

21. Geographical variation and biology of the Pacific white-sided dolphin, *Lagenorhynchus obliquidens*, in the north-eastern Pacific

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INTRODUCTION

The Pacific white-sided dolphin, *Lagenorhynchus obliquidens*, is a North Pacific endemic reported from Taiwan to the Kurile and Commander Islands on the west (Okada and Hanaoka 1939; Sleptsov 1961; Nishiwaki 1967; Tomilin 1967; Mitchell 1975), from 20°–21°N to 61°N on the east, and more-or-less continuously across temperate waters between 40° and 46°N (Leatherwood and Walker 1982, Leatherwood, Reeves, Bowles, Stewart, and Goodrich 1984). The species was described by Gill (1865) based on three co-types (U.S. National Museum Nos. 1961, 1962, 1963) reportedly taken 'off the California coast.' Though the exact locality is unclear, Poole and Shantz (1942) list the type specimen (three skulls with mandibles, in good condition) as having been taken by W. P. Trowbridge from near San Francisco, San Mateo County and catalogued 14 October 1885. They attribute these details to True (1889). A careful reading of the latter indicates that the specimens were indeed obtained 'on the coast of California by Lieutenant W. P. Trowbridge' but that for the types and for another specimen (USNM 14329) discussed in the same paragraph '... no particular localities are given in either instance.'

The species *Lagenorhynchus ognevi* Sleptsov (1955) was also described from the North Pacific, but it is now thought to be invalid. Tomilin (1967) demonstrated that the diagnostic characters based on cranial and postcranial morphology and meristics as well as external morphology and colouration are largely age-related features and well within the limits of variation found in *L. obliquidens*.

In the north-eastern Pacific, white-sided dolphins are widely distributed, at least seasonally, between about 23°N and the northern Gulf of Alaska and northern North Pacific. Within that range, seasonal fluctuations in apparent abundance, thought to be related to shifts in population centre(s), are reported for northern California, the Southern California Bight, and the west

coast of Baja California (Leatherwood and Walker 1982; Leatherwood *et al.* 1984).

In 1979 we began a study on geographical variation and biology of *L. obliquidens* in the eastern North Pacific. The primary objectives were to investigate the possible existence of subpopulations in the study area and to increase our knowledge of the general biology of the species.

METHODS

External measurements, ranging from total length only to a complete set of measurements, were available for 243 specimens.

Of all standard measurements taken for odontocetes, total length is that most likely to be taken consistently. Even so, length measurements were screened carefully before being used in any further analysis. We consider that all other measurements are less likely to be consistently reliable. They were taken over a long period (1905–1982) by a variety of workers using various and often unreported techniques. Therefore, we did not attempt to use such measurements in any analyses to differentiate populations.

Cranial measurements were selected and taken following Perrin (1975) (Table 1). As in previous studies of this kind, juvenile specimens were excluded from consideration because of ontogenetic growth changes and their effect on the analysis of population differences. Because rostral distal fusion, a feature used to indicate the onset of sexual maturity in *Stenella* spp. (Dailey and Perrin 1973) and *Tursiops* sp. (Walker 1981), does not occur in even physically mature specimens of *Lagenorhynchus obliquidens*, we determined state of maturity using other criteria:

- (1) reproductive condition, judged by direct analysis of organs or availability of other data indicating sexual maturity, such as notes on lactation or presence of a foetus;
- (2) evidence of fusion in thoracic vertebral epiphyses;
- (3) presence of seven or more growth layer groups in teeth; or
- (4) in the absence of other data, evidence from the overall development of cranial sutures that the animal was at least sexually mature.

One hundred and fifty-two crania (73 females, 60 males, and 19 animals of undetermined sex) from the north-eastern Pacific, between about 24°30'N and 61°N, were measured. One hundred and twelve of these (74%) were from the area of southern California between 32° and 37°N, 31 (20%) were from north of 37°N, and nine (6%) were from below 32°N. The gaps between the localities of the sample from southern California and those from the extreme northern and extreme southern portions of the eastern Pacific range were useful in grouping skulls for analysis.

In multivariate analyses, specimens with missing measurements are eliminated from the sample. To counter this problem and to maintain the highest

possible sample size, we eliminated those measurements which are commonly missing due to damage during collection and preparation of specimens (see Table 21.1).

Teeth were collected from near the middle of the left lower jaw of 142 animals (86 females, 56 males) for which total length and collection location were known. The teeth were prepared at NMFS/SWFC following procedures detailed by Myrick, Hohn, Sloan, Kimura, and Stanley (1983). Decalcification times ranged from 11.5 to 20.0 h, increasing with tooth and pulp cavity size. Staining times ranged from 30 to 60 minutes.

Dentinal growth layer groups (GLGs; terminology of Perrin and Myrick 1981) of *L. obliquidens* are composed of four alternating lightly and darkly stained bands. The first band or boundary layer (beginning with the neonatal line) is thin and either unstained or lightly stained. Within the GLG and advancing toward the pulp cavity this band is adjacent to first a broad darkly stained band, then a thin unstained mid-GLG band, and finally a broad dark band. Cemental GLGs are composed of two bands, one darkly and one lightly stained.

Each tooth section was independently read twice by each of two readers (Goodrich and Myrick). Following a cursory examination of the condition of the section, dentinal readings were made. Counts of dentinal layers were supplemented by counts of cemental layers, recognizing that the latter often occur in multiples of the former. Whenever the pulp cavity was occluded or dentinal layers were poorly stained, cemental layers were considered the most reliable indicators of GLGs.

'Best' and 'final' counts, considering size of the pulp cavity and condition of GLG layers (see protocol, Myrick *et al.* 1983), were averaged. If any 'best and final' readings were outside a pre-established interval from that mean (± 1 for 0–10 GLGs, ± 2 for 11–15 GLGs, ± 3 for 16–25 GLGs, ± 4 for 26–36 GLGs, and ± 5 for ≥ 37 GLGs) the tooth was reread. Results of all readings ('best' initial and reread values) were used to calculate mean GLGs for each specimen. The data are summarized in Walker, Goodrich, Leatherwood, and Stroud (1984).

Previously unpublished reproductive data from 88 specimens (50 females and 38 males) are presented (Tables 21.2 and 21.3). Laboratory procedures for preparation and examination of reproductive tissue samples followed Perrin, Coe, and Zweifel (1976).

As in previous studies, sexual maturity in the present sample was judged from presence of at least one corpus luteum or corpus albicans or presence of sperm in a testis section, supplemented by other data available, such as testis weight, lactation, or evidence of pregnancy.

Information on colour pattern in *L. obliquidens* was derived from examination of numerous photographs and the authors' (Walker and Leatherwood) personal observations of free-ranging and captive animals.

Stomach contents of 23 animals were available for analysis. All were from

TABLE 21.1. Skull measurements (in mm) and meristics of *Lagenorhynchus obliquidens* from the north-eastern Pacific

Variable	Sample	Range (mm)	Mean	Stand. Dev.
* 1 Condylbasal length	144	350-446	388.0	16.2
* 2 Rostrum length	144	171-228	195.6	10.3
* 3 Rostrum width at base	146	91-123	105.6	6.6
* 4 Rostrum width at 60 mm	145	66-95	78.6	6.2
* 5 Rostrum width at midlength	142	60-86	70.9	5.5
* 6 Premaxillary width at rostrum midlength	144	36-56	43.8	3.9
* 7 Rostrum width at $\frac{1}{2}$ length	142	43-70	54.6	5.2
* 8 Rostrum tip to external nares	144	208-273	237.9	11.3
* 9 Rostrum tip to internal nares	123	206-277	243.8	12.9
*10 Preorbital width	139	164-198	178.0	7.6
*11 Postorbital width	141	181-214	194.5	7.2
*13 External nares width	146	44-90	56.9	4.8
*14 Zygomatic width	144	178-218	195.1	8.3
*15 Greatest width of premaxillaries	147	80-103	89.9	3.6
*16 Parietal width	144	148-184	168.8	6.2
*19 Temporal fossa length	147	65-93	79.7	5.8
*20 Temporal fossa width	148	50-78	60.8	4.9
*25 Orbit length	141	47-65	53.9	3.0
*26 Antorbital process length	142	25-47	36.1	3.6
*27 Internal nares width	144	48-75	61.7	4.7
28 Pterygoid length	142	53-74	62.8	4.6
30 Bulla length	89	29-38	35.2	1.6
31 Periotic length	81	28-37	30.5	1.4
32 Upper tooth row length	142	154-213	179.1	9.9
33-36 Teeth (no.)	140/138 145/144	24-36/25-35 23-34/25-35	30.3/30.5 30.1/30.1	2.1/2.2 2.0/2.0
37 Lower tooth row length	140	165-214	180.6	9.0
38 Ramus length	137	231-366	320.2	15.6
39 Ramus height	139	60-81	68.6	3.9
40 Tooth width	127	3.2-6.5	4.6	0.5

*Indicates measurements in principal components analyses.

Note: Data from both populations are pooled. These calculations are presented solely to characterize cranial features of *Lagenorhynchus obliquidens* and to facilitate comparisons with other species of *Lagenorhynchus*.

TABLE 21.2. Summary of female reproductive data for *Lagenorhynchus obliquidens* from the north-eastern Pacific

Specimen No.	Location		Collection Date YMD	Mean GLG No.	Weight (kg)	Total Length (cm)	Gonad Weights		No. of Corpora		Source of Data or Reproductive Specimens	Reproductive Comments
	Lat (N)	Long (W)					Left	Right	Left	Right		
NMML 3223	37°42'	123°08'	66-03-25	7.8	65	159	3.3	2.7	0	0	NMML	Follicle diameter: 35-40 microns
L-02-19	34°07'	119°06'	67-07-13	—	—	162	5.5	5.5	—	—	NUC	Immature, follicle diameter: 0.5 mm
NMML 3208	35°04'	121°33'	66-03-09	4.0	66	162	1.2	1.2	0	0	NMML	Immature, follicle diameter: 0.9 mm
NMML 3277	46°14'	124°40'	68-02-26	6.8	67	165	1.3	1.1	0	0	NMML	Follicle diameter: left 1.7 mm; right 2.9 mm
NMML 3273	46°14'	124°40'	68-02-26	—	71	167	2.2	3.1	0	0	NMML	Follicle diameter: left 6.7 mm; right 3.1 mm
NMML 3790	36°25'	122°31'	65-06-19	7.2	73	168	6.3	3.8	0	0	NMML	No follicles over 100 microns
18-68	33°30'	118°25'	68-02-28	—	—	168	1.0	0.9	0	0	Harrison <i>et al.</i> (1972)	Follicle diameter: left 5.1 mm; right 1.9 mm
NMML 3765	37°46'	123°26'	66-02-25	9.8	73	168	4.8	2.3	0	0	NMML	Few small follicles 350 microns
06-63	33°45'	118°25'	63-05-04	—	68	169	—	—	0	0	Harrison <i>et al.</i> (1972)	Barely visible follicles on left ovary
TAC-59-3	35°42'	121°41'	59-02-27	—	85	170	—	—	0	0	Fisucs and Niggol (1965)	Follicle diameter: left 2.4 mm; right 2.6 mm
NMML 3212	36°29'	122°30'	66-03-05	6.8	69	171	3.0	2.6	0	0	NMML	Follicles well developed, no corpora present
HSU 2418	41°03'	124°09'	58-09-11	8.7	62	171	—	—	0	0	Houck (1961)	Follicle diameter: left 1.6 mm; right 2.0 mm
NMML 3221	37°37'	123°07'	66-03-25	24.5	83	172	4.0	2.0	17	6	NMML	Follicle diameter: left 1.6 mm; right 4.3 mm
NMML 3761	37°46'	123°26'	66-02-25	5.4	75	172	0.7	1.4	0	0	NMML	Lab report indicates no corpora present
L-02-12	33°50'	119°10'	64-06-02	—	80	173	—	—	0	0	NUC	Few follicles up to 500 microns in diameter
38-63	33°45'	118°25'	63-10-20	—	81	173	—	7.5	—	4	Harrison <i>et al.</i> (1972)	Follicle diameter: left 1.7 mm; right 1.1 mm
NMML 3209	36°29'	122°30'	66-03-05	7.0	78	173	3.8	3.2	0	0	NMML	

TABLE 21.2. *contd.*

Specimen No.	Location		Collection Date YMD	Mean GLG No.	Weight (kg)	Total Length (cm)	Gonad Weights		No. of Corpora		Source of Data or Reproductive Specimens	Reproductive Comments
	Lat (N)	Long (W)					Left	Right	Left	Right		
NMML 3222	37°40'	123°08'	66-03-25	8.5	72	173	3.1	2.3	0	0	NMML	Follicle diameter: left 2.7 mm; right 2.5 mm
NMML 3762	37°46'	123°26'	66-02-25	5.6	75	173	1.8	1.6	0	0	NMML	Follicle diameter: left 1.4 mm; right 1.7 mm
NMML 3218	35°08'	121°25'	66-03-10	5.5	83	174	5.5	2.4	1	0	NMML	Follicle diameter: left 4.0 mm; right 1.8 mm
SJSU C-195	36°48'	121°47'	77-05-04	—	—	174	—	—	—	—	SJSU	Pregnant, 84 cm fetus
NMML 3768	37°46'	123°26'	66-02-25	6.8	77	174	5.0	4.3	0	0	NMML	Follicle diameter: left 3.7 mm; right 1.9 mm
NMML 3269	46°14'	124°34'	68-02-25	—	75	174	2.6	1.8	0	0	NMML	Follicle diameter: left 4.1 mm; right 2.9 mm
TAC 21143	46°14'	124°40'	68-02-25	6.5	75	174	1.3	1.1	0	0	NMML	Follicle diameter: left 0.5 mm; right 0.4 mm
7-63	33°45'	118°25'	63-05-05	—	69	174	2.6	2.6	0	0	Harrison <i>et al.</i> (1972)	No follicles over 120 microns in either ovary
SBMNH 2347	35°06'	121°40'	81-05-03	25.0	—	175	7.2	7.1	—	—	SBMNH	Animal not pregnant or lactating
NMML 3271	46°14'	124°34'	68-02-25	—	84	175	6.1	2.1	6	0	NMML	Follicle diameter: left 2.6 mm; right 1.8 mm
NMML US-61-P1	51°45'	128°00'	61-01-26	—	89	175	2.2	—	0	—	NMML	Left ovary only: follicle diameter: 0.7 mm
32-66	33°53'	118°26'	66-08-15	5.6	66	175	2.0	2.5	0	0	Harrison <i>et al.</i> (1972)	No follicles over 120 microns in either ovary
NMML 3767	37°46'	123°26'	66-02-25	8.1	78	176	2.7	3.7	0	0	NMML	Follicle diameter: left 1.6 mm; right 1.7 mm
WAW 174	33°36'	118°09'	71-09-21	—	—	176	10.6	2.0	9	0	Swayer and Walker (1977)	—
NMML 3207	37°20'	123°38'	66-03-03	8.2	83	177	3.1	4.4	0	0	NMML	Follicle diameter: left 1.8 mm; right 3.2 mm
NMML 3270	46°14'	124°34'	68-02-25	20.0	86	177	7.8	4.1	15	0	NMML	Lactating; follicle diameter: left 1.3 mm; right 1.8 mm
NMML 3760	37°46'	123°26'	66-02-25	5.9	76	178	2.2	2.7	0	0	NMML	Follicle diameter: left 1.7 mm; right 3.0 mm

NMML 3764	37°46'	123°26'	66-02-25	5.0	78	178	5.5	4.2	0	0	NMML	Follicle diameter: left 2.7 mm; right 1.9 mm
NMML 3275	46°14'	124°33'	68-02-26	9.4	82	178	4.4	2.3	1	0	NMML	Follicle diameter: left 4.8 mm; right 2.0 mm
69-7-4	33°30'	118°25'	69-02-01	—	—	178	7.3	4.2	5	0	Harrison <i>et al.</i> (1972)	Follicle diameter: right ovary 2.0 mm
NMML 3210	36°29'	122°30'	66-03-05	8.0	89	179	3.0	6.3	0	4	NMML	Follicle diameter: left 2.3 mm; right 3.8 mm
VBS 1263	48°30'	124°20'	36-09-17	—	—	180	—	—	—	—	Scheffer and Slipp (1948)	Pregnant, 12.9 mm fetus [probably 12.9 cm]
NMML 1965-175 26-67	32°37'	118°56'	65-07-12	8.7	97	180	—	—	—	—	NMML	Animal pregnant, 45 cm fetus; not lactating
NMML 3217	33°46'	118°10'	67-08-21	14.2	55	180	6.5	3.0	9	0	Harrison <i>et al.</i> (1972)	No follicles over 120 microns
MVZ 140845	35°08'	121°25'	66-03-10	9.0	81	181	5.5	3.2	2	0	NMML	Follicle diameter: left 2.9 mm; right 2.5 mm
MLP 70-19-1	38°05'	122°55'	70-02-09	37.2	—	181	—	—	—	—	MVZ	Field records report numerous corpora albicantia on both ovaries
TAC 59-4	33°45'	118°25'	70-09-22	—	—	182	—	—	—	—	MLP	Captive animal; gave birth to 95 cm, 25 lb male calf; calf lived † hr
USNM 276395 69-6-2	36°58'	122°53'	59-03-05	—	88	182	—	—	—	—	Fiscus and Niggol (1959)	"numerous follicles"; animal considered nulliparous
TAC 59-1	37°45'	122°50'	48-12-12	—	—	183	—	—	—	—	Scheffer (1950)	Pregnant, 37 cm fetus
2-63	33°35'	118°25'	69-06-01	—	84	183	10.1	5.1	5	0	Harrison <i>et al.</i> (1972)	Animal aborted a near term fetus on 69-03-01
USNM 276395 16-62	35°16'	121°35'	59-02-14	—	84	183	—	—	—	—	Fiscus and Niggol (1965)	Numerous follicles; apparently nulliparous
13-62	33°30'	118°35'	62-10-00	—	74	183	—	4.1	—	0	Harrison <i>et al.</i> (1972)	No follicles over 120 microns in right ovary
LACM 54712	37°45'	123°10'	48-12-12	8.6	95	183	—	—	—	—	USNM	Pregnant animal. Ranged from 3-15 mm
NMML 1968-103	33°30'	118°25'	62-10-00	—	77	185	4.2	4.1	0	0	Harrison <i>et al.</i> (1972)	No follicles over 120 microns
	33°57'	118°25'	62-08-24	—	65	185	8.3	13.3	0	4	Harrison <i>et al.</i> (1972)	Numerous cystic follicles from 1-2 cm diameter
	33°45'	118°20'	70-10-26	21.5	86	185	—	—	11	—	LACM	Necropsy records reported 11 CA's on left ovary
	33°48'	119°43'	68-02-08	19.5	88	186	—	—	—	—	NMML	Necropsy records report "many CA's" on left ovary

TABLE 21.2. *contd.*

Specimen No.	Location		Collection Date		Mean GLG No.	Weight (kg)	Total Length (cm)	Gonad Weights		No. of Corpora		Source of Data or Reproductive Specimens	Reproductive Comments
	Lat (N)	Long (W)	YMD	YMD				Left	Right	Left	Right		
NMML 985	34°07'	120°46'	64-01-08		14.2	91	186	6.8	1.9	4	0	NMML	Not lactating; mammary thickness 10 mm
SJSU 2158	36°37'	121°54'	78-04-04		—	85	186	7.4	5.6	23	12	SJSU	Follicle diameter: left 2.2 mm; right 4.3 mm
15-62	33°30'	118°25'	62-10-00		—	76	186	4.4	6.1	—	—	Harrison <i>et al.</i> (1972)	No follicles over 120 microns in either ovary
"DEBBIE"	33°30'	118°25'	69-07-05		—	—	186	3.2	2.6	—	—	Harrison <i>et al.</i> (1972)	No follicles over 120 microns in either ovary
83-66	34°25'	118°30'	66-11-30		—	66	187	14.0	5.0	18	0	Harrison <i>et al.</i> (1972)	Aborted fetus two weeks prior to death
NMML 3219	36°02'	121°58'	66-03-22		9.8	93	188	5.5	2.5	3	0	NMML	Follicle diameter: left 3.1 mm; right 2.5 mm
HSU 2689	41°35'	124°06'	78-06-08		—	80	188	5.6	—	23	—	HSU	Lactating; left ovary follicle diameter: 3.1 mm
L-13-64	34°20'	119°25'	65-05-17		—	76	190	9.0	4.0	—	—	NUC	Pregnant, 72 cm male fetus; follicle diameter: left 2.4 mm; right 1.6 mm
NMML 3216	35°08'	121°25'	66-03-10		7.2	101	191	16.8	3.0	1	0	NMML	Pregnant, records indicate "full term fetus"
RB 2118	37°24'	122°27'	73-04-14		—	—	193	—	—	—	—	Ray Bandar priv. coll.	
USNM 504416	25°22'	112°52'	76-02-11		6.9	—	197	5.3	4.7	0	0	USNM	Immature
LACM 54711	33°20'	118°25'	70-10-20		11.8	—	197	—	—	0	9	LACM	Captive animal; aborted 29 cm fetus
WAW 150	34°00'	118°48'	72-03-04		—	—	199	8.8	4.2	7	0	Sawyer and Walker (1977)	
INIBP-Gr6501	27°10'	114°31'	65-09-18		—	—	200	—	—	0	0	NMML	"Immature, very tiny follicles"
LACM 54076	32°48'	117°17'	70-05-07		29.2	—	201	—	—	—	—	LACM	Pregnant, 81.0 cm male fetus
WFP 591	32°52'	117°15'	79-04-16		26.4	—	208	—	—	—	—	SWFC	Lab reports about 10 CA's; lactating; uterine condition postpartum

USNM 504412	25°22'	112°52'	76-02-11	18.8	142	212	28.6	4.2	4	2	USNM	Pregnant, 52 cm fetus; follicle diameter: 2.0 ; not lactating
MWD 183	26°20'	113°43'	79-08-25	19.5	145	212	15.5	5.8	14	1	SWFC	Follicle diameter: left 2.6 mm; right 3.8 mm
MM-126	33°30'	118°25'	76-07-00	—	—	213	6.9	2.7	5	1	Harrison and McBrearty (1977)	Lived 6 years in captivity
USNM 504415	25°22'	112°52'	76-02-11	26.6	140	215	12.0	3.2	10	0	USNM	Lactating; follicle diameter: left 1.4 mm; right 1.6 mm
MM-137	33°30'	118°25'	76-08-00	—	—	216	5.5	4.3	12	2	Harrison and McBrearty (1977)	Had two stillborn calves in captivity: one 101.6 cm, the other 109.2 cm
56-68	33°30'	118°25'	68-04-12	31.2	—	236	12.5	4.5	23	0	Harrison <i>et al.</i> (1972)	Few follicles 2.0 mm diameter

Source of specimens of data: NMMML = National Marine Laboratory, Seattle, Washington; NUC = Naval Undersea Center, San Diego, California; SJSU = San Jose State University, San Jose, California; SBMNH = Santa Barbara Museum of Natural History, Santa Barbara, California; MVZ = Museum of Vertebrate Zoology, Berkeley, California; MLP = Marineland of the Pacific, Rancho Palos Verdes, California; USNM = U.S. National Museum, Smithsonian Institution, Washington, D.C.; LACM = Natural History Museum of Los Angeles County, Los Angeles, California; SWFC = Southwest Fisheries Center, La Jolla, California; CPSU = California Polytechnic State University, San Luis Obispo, California; SDNHM = San Diego Natural History Museum, San Diego, California; HSU = Humboldt State University, Arcata, California.

TABLE 21.3. Summary of male reproductive data for *Lagenorhynchus obliquidens* from the north-eastern Pacific

Specimen Number	Location of Collection		Date of Collection	Length (cm)	Weight (kg)	Mean Number GLG's		Testis Weights (gr)		Testis Length (cm)		Tubule diameter (m)	Sperm Present Tubules	Epididymis Specimens	Source of Data or
	Lat (N)	Long (W)				Left	Right	Left	Right	Left	Right				
CPSU —	35°06'	120°38'	67-03-22	148	—	—	23.5	24.0	15.0	15.0	—	—	—	CPSU	
NMML 3215	36°29'	122°30'	66-03-05	151	58	5.0	15.0	12.0	—	9.0	40	No	No	NMML	
NMML 3272	46°13'	124°36'	68-02-26	152	59	—	5.1	5.2	—	7.5	40	No	No	NMML	
L-01-6	34°10'	119°15'	64-01-27	152	46	—	25-35	25-35	8-10	8-10	—	—	—	Ridgway and Green (1967)	
L-12-55	34°20'	119°16'	67-02-24	155	—	—	—	7.5	—	7.0	—	—	No	NUC	
19-67	33°52'	118°25'	67-05-10	164	64	—	14.7	18.0	8.0	8.0	90	—	No	Harrison	
NMML 3276	46°13'	124°36'	68-02-26	165	75	7.0	13.7	13.7	—	8.6	40	No	No	<i>et al.</i> (1972)	
29-64	33°53'	118°27'	64-10-16	170	56	—	—	—	—	—	110	—	No	NMML	
14-24	34°02'	118°50'	64-04-21	170	74	—	305.0	340.0	21.0	22.0	160	—	No	Harrison	
NMML 3766	37°46'	124°30'	66-02-25	172	79	3.6	15.0	16.0	—	9.5	50	No	No	<i>et al.</i> (1972)	
NMML 3214	36°29'	122°30'	66-03-05	174	82	14.2	130.0	140.0	—	19.0	—	—	—	NMML	
NMML 3211	36°29'	122°30'	66-03-05	177	84	15.2	130.0	150.0	—	21.0	—	—	—	NMML	
17-63	33°52'	118°23'	63-12-17	178	63	—	25.0	25.0	7.3	8.5	70	—	No	NMML	
82-66	33°25'	119°43'	66-12-21	178	55	—	14.0	22.5	8.5	8.0	70	—	No	Harrison	
NMML 3274	46°14'	124°33'	68-02-26	179	97	—	121.0	133.3	219.0	235.0	80	Yes	—	<i>et al.</i> (1972)	
17-62	38°17'	122°28'	62-12-17	180	61	—	21.0	22.1	50.0	90.0	70	—	No	NMML	
NMML 3206	36°23'	122°14'	66-02-17	180	78	4.8	18.0	25.0	—	120.0	70	No	No	Harrison	
SBMNH 11692	34°25'	119°43'	81-05-18	181	—	25.0	345.0	—	—	—	—	—	—	<i>et al.</i> (1972)	
TAC 59-2	35°28'	121°38'	59-02-22	181	90	—	—	—	—	—	—	—	—	NMML	
28-64	33°45'	118°25'	64-09-19	183	78	—	107.0	100.0	—	40.0	135	—	—	SBMNH	
L-2	33°30'	118°22'	64-11-27	183	76	—	17.8	17.2	8.6	8.8	70	—	No	NMML	
													—	Harrison	
													—	<i>et al.</i> (1972)	

NMML 3213 27-65	36°29' 34°02'	122°30' 118°29'	66-03-05 66-07-17	184 184	99	16.2	155.0 15.0	170.0 15.5	215.0 9.5	22.0 9.5	— 75	— —	— —	NMML Harrison <i>et al.</i> (1972)
NMML 3224	37°45'	123°13'	66-03-25	186	91	10.5	175.0	165.0	225.0	230.0	110	Yes	—	NMML SWFC NUC
WFP 082	32°52'	117°15'	71-05-16	187	77	14.0	455.0	454.0	—	—	—	—	—	
68-L-17	34°10'	119°45'	64-10-27	188	72	—	35.0	35.0	—	—	—	—	—	
SDNHM 21219	32°51'	117°16'	56-01-08	194	99	25.4	150.0	150.0	30.0	30.0	75	—	—	SDNHM LACM
JEH 1051	33°44'	118°05'	81-05-16	195	79	8.4	17.0	20.0	8.2	9.0	75	No	—	Harrison <i>et al.</i> (1972)
RMG 4605	25°30'	113°35'	69-04-23	198	—	—	52.0	59.0	14.0	14.0	—	—	—	
SDNHM 21223	33°30'	118°20'	57-01-24	191	125	24.6	250.0	—	30.0	—	—	—	—	SDNHM Harrison <i>et al.</i> (1972)
RMG 4-68	33°30'	118°20'	57-01-24	191	—	—	250.0	—	30.0	30.0	—	—	—	LACM
LACM 54714 04-68	33°35' 33°30'	118°12' 118°25'	70-12-09 68-02-16	193 194	90	11.2	162.0	154.0	32.0	30.0	—	—	—	Harrison <i>et al.</i> (1972)
SDNHM 981	34°22'	119°42'	75-06-16	199	133	24.5	900.0	900.0	37.0	37.5	—	—	—	SDNHM
CPSU M-1218	35°06'	120°38'	72-08-20	200	—	—	—	—	45.0	45.0	—	—	—	CPSU
R&G	34°04'	119°30'	65-08-15	200	102	—	548.0	559.0	24.0	24.5	200	—	—	Harrison <i>et al.</i> (1972)
10-67	33°25'	119°43'	66-11-00	201	73	10.9	104.0	106.0	19.0	17.0	100	—	—	Harrison <i>et al.</i> (1972)
104-L-20	34°30'	119°40'	67-08-02	213	100	—	540.0	510.0	35.0	35.0	—	—	—	NUC
MWD 182	26°20'	113°43'	79-08-25	219	157	18.4	—	580.0	—	—	180	Yes	—	SWFC
JEH 1042	33°40'	118°01'	81-02-16	220	124	37.4	634.0	—	30.0	—	164	Yes	—	LACM
USNM 504413	25°22'	112°52'	76-02-11	228	198	17.2	316.5	326.5	31.0	31.0	205	Yes	—	USNM

Source of specimens or data: NMML = National Marine Laboratory, Seattle, Washington; NUC = Naval Undersea Center, San Diego, California; SJSU = San Jose State University, San Jose, California; SBMNH = Santa Barbara Museum of Natural History, Santa Barbara, California; MVZ = Museum of Vertebrate Zoology, Berkeley, California; MLP = Marineland of the Pacific, Rancho Palos Verdes, California; USNM = U.S. National Museum, Smithsonian Institution, Washington, D.C.; LACM = Natural History Museum of Los Angeles County, Los Angeles, California; SWFC = Southwest Fisheries Center, La Jolla, California; CPSU = California Polytechnic State University, San Luis Obispo, California; SDNHM = San Diego Natural History Museum, San Diego, California; HSU = Humboldt State University, Arcata, California.

the Southern California Bight and off the west coast of Baja California, Mexico. Of the sample, 14 animals (61%) were collected as individual strandings. The remaining nine animals were collected at sea. Two stomachs were initially preserved in formalin, which dissolves otoliths. In these instances, fish remains were identified from intact skeletal elements. The other 21 specimens were either frozen or preserved in alcohol prior to examination.

Data on the occurrence of two air sinus parasites were recorded during the course of this study. The incidence of the genus *Nasitrema* spp. (Trematoda) was based solely on published accounts, examination of unreported museum samples, and the recent dissection of four intact animals collected off the west coast of Baja California, Mexico.

Documentation of the occurrence of the nematode *Crassicauda* sp(p). was based on dissection of 39 intact animals and examination of 197 prepared cranial specimens for evidence of *Crassicauda*-related bone lesions.

During the course of the study detailed records on post-cranial bone disease were also kept. A total of 63 skeletons was examined.

RESULTS AND CONCLUSIONS

External morphometrics

Dorsal fins in *Lagenorhynchus obliquidens* vary considerably in size, and range in shape from falcate and sharply pointed to lobate and more rounded on the tip (Kasuya 1981) (Fig. 21.1). We have observed fins of both shapes in the same herds and on both males and females in captivity. As none of the standard measurements taken on odontocetes (Norris 1961) are adequate to detect such differences in fin shape, we have no data to test the relationship of dorsal fin shape to sex, length, age, or state of maturity of specimens. We hypothesize that these differences are age related and that fins begin to become lobate with the onset of physical maturity.

The largest specimens known to us are a 250 cm male (specimen MVZ 116037, collected 23 July 1950 by Seth Benson at 28°00'N, 114°45'W) and a 236 cm female (specimen 56-68, collected by W. A. Walker 12 April 1968 at 33°33'N, 118°25'W—see Harrison, Boice, and Brownell 1969).

Cranial morphometrics

The scores of individual specimens for the first two principal component axes were plotted by latitude (Figs. 21.2 and 21.3). Geographic plots of PCA scores have been used in previous studies of animal populations (Kennedy and Schnell 1978; Menozzi, Piazza, and Cavalli-Sforza 1978; Schnell, Douglas, and Hough 1982; Douglas, Schnell, and Hough 1984). In evaluating the results of PCA, the first principal component is generally considered to



FIG. 21.1. Pacific white-sided dolphins, showing normal colouration and variability in dorsal fin size and shape (from Kasuya 1981).

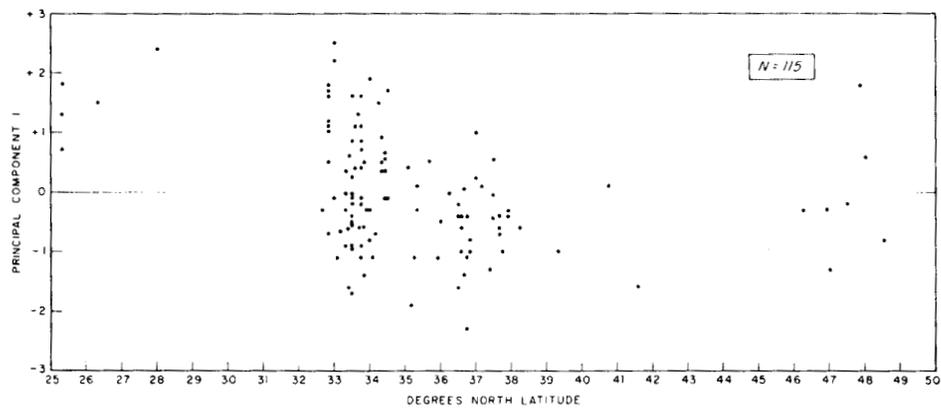


FIG. 21.2. Scores of individual cranial specimens for first principal component, by latitude.

represent specimen size, and the second to represent specimen shape (Cooley and Lohnes 1962; Seal 1964).

Though the sample in the present investigation was small, there appears to be marked separation between animals from the extreme northern (above 37°N) and southern (below 32°N) ranges of the sample with respect to size (see Fig. 21.2). The crania of southern animals tend to be larger than those of

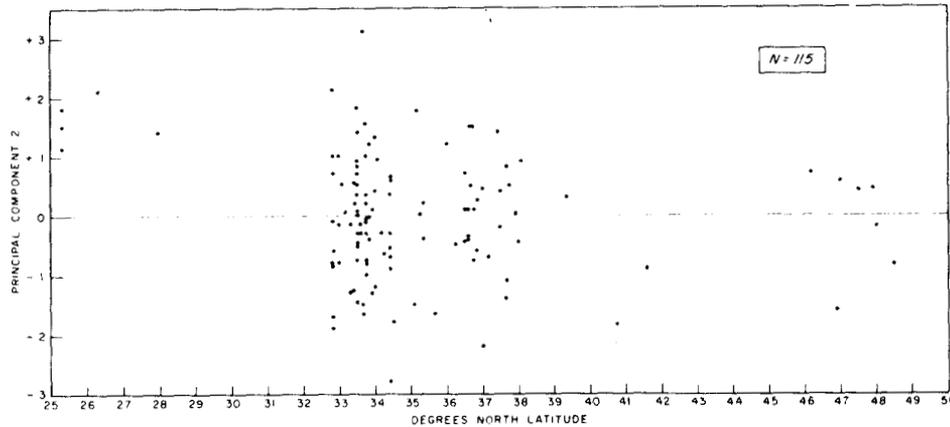


FIG. 21.3. Scores of individual cranial specimens for second principal component, by latitude.

northern animals (Fig. 21.4). We tentatively interpret these results as evidence of the existence of two populations in the north-eastern Pacific, one in the northern temperate and one in the southern temperate region. The distribution of scores for the second principal component (see Fig. 21.3) supports this interpretation, indicating that differences occur between these two putative populations in skull shape as well as skull size. It is worth noting that in both analyses there is significant variability in scores below about 37°N, with the most dramatic spread in values between 34°30'N and 32°30'N. We interpret this to possibly mean that there are specimens from both populations represented in the Southern California Bight sample. That interpretation is supported by the age-length data discussed below. The dramatic change in character of the sample latitudinally (see Figs. 21.2 and 21.3) corresponds to changes in oceanographic condition near Point Conception (approx. 34°30'N), changes which result in marked faunal differences north and south of the Point (Hubbs 1960).

The relationship between total length of the skull (CBL), and length of the temporal fossa also indicates the possible existence of two populations; the temporal fossae tend to be proportionally shorter in the southern than in the northern temperate population (Fig. 21.5).

Age relationships

No experimentally calibrated teeth were available. We have assumed that one GLG = one year. With that assumption, the animals we examined ranged in age from 0.4 to 46.0 years, with significant variability in length at any given age. Animals examined from above 37°N and below 32°N ranged from 1.5 to 37 years. A comparison of total length and skull length of the northern vs southern animals of comparable age (Figs. 21.4 and 21.6) confirm that the southern form is larger in overall size than the northern form.

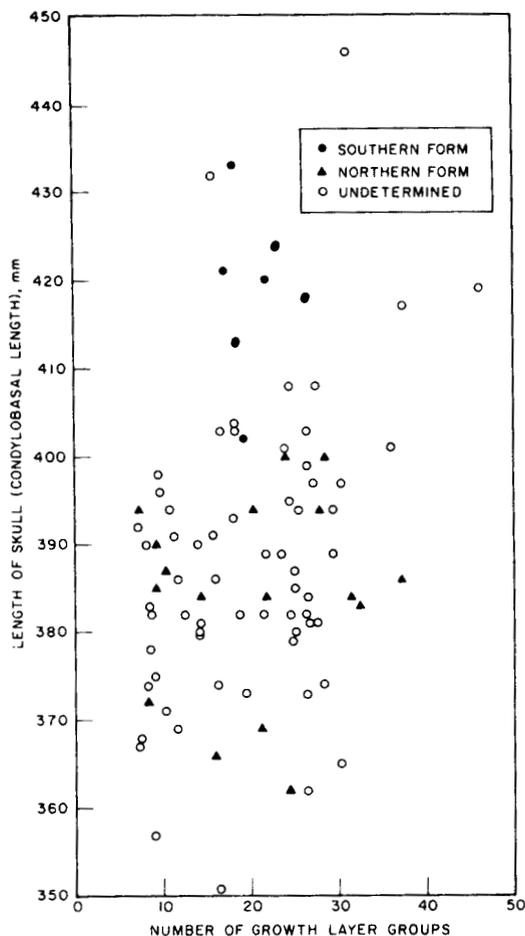


FIG. 21.4. Relationship between total length of skull (condylobasal length) and age. Southern form = specimens from south of 32°N; northern form = specimens from north of 37°N; undetermined = specimens from between 32°N and 37°N.

Reproduction

Published accounts of reproduction in *L. obliquidens* in the north-eastern Pacific are few. Since the extensive study of Harrison, Brownell, and Boice (1972), reproductive data on only four animals have appeared in the literature (Harrison and McBrearty 1977; Sawyer and Walker 1977). Perrin and Reilly (1984) recently reviewed reproductive parameters from the literature.

Based on 33 specimens (18 females and 15 males) from the Southern California Bight and a single male from Punta Abreojos, Baja California, Mexico, Harrison *et al.* (1972) noted, but were unable to explain, a considerable variability in the length at sexual maturity of either sex, or a

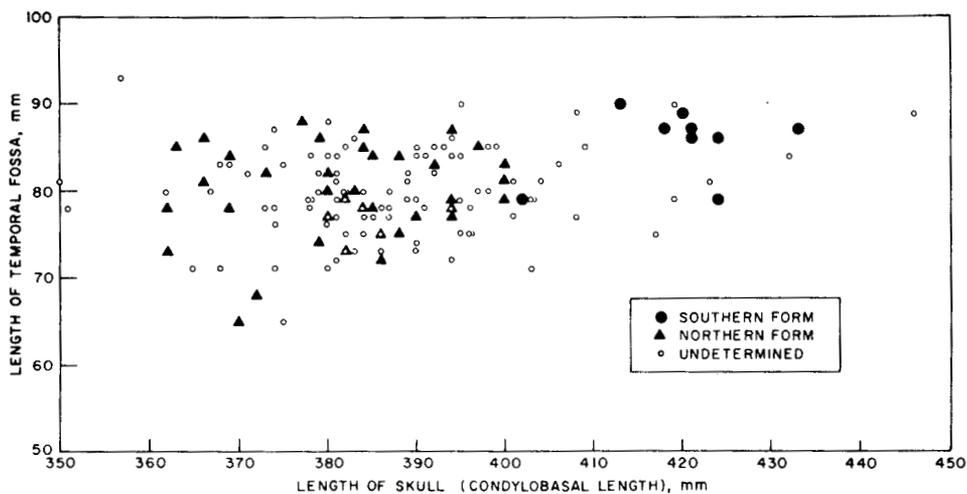


FIG. 21.5. Relationship between length of the skull (condylobasal length) and length of the temporal fossa. Southern form = specimens from south of 32°N; northern form = specimens from north of 37°N; undetermined = specimens from between 32°N and 37°N.

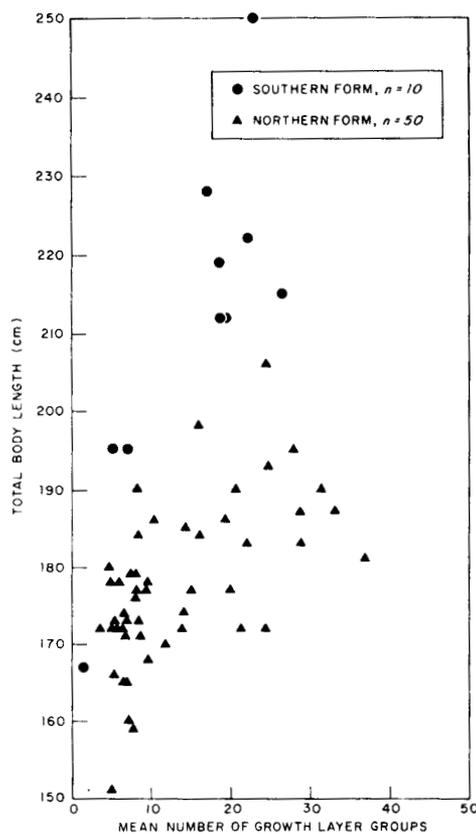


FIG. 21.6. Relationship between total body length and age. Southern form = specimens from south of 32°N; northern form = specimens from north of 37°N.

variability in body length and number of corpora of females. Data from the present sample contain comparable variability. For example, a 197 cm female estimated to be 6.9 years old had no corpora, while a 172 cm female estimated to be 24.5 years old had 23 corpora (Table 21.2), and a 179 cm male of undetermined age was sexually mature while a 213 cm male of undetermined age was sexually immature (Table 21.3). We hypothesize that such disparities relate, at least in part, to an overlap in distribution of the two populations between 32° and 37°N. Unfortunately, reproductive information available from below 32°N is insufficient to permit us to test this hypothesis.

Harrison *et al.* (1972) estimated length at birth to be about 95 cm. The largest foetus known to us was a 109 cm captive stillborn (Harrison and McBrearty 1977). Only one foetal specimen (52 cm) has been collected from the southern population. Due to the large differences in the overall size noted for the southern and northern temperate forms, using existing foetal length and length-at-birth data could lead to considerable error in estimation of foetal growth rate and gestation period.

Colouration

Pacific white-sided dolphins are strikingly marked, with a black dorsal surface, light gray sides, and a white ventrum (see Fig. 21.1). The black cape is interrupted on each side of the dorsal fin by a light stripe, originating in the light colour of the forehead and face, curving over the top of the melon, continuing along the side to below the dorsal fin, then turning downward and widening to form a prominent light gray patch on the flank. The beak is dark and a narrow stripe extending forward from the flipper is continuous with the black of the lips. The sides of the body in front of the dorsal fin and the forehead are gray. A thin dark band separates the gray and black zones of the side from the white ventrum. The dorsal fin is dark on the anterior third and light on the posterior two-thirds. The flippers are often similarly bi-coloured. The flukes are all dark.

Our impressions from numerous observations of free-ranging and captive individuals are that foetuses (Fig. 21.7) and newborn calves contain essential elements of adult colour patterns but in muted expression. The various components appear to intensify with age, and there is wide variability in component intensity even within a herd. We examined photographs of 13 known-length individuals (seven males and six females) but were unable to define any consistent patterns of variation.

Anomalous colour patterns have been observed. Brownell (1965) illustrated an animal with a black thoracic patch surrounded by exceptionally extensive and bright regions of white. A specimen so coloured was collected from 37°46'N, 124°30'W, 25 February 1966 (Fig. 21.7). Others have been seen in herds off Washington in April 1971 and off Southern California in February 1974 and 1976 (Leatherwood, unpublished observations). Brown and Norris (1956) noted three instances of what they interpreted as albinism

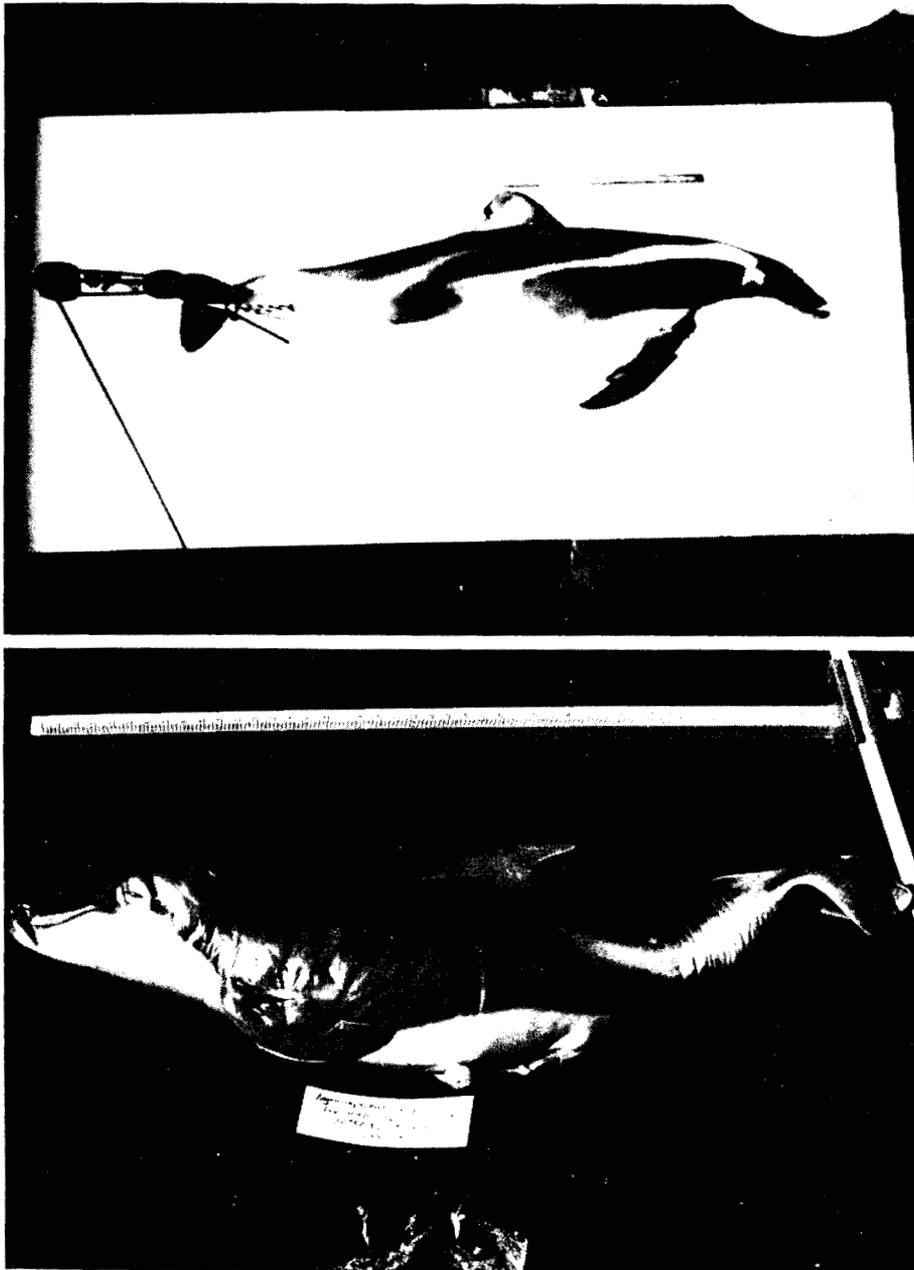


FIG. 21.7. (Top) A normally coloured foetus (Specimen MMD-1965-175, a male collected by D. W. Rice, 12 December 1965 at 32°37'N, 118°56'W). (Bottom) An anomalously coloured male (Specimen NMML 3766).

in the species, two off southern California and one off western Baja California, Mexico. Hain and Leatherwood (1982) added a report of a nearly all white individual off San Pedro Point, Santa Cruz Island in September 1968.

Food habits

Kajimura, Fiscus and Stroud (1980) and Stroud, Fiscus and Kajimura (1981) summarized food items in stomachs of Pacific white-sided dolphins from Japan, the north-western Pacific and western Bering Sea, and the west coast of North America for 1919 to 1969, and reported contents of stomachs of 44 new specimens they collected off California and Washington between 1958 and 1972. Jones (1981) summarized published accounts of stomach contents of 16 specimens from California, collected between 1958 and 1973, and added details of seven specimens he collected from beaches off northern California between 1968 and 1973. In the eastern North Pacific above Point Conception (about 34°30'N) these dolphins feed primarily on small schooling fishes and cephalopods from the epipelagic and mesopelagic zones.

Stomach contents have been reported from seven specimens collected south of Point Conception (Scheffer 1953; Brown and Norris 1956; Fitch and Brownell 1968; Kajimura *et al.* 1980; Stroud *et al.* 1981). Stomach contents from 23 additional animals collected in southern California and off Baja California, Mexico are summarized in Table 21.4. In terms of frequency of occurrence, the northern anchovy, *Engraulis mordax*, hake, *Merluccius productus*, and squid, *Loligo opalescens*, appear to be the most important prey species.

There is little information available on daily feeding cycles. Based on their observations that large stomach volumes were most often observed in animals collected before 10.00 hours, Kajimura *et al.* (1980) and Stroud *et al.* (1981) concluded that most feeding occurs at night or in the morning. Data from Jones (1981) and the present investigation are based primarily on samples from stranded specimens and shed little light on this question. Other observations, however, suggest feeding may occur at other times as well. For example, Leatherwood and Reeves (1983) reported that white-sided dolphins have been 'often seen feeding near dawn and dusk on small surfacing balls of unidentified bait.' Brown and Norris (1956), without indicating time of day, reported having many times seen these dolphins, scattered in small groups, milling around anchovy schools. Presence of numerous anchovy scales in the water on many of these occasions was taken as evidence the dolphins were feeding on anchovies. Data from a 184 cm female *L. obliquidens* radio-tagged 15 December 1972 and tracked sporadically from aircraft during daylight hours between 19 December 1972 and 26 January 1973 indicate dives during early and mid-morning (0730-1015) (Leatherwood and Evans 1979; Leatherwood, unpublished data). In the Southern California Bight, white-sided

TABLE 21.4. Summary of stomach contents from 23 specimens of *Lagenorhynchus obliquidens* from Southern California and the west coast of Baja California, Mexico

Food Item	Volume		Number		Occurrence	
	ml.	% of Total	No.	% of Total	No.	% (N = 23)
TOTAL	23800	100	5469	100	—	—
FISH	23490	98.70	5184	94.90	20	86.90
Clupeidae						
<i>Sardinops sagax</i>	243	1.00	9	0.20	3	13.00
Engraulidae						
<i>Engraulis mordax</i>	17936	75.40	4212	77.00	18	78.30
Bathylagidae						
<i>Leuroglossus stilbius</i>	tr.	—	1	0.02	1	4.30
Myctophidae						
<i>Diaphus theta</i>	tr.	—	1	0.02	1	4.30
<i>Triphoturus mexicanus</i>	tr.	—	9	0.02	2	8.70
Batrachoididae						
<i>Porichthys notatus</i>	tr.	—	21	0.40	3	13.00
<i>Porichthys myriaster</i>	tr.	—	16	0.30	2	8.70
Ophidiidae						
<i>Chilara taylora</i>	tr.	—	3	0.05	2	8.70
Merlucciidae						
<i>Merluccius productus</i>	507	2.10	778	14.00	14	60.90
Scorpaenidae						
<i>Sebastes sp.</i>	tr.	1	40	0.70	3	13.00
Anoplopomatidae						
<i>Anoplopoma fimbria</i>	tr.	—	2	0.04	1	4.30
Carangidae						
<i>Trachurus symmetricus</i>	1063	4.50	55	1.00	8	34.80
Sciaenidae						
<i>Genyonemus lineatus</i>	tr.	—	8	0.10	1	4.30
<i>Seriphus politus</i>	tr.	—	2	0.04	1	4.30
Scombridae						
<i>Pneumatophorus japonicus</i>	3741	15.70	20	0.40	1	4.30
Stromateidae						
<i>Peprilus simillus</i>	tr.	—	5	0.10	2	8.70
Cynoglossidae						
<i>Symphurus atricauda</i>	tr.	—	1	0.02	1	4.30
Pleuronectidae						
<i>Hypsosetta guttata</i>	tr.	—	1	0.02	1	4.30
CEPHALOPODS	310	1.30	285	5.10	14	60.90
Loliginidae						
<i>Loligo opalescens</i>	310	1.30	220	4.00	13	56.50
Gonatidae						
<i>Gonatus spp.</i>	tr.	—	28	0.50	1	4.30
Octopoteuthidae						
<i>Octopoteuthis sp.</i>	tr.	—	8	0.10	3	13.00
Onychoteuthidae						
<i>Onychoteuthis sp.</i>	tr.	—	23	0.40	3	13.00
Octopodidae						
<i>Octopus sp.</i>	tr.	—	6	0.10	2	8.70

dolphins are sometimes caught incidentally in anchovy purse-seine operations, set in daylight and darkness. Presumably, dolphins caught were feeding on anchovies.

A white-sided dolphin captured near dawn on 9 December 1970 in an anchovy purse-seine off Point Fermin, California, was transported to Marineland of the Pacific, where it lived until 17 December 1970. Although the dolphin was fed exclusively herring, *Clupea pallasii*, during its eight day internment, the stomach was found after death to also contain otoliths of anchovies (Walker, unpublished data). This observation cautions against assuming that the contents of a dolphin's stomach represent the last feeding before death.

Parasitism and disease

The occurrence of parasites in *L. obliquidens* is summarized in Dailey and Brownell (1972) and Dailey and Walker (1978). Of the eight genera of parasites documented from this species, only the air sinus parasites, *Nasitrema* spp. (Trematoda) and *Crassicauda* sp(p). (Nematoda) have been implicated in natural mortality of small cetaceans in the eastern North Pacific (Dailey and Perrin 1973; Dailey and Walker 1978; Perrin and Powers 1980; Walker, Hochberg, and Hacker 1984).

In the present sample, specimens of *Nasitrema* were found in dolphins collected at sea from 25°22'N to 37°46'N, and specimens of *Crassicauda* were recovered in free-ranging animals from 33°40'N to 46°14'N. The evidence for the incidence and distribution of *Crassicauda* was primarily the presence of intact parasites recovered during necropsy. Incidence of infections was low, occurring in only 10% (four of 39) of the animals examined.

We also examined 197 skulls for evidence of *Crassicauda* bone lesions, described by Dailey and Perrin (1973). Only one specimen, a 160 cm juvenile female collected by W. A. Walker 26 July 1971 at 33°53'N, 118°25'W, had such lesions. The animal's left petriotic bone was almost completely eroded (illustrated in Cowan, Walker, and Brownell 1985). The low rate of *Crassicauda* infection implied by the low incidence (0.5%) of bone lesions in the skull sample examined should be interpreted cautiously, as the sample was biased toward specimens of older age classes.

We examined 63 post-cranial skeletons for disease. Of these, 34 (54%) demonstrated some degree of vertebral bone disease (osteonecrosis) (Fig. 8). The extent of damage varied from necrosis and fusion of two to three adjacent vertebrae to extreme cases in which the entire lumbar region was fused and the associated vertebral centra were considerably distorted. In four instances, vertebral osteonecrosis was encountered during dissection of whole specimens. In none of the four cases was there gross evidence of pathology of adjacent muscles or integument. Examination of the data revealed no association between locality, sex, length, or age and this disease.

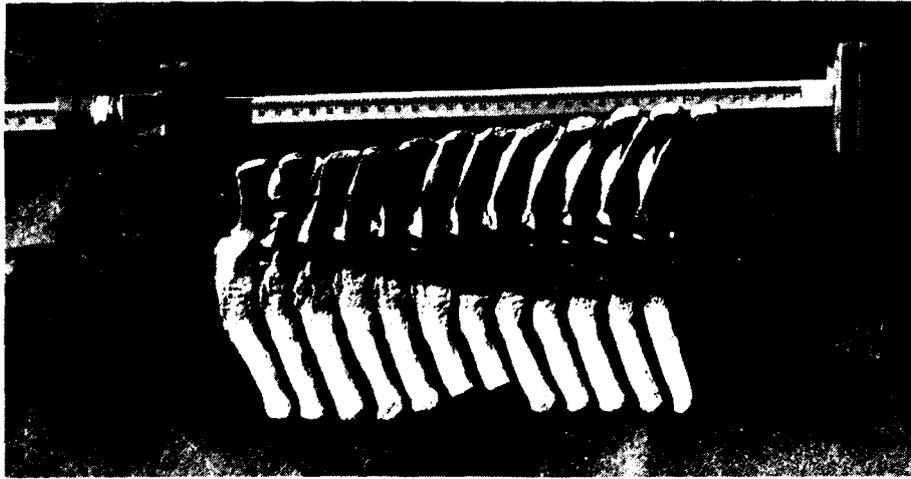


FIG. 21.8. A section of lumbar vertebrae showing osteonecrosis.

The incidence of osteonecrosis was the same in stranded animals (21 of 39 or 53.8%) and animals collected at sea (13 of 24 or 54.2%). We conclude, therefore, that this vertebral bone disease does not play a significant role in strandings. To date, the aetiology of the disease is unknown.

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Staff at NMFS/SWFC were instrumental in successful completion of this project; R. B. Miller processed ovarian specimens; A. C. Myrick, Jr., generously shared his laboratory facilities, patiently advised us on procedures and problems and generously participated in reading of specimens and interpretation of results during the age determination phase. J. Walker offered useful suggestions or approaches to data analysis.

The late J. E. Fitch identified the major portion of the fish otoliths for the food habits analysis.

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