

Feeding kinematics of *Kogia* and *Tursiops* (Odontoceti: Cetacea): characterization of suction and ram feeding

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Accepted 18 July 2005

Summary

The feeding kinematics of dwarf and pygmy sperm whales (*Kogia sima* and *K. breviceps*) and bottlenose dolphins *Tursiops truncatus* were characterized and compared incorporating the Ram–Suction Index (RSI). Mean RSI data support a suction feeding strategy for *Kogia* (-0.67 ± 0.29 ; mean \pm s.d.) and a ram feeding strategy for *Tursiops* (0.94 ± 0.11 ; mean \pm s.d.). *Tursiops* displayed two ram-based feeding behaviours: open gape approach, where gape was at least 50% of maximum in the first video field, and closed gape approach, where gape increased near food items. Four feeding phases were identified in both odontocetes: preparatory, jaw opening, gular depression and jaw closing. The mean *Kogia* feeding cycle duration (470 ± 139 ms) was significantly shorter ($P < 0.003$) than all *Tursiops* groups (pooled: 863 ± 337 ms; open gape approach: 1211 ± 207 ms; closed gape approach:

662 ± 207 ms). *Kogia* mean maximum gape angle ($39.8 \pm 18.9^\circ$), mean maximum opening and closing gape angle velocities (293 ± 261 deg. s^{-1} and 223 ± 121 deg. s^{-1} , respectively) were significantly greater ($P < 0.005$) than pooled *Tursiops* mean maximum gape angle ($24.8 \pm 6.6^\circ$), mean maximum opening and closing gape angle velocities (84 ± 56 deg. s^{-1} and 120 ± 54 deg. s^{-1} , respectively). Negative *Kogia* RSI values were correlated with increasing maximum gular depression and retraction, wide gape angle, and rapid opening gape angle velocity. Kinematic data support functional hypotheses that odontocetes generate suction by rapid depression of the hyoid and tongue.

Key words: odontocete feeding, kinematics, RSI, suction, ram, *Kogia*, *Tursiops*.

Introduction

Cetaceans have evolved highly derived feeding behaviors relative to terrestrial mammalian taxa. Even among cetaceans, feeding adaptations are diverse and are exemplified in the comparison of the suborders Mysticeti (baleen whales) and Odontoceti (toothed whales). Due to their extreme modifications of the oral apparatus, mysticetes have received more scientific attention regarding their feeding biomechanics than odontocetes, which share more similarities in the structure and function of the oral apparatus with terrestrial mammalian taxa than mysticetes (e.g. Pivorunas, 1977; Lambertsen, 1983; Orton and Brodie, 1987; Lambertsen et al., 1995). The stereotypical image of an odontocete is that of narrow, long-snouted delphinids such as bottlenose dolphins *Tursiops truncatus*, which chase down prey with a clap-trap type of jaw containing numerous homodont teeth (Winge, 1921; Howell, 1930; Slijper, 1962; Norris and Møhl, 1983; Heyning, 1989; Rommel, 1990). Foraging strategies for bottlenose dolphins are known to be diverse and many behavioral strategies have been documented, such as: beaching in pursuit of prey (Hoese, 1971; Rigley, 1983), crater-feeding (Rossbach and Herzing, 1997), cooperatively herding fish (Leatherwood, 1975; Hamilton and Nishimoto, 1977), and interacting with commercial fishery gear (Leatherwood, 1975; Fertl and Leatherwood, 1997).

However, non-delphinids possess a wider morphological diversity than delphinids (Gaskin, 1976). In contrast to the stereotypical odontocete image, many odontocetes possess blunt rostra and reduced dentition (Norris and Møhl, 1983; Heyning and Mead, 1996; Werth, 2000), feed on squid (teuthophagous), and may use suction as their primary mode of prey capture. Examples of such odontocetes include pilot whales (*Globicephala*; Brown, 1962; Werth, 2000), harbor porpoises (*Phocoena phocoena*; Kastelein et al., 1997), beaked whales (Ziphiidae; Heyning and Mead, 1996) and sperm whales (Physeteridae and Kogiidae; Caldwell et al., 1966; Werth, 2005).

The underlying mechanics of odontocete feeding have not been systematically investigated. Although there is a wealth of information on odontocete anatomy, surprisingly there are far fewer behavioral investigations to test functional hypotheses based on anatomical studies alone. The derived oral morphology in some species would appear to physically restrict the feeding mode to obligatory suction feeding. For example, male strap-toothed beaked whales *Mesoplodon layardii* possess a single pair of mandibular teeth that grow over the maxillae and constrain the jaws beyond a minimal gape that would make ram-based prey capture difficult

(Heyning and Mead, 1996). The throat grooves and enlarged hyolingual musculature of ziphiids, physeterids and kogiids are presumably adaptations for increasing oral volume related to suction feeding (Clarke et al., 1968; Reidenberg and Laitman, 1994; Heyning and Mead, 1996; Werth, 2005). Robust hyolingual musculature is also present in the short-finned pilot whale *Globicephala melas* (Werth, 1992; Reidenberg and Laitman, 1994), which is the only odontocete for which a kinematic feeding investigation has validated the use of suction (Werth, 2000). However, direct pressure measurements from captive *P. phocoena* also confirm that this species has the capability to employ suction (Kastelein et al., 1997).

Experimental investigations on the function of odontocete feeding require the cooperation of captive species. However, many species are not widespread in captivity, or do not adapt well to captivity. For example, *Kogia* (pygmy and dwarf sperm whales) have a poor success rate in captivity (Sylvestre, 1983). Yet, kogiids are of particular interest due to their basal phylogenetic position within Odontoceti and relatively distant evolutionary relationship to delphinids (Milinkovich et al., 1994; Berta and Sumich, 1999; Geisler and Sanders, 2003). Their enlarged hyoid apparatus, gular and tongue musculature, throat grooves and circular oral orifice suggest that *Kogia* use suction and that their suction capability could be one of the best developed among odontocetes (Caldwell and Caldwell, 1989; Reidenberg and Laitman, 1994). In addition, kogiids possess those characteristics that are typical of odontocetes that are thought to use suction. The snout is blunt and the mouth is short, with reduced dentition; few, if any, teeth are present in the maxillae. The relatively gracile underslung mandibles contain up to 16 pairs of fang-like teeth (Handley, 1966; Ross, 1978; Caldwell and Caldwell, 1989) that are likely advantageous for retaining squid in the mouth. As in other potential suction feeding odontocetes, kogiids are primarily teuthophagous (Pinedo, 1987; Aguiar Dos Santos and Haimovici, 2001; Wang et al., 2002).

Recently, we had the rare opportunity to conduct a detailed kinematic investigation of *Kogia* feeding behavior using two species that were kept alive in captivity for more than one year each (Manire et al., 2004). The objective of this study was to characterize the feeding performance and suction capability of *Kogia* sp. For comparison, we also investigated the feeding performance of a presumed ram-based feeder, *T. truncatus*. Ram and suction are two ends of a feeding continuum frequently studied in aquatic vertebrates and have been addressed by numerous investigators (e.g. Lauder, 1985; Aerts, 1990; Norton and Brainerd, 1993; Motta and Wilga, 2001; Wainwright, 2001; Carroll et al., 2004). Anecdotal observations and morphological data suggest that *Kogia* sp. and *T. truncatus* fall on opposite ends of the ram–suction spectrum. However, such indices have not been applied to odontocetes. Their apparently divergent feeding behaviors and distant evolutionary relationship within Odontoceti make *Kogia* sp. and *T. truncatus* interesting candidates for comparative investigations of odontocete feeding performance.

Materials and methods

Subjects

One female *Kogia sima* (Owen) calf ('Simone') and one female *K. breviceps* (Blainville) calf ('Ami') were subjects of behavioral performance investigations at Mote Marine Laboratory (MML; Sarasota, FL, USA). Data were also collected from two adult male *Tursiops truncatus* (Montagu) subjects at SeaWorld of Texas (San Antonio, TX, USA). Both kogiids stranded and were taken to MML for rehabilitation, where they became the only kogiids to survive for more than one year in a captive setting (Manire et al., 2004). At the time of feeding trials, 'Ami' was 10–11 months old, weighed 126.5 kg and was 203 cm in total length. 'Simone' was 10–12 months of age, had a mean mass of 60 kg and was 160 cm in mean total length over the 5 months of study. *Tursiops* subjects included 'Kai,' who was 26 years old, 344 kg and 308 cm in total length, and 'Clicker,' who was over 30 years old, 195 kg and 249 cm in total length at the time of the study. A total of 236 min of footage was collected from *Kogia* feeding trials. A total of 85 min of footage was collected from *Tursiops* feeding trials. All investigations of *Kogia* and *Tursiops* were approved by Texas A&M University Laboratory Animal Care (AUP#2003-72), SeaWorld and MML's Institutional Animal Care and Usage Committee.

Feeding trials

Feeding performance experiments with *Kogia* were performed during two, 2-day sessions at fixed 4 h daytime feeding intervals over 3 months. Trials were conducted in an 8 m wide circular pool maintained at a depth of 1.5 m (Fig. 1A). Subjects were recorded feeding from a lateral perspective using a Sony Handycam Vision DCR-TRV900 or DCR-TRV950 (Shinagawa-Ku, Japan) in an Equinox (Portage, MI, USA) underwater housing. Video footage was recorded at 60 fields s⁻¹ at a shutter speed of 1/500 s. *Kogia sima* subjects were recorded feeding on whole opalescent inshore squid (*Loligo opalescens*) that rested loosely in a trainer's hand, mantle towards subjects, until drawn into the subjects' mouths. To standardize camera-to-subject distance, the feeder and camera were stationed in 1 m quadrants placed 1 m apart. Subjects were offered food until they no longer showed interest. No *K. breviceps* subjects were in captivity during the study period. Footage of *K. breviceps* was provided subsequent to 'Ami's' death and sequences that met the orientation and landmark criteria of clarity were analyzed.

Tursiops truncatus feeding performance trials were conducted during four, 1-day sessions over 5 months. Subjects were held in a 4 m deep pool and their lateral perspective was videotaped through a metal grated door (Fig. 1B). Subjects were fed herring at a fixed location, 1 m from the camera. Herring were held underwater, head towards subjects, by a trainer outside of the pool until subjects approached within 2 m, at which time food was released. Feeding trials occurred between 1000 and 1600 h to minimize variation in light conditions. Natural landmarks such as the center of the eye

were identified and, when possible, high contrast zinc oxide dots were placed on facial and pectoral regions to assist in the identification of homologous landmarks during the digitizing process of data analysis (Fig. 2A,C).

Kinematic variables and analyses

A ram-suction index and 16 kinematic variables were calculated from feeding trial footage. A ram-suction index (RSI) was calculated following the method of Norton and Brainerd (1993):

$$RSI = (D_{\text{predator}} - D_{\text{prey}}) / (D_{\text{predator}} + D_{\text{prey}}),$$

where D_{predator} is the subject's net distance traveled and D_{prey} is the food item's net distance traveled. Kinematics from feeding trials of *Kogia* ($N=16$) and *T. truncatus* ($N=30$) were analyzed using a motion analysis software package (Peak Motus 8.1, Peak Performance Technologies, Denver, CO, USA). Homologous landmarks from each field (Fig. 2) were digitized in each feeding sequence analyzed. Kinematic variables analyzed included: (1) maximum gape, the maximum distance from maxillary tip to mandibular tip; (2) time to maximum gape, the duration from when the jaws began to open until maximum gape; (3) maximum gape

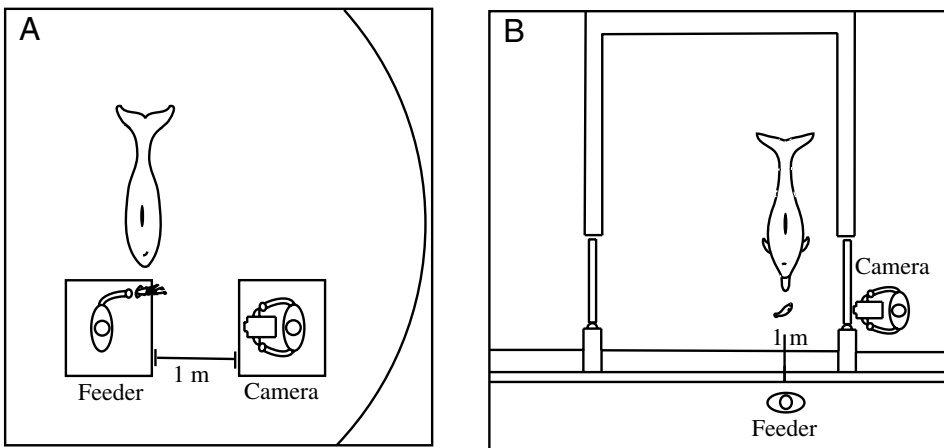


Fig. 1. Experimental setup. (A) *Kogia* at MML and (B) *Tursiops* at SeaWorld of Texas. All videotaping was conducted from the lateral perspective. Note the 1 m squares for *Kogia* videotaping to maintain a relatively constant distance to subject.

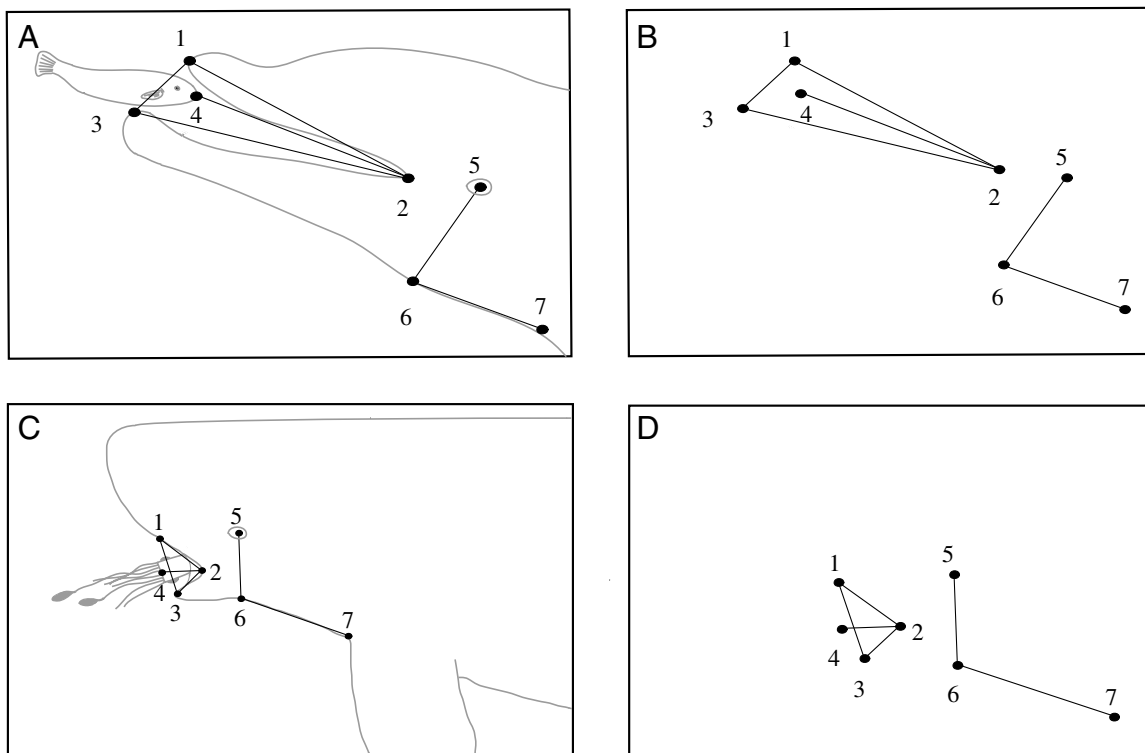


Fig. 2. Kinematic landmarks. (A) *Tursiops* digitized points identified from footage; (B) *Tursiops* spatial model within the motion analysis software; (C) *Kogia* digitized points from video footage and (D) *Kogia* spatial model. Points include (1) maxilla tip, (2) corner of mouth, (3) mandibular tip, (4) food, (5) center of eye, (6) rostral border of externally apparent hyoid and (7) cranial pectoral fin insertion.

angle, the maximum angle from the maxillary tip to mouth vertex or corner of the mouth (COM) to mandibular tip; (4) maximum opening gape angle velocity, the greatest angular rate of jaw opening; (5) maximum closing gape angle velocity, the greatest angular rate of jaw closure; (6) maximum gular depression, the greatest increase in distance from the eye to external rostral border of the hyoid; (7) time to maximum gular depression, the duration from start of gular depression to maximum gular depression; (8) maximum gular retraction, the greatest decrease in distance from the cranial pectoral fin insertion to external rostral border of the hyoid; (9) time to maximum gular retraction, the duration from start of gular retraction to maximum gular retraction; (10) maximum tongue retraction, the greatest decrease in distance from tongue tip to COM; (11) predator–food distance, the horizontal distance from the food item to maxillary tip at the start of the feeding cycle; (12) suction distance, the horizontal distance traveled by the food item during the feeding cycle; (13) ram distance, the horizontal distance traveled by the predator during the feeding cycle; (14) maximum food velocity, the greatest change in distance per time of the food in a feeding event; (15) maximum hydraulic jetting, the greatest distance traveled by food when ejected from the mouth during mouth closure; and (16) maximum hydraulic jetting velocity, the greatest change in distance per time of food while exiting the mouth.

Statistics

Normality was calculated with the Shapiro–Wilk normality test ($Z \geq 0.05$) and variance obtained with Levene's test for equality of variance ($s^2 \leq 0.05$). When both variance and normality requirements were met, analyses of variance (ANOVA) were performed to determine significant differences ($P \leq 0.05$) of kinematic variables between feeding trials. *Post-hoc* analyses utilized Scheffe's test to determine which subjects and subject groups were significantly different. If variance was significant but normality was met, data were analyzed by independent sample *T*-tests ($P \leq 0.05$). Non-parametric data were analyzed using Mann–Whitney *U* tests ($P \leq 0.05$). Correlation analyses assessed the positive or negative relatedness of RSI, timing of feeding events and gape and gular displacements. Pearson's '*r*' correlation test calculated significant correlations in parametric data and Spearman's rho test was implemented for non-parametric data.

Results

Kogia feeding behavior

Subjects either freely swam to food items, or were stationary as food items were placed in front of their mouths (Fig. 3A,B). *Kogia* feeding involved nearly simultaneous jaw opening, gular depression and retraction. Minute fluctuations in gape and gular movement were identified immediately prior to feeding. Observations indicated that food began an initial movement into the oral cavity with gape increase in response to presumed suction forces. However, food velocity did not

increase rapidly until gular depression was observed. Once jaw opening began, it progressed rapidly and extensively, with maximum gape angle frequently in excess of 60°. Suction generation was likely aided by a tissue structure on each side of the mandible that occluded lateral gape and assisted in forming a circular aperture. Jaw closure was slower than opening and involved the gular region's return to its initial position.

Kogia feeding kinematics

Kogia kinematic variables are summarized in Table 1. The *Kogia* feeding cycle (Fig. 4A) consisted of four phases: preparatory, jaw opening, gular depression and jaw closing. Phase I (preparatory) was observed when the maxillary tip, mandibular tip, COM, eye and external rostral border of the hyoid were identified within a single video field, and gape was 25% greater than minimum gape (to eliminate pre-feeding gape fluctuations). Phase II (jaw opening) was initiated when gape began to increase by ≥ 0.2 cm field⁻¹. Phase III (gular depression) began at maximum gape. Gular depression and retraction were not exclusive to the gular depression phase, but also occurred in jaw opening and closing phases. Phase IV (jaw closing) began when gape started to close by ≥ 0.2 cm field⁻¹ and ended when jaw closure decreased to ≤ 0.2 cm field⁻¹. Mean maximum gape angle, mean maximum opening gape angle velocity and mean maximum gape occurred during phase II, while maximum closing gape angle velocity, mean maximum gular depression, mean time to maximum gular depression, mean maximum gular retraction, and mean time to maximum gular retraction generally occurred in phase III.

Kogia correlation analysis showed a more negative RSI with decreased time to maximum gape (Spearman's rho; $P \leq 0.05$) and slower maximum closing gape angle velocity (Spearman's rho; $P \leq 0.05$). RSI values decreased in association with increased time to maximum gular depression (Pearson's '*r*'; $P \leq 0.05$) and increased maximum gular depression (Pearson's '*r*'; $P \leq 0.05$). RSI also decreased with increased time to maximum gular retraction (Pearson's '*r*'; $P \leq 0.01$) and increased maximum gular retraction (Pearson's '*r*'; $P \leq 0.01$). Maximum gular depression increased with maximum gular retraction (Spearman's rho; $P \leq 0.01$). Time to maximum gape increased with larger maximum gape and faster maximum food velocity (Pearson's '*r*'; $P \leq 0.05$).

Tursiops feeding behavior

Tursiops truncatus subjects exhibited feeding behaviors that were distinct from those of *Kogia*. Feeding was more locomotory in nature and subjects approached frozen herring from at least 3–4 m away. Some fluctuations in gape and gular movement were noted immediately prior to feeding. Pectoral fins were frequently flared or rotated outward with the lateral surface of the flipper faced forward (pronation), presumably as an effort to slow forward progress within centimeters of food items. Mandibular depression was slow and gular depression was extensive relative to *Kogia*. Gular depression and retraction were not limited to the gular depression phase and

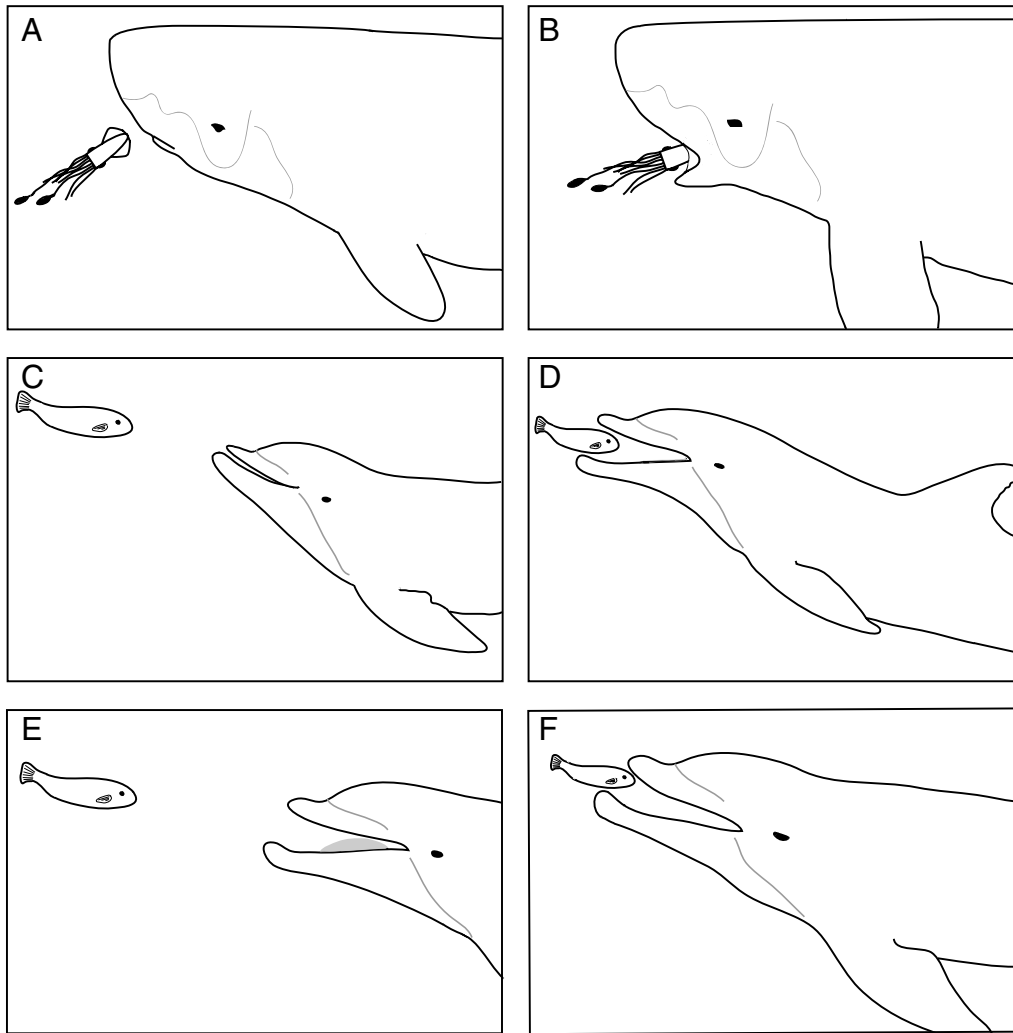


Fig. 3. *Kogia* and *Tursiops* feeding near the beginning of the observed feeding cycle and at maximum gape. (A) *Kogia* preparatory phase with minimal gape; (B) phase II ending with maximum gape. (C) *Tursiops* closed gape approach; feeding begins with slight gape, tucked pectoral fin and forward motion and (D) overtakes prey at maximum gape. (E) *Tursiops* open gape approach enters the frame at or near maximum gape, continues forward motion with open gape and (F) closes jaws as prey is overtaken.

were observed in jaw opening and jaw closing phases (Fig. 4B,C). Two distinct ram-based feeding patterns were identified: *Tursiops* open gape approach and *Tursiops* closed gape approach (Fig. 3C–F). Subjects performing *Tursiops* open gape approach feeding behavior entered the camera's view having 50% of maximum gape or more. Gape increased slowly to maximum while the subject swam to and captured the food item, at which time the jaws closed. *Tursiops* closed gape approach was utilized by both subjects, but *Tursiops* open gape approach was utilized only by 'Clicker.' Subjects performing *Tursiops* closed gape approach feeding behavior entered the first video field at or near closed gape (<3 cm gape); a preparatory phase was observed before the jaws rapidly opened to maximum gape within centimeters of food. Gular depression and retraction and tongue retraction were visible in most sequences.

Tursiops feeding kinematics

Pooled *Tursiops*, open gape approach and closed gape approach feeding variables are summarized in Table 1. Four feeding phases (preparatory, jaw opening, gular depression and jaw closing) were identified (Fig. 4B,C). Phase I began when

maxillary and mandibular tips were identified; gape was 25% greater than minimum gape. The mean maximum gape angle, mean maximum opening gape angle velocity, mean maximum gape and mean time to maximum gape occurred in phase II. Mean maximum closing gape angle velocity occurred in phase IV. *Tursiops* closed gape approach feeding behavior was more representative of the pooled data while *Tursiops* open gape approach feeding behavior was more divergent. Phase I was observed in only one of 11 *Tursiops* open gape approach feeding sequences, and the only trial in which tongue retraction was observed measured 1.31 cm and time to maximum tongue retraction was 300 ms.

Pooled *Tursiops* correlation analysis showed an increased maximum gape angle with both increased maximum opening and closing gape angle velocities (Pearson's 'r'; $P \leq 0.01$). *Tursiops* open gape approach correlations included increased maximum closing gape angle velocity with increased maximum opening gape angle velocities (Spearman's rho; $P \leq 0.05$). Maximum gape angle increased with both maximum opening and closing gape angle velocity (Pearson's 'r'; $P \leq 0.01$). Maximum gular depression increased with increased maximum gular retraction (Spearman's rho; $P \leq 0.01$). Within

Table 1. Summary of feeding mean kinematic variables for *Kogia*, pooled *Tursiops*, *Tursiops* open gape approach and *Tursiops* closed gape approach

Kinematic variable	<i>Kogia</i>	<i>Tursiops</i>		
		Pooled	Open	Closed
RSI	-0.67±0.29	0.94±0.11	0.95±0.08	0.93±0.12
Feeding cycle duration (ms)	470±139	863±337	1211±207	662±207
Phase I duration (ms)	39±65	59±110	20±60	83±125
Phase II duration (ms)	195±115	493±276	756±277	340±115
Phase III duration (ms)	36±75	45±88	77±127	26±51
Phase IV duration (ms)	200±85	266±176	359±248	212±86
Maximum gape angle (°)	40±19	25±6.60	25±7.33	25±6.34
Max. opening gape angle velocity (deg. s ⁻¹)	293±261	84±56	40±18	109±55
Max. gape (cm)	8.54±3.60	12±3.29	11±3.51	12±3.24
Time to max. gape (s)	282±147	564±251	782±253	438±142
Max. closing gape angle velocity (deg. s ⁻¹)	223±121	120±54	108±49	127±57
Max. gular depression (cm)	2.25±1.81	4.75±2.57	4.88±2.32	4.61±2.91
Time to max. gular depression (ms)	283±153	623±208	695±217	552±181
Max. gular retraction (cm)	2.67±2.35	5.57±3.07	1.79±0.11	4.11±3.35
Time to max. gular retraction (ms)	260±69	397±197	261±154	438±196
Max. food velocity (cm s ⁻¹)	41±23	n/a	n/a	n/a
Max. hydraulic jetting distance (cm)	2.59±1.13	n/a	n/a	n/a
Max. hydraulic jetting velocity (cm s ⁻¹)	22±5.90	n/a	n/a	n/a
Max. tongue retraction (cm)	n/a	4.65±3.73	n/a	5.13±3.76
Time to max. tongue retraction (ms)	n/a	167±57	n/a	148±20

RSI, Ram-Suction Index.

Values are means ± s.d.; n/a, not applicable. *N*=16 (*Kogia*), 30 (*Tursiops*).

Tursiops closed gape approach feeding mode, increased RSI correlated with decreased feeding cycle duration (Spearman's rho; $P \leq 0.01$) and decreased time to maximum gular depression (Spearman's rho; $P \leq 0.05$). Maximum closing gape angle velocity increased with maximum opening gape angle velocity (Pearson's 'r'; $P \leq 0.01$). Maximum gape angle increased with both increased maximum opening and increased closing gape angle velocity (Pearson's 'r'; $P \leq 0.01$).

Comparative Odontocete kinematics

Kogia and pooled *Tursiops*

Numerous significant differences were demonstrated between genera. Mean *Kogia* RSI values were significantly less than for any *Tursiops* group (pooled, open gape or closed gape trials; $P < 0.001$). *Kogia* suction distances were greater than for any *Tursiops* group ($P < 0.05$) (Table 2) and *Kogia* ram distances were less than any *Tursiops* group ($P < 0.001$). The mean total feeding cycle and jaw opening durations (phase II) were significantly shorter in *Kogia* than any *Tursiops* group ($P \leq 0.002$). Mean gular depression (phase III) duration was significantly longer in *Kogia* than *Tursiops* open gape approach ($P < 0.01$). Mean maximum gape angle was greater in *Kogia* than any *Tursiops* group ($P \leq 0.005$). Mean maximum opening and closing gape angle velocities were significantly faster in *Kogia* compared to any *Tursiops* group ($P < 0.01$). Mean maximum gape was significantly smaller in *Kogia* than any *Tursiops* group ($P < 0.01$). Mean time to maximum gape was shorter in *Kogia* compared to any *Tursiops* group

($P \leq 0.002$). Mean maximum gular depression was less in *Kogia* compared to pooled *Tursiops* and *Tursiops* open gape approach ($P < 0.05$). Mean time to maximum gular depression was significantly faster in *Kogia* than any *Tursiops* group ($P < 0.05$).

Tursiops open and closed gape approach feeding

Numerous significant differences were also demonstrated between *Tursiops* feeding modes. The mean ram distance of *Tursiops* open gape approach was significantly greater than pooled *Tursiops* and *Tursiops* closed gape approach ($P \leq 0.005$). Mean feeding cycle duration with *Tursiops* open gape approach was longer than the pooled *Tursiops* or *Tursiops* closed gape approach ($P < 0.02$). The mean jaw opening duration was also longer for *Tursiops* open gape approach than for pooled *Tursiops* ($P < 0.02$) and *Tursiops* closed gape approach ($P < 0.001$). The mean gular depression (phase III) duration was significantly longer in *Tursiops* open gape approach than *Tursiops* closed gape approach ($P < 0.01$). Mean maximum opening gape angle velocity was significantly slower in *Tursiops* open gape approach compared to pooled *Tursiops* ($P = 0.012$) and *Tursiops* closed gape approach ($P < 0.001$). Mean time to maximum gape was also significantly longer in *Tursiops* open gape approach than pooled *Tursiops* or *Tursiops* closed gape approach ($P < 0.05$). Mean maximum gular retraction was significantly greater in *Tursiops* open gape approach compared to *Tursiops* closed gape approach ($P < 0.05$).

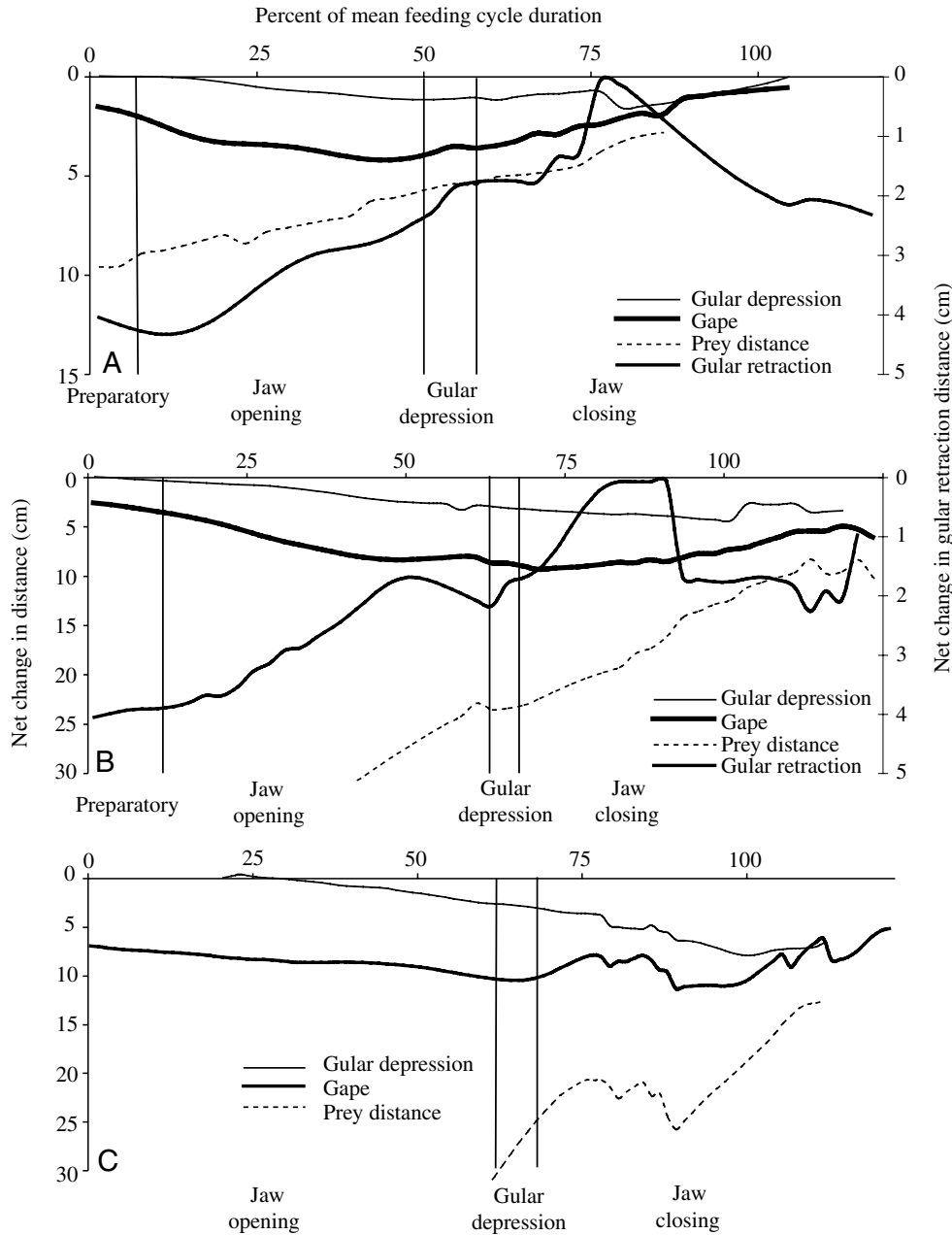


Fig. 4. Profiles of key kinematic variables in *Kogia* and *Tursiops* as a percentage of total feeding cycle duration: gape, gular depression, gular retraction and prey distance. Gular retraction is scaled along the right y-axis and all other variables on the left y-axis. (A) Kinematic profile of *Kogia*. (B) Kinematic profile of *Tursiops* closed gape approach. (C) Kinematic profile of *Tursiops* open gape approach (gular retraction is not depicted). Feeding phases I–IV (preparatory, jaw opening, gular depression and jaw closing) are denoted below each graph. *Kogia* and *Tursiops* closed gape approach display similar patterns in gular depression and retraction, gape and prey distance relative to the onset of each feeding phase; however, *Kogia* kinematics occurred at a much faster rate. *Tursiops* open gape approach included a notably delayed gular depression phase onset as a result of slow gape increase. Note gular return to baseline following completion of the feeding cycle.

Table 2. Capture distances and durations from onset of feeding cycle for two *Kogia* species and *Kogia* pooled data, pooled *Tursiops*, and *Tursiops* open gape and closed gape approaches

Predator	t_{capture} (ms)	Distance (cm)			RSI
		Predator–prey	Suction	Ram	
<i>Kogia sima</i>	482±145	8.80±5.24	4.45±3.00	0.54±1.68	-0.71±0.34
<i>Kogia breviceps</i>	447±136	15±6.24	5.93±2.73	1.78±0.55	-0.60±0.17
<i>Kogia</i> (pooled)	470±139	11±5.88	4.89±2.86	0.90±1.52	-0.67±0.29
<i>Tursiops truncatus</i> (pooled)	863±337	42±21	-2.45±6.87	46±21	0.94±0.11
<i>Tursiops truncatus</i> (OGA)	1211±207	66±8.21	-1.81±7.51	71±8.49	0.95±0.08
<i>Tursiops truncatus</i> (CGA)	662±207	29±12	-2.79±6.69	33±10	0.93±0.12

t_{capture} represents feeding cycle duration; RSI, Ram–Suction Index. Values are means ± s.d.; $N=16$ (*Kogia*), 30 (*Tursiops*).

Discussion

Kinematics of suction-based feeding

The current functional hypothesis for the generation of negative intraoral pressure by marine mammals for the purpose of ingesting food is the rapid depression and retraction of the tongue by the hyoid apparatus. Much anatomical data exist that support this hypothesis (e.g. Gordon, 1984; Reidenberg and Laitman, 1994; Heyning and Mead, 1996). However, few cetacean investigations have examined the mechanics of suction production. The major finding of this study is that the kinematic profile of presumed suction feeders, *K. breviceps* and *K. sima*, validates the use of suction by these odontocetes and supports the functional hypothesis that suction is produced by rapid depression and retraction of the tongue and associated gular structures, such as the hyoid apparatus.

The negative RSI values for *Kogia* were likely generated by the simultaneous depression and retraction of the hyoid apparatus, which in turn would have depressed and retracted the tongue. The rapidity of this movement, relative to *Tursiops*, would likely have produced negative intraoral pressures, and analysis of feeding trial footage verifies that suction is produced (food moved into the mouth). In addition, suction production was also likely influenced by the rapid increase in gape and gape angle relative to *Tursiops*. In general, the kinematic profile of *Kogia* resembles that of *Tursiops* closed gape approach (Fig. 4A,B), except for overall shorter durations of events. This rapidity of motion was likely significant in the development of intraoral pressures. The fact that *Kogia* gular depression and retraction were not as extensive as *Tursiops* is likely a scaling factor and not related to the relative magnitude of suction produced. *Kogia* subjects possessed a mandible that was largely recessed within the confines of the head, and only the distal one-third of the mandible was external compared to two-thirds for *Tursiops*. This resulted in a larger gape in *Tursiops* compared to *Kogia*. However, gape angle was greater in *Kogia* vs *Tursiops*, and this wide gape angle is probably one of the greatest of any odontocete, with the possible exception of *Physeter* (Werth, 2005). The short external mandible, in conjunction with the specialized ridges of tissue on the lateral perimeter of the mandible, served to occlude the lateral gape of the jaw and helped produce a tubular mouth opening; a surprising adaptation in an odontocete. Other marine mammals, such as walrus *Odobenus rosmarus* (Kastelein et al., 1991) and belugas *Delphinapterus leucas* (Brodie, 1989), use elaborated orofacial musculature to occlude this region. Several throat grooves present in the gular region of *K. sima* may have assisted in allowing greater depression and retraction of the gular region.

Kogia feeding must allow for the expulsion of water following food capture. *Kogia* subjects generally maintained a partial gape subsequent to phase IV, probably to allow water to exit. When *Kogia* subjects retained food after a feeding event, squid were often held in the mouth by the elongated mandibular teeth with the mouth still partially open. It appeared that only a light pressure was applied to retain food

and it was doubtful that a soft-bodied cephalopod could significantly encumber gape closure. Furthermore, more forceful jaw closure could hinder squid removal from the teeth. The opposite behavior to suction is the forceful jetting of water out of the mouth, or hydraulic jetting. Hydraulic jetting was observed in 25% of *Kogia* feeding trials and could be influential in the capture of benthic prey or in manipulation of prey.

Two major caveats of the *Kogia* data were that subjects were young and that feeding trials ended prematurely due to the death of both subjects. This event was not unexpected since kogiids have a poor success rate in captivity (Sylvestre, 1983). The situation in this study was unique in that these subjects survived for more than one year (Manire et al., 2004). *Kogia* subjects were less than one year old, at least partially dependent upon formula diets and did not swallow food in any recorded session. It is possible that sucking behavior could have been derived from suckling, as in other mammals (Gordon and Herring, 1987; German et al., 1992; Thexton et al., 1998), and is not completely representative of feeding in adult *Kogia*. Without more definitive techniques such as cineradiography and pressure transducer measurements to assess tongue movement and its affect on intraoral pressures (as used by Thexton et al., 2004), the precise mechanism of odontocete suction generation remains unclear. However, the *K. breviceps* subject had consumed whole squid for the last 15 of 21 months of captivity. Food was routinely manipulated and introduced into the mouth by both subjects. Only events that mimicked feeding were analyzed; manipulatory behaviors were eliminated from analyses. Due to their young age and inexperience, feeding behavior by *Kogia* subjects was likely uncoordinated. However, significant suction events were still recorded despite the subjects' inexperience. Further study of older kogiids may show an even stronger suction capability than reported in this study.

The rapid feeding cycle of *Kogia* is consistent with kinematic data from pilot whales *G. melas*. Werth (2000) also found a four-phase feeding cycle in *G. melas* that is unlike the feeding cycle of terrestrial mammals (Hiimae and Crompton, 1985), but likely derived from it. The mean *Kogia* feeding cycle duration was approximately 100 ms shorter than that of *G. melas* and 10–179 ms shorter in all phases except jaw closing (phase IV), where *G. melas* was 120 ms shorter. The more rapid *Kogia* feeding cycle suggests a greater suction capability than *G. melas* and this is supported by hyolingual data for both species (Reidenberg and Laitman, 1994). Once food had entered the oral cavity, greater water expulsion may have slowed *Kogia* jaw closure. A longer *Kogia* jaw closing phase duration than with *G. melas* may also have resulted from an ability of *Kogia* to retain food by their elongated teeth, which would not require the more rapid gape closure seen in *G. melas*.

Kinematics of ram-based feeding

Tursiops RSI values were distinctly ram-based, with little, if any, suction component to feeding. Effective suction occurs

over a limited distance and changes in RSI values result primarily from modulation of ram distance (Wainwright, 2001). The greater ram distances of *Tursiops* relative to *Kogia* are responsible for the greater RSI values of *Tursiops* and support a more locomotory feeding strategy for *Tursiops* in this study. Suction distance means (Table 2) likewise support a lesser degree of suction feeding in *Tursiops*, as food items frequently moved away from subjects, potentially due to bow waves formed at the rostral maxillae and mandibular tips of *Tursiops* subjects. A small *Tursiops* suction component may have been present to help reduce the affect of this positive pressure wave. Although a significant suction feeding component was not observed here, *Tursiops* is known to participate in a variety of feeding modes under different conditions and a significant suction component may be present under different conditions.

Tursiops gape kinematics were distinct from *Kogia*. The relatively slower gape velocities, time to maximum gape and jaw opening (phase II) durations of *Tursiops* likely resulted in more positive RSI values. The observation that maximum closing gape angle velocity was generally faster than maximum opening gape angle velocity in *Tursiops* was likely because of the need to capture food items once within reach and would be expected for a ram-based feeder.

As in *Kogia*, *Tursiops* gular movement occurred over most of the feeding cycle and was not limited to the gular depression phase. Forward motion of *Tursiops* was essential in food capture. In several cases, numerous capelin *Mallotus villosus* were simultaneously offered to *Tursiops* subjects. Gape and gular movements alone were insufficient to draw food items into the mouth and in several trials successful food capture did not involve any gular depression or retraction. This was a key behavioral difference between *Kogia* and *Tursiops*.

The function(s) of pectoral flares is unclear, but may increase the accuracy of capture attempts or reduce bow wave pressure formed on the rostral tip, which could minimize food being pushed away or allow for a suction component in the final moment before capture. In either case, pectoral flares may be an important feeding modulation in free-ranging *Tursiops* attempting to capture elusive prey. In this study, flares appeared to slow forward motion in *Tursiops* subjects when in close proximity to food, from about 50 cm s⁻¹ to near 0 cm s⁻¹. Although observed in most feeding sequences, flares did not always occur and may have been in response to the enclosed environment in which subjects were located. Pectoral pronation was similarly observed in a kinematic analysis of pilot whales (Werth, 2000) to slow forward motion in the final stages of food approach.

Tursiops open and closed gape approaches were different from each other, but were both strongly ram-based. The slowly increasing gape of *Tursiops* open gape approach resulted in all significant differences of gape and feeding duration variables between *Tursiops* open and closed gape approaches. Gular depression and retraction were observed even when a large partial gape was present. A preparatory phase was observed in only one of 11 trials of *Tursiops* open gape approach behavior

and was not included in the kinematic profile of *Tursiops* open gape approach feeding (Fig. 4C). However, it is likely that a preparatory phase was always present in *Tursiops* open gape approach, but occurred before the subject entered the video camera's field of view. Early gape may serve to reduce response time for capture of more elusive prey.

In summary, broad morphological differences between *Kogia* and *Tursiops* are reflected in their different feeding performances. *Kogia* was observed to feed primarily using suction, which likely relied upon rapid gape and gular kinematics to produce negative intraoral pressures and draw food into the mouth. *Tursiops* was primarily ram-based, exhibited slower gape and gular kinematics and always overtook food by locomotion. The *Tursiops* feeding repertoire in this study included two distinct feeding patterns that were dissimilar in the timing of gape increase. Kinematic data support the functional hypothesis that odontocetes can produce suction by the rapid depression and retraction of the hyolingual apparatus, but also demonstrate that rapid jaw opening and wide gape may serve to increase suction capability. Furthermore, these data serve to provide a foundation for future kinematic studies that can place odontocete feeding biomechanics within an evolutionary perspective.

We thank Dr Charles Manire of Mote Marine Laboratory and Dudley Wigdahl of SeaWorld of Texas for permitting access to study subjects. Petra and David Cunningham-Smith and Marcy Artavia provided valuable assistance during filming sessions. Alexander Werth provided valuable input in the development of this manuscript. The manuscript was improved by comments from M. Bloodworth, A. Werth, and two anonymous reviewers. This work was supported by Texas Institute of Oceanography, Department of Marine Biology at Texas A&M University at Galveston, Texas A&M University Regents Fellowship to B.B. and the Erma Lee and Luke Mooney Graduate Travel Grant.

References

- Aerts, P. (1990). Variability of the fast suction feeding process in *Astatotilapia elegans* (Teleostei, Cichlidae) – a hypothesis of peripheral feedback control. *J. Zool.* **220**, 653-678.
- Aguiar Dos Santos, R. and Haimovici, M. (2001). Cephalopods in the diet of marine mammals stranded or incidentally caught along southeastern and southern Brazil (21–34°S). *Fish. Res.* **52**, 99-112.
- Berta, A. and Sumich, J. L. (1999). Cetacean evolution and systematics. In *Marine Mammals: Evolutionary biology* (ed. A. Berta and J. L. Sumich), pp. 49-80. San Diego: Academic Press.
- Brodie, P. F. (1989). The white whale *Delphinapterus leucas* (Pallas, 1776). In *Handbook of Marine Mammals*, Vol. 3. *River Dolphins and the Larger Toothed Whales* (ed. S. H. Ridgeway and R. Harrison), pp. 119-144. London: Academic Press.
- Brown, D. H. (1962). Further observations on the pilot whale in captivity. *Zoologica-New York* **47**, 59-64.
- Caldwell, D. K. and Caldwell, M. C. (1989). Pygmy sperm whale *Kogia breviceps* (de Blainville, 1838): dwarf sperm whale *Kogia simus* Owen, 1866. In *Handbook of Marine Mammals*, Vol. 4 (ed. S. H. Ridgeway and R. Harrison), pp. 235-260. London: Academic Press.
- Caldwell, D. K., Caldwell, M. C. and Rice, D. W. (1966). Behavior of the sperm whale, *Physeter catodon*. In *Whales, Dolphins, and Porpoises* (ed. K. S. Norris), pp. 678-718. Berkeley: University of California Press.

- Carroll, A. M., Wainwright, P. C., Kuskey, S. H., Collar, D. C. and Turingan, R. G. (2004). Morphology predicts suction feeding performance in centrarchid fishes. *J. Exp. Biol.* **207**, 3873-3881.
- Clarke, R., Aguayo, A. L. and Paliza, O. (1968). Sperm whales of the southeast Pacific, I and II: introduction and size range, external characters and teeth. *Hyalradets Skrifter* **51**, 1-80.
- Fertl, D. and Leatherwood, S. (1997). Cetacean interactions with trawls: a preliminary review. *J. Northw. Atl. Fish. Sci.* **22**, 219-248.
- Gaskin, D. E. (1976). The evolution, zoogeography and ecology of Cetacea. *Oceanogr. Mar. Biol. Ann. Rev.* **14**, 247-346.
- Geisler, J. H. and Sanders, A. E. (2003). Morphological evidence for the phylogeny of Cetacea. *J. Mamm. Evol.* **10**, 23-129.
- German, R. Z., Crompton, A. W., Levitch, L. L. and Thexton, A. J. (1992). The mechanism of suckling in two species of infant mammal: miniature pigs and long-tailed macaques. *J. Exp. Zool.* **261**, 322-330.
- Gordon, K. R. (1984). Models of tongue movement in the walrus (*Odobenus rosmarus*). *J. Morphol.* **182**, 179-196.
- Gordon, K. R. and Herring, S. W. (1987). Activity patterns within the genioglossus during suckling in domestic dogs and pigs: interspecific and intraspecific plasticity. *Brain Behav. Evol.* **30**, 249-262.
- Hamilton, P. V. and Nishimoto, R. T. (1977). Dolphin predation on mullet. *Fla. Sci.* **40**, 251-252.
- Handley, C. O. (1966). A synopsis of the genus *Kogia* (pygmy sperm whales). In *Whales, Dolphins and Porpoises* (ed. K. S. Norris), pp. 62-69. Berkeley: University of California Press.
- Heyning, J. E. (1989). Comparative facial anatomy of beaked whales (Ziphiidae) and systematic revision of families of extant Odontoceti. *Contrib. Sci.* **406**, 1-65.
- Heyning, J. E. and Mead, J. G. (1996). Suction feeding in beaked whales: morphological and observational evidence. *Contrib. Sci.* **464**, 1-12.
- Hiiemae, K. M. and Crompton, A. W. (1985). Mastication, food transport, and swallowing. In *Functional Vertebrate Morphology* (ed. M. Hildebrand, D. M. Bramble, K. F. Liem and D. B. Wake), pp. 262-290. Cambridge: Harvard University Press.
- Hoese, H. D. (1971). Dolphin feeding out of water in a salt marsh. *J. Mammal.* **52**, 222-223.
- Howell, A. B. (1930). *Aquatic Mammals: Their Adaptations to Life in the Water*. Baltimore: C. C. Thomas.
- Kastelein, R. A., Gerrits, N. and Dubbeldam, J. (1991). The anatomy of the walrus head (*Odobenus rosmarus*). 2. Description of the muscles and of their role in feeding and haul-out behavior. *Aquat. Mammals* **17**, 156-180.
- Kastelein, R. A., Staal, C., Terlouw, A. and Muller, M. (1997). Pressure changes in the mouth of a feeding harbour porpoise (*Phocoena phocoena*). In *The Biology of the Harbour Porpoise* (ed. A. J. Read, P. R. Wiepkema and P. E. Nachtigall), pp. 279-291. Woerden: De Spil Publishers.
- Lambertsen, R. H. (1983). Internal mechanisms of rorqual feeding. *J. Mammal.* **64**, 76-88.
- Lambertsen, R. H., Ulrich, N. and Straley, J. (1995). Frontomandibular stay of Balaenopteridae: a mechanism for momentum recapture during feeding. *J. Mammal.* **76**, 877-899.
- Lauder, G. V. (1985). Aquatic feeding in lower vertebrates. In *Functional Vertebrate Morphology* (ed. M. Hildebrand, D. M. Bramble, K. F. Liem and D. B. Wake), pp. 210-229. Cambridge: Belknap Press of Harvard University Press.
- Leatherwood, S. (1975). Some observations of feeding behavior of bottlenose dolphins (*Tursiops truncatus*) in the northern Gulf of Mexico and (*Tursiops cd T. gilli*) off southern California, Baja California, and Nayarit, Mexico. *Mar. Fish. Res.* **37**, 10-16.
- Manire, C., Rheinhardt, H., Barros, N., Byrd, L. and Cunningham-Smith, P. (2004). An approach to the rehabilitation of *Kogia sp.* *Aquat. Mammals* **30**, 209-219.
- Milinkovich, M. C., Meyer, A. and Powell, J. R. (1994). Phylogeny of all major groups of cetaceans based on DNA sequences from three mitochondrial genes. *Mol. Biol. Evol.* **11**, 936-948.
- Motta, P. J. and Wilga, C. D. (2001). Advances in the study of feeding behaviors, mechanisms, and mechanics of sharks. *Environ. Biol. Fish.* **60**, 131-156.
- Norris, K. S. and Møhl, B. (1983). Can odontocetes debilitate prey with sound? *Am. Nat.* **122**, 85-104.
- Norton, S. and Brainerd, E. (1993). Convergence in the feeding mechanics of ecomorphologically similar species in the Centrarchidae and Cichlidae. *J. Exp. Biol.* **176**, 11-29.
- Orton, L. S. and Brodie, P. F. (1987). Engulfing mechanisms of fin whales. *Can. J. Zool.* **65**, 2898-2907.
- Pinedo, M. C. (1987). First record of a dwarf sperm whale from the southwest Atlantic, with reference to osteology, food habits and reproduction. *Sci. Rep. Whales Res.* **38**, 171-186.
- Pivorunas, A. (1977). The fibrocartilage skeleton and related structures of the ventral pouch of balaenopterid whales. *J. Morphol.* **151**, 299-314.
- Reidenberg, J. and Laitman, J. (1994). Anatomy of the hyoid apparatus in Odontoceti (toothed whales): specializations of their skeleton and musculature compared with those of terrestrial mammals. *Anat. Rec.* **240**, 598-624.
- Rigley, L. (1983). Dolphins feeding in a South Carolina salt marsh. *Whalewatcher* **17**, 3-5.
- Rommel, S. (1990). Osteology of the bottlenose dolphin. In *The Bottlenose Dolphin* (ed. S. Leatherwood and R. R. Reeves), pp. 29-49. San Diego: Academic Press.
- Ross, G. J. B. (1978). Records of pygmy and dwarf sperm whales, genus *Kogia*, from southern Africa, with biological notes and some comparisons. *Ann. Cape Prov. Mus. Nat. Hist.* **11**, 259-327.
- Rosbach, K. A. and Herzing, D. L. (1997). Underwater observations of benthic feeding bottlenose dolphins (*Tursiops truncatus*) near Grand Bahamas Island, Bahamas. *Mar. Mammal Sci.* **11**, 498-503.
- Slijper, E. J. (1962). Feeding. In *Whales* (ed. E. J. Slijper), pp. 253-293. New York: Basic Books.
- Sylvestre, J. (1983). Review of *Kogia* specimens (Physeteridae, Kogiinae) kept alive in captivity. In *Investigations on Cetacea*, Vol. 15 (ed. G. Pilleri), pp. 201-219. Berne: Brain Anatomy Institute.
- Thexton, A. J., Crompton, A. W. and German, R. Z. (1998). Transition from suckling to drinking at weaning: a kinematic and electromyographic study in miniature pigs. *J. Exp. Zool.* **280**, 327-343.
- Thexton, A. J., Crompton, A. W., Owerkowicz, T. and German, R. Z. (2004). Correlation between intraoral pressures and tongue movements in the suckling pig. *Arch. Oral Biol.* **49**, 567-575.
- Wainwright, P. C., Ferry-Graham, L. A., Waltzek, T. B., Carroll, A. M., Husley, C. D. and Grubich, J. R. (2001). Evaluating the use of ram and suction during prey capture by cichlid fishes. *J. Exp. Biol.* **204**, 3039-3051.
- Wang, M. C., Walker, W. A., Shao, K. T. and Chou, L. S. (2002). Comparative analysis of the diets of pygmy sperm whales and dwarf sperm whales in Taiwanese waters. *Acta Zool. Taiwan.* **13**, 53-62.
- Werth, A. J. (1992). Anatomy and Evolution of Odontocete Suction Feeding. PhD thesis, Harvard University, Cambridge, USA.
- Werth, A. J. (2000). A kinematic study of suction feeding and associated behavior in the long-finned pilot whale, *Globicephala melas* (Traill). *Mar. Mammal Sci.* **16**, 299-314.
- Werth, A. J. (2005). Functional morphology of the sperm whale (*Physeter macrocephalus*) tongue, with reference to suction feeding. *Aquat. Mammal.* **30**, 405-418.
- Winge, H. (1921). A review of the interrelationships of cetacea. *Smiths. Misc. Coll.* **72**, 1-97.