Bilateral Directional Asymmetry of the Appendicular Skeleton of the White-Beaked Dolphin (*Lagenorhynchus albirostris*)

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Abstract

Bilateral directional asymmetry of the lengths and diameters of the scapula, humerus, radius, and ulna were analyzed on a sample of 38 white-beaked dolphins (*Lagenorhynchus albirostris*) from Danish waters. The levels of asymmetry were consistent between the sexes and between physically mature and immature animals. The length and diameter of the humerus and the length of the radius showed significant asymmetry, all favouring the right side. The greatest asymmetry was found in the diameter of the humerus (1.88% SE 0.36). The results were somewhat different from what is known in the harbour porpoise (*Phocoena phocoena*) that show asymmetry favouring the right side in all of the dimensions investigated here. This may indicate a different pattern of employment of the flippers. The detected asymmetries, along with the many examples of lateralized behaviour recorded in cetaceans, point to the existence of lateralized use of the flippers in the white-beaked dolphin and possibly other delphinid and cetacean species. Although some evidence exists for flipper preference in the baleen humpback whale (*Megaptera novaengliae*) and turning preferences in other species, this needs to be confirmed through further behavioural studies.

Key Words: White-beaked dolphin, *Lagenorhynchus albirostris*, appendicular skeleton, directional asymmetry, lateralized behaviour

Introduction

In humans (*Homo sapiens*), skeletal bilateral directional asymmetries (DAs) are used as indicators of the influence of the mechanical environment on bone structure (e.g., Latimer & Lowrance, 1965; Hiramoto, 1993; Steele & Mays, 1995; Mays et al., 1999; Steele, 2000; Plochocki, 2004). DA occurs when one side of the skeleton is more developed than the other, and it is largely attributed to differential mechanical loading, as would occur with lateralized use of the appendages. Mechanical loading accelerates chondrocyte metabolism and hence bone growth (Plochocki, 2004). In humans, where *ca* 90% exhibit right-handedness (Annett, 1972), the right side of the upper body skeleton is usually more developed than the left, with the scapula being heavier and denser and the long bones (humerus, radius, and ulna) longer (Steele, 2000).

DAs of the skeleton of the pectoral appendage have only been detected in a few species besides humans; rhesus macaques (*Macaca mulatta*) (Falk et al., 1998), laboratory rats (*Rattus norvegicus*) (Fox et al., 1995), and walruses (*Odobenus rosmarus*) (Levermann et al., 2003).

In a recent study, Galatius (2005) found substantial DA in the flipper skeleton of the harbour porpoise (*Phocoena phocoena*), with the bones of the right flipper (scapula, humerus, radius, and ulna) having significantly larger dimensions and masses and the humerus and ulna having a more robust build. These results were interpreted as implying lateralized use of the flippers in the harbour porpoise and perhaps other cetaceans. Galatius implied that this might offer an explanation for some of the observations of lateralized turning preferences observed in cetaceans (Ridgway, 1986; Sobel et al., 1994; Marino & Stowe, 1997a, 1997b). Lateralized flipper use has been detected in a baleen cetacean; the humpback whale (*Megaptera novaeangliae*) shows a preference for using the right flipper for the "flippering"—behaviour in which the animal slaps a flipper against the water surface (Clapham et al., 1995).

The aim of this study was to investigate the DA of the flipper skeleton of another cetacean species and establish whether the pattern found in the harbour porpoise (Galatius, 2005) should be regarded as a general rule.

Materials and Methods

Data Collection
Thirty-eight white-beaked dolphin (*Lagenorhynchus albirostris*) skeletons from Danish waters, all held in the collections of the Zoological

Museum of Copenhagen and the Fisheries and Maritime Museum in Esbjerg, were investigated for directional asymmetries in the flipper skeleton.

The following measurements were made with a digital calliper to the nearest tenth of a mm for both right and left side bones (Figure 1): length of the scapula, length of the humerus, lateral diameter of the humerus, length of the radius, lateral diameter of the radius, length of the ulna, and lateral diameter of the ulna.

Measurements were only taken when bones were available on both sides without sign of injury or disease. Epiphyses were included in all measurements of the bones.

The repeatability of the measurements was assessed by measuring all dimensions twice on 10 specimens and calculating Dahlberg's Method Error (ME):
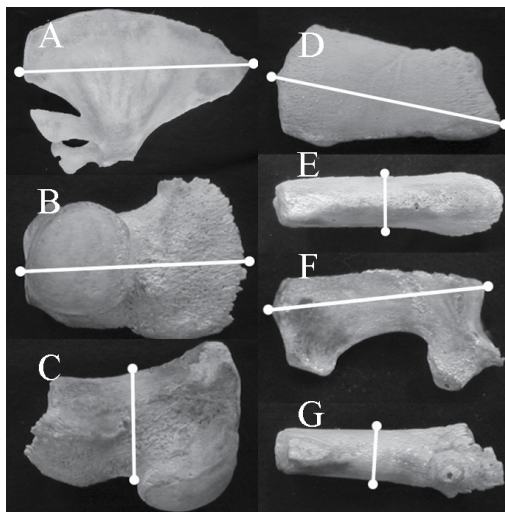
$$ME = \Sigma d^{2} / 2n$$

Figure 1. Bone measurements (not to scale): A: scapula length, B: humerus length, C: humerus diameter, D: radius length, E: radius diameter, F: ulna length, and G: ulna diameter

where, Σd^{2} is the sum of the squares of the difference between the two measurements and *n* is the number of the double registrations. The ME was < 0.30 mm for all measurements, and as such, measurement error should contribute little to the variance.

Data Analysis
The formula of Plochocki (2004) was used for calculating individual DA:

DA = [2(Right - Left) / (Right + Left)] x 100

thus, standardizing asymmetry to within-individual percentages, where a negative value indicated a larger left side and a positive value indicated that the right side was larger. Robustness of the bones was assessed by calculating the DA of the diameter/length ratio of the humerus, radius, and ulna. Adopting the Plochocki formula, the ratios were calculated as:

DA_n = [2((dRight/lRight) - (dLeft/lLeft)) / ((dRight/lRight) + (dLeft/lLeft))] x 100

where, d is the diameter of the bone and l is the length of the bone.

To investigate whether sexual dimorphism or ontogenetic development might influence the results, the sample was screened for significant differences in levels of DA between physically immature and mature (fully fused vertebral epiphyses) specimens and sexes by one-way MANOVA. Because of the limited size of the sample, tests for effects of sex and maturity were performed separately.

After ensuring that the groups did not differ significantly in asymmetry levels, the data were pooled and the presence of DA was tested using two-tailed Wilcoxon-Mann-Whitney tests on the raw data of all measurements, with a modified Bonferroni-correction of the *p*-values (Jaccard & Wan, 1996).

Table 1. Mean values for all measurements from mature male and female white-beaked dolphins; lengths and diameters are given in mm.

Variable	Males			Females		
	n	Right ± SE	Left ± SE	*n*	Right ± SE	Left ± SE
Scapula length	6	290.7 ± 5.9	294.2 ± 5.9	11	285.7 ± 4.2	282.8 ± 4.0
Humerus length	6	90.2 ± 1.6	89.5 ± 1.2	11	86.9 ± 0.9	86.3 ± 0.9
Humerus diameter	6	44.2 ± 1.1	43.5 ± 1.6	11	41.1 ± 0.4	40.7 ± 0.4
Radius length	6	118.5 ± 2.6	117.7 ± 2.8	11	114.3 ± 0.8	114.1 ± 0.8
Radius diameter	6	25.1 ± 1.0	25.1 ± 1.0	11	23.8 ± 0.3	23.9 ± 0.3
Ulna length	6	87.8 ± 0.8	87.4 ± 1.0	11	87.8 ± 1.6	87.6 ± 1.6
Ulna diameter	6	21.1 ± 1.1	21.4 ± 1.1	11	20.0 ± 0.3	19.7 ± 0.3

Results

Mean values of all left and right variables for physically mature males and females are presented in Table 1.

Neither significant sex nor maturity differences were found in the levels of directional asymmetry with the one-way MANOVAs ($p = 0.05$) (Table 2).

Table 2. MANOVA-screen for differences in DA by sexes and by maturity in white beaked dolphins

Effect	n	DF	F	p
Sex (♂, ♀)	20, 18	8	1.75	0.129
Maturity (immature, mature)	21, 17	8	0.52	0.829

After a Bonferroni adjustment, the Wilcoxon-Mann-Whitney tests for DA showed significant results for the humerus length, diameter, and robustness and for the radius length, all favouring the right side. The most asymmetric dimension was the diameter of the humerus with a mean directional asymmetry of 1.88% SE 0.35 (Table 3).

harbour porpoise, where the asymmetries are uniformly distributed over the entire analyzed flipper skeleton. This may be due to morphological differences or patterns of employment and movement of the flippers. The delphinids possess the most compact humerii of all cetaceans (Benke, 1993). This probably reflects a particularly high level of mechanical stress on this bone in delphinids. If so, the detected humeral DA may well be explained by bilaterally different levels of stress, and thus lateralized behaviour.

The asymmetries were found to be consistent across males and females and between immature and mature specimens. The most striking difference between the harbour porpoise and the white-beaked dolphin was the DA of the scapula that showed very strong DA in the porpoise where it was interpreted as indicative of a greater muscle-mass associated with the right flipper while there was no DA in the current study. This may again point to different patterns of employment of the flippers between the species.

The harbour porpoise's DAs seem to be constant over the entire lifespan of the animal. Given

Table 3. Two-tailed Wilcoxon-Mann-Whitney test results for pooled samples; mean directional asymmetry and distribution of asymmetry in white-beaked dolphins are given.

Variable	n	Mean DA ± SE	R > L	R = L	R < L	Z	p
Scapula length	38	0.35 ± 0.24	58%	5%	37%	1.23	0.221
Humerus length	38	0.51 ± 0.19	69%	5%	26%	2.76	0.006*
Humerus diameter	38	1.88 ± 0.36	84%	3%	13%	4.18	<0.001*
Humerus robustness	38	1.37 ± 0.41	76%	0%	24%	2.98	0.003*
Radius length	38	0.39 ± 0.13	66%	8%	26%	2.68	0.007*
Radius diameter	38	-0.23 ± 0.42	47%	3%	50%	0.21	0.833
Radius robustness	38	-0.62 ± 0.43	31%	3%	66%	1.47	0.137
Ulna length	38	0.39 ± 0.15	60%	11%	29%	2.53	0.012
Ulna diameter	38	0.39 ± 0.49	50%	3%	47%	1.08	0.281
Ulna robustness	38	0.00 ± 0.49	47%	3%	50%	0.11	0.913

R > L: proportion of specimens with asymmetry favouring the right side; R = L: specimens with asymmetry values 0.5<0>-0.5; R < L: proportion of specimens with asymmetry favouring the left side; Z: Wilcoxon Z-statistic; and *p*: significance before Bonferroni adjustment. * indicates statistical significance ($p < 0.05$) after Bonferroni adjustment.

Discussion

Significant DAs in the appendicular skeleton of the white-beaked dolphin were detected in humerus length and diameter and in radius length. Unlike the harbour porpoise (Galatius, 2005), no significant DAs were found in the other analyzed dimensions, although more significant results may have been obtained with a larger sample size. If analyzed in the light of a lateralized behaviour hypothesis, these results would indicate that the humerus is the bone exposed to the most stress in the white-beaked dolphin, as opposed to the

the limited sample size in this study, it is not possible to assess if this is the case in the white-beaked dolphin; however, the lack of difference in DA level between mature and immature specimens indicates that DA is developed quite early as is also the case in humans (Steele, 2000). Besides the harbour porpoise, DAs in the flipper skeleton have now also been detected in a delphinid species and is thus known in two cetacean genera.

In the light of the many recordings of lateralized behaviour in cetaceans (Kasuya & Rice, 1970; Hoese, 1971; Ridgway, 1986; Sobel et al., 1994; Clapham et al., 1995), it seems probable that the

detected directional asymmetries are caused by differential mechanical loading and, hence, lateralized use of the flippers, although this needs to be verified through behavioural studies dealing specifically with the flippers. The limited data available do not contradict such a hypothesis, however. The only direct study of flipper use in cetaceans suggests a right-flipper preference for "flippering" in the humpback whale (Clapham et al., 1995).

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