

Occurrence of long-beaked and short-beaked forms of *Delphinus* spp. off NW Africa appears to reflect differential use of habitat rather than taxonomy.

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ABSTRACT

The common dolphin has a widespread distribution and is present in all oceans of the world, where it occupies from cold to temperate and subtropical waters. This wide distribution range has led to the differentiation of a number of morphotypes. Little information is available on this regard from the tropical and subtropical waters of the northeastern Atlantic Ocean. From 1993 to 2006, bone samples (n=66) and skulls (n=41) from stranded common dolphins (*Delphinus* spp.) were collected from the segment of Mauritanian coastline extending from the Western Sahara to the Senegal River. Skull morphometrics and isotopic relative abundance of nitrogen and carbon were investigated to assess potential population structuring as well as position in the trophic web and preferred habitats. Morphometrics showed large variation, and the distribution of the RL/ZW ratios, the most indicative measurement to discriminate between long-beaked and short-beaked forms, followed a cline and it was not possible to differentiate, as in other oceans, two distinct clusters. Large variability was also observed for both isotopes: nitrogen isotope ratios (δN) ranged between 10.8 and 14.3, a difference of about one trophic level, while carbon isotope ratios (δC) ranged between -14.4 and -10.9, both indicating substantial heterogeneity in habitat use. Regression analysis between δN and δC revealed that individuals feeding at higher trophic level were more pelagic and prone to feed over the continental slope, whereas those foraging at lower trophic level were feeding over the continental shelf or around the shelf edge. More importantly, a joint analysis between RL/ZW ratios and stable isotopes revealed that the shorter-beaked animals were feeding at a lower trophic level than the longer-beaked animals. We conclude that the waters off Mauritania are inhabited by common dolphins with beak lengths that range from the typically short-beaked form to the typically long-beaked form, although it does not appear that these morphotypes can be ascribed to two separate species (*D. delphis* and *D. capensis*) or even populations. Dissimilarities in isotopic signature would suggest that the length of the beak would be more indicative of habitat use rather than of taxonomic segregation.

INTRODUCTION

Dolphins have evolved in marine waters and spread through the oceans, but their distribution is limited by the range of water temperatures that have become acceptable for each species. The common dolphin is a representative example of this evolutionary path, since it is present in all oceans of the world where it occupies from cold to temperate and subtropical waters (Evans, 1994, Perrin, 2002). Such an extensive distribution range has facilitated the differentiation of a number of morphotypes that until today remain of unclear taxonomic ascription (White, 1999). In many areas, two morphotypes have been distinguished: one long-beaked, mostly of coastal or neritic distribution, and one short-beaked, that occupies indistinctly inshore and offshore waters (Banks and Brownell, 1969; Evans, 1982). Banks and Brownell (1969) differentiated the two forms through their ratio of zygomatic width to rostrum length, and suggested that the anatomical difference was likely due to dissimilarities in food habits. The anatomical differentiation was later confirmed by Evans (1982), who conducted additional multivariate analysis of skull measurements on the species. In the Eastern North Pacific, Heyning and Perrin (1994) and Rosel *et al.* (1994) through morphological and genetic analysis, respectively, conclusively distinguished the two morphotypes and split

the genus into two species: the short-beaked common dolphin *Delphinus delphis* (Linnaeus, 1758) and the long-beaked common dolphin *Delphinus capensis* (Gray, 1828).

In the eastern North Atlantic, *Delphinus spp.* is present from ca65°N (south of Norway) to about the Equator. However, the region appears to be split between the two morphotypes: north of ca25°N (the southern border of the western Sahara) only the short-beaked form occurs, from there to the river Senegal both forms appear to coexist, and further south the long-beaked form would predominate (Van Bree and Gallagher, 1978; Amaha, 1994; Heyning and Perrin 1994; Van Waerebeek 1997; Rice, 1998; Perrin, 2002). Recently, a genetic study conducted by Natoli *et al.* (2006) concluded that the long-beaked individuals from Mauritania clearly differentiated from other long-beaked populations elsewhere and challenged the currently accepted hypothesis of a single long-beaked lineage worldwide. Additionally, they suggested that the long-beaked form originated independently in different regions; the adaptation to local environments would be driving local speciation. However, Natoli *et al.* (2006) based their study only on the genetics of a limited number of specimens, thus leaving uncertainty on the actual composition and adscription of the *Delphinus* forms in the region.

In this paper we report the results of a study on the population structuring of common dolphins from Mauritania using two independent tools: the relative abundance of nitrogen and carbon stable isotopes, and the morphometrics of the skull. We conclude that, concurrently with Natoli *et al.* (2006), taxonomic splitting is not justified in the region.

METHODOLOGY

Sampling

Samples were collected between 1992 and 2006 along the ca700 km of Mauritanian coastline that extends from Cape Blanc to the Senegal River, north-western Africa (Figure 1).

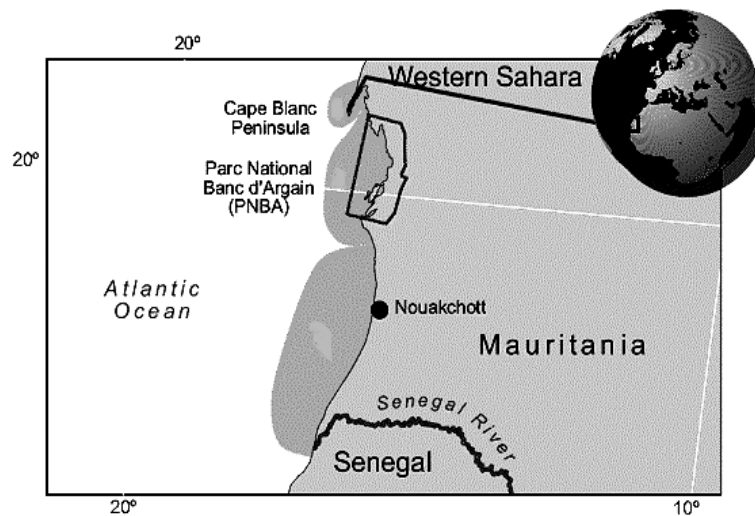


Figure 1 – Map of the study area.

The beaches were surveyed opportunistically or in dedicated expeditions during the study period and, when the remains of a dead dolphin were encountered, the skull was preserved. Sex, body length, geographical position and any indication of the cause of death were recorded whenever possible; however, most specimens were found in an advanced state of decomposition or as bone remains, so unfortunately there is no detailed biological information from many specimens.

Stable isotopes analysis

The relative abundance of heavy to light nitrogen isotopes ($^{15}\text{N}/^{14}\text{N}$, expressed as $\delta^{15}\text{N}$) and carbon isotopes ($^{13}\text{C}/^{12}\text{C}$, expressed as $\delta^{13}\text{C}$) was determined in bone. For the analysis, approximately one gram of tissue was rinsed with distilled water, dried for 3 days at 60°C and powdered with mortar and pestle. Because lipids mislead the analyses by decreasing the $\delta^{13}\text{C}$ (DeNiro and Epstein, 1977), they were removed

from the samples by rinsing the powdered tissue several times with a chloroform/methanol (2:1) solution (Bligh and Dyer, 1959). When conducting stable isotope analysis in bone, several authors have carried out preventive demineralization of the tissue by treating it with a 0.5 and 1.0 M hydrochloric acid (HCl) solution (Bocherens *et al.*, 1997; Newsome *et al.*, 2006). However, a test in our samples revealed that $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values did not change between demineralised and untreated samples, so this procedure was not followed subsequently. Approximately one milligram of lipid-free bone was weighed in tin capsules (3,3x5 mm) and analysed in a continuous flow isotope ratio mass spectrometer (Flash 1112 IRMS Delta C Series EA Thermo Finnigan), where the capsules were loaded and combusted at 1000°C. Atropine was used as a standard to check for elemental composition for C and N.

Stable isotope abundances were expressed in delta (δ) notation, in which the relative variations of stable isotope ratios are expressed in permil (‰) deviations from predefined international standards calculated as: $\delta X = [(R_{\text{sample}}/R_{\text{standard}}) - 1] \times 1000$, where X is ^{13}C or ^{15}N , R_{sample} is the ratio of the heavy to the light isotope of the sample ($^{13}\text{C}/^{12}\text{C}$ or $^{15}\text{N}/^{14}\text{N}$), and R_{standard} is the ratio of the heavy to the light isotope in the reference standards. The latter were the V-PDB (Vienna Pee Dee Belemnite) calcium carbonate for ^{13}C and the atmospheric nitrogen (air) for ^{15}N . International isotope secondary standards of known $^{13}\text{C}/^{12}\text{C}$ ratios, as given by the IAEA (International Atomic Energy Agency), namely polyethylene (IAEA CH7, $\delta^{13}\text{C} = -31.8\text{‰}$), graphite (USGS24, $\delta^{13}\text{C} = -16.1\text{‰}$) and sucrose (IAEA CH6, $\delta^{13}\text{C} = -10.4\text{‰}$), were used for calibration at a precision of 0.2‰. For nitrogen, international isotope secondary standards of known $^{15}\text{N}/^{14}\text{N}$ ratios, namely $(\text{NH}_4)_2\text{SO}_4$ (IAEA N1, $\delta^{15}\text{N} = +0.4\text{‰}$ and IAEA N2, $\delta^{15}\text{N} = +20.3\text{‰}$) and KNO_3 (IAEA NO₃, $\delta^{15}\text{N} = +4.7\text{‰}$), were used for calibration at a precision of 0.3‰.

Morphometric measurements

Skulls were measured using a vernier caliper (0.1mm accuracy). The sample only included skulls in which the premaxillary and maxillary bones were fused and that were therefore considered to have completed their growth and to correspond to physically mature individuals. Morphometric measures followed those of Heyning and Perrin (1994), although for the present report we only focus on the rostrum length/greatest zygomatic width (RL/ZW) ratio, which is the most indicative measurement to discriminate between short-beaked and long-beaked forms of common dolphins (Banks and Brownell, 1969; Evans, 1975; Van Bree and Gallagher, 1978; Amaha, 1994; Evans, 1994; Heyning and Perrin, 1994; Jefferson and Van Waerebeek, 2002).

Data analysis

Previous to other statistical examination, the data were tested for outliers and, whenever found, eliminated from subsequent analysis. The normality of the data was tested through the Lilliefors's test and their heteroscedasticity through the Levene's test. The relationship between stable isotopes of carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) was investigated through correlation analysis. Correlation analyses were also performed between isotopic abundances of nitrogen ($\delta^{15}\text{N}$) and carbon ($\delta^{13}\text{C}$), and the RL/ZW ratio. Regression analysis was conducted whenever significant correlations were found. The statistical software package SPSS 15.0 was used for all analyses.

RESULTS

In total, 66 specimens were examined, from which a sample of bone was collected for stable isotopes. Measurement of skulls was only possible from 41 of these, since part of the skulls were incomplete or sufficiently damaged to impede reliable measurement. Although the complete coastline was surveyed, most specimens were found north of the tip of Cape Blanc and south of Cape Timirist (the southern border of the Parc National du Banc d'Arguin). Thus, common dolphins were apparently absent or occurring at very low density in the shallow waters of the Banc d'Arguin.

The average isotopic values of the individuals sampled in this study were -12.4 ± 0.7 (‰; mean \pm SD) for the $\delta^{13}\text{C}$ and 12.5 ± 0.7 (‰; mean \pm SD) for the $\delta^{15}\text{N}$. A high intraspecific variability was observed for both stable isotopes: $\delta^{15}\text{N}$ ranged between 10.8‰ and 14.3‰, a difference of about one trophic level,

while $\delta^{13}\text{C}$ ranged between -14.4‰ and -10.9‰, indicating sensible differences in habitat use. Three outliers were found and removed from subsequent analyses. $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ were significantly and negatively correlated ($R^2=0.382$, $p<0.001$), and $\delta^{13}\text{C}$ decreased when $\delta^{15}\text{N}$ increased, this is, at higher trophic levels (Figure 2).

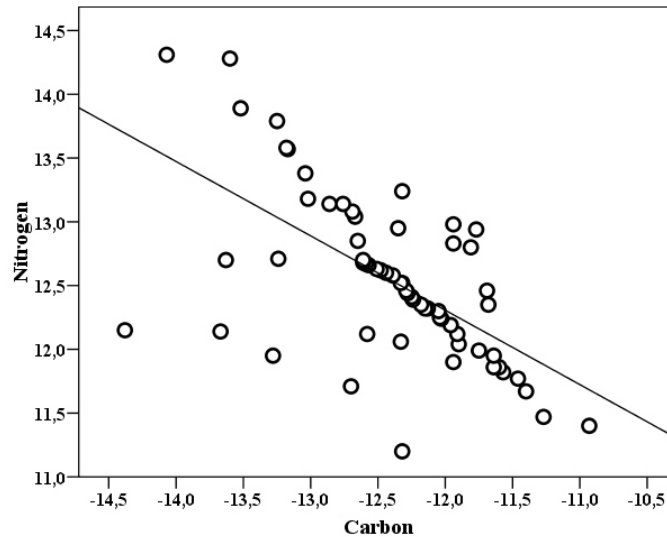


Figure 2 - Correlation between $\delta^{15}\text{N}$ (Nitrogen) and $\delta^{13}\text{C}$ (Carbon) for the common dolphins inhabiting Mauritanian waters ($R^2=0.382$, $p<0.001$, $n=63$).

The RL/ZW ratios of the individuals sampled in this study ranged 1.27-1.73 (mean: 1.48; SD: ± 0.12). The distribution of the RL/ZW ratios clearly followed a cline (Figure 3), and a separation between two putative groups attending to their relative beak length was not apparent.

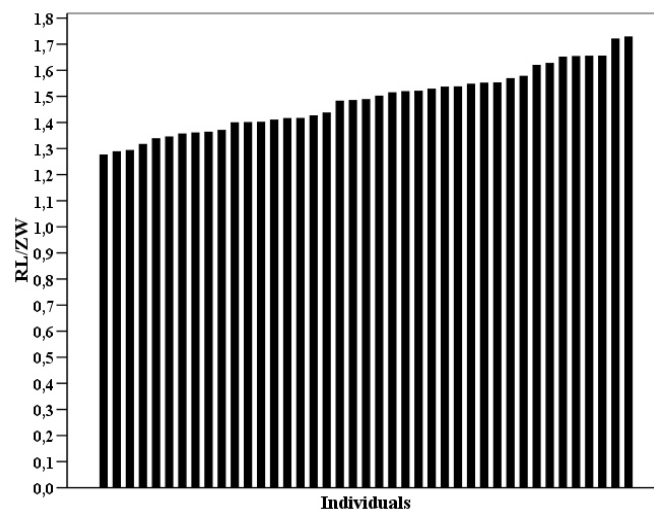


Figure 3 – Distribution of the RL/ZW ratios for the common dolphins sampled ($n=41$).

When investigating the correlations between isotopic abundances and the RL/ZW ratio, two outliers were found and removed from subsequent analyses. A positive significant correlation ($R^2=0.326$, $p<0.001$) was found between $\delta^{15}\text{N}$ and the RL/ZW ratio, indicating that the RL/ZW ratio increased when the $\delta^{15}\text{N}$ increased (Figure 4). Conversely, no correlation was found between $\delta^{13}\text{C}$ and RL/ZW ratios ($p=0.103$).

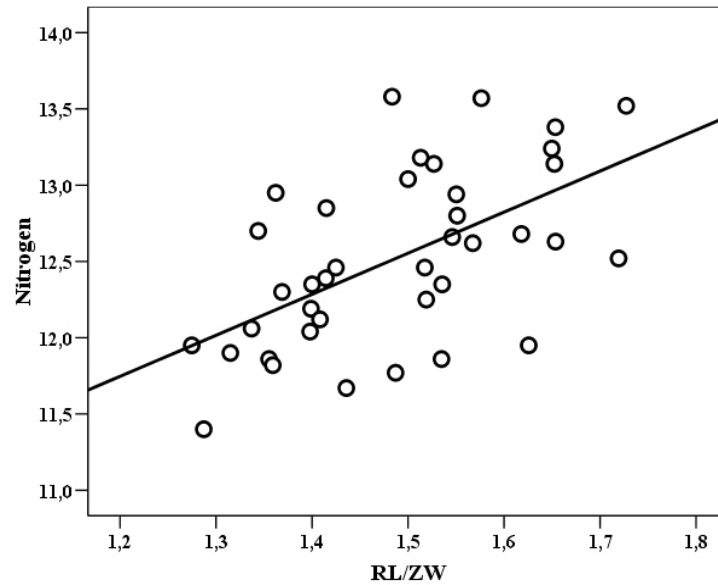


Figure 4 - Correlation between $\delta^{15}\text{N}$ and the RL/ZW ratio in the common dolphins inhabiting Mauritanian waters ($R^2=0.326$, $p<0.001$, $n=39$).

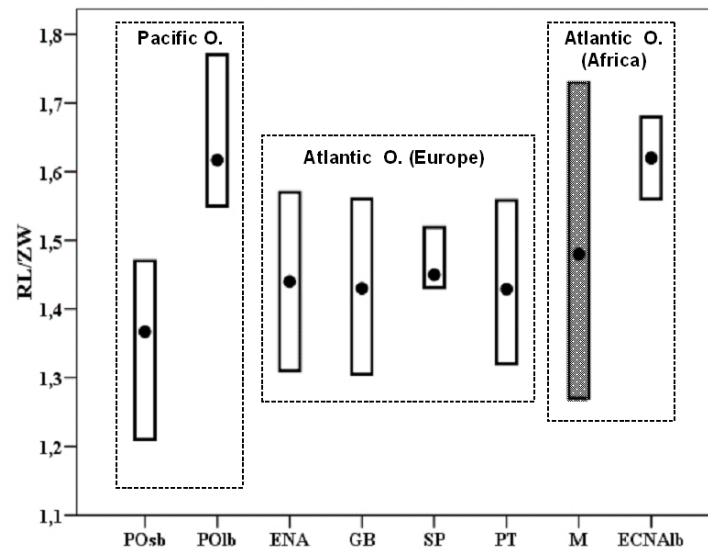


Figure 5 – Comparison of the RL/ZW ratios from *Delphinus spp.* populations worldwide. POsb: short-beaked common dolphin from the Pacific Ocean ($n=97$), POlb: long-beaked common dolphin from the Pacific Ocean ($n=31$) (Heyning and Perrin, 1994); ENA: short-beaked common dolphin from the Eastern North Atlantic ($n=111$), GB: short-beaked common dolphin from Great Britain ($n=47$), SP: short-beaked common dolphin from Spain ($n=10$), PT: short-beaked common dolphin from Portugal ($n=18$) (Murphy *et al.*, 2006); M: *Delphinus spp.* from Mauritania ($n=41$) (present study); ECNAIb: long-beaked common dolphin from Central West Africa ($n=21$) (Van Waerebeek, 1997).

Figure 5 shows a comparison between the RL/ZW ratios observed in this study and those previously published for short- and long-beaked forms elsewhere. The range of the RL/ZW ratios of common dolphin specimens from Mauritania (1.27-1.73, M, Figure 5) overlaps with *D. delphis* and *D.*

capensis populations from other parts of the world. The range for RL/ZW ratio described as *D. Delphis*, from the Eastern North Atlantic was 1.31-1.57 (ENA, Figure 5), which falls within the range of RL/ZW ratios (1.21-1.47) obtained for this species off California (POsb, Figure 5), as well as for the *D. capensis* RL/ZW ratios (1.55-1.77; POLb, Figure 5) (Heyning and Perrin, 1994). Van Waerebeek (1997) analyzed the RL/ZW ratios of common dolphins off Senegal (1.56-1.68, ECNAIb, Figure 5) and assumed to be all of them *D. capensis*.

DISCUSSION

The isotopic composition of an animal depends on that of its food sources (DeNiro and Epstein, 1978; 1981), but the relative abundance of the heavier isotope of carbon and, particularly, nitrogen, increases in each trophic level, thus rising progressively through the trophic web (Peterson and Fry, 1987; Cabana and Rasmussen, 1996). Thus, $\delta^{15}\text{N}$ is commonly taken as indicator of trophic level, with an increase of a mean of 3.4‰ per trophic level (Minagawa and Wada, 1984; Peterson and Fry, 1987), as well as a direct indicator of diet composition (DeNiro & Epstein, 1981). $\delta^{13}\text{C}$ also moderately reflects trophic level but, as coastal, benthos linked, food webs are more enriched in ^{13}C than oceanic/pelagic food webs (France & Peters, 1997; Hobson, 1999), this index is moreover informative of the main habitat used for foraging (France, 1995; Das *et al.*, 2003).

The large variability in both indices found in our sample suggests substantial differences in habitat use, with individuals occupying both inshore and offshore waters. Sightings data from the area are scarce and opportunistic, and they are never so accurate as to differentiate short-beaked from long-beaked individuals, but it has been suggested that common dolphins are rarely sighted close to the beach (Robineau and Vely, 1998). Regression analysis between δN and δC revealed that individuals feeding at higher trophic levels were more pelagic and prone to feed over the continental slope, whereas those foraging at lower trophic levels were feeding over the continental shelf or around the shelf edge. It thus appears that the use by common dolphins of different habitats is related to the exploitation of dissimilar food resources.

Individuals from Mauritania with higher $\delta^{15}\text{N}$ values, and thus feeding at a higher trophic level, were also found to have higher RL/ZW ratios than individuals with a lower $\delta^{15}\text{N}$. Published literature does not report obvious differences in the diet of *D. delphis* and *D. capensis* (Ohizumi *et al.*, 1998), but a survey on stomach contents by Schwartz *et al.* (1992) concluded that the short-beaked form may feed more extensively on squid, and therefore exploit a lower trophic level, than the long-beaked form, that would mostly rely on pelagic fish situated high in the trophic web. The results of the present study point in the opposite direction, this is, that individuals of shorter beak exploit lower trophic levels, while those of longer beak consume prey from the water column and situated higher in the food web.

The variability in relative beak lengths was very large as compared to other *Delphinus* populations studied in other parts of the world (Figure 5). Although the sample could not be stratified by sex, the observed variability is unlikely to be explained by a gender-effect, since the sexual dimorphism of *Delphinus* skulls is very limited (Heyning and Perrin, 1994; Van Waerebeek *et al.*, 1994). Overall, the ranges of variation were so large as to be only slightly smaller than the composite variation of the two North Pacific species, *D. delphis* and *D. capensis*, put together (Heyning and Perrin, 1994). The lower fringe of values encompassed the values typically found in the *D. delphis* from the eastern North Atlantic (Murphy *et al.*, 2006), while the northern fringe encompassed those found in Central West Africa and attributed to *D. capensis* (van Waerebeek, 1997).

The distribution of both the RL/ZW ratio and the isotopic indices formed a cline, and in neither case two distinct groups could be identified as it is the case with the skull morphometrics from the eastern North Pacific (Heyning and Perrin, 1994). Thus, despite the occurrence in the area of individuals that can be ascribed to the two *Delphinus* morphotypes, it appears that the area is inhabited by a single population with intrinsic large variation. This appears to confirm previous genetic research conducted by Natoli *et al.* (2006), which found long-beaked individuals from Mauritania to be taxonomically closer to the short-beaked form of the North Atlantic rather to *D. capensis* from other parts of the world.

We can thus conclude that both forms of common dolphin co-exist in Mauritania, even though the existence of two putative populations or species (*D. delphis* and *D. capensis*) should be put in doubt until more in-depth genetic analyses are conducted and other taxonomic relevant morphometric measurements are investigated. In this context, dissimilarities in isotopic signatures suggest that the length of the beak is more indicative of habitat use rather than of taxonomic segregation.

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