*J. CETACEAN RES. MANAGE.* 7(3):301–308, 2006

# How big is a beaked whale? A review of body length and sexual size dimorphism in the family Ziphiidae

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ABSTRACT

There is a paucity of data on the family Ziphiidae (the beaked whales) and even basic information, such as body length, is not available for some species. This review examines published records of body length for 20 of the 21 currently recognised species of beaked whale. It considers maximum, median and modal body lengths, where possible by sex. For Cuvier's, Blainville's and Gray's beaked whales, modal and median lengths were much shorter than the maximum reported lengths; this may reflect misidentification of the largest animals. Although males of some species reached a greater maximum size, there was only a significant difference in median body length for three species: True's beaked whale; the strap-toothed whale; and Gervais' beaked whale. In all three cases, females had a significantly larger median length. The apparent lack of consistent sexual dimorphism in body length suggests that, while male beaked whales use their tusks as weapons to compete aggressively for access to receptive females, large size does not give a competitive advantage. This may be a result of the way the sexually dimorphic tusks are used during combat. The only exception to this rule appears to be the northern bottlenose whale, for which males consistently reach greater body lengths than the largest females. Male-male combat appears to take a different form in this species.

KEYWORDS: MORPHOMETRICS; REPRODUCTION; AGGRESSION; BEAKED WHALES; STRANDINGS; WHALING

## INTRODUCTION

Beaked whales (Family Ziphiidae; Order Cetacea) remain the least well understood family of cetaceans and for several species even basic biological information, such as pigmentation and external morphology, is unknown (e.g. the spade-toothed whale, *Mesoplodon traversii*, is only known from three partial skeletons – van Helden *et al.*, 2002). Even for better known species, information on biological characters, such as body length, is often dispersed throughout the scientific literature with only small sample sizes. This review brings together and analyses as much of the information on body length in beaked whales as could be found. Previous studies examining body length have generally only considered the maximum body length (e.g. Mead, 1984; 1989a; b) although Mead (1984) tried to obtain additional data on, for example, mean length at sexual maturity. For most species, modal and median lengths have not previously been reported.

Body size is an important component of an animal's biology, influencing a variety of aspects of its life including metabolic requirements, prey size selection, locomotory abilities, habitat utilisation and competitive abilities (Guyton, 1974; Andersson, 1982; Cox *et al.*, 1982; Warner and Hall, 1988; Miquelle *et al.*, 1992; Poole, 1994; Whitehead, 1994; Olsson and Shine, 1996; Radloff and Du Toit, 2004). Understanding the body length (both as a characteristic of a species in its own right and as a proxy for mass) reached by the majority of individuals within a species, rather than just the largest, is thus important. This review addresses two questions: (1) what are the maximum and most common body lengths for each beaked whale species and (2) are beaked whale species sexually dimorphic in terms of body length?

## MATERIALS AND METHODS

Beaked whale data from published accounts of stranded animals, strandings databases and personal communications from other researchers have been collated into a global database (see D'Amico *et al.*, 2003 for details). In almost all cases, the measurements came from stranded animals with the associated potential problems this brings (see 'Results and Discussion'). The only exceptions to this were measurements of pygmy beaked whales (*M. peruvianus*) made from aerial photographs (Pitman and Lynn, 2001). Data from whaling records have been considered separately. Any records where the species identification was known to be uncertain, or where the body length was estimated or approximated, were not included in this analysis.

Due to problems associated with identifying beaked whales to the species level, even for experienced observers (e.g. see Dalebout *et al.*, 1998), it is not possible to rule out that some animals that have been misidentified may have been included in this analysis; if so, this could cause a bias when investigating body length. To address this potential problem, three different parameters were examined: maximum recorded body length; modal body length (for 10cm increments); and median body length. Maximum body length reflects the largest length a species reaches, but could be biased if large animals have been misidentified. When the maximum reported length was more than 0.5m larger than the next largest measurement, then both are given (Table 1). Modal body length shows the most common body length of stranded animals and is not greatly affected by erroneous identifications of larger animals. Modal lengths were identified only when there was a clear increase in the frequency of records at specific body lengths. However, the mode could potentially be affected by misidentifications of a significant proportion of the animals in a specific length class. In addition, when sample sizes are relatively small, the mode may be influenced by a small number of individuals within one length class that may not be representative of the species as a whole.

Three approaches have been adopted to investigate whether sexual dimorphism in body length occurs in beaked whales. Firstly, the percentage body length of the largest female to the largest male was calculated. Secondly, where there were a sufficient number of individuals, the Mann-Whitney test was used to compare the median length of males and females of the same species; the null hypothesis investigated was that the sexes did not differ in median body length. However, in this case it must be recognised that males and females may have similar median lengths but still be sexually dimorphic. For example, in sperm whales (*Physeter macrocephalus*) only the oldest males reach the greatest lengths (Rice, 1989) and therefore, a difference between males and females is only noticeable in the largest size classes. To try to account for this a third approach was used in which the frequency distributions were divided into length classes and the frequency of occurrence of males and females in the largest were compared using a chi square test. In this case, the null hypothesis was that there was no difference in the frequency of occurrence of males and females in the largest recorded length classes. The length classes chosen varied by species (0.4-1.0m) and the number of classes varied from two to three to ensure that the expected values were sufficiently large to avoid violating the requirements of the statistical test used.

## RESULTS AND DISCUSSION

The body lengths of 805 individual beaked whales from 20 of the 21 currently recognised species (Table 1) were found (excluding the whaling data). The final species, the spade-toothed beaked whale, is only known from skeletal remains, so no length data are available (van Helden *et al.*, 2002). Sufficient ($n$>10) data to estimate a modal length were available for 17 species. An investigation of possible sexual dimorphism was possible for 15 species although the length class approach could only be used for seven due to sample size considerations.

### Maximum and modal lengths

*Strandings data*

The longest beaked whale species is Baird's beaked whale (*Berardius bairdii*), with a maximum reliably reported length of 11.0m in our database (original source: Marine Mammal Strandings Database, National Museum of Science, Tokyo, Japan). The aptly-named pygmy beaked whale is the smallest beaked whale species, with a maximum reported length of 3.9m (Pitman and Lynn, 2001).

Modal lengths were notably smaller than the maximum reported lengths for all species. This suggests that the maximum length may not be the most suitable parameter to use when investigating how body size interacts with and influences other aspects of a species' biology. For some species the differences between maximum and modal length was sufficiently large to suggest that there are biases or errors within the data (Fig. 1). The greatest difference was in Hubbs' beaked whale (*M. carlhubbsi*), where the primary mode was at 2.5-2.6m, compared with a maximum reported length of 5.32m (Mead *et al.*, 1988). Mead (1984) estimated the average length at birth of Hubbs' beaked whale to be 2.5m, and the mode around this body length may represent a high proportion of juveniles in the relatively small total number of animals for the species ($n$=26). Secondary modes occurred at 4.9-5.0m and 5.3-5.4m and may be more reflective of typical adult length.

There were also large differences between maximum and modal length of northern bottlenose whales (*Hyperoodon ampullatus*), Blainville's beaked whale (*M. densirostris*), Gray's beaked whale (*M. grayi*) and Cuvier's beaked whales (*Ziphius cavirostris*). In these cases, these differences may represent a small number of unusually large individuals in the dataset, or errors in species identification or measurements. For example, Heyning (1989) considered all Cuvier's beaked whales measuring over 7m to represent misidentified individuals. The vast majority (93%) of Cuvier's beaked whale records examined here were under 7m and all larger records come from higher latitudes where Cuvier's beaked whale is sympatric with other larger beaked whale species (*Hyperoodon* and *Berardius* spp.), with which it could be confused. Heyning (1989) noted that the largest unquestionable length recorded for a stranded Cuvier's beaked whales is only 6.93m. Therefore, it is unlikely that the actual maximum length of Cuvier's beaked whales is greater than 7m (and see below).

Similarly, based on field observations of this species, the author does not consider Blainville's beaked whales to reach the maximum reported length (6.4m – Rosario-Delestre *et al.*, 1999) with any regularity. In fact, since the next largest record is only 4.725m (Ross, 1984) and the modal length classes are 3.9-4.0m and 4.3-4.4m (Fig. 1), it appears that this species rarely, if ever, reaches lengths over 4.8m and that most individuals are under 4.5m in length. The maximum reported length of Shepherd's beaked whale, *Tasmacetus shepherdi*, may also represent an error of some kind (Mead, 1989c), as at 9.1m this animal was 30% larger than the next longest individual. However, there are insufficient data to calculate a modal or median length for comparison. For the remaining animals, all measurements of body length that could be calculated were sufficiently similar to suggest they all may be an accurate indicator of actual values for the species.

*Comparison with whaling data (see Table 2)*

**BAIRD'S BEAKED WHALE**

Balcomb (1989) presented data on lengths of Baird's beaked whales caught off Japan ($n$=26) and California ($n$=14). He reported two modes for the California fishery, one at 10.6-10.7m and one at 10.9-11.0m. He also reported a maximum length of 11.2m off California and one of 'about 12.8m' for Japan. The latter animal was reported as being 42ft in Nishiwaki and Oguro (1971). The next largest they reported was 39ft (11.9m). A more recent extensive study by Kasuya *et al.* (1997) for whales off Japan examined by biologists reported that males ranged from 7.8-10.7m ($n$=88) and females from 8.2-11.1m ($n$=47). For both sexes, there was a single modal peak at 10.2-10.3m. The modal lengths of animals reported by Kasuya *et al.* (1997) were slightly larger than the modal lengths of the stranded animals analysed in this study (10.0-10.1m). The Kasuya *et al.* (1997) study incorporated the Japanese data from Balcomb (1989) and three stranded animals and does not make direct reference to the 'about 12.8m' animal. However, the authors noted that measurements taken by industry personnel may differ in methods and not be strictly comparable. This may explain the generally larger values in the Omura *et al.* (1955) study.

**NORTHERN BOTTLENOSED WHALE**

Data from whaling on body length are also available for northern bottlenose whales caught by Faroese and Norwegian whalers. Bloch *et al.* (1996) compared the lengths of 109 northern bottlenose whales caught off the Faroes by whaling vessels and in the local shore-based drive fishery. In the offshore fishery, males ranged from 3.41-11.16m and females from 3.41-8.47m, while animals caught in the drive fishery ranged from 3.98-8.81m for males and 3.66-7.62m for females. As Bloch *et al.* (1996) noted, the lengths for both sexes are thus greater for animals shot offshore than taken in the drive fishery. The authors suggest that this reflects a tendency for larger, more experienced

Table 1

Minimum, maximum, modal and median body lengths for each beaked whale species, with comparison of body length between males and females of each species, where possible. Whaling data are not included (see text and tables). For modal length, '-' indicates that there was no clear modal value (see Fig. 1). Median values were only calculated for sample sizes greater than five. Percentage column refers to the percentage of largest female to largest male. Where there is doubt about the largest size, the value in parentheses is for the next largest individual of that sex. *W* and *P* refer to Mann-Whitney test for comparing median values for males and females. Significantly different median values are indicated in bold with an asterisk after the letter denoting the larger sex. Records of Cuvier's beaked whale over 7m are considered unreliable (Heyning, 1989) and a 9.1m record of Shepherd's beaked whale possibly inaccurate (Mead, 1989c). All lengths are in metres.

| | All individuals (incl. unknown sex) | | | | | Females | | | | Males | | | | Females vs. males | | | Larger sex | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Species | Min. | Max. | Mode | Median | *n* | Max. | Mode | Median | *n* | Max. | Mode | Median | *n* | % | *W* | *P* | Max. | Mode | Median |
| *B. arnuxii* | 6.00 | 9.30 | - | - | 7 | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| *B. bairdii* | 5.80 | 11.00 | 10.0-10.1 | 10.0 | 22 | 11.00 | - | 10.50 | 10 | 11.00 | - | 9.60 | 5 | 100 | 84.5 | 0.624 | M=F | - | F |
| *H. ampullatus* | 2.70 | 10.00 | 6.1-6.2; 6.4-6.5 | 6.40 | 116 | 8.60 | - | 6.51 | 23 | 10.00 (8.70) | 6.5-6.6 | 6.40 | 32 | 86 (99) | 667.0 | 0.701 | M | - | F |
| *H. planifrons* | 4.63 | 7.50 | - | 6.50 | 15 | 7.45 | - | 6.50 | 5 | 6.93 | - | 6.425 | 5 | 108 | 29.0 | 0.834 | F | - | F |
| *M. pacificus* | 2.91 | 6.50 | - | - | 4 | 6.00 | - | - | 2 | - | - | - | - | - | - | - | - | - | - |
| *M. bidens* | 2.59 | 5.50 | 4.5-4.6; 4.8-4.9 | 4.50 | 95 | 5.10 | 4.8-4.9 | 4.49 | 40 | 5.50 (4.95) | 4.7-4.8 | 4.50 | 34 | 93 (103) | 1505.5 | 0.957 | M | F | M |
| *M. bowdoini* | 2.30 | 4.41 | 3.9-4.0; 4.2-4.3 | 4.03 | 15 | 4.36 | - | 4.075 | 6 | 4.41 | - | 4.22 | 7 | 100 | 36.0 | 0.3922 | M | - | M |
| *M. carlhubbsi* | 2.49 | 5.32 | 2.5-2.6 | 4.76 | 26 | 5.32 | - | 4.85 | 12 | 5.30 | - | 4.72 | 13 | 100 | 157.5 | 0.956 | F | - | F |
| *M. densirostris* | 2.30 | 6.40 (4.725) | 3.9-4.0; 4.3-4.4 | 4.15 | 63 | 4.71 | 3.9-4.0 4.5-4.6 | 4.135 | 34 | 6.4 (4.725) | 4.3-4.4; 4.6-4.7 | 4.10 | 26 | 74 (100) | 1028.0 | 0.899 | M (M) | M | F |
| *M. europaeus* | 2.17 | 4.85 | 4.2-4.3 | 4.23 | 72 | 4.85 | 4.5-4.6 | 4.32 | 35 | 4.57 | - | 4.09 | 29 | 106 | 1318.0 | 0.015 | F | - | **F*** |
| *M. ginkgodens* | 3.29 | 5.28 | 4.7-5.0 | 4.64 | 16 | 4.90 | 4.8-4.9 | 4.45 | 9 | 5.10 | - | 4.86 | 4 | 96 | 54.0 | 0.190 | M | - | F |
| *M. grayi* | 2.42 | 5.64 (4.80) | 4.7-4.8 | 4.56 | 14 | 4.80 | - | 4.67 | 5 | 5.64 (4.80) | - | 4.50 | 8 | 85 (100) | 42.0 | 0.340 | M (M=F) | - | F |
| *M. hectori* | 1.90 | 4.34 | 3.7-3.8 | 3.425 | 16 | 4.15 | - | 4.00 | 3 | 4.34 | 3.7-3.8 | 3.73 | 8 | 96 | 19.0 | 0.918 | M | - | F |
| *M. layardii* | 4.55 | 6.25 | - | 5.37 | 18 | 6.25 | - | 5.765 | 8 | 5.84 | - | 5.145 | 10 | 107 | 104.0 | 0.0145 | F | - | **F*** |
| *M. mirus* | 2.25 | 5.40 | 4.8-4.9 | 4.76 | 34 | 5.26 | 4.8-4.9 | 4.87 | 13 | 5.335 | - | 4.56 | 21 | 99 | 304.5 | 0.0067 | M | - | **F*** |
| *M. perrini* | 2.10 | 4.43 | - | - | 5 | 4.43 | - | - | 1 | 3.90 | - | - | 3 | 114 | - | - | F | - | - |
| *M. peruvianus* | 1.59 | 3.90 | 3.2-3.3; 3.6-3.7; 3.7-3.8 | 3.385 | 15 | 3.90 | - | - | 3 | 3.72 | - | - | 4 | 105 | - | - | F | - | - |
| *M. traversii* | - | - | - | - | - | - | - | - | - | - | - | - | - | | - | - | - | - | - |
| *M. stejnegeri* | 2.13 | 5.74 | 5.0-5.1 | 4.83 | 99 | 5.44 | 4.8-4.9 | 4.88 | 45 | 5.74 | 4.6-4.7; 5.0-5.1 | 4.76 | 48 | 95 | 2152.5 | 0.776 | M | M | F |
| *T. shepherdi* | 4.80 | 9.10 (6.97) | - | - | 5 | 6.60 | - | - | 1 | 9.1 (6.97) | - | - | 2 | 73 (95) | - | - | M | - | - |
| *Z. cavirostris* | 2.50 | 9.80 (9.10) | 5.4-5.5 | 5.50 | 148 | 8.50 (7.60) | 5.5-5.6 | 5.47 | 53 | 9.80 (7.92) | 5.5-5.6 | 5.50 | 53 | 87 (96) | 2830.5 | 0.977 | M (M) | M=F | M |

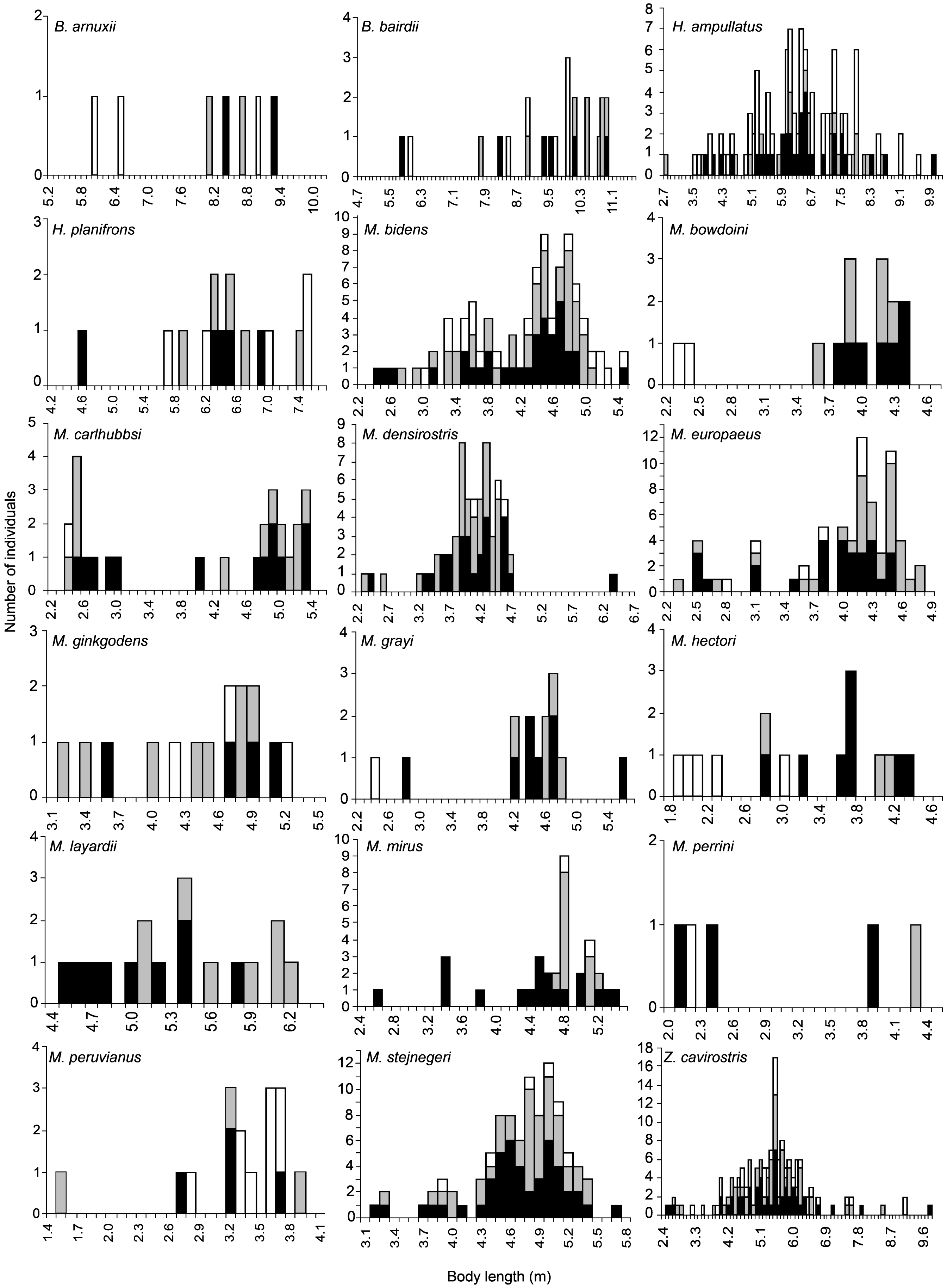

Fig. 1. Frequency distribution at 0.1m intervals of body length of stranded individuals of 17 beaked whale species (with the exception of photogrammetric measurements of pygmy beaked whales from Pitman and Lynn, 2001). Black bars – male, grey bars – female, white bars – sex unknown.

Table 2

Comparison of information from whaling data and strandings data.

| | Males (M) | | | Females (F) | | | F:M |
|---|---|---|---|---|---|---|---|
| | Max (m) | Mode (m) | *n* | Max (m) | Mode (m) | *n* | % maximum |
| ***B. bairdii*** | | | | | | | |
| Strandings (this paper) | 11.00 | 10.0-10.1[1] | 5 | 11.00 | 10.0-10.1[1] | 10 | 100 |
| Whaling (Kasuya *et al.*, 1997) - 1975; 1985-88 | 10.70 | 10.2-10.3 | 88 | 11.10 | 10.2-10.3 | 47 | 104 |
| Whaling (Nishiwaki and Oguro, 1971 )* - 1965-69 | 11.88 | 10.1-10.4 | 400 | 12.80 | 10.1-10.4 | 301 | 108 |
| Whaling (Omura *et al.*, 1955)* - 1948-52 | 11.60 | 10.4-10.7 | 631 | 12.20 | 10.7-11 | 293 | 105 |
| ***H. ampullatus*** | | | | | | | |
| Strandings (this paper) | 10.00(8.70)[2] | 6.5-6.6 | 32 | 8.60 | Not given | 23 | 86(99)[2] |
| Whaling (Bloch *et al.*,1996 - offshore) | 11.16 | 7-7.5[3] | 20 | 8.47 | 6.5-7[3] | 22 | 76 |
| Whaling (Bloch *et al.*,1996 - drive) | 8.81 | 7-7.5[3] | 36 | 7.62 | 6.5-7[3] | 31 | 86 |
| Whaling (Benjaminsen, 1972)* | 10.97 | | 5,043[3] | 8.80 | | 5,043[4] | 80 |
| ***Z. cavirostris*** | | | | | | | |
| Strandings (this paper) | 9.80(7.92)[2] | 5.5-5.6 | 53 | 8.50 (7.60)[2] | 5.5-5.6 | 53 | 87(96)[2] |
| Whaling (Nishiwaki and Oguro, 1972)* - 1965-70 | 7.00 | 6.10 | 132 | 6.70 | 6.10 | 57 | 96 |
| Whaling (Omura *et al.*, 1955)* - 1948-52 | 6.71 | 5.50 | 51 | 7.00 | 5.80 | 34 | 104 |

*Original measurements in feet. [1]Given the small sample size, the mode is for all individuals (including those of unknown sex) combined. [2]The values in parenthesis are for the second largest animals (see text). In the case of the northern bottlenose whale, the length of the largest whale in the strandings sample is not inconsistent with the whaling data. However, for Cuvier's beaked whale, the maximum lengths for both sexes for the strandings data are considerably larger than those for the whaling data. [3]It was not possible from the paper to determine the precise number of males and females so the total for all animals of known sex is given here.

animals to stay further from shore, particularly when accompanied by small calves. If true, this may also result in a bias in the body lengths of stranded animals. For males included in the database, the range (3.7-10m) was less than that for the 'offshore' Faroese fishery but greater than for the Faroese drive fishery. The same was not true for adult females (2.7-8.6m), although this can be assigned to the one extremely small individual and one female that was somewhat larger than others in this study (Fig. 1). For all the Faroese data combined, males had a modal length of 7-7.5m and females 6.5-7m. Data for the same species are also available for animals taken by Norwegian whalers in the North Atlantic Ocean (Benjaminsen, 1972). For all five main whaling areas (Labrador, Iceland, Svalbard, Andenes and Møre) there is a clear modal length for females at 7.3m with a maximum length rarely over 8.5m. For males, the modal length varied from 7.3m to 8.3m across these areas, with a maximum length rarely greater than 9.7m. These data from whaling compare to a modal length of 6.5-6.6m for males and 6.4-6.5m overall obtained in this study, and maximum lengths of 8.6m for females and 10m for males.

### CUVIER'S BEAKED WHALE

Nishiwaki and Oguro (1972) reported that the modal length of Cuvier's beaked whales of each sex (132 males and 57 females) caught by whalers in the North Pacific was 20ft (6.1m). The maximum lengths for males and females were 23ft (7.0m) and 22ft (6.7m) respectively. In this study, the modal values were 5.5-5.6m for each sex and 5.4-5.5m for the species as a whole, whilst the maximum values of over 7.0m were probably a result of misidentification according to Heyning (1989; see above).

### *Limitations of whaling and strandings data*

For both strandings and whaling data, the primary question is how representative are the data of the true 'population'? In the context of this study, the 'population' refers to the species as a whole. The examples above illustrate the potential strengths and limitations of both data sources.

In general, whalers will tend to select for larger individuals in the 'available' population. Exceptions to this might be expected if, for example (1) the animals are at low densities such that being overly selective is uneconomic or (2) the species being taken is not the primary target of the fishery (i.e. it is largely opportunistic). Bias may also occur if there is geographical and/or temporal segregation in the whale population by sex- and/or age-class and the whaling operations are limited in their geographical and/or temporal scope. The overall length distribution in a population may also vary due to exploitation. Given the propensity for selecting for large individuals, one might expect that the maximum length data are more 'representative' of the species than the modal lengths. Where whaling data are only recorded by whalers, there may be either deliberate inaccuracies due to possible commercial pressures to exaggerate length, e.g. due to higher bonus payments for large animals or to comply with length regulations or accidental inaccuracies due to carelessness, or different methods of measuring or stretching as the animal is hauled from the sea. It should be noted that no length limits were in force for the beaked whale operations considered here and that for many of the samples, measurements were taken by biologists (e.g. Kasuya *et al.*, 1997). Sample sizes are usually larger than for strandings data.

Strandings data also have a number of limitations and potential biases. For example, the likelihood of stranding may be indirectly length-related due to (1) differential survival by age-class, (2) geographical and/or temporal segregation by age-class in relation to prevailing currents and/or the efficiency/existence of the stranding scheme or (3) the nature of the stranding (e.g. mass stranding, individual stranding, stranding due to illness, stranding due to bycatch etc.). As a result, certain length classes may be over- or under-represented in databases constructed from strandings records. Inaccuracies may also occur due to lack of experience in identifying species, taking standard measurements or the decomposition state of the carcase.

For the three species where a comparison can be made animals killed by whalers tended to be larger than animals that stranded, as reflected in the modal lengths. This tends to suggest that the whalers were selecting for larger animals although it may also reflect under-representation of larger animals in the strandings record. Further investigation is required to determine which, if either, most accurately reflects the true modal lengths of the species concerned.

Such considerations must also be borne in mind in the discussion of sexual dimorphism below.

## Sexual dimorphism

### *Strandings data*

The maximum recorded length of females ranged from 74-114% of that for males (Table 1).

In six species, the percentage was less than 95% (i.e. females were smaller). However, as noted above, there are doubts over the maximum lengths recorded for males for four species (Blainville's, Gray's, Shepherd's and Cuvier's beaked whales); this is also true for the female Cuvier's beaked whale (see above). If for each of these, the largest female (or second largest for Cuvier's) is compared to the second largest male, the values all become between 95% and 103% (Table 1). For one of the remaining two species, Sowerby's beaked whale (*M. bidens*), the largest known sex animal is a male of 5.5m (there is also one of unknown sex at the same length), then three animals of unknown sex between 5.2-5.3m, followed by four of the next six animals being females (the other two being of unknown sex). For the final species (northern bottlenosed whale), there were three animals of unknown sex after the largest 10m male before the next known sex animals which were a male and a female, both around 8.6-8.7m. Mead (1989a) reported that the largest recorded male is 9.8m and the largest female 8.7m; similar to the results given here.

In five species, the percentage was 105% or greater (i.e. females were larger). However, for three of these species, the sample sizes were very small (5 or less, for either sex). For the remaining two species, Gervais' beaked whale (*M. europaeus*) and strap-toothed whale (*M. layardii*), there were several females larger than the largest male (Fig. 1). Therefore, from the strandings data, these are the only two species for which there is a clear and unequivocal difference between males and females in terms of the maximum size reached; in both of these species females reach a consistently larger size than males.

Turning to median values, there were only three species for which there were significant differences between the sexes and in each case, the females had the significantly larger value (Table 1). These species were Gervais' beaked whale, the strap-toothed whale and True's beaked whale (*M. mirus*).

In terms of the comparison of body lengths in the largest length classes, in only one of the seven species where this could be examined was there a significant difference (Table 3). For Gervais' beaked whales, males and females were found to differ significantly in their frequency of occurrence in the three longest classes ($\chi^2 = 6.136$, d.f.=2, $p$=0.047). In the longest class (4.4-4.8m) there were more females (14) and fewer males (4) than expected. The overall results concur with the examination of median values, i.e. there was no evidence of sexual dimorphism in length for most species and where there was evidence, females were larger in those three species. Of course, it should be remembered that this analysis does not take into account the animals of unknown sex which may be important in some cases (e.g. see the comments on northern bottlenosed and Sowerby's beaked whales above).

Therefore, Gervais' beaked whale is the only species in our database that shows a consistent sexual dimorphism in body length, when unknown sex animals are excluded for the three measures investigated. For this species, females were found to have a clear difference in maximum length, a greater median length and a greater occurrence in the largest size category.

Table 3

Comparison of male and female beaked whales in largest length categories for seven beaked whale species. In only one species, *M. europaeus*, was there a significant difference between the number of males and females in these categories. In this case, there were more females than expected in the largest length category.

| Length categories (m) | No. males | No. females | d.f. | $\chi^2$ | Probability |
|---|---|---|---|---|---|
| *H. ampullatus* | | | | | |
| 6.0-7.0 | 14 | 6 | | | |
| 7.0-8.0 | 5 | 7 | | | |
| >8.0 | 3 | 2 | 2 | 2.498 | 0.287 |
| *M. bidens* | | | | | |
| 4.0-4.4 | 4 | 4 | | | |
| 4.4-4.8 | 15 | 8 | | | |
| >4.8 | 5 | 13 | 2 | 5.668 | 0.059 |
| *M. mirus* | | | | | |
| 4.6-5.0 | 9 | 9 | | | |
| 5.0-5.4 | 5 | 4 | 1 | 0.018 | 0.892 |
| *M. europaeus* | | | | | |
| 3.6-3.99 | 4 | 2 | | | |
| 4.0-4.39 | 14 | 11 | | | |
| 4.4-4.8 | 4 | 14 | 2 | 6.136 | **0.047** |
| *M. densirostris* | | | | | |
| 3.6-3.99 | 4 | 8 | | | |
| 4.0-4.39 | 10 | 12 | | | |
| 4.4-4.8 | 5 | 9 | 2 | 0.601 | 0.741 |
| *M. stejnegeri* | | | | | |
| 4.4-4.8 | 18 | 8 | | | |
| 4.8-5.2 | 15 | 22 | | | |
| >5.3 | 6 | 6 | 2 | 5.059 | 0.080 |
| *Z. cavirostris* | | | | | |
| 5.0-5.5 | 15 | 11 | | | |
| 5.5-6.0 | 11 | 10 | | | |
| >6.0 | 6 | 7 | 2 | 0.475 | 0.788 |

However, questions of sample size for some analyses, the treatment of animals of unknown sex and the possible biases arising out of strandings data referred to above must temper any conclusions that can be drawn.

## Comparison with whaling data (see Table 2)

For Baird's beaked whales, whaling data appear to suggest little sexual dimorphism but with a tendency to slightly larger females. In the study by Nishiwaki and Oguro (1971) for catches between 1965 and 1969, they found similar modal lengths in the catches for each sex (33-34ft; 10.1-10.4m) although noting that 'roughly, larger lengths are of females'. The largest animal was a 42ft female (12.8m) while the largest male was 39ft (11.9m) – the female to male percentage is thus 108%. In the more recent Kasuya *et al.* (1997) study, the largest animal was an 11.1m female while the largest male was 10.7m – the percentage was thus 104%. Kasuya *et al.* (1997) also calculated growth curves and estimated asymptotic lengths of 10.45m for females 10.10m for males. An earlier study by Omura *et al.* (1955) for catches between 1948-52 also fitted this pattern (the percentage was 105%). The lengths for both sexes were generally larger than the later studies – this may reflect a real difference or different measuring methods.

For Cuvier's beaked whale, Heyning (1989) reported that whaling data indicated no significant difference in length between the sexes. The studies of Omura *et al.* (1955) and Nishiwaki and Oguro (1972), show the percentage of female maximum length to male maximum length vary from 96-104% and similar modes for both sexes (although lower in the earlier period).

The above whaling data are thus consistent with a general hypothesis of either a lack of sexual dimorphism in body length or with females being slightly larger in the family Ziphiidae.

Within the literature there is one species, the northern bottlenose whale, that has consistently been reported as being sexually dimorphic in terms of length (e.g. see Mead, 1989a). For the Faroese operations (*n*=109), males had both a larger modal body length than females and a larger maximum size (11.16m for males and 8.47m for females – Bloch *et al.*, 1996). For Norwegian operations, males had a greater modal length than females in all but one area and a greater maximum length in all areas (Benjaminsen, 1972). However, in the Faroese (Bloch *et al.*, 1996, fig. 6) and Norwegian whaling data (Benjaminsen, 1972, fig. 6), it is a relatively small proportion of males that are larger than the largest females. While the difference in maximum size was also apparent from the strandings data, there were only two known males that exceeded the maximum size of females (although an additional three animals of unknown sex exceeded this length) and there were no significant differences between males and females in terms of body length. The strandings data are more similar to the Faroese drive fishery data, supporting the view of Bloch *et al.* (1996) that the larger animals may be more common offshore.

The evidence therefore supports the view of limited sexual dimorphism with the largest males being somewhat larger than the largest females. Bloch *et al.* (1996), noted a change in the shape (from bulbous to flat) and colour (from grey to white) of the melon of males with length that may be related to sexual and physical maturity. Of 32 males examined, changes in head shape and colour began to be noticed between 6.54-6.92m, becoming more pronounced between 6.94-7.55m (grey but flat) and becoming fully white and flat from 8.33m. Benjaminson (1972) reported from a histological analysis that males became mature at 24-25ft (*n*=32) or about 7.3-7.6m. Thus it may be that males reach sexual maturity at around this length and physical and/or social maturity at around 8.3m. Differences in the length at attainment of sexual and physical and/or social maturity are not uncommon in cetaceans (e.g. sperm whales; Best *et al.*, 1984).

## CONCLUSION

Whilst recognising the limitations of the available data as discussed above, I believe that the analyses presented here are sufficient to propose that, as a family, most beaked whale species show either no sexual dimorphism in body length or have slightly larger females (e.g. Gervais' beaked whale). The only exception to this within the family Ziphiidae (for which there are sufficient data) appears to be for the northern bottlenose whale where a small proportion of males may be consistently larger than the largest adult females. Whether the same is true for the closely-related southern bottlenose whale (*H. planifrons*) is currently unclear due to a lack of sufficient data (*n*=5 for each sex).

In many marine mammal species where males compete aggressively for females, males are often significantly larger (e.g. elephant seals, *Mirounga* species – Modig, 1996; sperm whales – Rice, 1989). This is also the case for many terrestrial mammals, including those that use teeth as weapons (e.g. anthropoid primates – Leutenegger and Kelly, 1977). In most beaked whale species, males are thought to compete for females and use their tusks as weapons (Heyning, 1984). While a lack of sexual dimorphism in body length or having larger females might be thought unexpected, in the case of beaked whales, such dimorphism would only be expected if having a larger body size gave a competitive advantage (Ralls, 1976; Brownell and Ralls, 1986).

Scarring patterns indicate that in most species of beaked whale, males fight by making a series of passes at their opponents, analogous to humans jousting on horseback (MacLeod, 2002). The turning radius of a cetacean is related to its body length, thus when all else is equal a longer animal will have a greater turning radius (Fish, 2002; Fish *et al.*, 2003). As a result, shorter males might have an advantage since they can mount a new run at a larger opponent before the opponent can turn fully and be ready to re-engage. In this context, therefore, the selection pressure would be for shorter and more manoeuvrable males, all other things being equal. Other selective pressure may then either maintain a similar length between males and females, as seems to be the case in most beaked whales, or even be for larger females, as is apparently the case in Gervais' beaked whale.

Bottlenose whales appear to be the only beaked whale species that fight in a different manner, with males using their foreheads and their large underlying maxillary crests as battering rams (Gowans and Rendell, 1999). While repeated turning and re-engaging is also employed during such fights, it may be that body size also gives some competitive advantage. This could explain why the northern bottlenose whale is the only species for which there is evidence that some adult males are consistently larger than adult females.

In summary, this paper presents the first published modal and median values of body length for many beaked whale species. Analysis of these data revealed no clear evidence of sexual dimorphism in body length in most species for which there are sufficient data. Where clear sexual dimorphism in body length was found, this might be related to the nature of competition among males.

## ACKNOWLEDGEMENTS

This work was made possible through funding from the Office of Naval Research (Grant Number N00014-02-1-0253) to compile a database of global beaked whales records and the author would like to thank Jessica Ward, Ellen Keene, Glenn Mitchell, Angela D'Amico and Robert Gisiner for their collaboration and help in location and collation of beaked whale records and in the construction of the beaked whale database which was used as a source of records for this analysis. The author would also like to thank all those who contributed information to this database. A full list of published strandings data utilised in this analysis is available on request. Sources of unpublished data used in this analysis were Scottish Agricultural College Veterinary Division, Inverness, Scotland, the Natural History Museum, London, UK, the Irish Whale and Dolphin Group Strandings Database[1], the Marine Mammal Strandings Database, National Museum of Science, Tokyo, Japan[2] and the Port Elizabeth Museum, Port Elizabeth, South Africa. Finally, the author would like to thank Graham Pierce, Sonia Mendes, James Mead and Christina Lockyer for comments and suggestions for additional data for this manuscript.

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[1] *http://www.iwdg.ie/strandings.*

[2] *http://svrsh1.kahaku.go.jp/database_english/frameset.html.*

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Date received: October 2004
Date accepted: April 2005