

Abstract.—Variation in skulls of 415 dusky dolphins, *Lagenorhynchus obscurus*, was studied based on 37 standard cranial measurements and meristic variables and 28 non-metrical characters (NMC) by using both bivariate and multivariate analyses. Geographic variation was analysed in mature skulls from central Peru ($N=189$), Chile ($N=22$), New Zealand ($N=47$) and southwestern Africa ($N=40$). Advanced fusion in the frontal-supraoccipital suture is the most reliable (95% efficiency) cranial criterion of sexual maturity; distal fusion in premaxillary and maxillary cannot be used. Sexual dimorphism, verified with *t*-tests and analysis of covariance, was encountered in only 6 of 37 measurements and in none of the NMC characters. Although skull size is the same, males have a wider rostrum and a longer temporal fossa than females. Analyses of covariance and *t*-tests indicated highly significant differences between geographic groups. A discriminant analysis successfully classified 96.5%, 91.7%, and 90.9% of skulls from respectively the South-east Pacific (Peru and Chile pooled), New Zealand, and SW Africa. Such differentiation is considered of subspecific level. All methods indicated higher morphological similarity within the Peru/Chile and SW Africa/New Zealand grouped pairs than between the pairs. Most strikingly, skulls from New Zealand and SW Africa are on average 3.1 cm (8.5%) shorter than these from Peru and Chile, concordant with differences in body length. New Zealand specimens differ from SW African animals by smaller tooth size and a greater number of teeth. Nine cranial variables revealed significant variation between dusky dolphins from central Peru and northern Chile, but the degree of heterogeneity should be re-evaluated with a larger sample from Chile. NMC characters confirmed the trends mentioned but resolving power was limited; their use is not recommended as the principal method for subspecific discrimination. The Peruvian dusky dolphin is thought to represent the most ancestral (plesiomorph) form from which the others were derived through dispersion via the east-flowing Westwind Drift.

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Geographic variation and sexual dimorphism in the skull of the dusky dolphin, *Lagenorhynchus obscurus* (Gray, 1828)

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The dusky dolphin, *Lagenorhynchus obscurus* (Gray, 1828), is mainly encountered in temperate coastal waters off Peru, Chile, Argentina, New Zealand, and South Africa (Gaskin, 1968; Webber, 1987; Van Waerebeek, 1992, a and b). Records, either specimens or sightings, are also available from Namibia¹ (Rose and Payne, 1991) and Angola².

This species was originally suggested to have a continuous circumpolar distribution (Brownell, 1965; Hershkovitz, 1966; Mörzer Bruyns, 1971); however, owing to its coast-dwelling habits many authors favor the notion of a disjunct distribution and existence of several isolated stocks (Brownell, 1974; Anonymous, 1975; Leatherwood and Reeves, 1983; Webber, 1987; Webber and Leatherwood, 1990). Nevertheless, evidence to support this hypothesis is lacking. Possible pelagic occurrence of dusky dolphins in the southern oceans and off many oceanic islands remains unknown. Specimen records are documented from the Campbell, Auckland, and Chatham Islands around New Zealand (Gaskin, 1968; Baker, 1983; Webber, 1987), the Falkland Islands (British Museum of Natural History specimens; Brownell, 1965)

and from Gough Island (40°20'S, 10°00'W) on the mid-Atlantic Ridge³. Presence of dusky dolphins off southern Australia and Tasmania (reviewed by Webber, 1987; Van Waerebeek, 1993) and off the Kerguelen Islands (Robineau, 1991) could not be confirmed. Kasamatsu et al.⁴ reported a single sighting from south of Madagascar but no photographs were taken and both the unusual (for *L. obscurus*) sea surface temperature (25°C) and offshore location solicits some caution. The sighting of a group of *Lagenorhynchus* sp. in deep tropical waters of the South Pacific, for instance, resulted in considerable debate before they were identified as *L. australis*, despite the availability of excellent photographs (Leatherwood et al., 1991).

Incidental fishing mortality occurs throughout the range of dusky dolphin and it is heavily exploited in Peru (Read et al., 1988; Van Waerebeek and Reyes, 1990, 1993) and, locally, off northern Chile (Van Waerebeek and

³P.B. Best, South African Museum, unpubl. photographs, identification confirmed by the author.

⁴Kasamatsu, F., G. Joyce, P. Ensor, and J. Mermoz. 1990. Current occurrence of Cetacea in the southern hemisphere; results from the IWC/IDCR southern hemisphere minke whale assessment cruises, 1978/79–1987/88. Doc. SC/42/015 presented to the Int. Whal. Comm. Sci. Committee, 77 p.

¹P.B. Best, South African Museum, pers. commun. February 1991.

²P.B. Best, South African Museum, unpubl. photograph, identification confirmed by author.

Guerra, 1986⁵; Guerra et al., 1987). Population identification is needed so that breeding units can be managed separately. Cranial measurements have been used to discriminate populations in several delphinids including the common dolphin, *Delphinus delphis* (Evans, 1975, 1982; Heyning and Perrin⁶), bottlenose dolphin, *Tursiops truncatus* (Ross, 1977; Walker, 1981⁷), tucuxi, *Sotalia fluviatilis* (Borobia and Sergeant, 1989), pantropical spotted dolphin, *Stenella attenuata*, and spinner dolphin, *S. longirostris* (Perrin, 1975, a and b; Perrin et al., 1979; Schnell et al., 1982⁸, 1985; Douglas et al., 1984).

In addition to skull measurements, non-metrical cranial characters have also been employed in population studies: harbor porpoises, *Phocoena phocoena* (Sjovold, 1977; Kinze, 1985, 1990⁹), spotted and spinner dolphins (Perrin et al., 1982¹⁰; Yablokov et al., 1983) and common dolphins (Perrin et al., 1988¹¹, 1989). The resolving power of non-metrical methods has been difficult to assess, however, because the identities of the dolphin stocks on which the technique was applied were debatable and results somewhat equivocal (Perrin et al., 1988¹¹, 1989). Also, non-metrical methods are more prone to observer bias and drift in character-

state evaluation over time, especially if large samples are involved (e.g., Perrin et al., 1982¹⁰, 1989).

Of the six extant species of *Lagenorhynchus*, geographic variation has been examined for the three northern hemisphere species: Pacific white-sided dolphin, *L. obliquidens* (Walker et al., 1986), Atlantic white-sided dolphin, *L. acutus*, and whitebeaked dolphin, *L. albirostris* (Mikkelsen, 1991). The purpose of this paper is to quantify sexual dimorphism and individual and geographical variation in skulls of *L. obscurus* from Peru, Chile, southwestern Africa (including South Africa, Namibia and Angola), and New Zealand utilizing material currently available in scientific collections. Evidence for separate dusky dolphin populations, as presented below, should urge agencies responsible for marine resource management in aforementioned coastal states to take special steps to ensure the conservation of *L. obscurus* on a stock by stock basis, rather than to evaluate the status of the species on a global scale.

Material and methods

Skulls were obtained by the author from animals recently killed in fishery operations as well as from museum specimens with widely variable degrees of documentation. Of more than 300 cranial specimens of *L. obscurus* from central Peru, collected along a coastal strip between Huacho (11°10'S) and San Andrés (13°50'S) in the period 1984 to 1990, 239 skulls were adequate for study. The majority of these were obtained from freshly butchered dusky dolphins at the wharves of Pucusana (12°30'S) and Cerro Azul (13°00'S); the rest were retrieved from decomposed remains at local fish-offal dumps or were beach-cast. When available, biological data, including sex, standard body length (SL) and reproductive status, were recorded for each specimen. Skulls were deposited at the Centro Peruano de Estudios Cetológicos, Pucusana, Peru; the Zoölogisch Museum of the University of Amsterdam; the Koninklijk Belgisch Instituut voor Natuurwetenschappen (Brussels); and at the U.S. National Museum of Natural History, Washington D.C. Surveys to collect stranded and by-caught specimens in northern Chile were carried out in collaboration with colleagues from the Instituto de Investigaciones Oceanológicas, Universidad de Antofagasta, Antofagasta, Chile (Van Waerebeek and Guerra, 1986⁵; Guerra et al., 1987).

The remainder of cranial material was located at the following institutions: the American Museum of Natural History, New York; British Museum (Natural History), London; Canterbury Museum and Canterbury University, Christchurch, New Zealand;

⁵Van Waerebeek, K., and C. Guerra. 1986. Review of the distribution and status of the Burmeister's porpoise in Chile. Cetacean survey in II region of Chile, August-September 1986. Instituto de Investigaciones Oceanológicas, Universidad de Antofagasta, casilla 170, Antofagasta, Chile. Unpubl. Rep., 13 p.

⁶Heyning, J. E., and W. F. Perrin. 1991. Re-examination of two forms of common dolphins (genus *Delphinus*) from the eastern North Pacific; evidence for two species. Dep. Commer., NOAA, Natl. Mar. Fish. Serv., Southwest Fish. Sci. Cent., P.O. Box 271, La Jolla, CA 92038. Admin. Rep. LJ-91-28, 37 p.

⁷Walker, W. A. 1981. Geographic variation in morphology and biology of bottlenose dolphins (*Tursiops*) in the eastern North Pacific. Dep. Commer., NOAA, Nat. Mar. Fish. Serv., Southwest Fish. Sci. Cent., P.O. Box 271, La Jolla, CA 92038. Admin. Rep. LJ-81-03C, 54 p.

⁸Schnell, G. D., M. E. Douglas, and D. J. Hough. 1982. Geographic variation in morphology of spotted and spinner dolphins (*Stenella attenuata* and *S. longirostris*) from the eastern tropical Pacific. Dep. Commer., NOAA, Natl. Mar. Fish. Serv., Southwest Fish. Sci. Cent., P.O. Box 271, La Jolla, CA 92038. Admin. Rep. LJ-82-15C, 213 p.

⁹Kinze, C. C. 1990. Non-metric analysis of harbour porpoises (*Phocoena phocoena*) from the North and Baltic seas: implications for stock identity. Unpubl. Paper SC/42/SM35 presented to the IWC Sci. Committee, June 1990.

¹⁰Perrin, W. F., A. V. Yablokov, and V. L. Cass. 1982. Preliminary report on the use of non-metrical skull characters to discriminate populations of pelagic dolphins. Dep. Commer., NOAA, Natl. Mar. Fish. Serv., Southwest Fish. Sci. Cent., P.O. Box 271, La Jolla, CA 92038. Admin. Rep. LJ-82-14, 32 p.

¹¹Perrin, W. F., A. V. Yablokov, J. Barlow, and M. V. Mina. 1988. The use of non-metrical skull characters for analyzing geographical variation in the common dolphin, *Delphinus delphis*. Part 1: Selection of characters. Dep. Commer., NOAA, Natl. Mar. Fish. Serv., Southwest Fish. Sci. Cent., P.O. Box 271, La Jolla, CA 92038. Admin. Rep. LJ-88-20, 24 p.

Departamento de Ciencias del Mar, Universidad Arturo Prat, Iquique, Chile; Museo Nacional de Historia Natural, Santiago de Chile; National Museum of New Zealand, Wellington; Otago Museum and Otago University, Dunedin, New Zealand; Port Elizabeth Museum, Port Elizabeth, and South African Museum, Cape Town, South Africa; U.S. National Museum of Natural History, Washington D.C.; and the Zoologisch Museum, University of Amsterdam. Unfortunately, only a very few skeletal specimens from the SW Atlantic are available in Argentinian collections¹² and, for reasons of economy, it was impractical to examine these. Metrical and non-metrical data sets were collected by the author only, in order to reduce error and observer bias as a source of variation.

Cranial maturity

Juvenile specimens were excluded from the sample to reduce variability due to age. As many skull specimens did not have sexual maturity data, mature skulls were selected partly by using indirect criteria. To identify one or more cranial indicator(s) of sexual maturity in *L. obscurus*, selected sutures were inspected in 85 skulls (48 females, 37 males) from sexually mature specimens from Peru and in 31 skulls from subadults (large sexually immature specimens) from Peru, SW Africa, and New Zealand. Skulls which had been boiled (moderate heating for maceration excepted) or chemically treated were not included.

The degree of suture fusion between cranial elements was scored as: 0= no fusion, elements can be moved freely; 1= limited fusion, suture line clearly visible at all points; or 2= advanced fusion with partial obliteration of suture line. Occlusion of the pulp cavity in teeth (OCCL) was scored as: 0= wide open; 1= partially occluded; or 2= occlusion complete. The following seven cranial sutures were defined as follows:

SYM	symphysis mandibularis (between left and right ramus)
MXDIST	distal maxilla-premaxilla suture (rostral distal fusion)
PTPAL	pterygoid-palatine suture
PTBAS	pterygoid-basioccipital suture
LAC	lacrimal-maxilla/frontale suture
ZYG	zygomatic-parietal/exoccipital suture
FROC	frontal-supraoccipital suture.

The selection criteria for adult skulls were, in decreasing order of priority:

1 Skulls of sexual mature specimens as evidenced in males by presence of seminal fluid upon gross examination of the epididymis (Sergeant, 1962); in females by presence of at least one corpus luteum or corpus albicans in the ovaries or if lactating or pregnant, or both;

2 Advanced fusion (score 2) in the frontal-supraoccipital suture or advanced fusion in at least two of the other six defined cranial sutures.

The complete fusion of thoracic vertebral epiphyses, indicating physical maturity, was used to confirm cranial maturity of some specimens.

Metrical characters

Thirty-three standard metrical variables measured with vernier calipers to the nearest mm and four tooth counts, adapted from Perrin (1975a) and Schnell et al. (1982⁸) (see Table 3) were recorded for 381 dusky dolphin skulls. Standardized skewness and kurtosis were computed for all sample variables; if significant departure from normality was suspected, a Kolmogorov-Smirnov (*K/S*) one-sample test of the fit was applied. A ratio of variances test with 95% confidence limits was used to verify homogeneity of variance in all sample pairs. STATGRAPHICS version 4.2 programme (STSC Inc., 1989) was used on an AT286 personal computer for most statistical applications. The $\alpha=0.05$ level was the criterion chosen for significance. All *t*-tests were two-sided. Owing to the large series of *t*-tests, a few significant results (false positives) should be expected to occur by chance alone.

Sexual dimorphism in cranial measurements and tooth counts was studied by means of *t*-tests and analysis of covariance (ANCOVA, with condylobasal length as covariate) in skulls of sexually mature females (*N*=59) and males (*N*=50) from central Peru. To permit pooling of sexes and utilization of cranially mature skulls of unknown sex, the few sexually dimorphic characters were not further considered in the analysis of geographic variation.

Seasonal variation was examined for in all variables by using a multifactor analysis of covariance (MANCOVA) with three-monthly seasons (January–March, April–June, etc.) and sex as classification variables.

Geographic variation was analysed for skulls from Peru (59 females, 50 males and 80 of unknown sex), New Zealand (*N*=47), SW Africa (*N*=40) and Chile (*N*=22). Both a one-way analysis of variance (ANOVA) and an ANCOVA with skull CBL as covariate and with geographic region as classification variable were utilized to assess among-group variation in skull size and shape. Next, most morphologically similar group pairs,

¹²R. N. P. Goodall, Centro Austral de Investigaciones Cientificas, Ushuaia. Pers. commun. July 1988.

namely Peru/Chile and SW Africa/New Zealand were compared by means of *t*-tests to identify discriminating variables.

Discriminant analyses (DISCRIM) were performed on samples limited to specimens with a complete set of measurements. This sample included 135 skulls from Peru, 24 from New Zealand, 22 from SW Africa and 7 from Chile. A first DISCRIM with 21 characters maximized discrimination between geographic groups. Subsequently, a series of discriminant analyses was executed by considering various combinations of a small number of highly variable cranial characters so that an optimum segregation between groups was obtained. These discriminant functions can be used tentatively to assign undocumented museum skulls to respective populations. It must be cautioned however that no specimens from Argentina have been examined and the discriminant locus of that population remains unknown.

Non-metrical characters

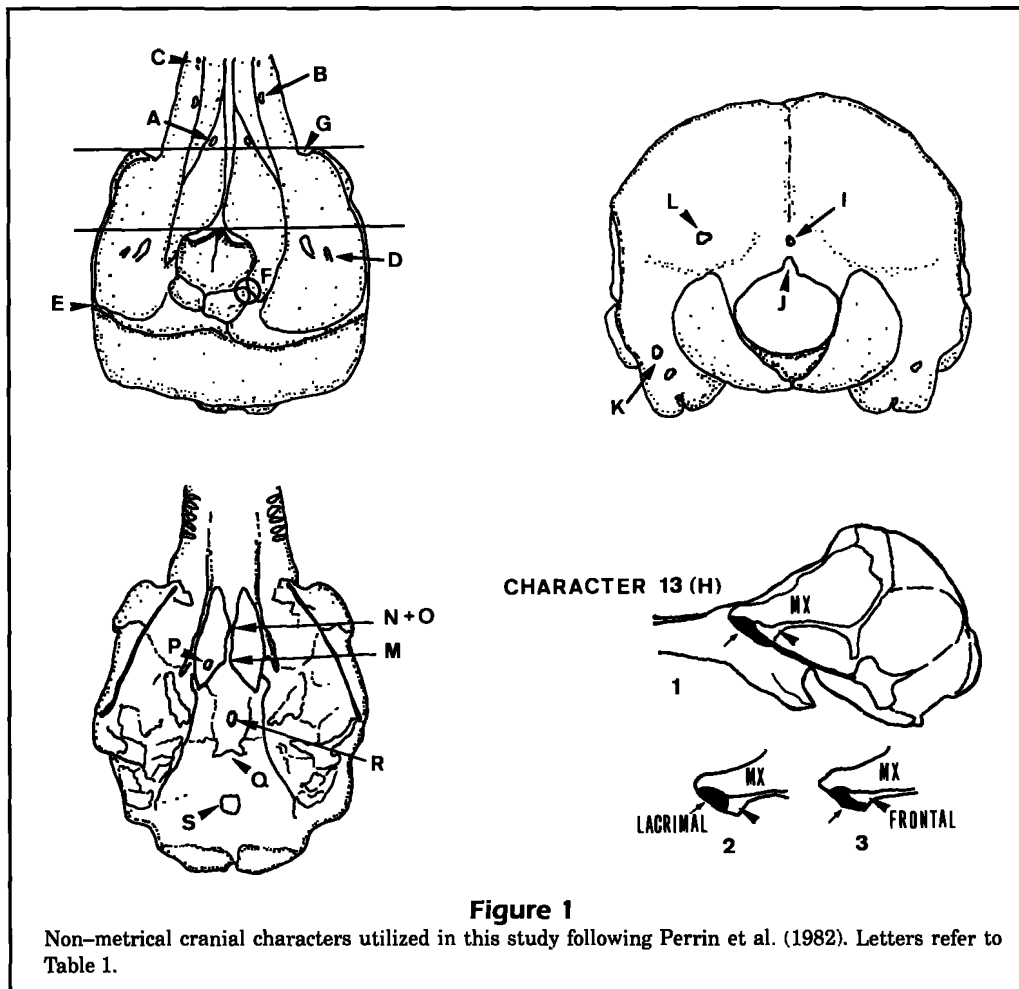
Initially, 35 non-metrical cranial characters (NMC), following Perrin et al. (1982¹⁰), were determined, but serious problems with score repeatability over time reduced the number of usable NMC to 27 (Table 1 and Fig. 1). Similar problems have been reported for the common dolphin by Perrin et al. (1988¹¹, 1989).

Analysis of sexual dimorphism was limited to skulls of sexually mature specimens from central Peru ($N=109$), eliminating influences of growth and geography. Sexually monomorphic characters (the full set, see Results) were then tested for dependence on cranial maturity status in 173 mature and 48 immature skulls. Geographic variation in non-metrical traits among the four geographic areas was studied after eliminating variables influenced by sex and maturity. All significance testing of variation in NMC was done by means of chi-square contingency analyses. Tooth counts were compared by *t*-tests.

Table 1

Non-metrical cranial characters utilized in present study (from Perrin et al., 1982⁹); see Figure 1.

Character 1L/1R (left/right).	Position of the foramen (A in Figure 1) in the premaxillary at the base of the prenasal triangle, relative to the level of the anteriormost projection of the antorbital processes. Codes: 1=at; 2=ahead; 3=behind the level.
Character 2L/2R.	Position of the anteriormost large foramina (B) in the maxillary relative to the level of the anteriormost projection of the antorbital processes. Codes: 1=at; 2=ahead; 3=behind the level.
Character 3.	Asymmetry of position of the two anteriormost large maxillary foramina (B). Codes: 1=symmetrical; 2=left foramen more anteriorly placed; 3=right foramen more anterior.
Character 5L/5R.	Number of small foramina (C) in the maxillary anterior to the anteriormost of the large foramina. Codes: 1=one foramen; 2=two foramina; 3 etc.; 6=no foramina.
Character 6L/6R.	Number of foramina (D) in the maxillary behind a line at the level of the anterior edge of the external nares and perpendicular to the long axis of the skull. Codes: 1=1 foramen; 2=2 foramina; 3 etc.; 6= no foramina.
Character 9L/9R.	Contact between maxillary and occipital, at point where occipital crest intersects margin of temporal fossa (E). Codes: 1=contact (or space of <1mm); 2=no contact.
Character 10.	Contact between premaxillary and nasal, on right side (F). Codes: 1=contact (or space of <1mm); 2=no contact.
Character 12L/12R.	Presence of an antorbital notch (G). Codes: 1=notch present; 2=not present.
Character 13.	Composition of the antorbital process, in lateral view, on left side (H). Codes: 1=formed by lacrimal; 2=formed by lacrimal and frontal; 3=formed by lacrimal and maxillary.
Character 16.	Accessory foramen above foramen magnum (I). Codes: 1=present; 2=absent.
Character 17.	Clear notch in upper margin of foramen magnum (J). Codes: 1=present; 2=absent.
Character 18L/18R.	Fenestrations in occipitals, near foramen magnum and in exoccipital region (K). Codes: 1=one fenestration; 2=two; 3 etc.; 6=no fenestrations.
Character 19.	Fenestrations in region of occipital swellings (L). Codes: 1=one fenestration; 2=two etc.; 6= no fenestration.
Character 23.	Posterior contact between pterygoid hamuli (M). Codes: 1=open (gap >1mm); 2=closed.
Character 24.	Anterior contact between hamuli (N). Codes: 1=open (gap >1mm); 2=closed.
Character 25.	Spine of palatines visible in anterior gap between hamuli (O). Codes: 1=visible; 2= not visible.
Character 30.	Mesial fenestration in basisphenoid (R). Codes: 1=foramen present; 2=absent.
Character 33L/33R.	Number of mental foramina. Codes: 1=1; 2=2; etc.
Character 34L/34R.	Arrangement of mental foramina. Codes: 1=foramina lie along a simple curve; 2=foramina do not lie along a simple curve.



Results

Cranial maturity

Relationships between the degree of fusion in cranial sutures and sexual maturity for *L. obscurus* are shown in Table 2. Less than 25% of the adults exhibited advanced rostral distal fusion (MXDIST=2) which, as in *L. obliquidens* (see Walker et al., 1986), eliminates MXDIST as a selection criterion for adult skulls in this species (too many useful skulls would be rejected). However, three other sutures, frontale-supraoccipitale (FROC), zygomatico-parietale/exoccipitale (ZYG), and lacrimale-maxilla/frontale (LAC), had advanced fusion (state=2) in 95%, 89%, and 85%, respectively of the sexually mature specimens. Equally important, only two sexually immature specimens from New Zealand showed full fusion in any of these sutures: one was a pubescent female with large follicles (ZM39957) and the other, an unusually large female without ovarian corpora (ZM39561, 187 cm). Moreover, based on over-

all size, those skulls fitted into the adult series. Skulls with at least some fusion (state 1 or 2) in either MXDIST, SYM, or PTPAL are very likely from sexually mature dolphins (see Table 2).

Metrical characters

Individual variation Summary statistics for cranial characters in adult female and male dusky dolphins of central Peru are presented in Table 3. Of 74 characters tested, only one (upper left tooth count, for females) departed significantly from normality (Kolmogorov-Smirnov, $P=0.017$), which could be attributed to chance fluctuations. Homogeneity of variance (95% confidence, TWOSAM, STSC Inc., 1989) was confirmed for all sex-paired characters.

Statistics summarizing individual variation in cranial characters are given also for mature dusky dolphins of northern Chile, southwestern Africa and New Zealand (Table 3). No significant departures from nor-

Table 2

Percent frequencies, rounded to nearest integer, for degrees of fusion seen in cranial sutures of *Lagenorhynchus obscurus* specimens of known sexual maturity status (sexes pooled). Mature animals are all from Peruvian waters; subadults include specimens from Peru, southwestern Africa, and New Zealand. States of fusion are: 0= unfused; 1= some fusion; 2= advanced fusion. Cranial sutures are defined in text.

Suture	Subadults (%) Fusion state			Mature (%) Fusion state				
	N	0	1	2	N	0	1	2
SYM	31	94	3	3	71	47	28	25
MXDIST	29	100	0	0	77	23	53	23
PTPAL	30	97	3	0	85	4	28	68
PTBAS	30	80	20	0	85	4	28	68
LAC	30	50	50	0	85	0	15	85
ZYG	31	81	13	6	85	1	9	89
FROC	31	45	48	6	85	0	5	95
OCCL	—	—	—	—	90	4	41	54

mality were encountered in any of the characters (K/S , $P>0.5$).

Sexual dimorphism The overall size of the adult dusky dolphin skull, based on condylobasal length and zygomatic width, is equal in males and females (t -tests, $P>0.50$; Tables 3 and 4). Highly significant sexual dimorphism (t -tests, $P<0.005$) was found in the width of the rostrum over most of its length (RW60, RW1/4, RW1/2, PMX1/2, RW3/4) and in the length of the temporal fossa; males had consistently higher mean widths. Analyses of covariance showed sexual dimorphism in exactly the same variables and with very similar significance levels as in the two-sided t -tests, indicating proportional differences (shape). However, it is uncertain whether the observed, small dissimilarities have biological meaning, particularly as there is wide overlap in ranges. I was unable to produce a satisfactory model to predict the sex of an unknown animal through stepwise variable selection in a multiple regression (see Douglas et al., 1986) exactly because of those subtle deviations.

Twenty-four of 36 characters showed significant correlations with the condylobased length (CBL) covariate, including five of the six dimorphic characters (Table 4), implying that much of the variability is explained by variation in CBL. Eliminating dimorphic characters from the geographic analysis therefore entails little loss of information.

Seasonal variation An analysis of seasonal variation was feasible only for Peruvian specimens. Skull size (CBL) was not seasonally dependent (MANCOVA, $F=1.45$, $df=3$, $P=0.23$) but six other skull characters (RW60, RW1/4, APL, RAL, TCUL, and TCUR) demon-

strated seasonal variation at a low level of significance (MANCOVA, $0.05 < P < 0.02$). However, at least in the case of RW60, RW1/4, and RAL, significant interactions due to sexual dimorphism in these measurements seemed to be the cause (P -values for 2-factor interactions were respectively 0.039, 0.047, and 0.037). In APL, TCUL, and TCUR, which are sexually monomorphic characters (see above), there were no sex/season interactions ($P>0.50$). The significance in these few cases could be due to chance in view of the large number of t -tests. This is supported by the results of a series of Runs tests (Runs above and

below median, Runs up and down, STSC Inc., 1989) on chronologically ordered CBL, tooth counts and tooth widths. These results did not suggest any non-randomness ($Z>0.05$ for all tests).

Geographic variation Exclusion of the few sexually dimorphic characters allowed combining samples of males and females and the use of cranially mature skulls of unknown sex. Highly significant differences between geographic regions were confirmed for 29 of 31 cranial characters (for all ANOVA, $P<0.005$ and mostly $P<0.0001$; Table 5). Tympanic bulla width (BW) proved divergent between groups but with less confidence (ANOVA, $F=4.1$, $df=3,117$, $P=0.019$) and no difference could be detected for periotic length (ANOVA, $F=0.24$, $df=3,201$, $P=0.87$). Variance generally was homogeneous (Cohran's C -test and Bartlett's test, $P>0.01$ and mostly $P > 0.05$); exceptions include TLL (Cohran's, $P=0.006$) and PEL (Cohran's, $P=0.003$; Bartlett's, $P=0.009$).

ANCOVA analyses revealed discernible variation in 16 of 30 skull characters which can not be attributed to divergences in skull size alone but are due to proportional differences (i.e., shape); 11 characters were highly significantly different between geographic groups ($P<0.01$, Table 5). Means and 95% confidence intervals are plotted for each variable against geographic region (Fig. 2). The most striking element is the overwhelming difference in skull size, reflected in most measurements, grouping skulls from Peru and Chile and specimens from New Zealand and Southwest Africa. Skulls of dusky dolphins from the latter pair-group have, on average, a CBL about 3 cm shorter than skulls from Peru and Chile.

Table 3

Skull measurements (in mm) and tooth counts of mature dusky dolphins *Lagenorhynchus obscurus* from different populations. Sexes are pooled except for Peru; tooth counts of Chilean specimens include some juvenile specimens. Skull selection criteria are explained in text.

Zealand	Peru: Females				Peru: Males				Chile				SW Africa				New			
	Variable	N	Mean	SD	Range	N	Mean	SD	Range	N	Mean	SD	Range	N	Mean	SD	Range	N	Mean	SD
Condylbasal length (CBL)	59	398.4	12.6	368-426	49	396.9	11.3	372-420	14	394.9	9.57	377-410	34	365.8	11.0	342-386	41	367.0	10.9	344-388
Rostrum length (RL)	59	221.8	9.19	198-224	49	219.5	8.29	202-241	13	220.8	9.41	208-235	36	198.8	7.0	178-214	42	198.4	9.0	178-215
Rostrum width at base (RWB)	59	101.1	4.63	87-112	50	101.5	4.84	92-113	21	100.5	4.71	89-109	39	97.7	5.4	75-107	45	97.2	4.6	89-108
R. width at 60 mm (RW60)	59	74.7	3.35	68-82	50	76.9	3.62	68-84	21	74.8	3.47	69-80	40	67.8	3.2	59-75	45	66.7	3.4	61-77
R. width at 1/4 length (RW1/4)	58	75.5	3.21	69-83	49	77.8	3.55	69-85	16	76.1	3.36	70-82	36	70.1	2.8	64-76	41	68.6	3.3	63-78
R. width at 1/2 length (RW1/2)	59	65.3	2.95	59-72	49	67.5	3.4	59-75	16	66.3	3.93	58-71	36	60.2	2.9	54-68	42	59.2	3.5	53-67
Premax. width at 1/2 length (PMX1/2)	59	35.5	2.44	29-41	49	37.2	2.68	32-43	16	36.7	2.55	33-41	36	34.1	2.1	30-40	42	32.8	2.5	27-39
R. width at 3/4 length (RW3/4)	59	48.2	2.44	42-54	49	50.8	2.78	45-57	16	49.4	4.45	41-55	33	45.5	3.0	39-53	39	44.9	3.1	39-50
Rostrum tip to ext. nares (RTEN)	58	264.1	11.0	232-228	46	262.2	9.33	245-284	14	259.9	12.8	229-277	35	237.3	8.0	214-250	40	239.8	12.1	198-261
Rostrum tip to int. nares (RTIN)	58	261.5	11.2	232-228	49	260.0	10.8	240-283	10	259.6	8.98	246-274	28	235.1	8.0	219-250	35	238.1	9.2	214-254
Preorbital width (PROW)	57	166.9	4.89	151-117	50	167.6	4.19	159-178	19	164.3	6.0	154-178	32	159	4.7	151-169	43	158.9	5.7	145-171
Postorbital width (POOW)	57	184.4	5.54	168-119	50	184.8	4.97	176-198	16	184.0	5.98	175-195	33	175.4	4.8	164-186	40	175.8	5.4	166-190
Zygomatic width (ZYW)	57	187.6	5.17	178-119	50	188.3	5.59	179-202	17	187.2	5.85	178-199	34	177.8	5.2	165-191	44	177.7	5.4	167-194
Parietal width (PARW)	59	152.6	6.11	137-116	50	153.9	5.96	135-166	15	154.6	6.16	146-166	37	150.8	5.1	136-160	46	150.2	5.5	138-160
Greatest width premax. (GWPMX)	59	78.0	2.98	72-85	50	77.3	2.76	72-83	22	78.2	3.16	74-86	40	76.0	3.2	68-85	47	75.9	3.6	67-85
External nares width (ENW)	59	55.4	2.56	48-62	50	54.5	2.31	50-59	22	54.2	2.22	50-59	39	54.4	2.6	47-61	47	53.2	2.6	49-61
Temporal fossa length (TFL)	59	71.4	3.87	62-80	50	74.2	4.9	63-86	13	74.0	3.51	66-79	36	69.6	4.4	59-78	47	69.6	4.0	60-76
Temporal fossa width (TFW)	59	52.4	3.41	43-62	50	52.8	3.98	44-65	16	52.5	3.08	48-57	37	51.1	3.8	41-60	47	49.5	3.0	43-56
Orbit length (ORL)	58	52.2	2.35	48-58	50	52.1	2.32	48-59	18	52.8	2.24	47-56	35	51.0	2.4	45-56	46	49.8	2.1	45-56
Antorbital process length (APL)	58	38.1	2.89	32-45	50	38.7	2.76	33-46	17	36.3	2.11	32-40	37	34.8	2.8	29-41	46	35.5	3.3	26-42
Internal nares width (INW)	59	57.7	3.04	51-65	50	57.7	2.81	52-64	18	56.9	3.07	53-63	37	52.4	2.5	47-57	44	53.7	2.7	48-60
Pterygold length (PTEL)	55	65.5	4.3	57-77	50	64.4	4.0	56-74	11	62.1	2.74	57-66	30	59.0	4.0	51-73	35	57.7	4.0	49-66
Upper tooth row length (UTRL)	59	192.9	8.38	171-221	49	190.1	7.58	171-207	13	191.2	7.25	180-204	32	171.2	6.4	153-182	43	170.2	8.2	151-183
Lower tooth row length (LTRL)	55	192.7	7.54	171-220	47	190.9	8.16	171-210	11	183.5	9.09	172-195	34	172.4	7.5	159-187	41	170.7	8.5	143-191
Ramus length (RAL)	55	335.4	9.97	312-360	47	334.5	11.3	309-360	11	327.9	10.52	311-346	32	308.6	10.1	286-330	40	306.3	9.6	284-326
Ramus height (RAH)	54	69.2	2.95	63-80	47	69.3	2.65	62-74	9	68.8	1.92	66-71	31	65.1	2.6	60-71	40	65.3	2.6	60-71
Tooth count upper left (TCUL)	58	32.0	1.59	29-37	49	31.8	1.73	29-36	17	30.9	2.07	26-34	29	30.4	1.6	28-34	36	31.9	1.8	28-37
Tooth count upper right (TCUR)	58	32.0	1.74	29-39	49	31.8	1.69	29-36	14	30.6	1.9	26-33	30	30.2	1.7	27-33	37	32.0	1.6	29-36
Tooth count lower left (TCLL)	55	31.1	2.06	26-37	47	31.3	1.58	28-36	14	30.2	1.97	28-35	31	29.6	1.5	26-32	40	31.5	2.2	28-39
Tooth count lower right (TCLR)	55	30.8	2.14	26-37	47	31.0	1.41	28-36	17	30.4	2.26	27-35	32	29.6	1.5	27-34	40	31.4	2.2	27-37
Tooth width at mid-jaw (TW)	55	4.4	0.36	3.7-5.1	49	4.4	0.35	3.6-5.5	16	4.3	0.28	3.7-4.7	36	4.18	0.37	3.3-5.2	32	3.65	0.35	2.9-4.3
Maximum bulla length (BL)	55	35.4	1.19	33-39	49	35.4	1.38	33-38	5	34.6	0.89	34-36	30	34.0	1.1	32-36	18	33.9	1.2	31.5-36
Maximum bulla width (BW)	20	19.8	0.69	19-21.5	20	19.7	0.85	18.5-21.5	—	—	—	—	30	19.5	0.6	18.5-20.5	15	19.3	0.7	18-20.5
Height braincase (HBR)	58	109.5	4.45	101-119	50	110.3	4.45	100-119	19	109.9	5.25	103-21	37	107.1	4.0	99-119	45	105.0	4.8	93-115
Length braincase (LBR)	58	126.9	4.6	113-138	50	127.9	4.04	118-134	19	125.9	3.93	117-133	37	122.5	4.3	113-131	45	121.6	4.2	112-131
Periotic length (PEL)	54	30.2	1.16	28-33	49	30.33	1.06	27-32	6	30.5	1.64	28-33	27	30.0	1.2	28-32	12	30.4	1.3	28-32
Height crest (HCR)	52	7.66	2.13	3.9-14.5	48	7.17	1.77	4-12.5	—	—	—	—	30	5.5	2.1	1-10	41	7.2	2.1	3.5-13

Table 4

Results of two-sided *t*-tests and multifactor analysis of covariance (MANCOVA) to determine sexual dimorphism and seasonal variation (see text) in skull measurements of mature female (*N*=59) and male (*N*=50) *Lagenorhynchus obscurus* from Peru. Condylbasal length (CBL) is used as the covariate. Measurements are defined in the text.

Variable	MANCOVA					
	Two-sided <i>t</i> -test		Covariate (CBL)		Factor 1 (sex)	
	<i>t</i>	<i>P</i>	<i>F</i> -ratio	<i>P</i>	<i>F</i> -ratio	<i>P</i>
CBL	0.63	0.53	—	—	0.37	0.55
RL	1.33	0.19	328	<0.0001	2.0	0.16
RWB	0.49	0.62	0.43	0.52	0.32	0.58
RW60	3.32	<0.002	12.3	<0.001	12.1	<0.001
RW1/4	3.62	<0.0005	4.87	<0.05	12.8	0.0005
RW1/2	3.58	<0.0001	12.3	<0.0001	13.1	0.0005
PMX1/2	3.59	<0.0001	0.29	0.59	10.4	0.002
RW3/4	4.2	<0.0001	8.72	<0.005	18.7	<0.0001
RTEN	0.93	0.36	201.5	<0.0001	0.001	0.98
RTIN	0.74	0.46	470.4	<0.0001	0.29	0.59
PROW	0.78	0.44	13.3	<0.0005	0.71	0.41
POOW	0.31	0.75	12.38	<0.001	0.04	0.84
ZYW	0.64	0.52	16.8	0.0001	0.62	0.44
PARW	1.17	0.24	2.41	.012	1.40	0.24
GWPMX	1.29	0.20	1.68	0.20	1.54	0.22
ENW	1.74	0.09	0.91	0.35	2.98	0.09
TFL	3.36	<0.005	7.35	<0.01	10.54	0.002
TFW	0.61	0.54	0.05	0.94	0.13	0.72
ORL	0.19	0.85	35.1	<0.0001	0.63	0.44
APL	1.26	0.21	2.70	0.10	1.54	0.22
INW	0.10	0.92	3.31	0.07	0.01	0.92
PTEL	1.39	0.17	30.5	<0.0001	1.1	0.30
UTRL	1.75	0.08	281.5	<0.0001	3.56	0.06
LTRL	1.10	0.27	135.1	<0.0001	0.26	0.61
RAL	0.42	0.67	386.2	<0.0001	0.54	0.47
RAH	0.06	0.95	13.4	<0.0005	0.07	0.79
TCUL	0.76	0.45	4.79	<0.05	1.41	0.24
TCUR	0.65	0.51	4.73	<0.05	0.95	0.34
TCLL	0.53	0.60	1.42	0.24	0.08	0.78
TCLR	0.54	0.60	1.32	0.25	0.09	0.77
TW	0.08	0.94	4.63	<0.05	0.36	0.55
BL	0.05	0.96	15.6	0.0002	0.003	0.96
BW	0.41	0.69	0.26	0.62	0.008	0.93
HBR	0.95	0.35	5.14	<0.05	1.72	0.19
LBR	1.20	0.23	42.3	<0.0001	2.55	0.11
PEL	0.64	0.52	29.1	<0.0001	0.84	0.37
HCR	1.26	0.21	2.67	0.11	1.98	0.16

Southwest African versus New Zealand population Results of two-sided *t*-tests comparing adult skulls from southwest Africa and New Zealand are presented in Table 6. Skulls from these regions do not differ in size, as indicated by condylbasal length (*t*=0.48, *P*=0.63) and zygomatic width (*t*=-0.074, *P*=0.94). Nevertheless, the two populations are strikingly divergent in dentition. Mean tooth width for New Zealand dusky dolphins (3.56 mm, SD=0.35, *N*=32) is highly significantly smaller (*t*=-7.14, *P*<0.0001) than in SW African

dusky dolphins (4.18 mm, SD=0.37, *N*=36); the difference is visually obvious even from a quick inspection of skulls. In addition, New Zealand crania have on average 1.5–1.8 teeth more in each row than African skulls (two-sided *t*-tests, *P*<0.001). Maximum tooth counts in the four rows range 32–34 (SA) and 36–39 (NZ). Finally, SW African crania have a significantly lower supraoccipital crest (*t*=3.43, *P*=0.005), slightly wider external nares and temporal fossa and, possibly, a somewhat higher braincase (0.05<*P*<0.01) than the New Zealand specimens.

Peruvian versus Chilean population Dusky dolphin crania from central Peru and northern Chile showed no meaningful overall size differences, as indicated by CBL and ZYG (Table 6). The antorbital process (APL) and the lower tooth row (LTRL) however were very significantly shorter (*t*-test, *P*<0.005) and mean tooth counts were lower in Chilean animals. Small but statistically discernible deviations (*P*<0.05) were detected also in PROW, PTEL, and RAL. These data suggest that at least some genetic distance exists between *L. obscurus* stocks from central Peru and northern Chile, but it is recommended that the sample size for Chile be increased before definite conclusions be made.

Multivariate analysis Results of the discriminant analyses (DISCRIM) with a maximum of characters (21) fully confirm findings from bivariate techniques (Table 7); scores on first and second axis are shown in Figure 3. The first discriminant function differentiated well between population pairs Peru/Chile and New Zealand/SW Africa; the second function largely separated SW Africa and New Zealand stocks (Fig.4), whereas the third function projected the Chile group at the positive extreme of the z-axis (see group centroids, Table 7). The discriminant functions successfully predicted the actual group most of the time, i.e., from 85.7% of cases in Chile to 91.7% in New Zealand. When Chilean and Peruvian animals were combined into a single "Southeast Pacific stock," 96.5% (137 of 142) of these were correctly allocated. Only two of 24 (8.3%) New Zealand skulls were misclassified as SW African but they were never mistaken for SE Pacific animals. Two skulls out of 22 (9.2%) from SW Africa were erroneously assigned, one each to the New Zealand and Peru stocks. The highest percentages of misclassifications (10.4% and 14.3%) occurred among

Table 5

Geographic variation in cranial characters of mature *Lagenorhynchus obscurus* (N = 298) from Peru, Chile, southwestern Africa and New Zealand. Sexes were pooled after removal of sexually dimorphic variables (see Table 3). NS = not significant, $P > 0.05$.

Variable	ANOVA			ANCOVA	
	F-ratio	df	P	F-ratio	P
CBL	120.2	3,275	<0.0001	—	—
RL	118.3	3,274	<0.0001	2.48	NS
RWB	10.1	3,287	<0.0001	0.66	NS
RTEN	63.5	3,261	<0.0001	0.83	NS
RTIN	82.4	3,245	<0.0001	1.05	NS
PROW	40.0	3,273	<0.0001	2.46	NS
POOW	44.6	3,264	<0.0001	3.78	<0.02
ZYW	54.5	3,276	<0.0001	4.14	<0.01
PARW	6.88	3,282	<0.0005	0.87	NS
GWPMX	4.39	3,294	<0.005	1.99	NS
ENW	5.35	3,293	<0.0005	1.66	NS
TFW	13.2	3,285	<0.0001	3.65	<0.02
ORL	18.0	3,280	<0.0001	3.31	<0.05
APL	22.9	3,280	<0.0001	3.38	<0.05
INW	34.1	3,282	<0.0001	4.82	<0.005
PTEL	33.5	3,242	<0.0001	2.89	<0.05
UTRL	122.0	3,270	<0.0001	4.33	<0.01
LTRL	109.3	3,242	<0.001	8.92	<0.001
RAL	118.3	3,239	<0.0001	6.18	<0.001
RAH	34.9	3,232	<0.0001	0.14	NS
TCUL	7.4	3,256	<0.0005	6.68	<0.0005
TCUR	9.65	3,256	<0.0001	7.74	<0.0005
TCLL	11.7	3,236	<0.0001	8.85	<0.0001
TCLR	10.1	3,237	<0.0001	8.25	<0.0001
TW	50.3	3,260	<0.0001	25.2	<0.0001
BL	13.9	3,208	<0.0001	0.35	NS
BW	4.1	3,117	<0.02	0.70	NS
HBR	19.5	3,285	<0.0001	4.59	<0.005
LBR	28.4	3,285	<0.0001	1.08	NS
PEL	0.24	3,201	NS	2.31	NS
HCR	6.33	3,235	<0.0005	3.47	NS

Peruvian and Chilean crania, explainable by the relatively greater morphological similarity and geographic proximity. Overall there were successfully identified to geographical population 164 out of 188 (87.2%) of the skulls, increasing to 179 out of 188 (95.2%) when skulls from Chile and Peru were pooled.

Six characters with high discriminatory power were identified from the standardized discriminant function coefficients, *t*-tests and ANOVA's and an additional discriminant analysis was performed using those variables (Table 8). Classification results and the discriminant function plot (Fig. 4) demonstrate that specimen prediction remains fairly effective (143 of 188 or 76.1% and 171 out of 188 or 91.0% when the SE Pacific sample is pooled as one group).

Non-metrical characters

Tooth counts—As expected, tooth counts derived from skulls were consistently greater ($P < 0.0001$) than counts made on heads in the flesh because small, apical teeth frequently do not erupt from the gums (see Van Waerebeek, 1992b). Differences of mean tooth counts between skull and fresh specimens varied from 2.29 to 2.67 per jaw arcade. Considering confidence intervals, the best estimate (closest integer) for each of the four arcades was two more teeth visible in skulls than in heads in the flesh.

Tooth counts are bilaterally symmetrical in upper and lower jaws and for all sample pairs (*t*-tests, $P > 0.16$). The upper jaw has significantly more teeth than the lower jaw, (one-sided *t*-tests; $P < 0.005$ in all cases); confidence intervals included one (tooth) as the largest integer but not zero.

Sexual dimorphism—The 28 non-metrical cranial characters (NMC) tested are, without exception, independent of sex (chi-square contingency tests, $P > 0.05$). Sexual dimorphism neither exists in the number of teeth in Peruvian dusky dolphins, both as counted from skulls and from fresh animals (*t*-tests, $P > 0.25$). It is considered safe to assume that this is generally true for the other populations of *L. obscurus* and therefore the sexual factor is disregarded in the subsequent analyses.

Developmental variation—Twenty-two of the 28 NMC characters tested (78.6%) in Peruvian dusky dolphins are independent of maturity status (Table 9). Variables which may be correlated with age to some degree (chi-square, $P < 0.05$) include position of the left premaxillary foramen at the base of the premaxillary triangle (1L), presence of fenestration(s) in occipitals (18L) or basisphenoid (30), visibility of palatine spine (25), and the number of mental foramina (33L). At least one of these is expected to be due to chance fluctuation ($\alpha = 0.05$). The more frequent occurrence of a notch in the upper margin of the foramen magnum (17) in immature animals as compared to adults proved highly significant (chi-square=8.83, $P < 0.005$).

Geographic variation—The six growth dependent characters were removed from the data set before variation between populations was tested. By doing this, samples available for geographic variation analysis were greatly enhanced as juvenile specimens (but not neonates) could be included. Table 10 lists absolute

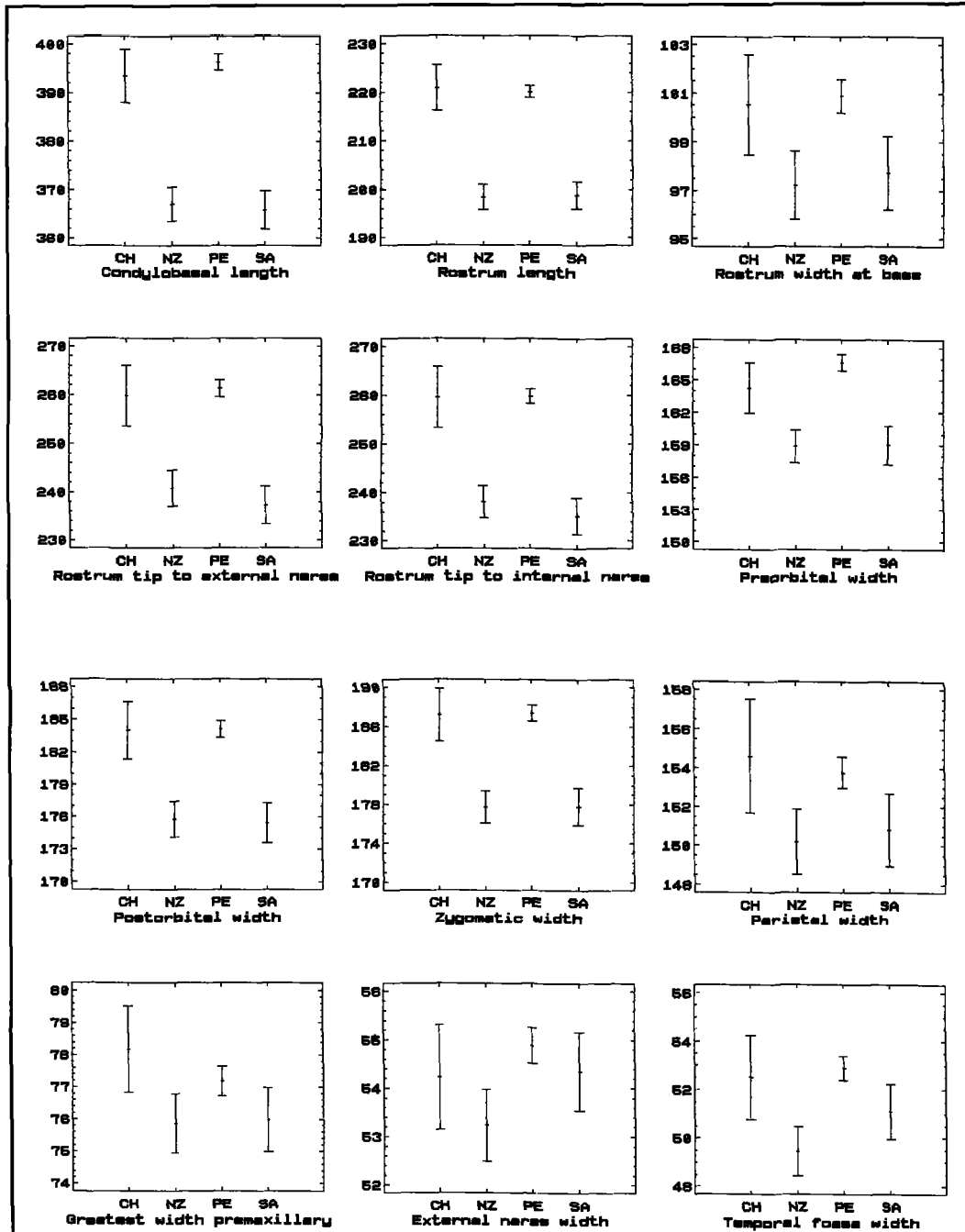
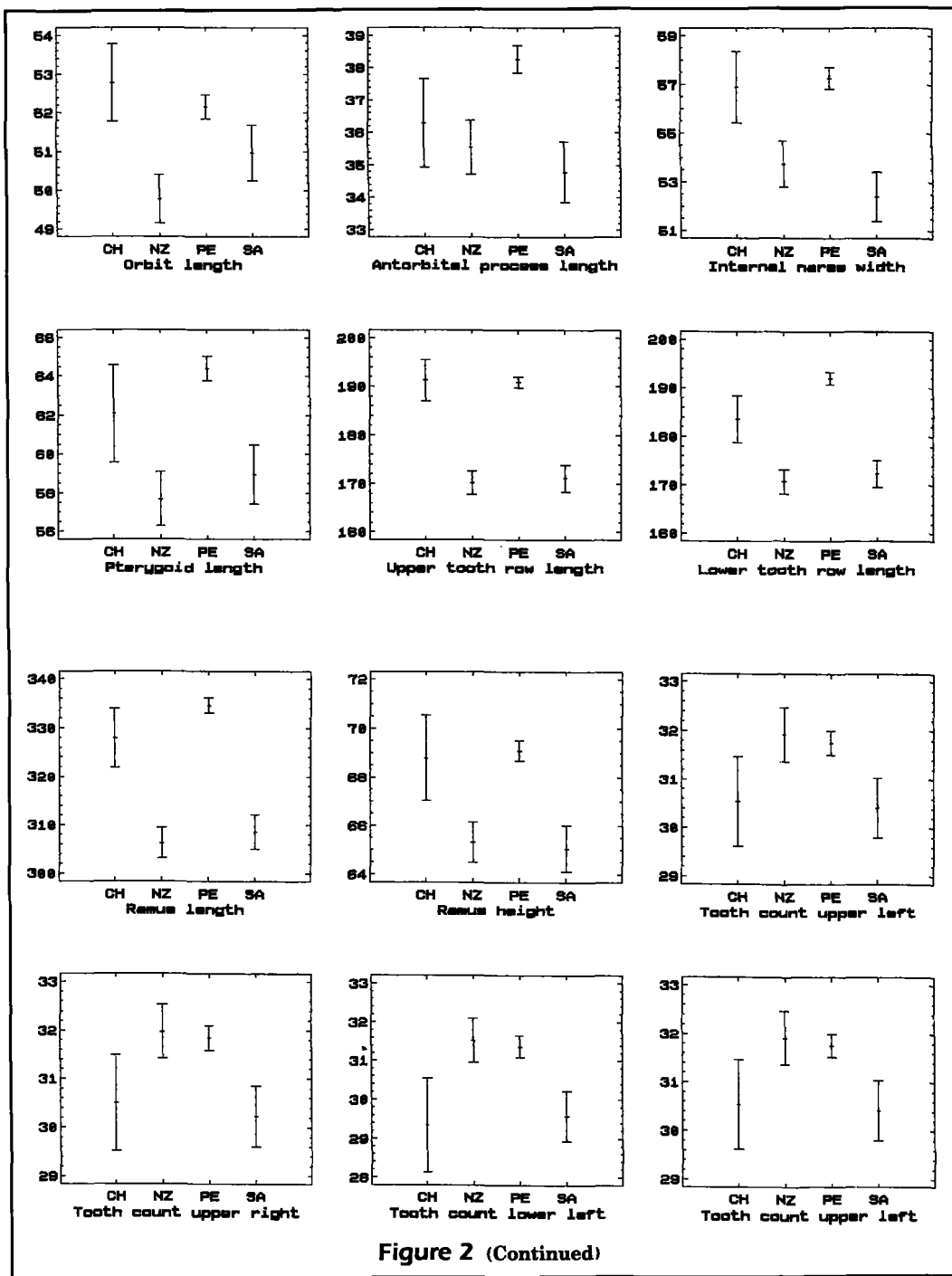


Figure 2
 Comparison of means in cranial measurements (in mm) and meristics for adult *Lagenorhynchus obscurus* from Chile (CH), New Zealand (NZ), Peru (PE) and southwestern Africa (SA). Error bars are 95% confidence intervals for means.

frequencies of NMC character states in skulls from Peru ($N=221$), Chile ($N=40$), New Zealand ($N=69$), and southwestern Africa ($N=65$). Surprisingly, only three characters out of 22 (14%) were found to demonstrate

significant differences between geographic groups (chi-square contingency analysis; see Table 10). These are relative position of the foramen in the right premaxillary at the base of the prenasal triangle (variable 1R,



$P < 0.0001$), presence of an accessory foramen above the foramen magnum (variable 16, $P = 0.02$), and the degree of contact, posteriorly, between pterygoid hamuli (variable 23, $P = 0.03$).

Upon comparison of frequencies for variables 16 and 23, two similarity pairs became apparent: New Zealand/southwestern Africa and Peru/Chile. Within

each subgroup the monomorphic status for both characters was confirmed (chi-square, $df = 1$, $P > 0.41$ in four tests). Southwest African *L. obscurus* differed very significantly in character 1R from all other stocks. By removing the African subsample, frequencies for 1R in the three remaining geographic units became homogeneous (chi-square = 0.58; $df = 4$, $P = 0.96$).

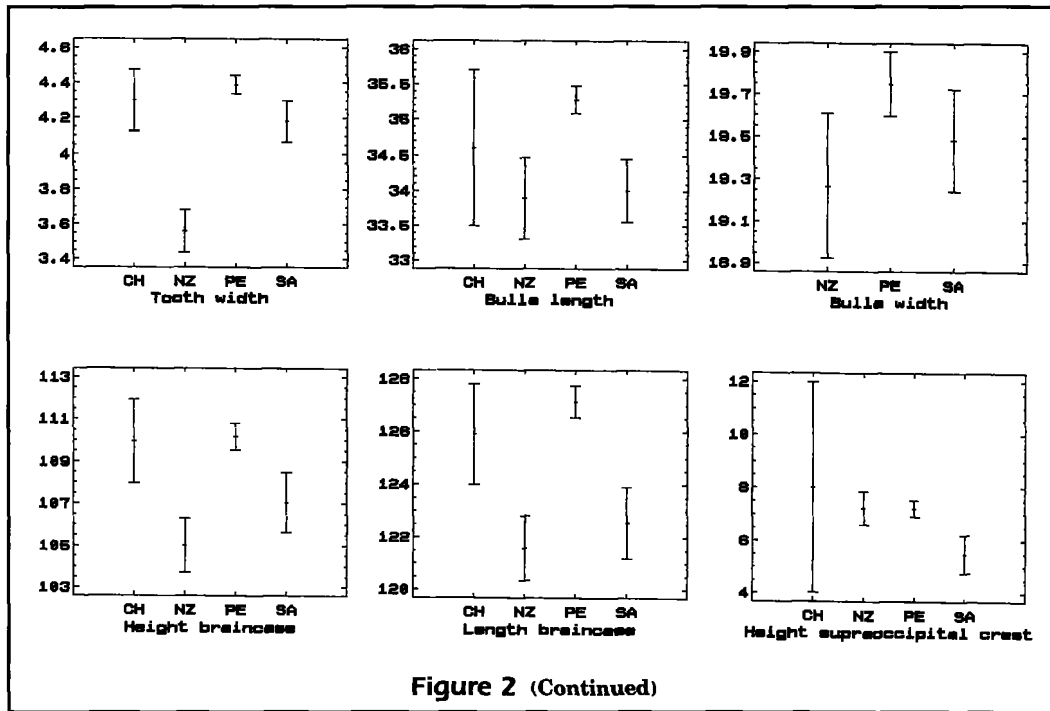


Figure 2 (Continued)

Discussion

Advanced fusion in the frontal-supraoccipital suture (FROC) is the most reliable single cranial criterion of sexual maturity in the dusky dolphin (95% efficiency). In combination with fusion=2 in LAC and ZYG cranial sutures, it can select sexually adult specimens from an undocumented series of *L. obscurus* skulls with even a higher degree of certainty. Distal fusion of premaxillary and maxillary bones has served as the indicator of choice for sexual maturity in *Stenella* spp. (Dailey and Perrin, 1973; Perrin, 1975a; Schnell et al., 1982⁸; Douglas et al., 1984, 1986; Perrin et al., 1981, 1987, 1989), common dolphin (Evans, 1975, 1982), and bottlenose dolphin (Walker, 1981⁷; Mead and Potter, 1990; Van Waerebeek et al., 1990). Its reliability and usefulness however depends on the species and the requirements of selection; Mead and Potter (1990) for instance reported that some immature *Tursiops* skulls were erroneously assigned to the adult group. Almost half of sexually mature dusky dolphins did not show any rostral distal fusion. The character reportedly was of no use in physically mature Pacific white-sided dolphins *Lagenorhynchus obliquidens* (Walker et al., 1986). Classification of specimens with heavily eroded sutures from weathering, boiling or chemical treatment is difficult, and if available sample size permits, these skulls should

probably not be used. Moderate heating applied over short periods, to soften tissues for instance, inflicts little damage.

Skulls of *L. obscurus* exhibit little sexual dimorphism, therefore it was not possible to define usable classification functions for sexing specimens. Of 28 non-metrical cranial characters, none exhibited dimorphism. In addition, the number of dimorphic metrical characters (6 of 37, 16.2%) was remarkably low in comparison with that in other small delphinids such as the pantropical spotted dolphin *Stenella attenuata* (23 of 36, 63.9%; Schnell et al., 1985) and the spinner dolphin *Stenella longirostris* (13 of 36, 36.1%; Douglas et al., 1986). *L. obscurus* and the named *Stenella* spp. share the characteristic of males having a broader rostrum and a longer temporal fossa than females, while the overall skull size is not different between sexes (see Schnell et al., 1985; Douglas et al., 1986). Intersexual differences in these species may be governed, at least partly, by similar selection factors. A number of authors have invoked common (genetic) ancestry between *L. obscurus* and the *Stenella* species group to explain certain morphological similarities (True, 1889; Fraser, 1966; Fraser and Purves, 1960; Mitchell, 1970). However, I concur with the opinion of W. F. Perrin¹³ that con-

¹³W. F. Perrin, Natl. Mar. Fish. Serv. Pers. commun. March 1992.

Table 6

Geographic variation in skull measurements and meristics of *Lagenorhynchus obscurus* from Peru (PE, N=189), Chile (CH, N=22), New Zealand (NZ, N=47) and southwestern Africa (SA, N=40).

Variable	PE versus CH		NZ versus SA	
	<i>t</i>	<i>P</i>	<i>t</i>	<i>P</i>
CBL	-0.48	0.40	0.48	0.63
RL	0.03	0.98	-0.26	0.80
RWB	-0.67	0.50	-0.45	0.65
RTEN	-1.12	0.27	1.6	0.11
RTIN	-0.34	0.73	1.32	0.19
PROW	2.50	<0.05	-0.094	0.93
POOW	-0.41	0.68	0.29	0.77
ZYW	-0.53	0.60	-0.074	0.94
PARW	0.84	0.40	-0.52	0.60
GWPMX	0.69	0.49	-0.14	0.89
ENW	-1.33	0.19	-2.02	<0.05
TFW	-0.11	0.91	-2.18	<0.05
ORL	1.03	0.30	-2.38	<0.05
APL	-2.89	<0.005	1.11	0.27
INW	-1.07	0.29	2.32	<0.05
PTEL	-2.23	<0.05	-1.28	0.21
UTRL	-0.17	0.87	-0.56	0.58
LTRL	-3.29	<0.005	-0.86	0.39
RAL	-2.10	<0.05	-0.97	0.36
RAH	-0.50	0.62	0.41	0.68
TCUL	-2.71	<0.01	3.45	<0.001
UR	-2.70	<0.01	4.25	<0.0001
TCLL	-3.01	<0.005	4.24	<0.0001
TCLR	-2.76	<0.01	3.95	<0.0002
TW	-1.05	0.30	-7.14	<0.0001
BL	-1.32	0.19	0.33	0.74
BW	—	—	-1.12	0.27
HBR	0.09	0.93	-2.09	<0.05
LBR	-1.37	0.17	-1.02	0.31
PEL	0.52	0.61	1.0	0.33
HCR	—	—	3.43	<0.005

vergence or parallelism is a more likely cause of the cited resemblances. The near absence of sexual dimorphism in the skull and external features of the dusky dolphin, coupled to the exceptionally large relative testis size, led me to suggest that sperm competition should occur in this species (Van Waerebeek, 1992b).

Both bivariate and multivariate analysis provide evidence of extensive geographic variation in skull morphology among the dusky dolphin stocks studied. Most strikingly, adult skulls from the Southeast Pacific stock are considerably larger than either New Zealand or SW African specimens (difference in weighted CBL means is 31 mm or 8.5% of CBL); skulls from New Zealand do not differ significantly in size from those of SW Africa. This is corroborated by the greater mean body length (roughly 10 cm) at sexual maturity and asymptotic length in Peruvian dolphins than in SW African and New Zealand specimens (Van Waerebeek, 1992b). Two non-metrical cranial characters also support the existence of the Peru/Chile and New Zealand/

Table 7

Statistics for discriminant analysis utilizing 21 cranial characters of adult *Lagenorhynchus obscurus* skulls from Chile (CH, N=7), New Zealand (NZ, N=24), southwestern Africa (SA, N=22) and Peru (PE, N=135). Group numbers (under centroids) refer to these used in the discriminant function plot (Fig.3). SEP= Southeast Pacific (Chile and Peru combined).

Discriminant function	Eigenvalue	Relative percentage	Canonical correlation
1	2.202	76.02	0.829
2	0.523	18.06	0.586
3	0.171	5.91	0.382

Unstandardized discriminant function coefficients

	1	2	3
CBL	0.0096	-0.0466	-0.0730
RL	0.0134	0.0025	0.0672
RWB	0.0038	-0.0618	-0.0057
RTEN	-0.0074	-0.0209	0.0268
PROW	-0.0285	-0.0416	-0.0647
POOW	0.0191	0.0528	-0.1291
ZYW	0.0152	-0.0285	0.1545
GWPMX	-0.0204	0.0431	0.0021
ENW	-0.0031	0.1414	-0.0817
TFW	0.0635	0.0256	-0.0028
ORL	-0.0190	0.0361	0.1625
APL	0.0683	-0.0198	-0.0739
INW	0.0481	-0.1066	0.0586
UTRL	0.0209	-0.0352	0.1097
LTRL	0.0664	0.0670	-0.1218
RAL	0.0067	0.0118	0.0047
TCUL	0.0195	-0.0537	-0.0424
TCUR	-0.1049	-0.1707	-0.1628
TW	0.6215	1.7912	0.6270
HBR	-0.0044	0.0669	-0.0467
LBR	0.0276	0.0058	0.0239
CONSTANT	-33.9754	5.8979	15.3204

Classification results

Actual group	Predicted group (percentage)				
	CH	NZ	SA	PE	SEP
CH	85.7	0	0	14.3	100
NZ	0	91.7	8.33	0	0
SA	0	4.6	90.9	4.6	4.6
PE	10.4	1.5	2.2	85.9	96.3

Group centroids

	Discriminant functions		
	1	2	3
CH (=1)	0.398	-0.705	2.040
NZ (=2)	-2.773	-1.254	-0.182
SA (=3)	-2.345	1.582	0.133
PE (=4)	0.855	0.0016	-0.095

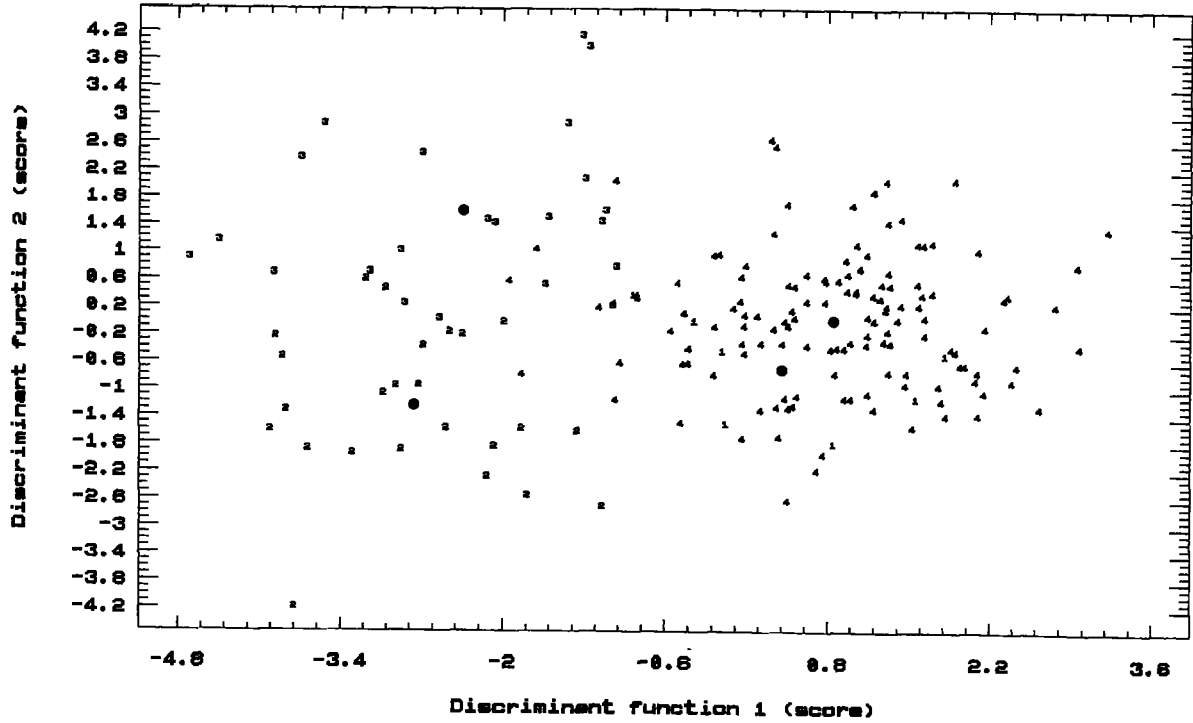


Figure 3

Scores of discriminant functions I and II based on 21 cranial characters for adult skulls of *Lagenorhynchus obscurus* from Chile (1), New Zealand (2), southwestern Africa (3), and Peru (4). Group centroids are indicated by a black dot. Corresponding statistics are presented in Table 7.

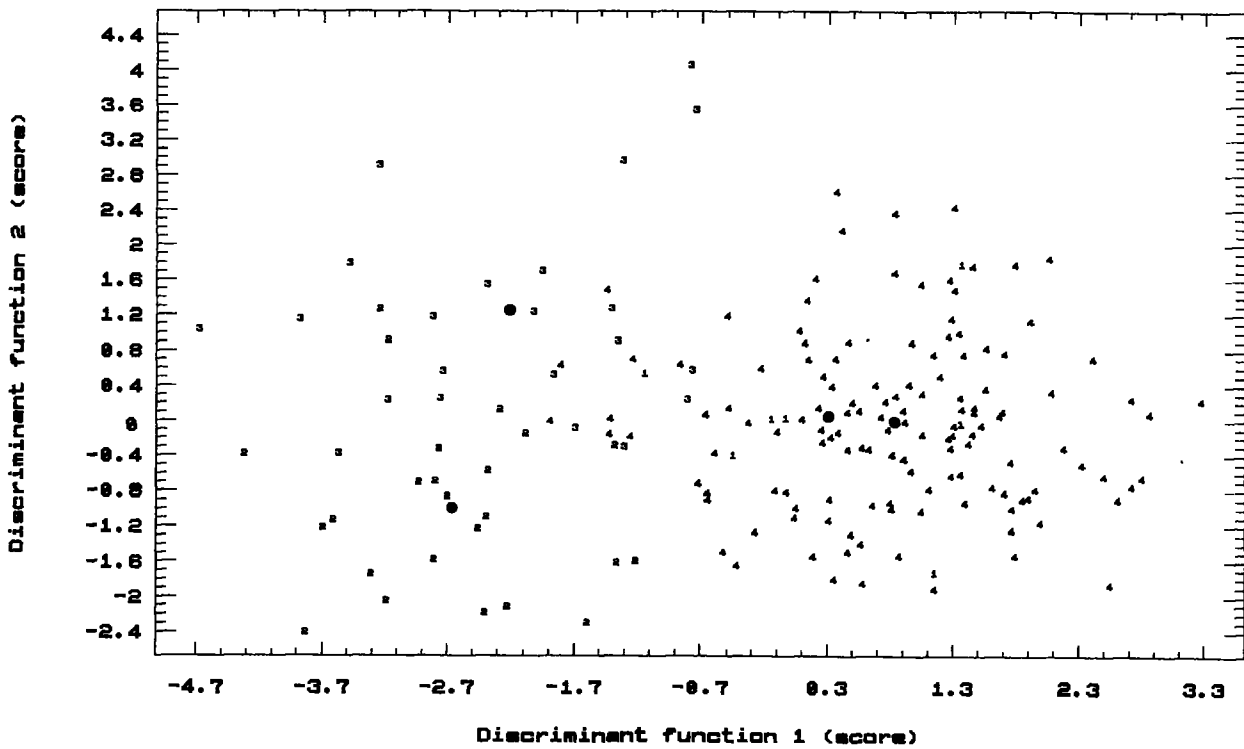


Figure 4

Scores of discriminant functions I and II based on the six most discriminating cranial characters (CBL, PROW, TFW, LTRL, TW, and TCUR) for adult skulls of *Lagenorhynchus obscurus* from Chile (1), New Zealand (2), southwestern Africa (3), Peru (4). Group centroids are indicated by a black dot. Corresponding statistics are presented in Table 8.

Table 8

Statistics of discriminant analysis utilizing a minimum number (6) of sexually monomorphic cranial variables with maximum discriminating power. Samples include adult skulls of *Lagenorhynchus obscurus* from Chile (CH, $N=7$), New Zealand (NZ, $N=24$), southwestern Africa (SA, $N=22$) and Peru (PE, $N=135$).

Discriminant function	Eigenvalue	Relative percentage	Canonical correlation
1	2.0188	84.35	0.818
2	0.3096	12.94	0.486
3	0.0649	2.71	0.247

Unstandardized discriminant function coefficients

	1	2	3
CBL	0.0350	-0.0588	-0.1105
PROW	0.0353	-0.0363	0.1205
TFW	0.0650	0.0484	0.0601
LTRL	0.0663	0.0449	0.1227
TW	0.7749	2.0950	-0.5369
TCUR	-0.0582	-0.3046	0.1422
CONSTANT	-36.6466	18.7270	-5.0552

Classification results

Actual group	Predicted group (percentage)				
	CH	NZ	SA	PE	SEP
CH	71.4	0	0	28.6	100
NZ	0	87.5	12.5	0	0
SA	9.1	18.2	72.7	0	9.1
PE	19.3	2.2	3.7	74.8	94.6

Group centroids

	Discriminant functions		
	1	2	3
CH (1)	0.301	0.0355	-1.281
NZ (2)	-2.674	-0.986	0.0236
SA (3)	-2.218	1.235	0.0400
PE (4)	0.821	-0.0278	0.0557

SW Africa similarity pairs. The New Zealand form is set apart from all others by minimal tooth size and is further distinguished from the SW African form by the significantly higher number of teeth.

A commonly used criterion of subspecific level difference between populations is whether or not 90% of the specimens can be unequivocally assigned to the proper group (Mayr, 1970). Perrin (1975a, 1990), for instance, described three subspecies of spinner dolphin, *Stenella longirostris*, based on this principle. Discriminant analysis allows correct identification of

a group (96.5%, 91.7%, and 90.9%) of *L. obscurus* skulls from respectively the Southeast Pacific, New Zealand, and SW Africa, which warrants allocation of subspecific status. It seems premature, however, to formally describe subspecies and assign trinomial names, because no skulls from Argentina have been studied and the Chilean sample was too small to permit definitive conclusions on the degree of heterogeneity in the Southeast Pacific group. In particular, no skulls have been examined from dusky dolphins occurring off southern Chile (south of 46°S), which are thought to belong to the Argentinian stock (Van Waerebeek, 1992a). Considering the persisting mortality levels in gillnet and harpoon fisheries off Peru and northern Chile and in purse-seine operations off Argentina (Van Waerebeek and Guerra, 1986⁵; Guerra et al. 1987; Crespo and Corcuera, 1990¹⁴; Van Waerebeek and Reyes, 1993; Van Waerebeek, unpubl. data), the question of separate subspecies or population status is of major importance with respect to conservation.

The MANOVA results, suggesting some seasonal morphological variation in *L. obscurus* caught off central Peru, were not confirmed by other tests. However, the picture may be blurred by multi-year pooling or other sampling bias. High-resolution molecular techniques, such as DNA-fingerprinting, should preferably be used to explore this issue.

Although results were complementary, the resolving power of non-metrical cranial characters (not including tooth counts) was inferior to that of measurements (i.e., fewer characters differed); therefore non-metrical characters are not recommended as sole method for subspecific discrimination. Based on studies of the common dolphin, *Delphinus delphis*, Perrin et al. (1989) independently concluded that non-metrical characters be used only in combination with metrical characters and that special attention be paid to controlling conditions to maximize comparability of data sets.

Although little information is available on parasite prevalences in dusky dolphins other than these from Peru, preliminary indications of differential infestations add weight to the morphological findings. Crassicaudid nematodes were practically absent in the cranial sinuses of many hundreds of Peruvian dusky dolphins but were retrieved from the cranial sinuses of one out of two specimens from SW Africa.

¹⁴Crespo, E. A., and J. F. Corcuera. 1990. Interactions between marine mammals and fisheries in some fishing areas of the coast of Argentina and Uruguay. Doc. SC/090/G2 presented to the IWC, La Jolla, CA, 20-21 October 1990.

Table 9

Frequency distributions for selected non-metrical character states (coded 1–6, see Perrin et al., 1982) in 173 mature (MAT) and 48 immature (IMM) skulls of *L. obscurus* (sexes pooled) from central Peru. Chi-square contingency analyses indicate levels of developmental variation. For df=1, a Yates' corrected chi-square was computed and the higher of the two values (lower *P*) tabulated. Characters are explained in Table 1.

		Non-metrical character states						χ^2	<i>P</i>	df
		1	2	3	4	5	6			
1L	MAT	72	61	40				8.5	0.014	2
	IMM	14	28	6						
1R	MAT	56	17	99				4.89	0.09	2
	IMM	22	7	19						
2L	MAT	5	167	1				1.71	0.43	2
	IMM	0	48	0						
2R	MAT	9	162	2				3.21	0.20	2
	IMM	0	48	0						
3	MAT	45	83	45				5.36	0.07	2
	IMM	6	23	19						
5L	MAT	5					166	0.09	0.77	1
	IMM	1					46			
5R	MAT	2	1				168	0.52	0.77	2
	IMM	1	0				46			
6L	MAT	147	22	3			1	1.14	0.77	3
	IMM	42	6	0			0			
6R	MAT	162	10				1	1.38	0.50	2
	IMM	47	1				0			
9L	MAT	2	171					0.56	0.45	1
	IMM	0	48							
9R	MAT	6	166					1.72	0.19	1
	IMM	0	48							
10	MAT		172					—	—	—
	IMM		48							
12L	MAT	173						—	—	—
12R	MAT	172						—	—	—
	IMM	48								
13	MAT	1		165	1			0.58	0.75	2
	IMM	0		48	0					
16	MAT	3	170				0.84	0.36	1	
17	MAT	77	96					8.83	0.003	1
	IMM	33	15							
18L	MAT	35	2				133	7.3	0.026	2
	IMM	8	4				36			
18R	MAT	41	3				126	0.97	0.61	2
	IMM	11	2				35			
19	MAT		2				169	0.57	0.45	1
	IMM		0				48			
23	MAT	149	5					1.36	0.24	1
	IMM	38	3							
24	MAT	123	34					3.15	0.08	1
	IMM	38	4							
25	MAT	118	38					5.97	0.01	1
	IMM	39	3							
30	MAT	9	158	0				6.20	0.04	2
	IMM	0	43	1						
33L	MAT		7	48	60	22	3	11.2	0.02	4
	IMM		0	24	12	2	1			
33R	MAT	1	12	52	52	18	4	4.57	0.47	5
	IMM	0	1	17	13	8	0			
34L	MAT	115	23	1				1.25	0.53	2
	IMM	35	4	0						
34R	MAT	118	21	0				1.43	0.23	1
	IMM	36	3	0						

Table 10

Geographic variation in non-metrical cranial (NMC) characters for 395 skulls of *Lagenorhynchus obscurus* from Peru (PE, $N = 221$), Chile (CH, $N = 40$), New Zealand (NZ, $N = 69$), and southwestern Africa (SA, $N = 65$). Frequency distributions of NMC states (coded 1-6, see Perrin et al. 1982) for each region and results of chi-square contingency analyses are presented. Samples include all sex/maturity groups except neonates; characters known to be maturity dependent (see Table 9) have been excluded.

NMC	REG	1	2	3	4	5	6	χ^2	P	df
1R	PE	78	24	118				31.8	<0.0001	6
	CH	10	4	16						
	NZ	21	6	37						
	SA	24	22	15						
2L	PE	5	215	1				2.8	0.83	6
	CH	0	30	0						
	NZ	1	62	0						
	SA	0	61	0						
2R	PE	9	210	2				5.9	0.43	6
	CH	0	30	0						
	NZ	1	62	0						
	SA	0	61	0						
3	PE	51	106	64				5.9	0.43	6
	CH	7	17	6						
	NZ	17	33	13						
	SA	11	27	23						
5L	PE	6	0				212	8.33	0.21	6
	CH	1	0				26			
	NZ	0	0				62			
	SA	3	1				55			
5R	PE	3	1				214	10.8	0.10	6
	CH	1	1				25			
	NZ	0	0				62			
	SA	3	0				57			
6L	PE	189	28	3			1	7.9	0.54	9
	CH	23	5	0			1			
	NZ	51	12	0			0			
	SA	49	10	0			1			
6R	PE	209	11				1	0.89	0.99	6
	CH	27	2				0			
	NZ	59	3				0			
	SA	57	3				0			
9L	PE	2	219					3.85	0.28	3
	CH	1	26							
	NZ	0	63							
	SA	0	60							
9R	PE	6	214					4.94	0.18	3
	CH	3	24							
	NZ	2	60							
	SA	3	57							
10	PE		220					—	—	—
	CH		28							
	NZ		64							
	SA		60							
12L	PE	221	0					7.38	0.06	3
	CH	27	0							
	NZ	61	1							
	SA	57	2							
12R	PE	220	0					7.38	0.06	3
	CH	28	0							
	NZ	62	1							
	SA	57	2							

Table 10 (Continued)

NMC	REG	1	2	3	4	5	6	χ^2	P	df
13	PE	1		213	1			2.41	0.88	6
	CH	0		25	0					
	NZ	1		62	0					
	SA	0		59	0					
16	PE	3	218					9.59	0.02	3
	CH	0	21							
	NZ	3	59							
	SA	5	53							
18R	PE	52	5	0			161	7.06	0.32	6
	CH	2	1	0			15			
	NZ	12	0	0			47			
	SA	7	0	1			48			
19	PE	0	2				217	6.48	0.37	6
	CH	0	0				16			
	NZ	0	0				60			
	SA	1	0				55			
23	PE	187	8					8.83	0.03	3
	CH	12	1							
	NZ	41	6							
	SA	41	7							
24	PE	161	38					3.8	0.28	3
	CH	12	2							
	NZ	34	13							
	SA	34	14							
33R	PE	1	13	69	65	26	4	7.24	0.95	15
	CH	0	0	7	4	1	0			
	NZ	0	5	16	16	5	1			
	SA	0	5	24	18	3	1			
34L	PE	150	27	1				8.59	0.20	6
	CH	5	5	0						
	NZ	36	8	0						
	SA	41	9	0						
34R	PE	154	24	0				2.41	0.49	3
	CH	10	3	0						
	NZ	36	8	0						
	SA	47	5	0						

Cyamid amphipods have never been found on *L. obscurus* from Peru (Van Waerebeek, 1992b), whereas in New Zealand they seem to be fairly common (Cipriano, 1985).

The actual distribution of *L. obscurus* populations is generally comparable to that of the four species of *Cephalorhynchus*, and the geographical dispersion may have similarly evolved under the influence of the eastflowing Westwind Drift, as proposed for *Cephalorhynchus* spp. by van Bree (1986) and Robineau (1989). The close affinity of the large-bodied Peruvian dusky dolphin with the Pacific white-sided dolphin (Webber, 1987; Van Waerebeek, 1992b) suggests that the former probably represents the most ancestral (plesiomorph) form of dusky dolphin from which the

Argentinian, and small-bodied SW African and New Zealand forms were derived.

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