Patterns of tooth wear in recent white whales (Cetacea: Monodontidae): implications for age determination in fossil cetaceans

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Introduction

Teeth of some cetacean taxa often show extensive wear, a fact that has been mentioned *passim* in various papers or books. In vertebrate palaeontology, tooth wear in whales has been used as characters in phylogenetic analyses (O'Leary, 1998), and the presence of wear facets in teeth is intermittently reported (for example: Fordyce, 1994; Hirota and Barnes, 1994; Dubrovo and Sanders, 2000). Determination of the ontogenetic age is usually supported by correlation with ossification patterns in the appendicular skeleton of living cetaceans (e.g. Wheeler, 1930; Ito and Miyazaki, 1990; Yoshida et al., 1994; Calzada et al., 1997). However, in specimens where the appendicular skeleton is missing or very in complete, determination of age through this method is impossible. In specimens where a number of teeth have been preserved, there exists the possibility of using the degree of tooth wear as an approximation of age in fossil specimens, under the assumption that tooth wear increases with age; i.e. one might expect a direct ratio between the proportion of severely worn teeth and age.

Unfortunately, statistical analyses of wear patterns in cetaceans or their possible causes are few. This study concerns analysis of the pattern of wear on the teeth of white whales (*Delphinapterus leucas*). This taxon was chosen in part because it is one of the cetacean taxa where extensive tooth wear has often been noted (e.g. Eschricht, 1869; Brodie, 1969, 1989; Sergeant, 1973), and a large population sample was available in the collections of the Zoological Museum of the University of Copenhagen.

White whale dentition

The teeth of white whales grow continuously and increase in thickness with age from 2 mm to 14-16 mm (Degerbøl and Nielsen, 1930). The adult tooth formula is usually 18/16 with supernumerary teeth in the upper jaw usually being rudimentary (Brodie, 1989). The teeth do not protrude through the gums in functional numbers until the second or third year of the animal (Degerbøl and Nielsen, 1930; Brodie, 1989). Teeth of the upper jaw erupt gradually from front to back, while lower jaw teeth erupt more or less simultaneously (Eschricht, 1869; Degerbøl and Nielsen, 1930). Tooth eruption is complete at an age of approximately six years and animal length of around 260 cm, and teeth of females do not erupt as far as those of males (Sergeant, 1973). In older individuals the teeth may disappear (Kükenthal quoted in Degerbøl and Nielsen, 1930). If tooth eruption of the upper jaw and their contact with the teeth of the lower jaw is gradual, one might expect a mathematical correlation between the proportion of severely worn teeth and age. This in turn would have its use as a proxy for ontogenetic dating of both recent and fossil material, not only in white whales but also in related odontocete taxa.

In white whales, tooth wear occurs only later in the life of the animal, and the teeth of females usually show less wear than teeth of males (Sergeant, 1973). Wear is due to the occlusion of upper and lower jaw and is not restricted to the tip of the crown; sometimes only the front, back or side of the tooth is removed (Sergeant, 1973; personal observation this study). The opposite teeth are well aligned which does not appear seem to be well adapted for grasping prey, although sharpening takes place (Brodie, 1989). For a species primarily feeding on fish, interlocking teeth would be expected to be more optimal for grasping prey, but instead the white whales apparently rely on feeding using suction (Brodie, 1989). This feeding method involves movements of the tongue used to cause low pressure in the mouth cavity, drawing the prey into the mouth without the use of teeth for grasping (Berta and Sumich, 1995). Calves feed on milk during the first year, but supplement it with easily captured prey such as molluscs, annelids or crustaceans during their second year (Brodie, 1989).

Material and methods

48 specimens of white whale skulls from the collections of the Zoological Museum, University of Copenhagen were measured. Only specimens with complete dentitions in a jaw half were included. All specimens used in the analysis originate from the Greenland population, and have been collected over a long period spanning from the nineteenth century to 1994. Some of the specimens have previously been figured by Eschricht (1869: Pl. 8) or described by Degerbøl and Nielsen (1930: Table VI). Some specimens were complete, while in others part of the skull was damaged or missing. Measurements up to 38 cm were made using a pair of steel outside callipers; measurements above 38 cm were made using a steel measuring tape. All measurements are listed in millimeters (mm). Data were analysed using the computer programme PAST version 1.42, which is tailor-made for biological and palaeontological statistical data analysis (Hammer et al., 2001).

Only jaw halves without missing teeth were included in the analysis and were separated into four distinct data sets: upper left, upper right, lower left and lower right jaw halves, respectively. For each jaw half the following sizes were counted: (1) the total number of teeth and (2) the number of teeth showing a distinct wear facet with clearly delimited edges. Teeth with intact or merely rounded tips were not counted as "worn". For each specimen the rostrum length, the distance from the tip of the rostrum to the anterior rim of the external nares, was also measured. Rostrum length was used later in the analysis as an age proxy. A total of 71 upper jaw halves and 58 lower jaw halves with associated data on rostrum length were available for analysis.

Results

Using the collected data, the percentage of worn teeth in the upper left, upper right, lower left and lower right jaws respectively were calculated. The data sets on percentage of tooth wear for left and right jaws were pooled into one data set for upper and lower jaws respectively. This pooling was justified by a Kolmogorov-Smirnov test showing that the two respective data sets are not statistically distinct (upper jaws: P_{same} = 0.936 and lower jaws: P_{same} = 0.99999). The division into upper and lower jaw data sets was made to avoid discrepancies in wear pattern with time due to the above-mentioned differences in the eruption pattern of upper and lower jaw teeth. Also, the exact number of teeth in the upper and low jaws is different (ranges of 9-11 vs. 8-9, respectively).

For each data set the percentage of worn teeth was plotted against rostrum length, which was used as an age proxy. Using the model function of the PAST computer program, the data were then fitted to a B-spline function. The data are fitted using a least-squares criterion to the sequential third order polynomials of the B-spline function. This results in the construction of a smooth curve through a noisy data (Hammer et al., 2003). A decimation factor of 10 was used on each data set. The curves indicate a fairly low level of tooth wear (0-20%) for animals with a rostrum length up to 300 mm followed by an abrupt increase (approx. 60-90%) in worn teeth at the 300-350 mm interval (Fig. 1A and 1B). After this point the level of tooth wear appears to stabilize.

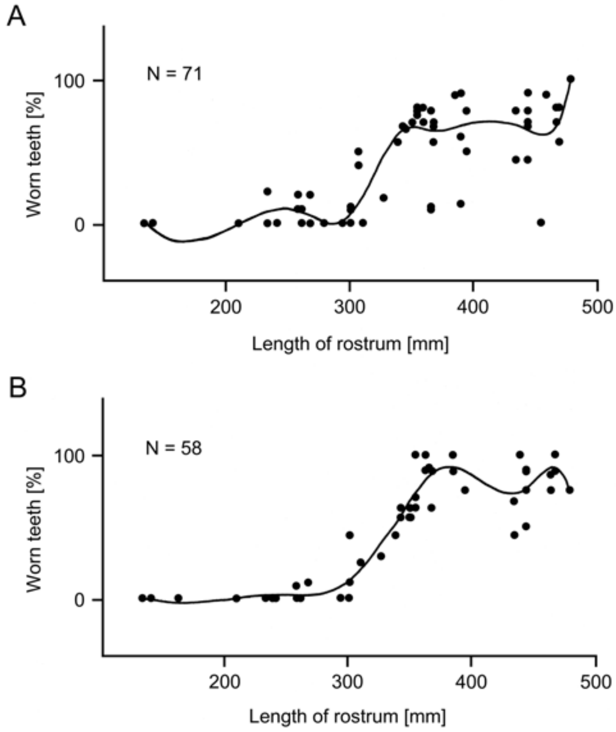

Fig. 1 — Percentage of worn teeth in jaw halves plotted against rostrum length, with B-spline curve. Note the steep increase in tooth wear percentage at a rostrum length of 300-350 mm. **A**: Upper jaw halves. **B**: Lower jaw halves.

To determine at which time in the age of the animal the steep increase in tooth wear occurs, the exact age of each specimen included in the analysis should be known. Unfortunately these data were not available for any of the specimens. Age determination in white whales is usually done by counting the number of mandibular layers or growth layer groups in thin sections of teeth (Sergeant, 1973, Brodie, 1969, 1989, Brodie et al., 1990). However, neither of theses approaches were possible due to the need to avoid damage to the studied material, some of which has historical value. Also growth layers are worn away from the age of approximately seven years (15 growth layers) in white whales (Brodie, 1969). Previous data on the age and maturity of white whales have been related to the total length of the animal (Degerbøl and Nielsen, 1930; Sergeant and Brodie, 1969; Brodie, 1971, 1989). Unfortunately the total length is only known only for a few of the specimens included in the analysis. Instead rostrum length, measured as the distance from tip of the rostrum to the anterior rim of the external nares, was used as an age proxy. This measurement is positively allometric during the growth of the animal (Degerbøl and Nielsen, 1930). Degerbøl and Nielsen (1930) list three animals (Table VI: Nos. 2, 10 and 22) from which both skull measurements and total length is known. These data were used to construct a growth curve showing relationships between rostrum length and total animal length (Fig. 2). Although the data points are few, they show a linear relationship between rostrum length (ROSEXNA) and total length (TOTLEN) of animal of TOTLEN = 10,27 * ROSEXNA – 45,48.

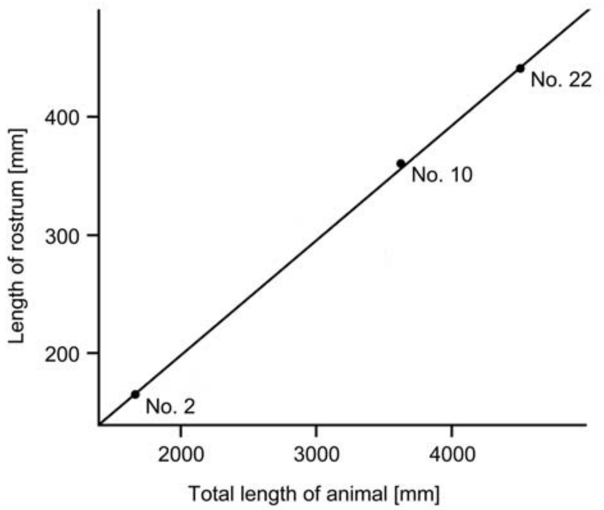

Fig. 2 — Plot of rostrum length against total body length of animals used for calculation of age proxy. Total length of animal = 10.27 * [Rostrum length] – 45.48. Numbers are specimen numbers from Degerbøl and Nielsen (1930) Table VI.

Using this formula, a rostrum length of 300 – 350 mm correlates with a total animal length of approximately 3–3.5 meters. Comparison of this to the previously calculated growth rate for white whales of Brodie (1971, 1989) indicates an age span of 4 to 6 years during which the sharp increase in tooth wear occurs.

Discussion

The results did not show the expected gradual increase in tooth wear with age. Instead, the percentage of worn teeth in white whales increases steeply during an age between approximately four and six years old and then stabilizes. The reason for this pattern, probably stems from the fact, that white whales do not use their dentition primarily for feeding. Teeth are instead used extensively in intraspecific superficial biting or scratching, especially among males, and biting appears to be an important form of communication (Brodie, 1989). Teeth are also used as “sounding blocks” in “jaw clap” signals, which is the dominant vocal method of communication in white whales (Brodie, 1989). Weaning takes place at around two years of age (Brodie, 1971), and the increase begins two years after. It apparently stabilizes at the age of six years, at which sexual maturity is attained (Brodie, 1989). Increased vocal communication and biting will probably result in much faster and more extensive wear of the teeth. An increase in interaction with the rest of the community is typically seen during the transition from juvenile to mature age. This correlation between the levels of tooth wear and social interaction is also supported by the observation that the teeth of females show less wear than teeth of males (Sergeant, 1973), who engage more in intraspecific biting or scratching (Brodie, 1989).

The results of this study therefore indicates that the degree of tooth wear in some odontocetes can reflect changes in the social behaviour pattern instead of ontogenetic age. The use of the level of tooth wear is therefore not necessarily an useful proxy for determining ontogenetic age in odontocetes, whether recent or fossil.

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