

## Species review of Blainville's beaked whale, *Mesoplodon densirostris*

B. M. Allen<sup>1,2</sup>, J. G. Mead<sup>2</sup>, and R. L. Brownell<sup>2,3</sup>

<sup>1</sup>National Marine Mammal Laboratory, Alaska Fisheries Science Center, National Marine Fisheries Service, National Oceanic and Atmospheric Administration, Seattle, WA, USA

<sup>2</sup>National Museum of Natural History, Smithsonian Institution, Washington, DC, USA

<sup>3</sup>Southwest Fisheries Science Center, National Marine Fisheries Service, National Oceanic and Atmospheric Administration, Pacific Grove, CA, USA

### **Mesoplodon densirostris (Blainville, 1817)**

Blainville's Beaked Whale, Dense-beaked Whale

Delphinus densirostris, Blainville 1817:178. Type locality unknown (Laboratoire d'Anatomie comparée du Muséum national d'Histoire naturelle, Paris - CAC: A. 3552).

Ziphius sechellensis, Gray 1846:28, pl. 6, figs 1,2. Type locality Seychelles Islands.

Dioplodon densirostris, Gervais 1850:16. Type species Delphinus densirostris, Blainville 1817.

Mesodiodon densirostre, Duvernoy 1851. Included species Delphinus densirostris, Blainville 1817.

M[esoplodon] densirostris, Flower 1878:684. First use of current name combination.

Nodus densirostris, Galbreath 1963:422. Use of Nodus Wagler 1830 as a senior synonym of Mesoplodon Gervais 1850. Melville (1985) suppressed Nodus and conserved Mesoplodon.

**CONTEXT AND CONTENT.** Order Cetacea, Suborder Odontoceti, Family Ziphiidae. There are 14 species recognized in the genus Mesoplodon. Gervais (1850) erected the genus Dioplodon for M. densirostris. M. densirostris is monotypic (Mead and Brownell, 2005).

### **Diagnosis:**

The most striking diagnostic features of M. densirostris are the shape of the mandible and the position of the paired mandibular teeth. Immediately posterior to the mandibular symphysis, the mandible is abruptly stepped dorsally in relation to the distal portion. Tooth size and shape is very distinctive for this species; however, these diagnostic characters are sexually dimorphic. The teeth of adult males are anteriorly inclined and develop in a raised crest situated well posterior to the mandibular symphysis of the mandible (Besharse, 1971; Ross, 1984). The single pair of laterally compressed teeth in M. densirostris is positioned more posteriorly relative to mandibular length than those of congeners (McCann, 1963; Moore, 1968; Heyning, 1984). Females of this species have less massive development of the mandible posterior to the mandibular symphysis; the teeth typically remain unerupted from the alveoli, not extending above the edge of the dentary groove (McCann, 1963; Besharse, 1971).

In dorsal view of the skull, the premaxillary bones extend forward of the nasal and frontal on the vertex, separating M. densirostris from Berardius and Ziphius. A sulcus along the anteromedial margin of the nasal bones results in a more anterior extension of the lateral portions of the nasal bones along the vertex, distinguishing M. densirostris from Tasmacetus and Indopacetus. When the skull is upright and the long axis of the anterior half of the rostrum is

horizontal, a horizontal plane transecting the dorsal margin of the maxillary prominences transects the mesethmoid bone, separating M. densirostris from Hyperoodon. The mandibular alveoli are positioned posterior to the mandibular symphysis, discriminating M. densirostris from all other beaked whale species except M. ginkgodens, M. peruvianus, and M. stejnegeri. On the vertex of the skull, the right premaxilla extends posteriorly beyond the right nasal a distance exceeding 70% of the dorsal length of the right nasal, separating M. densirostris from M. ginkgodens. In M. densirostris, the antorbital notches form obtuse angles, distinguishing it from M. peruvianus. The anterior margin of the pterygoid sinus fossa extends greater than 35 mm anterior to a transverse plane placed perpendicular to the long axis of the rostrum and transecting the apex of the left antorbital notch, which separates M. densirostris from M. stejnegeri.

M. densirostris can be diagnosed externally from cranial features. The melon slopes into a low forehead, and the rostrum is relatively short and wide. The arch of the mandible can protrude dorsally above the contour of the rostrum, especially in adult males. In lateral view, the arch of the gape is a distinguishing feature for both males and females.

Mesoplodon densirostris has a mean number of 4.2 connecting chambers (range 3-5, N=5) in its stomach (Mead 1993:80). The only known species that has fewer is M. perrini (incorrectly identified as M. hectori in Mead 1993) with 3. The other Mesoplodon species that have been investigated (M. bidens, europaeus, mirus, stejnegeri) range from 6-11 (Mead 1993).

## **General Characters:**

### **1) Coloration/ External Characters**

The body form of Mesoplodon densirostris is similar to all others in the genus in its laterally compressed, fusiform shape (McCann, 1963; Leatherwood and Reeves, 1983). Compared with other odontocetes, whales of the genus Mesoplodon have a relatively small head with a well-defined beak, a large thorax and abdomen, and a short caudal region (Leatherwood and Reeves, 1983:122; Mead, 1989).

Posterior to the rostrum, the head lacks a groove between the rostrum and forehead; the melon is relatively flat and merges seamlessly into the thick rostrum. The flukes have no deep median notch, and the posterior margin is straight or slightly crescentic (McCann, 1963; Leatherwood and Reeves, 1983; Mead, 1989). The blowhole is typically a broad, often asymmetric, semi-circle with the open side oriented anteriorly. Other features typical of Mesoplodon are a pair of throat grooves on the ventral side of the head between the lower jaws (following the angle of the converging mandibles), a small, sub-triangular dorsal fin positioned approximately two-thirds the total body length from the anterior end of the animal, and pectoral fins with a short phalangeal portion and a relatively long propodial portion (McCann, 1963; Kasuya and Nishiwaki, 1971; Mead, 1989; Pastene et al., 1990). Depressions, or "flipper pockets", in the ventrolateral region of the body appear to fit the flippers, possibly to reduce drag when the animal is swimming (True, 1910; Mead, 1989).

Pigmentation tends to change rapidly upon death (usually becoming dark with much of the details disappearing), making an accurate assessment from stranded animals difficult. Most adult males that have been described or photographed appeared dark gray both dorsally and ventrally; juveniles and adult females appear to be medium gray on the dorsal surface of the body and lighter on the ventral surface with no outstanding pigmentation details (McCann, 1963; Mead, 1989). The ventral surface is often lighter in color than the dorsal, particularly near the throat grooves, flippers, umbilical and genital regions (McCann, 1963; Kasuya and Nishiwaki, 1971; Paterson et al., 1993). Often, diatoms are present on the skin surface, particularly on the dorsal surface, which may give the animal a slight brown, tan, or yellow tinge.

Linear, oval, and punctate body scarring is often present. Linear scars are generally much more extensive on adult males than on females or juveniles, ranging in length from a few centimeters to over a meter, and often covering much of the body (McCann, 1963; Heyning, 1984; Mead, 1989). Males often possess many densely packed linear scars on the dorsal surface immediately posterior to the blowhole (McLeod, 2002). In the Mesoplodon species studied, it has been determined that the linear scarring patterns observed in males suggest that infliction occurs during intraspecific combat, as evidenced by matching scar patterns with the tooth structure and position of conspecifics (Heyning 1984; MacLeod 1998). The widely separated, more posterior position of the teeth of M.

densirostris results in widely separated parallel scars (Heyning, 1984, fig. 5). Oval or elliptical scars, usually attributed to cookie-cutter sharks (*Isistius brasiliensis*), are often scattered over the body (McCann, 1963). Upon dissection, Heyning and Mead (1996) found the epidermis of the anterior floor of the mouth of many beaked whale species to be white or lightly pigmented, possibly serving as an attractant for bioluminescent squid upon which the whales feed. Many adult males have white on the tip of the snout possibly as an intraspecific communication cue used to visually enhance the size of the erupted teeth (Heyning and Mead, 1996).

## 2) Morphometrics

The total length of *M. densirostris* ranges from 261 cm at birth to 473 cm for the largest reported adult (Mead 1984:93). *Mesoplodon* as a genus is relatively conservative in the placement of its various landmarks from which we traditionally measure. These measurements are from the tip of the snout taken as lengths parallel to the long axis of the body and are expressed as the mean of the measurement relative to the total length of the specimen: snout to center of blowhole (12.3%), eye (13.1%), angle of mouth (8.2%), ear (15.4%), distal end of throat grooves (7.7%). The measurements that have consistently the highest correlation coefficient with total length of the animal involve the position of the flipper (23.1%), tip of dorsal fin (66.4%), umbilicus (48.0%), anal slit (72.6%) and genital slit (68.5%) (Mead 1989:373). The girths are more variable. The mean relative girths are: at eye (30.1%), axilla (47.7%), maximum (54.9%), anus (33.4%) and girth midway between anus and fluke notch (18.5%).

## 3) Teeth/ Jaw / Skull Characters

The remarkably dense rostrum was considered by de Blainville to be such a significant diagnostic character for *M. densirostris* that this description was incorporated into the nomenclature of the species. At the time of its description, *M. densirostris* was the only member of the genus known to possess an extremely dense rostral ossification. This dense development of the rostrum is a proliferation of the vomer and mesethmoid into the mesorostral canal (Forbes, 1893:220; Moore, 1963:416), not a result of mesorostral cartilage ossification, as suggested by McCann (1963). Only mature males possess this hyperossification, in which the premaxilla, maxilla, and vomer eventually fuse into a massive rostral bone unit (Mead, 1989:391; Moore, 1963:400). Bone density of this structure has been measured at 2.612 to 2.686 g/cm<sup>3</sup> (de Buffrenil et al. 2000) and as much as 5.701 g/cm<sup>2</sup> from a dual energy X-ray absorptiometry (DXA) analysis (Zotti et al. 2009). These values are the highest density values measured for any mammalian bone tissue. Since then, several other beaked whale species have been described that share this osteological characteristic, including *M. carlhubbsi* and *Z. cavirostris*. The rostrum in *M. densirostris* is narrow posteriorly in dorsal view, expanding slightly at midlength, and tapering at the tip; at midlength the rostrum is deep in lateral view.

Unlike in delphinids, in which the pterygoid and palatine bones form thin, delicate walls lining the narrow, bilaterally paired pterygoid sinuses, the pterygoid bones of beaked whales are thick and robust (Rommel et al. 2006). The pterygoid sinuses of beaked whales are very large and lack bony lateral laminae, suggesting a difference in mechanical function (Rommel et al. 2006; Fraser and Purves 1960). Flower (1878) stated that *M. densirostris* has a well-developed basirostral groove; however, data from Ross (1984) support True (1910) and Besharse (1971) that this groove is not well marked in the species but is shallow and indistinct, particularly proximally.

Mandibular features have been used as key diagnostic characters of *Mesoplodon* species, specifically mandibular shape, tooth morphology, and tooth position along the mandible (Fraser, 1949; Mead, 1989; Moore, 1963, 1968; Ross, 1984). *Mesoplodon* species develop only a single pair of mandibular teeth, which varies in shape and position among species. (Heyning 1984). The teeth in *M. densirostris* are situated posterior to the mandibular symphysis on the elevated mandibular arch, with a slight anterior projection. *Mesoplodon* teeth are laterally compressed and secured deep in a bony socket by a narrow root (Moore 1968, Heyning 1984). Besharse (1971) was the first to compare an adult female specimen of *M. densirostris* with adult males, noting sexual dimorphism in tooth development and lack of tooth eruption in females. This lack of development of the teeth in females supports the notion that the teeth in ziphiids are not required for feeding, and therefore, develop in males to serve a different function (Moore, 1963:401).

Mature male *M. densirostris* teeth are large, measure greater than 100 mm in length, and extend above the edge of the dentary groove (Besharse, 1971). The teeth of mature females are small, considerably less than 100 mm in length, and do not extend above the dentary groove (Besharse, 1971). Paterson et al. (1993:294, fig. 7) present a

radiograph of an unerupted mandibular tooth of a female specimen. Measurements of this tooth were 52 mm high, 30 mm long, and 9 mm at greatest diameter, with the pulp cavity completely open. Another tooth, this one from the left mandible of a subadult female (JM9640), measured 54 mm in height, 47 mm in length, and 10 mm in greatest diameter, with the pulp cavity extensively obliterated (Paterson et al., 1993).

Heyning (1984) believes that the more posterior tooth position, in combination with situating the apex of the teeth above the level of the rostrum for a functionally more effective fighting tool, is indicative of an evolutionarily more advanced character, making M. densirostris the most derived of the Mesoplodon species. This differs from Moore's (1968) suggestion that, although the posterior position of the teeth in M. densirostris does make it one of the more derivative Mesoplodon species, inclination of the teeth should also be considered, which would not place this species in the most advanced position for tooth evolution (Heyning, 1984; Loughlin and Perez, 1985). Dalebout et al (2008) found what were considered ancestral and derived tusk forms have in fact arisen independently on several occasions, contradicting the linear-progression hypothesis, with M. densirostris and M. stejnegeri likely sister taxa. MacLeod (2000) suggested variation in the position and shape of teeth in Mesoplodon serves to aid in species recognition between sympatric, morphologically similar species.

### **Distribution:**

M. densirostris is seen infrequently at sea, and positive identifications in the field can be difficult unless key diagnostic characters of the head are observed. As a result, knowledge of the distribution of this species has been inferred almost entirely from stranding records. Photo-identification and tagging studies are possible in areas where these whales are known to reliably occur, typically around oceanic island groups such as the Bahamas Islands (Claridge et al. 2009), the Canary Islands (Johnson et al. 2007), and the Hawaiian Island (Schorr et al. 2009). Of all the Mesoplodon species, M. densirostris has the most extensive distribution; it is a cosmopolitan species, occurring in all oceans except the Arctic (Mead 1989, Jefferson et al. 2008). Its range is primarily tropical and warm temperate waters, including tropical oceanic islands and on continental or insular coasts along which warm currents flow. There are no records of either sightings or strandings from polar or other high-latitude regions. It is generally assumed that all ziphiids inhabit very deep waters (Moore, 1958; Shallenberger, 1981; Mead, 1989). Most observations of M. densirostris occur in deep waters.

The known range in the western North Atlantic extends from the Caribbean (Rosario-Delestre et al. 1999) and northern Gulf of Mexico (Waring et al. 2009) to Nova Scotia (McKenzie 1940), although reports from the latter area are believed to represent strays from Gulf Stream waters. In U.S. waters, strandings have been reported in most coastal states from Texas to Massachusetts. Records from the eastern North Atlantic include the west coast of Wales, United Kingdom (Herman et al. 1994), the Netherlands, Portugal, the Azores Islands, the Canary Islands, and the Mediterranean coast of Spain (Aguilar 1982).

In the North Pacific, records of this species range from California to Taiwan, and include sightings from the Hawaiian Islands, as well as strandings from the Line Islands, Midway, the Philippines, the Ryukyu Islands, Kuroshima, and Honshu, Japan (Miyazaki 1986).

Records of M. densirostris in the northern Indian Ocean are from Nicobar Islands (Evans 1987, Corbet and Hill, 1992), the Republic of Maldives (Ballance et al. 2001), and from equatorial waters around the Seychelles (Sathasivam 2004). As elsewhere, the lack of data from this region is probably due at least in part to low observer effort. Waters near Mauritius, western Australia, and eastern South Africa are localities of M. densirostris in the southern Indian Ocean (Ross 1984).

Known occurrences of M. densirostris in the South Atlantic are limited to specimens from Namibia, western South Africa (Ross 1984), and Brazil (Castello and Pinedo 1980, Secchi and Zarzur 1999). South Pacific accounts are concentrated mostly in the western ocean, including regions along the eastern Australian coast (Paterson 1993), Tasmania and Macquarie Island (Dixon and Frigo 1994), Lord Howe Island (Raven 1942), New Zealand, and New Caledonian archipelago and adjacent waters (Borsa and Robineau 2005). Other reports of M. densirostris have occurred from Papua New Guinea, Rarotonga, Vanuatu, Solomon Islands, and French Polynesia (Gannier 2000), with a single report from Chile extending the known range to the eastern South Pacific (Pastene et al. 1990).

Conclusions drawn from records of stranded animals must be viewed with caution, as the distribution of a species

may be influenced falsely by the likelihood that stranded animals were diseased or injured and strayed from their normal range; firm distributional conclusions should only be made when an area possesses a large sample size of strandings that remains temporally consistent. Emphasis should also be made on regions with negative data; this lack of data may be a result of no strandings occurring in these areas, or the presence of animals utilizing these waters and stranding on nearby coasts where there is limited or no cetological activity to bring these occurrences to the attention of the scientific community (Mead, 1989).

### **Fossil Record:**

There are no fossil records of Mesoplodon densirostris. General knowledge of ziphiid evolution is unclear. They first appear in the lower Miocene, are very well represented in the upper Miocene records, and appear to have slowly decreased in diversity since (Mead, 1975; 1989). Fossil records of the genus Mesoplodon are known from the Upper Miocene through the Upper Pliocene in Europe, the Upper Miocene in North America, and the Pliocene in Australia (Romer, 1966; Barnes et al., 1985). It has been suggested that the fossil genera Belemnozhiphius and Prorozhiphius are related to the extant genera Mesoplodon and Hyperoodon (Mead, 1975). Currently, Mesoplodon and Hyperoodon are grouped together and are believed to have derived from the same group as Tasmacetus (Moore, 1968); however, this arrangement is liable to change with investigations of the fossil remains (Mead, 1989). Numerous fossil fragments of Mesoplodon-like animals exist from England's Red Crag and Suffolk Crag (Upper Miocene) and from the phosphate beds of North and South Carolina. These fragments are not of sufficient quality and are too poorly understood for any reliable phyletic conclusions (Forbes, 1893; Mead, 1989). The pelagic habits of ziphiids may have resulted in the lack of preserved fossils.

### **Form and Function:**

#### **Vertebral numbers**

Osteological features typical of the genus Mesoplodon include a vertebral count of C7, T9-11, L8-11, Ca17-21, and 8 - 10 chevron bones associated with the anterior caudal vertebrae (Andrews, 1914; Mead, 1989; Raven, 1942; Ross, 1984). Total vertebral count ranges from 43-48 (Allen, 1906; Mead 1989; Paterson et al., 1993; Raven, 1942; Ross, 1984). Variance in vertebral counts among individuals may be a result of individual variation, as well as possible lost vertebrae occurring during preparation, as often occurs with the terminal caudal.

Physical maturity is determined by the state of fusion of the vertebral epiphyses (Mackintosh and Wheeler, 1929). The first three cervical vertebrae are often found solidly ankylosed; the remaining four often remain unfused to one another. The thoracic and lumbar vertebrae possess a high, thin spinous process and short transverse processes (Andrews, 1914). Raven (1942) reported on an irregular severance of the neural arches of the 5th and 6th cervical vertebrae of three specimens, and suggested this may be typical of this species.

#### **Rib numbers**

Documented rib counts range from 9-11, of which the anterior 5-7 are double-headed; most counts equal 10 pairs. Due to the slenderness of the posterior-most rib, the last pair of ribs is often not found and may lead to incorrect rib counts. The first seven pairs of ribs often articulate by means of a neck and a head, with the remaining posterior 3 pairs articulated at the tubercles. Andrews (1914) reported on a specimen with four unfused sternal segments. Fusion of sternal fusion appears to vary with age.

#### **Manus**

The manus consists of the ulnare (cuneiform), the intermedium (lunar), and the radiale (scaphoid) in the proximal row of carpals; the first carpal (trapezium), the fused second and third carpals, and the fused fourth and fifth carpals comprise the distal row (Mead, 1989). Reported phalangeal formulas often differ among specimens due to the incorporation of metacarpals in the count by some observers. Paterson et al. (1993) reported on two specimens that had a phalangeal formula of I:1; II:4; III:4; IV:3; V:2 derived from radiographs.

#### **Stomach**

Beaked whale stomachs differ from the typical cetacean stomach in their lack of a forestomach and the presence of more than two pyloric stomach compartments (Mead, 1993). The functional significance of this structural difference is unknown. The most highly derived stomachs of the beaked whales are found in Mesoplodon. Often the main stomach of Mesoplodon is divided into two compartments, the proximal and distal compartments, connected by several connecting chambers. The number of connecting chambers within the genus varies, with *M. densirostris* ranging in number from 3 to 5; this value is an exception from the typical Mesoplodon range of 7 to 11 connecting chambers (Mead, 1993). Many conflicts exist in the literature due to the lack of standardization in the definitions of the various stomach compartments, as well as differences in values obtained from external versus internal examination of the stomachs.

Much diversity exists in ziphiid stomach anatomy, particularly in the number of connecting chambers between the main and pyloric stomachs (Mead 2007). Ziphiid stomachs can be separated into at least three principal groups: generalized ziphiid stomach (one main stomach, one pyloric stomach), derived stomach type I (two main stomachs, one pyloric stomach), and derived stomach type II (two main stomachs, two pyloric stomachs). *M. densirostris* possess a generalized stomach morphology, lacking a forestomach, and possessing a simple mainstomach which forms a distal mainstomach compartment; leading off the mainstomach are a series of connecting chambers followed by the pyloric stomach compartments. The number of connecting chambers ranged from three to five in a sample of five *M. densirostris* specimens examined (Mead 2007). *M. densirostris* and *M. stejnegeri* differ from the generalized ziphiid stomach in having the development of a secondary pyloric stomach compartment in series with the original.

#### Feeding

Heyning and Mead (1996) suggest that beaked whales exhibit suction feeding. Such a suggestion is supported by the lack of teeth marks on squid found in the stomachs of the whales, the improbability of the use of the teeth for prey procurement and processing, and the presence of oral structures suitable for suction. The throat grooves allow ventral distention of the oral cavity floor, increasing the intraoral volume (Heyning and Mead, 1996). This increase in volume would allow suction feeding to occur by decreasing the intraoral pressure relative to the surrounding water, creating a suction adequate for prey acquisition. The existence of such a feeding mechanism is further supported by the limited extent to which ziphiids can open their mouths, a restricted aperture of the mouth effective for suctioning water in through a limited orifice, and the piston-like retraction capability of beaked whale tongues (Heyning and Mead, 1996). The palates of the whales contain small cornified papillae, and may replace the function of the teeth in other odontocetes in holding onto prey, particularly slippery squid (Heyning and Mead, 1996). The single pair of teeth found in Mesoplodon densirostris does not appear to be functional for prey acquisition, and the reduced tooth count could be considered an evolutionary selective advantage in the suction feeding mechanism.

#### Nasal diverticulae

Ziphiids in general possess a complex series of nasal sacs distal to the bony nares. They lack the vestibular sac that is present in delphinids and iniids. The diverticula arising from the nasal passage include the premaxillary and posterior nasal sacs. Internal investigations of Mesoplodon densirostris have revealed the absence or, in the case of one adult male specimen, significant reduction of the nasofrontal sacs found in all other species of Mesoplodon (Heyning, 1989). Due to the lack of a vestibular sac in ziphiids, it has been suggested that the posterior nasal sacs may serve as a mechanism of sound production (Heyning, 1989). Air filling the posterior nasal sac may be forcefully expelled when the antero-intenus muscles contract. This action would result in the vibration of the blowhole ligament, which could be transmitted to the adjacent right nasal plug (Heyning, 1989).

#### Nasal diverticulae and melon

The nasal plugs and associated vertex are relatively small compared with other mesoplodonts. The premaxillary sacs differ from those of other Mesoplodon in that the apertures to the nasal passages occur only along the lateral portion of the bony nares (Heyning, 1989). *M. densirostris* also appears to have more developed rostral muscles relative to congeners, as seen in the larger lateral rostral muscles inserted near the angle of the mouth (Heyning, 1989). The rostrum differs from that of other species in that it contains more dense connective tissue and less fat anteriorly, with the fat of the melon becoming distinguishable approximately 15 - 20 cm posterior to the tip of the rostrum (Heyning, 1989). In adult males, a dorsomedial cleft of dense connective tissue partially divides the

anterior melon (Heyning 1989). The blubber layer in this region contains significantly more connective tissue in adult males than in adult females, which may provide protection during intraspecific combat.

### **Ontogeny and Reproduction:**

#### **Age**

The relative age of an individual specimen can be approximated from the state of mesorostral ossification (Forbes, 1893; Moore, 1963; Heyning, 1984). Moore (1958) described a stranded specimen that he identified as being an adult male based on the size of its teeth in combination with the vomer filling, and rising above, the mesorostral groove. Perrin and Myrsk (1980) determined that absolute age estimation is most reliable by reading the growth layer groups (GLGs) in the cement; dentine deposition ceases or becomes irregular at a relatively early age, making an absolute age estimate using the dentine GLGs less accurate. It is assumed that GLG deposition occurs at the rate of one per year; however, there are presently no data to confirm this assumption in this species. The accelerated development and eruption of the teeth of adult males occurring near the onset of sexual maturity will need to be considered in the interpretation of GLGs in adult males (Heyning, 1984).

#### **Reproduction**

The maximum reported lengths for males and females are 473 cm and 471 cm, respectively (Mead, 1984). Minimum reported age at sexual maturity is 9 years based on the number of growth layer groups (GLGs) in the teeth (Mead, 1984). These GLGs, which are deposited annually in other odontocete species, were counted in the teeth of a female *M. densirostris* that was determined to have recently become sexually mature as evidenced by the presence of one corpus albicans in the ovaries (Ross, 1984). The testis of an immature male weighed 27 g. Minimum weight of the ovaries at sexual maturity is 12 g; maximum weight of ovaries is 25 g, with a total mean weight of ovaries of 14 g. The longest recorded fetus length was 190 cm, and the length of the shortest known calf was 261 cm. The length of the periods of gestation and lactation have not been determined.

A young female specimen was considered to be pubertal based on the lack of an observed corpus luteum or corpus albicans in the ovaries, and a diameter of about 1 mm was obtained for the largest Graafian follicle (Kasuya & Nishiwaki, 1971). Numerous primordial follicles, a few secondary follicles, occasional cystic atretic follicles and some small hyaline scars (which may represent corpora albicans) were observed in an ovary of a subadult female (Paterson et al., 1993). No corpora lutea were identified in this specimen. The same female was determined to be approaching or at sexual maturity from the presence of secondary follicles, but it was unclear whether ovulation had occurred. Ecchymosis, which may have been associated with calving, was observed around the urogenital opening in a lactating female found stranded in Charlestown, Rhode Island (Nawojchik 1994).

### **Ecology:**

#### **Food habits**

Squid has been described as the primary prey of beaked whales; however, large quantities of other invertebrates and fish may also be consumed (Ross, 1979; Mead, 1989; Heyning and Mead, 1996; MacLeod et al. 2003). Most information about the diet of *M. densirostris* has been obtained from the stomach contents of stranded specimens, to which investigators should apply the usual caveat that stranded animals may not reliably represent the overall population. The stomach of an adult female Blainville's beaked whale that stranded in South Africa contained 21 fish otoliths, identified as coming from *Cepola sp.* (1), *Scopelogadus sp.* (1), and *Lampanyctus sp.* (19) (Ross, 1979). Another *M. densirostris* from South Africa had two squid beaks in its stomach, identified as coming from *Todarodes sagittatus* and *Octopoteuthis sp.* (Ross, 1979; Aguilar et al., 1982). Preliminary analyses of the stomach contents of three *M. densirostris* uncovered no fish remains, and trace quantities of squid beaks (Mead, 1989). Based on the sparse nutritive data available, it appears that the diet of *M. densirostris* may be more extensive than the existing data suggest; however, it appears that mesopelagic squid and fish comprise the bulk of their diet. MacLeod et al. (2003) found the diet of *Mesoplodon* spp. to consist primarily of cephalopods from the families Cranchiidae, Histioteuthidae, and Gonatidae, as well as a large proportion of bottom-dwelling and deep-water fish species, and some crustaceans.

#### Predation

There are no documented observations of predation on M. densirostris. Well-healed tooth scars were described as superficial rake marks on an adult female (USNM 504217) that stranded at Buxton, North Carolina (Mead, 1989). These scars had a tooth spacing of at least 2 cm and were present on both sides of the ventral surface of the caudal peduncle. Based on the tooth spacing, either Orcinus orca or Pseudorca crassidens are believed to be the source of these marks. There was no evidence of serious injury resulting from infliction, and the scars did not penetrate the blubber.

#### Commensals

Conchoderma auritum is the only documented species of stalked barnacle occurring on the teeth of M. densirostris. Such barnacles attach only to hard surfaces; thus, the protrusive teeth of males are a suitable substrate for this commensal. Pringle (1963) reported on a M. densirostris specimen that washed ashore near Jeffreys Bay along the SE coast of southern Africa. This female [sic] specimen was described as having a mass of seaweed about 6 - 10 inches in length attached to the tip of each tooth. Ross (1984, table 23:216) determined that the sex of this whale was actually male based on the structure of the teeth, and the seaweed may have been a mistaken report of stalked barnacles which look very much like seaweed when they are desiccated (Mead, 1989:417). A photograph of an adult male M. densirostris with clumps, about 10 cm wide, of cf. Conchoderma attached to each tooth can be found in Minasian et al. (1984:116). This photo was taken at sea off Hawaii, and a similar observation was made on a specimen of M. densirostris that stranded on the North Carolina coast (USNM 486173). Pastene et al. (1990) described colonies of Conchoderma auritum that encrusted the teeth of either side of the lower jaw of a M. densirostris that was killed by fishermen of Pargua Bay, Chile. Other reports of barnacles occurring on M. densirostris include a report by G.J.B. Ross of Xenobalanus and an unidentified balanoid barnacle, deeply embedded on the flank of the whale stranded in South Africa.

#### Parasites

Known parasites of M. densirostris include unidentified adult cestodes that infected the proximal intestine of a juvenile male that stranded in New Jersey (Mead 1989:417). Nematodes, Anisakis spp., have been found in the stomachs of M. densirostris from Spain, South Africa, and New Zealand and acanthocephalan (Bolbosoma vasculosum) has been found in the intestines (Iglesias et al. 2008, Mattiucci et al. 2009).

Oval scars, usually 4 - 8cm in diameter, are frequently observed on the body of M. densirostris (Mead 1989:385). These scars are presumed to result from bites made by the small cookie-cutter or cigar shark. Photographs of multiple unsuccessful Isistius bites, resulting in faint crescent marks on a specimen of M. densirostris from California, are presented in Schonewald (1978:28). Paterson et al. (1993:291) also show a photograph of an M. densirostris with recent and well-healed Isistius lesions. The parasitic copepod Penella is often the cause of punctate scars, as seen in M. densirostris and can cause oval scars as well.

#### Pollutant residues

Moderate levels of organochlorine residues have been found in M. densirostris (Taruski et al., 1975; Aguilar et al., 1982). Aguilar et al. (1982) analysed muscle, blubber, and brain tissues from a female that stranded on the Spanish Mediterranean coast and found an abundance of DDT and PCBs in the samples. Similar contaminant load values were also found in two specimens from South Carolina and New Jersey (Taruski et al., 1975). Levels of both DDTs and PCBs appear to be lower in beaked whales than in other cetaceans. Alzieu and Duguay (1979) suggested that a teutophic diet could result in lower pollutant levels; however, findings from stomach content analysis suggest a more extensive diet for beaked whales, concluding that other biological factors may account for a relatively low organocontaminant load.

#### Fishery Interactions

No known fisheries exist that regularly target Mesoplodon. Occasional directed takes of M. densirostris have been recorded, mostly by small-scale harpoon fisheries (e.g. Kasuya and Nishiwaki, 1971). Two records exist of Japanese tuna fleets capturing single specimens of M. densirostris in the Indian Ocean. One of these captures occurred in the vicinity of the Seychelle Islands, the other off the west coast of Australia (McCann, 1963; McCann, 1964); there was

no mention of the method of which these animals were taken. Pastene et al. (1990) report on a male *M. densirostris* caught by fishermen off Pargua Bay, Chile (41° 28' S, 73° 00' W), the first documented occurrence in the eastern South Pacific. After pulling it to shore, the fishermen rendered the whale and obtained seven liters of oil. A report of the capture of a *M. densirostris* from Nova Scotia fishing waters occurred February 4, 1940 at Peggy's Cove, Nova Scotia (McKenzie, 1940). It is likely that this whale that was captured and killed under the wharf of Richard Crooks was ill, as this species had not previously been documented in these waters.

*Mesoplodon* are incidentally taken by fisheries around the world, particularly drift gillnet fisheries and longline fisheries (Forney 2004, Henshaw et al., 1997; Mead, 1989). It is unclear whether these entanglements occur from the whales randomly encountering nets that they did not know were there, or whether these individuals were attracted to the catch that were in the nets. Due to the difficulty of making reliable species identifications in the field, the varying level of taxonomic training of fisheries observers, and the limited knowledge of beaked whale population dynamics, the impact of fishery mortality on specific beaked whale populations has been difficult to assess (Henshaw et al., 1997). Use of acoustic pingers appears to have eliminated the bycatch of beaked whales in a California drift net fishery since their initial use in 1996 (Barlow and Cameron 2003, Carretta et al. 2008); however, occasional serious injuries and mortalities in fisheries still occur and some stranded beaked whales present with signs of potential entanglement (Waring et al. 2009, Carretta et al. 2009).

#### Adverse human interactions

Human activities other than fisheries have had deleterious effects on *Mesoplodon densirostris*. Live mass strandings of beaked whales, including *M. densirostris*, coinciding with nearby military activity noted at sea have occurred in several locations, including Fuerteventura, Canary Islands and Bahamas (e.g., Cox et al. 2006; Fernandez et al. 2004, 2005; Simmonds and Lopez-Jurado, 1991; Tyack et al. 2011; U. S. Department of Commerce and U. S. Navy 2001). These strandings are usually associated with the use of mid-frequency sonars and are atypical, involving multiple animals and often a mixed-species mass stranding. Tyack et al. (2011) found that tagged *M. densirostris* whales stopped echolocating during deep foraging dives, broke from foraging dives with long, slow ascents, and moved away when exposed to both multi-day naval exercises involving tactical mid-frequency sonars as well as playbacks of simulated sonar sounds. Whales returned to the study area 2-3 days after the sonar exercises ended, suggesting these sounds led to disruption of foraging and avoidance behavior. Plastic is occasionally found in the stomach contents of stranded beaked whales, including a Blainville's beaked whale that stranded off Brazil (Secchi and Zarzur 1999).

#### **Behavior:**

An analysis of fine-scale habitat utilization in waters off northern Bahamas found that seabed aspect (northeast), seabed gradient (68 to 296 m/km), and depth (136 to 1,319 meters) were important habitat criteria for determining the presence of *M. densirostris*; these factors are probably driven by the presence of prey species in this area (MacLeod and Zuur 2005). Blainville's beaked whales were found in the shallower (mean depth of 393 m), near-shore waters along the edge of the canyon wall of Great Bahama Canyon (Claridge 2006). Sub-adults were found further offshore and in deeper waters than adults, suggesting a habitat partitioning possibly driven by a dominance hierarchy. Acoustic vocalizations similar to those made by *M. densirostris* were detected at Cross Seamount southwest of Hawaii during April through October, with most detections occurring at night, suggesting that seamounts may be a habitat feature affecting the presence of beaked whales (Johnston et al. 2007).

Diving behavior of four *M. densirostris* whales in Hawaiian waters was studied using suction-cup-attached time-depth recorders (Baird et al. 2006). Mean dive depth was 922 m, with a maximum depth of 1,408 m for durations as long as 48-68 min during routine dives that exceeded 800 m. Although not noticeable difference between ascent and descent rates was detected for short dives, ascent rates for long, deep dives were significantly slower than descent rates (Baird et al. 2006). These whales also spent extended periods of time (approximately 1-2 hr) near the surface (less than 50 m), and had an increase in the number of respirations before and after long dives, presumably in preparation for and to recover from long dives. An adult male *M. densirostris* tagged off the Canary Islands made six foraging dives to maximum depths between 655 and 975 m over a 15.4 hour period, and an adult female made two deep dives to 730 and 815 m in 3 hours (Johnson et al. 2004). Long foraging dives were performed during both the day and night and are separate on average of 1.5 hrs (Aguilar de Soto 2006). All individuals in small groups were found to perform synchronized dives, even in groups containing juveniles (Aguilar de Soto 2006).

Abundance and density estimates of beaked whale species are difficult due to difficulty in identifying species, the affect of sea state on detection rates, and the long duration and depth of dives (Barlow et al. 2006). Beaked whale habitat in the eastern tropical Pacific Ocean may encompass a broader definition that previously proposed, ranging from the continental slope to the abyssal plain and in waters ranging from well-mixed to highly stratified (Ferguson et al. 2006).

*M. densirostris* echolocate for prey during deep foraging dives, including search, approach, and terminal phases (Johnson et al. 2004, 2006, 2007; Madsen et al. 2005). Non-invasive acoustic and orientation tags recorded high-frequency clicks (click duration ca. 250  $\mu$ s) of *M. densirostris* tagged in the waters off the Canary Islands (Johnson et al. 2004). No clicks were recorded until the animals reached 200 m, after which the whales clicked almost continuously at depth; on average, whales started clicked on descent at a depth of 400 m (range of 200-570 m) and stopped clicking on ascent at an average depth of 720 m (range of 500-790 m) (Johnson et al. 2004). Two distinct types of click sounds are produced: search clicks and buzz clicks (Johnson et al. 2006). Echoes from prey items suggest that the source level of *M. densirostris* clicks is in the range of 200-220 dB re 1 $\mu$ Pa at 1 m. The inter-click interval of search clicks ranged between 0.2 and 0.4 s with trains of regular clicks ending in a short burst, rapid increase in click rate, or “buzz”, as much as 250 clicks/ sec (Johnson et al. 2004, 2006, 2007). Buzzes were presumed to signify pursuit of prey since they were associated with a rapid acceleration of the tagged whale and terminated in impact sounds 65% of the time; an average of 23 buzzes was recorded per foraging dive with regular clicking resuming after the end of each buzz (Johnson et al. 2004). Click sounds have been previously reported for *M. densirostris* (Caldwell and Caldwell 1971); however, these recordings were made with a limited bandwidth. In addition to the high-frequency clicks >20 kHz (Johnson et al. 2004), mid-frequency sounds have been recorded in close proximity to a group of *M. densirostris* off the Hawaiian Islands, including one frequency-modulated whistle, and three frequency- and amplitude-modulated pulsed sounds, with energy between 6 and 16 kHz (Rankin and Barlow 2007).

#### Group size

Shallenberger (1981) reported on pods of three to seven *M. densirostris* sighted off Hawaii, one of the earliest reports suggesting that a small group size may be typical. Some information exists on small populations of *M. densirostris* near the Hawaiian, Bahama, and Canary Islands where repeated sightings of individuals and tagging studies have been conducted (Aguilar de Soto 2006, Baird et al. 2009, Claridge 2006). Shallenberger (1981) reported on pods of three to seven *M. densirostris* sighted off Hawaii, one of the earliest reports suggesting that a small group size may be typical. Small groups of Blainville’s beaked whales are typical in the waters near Great Abaco Island in the northern Bahamas, with a mean group size of 4.1 (SD = 1.9) individuals (Claridge 2006). Repeated sightings of individuals were confirmed with photo documentation, with a resight rate of 0.40 for individual whales. Adult females had the highest resight rate, revealing a harem mating system and some social segregation between adults and sub-adults based on analysis of association patterns of known individuals (Claridge 2006). Year-round populations of *M. densirostris* are found near shore off the island of El Hierro in the Canary Islands (Aguilar de Soto 2006).

#### Vocalizations

Airborne vocalizations of a stranded juvenile male *M. densirostris* described as “whistles” and “chirps” were recorded and some were analyzed as pulses (Caldwell and Caldwell, 1971). Acoustic recording tags (DTAGs) attached to *M. densirostris* recorded high frequency clicks during deep dives; tagged whales only clicked at depths below 200m and clicked almost continuously while at depth (Johnson et al. 2004). On decent, tagged whales started clicking at an average depth of 400 m (range 200 - 570 m) and stopped clicking at an average depth of 720 m on ascent (range of 500 – 790 m). *M. densirostris* produces numerous short, directional, ultrasonic clicks (no significant energy below 20 kHz); clicks have a relatively flat acoustic spectrum and a sharp low-frequency cut-off, with 0.2 to 0.4 s intervals between clicks (Johnson et al. 2004). Regular click patterns of tagged whales often terminate with a rapid increase in click rate, up to nearly 250 clicks per second; Johnson et al. (2004) defined this acceleration as a “buzz”. Echoes from the bottom and from prey in the water column were recorded on the tag from clicks produced by the tagged whale, with the prey echoes often detectable immediately prior to buzzes and regular clicking resuming after the end of each buzz. Buzzes are often associated with an increase in acceleration of the tagged whale, and 65% of buzzes ended with impact sounds, suggesting buzzes are closely associated with a sudden movement and attempt to capture prey (Johnson et al. 2004). An average of 23 buzzes was recorded per foraging

dive of tagged whales.

#### **Aggression - Scarring**

Adult male odontocetes commonly exhibit superficial scarring; this is especially true among ziphiids (Heyning, 1984; Evans, 1987; Mead, 1989). Linear scars as long as 2 meters can occur in pairs (both teeth employed) or singly (one tooth). These scars are observed most frequently on the dorsal body of adult males, and often match the tooth pattern of conspecifics, suggesting that these wounds are inflicted during intraspecific combat (Evans, 1987; Mead, 1989).

Only male *M. densirostris* exhibit a single pair of erupted teeth in the lower jaw, leading many to speculate that this feature has evolved through sexual selection. This hypothesis led Heyning (1989) to suggest that the dense structure of the rostrum of adult male *M. carlhubbsi* aids in exerting a considerable amount of force to inflict the deep wounds with the teeth on other males during combat, and that these wounds are inflicted with the mouth closed. This hypothesis can also be applied to similar observations of scars on male *M. densirostris* that match the tooth structure in combination with the significantly denser rostra of males compared with females. Although linear scars may also be inflicted by the teeth of other species of odontocetes, most evidence suggests that the scars are the result of intraspecific conflicts, and there is very little evidence of interspecific aggression (Heyning, 1989). MacLeod (1998) suggested scars caused by intraspecific interactions may serve as an indicator of male “quality” during aggressive interactions.

#### **Genetics:**

There has been little research on the genetics of *M. densirostris*. The species has not been karyotyped; however, two congeners (*M. europaeus* and *M. carlhubbsi*) have been shown to possess  $2n = 42$ , a characteristic that differs from the usual cetacean karyotype of  $2n = 44$  (Arnason et al., 1977). The chromosomes of the two studied mesoplodont species are very similar, and both include a large X chromosome (the largest yet found in any cetacean). The reduction in chromosome number among mesoplodonts appears to be due to a 2-pair fusion in the  $2n = 44$  karyotype. Although the  $2n = 42$  karyotype is also observed in some physeterids (sperm whales), Mesoplodont chromosomes exhibit more similarities with those of other cetaceans (Arnason et al., 1977, 1984).

Mead (1989) noted that nothing of systematic importance has been revealed in biochemical or karyological studies concerning the relationship between ziphiids and other cetaceans, and this contention remains largely valid today. Molecular phylogenetic studies of cetaceans have consistently failed to resolve the relative taxonomic position of ziphiids (Arnason & Gullberg, 1996; Milinkovitch et al., 1994; Rice 1998; Dalebout et al. 1998, 2004). Arnason & Gullberg (1996) conducted a parsimony analysis of cetacean mitochondrial cytochrome *b* sequences and found no support for Moore's (1968) suggestion of a distant position of *M. densirostris* relative to other mesoplodonts. Based on mtDNA analysis (Dalebout et al. 2004) and sequences from seven nuclear introns (Dalebout et al. 2008), *M. densirostris* and *M. stejnegeri* were identified as sister species.

#### **Conservation Status:**

Very little information exists on the status of populations of *M. densirostris*, with the exceptions of Hawaii, Bahamas, and Canary Islands where repeated sightings of individuals and tagging studies have been conducted (Aguilar de Soto 2006, Baird et al. 2009, Claridge 2006). This is due in large part to the pelagic and elusive nature of the species, which has made research exceedingly difficult. *M. densirostris* is not listed as endangered internationally by the Convention on International Trade in Endangered Species (CITES Appendix 2), nor as “threatened” or “endangered” in the U. S. under the Endangered Species Act, and is not considered “depleted” under the U. S. Marine Mammal Protection Act.

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