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Chapter 2

PRESENCE OF TWO MORPHOTYPES IN POPULATIONS OF *DELPHINUS DELPHIS*: OCCIPITAL BONE MORPHOLOGY

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ABSTRACT

The occipital bone is an area of great adaptive value for Cetaceans in general and Odontoceti specifically due to it containing critical systems for the animal, such as the blood supply system for the brain and the hindbrain, a neural system that in Odontoceti it is thought to play an important role in echolocation and navigation. The aim of this study is to study the variability of this region and its relationship with behavioural and environmental factors. This will be achieved by a biometry study of the skeletal part of the occipital area, since it allows more precise and extensive studies and it is to expect that variations in soft systems will reflect on these hard structures that gives them support. In order to do

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this, critical bone landmarks that reflect the configuration of soft structures will be used to conduct biometrical analysis in order to study morphological variability as well as asymmetry. It is to expect that the results from this analysis will not only increase our knowledge of biological components critical for the adaptation and survival of Cetaceans, but also information on population variability and environmental pressures that could be of great importance for future conservation plans in the face of the great-scale environmental changes the world is suffering.

In the present study we took measurements from the occipital bone of 652 *Delphinus delphis* specimens from the Natural History Museum of Los Angeles county and the Smithsonian National Museum of Natural History museums and two populations, one from the North Atlantic Ocean and other from the North Pacific Ocean. We used geometrical and statistical methods to estimate several characteristics of the occipital area such as occipital bone curvature and caudal fossa depth. Our results revealed the existence of two well-differentiated morphotypes, each of which could be divided further in two classes with a very different stranded to non-stranded ratio. This stranded to non-stranded ratio was negatively correlated to the curvature of the occipital bone and the caudal fossa depth. We conclude that these different morphotypes of the occipital bone area reflect anatomical factors that might influence the probabilities of stranding of a given individual.

Keywords: *Delphinus delphis*, morphotypes, occipital, biometry

INTRODUCTION

Despite the great interest marine mammals have drawn along the last decades that has made the adaptations of their anatomy to a new aquatic lifestyle the key point in the study of their evolution, the extent and nature of these changes has not yet been totally clarified. There are a huge number of studies regarding their ecology, behaviour, anatomy of their skeleton and soft tissues, and even some evolutive theories have to be already proven, but more likely one of the most interesting topics of study is the understanding of echolocation, phenomena related to the telescoping process that these animals suffered as an effect of their adaption to marine environment. The echolocation sense is been suggested to be responsible for the Cetacean skull asymmetry, that is also evident in the soft structures involved, and to allow the emission of two different sounds at the same time that might enhance the effectiveness of echolocation (Cranford et al., 1996, Yurick and Gaskin, 1988). The Cetacean hindbrain, which includes the cerebellum, pons, medulla oblongata and brainstem, is a special case. According to the "developmental constraint hypothesis", the relative size of brain components in mammals shows predictable allometric trends, that is to say, the relative size of the different parts of the brain tends to be constant (Finlay and Darlington,1995). Cerebellum size in Cetaceans is an exception to this rule with values around 15% of total brain size, which is significantly greater than that of other mammals such as Cercopitecids, with values of 8% of total brain size. Moreover, the average cerebellar size in a dolphin is 49.5% bigger than humans (whose cerebellum is also an exception to the developmental constraint hypothesis with a value of 10% of total brain size) with a similar noncerebellar brain volume (Marino et al., 2000). The pons also seems to be greatly enlarged, as well as the nucleus ellipticus and the medulla oblongata (Oelschlager and Oelschlager, 2002, Schwerdtfeger et al., 1984, Jansen and Jansen, 1969). The function of these enlarged structures remains open for speculation; although there is evidence that the cerebellum participates in a number of processes other than the traditionally associated motor control, such as cognition and language in humans (Leiner et al., 1993, Timmann and Daum, 2007), memory (Desmond et al., 1997, Andreasen et al., 1999) and sensory processing (Paulin, 1993, 2002). Some studies also suggest that the cerebellum acts as a tracking computer that deals with the spatial data incoming from the senses about the position and movement of both the animals and other objects around it in order to keep the animal aware of its surroundings and playing an important role in navigation (Paulin, 1993, 2002). This, along with the fact that there is evidence that the cerebellum is involved in biosonar acoustics, frequency sensitivity and sound location in bats (Kamada and Jen, 1990, Horikawa and Suga, 1986) and that certain cerebellar structures such as the paramedian lobules and paraflocculus appearing enlarged in echolocating bats and Cetaceans but not in non-echolocating species from both groups (Paulin, 1993, Ridgway, 1990, Henson, 1970) has led some authors to suggest that these enlarged hindbrain structures might play an important role in echolocation (Ridgway, 2000, Marino et al., 2000, Paulin, 1993). The occipital region has great evolutionary importance for Cetaceans for two main reasons. On the one hand, and as discussed in the previous paragraph, there is a conspicuous enlargement of several hindbrain structures that are thought to be related to echolocation and spatial awareness. On the other hand, the occipital region has great importance in terms of blood supply to the brain. This is due to the degeneration in the carotid artery delivery route in Cetaceans which implies that the spinal meningeal artery that enters the skull through the *Foramen Magnum*, is the main source of blood to the brain (Morgane and Jacobs, 1972, Breschet, 1836, Wilson, 1879, Galliano et al., 1966).

As a result of the above-mentioned reasons, we find that the occipital region is the location of two elements (hindbrain and vascular system) of great adaptive importance, and therefore an interesting subject for a variability study.

METHODS

The material examined (Supporting Information) consisted of 652 adult skulls of *Delphinus delphis* of both sexes from two different populations (North Atlantic and North Pacific Oceans). Both stranded and non-stranded specimens were included but specimens belonging to mass stranding events were not taken into consideration in order to avoid unknown variables. The morphometric analyses were conducted on the part of the occipital bone that has its embryological origin in the paraxial mesoderm (Gaupp, 1906, Al-Motabagani and Surendra, 2006) to avoid including osseous structures with different embryological origin, which might be subject to different developmental processes. The following anatomical measurements were taken with a digital caliper to the nearest 0.01 mm: (i) maximum width of the occipital bone, (ii) left width of the occipital bone, (iii) right width of the occipital bone, (iv) transverse diameter of the foramen magnum, and (v) total length of dolphin's body. These measurements need not to be taken in the same plane, because they are taken directly between points on the surface of the skull.

We assimilated the profile of the occipital bone to a conic curve. A conic can be defined by four points ABCD that belong to the set of conics inscribed on the quadrilateral formed by those points. Such conics are defined by the Cartesian equation of its sides:

$BA*DC+ \lambda BC*AD=0$ Eq.1

For each value of λ we obtain one of the infinite possible conics for that value, among which the distances between the four points may vary. The quadrilateral formed by the four points ABCD represents a degenerated conic (Figure 1).

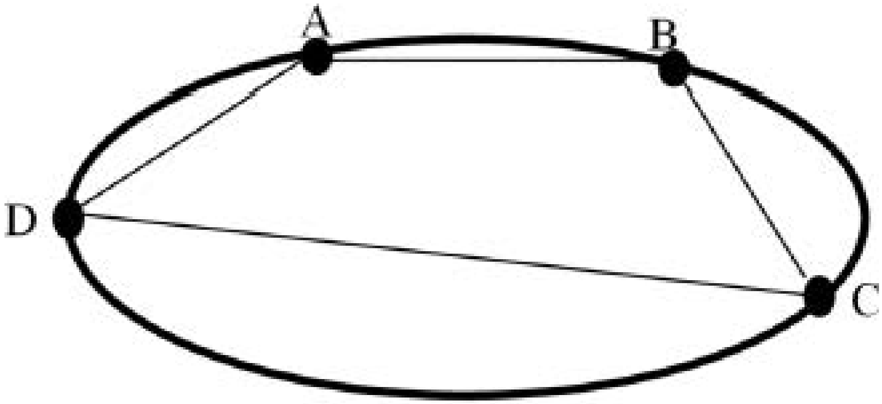

Figure 1. Quadrilateral formed by four points ABCD, which represents a degenerated set of conics.

The semiellipse (Figure 2 and 3) that fits the shape of the occipital bone can be defined by considering the distance *ab* as the line of the major axis of the ellipse (maximum width of the occipital bone), and four points *a*, *b*, *c* and *d* . The distances between these points will be named *ab* between *a* and *b*, *Ll* between *a* and *c* (left width of the occipital bone), *Lr* between *d* and *b* (right width of the occipital bone), and *W* (transversal diameter of the foramen magnum) (Figure 2). The measures taken for this study correspond to the four points and the line that can be used to define a conic and this conic can be used to make an estimation of the concavity of the occipital area (Figure 3).

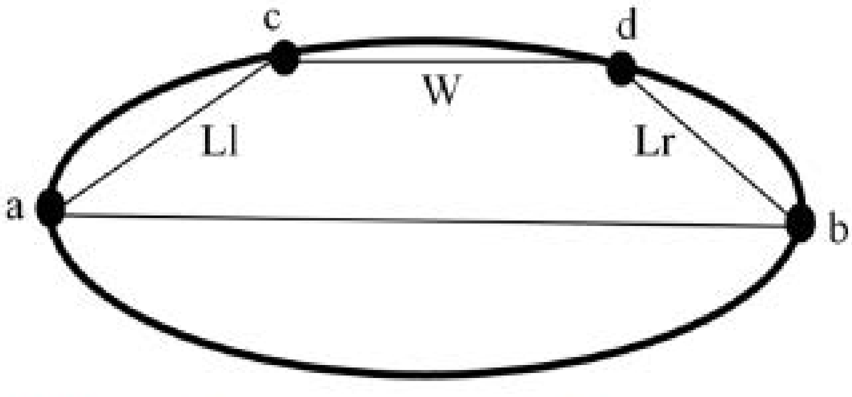

Figure 2. Ellipse defined by considering the distance *ab* as the line (máximum width of the occipital bone) of the mayor axis of the ellipse, and four points *a*, *b*, *c* and *d*. The distances between these points will be named *ab* (between *a* and *b*), *Ll* between *a* and *c* (left width of the occipital bone), *Lr* between *d* and *b* (rigth width of the occipital bone), and *W* (transversal diameter of the foramen magnum).

Figure 3. The points described in Figure 2, on the radiography of a skull from a specimen of *Delphinus delphis*.

The Cartesian equation of the conics that fit to the surface of the occipital bone, and defined by the four points *a, b, c* and *d* and the line *ab* is:

- $\lambda = W \times ab / Ll \times Lr$ Eq.2

Taking into account that the variables of equation 2 to calculate λ must meet the Kalya index equation (Eq.3) (Miramontes-Sequeiros et al., 2010) we find that the conics are limited by the variance (up to 10%) in the Kalya index specimen's values in the study species.

$\text{Kalya index}_{\mathit{Delphinus\ delphis}} = ((Lr+Ll+W)/ ab)^{*}\ 100 = 109.5 \pm 0.4$ Eq.3

where *Lr* is the right width of the occipital bone, *Ll* is the left width of the occipital bone, *W* is the transversal diameter of the foramen magnum, and *ab* is the maximum width of the occipital bone.

We can consider two extreme suppositions in order to test the theoretical limits of λ for the value of the Kalya index in *Delphinus delphis* (K index $_{Delphinus\ delphis}$ = 109.5):

a) Considering the minimum value of *W* as 1mm, and the maximum value of the *ab* as 100mm, and *Ll*=*Lr*, then λ=-0.03.
b) Considering the maximum value of *W*=*Lr*=*Ll*, and *ab* as 100mm, then λ=-27.4.

The variance in the Kalya index values represents the variation in the concavity of the occipital bone area, where λ represents the relation of *W* (transversal diameter of the foramen magnum) to *ab* (maximum width of the occipital bone), since the other variables are limited by the Kalya index at the species level (K index $_{Delphinus\ delphis}$ = 109.5). Moreover, λ is positively correlated to the caudal fossa depth, and its possible values are limited by the concavity and the point where *W* crosses the minor axis of the conic. For a given species, different λ values represent the possible combinations of proportions of the occipital variables that give rise to intra-species morphotypes (Miramontes-Sequeiros et al., 2010).

The first step was to discard the outlier values in order to normalize all the variables. Due to the lack of data in a large number of specimens related to the total length in our data, and in order to conduct the most accuracy statistical analysis, we assumed that the total length of the specimens is correlated to the maximum width of the occipital bone (*ab*) (Pearson's correlation = 0.8, Sig. (bilateral) = 0.01).

Once all the variables (cranial measurements, Kalya index and λ) were obtained for each of the specimens, we conducted a series of ANOVA tests in order to determine if there were any significant differences in the values of *ab*, Kalya index and λ between the stranded and captured specimens as a whole, the stranded and captured specimens from each population, and between the two populations (North Atlantic and North Pacific Oceans).

Afterwards, we created four *ab* size classes by three cross points: the mean and ± the standard deviation (*SD*). Then we conducted another series of ANOVA tests for the Kalya index and λ values between the different class sizes within each population and between stranded and captured specimens of each size class.

Once this was done, we took the most extreme subgroups defined by the most dissimilar values for Kalya index, λ and *ab*, which were North Atlantic stranded and North Pacific captured, and created two artificial morphotypes that would be used as a base for a statistical analysis. Hence, North Atlantic stranded would be the initial "Morphotype I" and North Pacific captured the initial "Morphotype II". Then, using those predicted values, we carried out a discriminant analysis that reclassified some of the specimens and gave new predicted values. Those predicted values were then used for a second discriminant analysis. This procedure was repeated up to five times, at which point there were no more specimens being reclassified. This procedure optimized the division between the initially artificial morphotypes, allowing us to assign the specimens from the subgroups with less extreme values to one of the real morphotypes. We further divided the morphotypes in a total of four classes using the mean and ± the standard deviation, and observed the stranded to captured ratio for each of them.

RESULTS

The mean *ab* is significantly different between both populations. We found that the North Atlantic population has a higher mean *ab* (Table 1). Kalya index and λ means are significantly different among both Oceans, being the North Atlantic population which has a lower Kalya and lower λ index mean value, and the North Pacific population which has a higher λ and higher Kalya index mean value (Tables 2 and 3). We did not find significant differences between Kalya index and λ mean values in stranded and captured specimens from each Ocean (Tables 2 and 3).

In the North Pacific population the Kalya index mean value is not significantly different among the *ab* classes, the λ mean value significantly increases as *ab* values increases. The stranding values are not significantly different in both variables (Tables 4 and 5).

In the North Atlantic population the λ mean value is not significantly different among the *ab* classes, the Kalya index mean value significantly decreases as *ab* values increases (Tables 6 and 7).

Table 8 shows the progressive separation of specimens between the two morphotypes by means of an iterated discriminant analysis. The final number of specimens of each class assigned to each morphotype can be seen in Table 9.

Table 1. Descriptive statistics of maximum width of the occipital bone (*ab*) in both Oceans. One-factor ANOVA in Atlantic and Pacific *Delphinus delphis* populations and in stranded or captured specimens in each Ocean

Ocean	*ab* mean	Standard deviation	ANOVA		Stranded/ captured samples	N	*ab* mean	Standar deviation	ANOVA	
			F	Sig.					F	Sig.
North Atlantic	143.27	6.93	36.76	0.00	Stranded	64	143.50	6.92	0.49	0.48
					Captured	10	141.84	7.19		
North Pacific	136.77	8.83			Stranded	112	138.25	6.47	4.06	0.04
					Captured	391	136.35	9.36		

Table 2. Descriptive statistics of Kalya index value in both Oceans. One-factor ANOVA in Atlantic and Pacific *Delphinus delphis* populations and in stranded or captured specimens in each Ocean

Ocean	Kalya index Mean	Standard deviation	ANOVA		Stranded/ Captured Samples	N	Kalya index Mean	Standard deviation	ANOVA	
			F	Sig.					F	Sig.
North Atlantic	108.62	2.65	10.72	0.00	Stranded	64	108.66	2.81	0.08	0.78
					Captured	10	108.40	1.27		
North Pacific	109.82	2.65			Stranded	112	110.03	2.98	0.69	0.40
					Captured	391	109.76	2.97		

Table 3. Descriptive statistics of λ values in both Oceans. One-factor ANOVA in Atlantic and Pacific *Delphinus delphis* populations and in stranded or captured specimens in each Ocean

Ocean	*Lambda* Mean	Standard deviation	ANOVA		Stranded/Captured Samples	N	*Lambda* Mean	Standard deviation	ANOVA	
			F	Sig.					F	Sig.
North Atlantic	-1.52	0.16	28.06	0.00	Stranded	64	-1.55	0.16	0.02	0.87
					Captured	10	-1.56	0.19		
North Pacific	-1.44	0.16			Stranded	112	-1.41	0.16	3.19	0.07
					Captured	391	-1.45	0.16		

Table 4. Descriptive statistics and ANOVA of the Kalya index mean values and stranded and captured specimens of *Delphinus delphis* from the North Pacific Ocean population in function of the maximum width of the occipital bone (*ab*) grouped in four classes by three cross points: the mean and ± the standard deviation (*SD*)

ab classes	N	Kalya index Mean	*SD*	ANOVA		Stranded/ Captured Samples	% Stranded	N	Kalya index Mean	*SD*	ANOVA	
				F	Sig.						F	Sig.
≤128.86	78	109.26	3.32	1.18	0.32	Stranded	7.7%	6	111.03	4.80	1.84	0.18
						Captured		72	109.11	3.17		
128.87- 137.67	170	110.00	3.16			Stranded	25.9%	44	110.59	2.97	2.06	0.15
						Captured		126	109.79	3.20		
137.68 -146.48	202	109.85	2.67			Stranded	25.7%	52	109.58	2.64	0.70	0.40
						Captured		150	109.94	2.69		
>146.49	53	109.96	2.87			Stranded	18.9%	10	109.28	3.26	0.67	0.41
						Captured		43	110.12	2.79		

Table 5. Descriptive statistics and ANOVA of the λ mean values and stranded and captured specimens of *Delphinus delphis* from North Pacific Ocean population, in function of the maximum width of the occipital bone (*ab*) grouped in four classes by three cross points: the mean and ± the standard deviation (*SD*)

ab classes	N	*Lambda* Mean	*SD*	ANOVA		Stranded/ Captured Samples	% Stranded	N	*Lambda* Mean	*SD*	ANOVA	
				F	Sig.						F	Sig.
≤128.86	78	-1.50	0.15	10.60	0.00	Stranded	7.7%	6	-1.52	0.21	0.17	0.68
						Captured		72	-1.50	0.15		
128.87- 137.67	170	-1.47	0.17			Stranded	25.9%	44	-1.45	0.18	0.69	0.40
						Captured		126	-1.47	0.16		
137.68- 146.48	202	-1.42	0.16			Stranded	25.7%	52	-1.39	0.15	2.04	0.15
						Captured		150	-1.43	0.16		
>146.49	53	-1.36	0.16			Stranded	18.9%	10	-1.35	0.15	0.13	0.72
						Captured		43	-1.36	0.16		

Table 6. Descriptive statistics and ANOVA of the Kalya index mean values and stranded and captured specimens of *Delphinus delphis* from North Atlantic Ocean population, in function of the maximum width of the occipital bone (*ab*) grouped in four classes by three cross points: the mean and ± the standard deviation

ab grouped	N	Kalya index Mean	Standard deviation	ANOVA		Stranded/Captured Samples	N	Kalya index Mean	Standard deviation
				F	Sig.				
≤128.86	3	108.54	1.45	6.01	0.00	Stranded	2	108.55	-------
						Captured	1	108.51	-------
128.87- 137.67	12	109.22	2.46			Stranded	10	109.49	2.53
						Captured	2	107.86	-------
137.68- 146.48	35	109.58	2.34			Stranded	32	109.67	2.40
						Captured	3	108.61	-------
>146.49	24	106.93	2.55			Stranded	20	106.62	2.65
						Captured	4	108.49	-------

Table 7. Descriptive statistics and ANOVA of the λ mean values and stranded and captured specimens of *Delphinus delphis* from North Atlantic Ocean population, in function of the maximum width of the occipital bone (*ab*) grouped in four classes by three cross points: the mean and ± the standard deviation

ab grouped	N	Lambda Mean	Standard deviation	ANOVA		Stranded/Captured Samples	N	Lambda Mean	Standard deviation
				F	Sig.				
≤128.86	3	-1.61	0.07	0.97	0.41	Stranded	2	-1.58	--------
						Captured	1	-1.65	--------
128.87-137.67	12	-1.59	0.17			Stranded	10	-1.59	0.11
						Captured	2	-1.57	--------
137.68- 146.48	35	-1.56	0.18			Stranded	32	-1.56	0.18
						Captured	3	-1.58	--------
>146.49	24	-1.51	0.12			Stranded	20	-1.50	0.13
						Captured	4	-1.51	--------

Table 8. Optimization of the assignment of samples to either Morphotype I or II. With each iteration (1 to 5) the grouping variable takes the values of the group predicted in the last iteration starting from the assumed values (iteration 0) of the classes NAtlantic Stranded and NPacific Captured which were initially assigned to morphotypes I and II respectively. The result indicates the real division of the samples between both morphotypes

		Combined intra-group correlations between the discriminant variables and the typified canonic discriminant function.					
	Iterations	0	1	2	3	4	5
Discriminant variables	*ab* (grouped)	0.680	-0.479	0.468	-0.445	-0.434	0.425
	Lambda	-0.555	0.426	-0.428	0.447	0.457	-0.465
	Kalya index	-0.337	0.230	-0.203	0.205	0.199	-0.192
Test df=3 ; Sig.=0.000	Canonic correlation	0.360	0.800	0.807	0.809	0.810	0.810
	Wilks' Lambda	0.870	0.359	0.349	0.346	0.344	0.344
	Chi-square	62.75	462.15	474.94	478.76	481.68	481.58
N samples for each of the predicted groups	Morphotype I	64	161	175	182	188	189
	Morphotype II	391	294	280	273	267	266
	TOTAL	455	455	455	455	455	455

Table 9. Descriptive statistics of the final number of specimens of each class assigned to morphotype I and II. NA is North Atlantic Ocean and NP is North Pacific Ocean

Morphotypes	Variables	Descriptive statistics		
		N	Mean (mm)	Standard Deviation
NA Stranded Morphotype I	*Ab*	47	145.67	5.66
	Kalya index		108.22	2.90
	Lambda		-1.59	0.16
NP Captured Morphotype II	*Ab*	249	133.57	9.25
	Kalya index		110.27	2.89
	Lambda		-1.38	0.13
NP Captured Reclassified in Morphotype I	*Ab*	142	141.23	7.36
	Kalya index		108.87	2.90
	Lambda		-1.57	0.14
NA Stranded Reclassified in Morphotype II	*Ab*	17	137.50	6.65
	Kalya index		109.87	2.18
	Lambda		-1.45	0.12

With the fifth discriminant function we extrapolated the belonging to one of the morphotypes of the specimens from the two groups with less extreme values: North Atlantic captured and North Pacific stranded (Table 10). According to these analyses, Morphotype I is present in the 73.4% of the stranded specimens of NA (Table 9), in contrast to the 19.8% of the stranded of NP (Table 10). Morphotype I in the captured specimens from NP represents up to 36.3 % (Table 9), while in the NA we do not have a significant number of data.

Taking into account the results obtained in Table 9 we can design a point diagram between the typified canonical discriminant function of the fifth iteration (axis Y) and the *ab* values disregarding the classes (axis X) where the differences between Morphotype I and Morphotype II are visible (Figure 4).

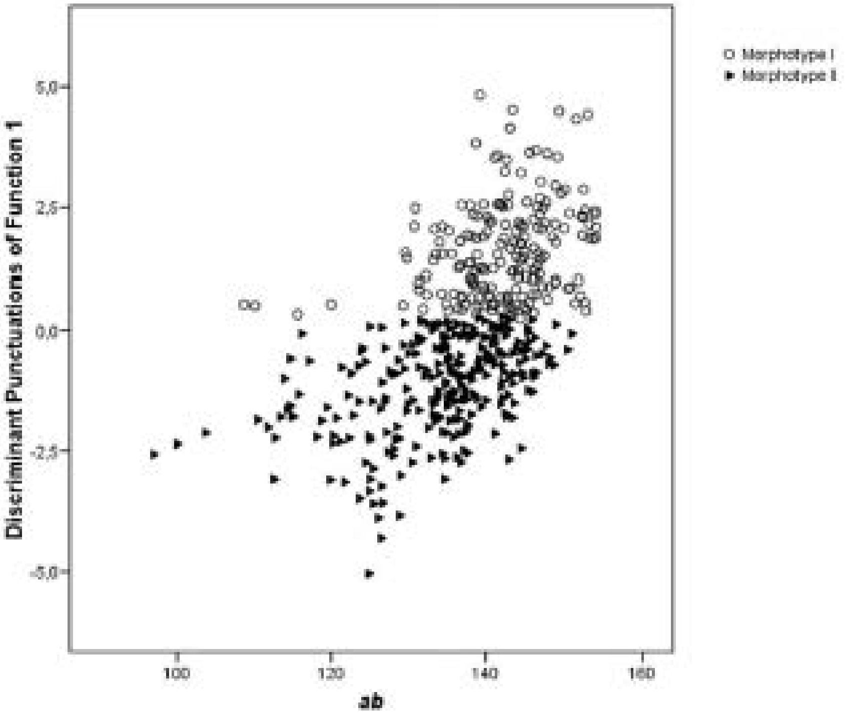

Figure 4. Differences between stranded and captured specimens from NA and NP Oceans, obtained from the final number of specimens of each class assigned to morphotype I and II.

In the graphic representation of the two most dissimilar morphotypes, I and II (Figure 5), we do not consider neither the reclassified nor extrapolated specimens to either Morphotype. These morphotypes I and II can be assimilated to the ones described by Miramontes-Sequeiros et al. (2010).

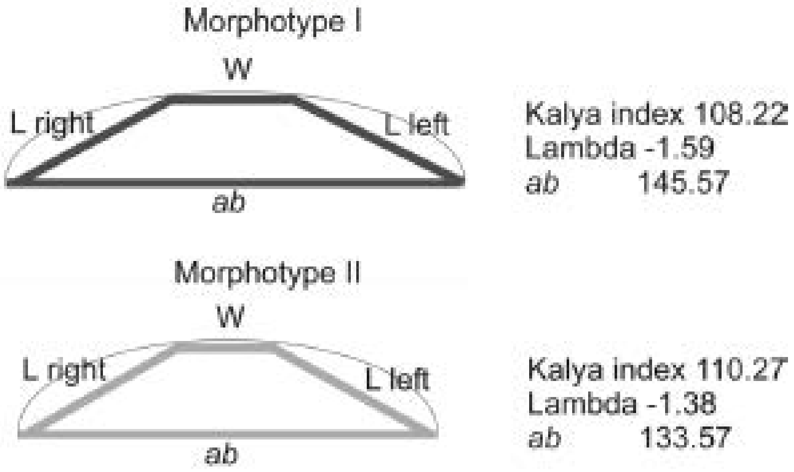

Figure 5. Representation in scale of the absolute value (table 13) of the two most dissimilar morphotypes I and II obtained in this study. Morphotype I has a lower concavity and depth, whilst the width of the occipital bone (*ab*) and foramen magnum is larger when compared to Morphotype II.

Table 10. Descriptive statistics of the extrapolated stranded specimens from North Pacific Ocean, applying the values of the fifth typified canonical discriminant function

Morphotypes	Variables	N	Mean	Standard deviation
extrapolated to morphotype I	*Ab*	35	139.62	6.40
	Kalya index		109.62	2.52
	Lambda		-1.57	0.15
extrapolated to morphotype II	*Ab*	142	141.22	7.36
	Kalya index		108.86	2.90
	Lambda		-1.56	0.14

When representing a scale in absolute value (Table 11) of morphotypes I and II obtained in this study we observed that the Morphotype I shows a lower concavity and depth, whilst the width of the occipital bone (*ab*) and foramen magnum is larger, in comparison to the Morphotype II (Figure 5).

Afterwards we applied the fifth discriminant function which best defines morphotypes I and II, and we divided them in four classes by three cross points: the mean and ± 2 times the standard deviation of all our data considering stranded and captured. The ratio stranding *vs* captured (S:C) reaches the highest values in Morphotype I class 1, and its values decrease until the lowest value in Morphotype II class 2 (Table 12).

Table 11. Descriptive statistics of the two most dissimilar morphotypes I and II (table 11) which are scaled represented in figure 5

Models	Variables	N	Mean	SD
North Atlantic Stranded Morphotype I	*W*	47	38.48	2.23
	LR		60.36	2.91
	LL		58.72	2.93
	ab		145.67	5.67
	K index		108.22	2.907
	Lambda		-1.59	0.16
North Pacific Captured Morphotype II	*W*	249	33.36	2.29
	LR		57.76	5.34
	LL		56.22	4.85
	ab		133.57	9.25
	K index		110.27	2.90
	Lambda		-1.38	0.14

Table 12. Final grouping of all the specimens in function of the fifth discriminant function which best defines morphotypes I and II by using three cross points: the mean and ± 2 times the standard deviation. The stranded to captured ratio of each category is also shown

Morphotype	Class	Discriminant punctuations of function 1 (grouped)		N	Ratio S:C
I	1	< -2.580	Stranded	18	0.9:1
			Captured	20	
	2	-2.579 to -0.280	Stranded	64	0.5:1
			Captured	129	
II	1	-0.279 to 2.020	Stranded	81	0.4:1
			Captured	199	
	2	>2.021	Stranded	13	0.2:1
			Captured	55	

DISCUSSION

We found significant differences between the percentage of stranded specimens between both Atlantic and Pacific oceans. However, due to the museum specimens not being sampled following a standardized procedure we cannot take these results as absolutely certain.

The mean body length (based on *ab* value) was found to be greater in the Atlantic population (Table 1); furthermore, Kalya index values were smaller in the Atlantic population (Table 2) and λ values were also smaller (Table 3).

When dividing the specimens in size classes, individuals from the North Pacific show a definite trend towards increasing their λ values as size class increases (Tables 4 and 5).

Specimens from the North Atlantic show no significant variation in λ values as size increases (Table 6). Kalya index, however, decreases significantly as size increases (Table 7). However, due to the different sampling sizes, individual sizes and stranded/captured ratios of each ocean, we cannot take these result as definitive. In fact, when taking both oceans as a single population, there was a lack of significant effects.

We thought that these partial significances of each ocean for λ and Kalya index were due to great interactions between all the variables (measurements, size, sample size, oceans and number of stranded and captured dolphins from each ocean). Furthermore, stranding is never expressed as a certainty, but a probability, some of the strandings could be due to reasons other than anatomical features, and some of the captured dolphins might have stranded at some point in the future. This is the reason why we decided to use the technique described in the "methods" section and Table 8 to separate all the specimens depending on their probability of belonging to one of two initially theoretical extreme morphotypes.

Our results point to the existence of two well-differentiated morphotypes that can be subject to further divisions in two classes for each morphotype. This division is made through a discriminant function that takes into account the Kalya index (equivalent to the curvature of the occipital bone), λ (positively correlated to the caudal fossa depth) and *ab* value (maximum width of the occipital bone, highly correlated with specimen body length).

When observing the relation of these morphotypes with the ratio of stranded: captured specimens it is possible to see a gradient from Morphotype I.1 (with the highest number of stranded specimens) to Morphotype II.2 (with the lowest number of stranded specimens). This gradient is shown in Table 12. Moreover, there is also a gradient of the three implied variables between the different classes. Morphotype I.1 has the greatest *ab* value (again, highly correlated with specimen's body length), the lowest curvature of the occipital bone, and the lowest depth of the caudal fossa. These variables keep changing steadily within the different classes until Morphotype II.2, where we find the lowest *ab*, the highest occipital bone curvature and the highest caudal fossa depth.

The conclusion of this study is that, among *Delphinus delphis* populations, there are several associated characters of the occipital bone that form a gradient, which in turn is highly correlated with the probability of stranding. Each half of this gradient can be represented by one of the morphotypes presented in figure 5. These characters are the occipital bone curvature and caudal fossa depth, both of them negatively correlated with the stranding probability.

This conclusion opens very interesting questions that shall be addressed in future studies, the main of which is why these occipital bone morphologies show such a strong relation with stranding. Previous studies (Marino *et al.*, 2000, Ridgeway, 2000) have pointed at a significantly greater size of the cerebellum in dolphins that in humans and other primates, and suggested that this oversizing might result from it playing an important role on the processing of the acoustic signals they use to orient themselves, Marino bases this suggestion partly on works on echolocating bats, such as the one by Kamada and Jen (1990) about the sensitivity to acoustic signals of cerebellar cells in brown bats (*Eptesicus fuscus*).

If cerebellar size was indeed an adaptive character for dolphins then caudal fossa depth and curvature, on which the total capacity of the caudal fossa is dependent on, would also be of evolutive importance; future studies will address the relationship between these soft and hard anatomical structures (cerebellum and occipital bone) and the way they affect populations of *Delphinus delphis*.

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APPENDIX

Table S1. Sample details, anatomical measures, Kalya index and Lambda values

N: specimen number.
Catalogue: Museum Catalogue Number.
Museum: LA = Museum of Natural History, Los Angeles County; WCD =Smithsonian National Museum of Natural History, Washington DC.
T Length: Total dolphin length cm.
Sex: 1 = Female 2 = Male.
Ocean: 1 = North Atlantic; 2 = North Pacific.
Stran-Capt: Stranded; Captured.
W: transverse diameter of the foramen magnum mm.
ab: width of the occipital bone mm.
Lr: width of the right occipital bone, excluding the foramen magnum mm.
Ll: width of the left occipital bone, excluding the foramen magnum mm.
K index: Kalya index. **Lambda**.

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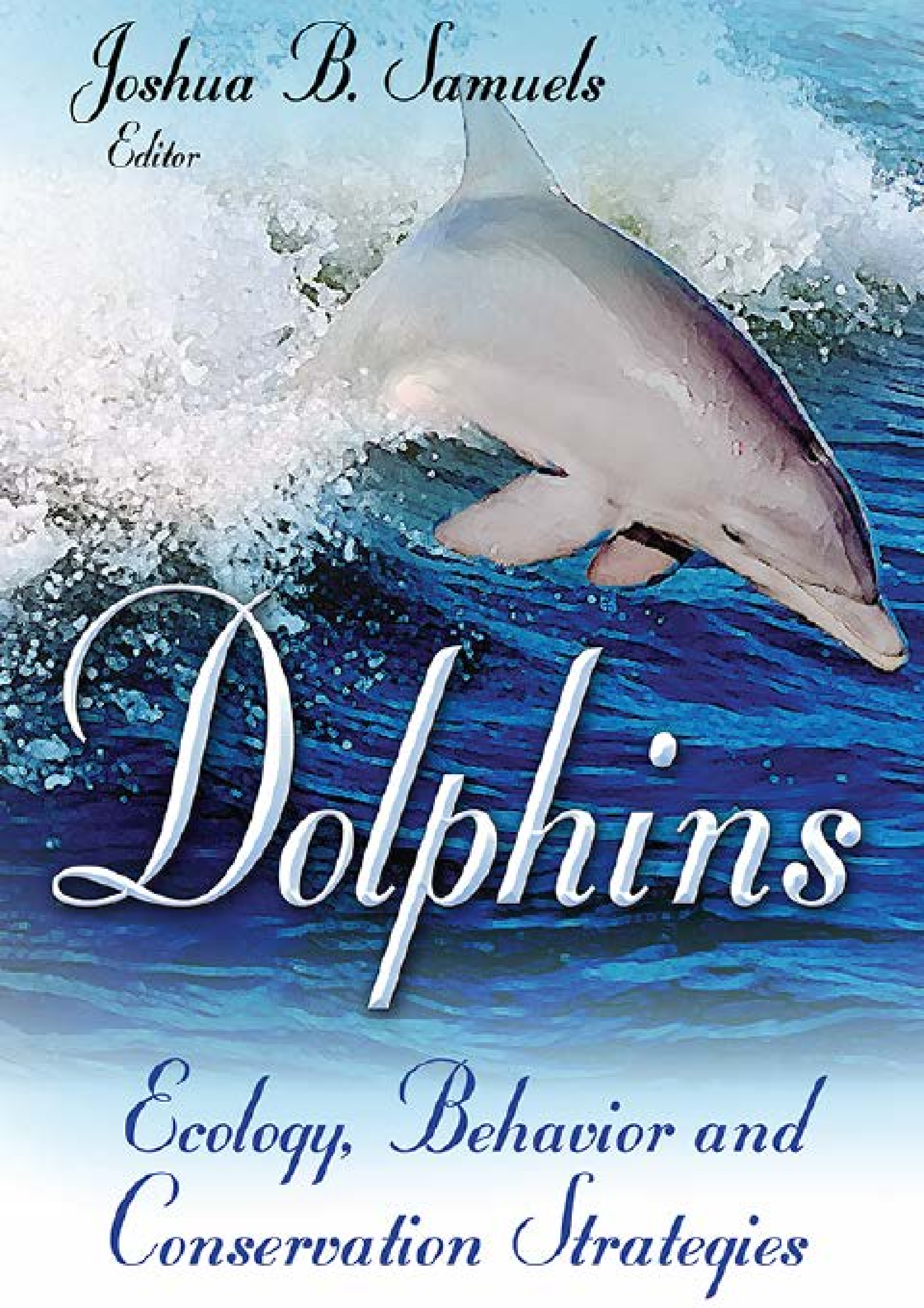

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