8	2.41	43-51	
29. NTLR	7	47.7	2.43	45-52	13	46.8	2.19	43-51	
30. LLTR	8	231.8	7.23	223.1-243.0	13	234.5	8.08	222.9-255.0	
31. LRAM	8	393.4	7.90	380.0-406.0	13	396.5	13.18	378.2-431.0	
32. HRAM	8	70.7	3.10	66.7-74.2	13	71.2	2.81	65.5-76.0	
33. LMF	8	131.0	3.57	127.9-138.9	13	129.9	8.08	120.1-144.0	
34. LBH	8	45.1	3.41	40.6-51.3	10	46.8	4.37	39.6-52.7	
35. WBH	8	47.9	2.04	45.6-51.3	10	46.8	4.29	40.6-53.1	
36. WTH	8	23.1	2.02	21.1-26.8	11	23.1	2.67	19.5-28.4	
37. LTH	8	69.6	4.03	63.2-75.9	11	67.2	5.8	58.6-75.4	
38. WSH	7	18.2	2.38	14.8-21.5	11	16.4	2.38	12.7-21.6	
39. LSH	7	89.1	5.79	82.4-97.8	11	87.5	7.78	73.0-100.2	