Functional Morphology of the Sperm Whale (*Physeter macrocephalus*) Tongue, with Reference to Suction Feeding

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Abstract

Gross and microscopic examination of the tongue and hyolingual apparatus of the sperm whale (*Physeter macrocephalus*) revealed numerous distinct differences from those of other toothed whales and dolphins, largely reflecting the tongue's atypical position, relations, and size, and its primary role in suction ingestion, rather than prey prehension or transport, as in many other odontocetes. Unlike other odontocetes, the sperm whale has a short, wide tongue that is uniquely situated at the rear of the open oral cavity. Since the tongue does not extend to the tooth row, which runs along the elongated median mandibular symphysis, it cannot easily reorient grasped prey items, yet it can position them to be swallowed or sucked directly into the oropharyngeal opening. The scarcity of intrinsic lingual musculature (*m. lingualis proprius*), coupled with the relatively large paired extrinsic muscles inserting in the tongue—notably the *m. hyoglossus*, whose profuse fibers comprise much of the tongue root, and the *m. genioglossus*—suggests the tongue mainly undergoes positional, rather than shape, changes as it is retracted by the hyoid to generate negative intraoral pressures to capture and ingest prey items via suction. The tongue possesses numerous longitudinal folds or plicae, but almost no free tip; its slightly convex dorsum bears deep fissures and few sensory receptors in a multilayered and predominantly aglandular horny epithelium.

Key Words: sperm whale, *Physeter macrocephalus*, tongue, hyoid, myology, morphology, suction feeding

Introduction

By far the largest odontocete or toothed whale is the sperm whale (*Physeter macrocephalus*), whose familiar, distinctive profile boasts an enormous barrel-shaped head (up to one-third of the body length) housing the spermaceti organ (Figure 1). The huge head overlies a narrow, rod-shaped, underslung mandible which fits into a palatal recess. The long mandible can reach 5 m, and its two bones are fused along much of their length so that the median mandibular symphysis occupies up to 54% of the length of the mandibular bodies in adults (Rice, 1989; Tomilin, 1967). Nearly all mandibular teeth project from along the symphysis, though a few teeth may erupt caudal to it (Figure 2). Vestigial maxillary teeth erupt very rarely (Berzin, 1972; Boschma, 1938).

The odontocete tongue covers much of the mouth floor, extending rostrally to the mandibular symphysis and, hence, in most odontocete species, to the rostral tip of the tooth rows. Because this symphysis is so long in *Physeter*, however, the sperm whale tongue reaches only the most caudal teeth (Figure 2). Hence, although the sperm whale's tongue is rather large (about one m long in adult males; Tomilin, 1967), relative to the tongues of other odontocetes, it is exceptionally short, wide, and thick (Figure 2).

Despite its great size—or perhaps owing to it—the sperm whale's tongue has never been described in published literature aside from a brief mention by Berzin (1972); his monograph described surface features rather than gross or microscopic structure. The lingual anatomy of another physeterid odontocete, the much smaller pygmy sperm whale (*Kogia breviceps*), was investigated in studies that relied on a fetal specimen (Kernan & Schulte, 1918; Schulte & Smith, 1918). Most studies of odontocete lingual and gular musculature and histology have involved delphinids and river dolphins (Arvy & Pilleri, 1970; Donaldson, 1977; Lawrence & Schevill, 1956, 1965; Li, 1983; Murie, 1873; Ping, 1927; Sokolov & Volkova, 1973; Sonntag, 1922). The present study examined the gross and microscopic anatomy of the sperm whale tongue and hyoid apparatus and explored their function, particularly with regard to their presumed role in prey capture and ingestion.

Materials and Methods

All dissection specimens for this study were obtained from the New England Aquarium
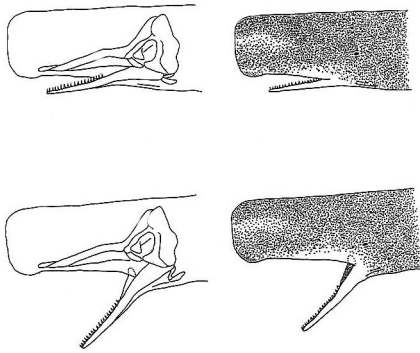
Figure 1. Profiles of *Physeter* showing closed and open oral cavity with normal and wide gape in internal (on left) and external (right) views; note round oropharyngeal opening (dotted line), ventral gular grooves, and hyoid apparatus (flexed and extended), which is ideally situated to retract the tongue and generate suction pressures to suck prey through this orifice.
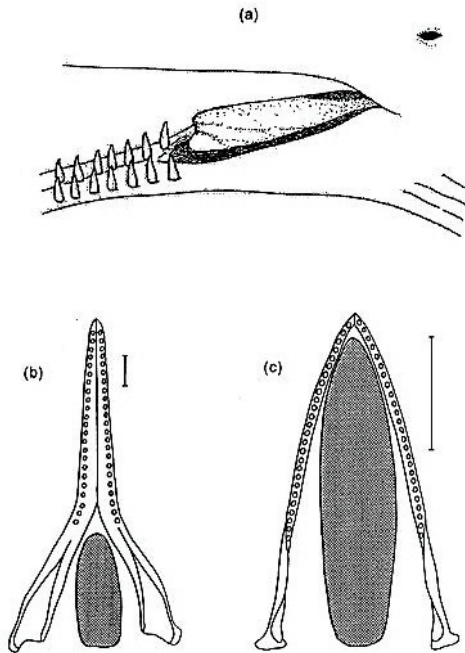
Figure 2. (a) Depiction of the atypical location of the sperm whale tongue behind the tooth rows, with schematic diagrams showing positions of tongue (shaded) and jaws in (b) sperm whale and (c) Atlantic white-sided dolphin (*Lagenorhynchus acutus*) (scale bar = 10 cm)

(NEAq), Boston, Massachusetts, USA, in accordance with statutes governing possession and disposition of marine mammal material. Specimens (Table 1), all obtained from strandings, are listed by NEAq accession catalogue numbers. Dissection relied mainly upon a neonatal female sperm whale (MH.88.522.Pc) retrieved (dead but in fresh condition, with no decomposition) on 12 August 1988 from Plymouth Beach Point, Plymouth, Massachusetts. It was judged a neonate because of the presence of fetal folds, raw umbilicus, and lack of erupted teeth. Two stranded adult males (MH.90.651.Pc, MH.91.673.Pc) were examined postmortem on the beach; tongues were dissected but not removed for further analysis. For myological comparison, the hyolingual apparatus and general oral and gular regions of three pygmy sperm whales (MH.86.202.Kb, MH.89.517.Kb, MH.90.555.Kb), one killer whale (*Orcinus orca*, MH.89.515.Oo), 30 Atlantic white-sided dolphins (*Lagenorhynchus acutus*), and 24 harbor porpoises (*Phocoena phocoena*) were dissected concurrent with standard necropsy procedures, as teeth were removed for age study and tissue samples taken for chemical assay. A few *L. acutus* and *P. phocoena* specimens were dissected in fresh condition at NEAq; all other specimens had been stored in a freezer there at -10° C. During dissection, measurements were taken by tape measure of the tongue and other structures *in situ*. Structures were photographed, videotaped, and sketched with scale bars for later study and measurement. Many muscles were removed for weighing, closer inspection, and microscopic analysis. Specimens of additional odontocete species (five long-finned pilot whales, *Globicephala melas*; three Risso's dolphins, *Grampus griseus*; two bottlenose dolphins, *Tursiops truncatus*; 11 *Delphinus delphis*; one white-beaked dolphin, *Lagenorhynchus albirostris*; and five striped dolphins, *Stenella coeruleoalba*) were consulted for qualitative examination of lingual musculature for comparison with *Physeter*; however, these specimens were not used in the quantitative analysis and are not listed in Table 1.

Tissues were saved for histological study from the juvenile sperm whale and from four Atlantic white-sided dolphins and harbor porpoises each, according to procedures summarized in Simpson & Gardner (1972) and Tarpley (1985). Tissues were fixed in 10% neutral buffered formalin. After a two- to four-week fixation period, multiple tissue blocks were trimmed for light microscopy, placed in labeled stainless steel tissue baskets, and again placed in 10% phosphate buffered formalin for a minimum of 24 h. Tissue samples were then washed in running tap water overnight to remove the fixative and placed in 70% ethanol for 48 h. For dehydration, samples were passed through a graded series of ethanol (95%, 95%, 100%, 100%) for 90 min each and then cleared through two changes of xylene. They were then

Table 1. Specimens used in this study (all used for general dissection and myological study unless otherwise noted); all measurements were taken postmortem.

Accession #	Sex	Mass (kg)	Body length (cm)[1]	Accession #	Sex	Mass (kg)	Body length (cm)[1]
Physeter macrocephalus							
[2, 3, 4]MH.88.522.Pc	F	--	375				
MH.90.651.Pc	M	--	1286				
MH.91.673.Pc	M	--	1432				
Kogia breviceps							
MH.86.202.Kb	F	398	336				
MH.89.517.Kb	M	344	291				
MH.90.555.Kb	M	410	347				
Orcinus orca							
MH.89.515.Oo	M	--	663				
Lagenorhynchus acutus							
MH.87.295.La	M	185	184	[3]MH.88.461.La	M	208	253
MH.87.417.La	M	32	137	[3]MH.88.456.La	M	146	209
MH.87.418.La	M	198	217	[3]MH.88.526.La	F	45	174
MH.87.436.La	F	133	164	[3, 4]MH.89.442.La	M	176	239
MH.87.442.La	M	294	252	[3]MH.89.443.La	F	67	168
MH.87.443.La	M	207	255	[3]MH.89.487.La	F	135	189
MH.87.446.La	F	109	156	[4]MH.90.400.La	M	155	221
MH.87.464.La	M	204	235	[4]MH.90.408.La	F	104	211
MH.87.542.La	F	178	227	[4]MH.90.418.La	M	180	212
MH.87.561.La	M	165	181	[4]MH.90.424.La	F	88	183
[2]MH.88.422.La	F	59	151	[4]MH.90.425.La	M	97	166
[2]MH.88.424.La	F	92	203	[4]MH.90.426.La	M	136	207
[3]MH.88.437.La	M	64	176	[4]MH.90.429.La	M	144	208
[2, 3]MH.88.442.La	F	133	214	[4]MH.90.430.La	F	127	186
[2]MH.88.447.La	M	52	160	[4]MH.90.434.La	M	178	233
Phocoena phocoena							
MH.86.296.Pp	M	52	144	[3]MH.87.566.Pp	F	51	145
MH.87.419.Pp	F	63	157	[2, 3]MH.88.428.Pp	M	59	156
MH.87.421.Pp	F	59	153	[2, 3, 4]MH.88.430.Pp	F	45	151
MH.87.424.Pp	M	38	129	[2, 3, 4]MH.88.450.Pp	F	60	158
MH.87.425.Pp	M	47	145	[3, 4]MH.89.437.Pp	M	38	131
MH.87.432.Pp	M	60	156	[4]MH.89.441.Pp	M	46	145
MH.87.450.Pp	F	47	143	[4]MH.89.446.Pp	M	42	144
MH.87.462.Pp	M	56	150	[4]MH.89.543.Pp	F	53	160
MH.87.468.Pp	M	39	132	[4]MH.90.421.Pp	M	55	159
[2]MH.87.471.Pp	F	71	168	[4]MH.90.428.Pp	F	74	165
[3]MH.87.475.Pp	F	55	157	[4]MH.90.443.Pp	F	63	157
[3]MH.87.477.Pp	M	44	131	[4]MH.90.463.Pp	M	49	145

[1] Measured from tip of rostrum to fluke notch

[2] Used for histological study

[3] Used for comparison of muscle mass

[4] Used for comparison of cross-sectional area

transferred through three paraffin baths in a Freas Model 524 paraffin oven set at 65° C. Specimens remained in the first two baths for approximately one h each; they were left in the third bath overnight. Tissues were then removed from the steel baskets and embedded in paraffin in plastic rings. Tissue thin sections were cut on an American Optical 820 rotary microtome from these blocks at a thickness of approximately 6 μm. Ribbons were placed briefly on a slide warmer, then two

or three sections of each block were affixed onto glass slides. At least 20 slides were prepared from each block. Three slides (1, 7, and 13) were stained with hematoxylin and eosin (H & E) to demonstrate general structure. Three slides (2, 8, and 14) were exposed to Alcian blue/periodic acid Schiff (AB/PAS) to check for the presence of mucopolysaccharides; three (3, 9, and 15) were stained with Verhoeff Van Gieson's stain (VVG) to differentiate collagenous and elastic fibers; three (4, 10, and 16) were stained with Masson's trichrome (MT) to distinguish muscle and collagen. Remaining slides initially were left unstained for special or repeat staining as needed. Some of these slides were later stained with Best's carmine (BC) to test for the presence of glycogen.

Examination of prepared slides relied on a Zeiss Standard Model 14 binocular light microscope equipped with 10x ocular lenses with micrometer and 2.5x planar and 10x, 25x, 40x, and 100x (oil) nonplanar objectives. Histologic arrangements were described and the structural dimensions were recorded. Total mucosal thickness was determined as a range and mean from a minimum of 12 tissue sections, as were the depths of the stratum corneum, stratum spinosum, foveolae, and lamina propria as appropriate. Photographs of selected slides were made using an Ortholux Leitz binocular microscope with planar objectives fitted with an Orthomat 1 camera. Photographic data were recorded on Kodachrome 64 film for preparation of color slides and on Panatomic X film to produce standard 35 mm negatives. Black and white printing was accomplished using a Beseler II enlarger (Model 23C-II) fitted with a 50 mm Nikkor lens. Ilfospeed 3.1M, F3 photographic paper was used for printing. Final magnification of the image was determined from direct measurements made from the photograph of a known scale taken through the same microscope objective and printed at the same enlarger setting.

Following the removal of small histological samples from representative regions of the neonate sperm whale tongue, the entire tongue was excised and returned to the freezer. One week later it was thawed in air and running cold water, then perfused with approximately 3 l of embalming fluid. To keep the specimen moist, it was wrapped in a towel soaked in embalming fluid and glycerine, enclosed in two thick plastic bags, and sealed in a plastic bucket for storage.

As noted, some tissues not set aside for histological study were used for comparative myological analysis. No such samples were fixed or otherwise preserved; all relied on fresh or previously frozen muscle. The masses of different tongue muscles from three odontocete species dissected for this study (Table 1) were compared (*Physeter*: $n = 1$; *L. acutus*: $n = 8$; *P. phocoena*: $n = 7$). In order to determine quantitatively the relative contribution of various lingual muscles (especially extrinsic muscles—those originating outside the tongue), muscles were weighed and standardized as a proportion of total tongue mass. When possible, whole muscle organs were removed in one piece from the tongue. In some cases pieces of a single muscle organ (e.g., the *m. hyoglossus*) were added together for weighing after they were excised from 5 cm thick serial sections that had previously been cut. Care was taken to exclude nonmuscular (i.e., connective tissue) fibers. When possible, origins of such muscles extraneous to the tongue were included for weighing.

The cross-sectional area, a good indicator of muscle strength, was also compared for differing lingual muscles of specimens (*Physeter*: $n = 1$; *L. acutus*: $n = 10$; *P. phocoena*: $n = 10$) at different serial (5 cm) intervals, using photographic projections of transverse tongue sections in which distinct muscle organs and/or fascicles had been delineated with dark thread to make them more visible. Photographs were taken with a Nikon N6000 camera equipped with a Nikkor 35-70 mm f/3.3~f/4.5 zoom lens. Outlines were projected to the same scale, then traced onto paper as well as scanned with a Microtek Model 3700 Scanmaker, then digitized with a CalComp Model 31120A Drawing Slate, attached to a Macintosh Performa 6214 running *Adobe Premiere* v. 4.2, to calculate the percentage of the total tongue body area occupied by a given muscle.

Results

Gross and Microscopic Anatomy

The main dissection specimen was a juvenile female (MH.88.522.Pc) judged neonatal due to the presence of fetal folds, a raw umbilicus, and absence of erupted teeth. Ten small tooth germ bumps (five per side) rose at the caudal-most point of the mandibular symphysis, 1-2 cm apart, each rising 4-7 mm above the gingiva. A thick, cream-colored liquid (200 ml), most likely milk tinged with blood, was removed from the first chamber of the stomach. The animal appeared thin, with a few light scratches and rake marks on both sides of its body. Three lice were found on the body (two in the umbilicus; one under the left flipper). There were no internal parasites. Blubber thickness, excluding epidermis, was measured from three samples taken from the axillary area (axillary girth = 194 cm): (1) dorsal = 5.0 cm, (2) lateral = 5.5 cm, and (3) ventral = 4.0 cm. All measurements that follow refer to this specimen unless stated otherwise.

Externally, the sperm whale tongue is notably short (78 cm in the neonate; 114 and 123 cm in the two adults) and wide (neonate, 33 cm; adults, 38

and 40 cm, respectively). The broad, mostly flat dorsum (slightly convex toward the root; flatter rostrally) has no median sulcus, yet bears numerous deep, convoluted folds or scalloped fissures along its caudal third and root. The small free tip is smooth, with no marginal papillae yet a few marginal folds in juveniles (likely attributable to suckling; Kastelein & Dubbeldam, 1990; Yamasaki et al., 1976), but not in adults. In all ages, the coloration of the tongue (dark pink with isolated patches of pale gray, mainly along the dorsum), and mouth and palate (white) stand in stark contrast to the dark slate gray and black of the body. Two very prominent and large (12 cm long), distensible gular grooves were located externally, ventral to the throat. These were concave (facing away from each other) and 9 cm apart at their closest point medially. The highly arched palate is reminiscent of the walrus (Gordon, 1984; Kastelein & Gerrits, 1990). A small lateral flap on each side of the upper jaw overlaps the mandible by 1-2 cm at the angle of the mouth; these flaps were relatively smaller (2-3 cm) in adult sperm whales.

In terms of microscopic structure, the tongue has a flat, stratified squamous mucosa with a horny, cornified corium that is thick except at the tongue apex. There are few true surface papillae (vallate or other) along the dorsum, although spherical groups of nonkeratinized cells within connective tissue papillae penetrate through the multilayered epithelium, especially along the fissures near the tongue root. These resemble taste buds; Berzin (1972) speculated they are chemosensory in nature. Studies of odontocetes gustatory ability have been limited, but Friedl et al. (1990) demonstrated that the bottlenose dolphin (*Tursiops truncatus*) can detect the four primary tastes. No obvious mechanosensory receptors are located on the tongue. Mucous and serous lingual glands were found but are less widespread than in typical terrestrial mammals, as is typical of cetaceans (Donaldson, 1977; Slijper, 1962; Sokolov & Volkova, 1973). Numerous deep, parallel longitudinal folds or fimbriated plicae, each with much smaller transverse folds, run along the sides of the tongue; these also are covered with a thick epithelium, albeit smoother and less keratinized. There is also a short frenum under the tip, with a large protuberance that represents the genioglossal origin. Caudally, there is no obvious demarcation between the tongue and oropharynx, although, as in *K. breviceps* (Kernan & Schulte, 1918), the abrupt junction of genioglossal fibers with the oropharyngeal connective tissue sheath can be taken as the caudal limit of the tongue.

Myology
The sperm whale tongue is firm and highly muscular (Figure 3), without the large accumulations of adipose and other loose connective tissues that characterize tongues of other "great" [mysticete] whales. There are scattered intrinsic lingual muscle
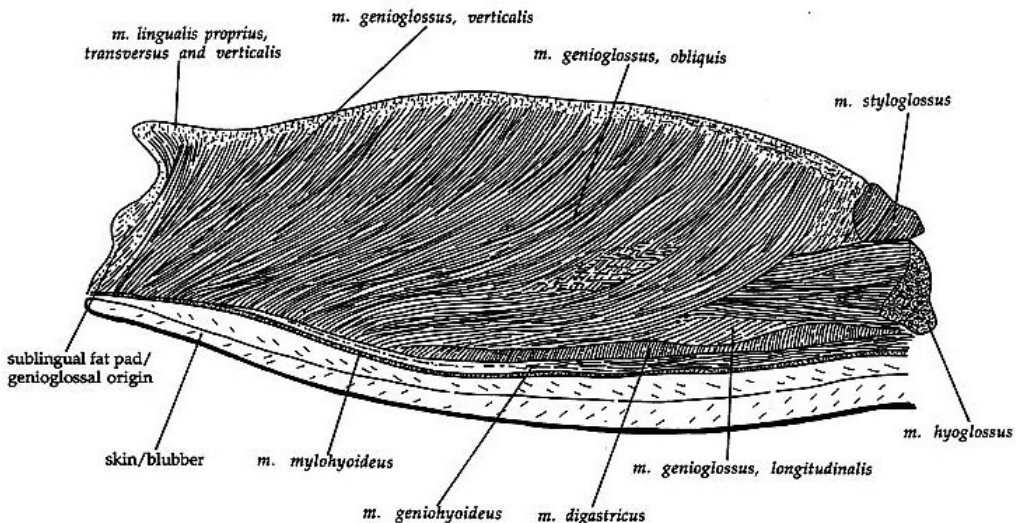
Figure 3. Longitudinal section of a *Physeter* tongue and the floor of the mouth in deep dissection (approximately mid-sagittal, rostral to left), showing all lingual muscles, except the small palatoglossus, whose fibers insert too far laterally to be seen here; note the large contribution of genioglossal fibers, which are divided into three heads that extend to the tongue dorsum and interdigitate with hyoglossal fibers caudally.

fibers (*m. lingualis proprius*), notably some verticalis (*perpendiculares*) and superficial longitudinal fibers, mostly in the rostral half of the tongue. Intrinsic lingual fibers were more visible and prominent in the neonate specimen than in the two adult whales dissected. Paired extrinsic lingual muscles comprise the vast majority of tongue musculature in juvenile and adult sperm whales, however.

Foremost among these is *m. genioglossus*, a large, complex muscle which originates along the medial surface of the mandible just caudal to the elongated symphysis. Its fan-shaped fibers are arranged in three characteristic bundles of vertical, oblique, and longitudinal fibers, although these heads are less distinct than in most mammals (Evans & Christensen, 1979), and even less so than in most odontocetes (Lawrence & Schevill, 1965; Sonntag, 1922). All fibers join medially into a long raphe, which rises vertically and spreads to constitute the bulk of the tongue musculature, especially rostrally, but along the entire tongue length. A few medial genioglossal fibers also continue caudally to mingle with fibers of the *m. palatoglossus* that descend to enter the tongue laterally at its root. The latter muscle, relatively small yet distinct, looks like a pharyngeal constrictor yet its fibers clearly insert in the tongue.

The paired *m. styloglossus* originate on the stylohyal, from which they extend ventrally and rostrally as flat, narrow straps. Schulte & Smith (1918) claimed the styloglossi of *K. breviceps* are "not rudimentary . . . but of good size" (p. 38); they are distinct yet thicker and rounder in *Physeter* than in other odontocetes described (Lawrence & Schevill, 1965; Sonntag, 1922) or dissected for this study. Also notable is that the insertion runs more along the base of the tongue than its sides. The thick, broad *m. hyoglossus* originates on the hyoid skeleton (mainly from the thyrohyal and basihyal elements, but also from the proximal part of the stylohyal) and passes rostrally just dorsal to the styloglossus yet ventral to the palatoglossus before inserting on the ventral portion of the tongue; a small lateral division spreads along the side of the tongue body. The geniohyoid is flat and thin; the digastric, sternohyoid, occipitohyoid, and thyrohyoid are all of relative size and position characteristic of odontocetes (Lawrence & Schevill, 1965; Sonntag, 1922). No inferences were made as to other infrahyoid muscles because these were not present in their entirety in the main dissection specimen. Overall, *Physeter*'s lingual myology appears closest (based on published descriptions and other species dissected for this study) to that of the long-finned pilot whale (*Globicephala melas*) (Murie, 1873) and the beluga (*Delphinapterus leucas*) (Watson & Young, 1880). Aside from the unusually large

genioglossus and hyoglossus, however, the lingual and gular musculature is not atypical for an odontocete (Lawrence & Schevill, 1965; Sonntag, 1922).

Dissection revealed no remarkable amounts or arrangements of connective tissue fibers in the sperm whale tongue; however, a marked concentration of dense fibers (mostly collagenous but some elastic) along the ventral part of the median septum encapsulates a long, firm, rod-like body of adipose cells. This is strikingly reminiscent of the lyssa of the dog tongue, presumed to be a stretch receptor (Chibuzo, 1979). A large sublingual space is evident between the geniohyoid and mylohyoid musculature. Many lingual veins extend close to the lateral surface of the tongue; an extensive network of large lingual veins lies in close proximity to (nearly surrounding) paired lingual arteries. The hypoglossal nerve (XII), which supplies motor innervation to the tongue, is large and readily apparent, as is the mandibular branch of the trigeminal nerve (V), which carries somatic afferent fibers as the lingual nerve (*n. lingualis*). The glossopharyngeal nerve is present yet small. Two other paired cranial nerves (VII and X) innervate the mammalian tongue (Chibuzo, 1979; Williams & Warwick, 1980); these were not found but are presumed present in the sperm whale tongue.

Relative Contributions of Lingual Musculature

The comparison of proportional contributions of extrinsic muscles in *Physeter*, *L. acutus*, and *P. phocoena* by mass (Figure 4) revealed that the genioglossus and hyoglossus muscles were substantially greater relative contributors to the total mass of the tongue in the sperm whale. The genioglossus in particular is much larger in *Physeter*; it is almost twice as massive in the sperm whale as in the harbor porpoise (99% more muscle mass) and more than twice as massive (138%) as in the Atlantic whitesided dolphin. The styloglossus and palatoglossus, in contrast, were relatively smaller contributors to the total tongue mass in the sperm whale (Figure 4), though the overall (absolute) masses of all muscles were much larger in *Physeter*. Ultimately, although this comparison by mass proved useful and conclusive, it was somewhat unsatisfactory, largely because the values used were for total muscle masses—not merely the portions projecting into and inserting in the tongue, which were all that remained in the principal *Physeter* specimen. [Attempts to recalculate using only fibers within the tongue were not satisfactory.] Additionally, tongues of these three species differ in the content and distribution of adipose and other tissue.

Comparison of cross-sectional area was therefore used as well; this proved equally productive. According to this criterion, the genioglossus is
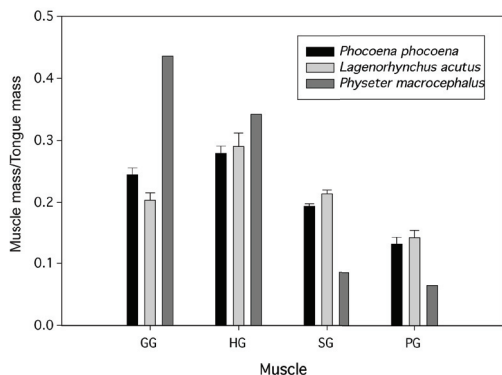
Figure 4. Comparison of extrinsic lingual musculature [gg = genioglossus, hg = hyoglossus, sg = styloglossus, and pg = palatoglossus] by proportional mass in sperm whale (*Physeter*: n = 1) and other odontocete species (Atlantic white-sided dolphin [*Lagenorhynchus acutus*]: n = 8; harbor porpoise [*Phocoena phocoena*]: n = 7), showing that the genioglossus [gg] and hyoglossus [hg] muscles weigh significantly more, as a fraction of the total tongue mass, in *Physeter* than in *L. acutus* or *P. phocoena*, whereas the styloglossus [sg] and palatoglossus [pg] contribute proportionately less in *Physeter*; error bars show standard error. Values for each species do not add up to 100% because the total tongue mass includes other (intrinsic) lingual muscles and nonmuscular (e.g., connective) tissues.
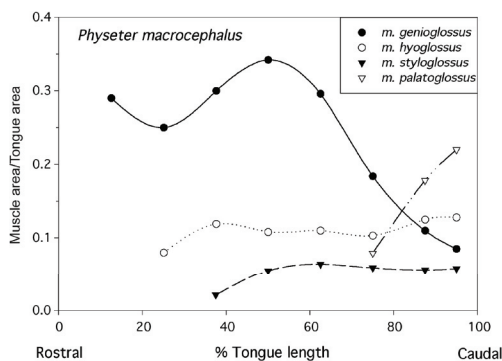
Figure 5. Graph depicting relative cross-sectional area, analyzed from serial (5 cm) transverse tongue sections, demonstrating the substantial contribution of the genioglossus muscle which inserts, via three separate heads, in the sperm whale tongue

the prime contributor to the tongue musculature in *Physeter* (Figure 5), except caudally near the tongue root, where the hyoglossus and palatoglossus predominate. The genioglossus is most extensive at the midpoint of the tongue's length, where fibers of its three heads—verticalis, obliquis, and longitudinalis—are all found, and where together they comprise just over a third of the tongue's total

cross-sectional area (Figure 5). The palatoglossus inserts only into the caudal-most quarter of the tongue and declines precipitously in size as it extends rostrally. Cross-sectional areas of the styloglossus and hyoglossus do not change appreciably throughout the tongue's length. These four extrinsic lingual muscles followed a pattern of insertion similar to that seen in dolphins and porpoises, yet they occupied a significantly greater volume of the sperm whale's tongue, with major implications for its function. Genioglossal insertion in the tongue of *L. acutus* is virtually identical to that of *Physeter*, with the greatest cross-sectional area at the longitudinal midpoint of the tongue (Figure 6). Although this muscle is not the chief extrinsic contributor to the tongue of *L. acutus* (Figure 4), it is still large; however, its area is never greater than 16% of the total tongue area (Figure 6), less than half of the 34% seen in the massive genioglossus of *Physeter*. The hyoglossus is likewise considerably larger in *Physeter* than in *L. acutus* (Figure 7). Though these follow slightly different paths of insertion, in both species, hyoglossal fibers diminish in number as they pass rostrally.
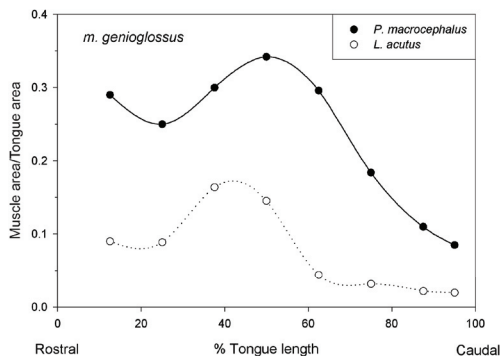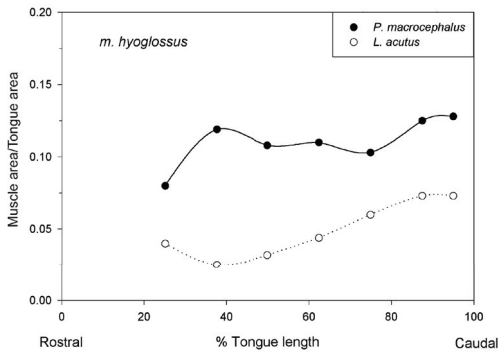

Figure 6. Comparison of the cross-sectional area (relative to the entire tongue area analyzed from serial sections) of the genioglossus muscle in *Physeter* and *L. acutus*, demonstrating the much greater proportion of this muscle, at all tongue locations, in the former species

Discussion

Sperm Whale Hyolingual and Dental Function
The sperm whale's tongue has an anomalous shape and occupies an unusual position relative to that of other odontocetes. Functional analysis of relative masses and cross-sectional areas revealed that extrinsic lingual muscles—those originating outside the tongue, especially the *m. genioglossus* and *m. hyoglossus*—are substantially larger in *Physeter* than in a representative dolphin and porpoise species. Dissection indicated that the sperm whale tongue's innervation is not unlike that of

Figure 7. Comparison of the cross-sectional area (relative to the entire tongue area analyzed from serial sections) of the hyoglossus muscle in *Physeter* and *L. acutus*, demonstrating the much greater proportion of this muscle, at all tongue locations, in the former species

other odontocetes (Behrmann, 1988). Delphinid tongues possess clear gustatory function (Friedl et al., 1990; Suchowskaja, 1972; Yamasaki et al., 1978), and this may be the case in *Physeter* as well. Ping (1927) and Sonntag (1922) speculated that certain lingual papillae might also serve as mechanoreceptors, but no clear mechanoreceptors were found in this study. Sokolov & Volkova (1973) suggested glands of the odontocete tongue may function not in salivation but in extrarenal salt excretion. It is possible that the sperm whale tongue also functions in thermoregulation, by conserving or alternately radiating excess heat. As noted, the sperm whale tongue possesses numerous large surface veins, some of which are situated adjacent to (occasionally surrounding) paired and anastomotic lingual arteries. These could serve as countercurrent periarterial retia. The potential thermoregulatory role of the tongue is notable in light of M. R. Clarke's hypothesis (1970) that the spermaceti organ acts, via temperature changes and conversion of spermaceti oil between solid and liquid phases, as a ballast tank.

Given the absence of direct experimental or observational evidence on sperm whale feeding, speculative inference combining morphological information (e.g., inferred muscle actions) with ecological and behavioral findings is the best alternative. Anatomical evidence from this study suggests the sperm whale tongue functions in prey capture via suction. The tongue also functions in deglutition by forcing prey into the oropharynx while simultaneously or subsequently expelling water.

Ubiquitous illustrations of sperm whales locked in mortal combat with giant architeuthid squids notwithstanding, there are no reliable direct (first person) accounts of sperm whale feeding; however, copious consilient data strongly suggest

Physeter captures and ingests prey via suction as is the case in many odontocete species (Werth, 1992, 2000a, 2000b). The size, type, and condition of sperm whale prey (often whole and undisturbed, lacking bite marks, and occasionally flopping alive in stomachs of commercially caught whales; Berzin, 1972; Caldwell et al., 1966; R. Clarke, 1955; Norris & Møhl, 1983; Okutani & Nemoto, 1964); the frequency of stones and other inorganic debris in sperm whale stomachs (Lambertsen & Kohn, 1987; Nemoto & Nasu, 1963); the frequent presence of barnacles (primarily *Conchoderma* or *Coronula*) or other epizoic organisms that cover and overgrow erupted dentition (R. Clarke, 1966; Kleinenberg et al., 1969; Millais, 1906; Rice, 1989), preventing normal occlusion and, in fact, indicating a total lack of tooth use (Norris & Møhl, 1983); and the ability of whales with broken or congenitally deformed mandibles (Beale, 1839; R. Clarke, 1956; Fischer, 1867; Murie, 1865; Nakamura, 1968; Nasu, 1958; Nishiwaki, 1972; Pouchet & Beauregard, 1889; Slijper, 1962; Spaul, 1964; Thomson, 1867) to feed on the same type and size prey as healthy whales (Bullen, 1902; R. Clarke et al., 1988) all indicate that, as in several odontocetes species, teeth serve as a male secondary sexual feature but are not necessary for feeding (Kato, 1984; Raven, 1942; Werth, 2000a).

Although the standard complement of scars and marks sported by sperm whales (Berzin, 1972; Best, 1979; Kato, 1984; Roe, 1969) commonly are attributed to dramatic battles with giant squid; their parallel patterns often are indicative of teeth marks rather than cephalopod beaks or sucker scrapes. Circular scars could be due to cephalopod suckers, yet the distance between parallel scratch marks matches the spacing of sperm whale teeth and their width and is comparable to the thickness of the crown (Best, 1979; Boschma, 1938; Slijper, 1962). Also, these scars are rarely, if ever, found on female sperm whales (Berzin, 1972; Kato, 1984), which do not fight although their feeding method (judged by diet) is presumed identical to that of males. Berzin (1972) attempted to use differences in scarring to claim that females feed on different prey (smaller, less fierce squid), but his idea is not supported by dietary data (Kawakami, 1980; Tarassevich, 1963) because the food of male and female sperm whales differs only in quantity. Ommanney (1971) reported that scarring in sperm whales varies by region but is very common in solitary bachelor bulls, typically recipients of the most hostility.

Twenty to 25 pairs of prominent, conical lower teeth occur along the mandibular symphysis, though the sperm whale's tiny, vestigial maxillary teeth do not erupt. [Apparently whalers were not alone in

believing sperm whales to have only lower teeth; Boschma (1938) lists 90 papers in which the authors were either unaware of or categorically denied the presence of maxillary teeth in this species.] As in other odontocete species, weaned juvenile sperm whales that have ceased nursing yet feed as adults (based on stomach contents and behavioral observations) often have no erupted teeth (R. Clarke et al., 1988; Ellis, 1985). Sperm whale mandibular teeth do not fully erupt until sexual maturity, when the average body length is 9 m (R. Clarke, 1956). This is further evidence that the battery of teeth possessed by sperm whales is not needed for feeding as is the case in adults of some other odontocete species. Scammon (1874) claimed that "being deprived of the natural means of obtaining food, [old sperm whales with worn teeth] become emaciated and at last expire" (p. 19), but whalers found that this is far from true (R. Clarke et al., 1988). Clarke et al. quantitatively demonstrated that such whales have blubber thicknesses comparable to normal individuals and that the prey of such deformed whales are equal in size to those of whales with normal jaws and dentition. Whether the jaw is twisted or broken, or if for whatever reason an individual has no or few functional teeth, the whale is invariably as healthy and robust as conspecifics with normal, occluding jaws and dentition, implying that these deformed animals feed normally, and thus, that the jaws and dentition are not necessary for feeding.

The sperm whale's tongue and hyoid skeleton lend credence to this claim. The huge hyoid skeleton discloses its role in retracting the short, yet firm, piston-like tongue to generate negative pressures in the "mouth" or throat, as in the walrus (*Odobenus rosmarus*) (Gordon, 1984; Kastelein & Gerrits, 1990; Kastelein et al., 1991, 1994, 1997a). *Physeter*'s greatly enlarged hyoglossus and genioglossus muscles serve to retract and protract the tongue, respectively, and the unusually ventral (rather than lateral) insertions of the styloglossi indicated that instead of directing the tongue to one or the other side, these also depress and retract the tongue, which would aid in suction generation. Results of this study indicate that the mobile tongue undergoes mainly rostrocaudal and dorsoventral positional changes (i.e., translocation) rather than shape transformations. The tongue is likely less important in orienting captured prey in sperm whales than in other odontocetes, due to its relatively short length and the absence along the tooth rows of the long median mandibular symphysis (Berzin, 1972). Thus, aside from its musculature, the tongue's position also would seem to preclude much of a role in prey prehension, positioning, or processing.

The sperm whale's prominent gular grooves, sublingual space, and longitudinal plicae clearly aid in lingual depression and the subsequent expansion of the oropharynx for suction ingestion, however (R. Clarke et al., 1968; Werth, 2000a). *Physeter* possesses two large and many smaller external throat grooves (total averaging 7 in females and 11 in males; R. Clarke et al., 1968), which are present as parallel or wishbone-shaped creases, as in some other large odontocetes, notably beaked whales (Ziphiidae). The male-female disparity in number of these folds is not indicative of differences in prey size or foraging method, but simply of body size (R. Clarke et al., 1968). Boschma (1938) and R. Clarke (1956) considered the function, if any, of sperm whale grooves; both suggested they allow for gular expansion with the engulfment of large quantities of water. Berzin (1972) doubted their role in throat distention based on their "great" variation and appearance *in utero*. Kükenthal (1914), however, did not find throat creases in his developmental studies, although they are found without exception in adults, and were plainly evident in the neonatal dissection specimen. Ross (1987) proposed that gular grooves are present in large suction feeders where such expansion would otherwise be prohibited by the thickness and rigidity of the overlying blubber, and that since smaller odontocetes have thinner blubber, they have no need for such substantial folds. [The presence of a sublingual space in adolescent balaenids (Werth 2000a, 2001), the only mysticete family lacking external throat grooves, could provide room for tongue depression and oral cavity enlargement in suckling juvenile right and bowhead whales.] Dissection confirmed that these grooves are extremely distensible and suggested they are not passive but perhaps are controlled by contraction of superficial ventral musculature (Heyning & Mead, 1991), likely the *m. sphincter colli* (= *m. panniculus carnosus*) profundus or primitivus or a novel offshoot of these muscles.

Dissection confirmed that the sperm whale hyoid apparatus is remarkably large in both juveniles and adults, possessing greatly flattened, rounded thyrohyal elements and robust stylohyals. The massive hyoid is particularly impressive in adults when compared to mysticetes of similar body size, or when compared in young sperm whales to similarly sized odontocetes such as *Orcinus*. Ossification centers of the odontocete hyoid body, unlike those of other cetacean bones, are notable for their fusion at an early (yet unspecified) age (Lawrence & Schevill, 1965), although this is less definite in physeterids, in which the robust hyoid elements typically remain distinct and unfused for an extended period (Flower, 1869, 1885). Flower (1885) noted that the hyoid of *Physeter* and *Kogia* is remarkable not only for its great mass and breadth, but also because it does "not

usually become ankylosed as in most dolphins" (p. 219). Whether this is due to functional or environmental influence (e.g., from extreme tensile forces generated by large hyolingual muscles that originate or insert there, or relating to high pressures from diving to great depth) or, more likely, simply because hyoid bones, like the remainder of the skeleton, develop more slowly in physeterids (Flower, 1869) is unclear. It is possible that the lack of hyoid element fusion in many adult sperm whales results in an even more flexible hyoid, which could be beneficial for the generation of intraoral suction.

Developmental Changes in Tongue Morphology and Function

Lingual morphogenesis must be addressed given the neonatal condition of the principal dissection specimen plus the obvious transition from juvenile suckling to primarily teuthophagous (squid-eating) adult suction feeding. It is likely, however, that odontocete suction ingestion evolved from initial use of suction for intraoral transport of grasped prey in long-snouted raptorial odontocetes (as suction is similarly used in gars and other long-snouted fishes; Werth, 2000a), with later loss of grasp and transport steps and attendant loss of elongated jaws and elaborate dentition in many taxa, simplifying and expediting the feeding process and freeing teeth for adaptation to social functions (Werth, 1992, 2000a). The evolution of adult suction feeding from neonate suckling is unlikely given the anomalous nature of cetacean lactation, in which contraction of smooth muscles surrounding the mammary glands actively pumps milk into the calf's mouth (Arvy, 1974; Slijper, 1962). Still, muscle actions involved in both suckling and adult suction ingestion are presumed identical.

No age differences were seen in sperm whale lingual musculature, whether in relative size, position, or relations. Hyoid growth is presumed isometric based on a comparison of neonate and adult hyoid elements. The sole noteworthy disparity found in the neonate was the limited lateral folding of the tongue, which is absent in adults. Marginal papillae on dolphin and porpoise tongues have been attributed to suckling (Kastelein & Dubbeldam, 1990; Yamasaki et al., 1976). The small lateral flaps from the upper jaw that overlap the mandible slightly (by approximately 2 cm in all ages) at the angle of the mouth were relatively smaller in adults; these might serve to reduce the mouth opening, perhaps to aid suckling in juveniles. Lingual depression and retraction (generated by the remarkably large genioglossus and hyoglossus muscles and hyoid skeleton) would serve both suckling behavior (Arvy, 1974; Triossi et al., 1998) as well as adult suction feeding; no

developmental changes in morphology would be expected.

Sperm Whales as Aberrant Suction Feeders

Most suction feeding vertebrates are distinguished by their perfectly round, terminally located oral orifices, generally accompanied by a blunt, rounded head with short jaws. This is especially true of one of the best documented marine mammal suction feeders, the walrus (Kastelein et al., 1994, 1997a). Most documented cases of odontocete suction generation involve blunt-headed species: beaked whales (Ziphiidae; Heyning & Mead, 1996), porpoises (Phocoenidae; Kastelein et al., 1997b), pilot whales (*Globicephala* spp.; Werth, 2000b), and the beluga (*Delphinapterus leucas*; Ray, 1966). The sperm whale clearly stands in marked contrast to these species due to its long, narrow jaws and oral opening that is positioned relatively further from the tip of the rostrum.

The oral cavity proper (*cavum oris proprium*) is defined in humans as the space bounded laterally and rostrally by the alveolar arches, teeth, and gums (Williams & Warwick, 1980). The palate forms the roof of this cavity and the tongue part of the floor. The vestibule of the mouth, outside the oral cavity, is limited to the narrow space between the dentition and lips and cheeks. This definition applies to other mammals (Evans & Christensen, 1979) and, in fact, to most vertebrates. According to this definition, sperm whales have no oral cavity. The corresponding space in *Physeter* is completely open to the environment (Figure 1). Sperm whales have no true lips or cheek. The teeth are not situated in a closed cavity; instead, they are fully exposed. The short, wide tongue lies entirely caudal to the dentition (Figure 2). When adducted, the lower jaw fits into a small, shallow depression in the roof of the mouth, whose edges partially surround the dentition. Large, deep sockets in the palate neatly accommodate the lower teeth, effectively and completely closing what little space could be properly referred to as an oral cavity.

How can this atypical anatomy be reconciled with abundant evidence of suction feeding? How could the sperm whale create a round mouth opening when it does not possess a proper mouth? The answer lies in the structure taken as the caudal border of the oral cavity, the oropharyngeal isthmus, which serves as the entrance to the pharynx. This isthmus, between the palatoglossal folds just rostral to the fauces, presents a round opening analogous to a proper oral orifice (Figure 1). This space represents the true opening to, and in a sense the first cavity of, the sperm whale digestive tract.

The phenomenon displayed by sperm whales of extremely wide gape, in which the jaw is lowered

at a nearly right angle to the body, is well-documented. The sperm whale illustrated in Scammon's (1874) classic volume on marine mammals is shown in this pose, and there is a lengthy, detailed description of this striking behavior in *Moby-Dick* (Melville, 1851). The significance of such widely opened, pendulous jaws relates partly to their potential role in fighting among males as well as in stirring up benthic or demersal prey, and, thus, unintentionally, in becoming entangled in deep sea cables (Heezen, 1957). Millais' 1906 description of a sperm whale covered with mud is further evidence of benthic foraging. Such wide gape would also be important for suction feeding, by exposing the circular oropharyngeal opening and forming a round "mouth" (Figure 1). The tongue and hyoid of *Physeter* are situated far enough caudally—and they have, as dissection and comparative muscular analysis revealed, such size and relations—that sufficient suction pressures should be generated to suck prey through this opening.

Analysis of suction feeding in captive long-finned pilot whales (*Globicephala melas*) (Werth, 2000b) indicated that some odontocetes not only use intraorally generated suction for prey capture, ingestion, and transport, but can also use gular (i.e., throat) suction to swallow prey directly into the oropharynx, as is likely for the sperm whale. It is possible that other odontocete species suck prey behind the tooth rows and into the oropharynx. In fact, in several odontocete species (notably ziphiids) that possess erupted dentition, the teeth are situated partially or completely outside the oral cavity and can play no role in seizing or holding prey (Kleinenberg et al., 1969). No other odontocetes display the incredibly wide (near 90°) gape or completely open oral "cavity" seen in *Physeter*, but all possess a round oropharyngeal opening and less than perfectly round mouth openings. [An exception is the beluga, a documented suction feeder (Ray, 1966), whose robust facial muscles, especially the buccinator and orbicularis oris, allow this species to "purse" its lips, closing lateral gape and producing a near-circular mouth (Brodie, 1989).] Ingesting prey directly into the oropharynx rather than into the oral cavity might exempt odontocetes from presenting the type of circular oral orifice seen in suction feeding fishes and salamanders (Lauder, 1985), and this would explain how and why prey of known and presumed suction feeding odontocetes can be captured without bites or tooth marks (as documented by stomach content data; Berzin, 1972; Caldwell et al., 1966; R. Clarke, 1955; Norris & Møhl, 1983; Okutani & Nemoto, 1964). If prey are sucked directly into the oropharynx, it is possible (if unlikely) that water is drawn into, and expelled from, the muscular forestomach (Harrison et al., 1967).

An intriguing hypothesis proposed by Beale (1839) suggested that squid bioluminescence rubs off on the sperm whale's white mouth, which stands in striking contrast to its black body, enabling it to lure prey visually. Instances of glowing sperm whale mouths, with a luminous substance that rubs off the bodies of bioluminescent squid, have been reported (Gaskin, 1967; Madsen & Herman, 1980). Passive luring might help to explain how sperm whales can capture exceedingly elusive squid via suction and swallow them with few or no bite marks. The observation that *Physeter* often dives and surfaces in the same spot (M. R. Clarke, 1979) also sheds doubt on the presumption that sperm whales actively chase prey; however, while Fristrup & Harbison (2002) agreed that vision is probably central to sperm whale foraging, they argued it is more likely that sperm whales locate mesopelagic prey visually by floating or swimming upside down and tracking items silhouetted against lighter colored upper waters. Norris and Møhl (1983) adduced much evidence from odontocete (especially sperm whale) anatomy to support their prey stunning hypothesis. Their findings—reduced dentition, altered head shape—are consistent with the claim of sperm whale suction feeding without the need for reliance on prey stunning, although it is possible that stunning and/or luring may bring squid and other highly evasive prey sufficiently close to be ingested via intraoral suction.

Acknowledgments

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