

EXTERNAL FEATURES OF THE DUSKY DOLPHIN
Lagenorhynchus obscurus (GRAY, 1828) FROM PERUVIAN WATERS

CARACTERÍSTICAS EXTERNAS DEL DELFÍN OSCURO
Lagenorhynchus obscurus (GRAY, 1828) DE AGUAS PERUANAS

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ABSTRACT

Individual, sexual and developmental variation is quantified in the external morphology and colouration of the dusky dolphin *Lagenorhynchus obscurus* from Peruvian coastal waters. No significant difference in body length between sexes is found ($p = 0.09$) and, generally, little sexual dimorphism is present. However, males have a more anteriorly positioned genital slit and anus and their dorsal fin is more curved, has a broader base and a greater surface area than females. Although the dorsal fin apparently serves as a secondary sexual character, the use of it for sexing free-ranging dusky dolphins is discouraged because of high overlap in values. Relative growth in 25 body measurements is characterized for both sexes by multiplicative regression equations. The colouration pattern of the dorsal fin, flank patch, thoracic field, flipper stripe and possibly (χ^2 , $p = 0.08$) the eye patch, are independent of maturity status. Flipper blaze and lower lip patch are less pigmented in juveniles than in adults. No sexual dimorphism is found in the colour pattern. The existence of a discrete "Fitzroy" colour form can not be confirmed from available data. Various cases of anomalous, piebald pigmentation are described, probably equivalent to so-called partial albinism. Adult dusky dolphins from both SW Africa and New Zealand are 8-10 cm shorter than Peruvian specimens, supporting conclusions of separate populations from a recent skull variability study.

KEY WORDS: colouration, external morphology, dusky dolphin, population, Southeast Pacific.

RESUMEN

Se cuantifica la variación individual, sexual y de desarrollo en la morfología externa y la coloración del delfín oscuro *Lagenorhynchus obscurus* de aguas costeras peruanas. No se detecta diferencia significativa en longitud corporal ($p = 0,09$) y, en general, poco dimorfismo sexual está presente. La ranura genital y el ano se sitúan más anteriormente en los machos que en las hembras. Además, la aleta dorsal en los machos muestra una mayor inclinación, tiene una base más larga y una superficie mayor. Aunque, aparentemente, la aleta dorsal sirve como característica sexual secundaria, no se recomienda usarlo para determinar el sexo de delfines oscuros en alta mar por un alto nivel de sobreposición en valores. Ecuaciones de regresión multiplicativa caracterizan el crecimiento relativo en 25 medidas corporales, en ambos sexos. El patrón de coloración de la aleta dorsal, mancha del flanco, mancha torácica, banda de la aleta pectoral y, posiblemente (χ^2 , $p = 0,08$), la mancha del ojo son independientes del estado de madurez; la mancha pectoral y la mancha del labio inferior en los juveniles se ven menos pigmentadas que en los adultos. La existencia de una forma discreta de coloración llamada "Fitzroy" no se puede confirmar con los datos presentes. Se describe una anomalía de la pigmentación que probablemente es equivalente con albinismo parcial, conocido en otros mamíferos. Los delfines oscuros adultos del suroeste de África y de Nueva Zelandia miden unos 8-10 cm menos que los especímenes del Perú, confirmando conclusiones que forman poblaciones separadas, basado en un estudio reciente de variabilidad craneal.

INTRODUCTION

Particularities in the external features of whales and dolphins can offer valuable insight in their general biology. Differences in colouration pattern, adult size and body shape often indicate reproductive isolation, and have contributed to the definition of populations or management units of exploited species (e.g. YONEKURA *et al.*, 1980; EVANS *et al.*, 1982; BAIRD & STACEY, 1988; KASUYA *et al.*, 1988; HEYNING & PERRIN, 1991; PERRIN, 1990; PERRIN *et al.*, 1991). External features, such as sexual dimorphism, play an important role in the visual communication of gregarious cetaceans, and they seem closely related to social interactions, especially mating behaviour (see reviews by WÜRSIG *et al.*, 1990; JEFFERSON, 1990). Ecological and behavioural field studies are greatly enhanced if sex and some appreciation of age or maturity can be deduced for individuals from visible clues. It is therefore rather surprising that the external morphology and colouration for only a few small cetaceans have been studied in detail and with adequate sample sizes. All six species of the dolphin genus *Lagenorhynchus* remain largely undocumented.

External measurements are available for only four (sub)adult dusky dolphins *Lagenorhynchus obscurus* (GRAY, 1828; WATERHOUSE, 1838; LAHILLE, 1901; GALLARDO, 1912) and for one neonate from New Zealand (ALLEN, 1977) and these are of limited use, for it is unclear how they were taken. WEBBER (1987) offered a body length-weight plot for 15 New Zealand dusky dolphins (mean adult length = 172.6 cm, range 166-184 cm) and compared colour patterns qualitatively between *L. obscurus* and *L. obliquidens*. Original observations on the colouration of *L. obscurus* were published by GRAY (1828), WATERHOUSE (1838), LAHILLE (1901) and GALLARDO (1912); important comparative discussions are by KELLOGG (1941), BIERMAN & SLIJPER (1947, 1948) and FRASER (1966). MITCHELL (1970) in an excellent paper standardized colour pattern components. Descriptions of colouration by GASKIN (1972), LEATHERWOOD & REEVES (1983), and WEBBER and LEATHERWOOD (1990), presumably, were mostly inspired by observations on New Zealand dolphins; those authors conducted much research in that area. DAWSON (1985) reported "considerable geographic variation in colour pattern, and some pattern variation within local groups" in New Zealand. A mere three photographs of SE Pacific dusky dolphins have been published (BINI, 1951; ANDRADE & BÁEZ, 1980; GUERRA *et al.*, 1987) without any discussion.

In New Zealand and Argentina, sex (and identity) of free-ranging dusky dolphins have been determined through live-capture and photo-identification based on distinctive scars and nicks of the dorsal fin and unusual pigment patterns (WÜRSIG & WÜRSIG, 1978; WÜRSIG & JEFFERSON, 1990). Capture however is exceedingly impractical while photo-identification permitted researchers to recognize only 20%, or less, of individuals. Some visual marker of sex and maturity that would permit real-time classification of specimens would obviously be much welcomed.

Recently, large numbers of fresh dusky dolphins have become available for study in Peru as a result of high catch levels in coastal small-scale fisheries (READ *et al.*, 1988; VAN WAEREBEEK & REYES, 1990, in press). In the present paper I quantify and discuss the variation in external morphology and colouration in Peruvian *L. obscurus* and offer a preliminary comparison with animals from other areas.

MATERIAL AND METHODS

Field procedures

Most of the information presented herein I took from dusky dolphins landed at Pucusana (12° 30' S) and Cerro Azul (13° 00' S), ports located 60 km and 140 km, respectively, south of Lima, Peru. Estimated post-mortem time of specimens ranged from a few hours to about 12 hours, exceptionally up to 18 hours. The close examination of a few live-caught animals helped to define natural patterns and avoid recording post-mortem artifacts. Data collection was executed at all seasons in the period 1985-1990; many different herds, but apparently a single population, were sampled (VAN WAEREBEEK, 1992, 1993). The long collecting period and sample size ensured that most of the existing colour variation was documented.

A series of 26 external measurements (Fig. 1), recorded to the nearest 0.5 cm and modified from standardized methods by NORRIS (1961), was obtained for 394 dusky dolphins (208 females, 186 males) of all sizes. However, standard length was available for 693 dolphins. Ten axial and nine point-to-point measurements of appendages were taken with a semi-rigid metal tape (usually on the left side of the body), and seven girths were measured with a flexible plastic tape. In a few cases, the fluke span had to be inferred from the width of a single fluke by

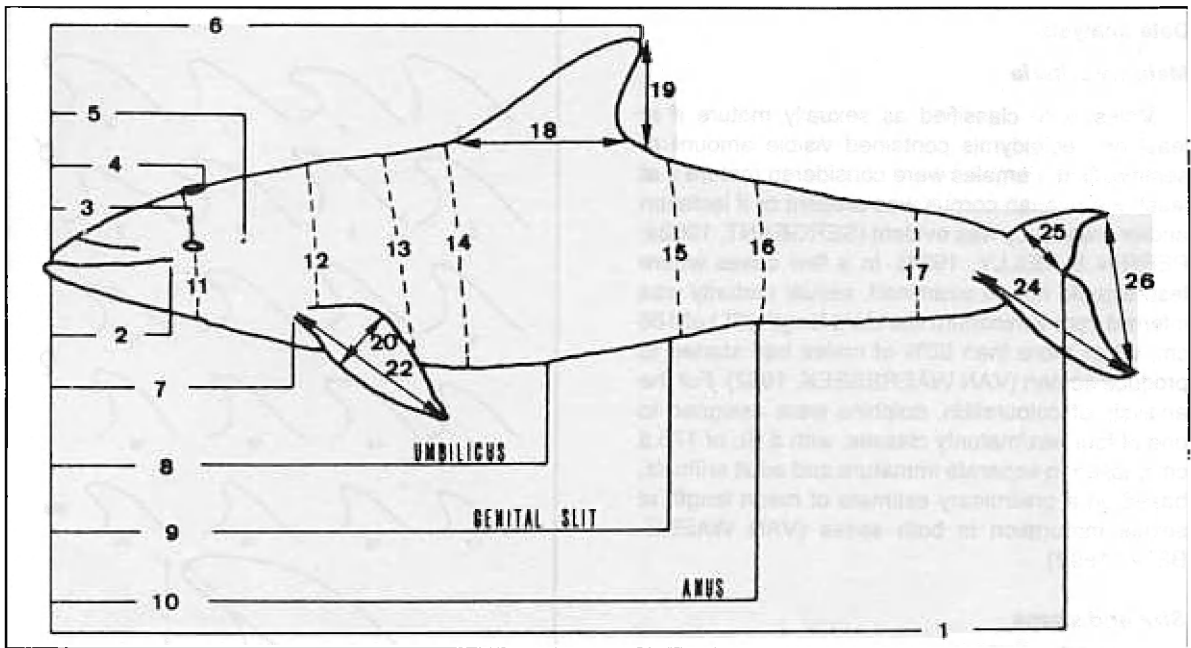


FIG. 1. External measurements taken of Peruvian dusky dolphins, including axial (nos. 1-10), girths (nos. 11-17) and point-to-point measurements (nos. 18-26). Numbers in square brackets refer to equivalent variables of Norris (1961).

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| <p>(1) Standard length: tip of upper jaw to deepest part of notch between flukes. [1]</p> <p>(2) Length of gape: tip of upper jaw to angle of gape. [3]</p> <p>(3) Length, tip of upper jaw to center of eye. [2]</p> <p>(4) Length, tip of upper jaw to posterior edge of blowhole.</p> <p>(5) Length, tip of upper jaw to external auditory meatus. [5]</p> <p>(6) Length, tip of upper jaw to tip of dorsal fin. [11]</p> <p>(7) Length, tip of upper jaw to anterior insertion of flipper. [10]</p> <p>(8) Length, tip of upper jaw to midpoint of umbilicus. [12]</p> <p>(9) Length, tip of upper jaw to anterior border of genital slit.</p> <p>(10) Length, tip of upper jaw to midpoint of anus. [14]</p> <p>(11) Girth, at level of eyes.</p> <p>(12) Girth, at level of axilla. [21]</p> <p>(13) Girth, at midpoint between axilla and anterior insertion of dorsal fin.</p> <p>(14) Girth, at anterior insertion of dorsal fin. [22]</p> | <p>(15) Girth, at posterior insertion of dorsal fin.</p> <p>(16) Girth, at level of anus. [23]</p> <p>(17) Girth, at midpoint between anus and deepest part of notch between flukes.</p> <p>(18) Length base of dorsal fin. [33]</p> <p>(19) Height of dorsal fin: fin tip to base. [32]</p> <p>(20) Maximum width of left flipper. [31]</p> <p>(21) Width of left flipper base at insertion.</p> <p>(22) Anterior length left flipper, from anterior insertion to tip. [29]</p> <p>(23) Posterior length left flipper, from axilla to tip. [30]</p> <p>(24) Length of fluke: from insertion to tip of left fluke.</p> <p>(25) Depth of fluke: shortest distance from notch to anterior border of fluke. [35]</p> <p>(26) Fluke span: width of from tip to tip. [34]</p> <p>(27) Number of visible teeth: upper left.</p> <p>(28) Number of visible teeth: upper right.</p> <p>(29) Number of visible teeth: lower left.</p> <p>(30) Number of visible teeth: lower right.</p> |
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doubling this value. One of the girths (N° 17) was abandoned for not having been taken rigorously throughout the study. A dorsal fin contour (DFC) was obtained for 119 sexually mature dolphins (51 females, 68 males) and 67 immature specimens (22 females, 45 males). Gonads were examined whenever available to determine maturity status.

When feasible, a colour pattern data form was filled out *in situ*. Colour transparencies (35 mm; 100 ASA) were taken by daylight of the freshest specimens only; unusual patterns were documented by

the best means available. Contrast and vividness of colours improved considerably after carcasses were doused for a few moments with running seawater. Because the colour pattern was bilateral symmetrical, only a single side (usually the left) was photographed. Transparencies of 257 Peruvian dusky dolphins were of sufficient quality to be used in a comparative study. For reasons of space, data are presented here in summarized form; the raw data set is deposited at the Centro Peruano de Estudios Cetológicos (CEPEC), Pucusana, Peru.

Data analysis

Maturity criteria

Males were classified as sexually mature if at least one epididymis contained visible amount of seminal fluid. Females were considered mature if at least one ovarian corpus was present or if lactation and/or pregnancy was evident (SERGEANT, 1962a; PERRIN & REILLY, 1984). In a few cases where testes could not be examined, sexual maturity was inferred from a minimum standard length (SL) of 186 cm, when more than 90% of males had started to produce semen (VAN WAEREBEEK, 1992). For the analysis of colouration, dolphins were assigned to one of four sex/maturity classes, with a SL of 175.5 cm chosen to separate immature and adult animals, based on a preliminary estimate of mean length at sexual maturation in both sexes (VAN WAEREBEEK, 1992).

Size and shape

Sexual dimorphism in external measurements was studied in 220 adult Peruvian dusky dolphins (126 females, 94 males). Size differences were probed by two-sided *t*-tests, variation in body shape by covariance analysis (ANCOVA, SL as covariate). To reveal potential sexual dimorphism in growth rate, measurements of specimens of all ages were plotted against body length. The model with highest coefficient of determination (r^2) was fitted to the data by least-square regression for females and males separately; the significance of difference in growth slopes was then verified with *t*-tests according to ZAR (1974).

Variation in the dorsal fin was correlated with sex and SL. Elevation (α) of the dorsal fin tip was measured on the contour sheets as indicated in Fig. 2; fin surface area (*S*) was digitized with a Hewlett Packard 9,826 tablet and computer. Dimorphism in these variables was verified by one-way analyses of (co)variance.

All numerical variables were screened for normality using standardized skewness and kurtosis tests and, when significant deviation was suspected (values exceeding ± 2.0), subjected to a Kolmogorov-Smirnov one-sample test of the fit. Homogeneity of variances between sample pairs was verified by a variance ratio test with 95% C.I. (ZAR, 1974). For most computations the STATGRAPHICS 4.2 programme (STSC Inc., 1989) was used. Significance, unless stated otherwise, is employed in its statistical sense at the 0.05 level of probability.

Colour pattern

Traditionally, colouration of dolphins and porpoi-

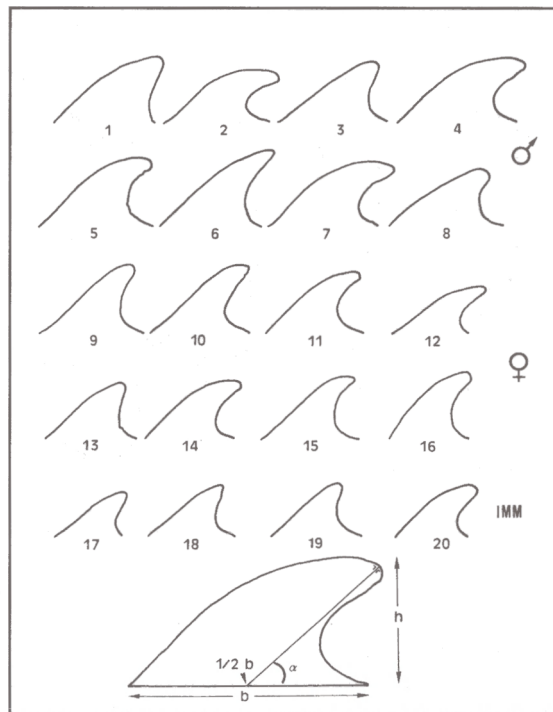


FIG. 2. Variability in shape and size of the dorsal fin (from fin tracings, scale 1:8) of Peruvian dusky dolphins: sexually mature males (Nos. 1-8), sexually mature females (Nos. 9-16) and immatures (Nos. 17-20). Specimens include: (1) KVV-1150, 202.5 cm; (2) KVV-1720, 199.5 cm; (3) KVV-1727, 186.5 cm; (4) KVV-1946, 194.5 cm; (5) KVV-2014, 209.5 cm; (6) KVV-1272, 197 cm; (7) KVV-1728, 201.5 cm; (8) KVV-1937, 187 cm; (9) KVV-1337, 195 cm; (10) JCR-1473, 194.5 cm; (11) KVV-1312, 187.5 cm; (12) KVV-1286, 185 cm; (13) KVV-1285, 195.5 cm; (14) KVV-539, 205 cm; (15) KVV-1399, 198 cm; (16) KVV-1287, 186.5 cm; (17) KVV-598, male 160 cm; (18) KVV-2134, male 163 cm; (19) KVV-1827, female 166 cm; (20) KVV-1283, female 149 cm. *h*=total height; *b*=base length; α =angle of dorsal fin tip.

ses has been described based on the pattern observed in a few specimens, granting little attention to individual, sexual, developmental or geographic variation. Even in recent years, studies which treated the subject with adequate samples and rigorous statistical analysis are few. EVANS *et al.* (1984) found that the intensity of expression of several [colour] traits in the short-finned pilot whale *Globicephala macrorhynchus* GRAY, 1846 varies in the same individual as a function of time and environmental condition. If this occurs in other toothed whales as well, small samples collected over short periods of time should be interpreted with utmost caution only.

I employed a categorical method, first success-

fully applied by EVANS (1975) for the common dolphin *Delphinus delphis*, in which colour components (fields) are scored for large series of specimens ($N > 100$). Despite the generally subtle, non-discrete variation encountered in the dusky dolphin, variants of eight colour components were defined for which variation was most straightforward (Fig. 3; general terminology taken from MITCHELL, 1970):

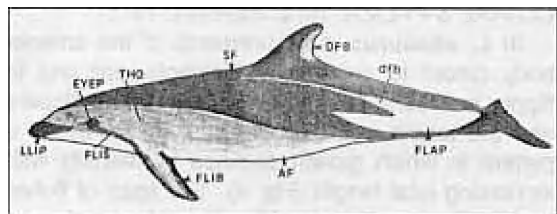


FIG. 3. Colour pattern of the dusky dolphin, slightly modified from Mitchell (1970), with AF = abdominal field, DFB = dorsal fin blaze, dfb = dorsal flank blaze, EYEP = eyepatch, FLAP = flank patch, FLIB = flipper blaze, FLIS = flipper stripe, LLIP = lower lip patch, SF = spinal field, THO = thoracic field.

DORSAL FIN BLAZE (DFB): 1 = a very conspicuous, whitish patch covering most of the dorsal fin; 2 = muted but clearly present, mostly light grey; 3 = hardly or not visible; dorsal fin usually dark grey to blackish overall;

FLIPPER BLAZE (FLIB): 1 = flipper uniformly light grey, without contrasting trailing edge; 2 = flipper light to dark grey with contrasting blackish trailing edge and flipper tip; 3 = dorsal surface of flipper almost uniformly dark grey to black;

EYE PATCH (EYEP): 1 = hardly noticeable, or very lightly coloured; 2 = prominent, dark grey to black;

FLANK PATCH (FLAP): 1 = white of flank patch and abdominal field (AF) blend into each other; 2 = FLAP and AF separated by grey to blackish, ill-defined stripe of varying width; 3 = FLAP and AF separated by broad uninterrupted, blackish band;

THORACIC FIELD (THO): 1 = entirely white, continuous with abdominal field, extending above flipper and often even above eye; 2 = anterior part of THO above flipper greyish, posterior part white and, laterally, gradually fusing with abdominal field without a clear dividing line; 3 = entire THO light or dark grey, demarcation with abdominal field fairly sharp;

LOWER LIP PATCH (LLIP): 1 = greyish, minimum definition; 2 = dark grey, moderately defined, extending over two thirds of length of gape; 3 =

prominently black, covering (almost) entire length of gape;

YELLOW FRINGE (YEL)¹: 1 = unmistakable brown-yellowish hue visible in interface of abdominal field with thoracic field and LLIP, occasionally at interface of thoracic and dorsal fields; 2 = yellowish hue not clearly visible or absent;

FLIPPER STRIPE (FLIS)²: 1 = moderately visible to very prominent, light to dark grey band extending from anterior insertion of flipper to EYEP; 2 = flipper stripe absent or hardly discernible.

Transparencies were viewed with daylight slide viewers and characters were scored independently by Laura Chávez (University of Hamburg, Germany) who had field experience with the study species and I. Diverging scores were re-evaluated and, in the absence of an immediate consensus, the character was left blank for that specimen.

Because of indications of observer drift over time in character state definition, scores recorded directly on the field but not supported by photographic material were not further considered, except for the "prominent" state (score 1) of characters YEL and FLIS which were deemed unequivocal. Differences among sex and maturity groups were tested with χ^2 contingency analyses.

Other populations

Original data on adult body lengths and photographic material of *L. obscurus* from other regions were generously supplied by several researchers (see acknowledgements). Limited morphometric information for New Zealand dusky dolphins has been presented by WEBBER (1987) in processed form. Additional photographs were consulted in the literature: WÜRSIG & WÜRSIG (1978), GASKIN (1982), BAKER (1983), LEATHERWOOD & REEVES (1983), MINASIAN *et al.* (1984), HARRISON & BRYDEN (1988); QUAYLE (1988); WÜRSIG *et al.* (1989); WEBBER & LEATHERWOOD (1990) and WÜRSIG (1991). The characterization of geographic variation in colouration I offer here is preliminary. A quantitative analysis was deemed premature because of small and heterogeneous samples (e.g. live animals besides specimens of variable post-mortem time) and unverifiable identity of specimens photographed at sea (i.e. a single individual may appear on different frames).

¹Data exclusively based on direct field observations (data form).

²Data partly based on direct field observations.

RESULTS AND DISCUSSION

External size and shape

Individual variation

Taking into account the robustness of *t*-tests and ANCOVAs (WONNACOTT & WONNACOTT, 1969), none of the 29 variables for either sex showed unacceptable departure from normality (Kolmogorov-Smirnov, $p > 0.01$), bar the lower right tooth count for males. The latter, however, may be due to chance fluctuation because of the large number of *t*-tests performed. Two character pairs (E10 and E26) deviated slightly from the required homogeneity of variance between sexes ($0.01 < p < 0.05$), but one or two pairs were expected to do so by chance at the 0.05 level of significance. Statistics of individual variation in external measurements and counts of visible teeth are presented for 220 sexually mature Peruvian dusky dolphins (126 females, 94 males) in Table 1. Considerable variation was observed in the size and shape of the dorsal fin (Fig. 2) as discussed in detail below. A keel on the caudal peduncle as in the Atlantic white-sided dolphin *Lagenorhynchus acutus* (e.g. LEATHERWOOD & REEVES, 1983) was not present.

Sexual dimorphism

I found no statistically significant difference ($t = 1.68$; $p = 0.09$) in total body length between adult females and males. Alternatively, small but highly significant differences ($p < 0.005$; *t*-tests and ANCOVAs) were present in six body measurements, namely: girth at anus, maximum width of flipper, base length of dorsal fin, depth of flukes (all greater in males), snout to vent and snout to anus (greater in females). Some proportional dimorphism was apparent also in the anterior and posterior length of the flipper and the length of the fluke, which were somewhat greater in males than in females (ANCOVA, $p < 0.05$). The slightly greater absolute values for maximum girth (E13, Table 1) and girth in front of the dorsal fin (E14) in females (*t*-tests, $p < 0.05$) are direct consequence of the bigger size of the females in the sample; indeed, corresponding *F*-statistics (ANCOVA) are not significant. All measurements were highly correlated with the body length covariate (ANCOVAs, $p < 0.0005$). Tooth counts, logically, showed no significant correlation (ANCOVAs, $0.30 < p < 0.70$).

Developmental variation

Developmental change in body proportions is a widespread phenomenon among mammals

(GOULD, 1966) and *L. obscurus* is no exception. Growth is characterized by least-squares regression equations of the form $Y = b.X^a$, where *Y* is a particular body measurement, *X* is total body length, *a* is the growth coefficient and *b* is a constant (Table 2). During ontogeny, body dimensions change either isometrically ($a < 1$) or allometrically with total length; in the latter case the growth rate can taper off with increasing length ($a < 1$) or intensify ($a > 1$) (see also CLARKE & PALIZA, 1972; PERRIN, 1975).

In *L. obscurus*, measurements of the anterior body (snout to gape, eye, blowhole, ear and to flipper insertion), as well as the size of the flippers and the length and depth of the flukes, follow a pattern in which growth declines in intensity with increasing total length (Fig. 4). The span of flukes and the base and height of the dorsal fin are characterized by a positive allometric growth. Development in girths ranges from a diminishing growth at the level of the eyes, and a roughly isometric expansion at mid-body (from axillae to dorsal fin), to an increased growth in the body posterior to the dorsal fin (Fig. 4).

The growth rate (slope) is significantly different between sexes in 12 of 24 variables (Table 2). The type of growth allometry (positive or negative), however, is equal in males and females, with the possible exception of girth at axillae (E12). Individual variation is negligible in juveniles, but it is greatly amplified in adult animals, a feature also found in oceanic dolphins of the genus *Stenella* (PERRIN, 1975).

Variation in the dorsal fin

Males have a broader-based dorsal fin than females (E18, $t = 3.31$, $p > 0.002$), but there is no significant difference in fin height (E19, $t = 0.34$, $p = 0.74$). Also, the tip of the dorsal fin is markedly less erect, so the fin is more hooked ($F = 12.2$; *df* 1, 118; $p < 0.001$) in mature males (mean elevation $\alpha = 49.6^\circ$, $SE = 0.66^\circ$), than in females (mean $\alpha = 53.2^\circ$, $SE = 0.83^\circ$). In addition, the dorsal fin becomes more hooked with increasing body length (SL); a linear regression with sexes pooled of dorsal fin tip elevation against standard body length (SL, in cm) yielded the following highly significant correlation:

$$\alpha = 69.7^\circ - 0.097 (SL) (F = 20.6; \text{df } 1, 182; p < 0.0001).$$

However, only 10.2% (*r*) of total variation was explained by the model. The large residual variation is believed to represent measuring error caused by difficulties in determining the correct base line on the DFC sheets; with a more accurate method for measuring fin angles, *r* is expected to improve. Nothing

TABLE 1

External measurements (in cm) and tooth counts of sexually mature female (N = 126) and male (N = 94) dusky dolphins, *Lagenorhynchus obscurus*, from central Peruvian waters. Maturity criteria are defined in text. CV = coefficient of variation

VARIABLE	FEMALES					MALES				
	N	RANGE	MEAN	SD	CV	N	RANGE	MEAN	SD	CV
SL: Standard length	126	168-205	189.0	7.0	0.037	94	175.5-209.5	187.4	7.1	0.038
E2: Snout to gape	101	19-24.5	21.6	1.28	0.059	83	19.5-25.5	21.4	1.13	0.053
E3: Snout to eye	101	21.5-29	25.1	1.39	0.055	84	22.5-28.5	24.8	1.2	0.048
E4: Snout to blowhole	100	25-31.5	27.8	1.37	0.049	83	24-31	27.5	1.39	0.051
E5: Snout to ear	98	26-35	31.0	1.68	0.054	77	28-34.5	30.7	1.4	0.046
E6: Snout to dorsal fin tip	92	102.5-126.5	116.3	4.4	0.038	76	102.5-129	115.8	4.97	0.043
E7: Snout to flipper insertion	100	35-47	42.5	2.14	0.05	82	37.5-49.5	42.4	2.18	0.052
E8: Snout to umbilicus	93	78-99	88.4	3.52	0.04	75	80-95	87.4	3.52	0.04
E9: Snout to vent, anteriorly	93	106.5-133	131.5	5.24	0.04	74	94-118.5	108.0	4.87	0.045
E10: Snout to anus	97	125-149	137.3	4.76	0.035	77	124-153	134.9	5.95	0.044
E11: Girth at eyes	121	61.5-75	67.6	2.59	0.038	81	61-74.5	67.8	2.42	0.036
E12: Girth at axillae	118	89.5-115	103.9	4.37	0.042	80	93.5-115.5	103.4	4.74	0.046
E13: Maximum girth	113	100-125.5	111.5	5.02	0.045	79	99-121	109.8	5.2	0.047
E14: Girth in front dorsal fin	115	99.5-127.5	112.0	5.61	0.05	80	100-122.5	110.2	5.4	0.049
E15: Girth behind dorsal fin	115	80-108	93.4	5.92	0.063	80	80-106	91.9	6.34	0.069
E16: Girth at anus	121	53.5-71	62.6	3.54	0.056	81	58-75	64.3	3.53	0.055
E18: Base length of dorsal fin	101	23.5-33.5	29.0	2.37	0.082	83	24.5-37	30.2	2.65	0.088
E19: Height of dorsal fin	96	15-23.5	19.3	1.61	0.083	83	16-27	19.4	1.73	0.089
E20: Maximum width of flipper	101	9-11.5	10.3	0.47	0.046	83	9-11.5	10.5	0.52	0.049
E21: Width of flipper base	101	10.5-13	11.7	0.64	0.055	83	10-13.5	11.8	0.66	0.056
E22: Anterior length of flipper	101	28.5-37	33.4	1.71	0.051	82	29.5-38	33.8	1.53	0.045
E23: Posterior length of flipper	101	20-27.5	24.3	1.29	0.053	82	20-28	24.7	1.26	0.051
E24: Length of fluke	99	27-34.5	30.6	1.74	0.057	79	26.5-36	31.1	1.81	0.058
E25: Depth of fluke	100	10-15	12.1	0.78	0.065	81	10.5-15	12.5	0.87	0.07
E26: Fluke span	96	41-55	48.3	2.95	0.061	84	40-59	48.9	3.86	0.079
Number of teeth upper left	80	25-36	29.7	1.91	0.064	76	26-36	29.5	1.73	0.059
Number of teeth upper right	80	24-35	29.6	2.0	0.068	77	26-36	29.3	2.03	0.069
Number of teeth lower left	80	24-32	28.5	1.83	0.064	77	25-33	28.7	1.78	0.062
Number of teeth lower right	80	24-33	28.5	2.01	0.071	78	25-33	28.4	1.66	0.058

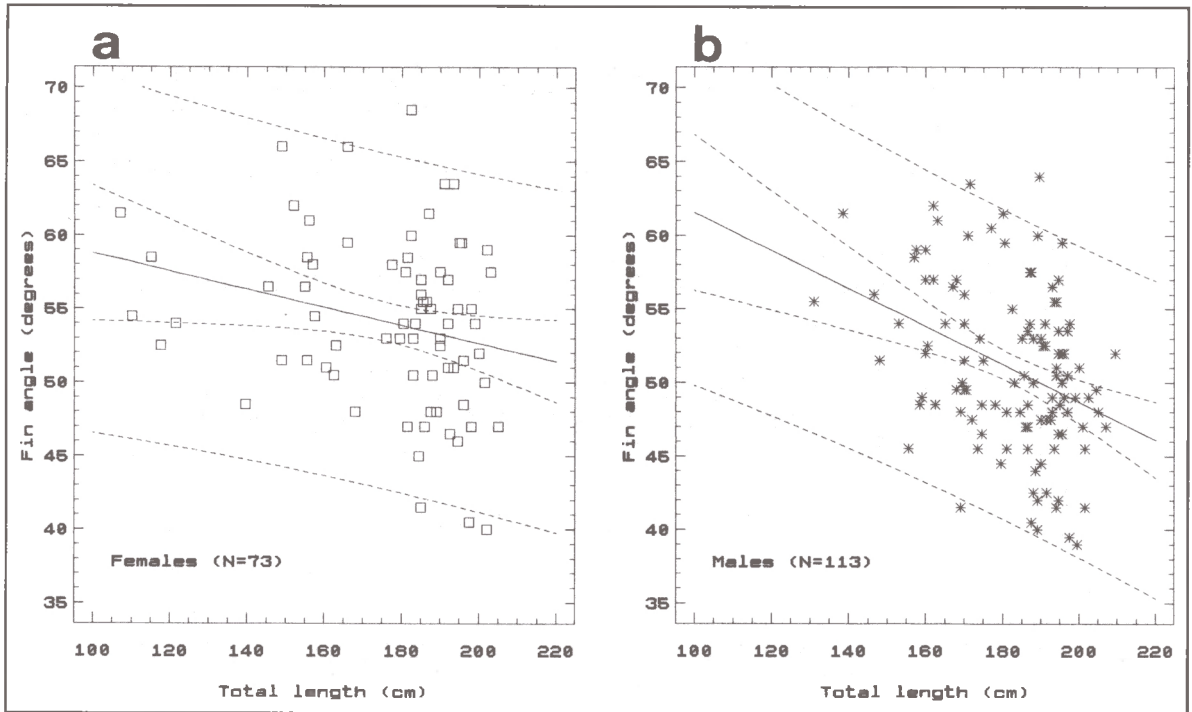


FIG. 4. Scatterplot of dorsal fin-tip elevation against total body length in female (a) and male (b) *L. obscurus* from Peru. As dolphins grow larger, dorsal fin tip increasingly curves more backward, especially in males. Linear regression lines, 95% confidence limits (closest dashed lines) and expectation limits for single observations (outer pair of dashed lines) are drawn. Females: $Y = 64.9 - 0.0061 X$ ($r = 0.25$; $p < 0.05$); Males: $Y = 74.4 - 0.129 X$ ($r = 0.36$; $p = 0.0001$).

suggests that the process of fin tip curving stops at any given length and it probably continues even in old age. Linear regressions of dorsal fin angles for each sex separately reveal a slightly steeper slope in males (Fig. 4a, b). While this difference could not be confirmed statistically (t -test, $p > 0.05$), it is likely to be real, considering the fin dimorphism in adults (see above).

The mean surface area (A) of the dorsal fin in adult males (350 cm^2 , $SE = 6.1 \text{ cm}^2$) proved very significantly greater (ANCOVA, $F = 43.3$; $df 1, 118$; $p > 0.0001$) than the equivalent in adult females (290.4 cm^2 , $SE = 5.5 \text{ cm}^2$). If development of the dorsal fin were isometric, the area would increase quadratically with body length and have a slope = 2 after log transformation. In reality, a negative allometric growth is seen in females (Fig. 5a) while the opposite is true in males (Fig. 5b) ($t = 5.47$, $df 1, 177$, $p < 0.0001$):

Males $\log_e A = -3.44 + 2.64 \log_e L$ ($r = 0.90$, $p < 0.0001$, $N = 111$)
 Females $\log_e A = 1.003 + 1.77 \log_e L$ ($r = 0.91$, $p < 0.0001$, $N = 66$)

The Pacific white-sided dolphin is also reported to have a widely variable dorsal fin, ranging in shape from falcate and sharply pointed to lobate and rounded; the latter form, it was suggested (BROWN & NORRIS, 1956; KASUYA, 1981; WALKER *et al.*, 1986), correlates with the onset of physical maturity. However, these authors did not attempt to quantify their observations. Lobate fins as present in *L. obliquidens* (see WALKER *et al.*, 1986, fig. 21.1) have not been encountered in *L. obscurus*.

Geographic variation in body length

In absence of meaningful sexual dimorphism in body length of adult Peruvian dusky dolphins, sexes were pooled for geographic comparison (mean SL = 187.7 cm , $SD = 5.0 \text{ cm}$, $N = 220$). The largest male recorded in this study ($N = 693$) was 209.5 cm long, the largest female measured 205.0 cm . A male harpooned off Huacho, Peru reportedly measured 211 cm (U.S. National Museum of Natural History N° 270418; BROWNELL, 1974), although it is unknown whether this measurement was taken in a standardized way.

TABLE 2

Growth pattern external measurements (VAR, see Table 1) in function of total body length (X) in *Lagenorhynchus obscurus* of Peru. Least-squares regression power equations and coefficient of determination (r^2) are indicated for females and males separately. All equations have highly significant slopes (ANOVAs, covariate $p < 0.0002$). Significance level of sexual dimorphism in slope is indicated (ns = not significant). Growth equations not significantly different (95% C.I.) from the linear model are marked by L.

Var	FEMALES Equation Y=	r^2	MALES Equation Y=	r^2	Dimorphism p
E2	$0.27 X^{0.84}$	93.4	$0.16 X^{0.93}$	92.6	< 0.005
E3	$0.36 X^{0.81}$	93.7	$0.26 X^{0.88}$	92.8	< 0.01
E4	$0.23 X^{0.92}$	94.4	$0.16 X^{0.99}$ (L)	94.5	< 0.05
E5	$0.51 X^{0.78}$	93.6	$0.45 X^{0.81}$	91.1	ns
E6	$0.77 X^{0.96}$	98.9	$0.68 X^{0.98}$ (L)	98.6	< 0.05
E7	$0.58 X^{0.82}$	96.8	$0.41 X^{0.89}$	96.1	< 0.005
E8	$0.71 X^{0.92}$	99.1	$0.64 X^{0.94}$	98.8	ns
E9	$0.77 X^{0.97}$	99.0	$0.74 X^{0.95}$	98.9	ns
E10	$0.68 X^{1.01}$	99.7	$0.70 X^{1.00}$ (L)	99.4	ns
E11	$1.44 X^{0.73}$	95.1	$1.37 X^{0.75}$	97.3	ns
E12	$0.51 X^{1.01}$ (L)	85.0	$0.64 X^{0.97}$	96.5	< 0.05
E13	$0.52 X^{1.02}$ (L)	96.7	$0.63 X^{0.98}$ (L)	96.7	ns
E14	$0.52 X^{1.02}$ (L)	95.5	$0.61 X^{0.99}$ (L)	96.8	ns
E15	$0.24 X^{1.13}$	94.0	$0.41 X^{1.03}$ (L)	95.0	< 0.005
E16	$0.19 X^{1.10}$	95.1	$0.24 X^{1.07}$	95.6	ns
E18	$0.12 X^{1.04}$	93.3	$0.11 X^{1.07}$	93.6	ns
E19	$0.09 X^{1.03}$ (L)	93.2	$0.05 X^{1.13}$	93.0	< 0.01
E20	$0.077 X^{0.94}$	95.9	$0.10 X^{0.88}$	95.7	< 0.005
E21	$0.14 X^{0.85}$	95.6	$0.094 X^{0.92}$	95.3	< 0.005
E22	$0.32 X^{0.89}$	96.4	$0.27 X^{0.92}$	96.2	ns
E23	$0.20 X^{0.91}$	95.7	$0.17 X^{0.95}$	93.8	ns
E24	$0.31 X^{0.88}$	94.9	$0.19 X^{0.97}$ (L)	94.5	< 0.005
E25	$0.19 X^{0.79}$	93.0	$0.13 X^{0.88}$	93.0	< 0.005
E26	$0.12 X^{1.14}$	96.6	$0.13 X^{1.13}$	94.6	ns

Dusky dolphins from southwestern Africa, with a mean adult length of 179.9 cm (SD = 7.18 cm, $N = 20$, sexes pooled) and a maximum recorded length of 190.5 cm ($N = 58$) (P.B. BEST, South African Museum, unpubl. data), are comparable in size ($t = 0.29$, $p = 0.77$) to mature animals from New Zealand which average 179.1 cm (SD = 8.97 cm, $N = 12$) and attain a maximum length of 195.5 cm (data provided by A.N. BAKER, National Museum of New Zealand and P.J.H. VAN BREE, Zoological Museum, University of Amsterdam). SW African and New Zealand dusky dolphins each are noticeably smaller than their Peruvian counterparts (t -tests, $p < 0.0001$); mean and maximum lengths differ some 8-10 cm. This further supports conclusions from cranial variation analysis that these groups constitute separate populations, and possibly even valid subspecies. Despite a few (statistically) significant cranial differ-

ences, Peruvian and Chilean dusky dolphins probably form a single SE Pacific population (VAN WAEREBEEK, 1992, 1993). A greater sample from Chile is needed to permit a definitive conclusion. Little can be said about *L. obscurus* from Argentina, due to an almost total lack of data. Body lengths of two females of unknown maturity have been published: one 162.5 cm and the other 165.5 cm (WATERHOUSE, 1838; LAHILLE, 1901). The standard body length of a specimen discussed by GALLARDO (1912) probably was 175.5 cm (GALLARDO's "100%"), and not 183 cm ("maximum length, 104,6%") as interpreted by KELLOGG (1941).

Colouration

Variation within the Peruvian population

Individual variation in colouration is extensive

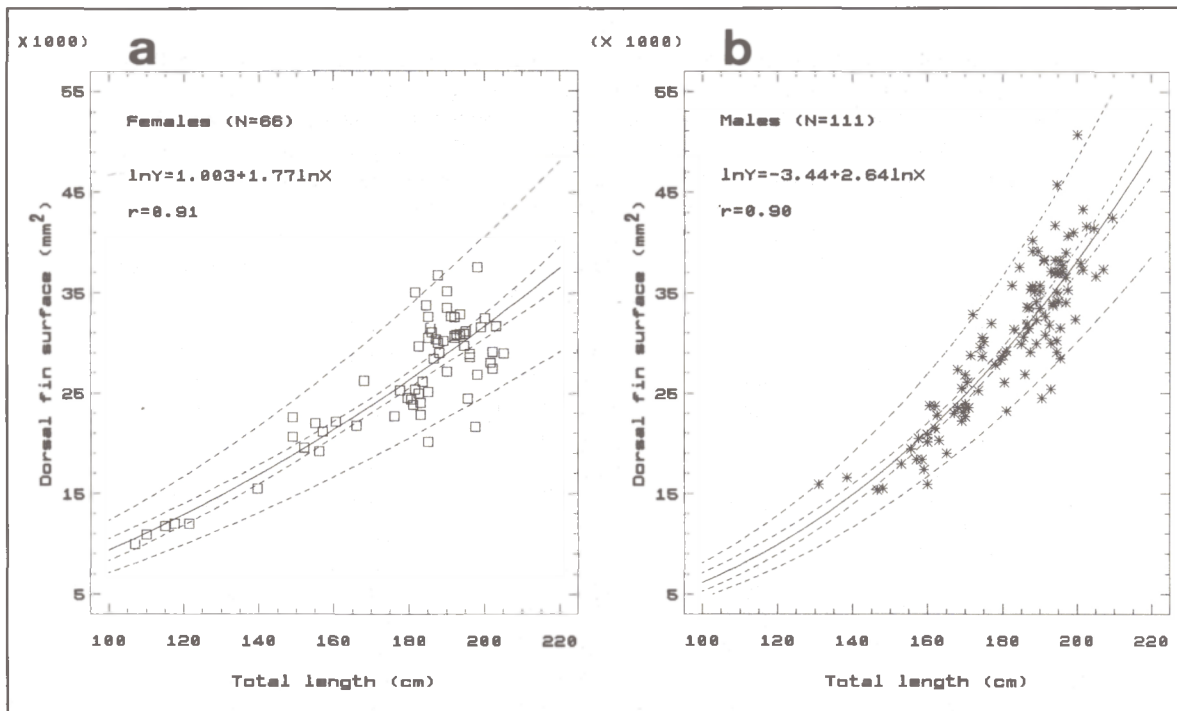


FIG. 5. Scatterplot dorsal fin surface area against total body length of female (a) male (b) *L. obscurus* from Peru. Least-square regression curve with 95% confidence limits and expectation limits for single observations are shown.

(see photographs in VAN WAEREBEEK, 1992) but non-discrete, with the result that appreciable numbers of specimens could not be scored confidently for particular colour components and had to be skipped.

DORSAL FIN BLAZE-DFB varied from almost invisible (i.e. the fin appeared entirely dark, in 36 of 156 dolphins (23.1%) to a light grey or white patch covering the larger part of the fin (23.1%), but more than half of the animals (84 of 156 or 53.8%) showed the intermediary configuration. DFB was independent of sex ($\chi^2 = 0.66$; df 2; $p = 0.72$) and maturity status ($\chi^2 = 4.15$; df 2; $p = 0.13$).

FLIPPER BLAZE - Most commonly (120 of 163, 73.6%) the upper side of the flipper was light to dark grey with a blackish trailing edge widening into a dark flipper tip. Rarely (6 of 163, 3.7%) was this black too faint to be visible. When the flipper was mostly dark grey, the blackish trailing edge and tip were hardly discernible (37 of 163, 22.7%), and the flipper could appear all black (see also MITCHELL, 1970). Lightly coloured flippers were more frequently seen in younger than in adult animals ($\chi^2 = 10.0$; df 2; $p < 0.01$) but no significant difference was found between males and females (Yates corrected $\chi^2 = 1.20$; df 1; $p = 0.27$).

EYE PATCH. A prominent, blackish eye patch was present in 154 of 183 (84.2%) specimens; in the remaining 29 animals (15.8%), the eye patch was faintly coloured or absent. More juveniles than adults showed the latter colouration, but the difference was not statistically significant ($\chi^2 = 3.11$; df 1; $p = 0.08$). The frequency of the eye patch types was not statistically different between sexes (Yates corrected $\chi^2 = 3.62$; df 1; $p = 0.06$).

FLANK PATCH-MITCHELL (1970) recognized a ventral flank blaze (vfb) and a dorsal flank blaze (dfb) associated with the flank patch (FLAP). Our observations demonstrate that the ventral flank blaze is nothing else than the cranial part of the flank patch. Conversely, the dorsal flank blaze indeed constitutes a separate overlay blaze merging with the large flank patch, as is evidenced by clear differences in intensity of white in these components in some individuals. The flank patch varies chiefly in its position relative to the abdominal field (AF) and in its overall size and shape. In the majority of specimens (161 of 208, 77.4%), the flank patch is separated from the abdominal field by a medium grey to black ill-defined stripe of varying width. In another form, an uninterrupted, broad black band separates the flank patch from the ventral field (39 of 208, 18.8%); ex-

ceptionally (8 of 208, 3.8%) the white of both fields blend clearly into each other. The frequency of FLAP variants had no relation to either sex ($\chi^2 = 1.42$; df 2; $p = 0.49$) or maturity ($\chi^2 = 2.39$; df 2; $p = 0.30$) of the dolphins.

THORACIC FIELD- The most common form of thoracic field in present sample (111 of 190, 58.4%) was pigmented overall and therefore clearly differentiated from the ventral field; in ten animals (5.3%) the thoracic field appeared mostly white, while 69 specimens (36.3%) were intermediately coloured. The intensity of pigmentation was independent of maturity ($\chi^2 = 0.70$; df 2; $p = 0.70$) and sex ($\chi^2 = 4.37$; df 2; $p = 0.11$).

LOWER LIP PATCH- Of 167 dusky dolphins examined, 22 (13.2%) showed a lower lip patch (LLIP) with minimal pigmentation; 93 (55.7%) had a moderately pigmented and 52 (31.1%) a heavily pigmented LLIP. Sexual dimorphism was absent ($\chi^2 = 2.88$; df 2; $p = 0.24$), but juveniles had a less pigmented lower lip than adults ($\chi^2 = 13.37$; df 2; $p = 0.0013$).

YELLOW FRINGE- A brown-yellowish lateral fringe (YEL) was clearly visible in 33 of 190 (17.4%) dolphins. A first χ^2 test classified this trait as independent of sex and maturity, but statistical values were lost and could not be re-calculated since the data set was inaccessible at time of writing.

FLIPPER STRIPE- The presence of a prominent eye to flipper stripe was fairly infrequent, namely in 36 of 224 (or 16.1%) of individuals examined. The frequency of occurrence was independent of sex ($\chi^2 = 3.06$; df 1; $p = 0.08$) and maturity ($\chi^2 = 0$; df 1, $p = 1.00$, with Yates' correction).

Geographic variation

Variants of colour fields in New Zealand dusky dolphins, evaluated from photographic material of mostly live animals, were not qualitatively different from these found in Peruvian specimens. As indicated earlier, no quantitative analysis was possible, but the form with an entirely white thoracic patch (THO = 1), relatively rare in Peru (5.3%), may be the more common form in New Zealand. DAWSON (1985), discussing the latter, referred to the thoracic patch as "a blaze of white extending from the snout, above the eye, and along the flank to join the white of the belly", coinciding with our THO = 1 definition. Several *L. obscurus* specimens from New Zealand presented a (to Peruvian standards) unusually small and delicate flank patch. A comparison of colouration with SW African dusky dolphins also revealed no obvious deviations from the pattern seen in Peruvian animals, but further research is necessary.

Dusky dolphins from the Peninsula Valdez area

(Chubut, Argentina) also greatly vary in degree of melanisation, possibly even more so than in Peru (see WÜRSIG & WÜRSIG, 1978; 64,66). In a heavily melanised phenotype, upper and lower lip patches and the eye patch are strikingly black; a conspicuous flipper stripe forms a broad, continuous black band that fuses with an equally dark flipper. The dorsal fin is almost entirely black and a yellowishbrown hue of varying intensity may line the borders of the white fields along the body. In a light-coloured phenotype, the flipper, flipper stripe, eye patch and lip patches are so faintly pigmented as to appear almost absent (e.g. GALLARDO, 1912; WÜRSIG & WÜRSIG, 1978). Limited photographic material suggests that the frequency of occurrence of these phenotypes may be group-specific; moreover most specimens seem to be intergrades between the two extreme types.

In live animals the anterior portion of the dorsal flank blaze (dfb) is visible anterodorsally some distance beyond the dorsal fin. Due to quick post-mortem fading this trait was rarely obvious in the Peruvian specimens.

Fitzroy form

A female dusky dolphin harpooned from the *Beagle* in Bahía San José (Argentina), was described by WATERHOUSE (1838) as *Delphinus fitzroyi*, subsequently referred to the genus *Lagenorhynchus* by FLOWER (1885). After more than a century of confusion (reviewed by HERSHKOVITZ, 1966) *L. fitzroyi* was still considered a separate species by for instance NISHIWAKI & NORRIS (1966). Other authors including KELLOGG (1941), YÁÑEZ (1948) and FRASER (1966) justly synonymized it with *L. obscurus*. More recently it has been regarded by some authors as a separate "Fitzroy" colour form of the dusky dolphin (WATSON, 1981; LICHTER & HOOPER, 1984; MINASIAN et al. 1984; CÁRDENAS et al., 1986). For reasons of clarity I reproduce here (my comments in square brackets) the original description of the colour pattern by WATERHOUSE (1838):

"Upper parts of the body black, under parts pure white, the two blended into each other by gray: extremity of snout a ring round the eye [EYEP = 2], the edge of the under lip, and the tail fin, black [LLIP = 3]; dorsal [DFB = 3] and pectoral fins [FLIB = 3] dark gray; a mark extends from the angle of the mouth to the pectoral fin [FLIS = 1]; above which, the white runs through the eye and is blended into grey over the eye; two broad deep-gray bands are extended in an oblique manner along each side of the body, running from the back downwards and backwards [FLAP = 1 or 2]."

The description and the accompanying lithograph made by Captain Fitzroy "after an excellent coloured drawing, when fresh killed" indicates that the Fitzroy specimen is similar to the heavily melanised colour type, as referred to above, from photographs presented by WÜRSIG & WÜRSIG (1978). The reported colouration of the Fitzroy specimen is aberrant in that "the white runs through the eye" and in the unusual, indistinct shape of the flank patch (see WATERHOUSE, 1838: plate 10). The animal was either an anomalous case of the melanised form or, despite claims by WATERHOUSE (op. cit.), has not been accurately depicted. The flank patch of the GALLARDO (1912, Fig. 1) specimen was also fairly unusual, so perhaps this patch is more variable in Argentinian than in Peruvian *L. obscurus*. If in an adequate sample from Argentina, the melanised form would prove to be a discrete phenotype, it could be referred to as the "Fitzroy form"; if not, and in the meantime, this name should be reserved for historical reviews only.

Anomalous pigmentation

Five Peruvian dusky dolphins and one specimen from SW Africa showed anomalous piebald pigmentation in the form of irregular white flecks of blotches superposed on the normal pattern (Table 3). White patches on (black) skin have been associated with *Candida* spp. infections in captive SW African dusky dolphins (FOTHERGILL & JOGESSAR, 1986), but the abnormalities reported here were presumably

not of an infectious nature, since the affected skin surface was smooth and apparently healthy. The phenotypic condition is highly reminiscent and probably equivalent to piebaldness (Dr. P.J.H. VAN BREE, *in litt.* 19 May 1992), a genetic melanisation defect well-known in humans and domestic animals, also referred to as "Weiszschekung" or "partial albinism" (SUNDFOR, 1939; HOEDE, 1940; COOKE, 1952; COMINGS & ODLAND, 1966; HULTÉN *et al.* 1987). Probability considerations suggest consanguinity for two affected animals (one a severe case) landed the same day at the Pucusana wharf (Table 3). Differential frequencies of this dominantly inherited trait perhaps could help delineate local breeding groups, however for large-scale population discrimination (e.g. Peru versus SW Africa) it is probably useless. Indeed, its occurrence in humans of various races and widely separated areas suggest that it can arise, apart from direct inheritance, by new mutation (see SUNDFOR, 1939). Whether piebaldness is identical with Chidiak-Higashi syndrome, previously reported from a killer whale (RIDGWAY, 1976, quoted in MATKIN & LEATHERWOOD, 1986, Fig. 3.3) is still unclear. In any case, the partial skin melanisation and the normal pigmentation of the eyes clearly distinguishes it from albinism (see HOEDE, 1940; HAIN & LEATHERWOOD, 1982).

In the genus *Lagenorhynchus* aberrant pigmentation, but not piebaldness, has otherwise been described solely from *L. obliquidens* (BROWN & NORRIS, 1956; BROWNELL, 1965; BLACK, 1989).

TABLE 3
Known cases of piebald colouration in *Lagenorhynchus obscurus*

Number	Locality	Date	Sex	SL(cm)	Description and source
s.n.	Ancón, Perú	Sept. 85	?		white blotches on anterior body and lower lip; photograph by J.C. Reyes (CEPEC)
s.n.	Pucusana, Peru	Aug. 86	?	?	white blotches on flukes and tail stock; photograph by J.C. Reyes (CEPEC)
KVW1018	Pucusana, Peru	25 Dec. 87	M	194.5	blotches on flank and thoracic patch, dorsal flank blaze absent; photographs by author, skin sample
KVW1288	Pucusana, Peru	2 Jun. 88	M	190.0	flecked pattern over most of body, superposed on normal pattern; photographs by author, skin sample
KVW1313	Pucusana, Peru	2 Jun. 88	F	196.0	flecked patches; photograph by author
SAM37754	Hout Bay, South Africa	7 Mar. 76	F	168.0	unpublished photograph courtesy of Dr. P.B. Best (South African Museum, Cape Town)

CONCLUSIONS

Although sexual dimorphism is statistically significant in several external measurements, only differences in the position of the genital slit and anus and the shape/size of the dorsal fin are of sufficient magnitude to manifest a biological function. The more forward positioned genital aperture and anus in male dusky dolphins are typical cetacean features (e.g. SERGEANT, 1962b; SLIJPER, 1962; PERRIN, 1975; YONEKURA *et al.* 1980). The slightly greater girth at the anus in males can be related to this. There is no vertical thickening of the caudal stock behind the anus as for instance is seen in mature males of the eastern spinner dolphin *Stenella longirostris orientalis* (PERRIN, 1975; PERRIN *et al.* 1991).

The dorsal fin of the male is more strongly curved and broader-based and has a substantially greater surface area than that of the female. These disparities are accentuated with increasing body length. I propose that the dorsal fin, besides its hydrodynamic function, serves as a secondary sexual character, a morphological signature of sexual maturity and, indirectly, social status. In any case, the dorsal fin of *L. obscurus* is more variable than either its flippers or flukes, which suggests that additional selective pressures are at work. The same argument probably goes for various other cetaceans, including killer whales, eastern spinner dolphins, Dall's porpoises *Phocoenoides dalli* (JEFFERSON, 1990; PERRIN *et al.*, 1991) and Pacific white-sided dolphins (BROWN & NORRIS, 1956). In adult spinner dolphins and Dall's porpoises, males have a more erect dorsal fin than females (JEFFERSON, 1990; PERRIN, 1990; PERRIN *et al.*, 1979, 1991). The reverse is true for the dusky dolphin and, possibly, the Pacific white-sided dolphin. Other *Lagenorhynchus* spp. should be checked to see whether this trait is idiosyncratic for the genus. Unfortunately, individual variation and overlap in dorsal fin size and shape are too great to permit reliable sexing of free-ranging dusky dolphins. In killer whales, gender has been judged on the basis of ratio of dorsal fin height to basal length, although that method as well was thought not to be foolproof (MATKIN & LEATHERWOOD, 1986).

No significant sexual dimorphism was found in the colouration of *L. obscurus*. However, it is perhaps worth to warn here for undue definitive conclusions concerning (absence of) dimorphism where borderline values for p were found (e.g. eye patch and measurements E8 and E24, with $0.05 < p \leq 0.07$) since the probability that these characteristics are slightly dimorphic but were not detected at chosen α

level and sample size (so-called β error, see WONNACOTT & WONNACOTT, 1990), may be fairly high. At any rate differences are subtle at best, and one may safely state that, based on size, shape and colouration, female and male dusky dolphins are hard to distinguish from each other. This fact, together with equal length at (50%) sexual maturity for males and females (175 cm), huge testis size, and apparent absence of wide-spread male antagonistic behaviour suggests a promiscuous mating system with sperm competition in the dusky dolphin (VAN WAEREBECK, 1992; VAN WAEREBECK & READ, *in press*).

Of eight colour components tested, the flipper patch, lower lip patch and eye patch are substantially less pigmented in juveniles than in adults. Full pigmentation, at least in some elements of the colour pattern, tends to be reached only at maturity, which is in agreement with findings for other delphinids. WALKER *et al.* (1984, 1986) found muted expression of elements of the adult colour pattern in foetuses and newborn calves of the Pacific white-sided dolphin and intensification with age. PERRIN (1972) noted a progressive obscuring of the dorsal cape in the spinner dolphin. GWINN & PERRIN (1975) through microscopic examination found some evidence of pigment aggregation with development, in the epidermis of gray and black areas of the common dolphin. Yellowish-brown pigment is rare in cetaceans and has been reported only from the common dolphin, the Atlantic white-sided dolphin *Lagenorhynchus acutus* and some young specimens of the killer whale (MITCHELL, 1970; GWINN AND PERRIN, 1975; ELLIS, 1989). Thus the discovery of a yellow fringe in *L. obscurus* is not without importance. Although our current colouration record for the various populations is incomplete, there are indications that divergences may exist in relative frequencies of colouration pattern variants.

The striking differences in mean and asymptotic body length between Peruvian and both New Zealand and SW African dusky dolphins support the recognition of discrete populations (and possibly even separate subspecies) based on craniometric and geographic considerations (VAN WAEREBECK, 1992, 1993).

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REFERENCES

- ALLEN JF 1977. Dolphin reproduction in oceanaria in Australasia and Indonesia. In *Breeding Dolphins, Present Status, Suggestions for the future*. SH Rigway & K Bernirschke (eds.). Rep. MMC-76/07 to US Marine Mammal Commission, pp. 85-100.
- ANDRADE H & p. BÁEZ 1980. Presencia del delfín listado: *Lagenorhynchus obscurus* (GRAY, 1828) en la costa de Valparaíso. *Noticiario Mensual del Museo Nacional de Historia Natural* 288/289: 7-9.
- BAIRD RW & PJ STACEY 1988. Variation in saddle patch pigmentation in populations of killer whales (*Orcinus orca*) from British Columbia, Alaska, and Washington State. *Canadian Journal of Zoology* 66: 2582-85.
- BAKER AN 1983. Whales and Dolphins of New Zealand and Australia. Victoria University Press, 133 pp.
- BIERMAN WH & EJ SLIJPER 1947. Remarks upon the species of the genus *Lagenorhynchus*. *Koninklijke Nederlandse Akademie voor Wetenschappen* 50: 1353-64.
- BIERMAN WH & EJ SLIJPER 1948. Remarks upon the species of the genus *Lagenorhynchus*. *Koninklijke Nederlandse Akademie voor Wetenschappen* 51(1): 127-33.
- BINI G 1951. Osservazioni su alcuni mammiferi marini sulle coste del Cile e del Peru. *Boll. Pesca Piscicoltura Idrobiol* 6 (n.s.) 1: 79-93.
- BLACK N 1989. Pacific white-sided dolphins in Monterey Bay. *Whalewatcher* 23(1): 5-8.
- BROWN DH & KS NORRIS 1956. Observations of captive and wild cetaceans. *Journal of Mammalogy* 37(3): 311-26.
- BROWNELL RL Jr. 1965. An anomalous color pattern in a Pacific striped dolphin. *Bulletin of the Southern California Academy of Sciences* 64(4): 242-3.
- BROWNELL RL Jr. 1974. Small odontocetes of the Antarctic. *Antarctic Map Folio Series* 18: 13-19.
- CARDENAS JC, STUTZIN ME, OPORTO JA, CABELLO C & D TORRES 1986. Manual de identificación de los cetáceos chilenos. CODEFF, Santiago, Chile, 102 pp.
- CLARKE R & O PALIZA 1972. Sperm whales of the Southeast Pacific. Part III: Morphometry. *Hvalradets Skrifter* 53. Det Norske Videnskap-Akademii Oslo, 106 pp.
- COMINGS DE & GF ORLAND 1966. Partial albinism. *Jama* 195 (7): 519-523.
- COOKE JV 1952. Familial white skin spotting (Piebaldness) ("Partial albinism") with white forelock. *Journal of Pediatrics* 41(1): 1-12.
- DAWSON S 1985. The New Zealand Whale and Dolphin Digest. Brick Row Publ. Co., Auckland, 130 pp.
- ELLIS R 1989. Dolphins and porpoises. A.A. Knopf, New York, 270 pp.
- EVANS ME 1975. The biology of the common dolphin, *Delphinus delphis*, Linnaeus. Ph. D. thesis, University of California.
- EVANS WE, THOMAS JA & DB KENT 1984. A study of pilot whales (*Globicephala macrorhynchus*) in the southern California bight. Admin. Report LJ-84-380, NMFS/SWFC, La Jolla, California, 47 pp.
- EVANS WE, YABLOKOV AV & AE BOWLES 1982. Geographic variation in the color pattern of killer whales. *Reports of the International Whaling Commission* 32: 687-94.
- EVANS WE, THOMAS JA & DB KENT 1984. A study of pilot whales (*Globicephala macrorhynchus*) in the southern California bight. Adm. Rep. LJ-84-380, NMFS/SWFC, La Jolla, California: 1-47.
- FLOWER W 1885. List Cetacea of the British Museum. *Proceedings of the Zoological Society*, London.
- FOTHERGILL M & VB JOGESSAR 1986. Haematological changes in two *Lagenorhynchus obscurus* treated with Ketoconazole. *Aquatic Mammals* 12(3): 87-91.
- FRASER FC 1966. Comments on the Delphinoidea. In *Whales, Dolphins and Porpoises*. KS Norris (ed.). University of California Press, Los Angeles, pp. 7-30.
- GALLARDO A 1912. El delfín *Lagenorhynchus fitzroyi* (Waterhouse) Flower, capturado en Mar

- del Plata. **Anales del Museo Nacional de Historia Natural de Buenos Aires** 23: 391-7.
- GASKIN DE 1972. Whales, Dolphins and Seals: With Special Reference to the New Zealand Region. Heinemann Educational Books, London and Auckland, 200 pp.
- GASKIN DE 1982. The Ecology of Whales and Dolphins. Heinemann Educational Books, London, 459 pp.
- GOULD SJ 1966. Allometry and size in ontogeny and phylogeny. **Biological Reviews** 41: 587-640.
- GRAY JE 1828. Spicilegia Zoologica - Or original figures and short systematic descriptions of new and unfigured animals. London, pt. 1: 1-8.
- GUERRA C, VAN WAEREBECK K, PORTFLITT G & G LUNA 1987. Presencia de cetáceos frente a la segunda región de Chile. **Estudios Oceanológicos** 6: 87-96.
- GWINN S & WF PERRIN 1975. Distribution of melanin in the color pattern of *Delphinus delphis* (Cetacea; Delphinidae). **Fishery Bulletin** 73(2): 439-44.
- HAJN JHW & S LEATHERWOOD 1982. Two sightings of white pilot whales, *Globicephala melae-na*, and summarized records of anomalously white cetaceans. **Journal of Mammalogy** 63(2): 338-43.
- HARRISON R & MM BRYDEN 1988. Whales, dolphins and porpoises. Facts on File Publications, New York, 240 pp.
- HERSHKOVITZ P 1966. Catalog of living whales. Smithsonian Institution, Washington D.C.: 259 pp.
- HEYNING JE & WF PERRIN 1991. Re-examination of two forms of common dolphins (genus *Delphinus*) from the eastern North Pacific; evidence for two species. SWFC/NMFS Adm. Report. LJ-91-28, 37 pp.
- HOEDE K 1940. Erbpathologie der menschlichen Haut. In: Erbbiologie und Erbpathologie körperlicher Zustände und Funktionen. I. Von Julius Springer, Berlin.
- HULTEN MA, HONEYMAN MM, MAYNE AJ & MJ TARLOW 1987. Homozygosity in piebald trait. **Journal of Medical Genetics** 24: 568-71.
- JEFFERSON TA 1990. Sexual dimorphism and development of external features in Dall's porpoise *Phocoenoides dalli*. **Fishery Bulletin** 88: 119-32.
- KASUYA T 1981. Identification manual of dolphins and porpoises in the Japanese waters. Research Division, Japan Fisheries Agency: 41 pp. In Japanese. [Not seen].
- KASUYA T, MIYASHITA T & F KASAMATSU 1988. Segregation of two forms of short-finned pilot whales off the Pacific coast of Japan. **Scientific Reports of the Whales. Research Institute** 39: 77-90.
- KELLOGG R 1941. On the identity of the porpoise *Sagmatias ambodon*. **Field Museum of Natural History, Zoological Series** 27: 293-311 + 7 pls.
- LAHILLE F 1901. El delfín de Fitzroy. *Lagenorhynchus fitzroyi* (Waterh.) Flow. **Boletín de Agricultura y Ganadería** 1(4): Buenos Aires: 3-6. [Not seen].
- LEATHERWOOD S & RR REEVES 1983. The Sierra Club Handbook of Whales and Dolphins. Sierra Club Books, San Francisco, 302 pp.
- LICHTER A & A HOOPER 1984. Guía para el reconocimiento de cetáceos del Mar Argentino. Fundación Vida Silvestre Argentina, 96 pp.
- MATKIN CO & S LEATHERWOOD 1986. General biology of the killer whale. *Orcinus orca*: a synopsis of knowledge. In Behavioral Biology of Killer Whales. BC Kirkeveld & JS Lockard (eds.). Alan R. Liss, Inc., New York, pp. 35-68.
- MINASIAN SM, BALCOMB III KC & L FOSTER 1984. The World's Whales. Smithsonian Institution, 244 pp.
- MITCHELL E 1970. Pigmentation pattern evolution in delphinid cetaceans: an essay in adaptive coloration. **Canadian Journal of Zoology** 48(4): 717-40.
- NISHIWAKI M & KS NORRIS 1966. A new genus, *Peponocephala*, for the odontocete cetacean species *Electra electra*. **Scientific Reports of the Whales Research Institute** 20: 95-100.
- NORRIS KS (ed.) 1961. Standardized methods for measuring and recording data on the smaller cetaceans. The Committee on Marine Mammals, American Society of Mammalogists. **Journal of Mammalogy** 42(4): 471-76.
- PERRIN WF 1972. Color patterns of spinner porpoises (*Stenella cf. longirostris*) of the eastern Pacific and Hawaii, with comments on delphinid pigmentation. **Fishery Bulletin of the Fish and Wildlife Service US**, 70: 983-1003.
- PERRIN WF 1975. Variation of spotted and spinner porpoise (genus *Stenella*) in the eastern Pacific and Hawaii. **Bulletin Scripps Institute of Oceanography** 21: University of California Press, Berkeley, 206 pp.
- PERRIN WF 1990. Subspecies of *Stenella longirostris* (Mammalia: Cetacea: Delphinidae). **Proceedings of the Biological Society of Washington** 103(2): 453-463.
- PERRIN WF, AKIN PA & JV KASHIWADA 1991. Geographic variation in external morphology of

- the spinner dolphin *Stenella longirostris* in the eastern Pacific and implications for conservation. **Fishery Bulletin**, 89: 411-428.
- PERRIN WF & SB REILLY 1984. Reproductive parameters of dolphins and small whales of the family Delphinidae. **Reports of the International Whaling Commission, Special Issue 6**: 97-133.
- PERRIN WF, SLOAN PA & JR HENDERSON 1979. Taxonomic status of the "southwestern stocks" of spinner dolphin *Stenella longirostris* and spotted dolphin *S. attenuata*. **Reports of the International Whaling Commission 29**: 175-184.
- QUAYLE L 1988. Dolphins and Porpoises. Gallery Books, New York, 144 pp.
- READ AJ, VAN WAEREBEEK K, REYES JC, MCKINNON JS & LC LEHMAN 1988. The exploitation of small cetaceans in coastal Peru. **Biological Conservation 46**: 53-70.
- RIDGWAY SH 1976. Statement at Hearings before the Subcommittee on Fisheries and Wildlife and the Environment, U.S. House of Representatives Merchant Marine and Fisheries Committee, May 4, 1976 [not seen].
- SERGEANT DE 1962a. The biology of the pilot whale or pothead whale *Globicephala melaena* (Traill) in Newfoundland waters. **Bulletin Fisheries Research Board of Canada 132**: 1-84.
- SERGEANT DE 1962b. On the external characters of the blackfish or pilot whales (genus *Globicephala*). **Journal of Mammalogy 32**(3): 395-413.
- SLIJPER EJ 1962. *Whales*: Basic books, 511 pp.
- STSC, Inc. 1989. STATGRAPHICS [software]. Statistical Graphics System by Statistical Graphics Corporation, Rockville, USA.
- SUNDFOR H 1939. A pedigree of skin-spotting in man - 42 piebalds in a Norwegian family. **Journal of Heredity 30**: 67-77.
- VAN WAEREBEEK K 1992. Population identity and general biology of the dusky dolphin *Lagenorhynchus obscurus* (Gray, 1828) in the Southeast Pacific. Ph.D. thesis, University of Amsterdam. 160 pp.
- VAN WAEREBEEK K 1993. Geographic variation and sexual dimorphism in the skull of the dusky dolphin *Lagenorhynchus obscurus* (Gray, 1828). **Fishery Bulletin 91**(4): 754-774.
- VAN WAEREBEEK K & AJ READ. In press. Reproduction of dusky dolphins *Lagenorhynchus obscurus* from coastal Peru. **Journal of Mammalogy**.
- VAN WAEREBEEK K & JC REYES. 1990. Catch of small cetaceans at Pucusana port, central Peru, during 1987. **Biological Conservation 51**(1): 15-22.
- VAN WAEREBEEK K & JC REYES. In press. The interaction of small cetaceans and Peruvian fisheries, catch statistics 1988-1989 and analysis of trends. In *Mortality of Cetaceans in passive Fishing Nets and Traps*, International Whaling Commission (Special Issue).
- WALKER WA, GOODRICH KR, LEATHERWOOD S & RK STROUD 1984. Population biology and ecology of the Pacific white-sided dolphin, *Lagenorhynchus obliquidens*, in the northeastern Pacific. Part II: biology and geographical variation. Adm. Report LJ-84-34C, NMFS/SWFC, La Jolla, California, 39 pp.
- WALKER WA, LEATHERWOOD S, GOODRICH KR, PERRIN WF & RK STROUD 1986. Geographical variation and biology of the Pacific white-side dolphin, *Lagenorhynchus obliquidens*, in the north-eastern Pacific. In *Research on Dolphins*. MM Bryden and Harrison (eds.). Oxford University Press, Oxford, pp. 441-465.
- WATERHOUSE GR 1838. The Voyage of H.M.S. Beagle during the years 1832-1836. Mammalia, part II. London, 96 pp.
- WATSON L 1981. *Whales of the World*. Hutchinson & Co., London, 302 pp.
- WEBBER M 1987. A comparison of dusky and Pacific white-sided dolphins (Genus *Lagenorhynchus*): morphology and distribution. M.Sc. thesis, San Francisco State University, 102 pp.
- WEBBER M & S LEATHERWOOD 1990. Dusky dolphin, *Lagenorhynchus obscurus*. In *Whales and dolphins*. A.R. Martin (ed.). Salamander Books, London, pp. 154-155.
- WONNACOTT TH & RJ WONNACOTT 1969. *Introductory Statistics*. Fifth edition 1990, John Wiley & Sons, New York, 711 pp.
- WÜRSIG B 1991. Cooperative foraging strategies: an essay on dolphins and us. **Whalewatcher 25**(1): 3-6.
- WÜRSIG B & TA JEFFERSON 1990. Methods of photo-identification for small cetaceans. **Reports of the International Whaling Commission, Special Issue 12**: 43-52.
- WÜRSIG B, KIECKHEFER TR, JEFFERSON TA 1990. Visual displays for communication in cetaceans. In *Sensory Abilities of Cetaceans*. J. Thomas & R. Kastelein (eds.), Plenum Press, New York, pp. 545-559.
- WÜRSIG B & M WÜRSIG 1978. Day and night of the dolphin. **Natural History 88**(3): 60-67.
- WÜRSIG B, WÜRSIG M & F CIPRIANO 1989. Dolphins in different worlds. **Oceanus 32**(1): 71-75.
- YÁÑEZ P 1948. Vertebrados marinos chilenos I: mamíferos marinos. **Revista de Biología Marina (Chile) 1**(2): 103-23.

YONEKURA M, MATSUI S & T KASUYA 1980. On the external characters of *Globicephala macrorhynchus* off Taiji, Pacific coast of Japan.

Scientific Reports of the Whales Research Institute 32: 67-95.

ZAR JH 1974. Biostatistical Analysis. Second Ed. 1984. Prentice-Hall Inc., New Jersey, 718 pp.