

TAXONOMIC STATUS AND GEOGRAPHICAL
CRANIAL VARIATION OF COMMON DOLPHINS
(*DELPHINUS*) IN THE EASTERN NORTH
ATLANTIC

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ABSTRACT

The common dolphin has a widespread distribution and is relatively abundant in the temperate to subtropical waters of the eastern North Atlantic. However, it is not known whether different species, subspecies, or populations occur in this region. We examined 393 common dolphin skulls obtained from both stranded and bycaught individuals collected between 1901 and 2005. The series included skulls of 152 females and 199 males, from animals ranging in body length from 93 to 230 cm and 105 to 244 cm, respectively. The ranges of total body length, skull size, RL/ZGW ratio and maximum upper alveolar (tooth) count of common dolphins in the eastern North Atlantic overlapped with those of both short- (*D. delphis*) and long-beaked (*D. capensis*) species found off the Californian coast. However, in the absence of additional data, the common dolphin in the eastern North Atlantic is regarded here as a large form of *Delphinus delphis*. Sexual dimorphism and possible sex-linked characters were identified within the sample. Results of the current study

indicate some population differentiation within the eastern North Atlantic, with common dolphins off Portugal showing segregation in morphometric characteristics from common dolphins in other areas.

Key words: common dolphin, *Delphinus delphis*, cetaceans, morphometrics, eastern North Atlantic.

Common dolphins, *Delphinus* spp., have a worldwide distribution mainly in tropical and subtropical waters, but extend as far north as 65°N in the eastern North Atlantic, owing to the warming influence of the North Atlantic Drift (Murphy 2004, and ref. therein). Common dolphins are abundant in the eastern North Atlantic, being among the most frequently stranded cetaceans as well as being incidentally bycaught in large numbers (Sheldrick 1989, Kuiken *et al.* 1994, Sheldrick *et al.* 1994, Berrow and Rogan 1997, Tregenza and Collet 1998, Harwood *et al.* 1999, Morizur *et al.* 1999, Rogan *et al.* 2001, López *et al.* 2002, López *et al.* 2003, Silva and Sequeira 2003). There are indications that the number of common dolphins in the southern North Sea has fluctuated during the 20th century, with an increase in strandings between the 1920s and the 1950s, followed by a decline thereafter (Bakker and Smeenk 1987, Evans 1990). However, on the whole, in the eastern North Atlantic there is no detailed information on long-term or seasonal movements of common dolphins, or on changes in their distribution and abundance. Information about stock structure and identity, essential to assess the impact of incidental captures in fisheries, is likewise unavailable.

Given their wide geographical distribution, it is not surprising that common dolphins show considerable morphological variation, which has led to the description of several species and subspecies. However, most recent studies of the taxonomic status of common dolphin populations have been restricted to local areas, so that globally taxonomy remains confused. Based on skeletal characters, external morphology, pigmentation patterns and genetic studies (mtDNA and cytochrome *b* sequences), and taking into account sexual dimorphism and ontogenetic development, two species of common dolphin are now recognized, the short-beaked common dolphin, *Delphinus delphis* Linnaeus, 1758 and the long-beaked common dolphin, *D. capensis* Gray, 1828 (Banks and Brownell 1969, Evans 1975, Heyning and Perrin 1994, Rosel *et al.* 1994), although this was established mainly with reference to two sympatric populations inhabiting waters off the Californian coast. Genetic analysis of individuals from the inshore long-beaked group and the offshore short-beaked group off California by Rosel *et al.* (1994) revealed reciprocal monophyly, genetic divergence of 1.11%, and fixed differences. Further genetic research, using amplified fragment length polymorphism, suggested that the two species *D. delphis* and *D. capensis* had diverged very recently (Kingston and Rosel 2004). Within *D. delphis*, individuals off southern California were compared with those inhabiting waters in the eastern tropical Pacific and the Black Sea, and results showed that the three populations differed only by 0.02% (Rosel *et al.* 1994).

Geographical variation in skull morphology has been found within local and geographically separated populations of short-beaked common dolphins. Preliminary genetic analysis suggested no differentiation between common dolphins inhabiting inshore and offshore waters off southern Australia (White 1999). However, skulls from shallow-water animals were significantly smaller than those from deep-water animals, suggesting that *D. delphis* is also a morphologically variable species (Bell *et al.* 2002). Further geographical variation in the morphology of the short-beaked

form has been recorded in the Black Sea, where *D. delphis* has the smallest skull, possibly as a result of dwarfism owing to their restriction to an almost isolated inland sea (Perrin 1984, Amaha 1994). Perrin *et al.* (1994) compared skulls from *D. delphis* inhabiting waters in the Black Sea, eastern tropical Pacific and the western North Atlantic. Although a significant difference was found between all three areas, the western North Atlantic sample was the most isolated, showing the least genetic exchange with other populations. However, the western North Atlantic sample was drawn from a larger area (western and mid north Atlantic) and may have been more heterogeneous (Perrin *et al.* 1994).

Limited earlier studies indicated that only one species of common dolphin (*D. delphis*) is present in European waters (Lilljeborg 1866, Flower 1880, van Bree and Gallagher 1978). As part of a global study, Amaha (1994) showed that *D. delphis* was indeed found in the North Atlantic, the North Sea, and the Mediterranean. However, in this study the sample size for the eastern North Atlantic was small and localized (23 skulls examined from dolphins that stranded along the Atlantic coast of France). The range of *D. delphis* in the eastern North Atlantic is believed to extend as far south as Senegal (Heyning and Perrin 1994, Van Waerebeek 1997). In waters off eastern Central Africa, Amaha (1994) analyzed 15 common dolphin skulls and reported the presence of only *D. capensis*. However, Van Waerebeek (1997) has described *D. delphis* inhabiting waters off Gabon and Angola, and occurring sympatrically with *D. capensis*, although this was based on only 21 skulls.

In the present study we aim to clarify the taxonomic status of common dolphin populations in the eastern North Atlantic, and identify whether separate stocks exist, using a morphometric analysis of measurements of 393 skulls collected between 1901 and 2005. We also examine aspects of sexual dimorphism and ontogenetic development within populations, using additional information on length, sex, age, and maturity, in order to differentiate inter- and intraspecific differences in skull morphology.

MATERIALS AND METHODS

Data Collection

In total, 393 common dolphin skull specimens were measured from the eastern North Atlantic, from latitudes between 60°04'35"N and 37°02'00"N (Fig. 1.). These comprised 199 male, 152 female, and 42 unsexed skulls of common dolphins, all of which were measured by SM. Sample sizes and locations of skulls are given in Appendix 1.¹ The data set was divided into six geographical areas (see Fig. 1): Area 1, Wales and England; Area 2, Ireland; Area 3, Scotland; Area 4, the Netherlands; Area 5, Spain; and Area 6, Portugal. This is the first study to examine geographical variation in this species within the eastern North Atlantic, and the different geographical areas outlined above represent political borders and/or jurisdictions of different stranding schemes.

For each dolphin, the following information was obtained whenever possible: total body length, sex, age, and location of stranding or incidental capture of the individual. Although the sampling period ranged from 1901 to 2005, except for animals from the Netherlands, the majority of the skulls were obtained since 1990, reflecting the increased efforts of local strandings projects. Most of the Dutch skulls ($n = 13$) were

¹ Appendices 1–4 are available online as part of supplemental material. See the end of this article for details.

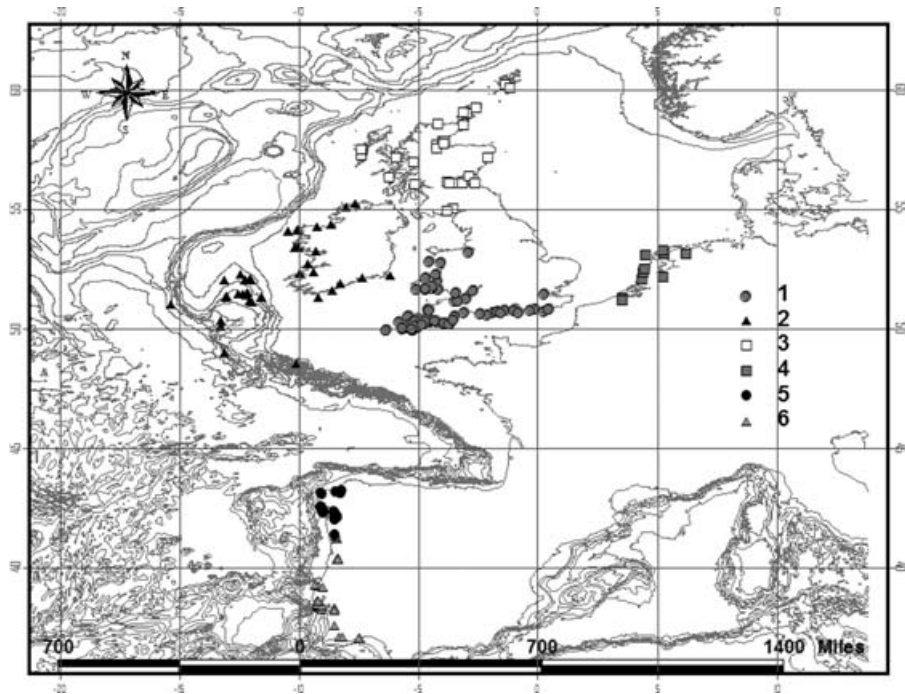


Figure 1. Distribution of sampling locations in the eastern North Atlantic, of common dolphins whose skulls were analyzed in this study. Area 1 = England and Wales, Area 2 = Ireland (stranded and bycatch samples), Area 3 = Scotland, Area 4 = The Netherlands, Area 5 = Spain, and Area 6 = Portugal.

collected from 1926 to 1953, as a result of an increase in common dolphin strandings during this period. Age was determined by analyzing growth layer groups in the dentine of teeth, adapted from the methods of Lockyer (1995). As ages were recorded by a number of different researchers and were not cross calibrated, they were used only as an indicator for assessing maturity. Thirty-six measurements were taken from each skull to an accuracy of 0.1 mm using standard vernier calipers without prior knowledge of body length, age, or sex (Table 1). Measurements were based mostly on those used in a number of previous studies including Evans (1975), Ross (1984), Heyning and Perrin (1994), Börjesson and Berggren (1997), and Amano *et al.* (2000). Four meristic characters were also recorded: the alveolar (tooth socket) counts for right and left sides of the rostrum, and the right and left sides of the mandible.

In addition to the 39 previously used characters, one additional character was defined for this study: the distance between right antorbital notch and midpoint between occipital condyles (ANOC), which measures the length of the cranium. Owing to skull asymmetry, measurements MD, ML, LMF, MDSS and LL, LO, LTF, and WFT were normally taken from the left mandible and the left-hand side of the skull, except if wear or breakage prevented this. Finally, ANOC was always measured on the right side of the skull. Four measurements used in previous studies were not included here because it proved impossible to measure them consistently. These were: width of premaxillae at three-quarters length of rostrum, the greatest length of left and right pterygoids, and the greatest width of occipital condyle.

Table 1. Description of cranial measurements and meristic characters for common dolphins *Delphinus delphis* used in the present study.

Morphometric and meristic characters	No.	Abbreviation
Condylobasal length	1	CBL
Length of rostrum, from tip to midpoint between posterior limits of antorbital notches	2	RL
Length between right antorbital notch to midpoint between occipital condyles (right side)	3	ANOC
Width of rostrum at base, along line between posterior limits of antorbital notches	4	WRB
Width of premaxillae, along line between posterior limits of antorbital notches	5	WPB
Width of rostrum 60 mm anterior to midpoint between posterior limits of antorbital notches	6	WR60
Width of premaxillae 60 mm anterior to midpoint between posterior limits of antorbital notches	7	WP60
Width of rostrum at $\frac{3}{4}$ length, measured from proximal end	8	WR3/4
Width of rostrum at $\frac{1}{2}$ length, measured from proximal end	9	WR1/2
Width of premaxillae at $\frac{1}{2}$ length of rostrum, measured from proximal end	10	WP1/2
Greatest width of right premaxilla, measured adjacent to external nares	11	WRPR
Greatest width of left premaxilla, measured adjacent to external nares	12	WLPR
Greatest width of external nares	13	WEN
Greatest width of premaxillae, measured adjacent to external nares	14	WPR
Tip of rostrum to anterior border of external nares	15	TREN
Posterior end of left tooththrow to tip of rostrum	16	LUTR
Posterior end of right tooththrow to tip of rostrum	17	RUTR
Tip of rostrum to midpoint between mesial ends of posterior margins of pterygoids	18	TRPT
Width of pterygoids	19	WPT
Greatest width across zygomatic process of squamosal	20	GZW
Greatest postorbital width	21	GPOW
Greatest preorbital width	22	GPRW
Length of antorbital process of left lacrimal (left side)	23	LL
Greatest length of orbit (left side)	24	LO
Greatest height of left temporal fossa (left side)	25	LTF
Greatest width of left temporal fossa, at right angles to greatest height (left side)	26	WTF
Greatest depth from frontal crest to basioccipital at condyle	27	DFTC
Greatest parietal width, between temporal fossae	28	WBTF
Length of mandible (left side)	29	ML
Depth of mandible at coronoid process	30	MD
Greatest length of left tympanic bone	31	LLTB
Greatest length of right tympanic bone	32	LRTB
Length of mandibular fossa (left side)	33	LMF
Posterior end of left tooththrow to tip of mandible	34	LLTR
Posterior end of right tooththrow to tip of mandible	35	RLTR
Maximum depth of mandible at subapical swelling (left side)	36	MDSS
Number of alveoli, lower right	37	LRTS
Number of alveoli, lower left	38	LLTS
Number of alveoli, upper right	39	URTS
Number of alveoli, upper left	40	ULTS

Data Treatment

To check for transcription errors from original data sheets, outliers, and for any left/right-sided differences in MD, LMF, MDSS, LL, LO, LTF, and WFT, each morphometric measurement was regressed against condylobasal length, for each sex (MINITAB statistical software Version 13). At this stage of the analysis we were unable to repeat any measurements, therefore any correctly transcribed data point found to be more than four standardized residuals from the fitted line was omitted from the data set.

Following Collet (1981) and Murphy (2004), mature female common dolphins were defined using at least two of the following criteria: 9 yr or older, ≥ 190 cm in TBL, with a CBL ≥ 400 mm and a fused rostrum, whereas mature male common dolphins were defined using at least two of the following criteria: 10-yr old or older, ≥ 200 cm in TBL, CBL ≥ 420 mm, and a fused rostrum.

Taxonomic Status

All skull data were examined to ascertain the taxonomic status of common dolphins in the eastern North Atlantic, by determining the rostrum length/greatest zygomatic width ratio (Banks and Brownell 1969, Evans 1975, van Bree and Gallagher 1978, Amaha 1994, Evans 1994, Heyning and Perrin 1994, Jefferson and Van Waerebeek 2002) and recording the maximum upper tooth (alveolar) count from either the right or left side of the rostrum (after Amaha 1994).

Data Analysis

Data were analyzed using the SPSS statistical software package (Version 12). Levene's test for unequal variance was carried out for each sex separately, and all morphometric data were transformed to a logarithmic scale ($\log_{10}(x)$). In the remaining analyses only mature individuals were analyzed, as a number of measurements could not be taken in immature individuals owing to unfused skulls or broken bones. Also, for a number of measurements, there were significant differences in the regression slopes between juvenile and mature dolphins, as shown using general linear model (GLM) analysis with CBL as the covariate. In the present study, condylobasal length was used as a covariate/predictor for comparisons of measurements between areas for both univariate and multivariate analyses. Combining data on mature dolphins from all areas, homogeneity of the regression slopes on CBL was tested separately for each measurement and for both sexes. Any measurements found to violate the assumption of homogenous slopes were removed from any analysis in which CBL was used as a covariate.

Geographical Variation Analysis

Multivariate analysis of covariance—Multivariate analysis takes into account the correlation between dependent variables and is more powerful than univariate analysis. However, multivariate analysis is sensitive to missing values. In this study, individual dolphins were excluded from the data set if they had missing values for more than five measurements. The remaining missing values were calculated using multiple missing-value regression analysis, separately for each sex with CBL as the independent variable. By calculating the regressions on pooled samples from all areas, the

possibility of making a statistical Type 1 was minimized (Börjesson and Berggren 1997). The revised complete data set was used to carry out multivariate analyses of covariance with CBL as the covariate, separately for mature males and females. In order to further examine geographical variation in individual measurements, ANOVA and ANCOVA with Tukey *post hoc* tests, using CBL as the covariate, were carried out separately on data from mature males and females. For areas with fewer than five skulls, the data were excluded from univariate analyses and filled-in values were not used. When multiple comparisons were carried out simultaneously, ANOVA and ANCOVA were run with and without Bonferroni adjustment.

Canonical Discriminant Analysis (CDA)—In addition to MANCOVA, CDA was carried out in order to determine the overall degree of variation in size and shape of mature common dolphin skulls in the eastern North Atlantic. Analysis of variations in skull shape is important for elucidation of population structure and for making conservation and management decisions. Discriminant analysis was carried out on both unstandardized and standardized data. When using data that are not standardized for size, the first canonical axis primarily reflects variations in size, whereas shape is reflected in the other axes. In the current study the data were standardized, because CDA plots on unstandardized data may reflect sampling biases in absolute size. Sampling biases may have occurred, as samples were not obtained randomly but arose primarily from stranding projects.

In order to standardize the data, a GLM was fitted to the data for each particular character measurement for each sex. Each individual character measurement (excluding condylobasal length) was corrected for skull size by using the following formula:

$$Y' = Y - b(X - \bar{X})$$

where Y' is the standardized measurement, Y is the original observation, b is the average group regression slope obtained from ANCOVA, and X is the condylobasal length (Thorpe 1976). Characters that violated homogeneity of slopes against CBL were not used in this analysis. Before the data were standardized, slopes of each character were compared between areas using a GLM with CBL as the covariate. No significant variations in slope were found between areas for mature female common dolphins for any of the characters, although GPRW, LL, and LO were excluded from the analysis due to a small number of samples for these measurements from the Netherlands. Significant variations in slopes were found for character ML in mature males, so that this character was not standardized (and not used in analyses of standardized data). Prior to carrying out the discriminant analysis, missing variables were again filled in using multiple missing-value regression analysis, and individual dolphins missing >5 characters were also excluded from the analyses. As the data formed an unbalanced design, the prior probabilities were based on the observed group sizes.

RESULTS

The data set comprised 393 skulls obtained from common dolphins collected in the eastern North Atlantic. Ranges of total body length, condylobasal length, and rostrum length for each area are shown in Table 2. It should be noted that the total body length ranges do not include all stranded animals, but only those for which skulls were collected and analyzed in this study. Male common dolphins ranged in

Table 2. Ranges in total body length, age, condylobasal length, rostrum length, and rostrum length/greatest zygomatic width ratio for each area. Means and standard deviations for upper tooth count outlined in Figure 2.

Country (n)	BL (n)	CBL (n)	RL (n)	RL/GZW ratio (n)
Male: England (66) + Wales (5)	134–244 cm (68)	336.7–480.0 mm (37)	185.7–299.8 mm (38)	1.15–1.51 (34)
Female: England (63) + Wales (6)	117–226 cm (66)	333.8–450.4 mm (35)	189.8–280.8 mm (35)	1.21–1.51 (34)
Male: Ireland (40)	105–220 cm (35)	270.1–455.6 mm (20)	137–291.2 mm (20)	1.13–1.50 (18)
Female: Ireland (21)	93–210 cm (21)	307.8–436.4 mm (13)	144.4–276.9 mm (13)	1.37–1.49 (8)
Male: Scotland (17)	148–230 cm (17)	359.2–470.9 mm (12)	200.2–291.8 mm (13)	1.28–1.47 (11)
Female: Scotland (18)	137–211 cm (17)	381.7–448 mm (10)	227.5–282.5 mm (10)	1.33–1.57 (9)
Male: The Netherlands (10)	182–243 cm (10)	435.9–468.6 mm (8)	271.2–294.6 mm (7)	1.42–1.56 (7)
Female: The Netherlands (5)	145–230 cm (4)	435.9–458.1 mm (3)	268.5–283.5 mm (3)	1.39–1.48 (3)
Male: Spain (23)	168–230 cm (19)	246–487.1 mm (18)	200–290 mm (16)	1.17–1.53 (16)
Female: Spain (14)	173–203 cm (14)	371–448.8 mm (10)	215–272 mm (12)	1.29–1.47 (11)
Male: Portugal (41)	108–226 cm (32)	253.6–466.9 mm (38)	131.9–282.3 mm (30)	1.12–1.52 (28)
Female: Portugal (29)	95.5–227 cm (28)	263.8–465.5 mm (24)	136.8–294.4 mm (21)	1.21–1.55 (18)

body length from 105 to 244 cm ($n = 181$), although most individuals (98%) were ≤ 230 cm. Mature males ranged in length from 190 to 244 cm ($n = 84$), condylobasal length from 421.2 to 487.1 mm ($n = 67$) and rostrum length from 251.3 to 299.8 mm ($n = 61$). The two largest male common dolphins were 244 cm (England) and 243 cm (the Netherlands) in body length. Female common dolphins ranged in body length from 93 to 230 cm ($n = 150$), and mature females ranged in length from 185 to 230 cm ($n = 75$), condylobasal length from 395.8 to 466.1 mm ($n = 54$) and rostrum length from 233.6 to 294.4 mm ($n = 55$). Ages ranged from 0.5 to 23 yr ($n = 95$) for males, and 0 to 24 yr ($n = 97$) for females.

Taxonomic Status

Taxonomic status was determined from alveolar count data and the rostrum length/zygomatic width ratio (RL/GZW). The range obtained for upper alveolar count was 41–56. The upper tooth count range for animals from Area 1 ranged from 41 to 54, Area 2 from 42 to 52, Area 3 from 42 to 52, Area 4 from 42 to 56, Area 5 from 41 to 53, and Area 6 from 43 to 52. Mature common dolphins ranged in RL/GZW ratio from 1.31 to 1.57 ($n = 111$) (Table 2), but most (95%) ratio values were less than 1.52. Two of the highest RL/GZW ratios were for individuals in the North Sea that stranded on the Scottish and Dutch coasts. In mature common dolphins, plots of RL/GZW ratio and upper tooth count showed no differentiation between geographical areas (Fig. 2 and Appendix 2¹). Furthermore, no significant difference between areas was observed for mean RL/GZW ratios in either mature male (ANOVA, $P = 0.149$) or mature female (ANOVA, $P = 0.721$) common dolphins. ANOVA also showed no significant differences between areas for mean upper tooth socket counts in either males ($P = 0.158$) or females ($P = 0.108$).

Geographical Variation

Multivariate Analysis of Covariance (MANCOVA)—MANCOVA indicated significant geographical variation in the skulls of mature males (Wilk's $\lambda = 0.036$, $F = 1.572$, $P = 0.005$). MANCOVA also revealed significant geographical variation in mature females (Wilk's $\lambda = 0.038$, $F = 1.802$, $P = 0.001$). When the small samples of the Netherlands and Spain were excluded from the analysis, a significant geographical variation was still found in mature females (Wilk's $\lambda = 0.122$, $F = 1.613$, $P = 0.031$).

Univariate analysis of variance and covariance—Using ANOVA with a Bonferroni adjustment, significant geographical variation in absolute size was found in TBL and 12 skull measurements in mature males (Table 3). Spanish dolphins had significantly shorter total body lengths compared to those from the Netherlands, Ireland, Scotland, and England and Wales. Overall, there appears to be a slight cline in size, with dolphins in higher latitudes having a greater mean TBL than animals off the Spanish and Portuguese coasts. Tukey tests showed male common dolphin skulls from Spain also had significantly smaller WR60, GZW, GPOW, WPT, WPR, MD, and ML compared to skulls from Scotland, and significantly smaller WP60, GZW, GPOW, GPRW, ML, and MD compared to those from England and Wales. Furthermore skulls from Portugal had significantly smaller GZW, MD and WR1/2 compared to skulls from Scotland, and significantly smaller MD compared to skulls from England and Wales.

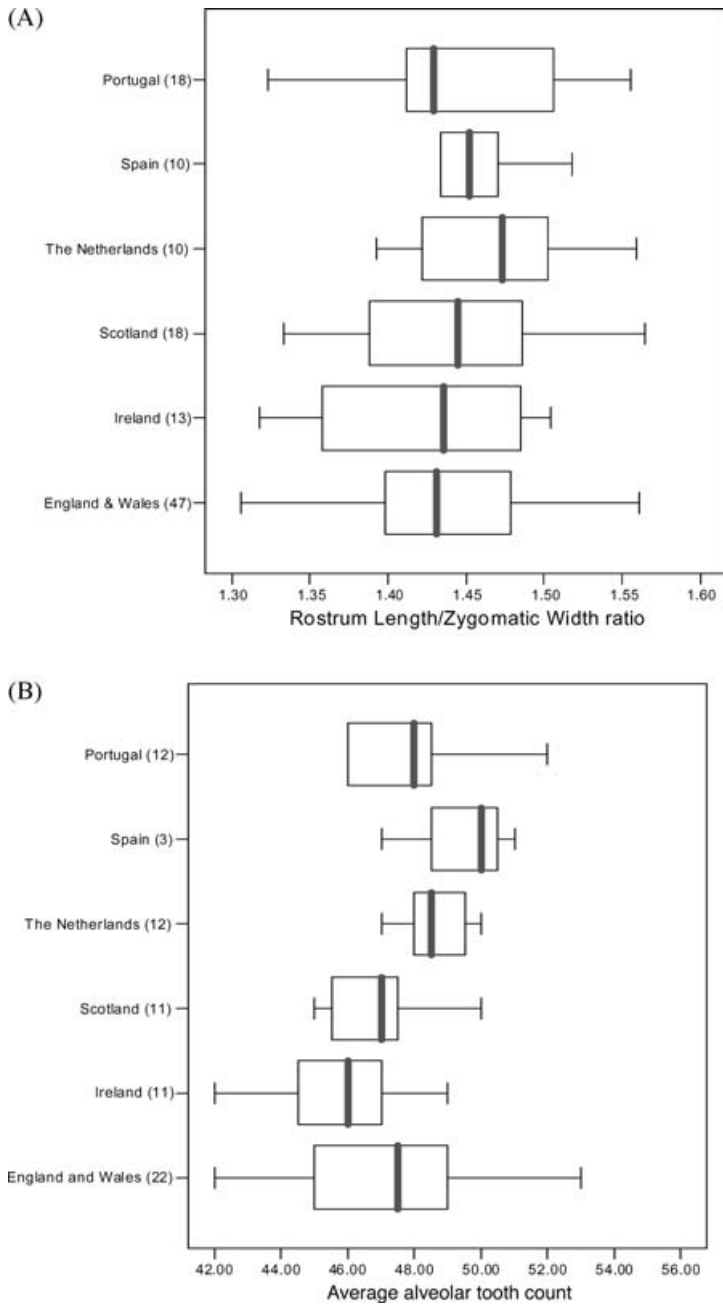


Figure 2. Range, median, and upper and lower quartiles of (A) rostrum length/zygomatic width ratio and (B) upper alveolar count by geographic area for mature dolphins. Gray lines inside the box are the medians, hinges at the left and right of the box are the upper and lower quartiles, horizontal lines left and right of the box represent the ranges, and numbers are sample sizes.

Table 3. ANOVA and Tukey test results for geographical variation in mature male common dolphins.

Characters	Eng/Wales Area 1	Ireland Area 2	Scotland Area 3	The Netherlands Area 4	Spain Area 5	Portugal Area 6	ANOVA	Tukey tests	P	Bonferroni adjustment
Male common dolphins										
TBL										
Log10-adjusted mean	2.328	2.330	2.338	2.339	2.294	2.314	0.002	Area 5 vs. Area 1	0.007	0.009
SE	0.004	0.009	0.007	0.008	0.009	0.008		Area 5 vs. Area 2	0.047	0.064
n	40	8	11	9	8	9		Area 5 vs. Area 3	0.003	0.003
								Area 5 vs. Area 4	0.004	0.005
ANOC										
Log10-adjusted mean	2.253	2.245	2.256	2.233	2.249	2.239	0.002	Area 4 vs. Area 1	0.006	0.007
SE	0.002	0.005	0.005	0.006	0.006	0.005		Area 4 vs. Area 3	0.015	0.018
n	39	10	10	9	7	9				
WPB										
Log10-adjusted mean	1.731	1.720	1.721	1.739	1.709	1.746	0.031	Area 5 vs. Area 6	0.038	0.050
SE	0.004	0.008	0.008	0.008	0.009	0.008				
n	38	9	11	9	8	9				
WR60										
Log10-adjusted mean	1.810	1.791	1.823	1.803	1.776	1.793	0.017	Area 3 vs. Area 5	0.024	0.030
SE	0.005	0.010	0.009	0.012	0.012	0.010				
n	36	10	11	7	7	10				
WP60										
Log10-adjusted mean	1.419	1.404	1.408		1.353		0.040	Area 1 vs. Area 5	0.028	0.035
SE	0.014	0.021	0.016		0.017					
n	11	5	8		7					
WR1/2										
Log10-adjusted mean	1.752	1.729	1.760	1.752	1.724	1.720	0.010	Area 3 vs. Area 6	0.044	0.060
SE	0.006	0.010	0.009	0.011	0.010	0.010				
n	20	7	9	6	7	8				

Table 3. Continued.

Characters	Eng/Wales Area 1	Ireland Area 2	Scotland Area 3	The Netherlands Area 4	Spain Area 5	Portugal Area 6	ANOVA	Tukey tests	P	Bonferroni adjustment
GZW										
Log10-adjusted mean	2.285	2.276	0.294		2.266	2.275	0.001	Area 5 vs. Area 1	0.023	0.029
SE	0.003	0.005	0.005		0.006	0.005		Area 5 vs. Area 3	0.002	0.003
n	36	9	11		8	10		Area 3 vs. Area 6	0.049	0.065
GPOW										
Log10-adjusted mean	2.289	2.280	2.298	2.286	2.271	2.280	0.006	Area 5 vs. Area 1	0.038	0.051
SE	0.003	0.005	0.005	0.006	0.005	0.005		Area 5 vs. Area 3	0.007	0.008
n	35	9	10	7	8	10				
GPRW										
Log10-adjusted mean	2.245	2.241	2.238	2.234	2.219	2.235	0.022	Area 5 vs. Area 1	0.007	0.009
SE	0.003	0.007	0.008	0.006	0.007	0.007				
n	30	7	6	9	8	8				
WPT										
Log10-adjusted mean	1.682	1.667	1.704	1.684	1.647	1.673	0.025	Area 3 vs. Area 5	0.011	0.013
SE	0.006	0.012	0.010	0.014	0.014	0.013				
n	27	7	9	5	5	6				
WPR										
Log10-adjusted mean	1.876	1.872	1.895	1.872	1.859	1.874	0.012	Area 3 vs. Area 5	0.004	0.004
SE	0.003	0.006	0.006	0.007	0.007	0.007				
n	38	10	11	9	8	9				
MD										
Log10-adjusted mean	1.840	1.819	1.847	1.872	1.808	1.817	0.000	Area 1 vs. Area 5	0.010	0.011
SE	0.003	0.007	0.006	0.007	0.009	0.006		Area 1 vs. Area 6	0.012	0.014
n	38	9	11	7	6	12		Area 3 vs. Area 2	0.037	0.047
								Area 3 vs. Area 5	0.006	0.007
								Area 3 vs. Area 6	0.010	0.011
ML										
Log10-adjusted mean	2.587	2.585	2.586	2.590	2.563	2.584	0.016	Area 5 vs. Area 1	0.012	0.015
SE	0.004	0.005	0.005	0.005	0.006	0.005		Area 5 vs. Area 3	0.033	0.045
n	15	8	9	7	6	8		Area 5 vs. Area 4	0.013	0.016

Table 4. ANOVA and Tukey test results for geographical variation in mature female common dolphins. The Netherlands and Spain were excluded from the analysis due to their small sample sizes.

Characters	Erg/Wales Area 1	Ireland Area 2	Scotland Area 3	Portugal Area 6	ANOVA	Tukey tests	P	Bonferroni adjustment
Female common dolphins								
TBL								
Log10-adjusted mean	2.308	2.298	2.294	2.316	0.030	Area 3 vs. Area 6	0.039	0.048
SE	0.003	0.006	0.006	0.006				
n	37	10	11	10				
WR3/4								
Log10-adjusted mean	1.635	1.616	1.593	1.618	0.026	Area 1 vs. Area 3	0.018	0.022
SE	0.006	0.011	0.011	0.011				
n	21	7	6	7				
GPOW								
Log10-adjusted mean	2.273	2.265	2.264	2.280	0.036	Area 6 vs. Area 3	0.058	0.075
SE	0.002	0.005	0.004	0.004				
n	37	7	10	8				
LO								
Log10-adjusted mean	1.702	1.711	1.687	1.733	0.002	Area 6 vs. Area 1 Area 6 vs. Area 3	0.009 0.001	0.010 0.001
SE	0.005	0.011	0.009	0.008				
n	32	6	9	11				

ANCOVA revealed significant geographical differences in relative size, in skulls of mature males, for five characters: RL, MD, ANOC, WR1/2, and TREN (Table 5). Pairwise comparisons, with a Bonferroni adjustment, on significantly different characters showed dolphins from the Netherlands sample had significantly larger relative RL compared to those from England, Wales, Spain, and Portugal, and smaller relative ANOC compared to samples from Spain, Ireland, Scotland, and England and Wales. Portuguese skulls were also significantly smaller in relative ANOC compared to those from England, Wales, Ireland, and Spain. Pairwise comparisons also showed that dolphins from Portugal were significantly smaller in RW1/2 and TREN compared to dolphins off Scotland, the Netherlands, and England and Wales.

In contrast to the male body length data, female common dolphins inhabiting waters off Portugal were found to be significantly larger in absolute body length, compared to animals off the Scottish coast (Table 4). Therefore, this may reflect a sampling bias in the current study. Three skull measurements, WR3/4, GPOW, and LO, were significantly different in both absolute and relative size between the areas (ANOVA and ANCOVA, Table 4, 6). Tukey tests revealed that females from Scotland were significantly smaller in absolute and relative size of WR3/4 compared to those from England and Wales, and in relative size of LO compared to animals off the Irish coast. Portuguese dolphin skulls were significantly larger in absolute and relative size of GPOW and LO compared to those from Scotland, and in LO compared to those from England and Wales. On the whole, it appears that LO is inversely correlated with increasing latitude (Fig. 3). Interestingly for each sex, different measurements showed significant geographical variation, as revealed using ANCOVA, which suggests that these may be sex-linked.

Canonical Discriminant Analysis (CDA)—Even though sample sizes were small, it was not possible to combine data from the mature male and female dolphin skulls, for each area, because of the existence of sexual dimorphism in the sample (Area 1)² and possible sex-linked measurements.

Unstandardized Data

The CDA revealed significant geographical variation in skulls of both males and females in the eastern North Atlantic ($P = 0.004$, $P = 0.000$, respectively). Canonical discriminant functions 1 and 2 accounted for 42.7% and 24.2%, respectively, of the variation in male skulls and 38.9% and 32.6% of the variation in female skulls. In females both the discriminant functions were significant, but in the males only function 1 was significant. Discriminant functions misclassified 14% of males from England and Wales, 22% of males from Scotland, 14% of males from the Netherlands, 29% of males from Spain, and 43% of males from Portugal (Appendix 3¹). Although the Portuguese sample size was small, the CDA reclassified two individuals into Area 1 (England and Wales), and one individual into Area 2 (Ireland). Discriminant functions misclassified 9% of females from England and Wales, 14% of females from Ireland, and 25% of females from Scotland (Appendix 3).

The CDA plot for unstandardized male data suggests an overlap in skull size/shape for mature male common dolphins from the Netherlands, Ireland, and Portugal (Fig. 4B). Function 1 (which was the only significant one), indicated a slight overlap in

² Murphy, S. 2006. Sexual dimorphism in cranial measurements of *Delphinus delphis* in the eastern North Atlantic. Available online as supplemental material; see the end of this article for details.

Table 5. ANCOVA and pairwise comparisons results for geographical variation in relative size characters in mature male common dolphins.

Relative Character	Eng/Wales Area 1	Ireland Area 2	Scotland Area 3	The Netherlands Area 4	Spain Area 5	Portugal Area 6	ANCOVA	Pairwise comparisons	P	Bonferroni adjustment
Male common dolphins										
RL										
Log ₁₀ -adjusted mean	2.440	2.445	2.441	2.449	2.437	2.434	0.018	Area 2 vs. Area 6	0.019	0.291
SE	0.002	0.003	0.003	0.003	0.004	0.003		Area 4 vs. Area 1	0.020	0.300
n	22	7	9	8	5	9		Area 4 vs. Area 5	0.020	0.307
								Area 4 vs. Area 6	0.001	0.011
ANOC										
Log ₁₀ -adjusted mean	2.255	2.246	2.254	2.233	2.252	2.238	0.000	Area 4 vs. Area 1	0.000	0.001
SE	0.002	0.004	0.004	0.004	0.005	0.004		Area 4 vs. Area 2	0.043	0.649
n	24	7	9	8	6	9		Area 4 vs. Area 3	0.001	0.008
								Area 4 vs. Area 5	0.005	0.082
								Area 6 vs. Area 1	0.000	0.007
								Area 6 vs. Area 3	0.005	0.070
								Area 6 vs. Area 5	0.030	0.448
WR1/2										
Log ₁₀ -adjusted mean	1.746	1.732	1.757	1.749	1.739	1.719	0.043	Area 2 vs. Area 3	0.045	0.682
SE	0.006	0.009	0.008	0.010	0.011	0.009		Area 6 vs. Area 1	0.013	0.191
n	19	7	9	6	6	8		Area 6 vs. Area 3	0.002	0.037
								Area 6 vs. Area 4	0.029	0.430
TREN										
Log ₁₀ -adjusted mean	2.518	2.523	2.520	2.522	2.518	2.508	0.023	Area 2 vs. Area 6	0.002	0.037
SE	0.002	0.003	0.003	0.003	0.004	0.004		Area 6 vs. Area 1	0.007	0.112
n	20	6	9	8	5	7		Area 6 vs. Area 2	0.002	0.037
								Area 6 vs. Area 3	0.005	0.082
								Area 6 vs. Area 4	0.003	0.039
MD										
Log ₁₀ -adjusted mean	1.839	1.815	1.840		1.829	1.823	0.040	Area 1 vs. Area 2	0.010	0.103
SE	0.004	0.008	0.007		0.010	0.006		Area 1 vs. Area 6	0.028	0.281
n	23	6	9		5	11		Area 2 vs. Area 3	0.020	0.205

Table 6. ANCOVA and pairwise comparisons results for geographical variation in relative size characters in mature female common dolphins.

Relative Character	Eng/Wales Area 1	Ireland Area 2	Scotland Area 3	The Netherlands Area 4	Spain Area 5	Portugal Area 6	ANCOVA	Pairwise comparisons	P	Bonferroni adjustment
Female common dolphins										
WR3/4										
Log10-adjusted mean	1.634	1.619	1.596			1.613	0.030	Area 1 vs. Area 3	0.005	0.032
SE	0.006	0.011	0.011			0.011				
n	21	6	6			7				
GPOW										
Log10-adjusted mean	2.275	2.273	2.262			2.283	0.018	Area 1 vs. Area 3 Area 6 vs. Area 3	0.012 0.002	0.072 0.013
SE	0.002	0.005	0.004			0.004				
n	23	5	7			7				
LO										
Log10-adjusted mean	1.700	1.715	1.682			1.727	0.008	Area 2 vs. Area 3 Area 6 vs. Area 1 Area 6 vs. Area 3	0.026 0.009 0.002	0.156 0.057 0.014
SE	0.005	0.010	0.010			0.009				
n	23	6	6			9				

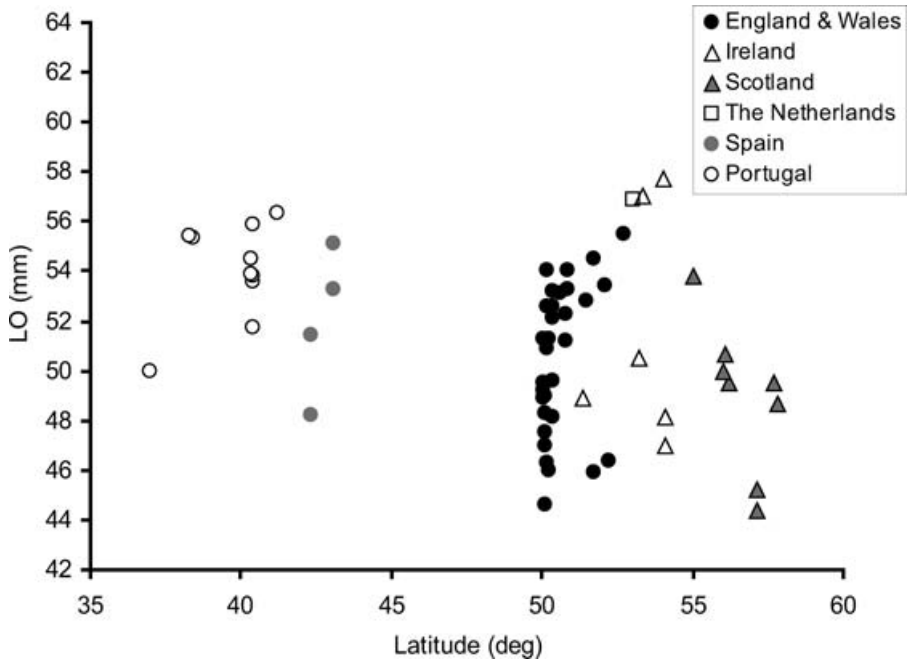


Figure 3. Scatterplot of the greatest length of orbit (mm) against latitude (deg) for mature females.

the measurements of skulls from dolphins from the Netherlands, Spain, and Scotland with those off the English and Welsh coast. The main discriminating characters in function 1 were the negative coefficient value of GPRW, and the positive coefficient values of WR60, ANOC, and MD. The female (unstandardized) CDA plot separated skulls of Spanish (from Galicia in northern Spain), Portuguese, and Dutch animals from all other groups (Fig. 4A). However, a slight overlap exists between skulls from Scotland, Ireland, and England and Wales. The main discriminating variables in Function 1 were GPRW and TRPT, both of which had highly positive coefficients. For function 2, which should show variations in skull shape, the main discriminating variables included both length and skull width characters such as RL, GZW, WR3/4, and LO (Appendix 4¹). These were some of the variables which univariate analysis of variance and covariance showed to be significantly different between areas (LO, WP3/4, and GPOW).

Standardized Data

The CDA revealed significant geographical variation in skull shape in male common dolphins ($P = 0.000$), but not in females ($P = 0.096$). The absence of significant geographical variation in the female data may in part be due to the reduction in the number of variables analyzed from 16 to 13. This reduction excluded the variables GPRW and LO, which were among the main discriminating variables in the unstandardized data. In males canonical discriminant functions 1 and 2 accounted for 49.1% and 17.6% of variation, respectively. Discriminant functions misclassified

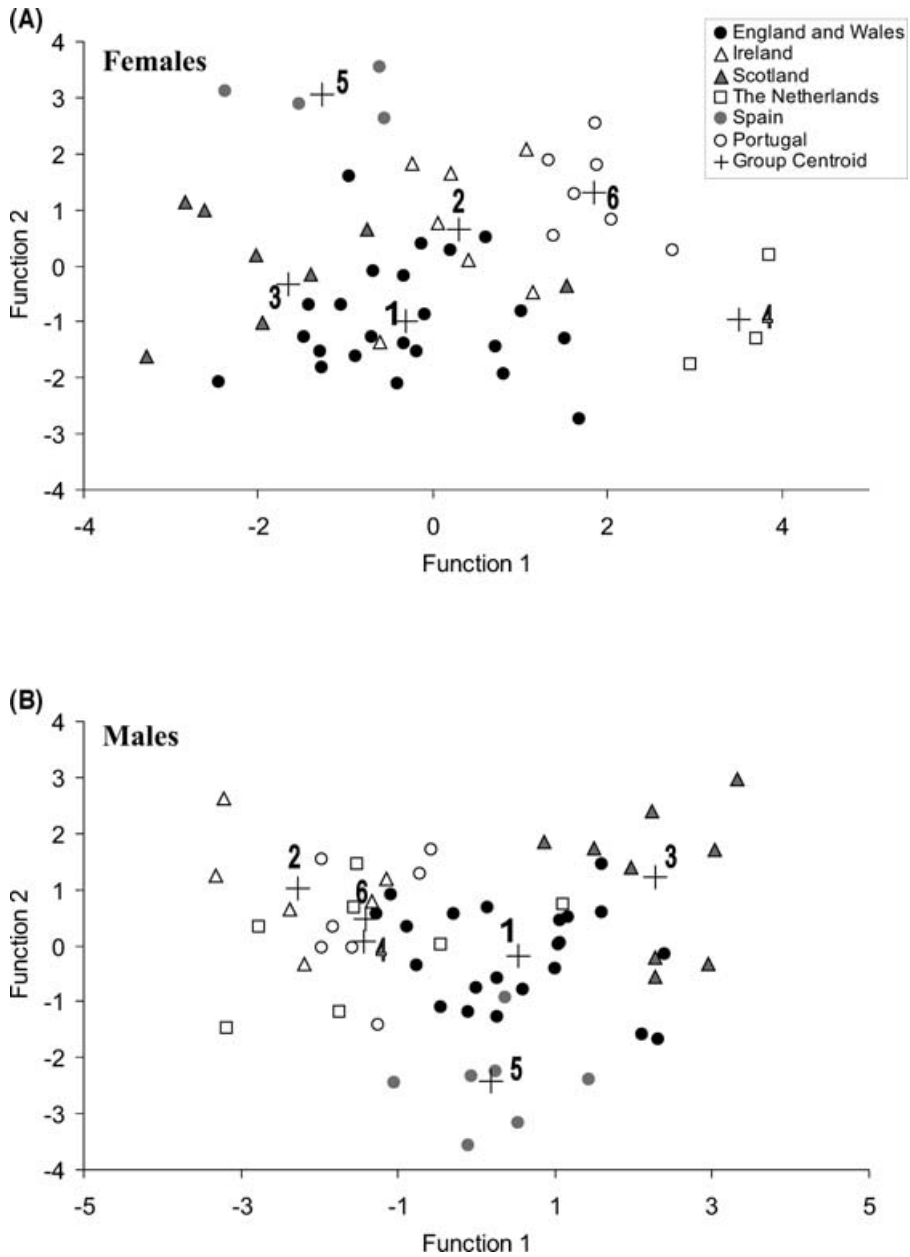


Figure 4. Plots of Canonical Discriminant Function Coefficients on the first and second axes, based on unstandardized data for (A) females and (B) males. Area 1 = England and Wales, Area 2 = Ireland, Area 3 = Scotland, Area 4 = The Netherlands, Area 5 = Spain, and Area 6 = Portugal.

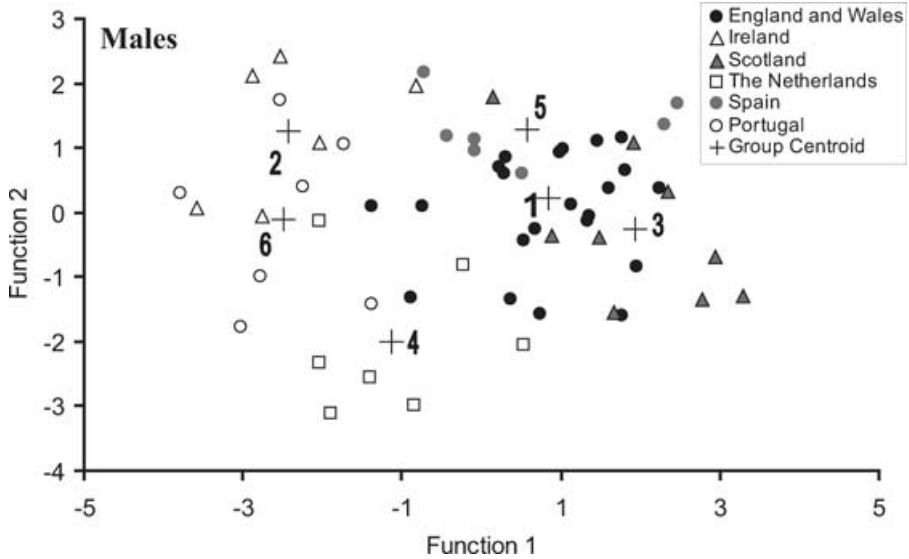


Figure 5. Plots of Canonical Discriminant Function Coefficients on the first and second axes, based on standardized data for males.

only 5% of males from England and Wales, 11% of males from Scotland, and 14% of males from Portugal. However, 57% of males from Spain were misclassified, although sample sizes from Spain were small. The CDA reclassified three animals from Spain (Area 5) into Area 1 (England and Wales) (Appendix 3). In males function 1 was significant, but function 2 was not quite significant ($P = 0.054$). The CDA plot is similar to the unstandardized CDA plot, and function 1 suggests an overlap in skull shape in mature males from Ireland and Portugal; and an overlap of skull shapes from Spain, Scotland, and England and Wales (Fig. 5). Allowing that function 2 was almost significant, results suggest a distinct difference between males in Ireland and Portugal from those in Spain, Scotland, and England and Wales; also separation of Dutch males from Scottish males, but with a slight overlap of Dutch males with those from England and Wales. In function 1 the main discriminating variables were related to skull width, the highly negative coefficient of GPRW, and highly positive coefficient of GZW (Appendix 4).

DISCUSSION

Taxonomic Status

The range for rostrum length/greatest zygomatic width ratio was 1.31–1.57 (mean = 1.44, $n = 111$) in mature specimens from all areas, although 95% were less than 1.52. The majority of skulls in this study thus fall within the RL/GZW ratio range (1.21–1.47) defined by Heyning and Perrin (1994) for *Delphinus delphis*. However, common dolphins in the current study also slightly overlap in RL/GZW ratio outlined for *D. capensis* (1.55–1.77) and therefore show signs of being an intermediate form. *D. delphis* in the eastern North Atlantic is larger in size than animals of

this species found off the Californian coast (Heyning and Perrin 1994). For example, minimum and maximum values for total body, condylobasal, and rostrum lengths of mature Californian *D. delphis* were 164–201 cm, 382–445 mm, and 218–275 mm, respectively (Heyning and Perrin 1994), compared with 185–244 cm (TBL), 395.8–487.1 mm (CBL), and 233.6–299.8 mm (RL) for dolphins in this study. However, in the current study, not only are common dolphins larger in TBL than *D. delphis* off the Californian coast, they are also larger than the majority of *D. capensis* in that region. Ranges for mature *D. capensis* from California were 193–235 cm for TBL, 445–498 mm for CBL and 281–321 mm for RL (Heyning and Perrin 1994). Common dolphins in the eastern North Atlantic are also larger (see Table 5), with respect to mean values obtained for the greatest postorbital, preorbital, and zygomatic widths, than both the short-beaked and long-beaked species off the Californian coast. However, even though common dolphins in the eastern North Atlantic appear more similar in size to *D. capensis* than *D. delphis* off California, they have not developed rostra as long as those identified in the long-beaked form. Furthermore, alveolar count data from the present study are, on average, within the range for *D. delphis* off the Californian coast.

Amaha (1994) also noted size differences between common dolphins in the eastern North Atlantic and the short-beaked form off the Californian coast. Amaha concluded that the eastern North Atlantic animals showed more similarities to *D. delphis* than *D. capensis* and did not exhibit signs of being an intermediate group. However, Mediterranean common dolphins were assigned to an intermediate form, although the sample size was very small ($n = 8$), and there was no information on year of stranding/capture for the specimens (Amaha 1994). Interestingly, Amaha (1994) found that eastern North Atlantic common dolphins had a longer skull length than that of the long-beaked form *D. capensis* inhabiting waters in the central eastern Atlantic (the majority of skulls analyzed being obtained from Senegal), and there was no difference in the tooth count (alveolar) data. However, the common dolphins in the eastern North Atlantic (off the French Atlantic coast) did have shorter and wider rostra than those of the central eastern Atlantic population (Amaha 1994). Further research by Van Waerebeek (1997) on common dolphins in the central eastern Atlantic suggested that both the common dolphin species inhabit waters in this region (from Gabon south to Central Angola), and they may live sympatrically. These skulls were obtained during the 1970s, and out of 21 skulls examined, two short-beaked dolphins were identified, both with a RL/GZW ratio of 1.49. Condylobasal length and RL/GZW ratio for adult *D. capensis* identified off the eastern Central Africa ranged 442–475 mm and 1.56–1.68 (Van Waerebeek 1997), in both cases overlapping with ranges obtained for common dolphins in the current study, although only slightly in relation to RL/GZW ratio.

Common dolphins from southern Australia and New Zealand also exhibit an intermediate morphology when compared to the short- and long-beaked species from Californian waters (Amaha 1994). A maximum TBL of 235 cm, and mean RL/GZW ratios of approximately 1.5 and 1.6 were recorded in two separate studies, while upper tooth count data ranged from 45 to 53 (Amaha 1994, Jefferson and Van Waerebeek 2002). As mentioned previously, a genetic study of the mitochondrial DNA control region and cytochrome *b* showed that only *D. delphis* inhabits waters off southern Australia (White 1999). Bell *et al.* (2002) also found that common dolphin skulls off southern Australia overlap in size with both the long- and short-beaked species in the eastern North Pacific. However, these Australasian animals exhibit a greater range of variation, not only when compared to *D. delphis* in the eastern North Pacific, but also

when compared to common dolphins in the eastern North Atlantic (this study). For example, southern Australian dolphins had RL/GZW ratios ranging from 1.36 to 1.73 (mean 1.52) and longer rostra (range 225–311 mm; Bell *et al.* 2002) compared to common dolphins in the present study.

Perrin *et al.* (1994) compared metric characteristics between *D. delphis* inhabiting waters in the eastern tropical Pacific, the Black Sea and the western North Atlantic. Although information on RL/GZW, body length, and tooth count data were not presented, information on CBL and RL suggests that skulls of common dolphins in western North Atlantic (combined data from the western and mid North Atlantic) ($n = 71$, CBL = 409–478 mm, RL = 240–299 mm) and the eastern tropical Pacific ($n = 73$; CBL = 397–460 mm, RL = 233–286 mm) are similar in size compared to individuals in this study (CBL = 395.8–480 mm, RL = 233.6–299.6 mm). Amaha (1994) also found similarities between skull samples obtained from the western and eastern North Atlantic, and noted less variation in skulls between the eastern and western basins of the Atlantic, as compared to within the Pacific. Total body length range for mature *D. delphis* in the western North Atlantic reported by Amaha (1994) was 198–236 cm. In the eastern tropical Pacific, maximum total body length described by Amaha (1994) for *D. delphis* was 221 cm, although Perrin (2002) reported an animal measuring 235 cm in length.

Analyses of microsatellite DNA have shown high levels of genetic differentiation and little or no gene flow between common dolphins in the Black Sea and those in both the Mediterranean and the eastern North Atlantic (Natoli *et al.* 2003). It is believed that the Black Sea contains an isolated population, with a lower effective population size, compared to the relatively high levels of gene flow and population size in the Mediterranean and eastern North Atlantic (Natoli *et al.* 2003). *D. delphis* in the Black Sea are smaller in both CBL (374–420 mm) and RL (218–258 mm), compared to *D. delphis* in the North Atlantic (Perrin *et al.* 1994). However, *D. delphis* in the Black Sea and off the Californian coast are similar in body size, as average length of mature individuals was 180 cm and 170 cm for males and females in the Black Sea, and 189.5 and 180.1 cm for males and females in Southern Californian Bight (Amaha 1994, Heyning and Perrin, 1994).

Different explanations for variability in size within *D. delphis* have been proposed for different areas. For example, it has been suggested that off the Californian coast, where *D. delphis* lives sympatrically with the long-beaked *D. capensis*, the overall body size and skull size of *D. delphis* has decreased, possibly due to character displacement (Perrin 1984). In contrast, common dolphins in the Black Sea are believed to have become reduced in size over time, owing to their restriction to an almost isolated inland sea (Perrin 1984). However, common dolphins in the North Pacific Ocean are also similar in body size to *D. delphis* in the Black Sea, and animals off the Californian coast, as asymptotic lengths calculated for mature males and females were 188.1 and 179.4 cm, respectively (Ferrero and Walker 1995). However, there is no published information suggesting that common dolphins in the North Pacific Ocean have over time, reduced their overall body size. Therefore, if the common dolphin in the eastern North Atlantic is not an intermediate form between *D. delphis* and *D. capensis*, but only a larger form of *D. delphis*, there is a possibility that “dwarfism” (relative to the size of common dolphins in the eastern North Atlantic and the Mediterranean) in body and skull sizes may not have occurred to common dolphins in the Black Sea—as had been previously suggested by Perrin (1984) and Amaha (1994). Instead, the common dolphins in the eastern North Atlantic may have evolved a much larger size than that of animals from populations of *D. delphis* in the eastern and northern Pacific

Ocean, and the Black Sea. If so, this probably also occurred to *D. delphis* inhabiting waters off southern Australia, New Zealand, and the western North Atlantic.

To date, two species of common dolphin and one subspecies are generally recognized. Based on tooth counts and absolute length of rostrum, it appears that common dolphins in the eastern North Atlantic are most similar to *D. delphis* as described by Heyning and Perrin (1994). However, large-scale morphological variation within this species is evident and in some geographical locations identification based on Heyning and Perrin's (1994) classification of long- and short-beaked forms is difficult. In conclusion, identification of *D. delphis* based on morphological criteria is not as easy as originally proposed, owing to the high variability in this species. However, until further analyses are carried out, the common dolphin in the eastern North Atlantic should be classified as a large form of the short-beaked common dolphin *D. delphis*.

Geographical Variation

Overall there appears to be a slight latitudinal cline in size, with mature male common dolphins in higher latitudes being slightly larger in terms of absolute skull width, mandible length, mandible depth, and total body length compared to dolphins off the northwest coast of Spain. Spanish mature male common dolphins were significantly smaller in a number of measurements compared to dolphins in other areas. However, the composition of the Spanish sample indicates a lack of mature males with a TBL of 202–225 cm, resulting in a lower-than-expected mean TBL for this sample. The lack of data in this range is due to sampling bias in the current study, as strandings data for the common dolphin in Galicia do not show any inconsistency in TBL data (see López *et al.* 2002). However, the female data appear to show a latitudinal cline in both absolute and relative length of the orbit, which appears to be inversely proportional to increasing latitude.

On the whole, comparisons of quantitative estimates between areas must be interpreted cautiously, because some of the sample sizes in the current study were small. However, in males geographical variation in absolute and relative skull size was apparent, with skulls of Portuguese and Irish male common dolphins distinct from skulls from Spain, Scotland, and England and Wales, as seen in both unstandardized and standardized CDA plots. The main discriminating factors using standardized data separating the skulls of Irish and Portuguese male common dolphins from those of other areas were related to the width of the skull (GPRW GZW). The unstandardized CDA plot for females suggested that Irish, Scottish, and English and Welsh common dolphins formed a group distinct from other areas. The main discriminating variables included skull length and width measurements (RL, TRPT, TREN, LO, GPRW, and GZW). As mentioned above, Portuguese females differed significantly in orbital measurements from females in areas in more northerly latitudes. In the eastern North Atlantic, there is evidence of ecophysiological separation of Portuguese common dolphins from those off the French Atlantic coast. Zhou *et al.* (2001) found lower mercury concentrations in Portuguese animals, possibly as a result of different feeding ecologies. Analysis of heavy metals in sardines (*Sardina pilchardus*) caught off Portugal, which is the main prey species of Portuguese common dolphins, demonstrated low concentration of mercury and other trace metals in this fish species (Zhou *et al.* 2001).

Some evidence from the current study suggests that Portuguese female common dolphins may be reproductively isolated and may not interbreed with common

dolphins from other areas in this study, even though Portuguese males may disperse northward. However, it is not possible to determine whether the mixing between Irish and Portuguese male common dolphins is due to Portuguese males migrating northward, or a southern migration of Irish males. Evidence of female philopatry has been suggested for a number of cetacean species. In Shark Bay, Australia, dispersal of female bottle-nosed dolphins (*Tursiops aduncus*) is more restricted than that of males (Krützen *et al.* 2004). Female philopatry has also been found in harbor porpoises (*Phocoena phocoena*). For example, females from the Baltic Sea are morphologically distinct from females in the Kattegat and Skagerrak seas, suggesting that porpoises from these areas do not interbreed. In contrast, a lack of geographical variation in males suggests that they move between these seas (Börjesson and Berggren 1997). The most probable explanation for the results in the current study is the mixing of common dolphins off the Portuguese coast with common dolphins in the Mediterranean and farther south of the sampling area. Natoli *et al.* (2003) found no significant variation, using microsatellite markers, between common dolphins in the western Mediterranean (samples obtained from the Alboran Sea and Algeria) and the contiguous North Atlantic (samples obtained from the Strait of Gibraltar and Portugal), which indicates gene flow between those areas.

The Dutch sample was obtained mainly from 1926 to 1953, a period coincident with an increase in common dolphin strandings. Results from analysis of unstandardized data showed that skulls of female common dolphins from the Netherlands were significantly different from those from other areas, despite the very small sample size ($n = 3$). The main discriminating factors in functions 1 and 2 were related to the skull length (TRPT and RL, respectively), so that the observed differences may be due to skull size, and not skull shape. Furthermore, in the discriminant analysis, the centroid of the Dutch data appears to be situated along the same plane (with respect to function 2, skull shape) as skulls from England and Wales. In males plots for both unstandardized and standardized data show an overlap of skulls from the Netherlands with those from England and Wales, but separation of samples from the Netherlands and Scotland. These findings all suggest movement of common dolphins into the southern North Sea via the English Channel during the above time period. This is consistent with the English strandings data, because in 1930s and 1940s there was an increase in the number of strandings of common dolphins along the east coast of England (East Sussex to southern Lincolnshire), in the southern North Sea (see Fraser 1946, 1953).

However, the Scottish sample in the present study is probably not representative of animals living off the Scottish coastline during the 1920s–1950s, as the distribution and abundance of common dolphins in this area has fluctuated over the last century. All animals analyzed in the CDA analysis were obtained between 1993 and 2005, a period when both abundance of common dolphins increased off the northwest Scottish coast and an increase in stranding records of this species was noted (MacLeod *et al.* 2005). This change in the abundance of common dolphins off the northwest Scottish coast has been attributed to increasing water temperature in recent years (period examined 1948–2003; MacLeod *et al.* 2005). This raises the question of where these animals have migrated from since the early 1990s. Examination of the CDA plots revealed that, although the skulls of Scottish animals appear slightly different to those from other areas, there is an overlap with skulls from England and Wales, but not with those from Ireland. The slight difference, however, of some Scottish animals from the English and Welsh animals suggests that there may be movement of animals from other areas *e.g.*, further offshore, or else that sampling biases have occurred in

the collection of specimens. Though a larger sample size of skulls from Scotland and Ireland is needed to clarify the interpretation of the data.

However, changes in water temperature in western European waters also occurred earlier in the century, which again led to changes in the distribution of common dolphins at that time. Between the 1930s and the 1960s, a decline in strandings of common dolphins occurred along the southwest coast of the United Kingdom, and Ireland (Fraser 1934, 1946; Sheldrick 1976; Evans and Scanlan 1989; Murphy 2004). During this period, it is believed that due to changes in prey availability and increasing water temperatures off the south coast of the United Kingdom (Russell cycle), a northward shift occurred in the distribution of the common dolphin (Evans and Scanlan 1989, and references therein). Movements of common dolphins into the northern North Sea from the Atlantic were documented in the 1930s, with unusually large number of strandings reported from the east coast of Scotland, at a time when there was an invasion of the North Sea by a large number of the squid *Todarodes sagittatus*, which is a prey species of the common dolphin (Fraser 1937, 1946; Evans and Scanlan 1989). Therefore, although results of the current study suggest that common dolphins stranded along the Dutch coastline between the 1920s and 1950s entered the southern North Sea via the English Channel, it is possible that some of these animals migrated northward from off the southwest coast of the United Kingdom, and entered the northern North Sea *via* the Atlantic.

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Supplementary Material

The following supplementary material is available for this article online:
Article on sexual dimorphism and four appendices.