BEHAVIORAL PERFORMANCE AND EVOLUTION OF FEEDING MODES IN ODONTOCETES

A Thesis

by

EMILY ALISON KANE

Submitted to the Office of Graduate Studies of
Texas A&M University
in partial fulfillment of the requirements for the degree of

MASTER OF SCIENCE

May 2009

Major Subject: Wildlife and Fisheries Sciences

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Approved by:

Chair of Committee,	Christopher D. Marshall
Committee Members,	Antonietta Quigg Bernd Würsig
Head of Department,	Thomas Lacher

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ABSTRACT

Behavioral Performance and Evolution of Feeding Modes in Odontocetes. (May 2009)
Emily Alison Kane, B. S., Southampton College of Long Island University
Chair of Advisory Committee: Dr. Christopher D. Marshall

Vertebrate evolution has resulted in a diversity of feeding mechanisms. Cetaceans are secondarily derived tetrapods that have returned to a marine habitat. As a result, they display feeding modes that have converged with more basal aquatic vertebrates, but display a diversity of new solutions and adaptations. To begin to explore the diversity of feeding adaptations among odontocetes, kinematics of feeding modes and feeding adaptations for belugas (*Delphinapterus leucas*), Pacific white-sided dolphins (*Lagenorhynchus obliquidens*), and long-finned pilot whales (*Globicephala melas*) were characterized. In addition, direct measurements of intraoral pressure were collected to determine maximum suction performance. Characters from these analyses were combined with data for other odontocetes, and were mapped onto a phylogeny of Odontoceti to begin to explore where changes in feeding modes took place. Feeding modes were diverse in belugas, Pacific white-sided dolphins, and pilot whales and included suction, ram, and a combination of both. In general, four phases were observed: (I) preparatory, (II) jaw opening, (III) gular depression, and (IV) jaw closing. Suction was a large component of the prey capture method in belugas and subambient pressures in excess of 100 kPa were generated. Belugas were also capable of lateral lip gape occlusion and anterior lip pursing to form a small anterior aperture. Pacific white-sided dolphins relied on ram to capture prey. However, some degree of pursing and resultant subambient pressure was observed that was likely used to compensate for high ram speeds or for prey manipulation and transport to the esophagus. Pilot whales were more similar to belugas in kinematics, but maintained high approach velocities and did not generate significant suction pressures; suction and ram were used in combination. Belugas and pilot whales appeared to employ hyolingual depression as a primary suction generation mechanism, whereas Pacific white-sided dolphins relied on fast jaw opening. Ancestral state reconstructions indicated that suction feeding capability evolved independently at least six times within Odontoceti. These results indicate the diversity of feeding behaviors in odontocetes and provide directives for future studies on the diversity of feeding in secondarily aquatic mammals.

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1. INTRODUCTION

1.1 Evolution of odontocete cetaceans

Approximately 550 million years of vertebrate evolution has resulted in one of the most derived clades of vertebrate taxa, namely members of the Order Cetacea. The feeding apparatus of vertebrates has undergone numerous changes throughout a long history of transitions from aquatic, to terrestrial, and back to aquatic environments. Approximately 400 million years ago, tetrapods transitioned to terrestrial environments, and within the last 50 million years, cetaceans have returned to an aquatic environment (Lipps and Mitchell, 1976; Fordyce and Barnes, 1994; Rice, 1998; Thewissen and Williams, 2002). The diversity of the vertebrate feeding apparatus ranges from jawless forms to highly kinetic skulls, specialized hyolingual adaptations for ballistic tongue projection, and jaws designed for mastication. Mammals that have secondarily adapted to the aquatic environment include filter feeding baleen whales (Mysticetes), as well as odontocetes that range in feeding morphology from species with many teeth and long rostra to species with few teeth and blunt rostra. However, these odontocete adaptations for capturing prey in an aquatic environment have largely been unexplored.

The ancestors of cetaceans were Suborder Archaeoceti, which currently exhibit a highly unresolved paraphyletic phylogeny. Archaeocetes were comprised of six families that ranged in morphology from *Pakicetus* with almost no aquatic adaptations to the *Dorudon*, the first oceanic whales (Fordyce and Barnes, 1994; Roe et al., 1998; Thewissen and Williams, 2002); the Dorudontines are thought to have given rise to modern baleen feeding mysticetes, and toothed odontocetes (Uhen, 1998). The divergence of Archaeocete cetaceans from their terrestrial mammalian ancestors may have been facilitated by a specialization of the feeding apparatus to fill available feeding niches (Lipps and Mitchell, 1976; Thewissen, 1998; O'Leary and Uhen, 1999). Despite the considerable morphological variation among archaeocetes, all possessed heterodont teeth with shearing facets that distinguished them from their terrestrial ancestors

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This thesis follows the style of *The Journal of Experimental Biology*.

(O'Leary and Uhen, 1999). Modern cetaceans emerged as recently as 35 million years ago (Fordyce and Barnes, 1994; Rice, 1998) with extensive modifications to the ancestral mammalian body plan (Bryden, 1988). Within the lineage that retained teeth (Odontoceti), the trend was toward long jaws with numerous, homodont teeth (Thewissen and Williams, 2002). This morphology is convergent with long snouted ram feeding aquatic vertebrates such as gars, needlefish, barracuda (Porter and Motta, 2004), and gharials (Thorbjarnarson, 1990). Some odontocete families retained these ancestral feeding traits, while others evolved blunt rostra, reduced dentition and a capability to form a circular oral aperture, traits that are convergent with other suction feeding aquatic vertebrates (Norris and Møhl, 1983; Werth, 2006).

According to the phylogeny presented by Price et al. (2005), there are 67 known cetacean species belonging to suborder Odontoceti (Fig. 1). Although the phylogenetic resolution of river dolphins (Families Platanistidae, Pontoporiidae, Iniidae, and Lipotidae) is poor and described as paraphyletic, river dolphin species typically exhibit the feeding morphology closest to that of ancestral odontocetes: long, slender snapping jaws and numerous homodont teeth (Reeves et al., 2002; Werth, 2006). River dolphins use these long narrow jaws to feed on fish, invertebrates, and turtles (Barros and Clarke, 2002). Superfamily Physeteroidea (sperm whales, pygmy and dwarf sperm whales), and Families Ziphiidae (beaked whales), Monodontidae (belugas and narwhals), and Phocoenidae (porpoises), tend to exhibit divergent feeding morphologies and ecologies from that of the ancestral archaeocetes and basal odontocetes. Physeteroideans and Ziphiids are deep diving species that specialize on squid prey (Clarke, 1996; Barros and Clarke, 2002; Marcoux et al., 2007; Santos et al., 2007). Additionally, Physeteroideans, Ziphiids, Monodontids, and Phocoenids typically have a reduced dentition (Reeves et al., 2002). However, monodontids possess more blunt rostra than that of the Physeteroidea or Ziphiidae (Werth, 2006), consume a variety of prey items that include fish, squid, and benthic invertebrates (Finley and Gibb, 1982; Seaman et al., 1982; Dahl et al., 2000; Barros and Clarke, 2002; Laidre and Heide-Jorgensen, 2005), and have been observed using facial muscles to purse their lips. This behavior is thought to enhance suction

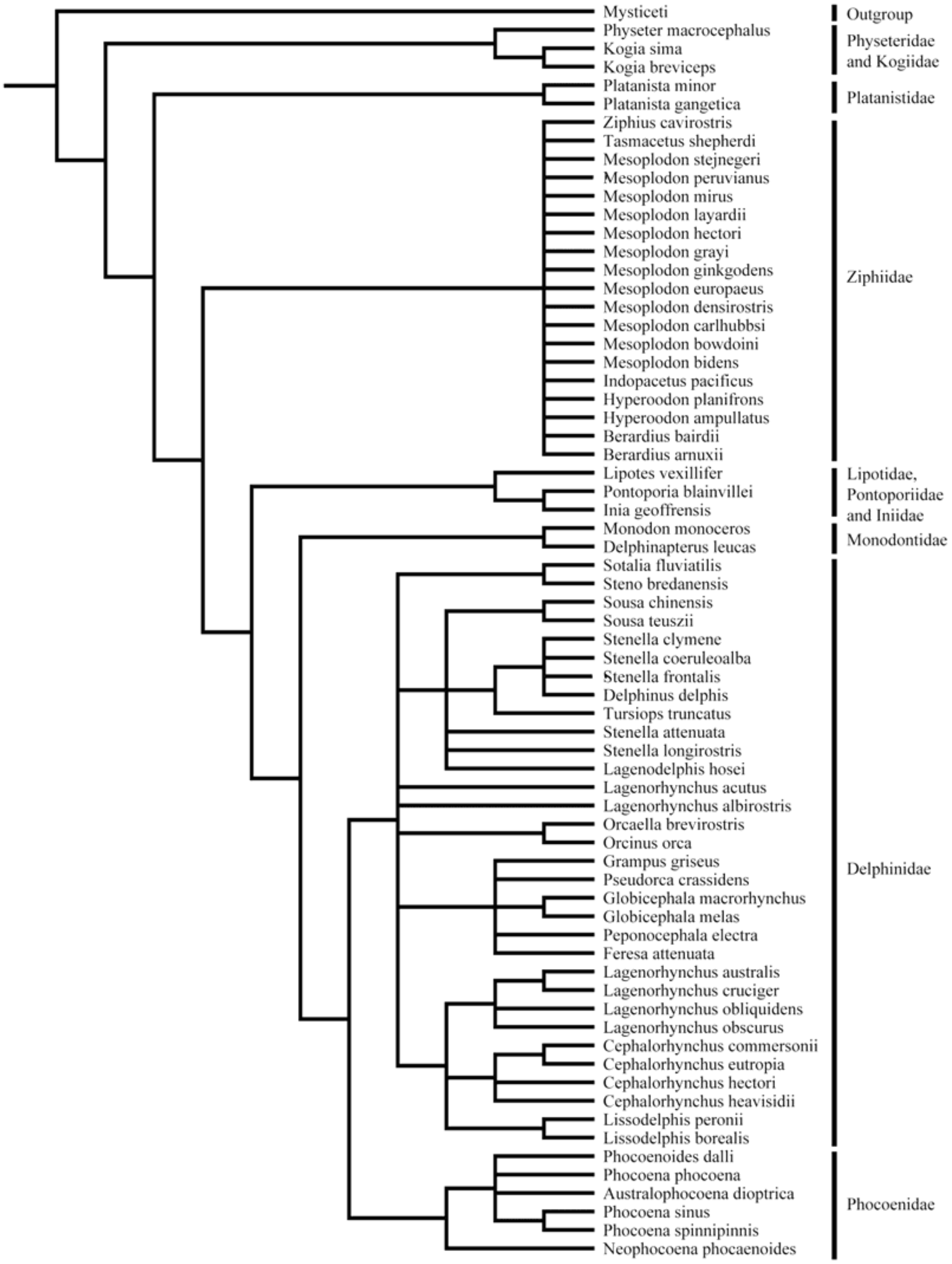

Fig. 1 Widely accepted phylogeny of extant Odontoceti. Adapted from a supertree of mammalian phylogeny constructed by Price et al. (2005). Phylogenies produced by Le Duc et al. (1999) and Rosel et al. (1995) were used to enhance resolution of Delphinidae and Phocoenidae, respectively.

generation (Ray, 1966). The Family Phocoenidae (porpoises) is the sister group to Delphinidae (dolphins), and generally resembles the monodontids in craniodental morphology in that rostra are short and blunt and dentition is reduced in porpoises (Reeves et al., 2002; Werth, 2006). Phocoenids are also similar to monodontids in their generalist diet, which includes a variety of pelagic and benthic fish, squid, and invertebrates (Clarke, 1996; Barros and Clarke, 2002). The most derived group of odontocetes are the Delphinids, which include a diverse array of taxa that range from teuthophagous pilot whales with shorter, more blunt rostra to piscivorous spinner dolphins with long pincher-like jaws and rostra (Barros and Clarke, 2002; Reeves et al., 2002; Werth, 2006). Delphinids represent a continuum of feeding morphologies that should be reflected in feeding strategies and kinematics that range from ram to suction feeding.

1.2 Aquatic feeding modes

Four generalized methods of prey capture are recognized in an aquatic environment: filter feeding, biting, ram feeding, and suction feeding (e.g. Moss, 1972; Lauder, 1985; Liem, 1993; Norton, 1995; Alfaro et al., 2001; Motta and Wilga, 2001; Motta et al., 2002). Filter feeding involves the flow of water over a filtering apparatus that actively or passively traps suspended prey items. North American paddlefish (*Polyodon spathula*) are well known filter feeders (Rosen and Hales, 1981). Within Order Cetacea, Suborder Mysticeti filters small fish and invertebrates from the water with sieve-like baleen plates. Biting involves cessation of forward motion and forceful contact of the prey with the jaws, often removing smaller pieces. This mode of prey capture is exemplified by parrotfish (Scaridae, Bellwood and Choat, 1990) and is evident in cetaceans that remove smaller pieces from large prey items, such as killer whales (*Orcinus orca*) that feed on large marine mammals. However, ram feeding involves rapid acceleration to overtake the prey, engulfing it entirely. This behavior has been documented in hammerhead sharks (*Sphyrna tiburo*, Wilga and Motta, 2000) and some cetaceans such as bottlenose dolphins (*Tursiops truncatus*, Bloodworth and Marshall, 2005). Suction feeding is characterized by buccal expansion that creates subambient intraoral pressure to draw water and prey into the mouth. This mode of feeding is the most widespread among aquatic vertebrates (Lauder, 1985, 1986) and has been documented in several odontocetes (Heyning and Mead, 1996; Kastelein et al., 1997; Werth, 2000a; Bloodworth and Marshall, 2005). While these four feeding modes are distinct, they are not mutually exclusive and are often combined to take advantage of available resources (Liem, 1993).

Suction feeding generates a flow of water directly in front of the mouth, and the strongest suction is dependent on the magnitude of the subambient pressure gradient generated (Wainwright and Day, 2007). This pressure gradient is generated by rapid buccal cavity expansion and concomitant increase in buccal volume. This sudden increase in volume creates subambient pressure that draws water and prey into the mouth (Muller et al., 1982). Flow velocity into the mouth is correlated with the magnitude and speed of volume change, as well as the surface area of the mouth aperture; large and fast volume changes, in combination with a small oral aperture result in high rates of fluid flow (Wainwright and Day, 2007). Stronger subambient buccal pressures result in high water flow rates. However, fluid velocity and pressure decay exponentially, and are generally insignificant at distances greater than one mouth diameter (Svanback et al., 2002; Day et al., 2007). In addition to creating a positive inertia on the prey toward the predator’s mouth (inertial suction), suction can also be used to compensate for the pressure wave generated by swimming toward the prey (compensatory suction) (Summers et al., 1998).

Kinematic studies of feeding that incorporate the use of pressure transducers to directly measure pressure magnitude have been used to characterize suction and ram feeding modes in a variety of primarily and secondarily aquatic vertebrates, including elasmobranchs, teleost fishes, salamanders, turtles, and mammals (for example, Lauder, 1985; Reilly and Lauder, 1990; Bels and Renous, 1992; Ferry-Graham and Lauder, 2001; Wilga et al., 2007; Marshall et al., 2008). Effective inertial suction feeders are able to generate a subambient pressure gradient at the mouth, and to do so, they typically have a limited gape with rapid gape opening and closing velocities. Whereas sharks and rays initiate buccal expansion through depression of the floor of the mouth, teleost fishes use their highly kinetic skulls for lateral expansion, thereby creating generally greater subambient pressures. Although marine mammals are phylogenetically constrained in their skull morphology, they have evolved a convergent mechanism to generate subambient intraoral pressure. Marine mammals use hyolingual musculature to depress and retract a piston-like tongue to create a rapid and large change in buccal volume; a greater hyolingual displacement indicates greater suction generation capability (Gordon, 1984; Heyning and Mead, 1996; Werth, 2000b; Marshall et al., 2008). However, the combination of hyoid shape, tongue shape, and orofacial morphology likely has a large influence on suction capability (Bloodworth and Marshall, 2007). Several anatomical studies of the feeding apparatus of odontocetes (e.g. Reidenberg and Laitman, 1994; Werth, 2006; Bloodworth and Marshall, 2007) have been conducted, and these serve as functional hypotheses that can be tested using feeding performance studies. However, since few data exist on the kinematics and suction performance of marine mammals, this study collects kinematic and biomechanical data for comparison with other marine mammals and other vertebrates.

1.3 Evolution of odontocete feeding modes

Suction is the most common feeding mode among aquatic vertebrates, and has been highly selected for due to the high density and viscosity of water (Lauder, 1985). However, during the transition to a terrestrial environment, suspension and suction feeding modes became ineffective and were abandoned. Processing of prey items by tetrapods became more complex and resulted in the evolution of mastication, or chewing, which is a defining characteristic of class Mammalia (Herring, 1993). However, when marine mammals such as odontocetes re-invaded the aquatic environment, mastication was abandoned and many aquatic adaptations, such as suction feeding, evolved secondarily.

The morphology of ancestral odontocetes was similar to that of extant aquatic ram feeding piscivores, and ram feeding is hypothesized to be the dominant method of prey capture in the first cetaceans (Werth, 2006). Some modern odontocete families are thought to have retained these ancestral feeding traits while others display divergent morphologies, such as blunt rostra, reduced dentition and capability to form a circular oral aperture. These adaptations likely occurred independently multiple times and resulted in suction feeding specialists that converge with other suction feeding aquatic vertebrates (Werth, 2006). While some odontocetes are considered specialists on either end of the ram-suction feeding spectrum, most are thought to utilize a mixture of both suction and ram feeding modes. Captive observations of a few cetacean species have demonstrated that both feeding modes are present in several taxa (Kastelein et al., 1997; Werth, 2000; Bloodworth and Marshall, 2005). However, behavioral performance studies on additional taxa will provide much needed comparative data to characterize the breadth of odontocete feeding behavior and to place odontocete feeding in an evolutionary context.

Characterizing the phylogeny of structure and function is common in evolutionary systematics, and is often performed by mapping observed changes in characters (e.g., morphology or performance) onto an existing phylogenetic tree. However, many data are continuous and can present difficulties in character mapping. As a solution, Mickevich and Johnson (1976) used gap coding to code continuous data into discrete character states, which were then easily mapped onto the phylogeny of silversides (*Menidia* spp.). Gap coding numerically orders the data to determine the difference (gap) between subsequent data points. These gaps are then compared to the group standard deviation to determine changes in character states. However, some datasets that are highly variable can fail to generate gaps, which can fail to determine character states. This leads to an inability to map character states onto a phylogeny (Riska, 1979). Throughout the past few decades, several alternative methods to gap coding have been proposed (for reviews, see Thorpe, 1984; Archie, 1985; Harvey and Pagel, 1991; Westneat, 1995; Garcia-Cruz and Sosa, 2006). Nonetheless, simple gap coding has withstood scrutiny and remains an accepted method for determining differences in character states among populations (Westneat, 1995), and may prove useful in the analysis of the evolution of odontocete feeding modes.

The numerous odontocetes in captivity are useful subjects for exploring the evolution of feeding modes in secondarily aquatic mammals. Belugas (*Delphinapterus leucas*), common in captivity, are anecdotally known for their suction capability (Ray, 1966; Brodie, 1989), and are an important group phylogenetically since they belong to a basal clade within Odontoceti (Monodontidae). In contrast, Pacific white-sided dolphins (*Lagenorhynchus obliquidens*) belong to the most derived clade (Delphinidae) and have been observed to rapidly herd and overtake a variety of fish prey organized as bait balls (Fiscus and Kajimura, 1980; Heise, 1997; Morton, 2000) in a behavior similar to that of their southern hemisphere congener (dusky dolphins, *Lagenorhynchus obscurus*, Würsig and Würsig, 1980; Vaughn et al., 2008). This behavior indicates the likely use of a ram feeding mode. Long-finned pilot whales (*Globicephala melas*), also members of Family Delphinidae, have been observed to use suction to ingest prey (Brown, 1962; Werth, 2000), a feeding mode indicated by their morphology, diet, and behavior. The comparison of three species of odontocetes with divergent feeding modes and phylogenetic distinctions allows for a comparison of suction generation among odontocetes and, in combination with other odontocetes for which kinematic data are available, forms a starting point to begin to explore the evolution of suction feeding in cetaceans.

1.4 Objectives

The primary objective of this study is to characterize and compare the kinematics and behavioral performance of feeding among presumed suction feeding and ram feeding odontocetes. The secondary objective of this study is to integrate odontocete feeding behavior data with data from the literature to begin to explore the evolution of feeding modes of odontocetes. The specific aims of this study are to:

1) Characterize the kinematics of feeding in three species of odontocetes.
    A) Define the kinematic profiles of belugas, Pacific white-sided dolphins, and long-finned pilot whales, and test the hypothesis that presumed suction feeding species will exhibit reduced gape, increased hyolingual depression, and adaptations to occlude lateral gape.
    B) Calculate ram-suction index (RSI) and test the hypothesis that presumed ram feeders will tend to have RSI values closer to +1 and presumed suction feeders, will tend to have RSI values closer to -1.
2) Characterize adaptations for lateral gape occlusion and pursing behavior in odontocetes, and test the hypothesis that each species in this study will display various degrees of pursing capability.
3) Measure the *in vivo* intraoral pressure changes during feeding events in belugas, Pacific white-sided dolphins, and pilot whales. Determine if species can produce subambient pressure and test the hypotheses that presumed suction feeding species will be able to generate greater subambient intraoral pressure than presumed non-suction feeders.
4) Begin to explore the evolution of feeding modes among odontocetes by determining where suction capabilities have occurred within odontocete phylogeny. Kinematic and pressure variables from this study as well as kinematic variables, pressure variables, and morphological characters from the literature, will be combined and mapped onto a widely accepted cladogram of suborder Odontoceti. This will be done to begin to systematically explore the evolution of suction feeding in Odontoceti and determine where changes in feeding modes may have taken place.

2. MATERIALS AND METHODS

2.1 Study animals and facilities

All subjects used in the study were captive animals held at two Sea World facilities (Sea World of Texas, San Antonio, TX and Sea World of California, San Diego, CA). Subjects included seven beluga whales (*Delphinapterus leucas* Pallas, 1976) and seven Pacific white-sided dolphins (*Lagenorhynchus obliquidens* Gill, 1865) housed at Sea World of Texas. Two female long-finned pilot whales (*Globicephala melas* Lesson, 1828) housed at Sea World of California were also used. Mean subject lengths and weights were 332 ± 43.9 cm and 577 ± 153 kg for belugas, 193 ± 27.8 cm and 108 ± 19.2 kg for Pacific white-sided dolphins, and 450 ± 32.3 cm and 1081 ± 348 kg respectively for pilot whales (Table 1). The use of all subjects was approved by Sea World, Inc. and the Institutional Animal Care and Use Committee (AUP 2006-237) of Texas A&M University.

2.2 Kinematic trials and analyses

Feeding kinematic data for presumed suction and non-suction feeding odontocetes was collected during controlled feeding trials. Herring (*Clupea harengus*), capelin (*Mallotus villosus*), mackerel (*Scomber japonicus*), and squid (*Loligo opalescens*) were presented to the subjects by hand (following Bloodworth and Marshall, 2005). Prey items were distributed according to the daily diet regimen for each individual; belugas primarily received herring, Pacific white-sided dolphins primarily received capelin, and pilot whales received herring, mackerel and squid. When cued, the subject was released from its station to freely capture the prey item via its preferred feeding mode (Fig. 2). Feeding trials were recorded using a Sony TRV950 video camera with a 500 ms shutter speed at 30 frames per second. The camera was either fitted into a handheld Equinox underwater housing (Galesburg, MI, USA) placed in the tank or was mounted onto a stationary tripod outside of an underwater viewing window. A calibration square of known dimensions was placed perpendicular to the video camera and in the plane of the subject before or after each feeding trial.

Table 1 Sex (M, male; F, female), age, length and weight of subjects used. Species abbreviations (in parentheses) and individual codes were used instead of species and animal names throughout the analysis.

Species	Individual	Code	Sex	Age (yrs)	Length (cm)	Weight (kg)
Beluga (DL)						
	Chrissy	1	F	23	351	571
	Luna	2	F	5	284	429
	Martha	3	F	23	335	542
	Nanuq	4	M	28	396	873
	Sikku	5	F	23	335	608
	Martina	6	F	23	356	603
	Whisper	7	F	6	267	411
Pacific white-sided dolphin (LO)						
	Avalon	8	F	6	188	100
	Betty	9	F	26	206	118
	Catalina	10	F	12	221	127
	Dart	11	M	2	152	116
	Hailey	12	F	6	180	86
	Lorelai	13	F	26	231	129
	Munchkin	14	F	5	173	82
Pilot whale (GM)						
	Bubbles	15	F	46	472	1327
	Niner	16	F	27	427	834

Lateral kinematic variables were calculated to describe the movement of the jaws during feeding. Videos of feeding trials were imported into the Peak Motus Motion Analysis System version 9 (Vikon, Denver, CO, USA). Seven anatomical landmarks were digitized (Fig. 2) and used for kinematic calculations, including: (1) rostral tip of upper jaw, (2) most anterior extent of lateral gape occlusion, where the lips were sealed to form an occluded lateral gape, (3) corner of the mouth, the vertex of the jaw, (4) rostral mandibular tip, (5) point on the prey item furthest from the subject, (6) center of the eye of the subject, and (7) rostral border of the externally apparent hyoid. A total of 23 lateral kinematic variables were calculated (Table 2). Feeding events began at the first frame in which gape angle opening velocity increased from 0 and gape began to increase, and ended at the last frame in which gape angle closing velocity returned to 0 and gape returned to the original closed position. To characterize the possible pursing behavior in belugas, and to compare pursing capability among species, five additional lateral gape occlusion kinematic variables were calculated and are also listed in Table 2.

Criteria for using video footage in kinematic analyses were that: (1) prior to jaw opening, both the prey item and the subject were visible in the frame and below the surface of the water, (2) all anatomical landmarks were visible in all frames, (3) the subject was perpendicular to the camera and any yaw or roll by the subject was less than 15°, (4) the video sequence was in focus, and (5) ingestion was observed. The five feeding events per subject that best fit these criteria were digitized frame-by-frame and homologous landmarks were analyzed using Peak Motus. For subjects with fewer than five sequences (25% of individuals: 2 belugas and 2 pacific white-sided dolphins), all usable feeding events were analyzed.

Ram-suction index (RSI) is as a quantitative measure of suction performance among aquatic vertebrates (Norton and Brainerd, 1993). RSI was calculated for each trial following Norton and Brainerd (1993):

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

where D_{predator} is the net distance traveled by the subject and D_{prey} is the net distance traveled by the food item. Anatomical landmarks assigned to the point on the prey

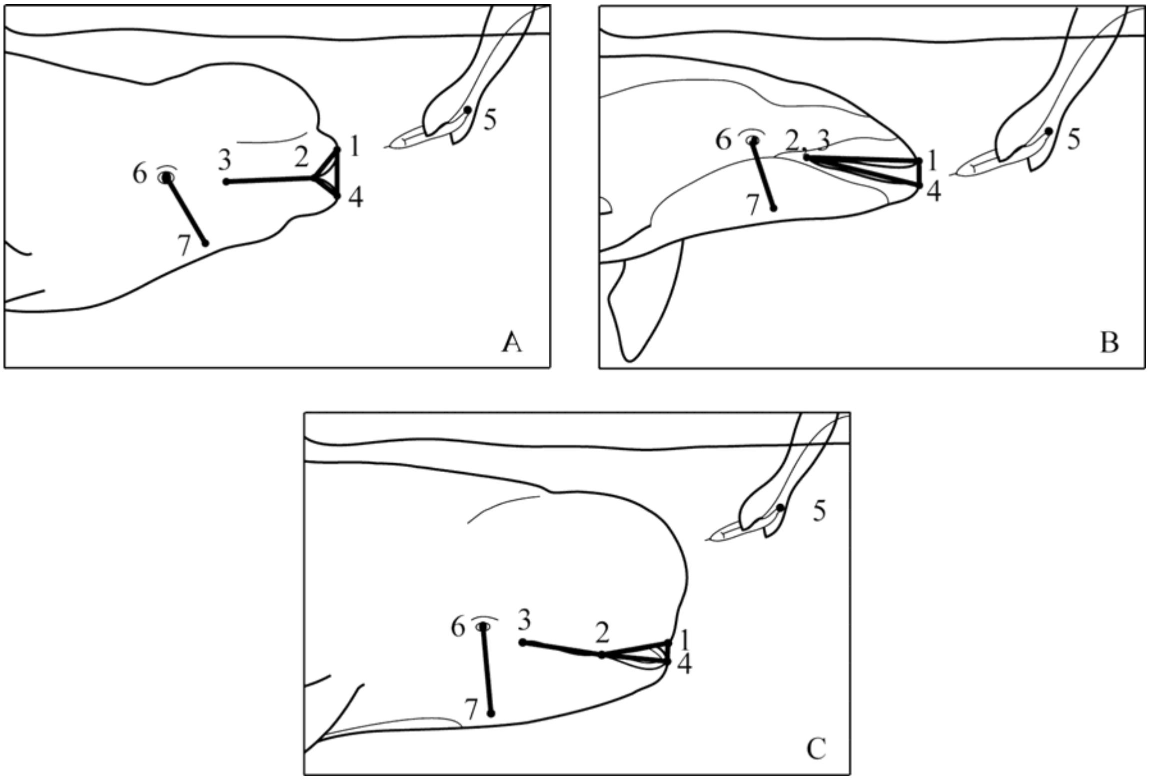

Fig. 2 Lateral anatomical landmarks. Schematic depicts experimental setup from the camera’s perspective, with lateral digitized landmarks and spatial model displayed for (A) belugas, (B) Pacific white-sided dolphins, and (C) pilot whales. Drawings are scaled independently. The pressure transducer was threaded through the gill of the fish and protruded approximately 2 cm from the fish’s mouth. Anatomical landmarks were: (1) rostral tip of upper jaw, (2) most anterior extent of lateral gape occlusion, where the lips were occluded to form a pursed lateral gape, (3) corner of the mouth, the vertex of the jaw, (4) rostral mandibular tip, (5) point on the prey item furthest from the subject, (6) center of the eye of the subject, and (7) rostral border of the externally apparent hyoid. In the event that pursing did not occur, landmarks 2 and 3 overlapped (B).

Table 2 Definitions and abbreviations for kinematic variables. Lateral variables include non-pursing variables, pursing variables, and ram-suction index variables which were measured from lateral perspective videos. Frontal variables were measured from frontal perspective videos.

Kinematic variable	Abbreviation	Definition
Lateral Kinematic Variables		
Maximum gape	GAPE	greatest distance of rostral tips of mandible and maxilla
Time to maximum gape	tGAPE	elapsed time from the onset of gape opening to the frame of maximum gape
Maximum gape angle	GANG	greatest angle from maxillary tip through the actual corner of mouth to the mandibular tip
Time to maximum gape angle	tGANG	elapsed time from the onset of gape opening to the frame of maximum gape angle
Maximum gape angle opening velocity	GAOV	greatest angular rate of gape angle opening
Time to maximum gape angle opening velocity	tGAOV	elapsed time from the onset of gape opening to the frame of maximum gape angle opening velocity
Maximum gape angle closing velocity	GACV	greatest angular rate of gape angle closing
Time to maximum gape angle closing velocity	tGACV	elapsed time from the onset of gape opening to the frame of maximum gape angle closing velocity
Maximum subject velocity	Vsubj	greatest rate of subject movement toward the prey
Time to maximum subject velocity	tVsubj	elapsed time from the onset of gape opening to the frame of maximum subject velocity
Maximum prey velocity	Vprey	greatest rate of prey movement toward the subject
Time to maximum prey velocity	tVprey	elapsed time from the onset of gape opening to the frame of maximum prey velocity
Time to prey ingestion	tING	elapsed time from the onset of gape opening to the last frame that prey is visible in the subject's mouth
Time to prey movement	tMVT	elapsed time from the onset of gape opening to the first frame in which prey movement toward the subjects mouth is visible
Maximum hyolingual depression	GULD	change in linear distance between the eye and hyoid from the first frame to the frame of maximal distance between the eye and hyoid
Time to maximum hyolingual depression	tGULD	elapsed time from the onset of gape opening to the frame of maximum hyolingual depression
Total duration	tDUR	elapsed time from the onset of gape opening to the last frame of gape closing

Table 2 continued.

Kinematic variable	Abbreviation	Definition
Percent occlusion	OCC	greatest distance from the vertex of the mouth to most anterior extent of lateral gape occlusion, divided by the length of the rostrum from the vertex to the rostral tips, x 100; taken at the frame of first visible prey movement toward the subject
Maximum posterior velocity of the pursed corner of the mouth	Vpost	greatest linear rate of posterior movement of the pursed corner of the mouth, corrected for subject velocity
Time to maximum posterior velocity of the pursed corner of the mouth	tVpost	elapsed time from the onset of gape opening to the frame of maximum posterior velocity of the pursed corner of the mouth
Maximum anterior velocity of the pursed corner of the mouth	Vant	greatest linear rate of anterior movement of the pursed corner of the mouth, corrected for subject velocity
Time to maximum anterior velocity of the pursed corner of the mouth	tVant	elapsed time from the onset of gape opening to the frame of maximum anterior velocity of the pursed corner of the mouth
Suction distance	Dprey	net distance traveled by the food item
Ram distance	Dpredator	net distance traveled by the subject
RSI	RSI	Ram-Suction Index value
Frontal Kinematic Variables		
Maximum gape	GAPE	maximum distance between maxillary and mandibular rostral tips at the midsagittal plane
Time to maximum gape	tGAPE	elapsed time from the onset of gape opening to the frame of maximum gape
Aperture width	WIDTH	horizontal distance between right and left pursed corners of the mouth at the frame of maximum gape
Total duration	tDUR	elapsed time from the onset of gape opening to the last frame of gape closing

farthest from the subject (landmark 5) and the subject's eye (landmark 6) were used to extract *x* and *y* coordinates of the subject and the prey. Calculations were made at the onset of the feeding event (see above) and the frame of prey capture, when the subject's lips came into contact with the prey. The change in position in the *x* and *y* direction of both subject and prey were used to measure the net distance traveled by both predator and prey and a RSI value was calculated for the trial. RSI values ranged from pure suction (-1) to pure ram (+1). The mean RSI was calculated for each species.

To determine whether observed gape and gape angle during feeding approximated maximum biological capability, digital photographs of an open mouth behavior were taken using a Minolta Maxxum 5 digital camera (Konica Minolta, Tokyo, Japan; Konica Minolta AF DT zoom 18-70 mm lens; 2256 x 1496 pixels; saved in TIFF format). Subjects were photographed with a scale when cued by a trainer to open their mouth, cued to vocalize, or when fed, all of which resulted in the subject opening its mouth to its widest possible extent. Mean maximum gape and gape angle were measured using Image J image analysis software (NIH, Bethesda, MD, USA) for five photos of each subject, which were then compared to corresponding kinematic data to determine what percentage of gape and gape angle were used during feeding trials.

To determine the degree of circularity of the oral aperture at the anterior lips, additional feeding sequences were recorded from the frontal perspective. The frontal perspective anatomical landmarks were: (1) center of the upper lip at the midsagittal plane, (2) right corner of the mouth, (3) center of lower lip at the midsagittal plane, and (4) left corner of the mouth (Fig. 3). Feeding events began with the first frame that the linear velocity of the upper and lower lips increased from zero, and the mouth began to open, and ended at the frame in which the linear velocity of the upper and lower lips returned to zero, and the mouth closed. Four frontal kinematic variables were also measured and are listed in Table 2. Area and circumference of the oral aperture at maximum gape were measured using Image J. Gape and width at the frame of maximum gape were used to calculate the ratio of vertical:horizontal diameter of the oral aperture (aperture ratio), as a measure of aperture circularity.

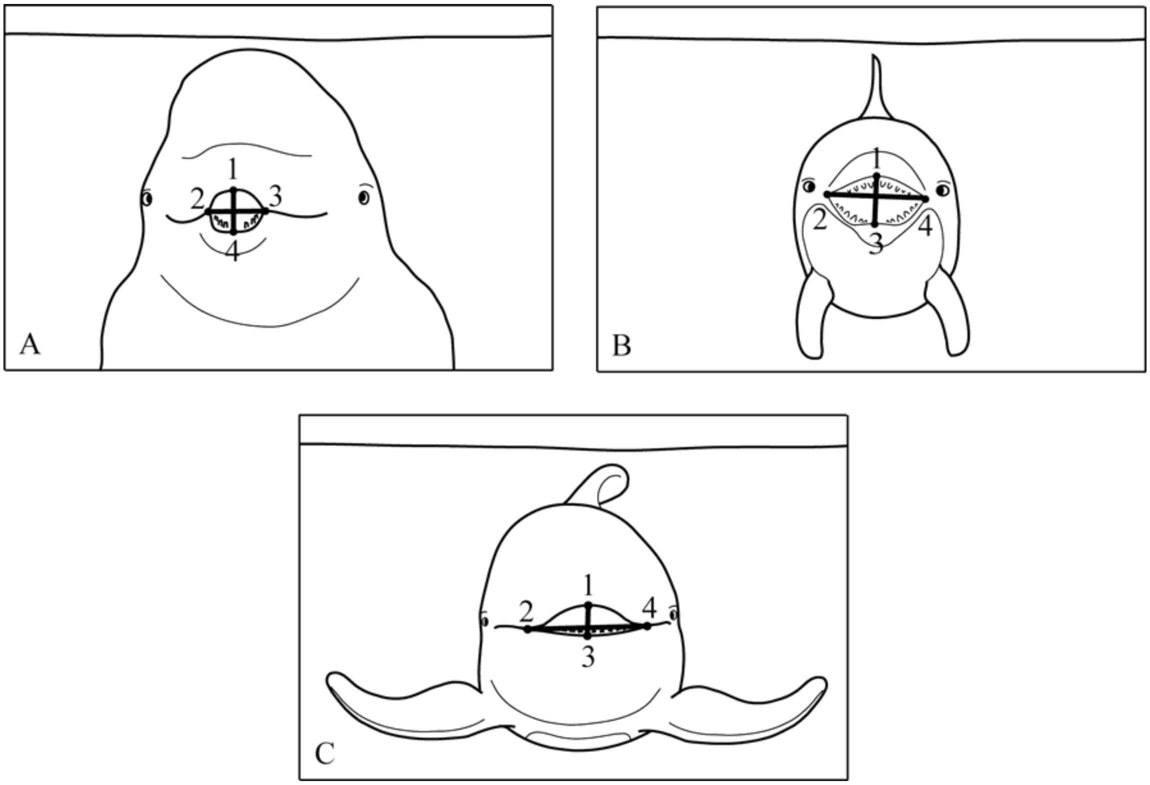

Fig. 3 Frontal anatomical landmarks. Schematic depicts digitized landmarks and the corresponding spatial models used in motion analysis for (A) belugas, (B) Pacific white-sided dolphins, and (C) pilot whales. Drawings are scaled independently. Landmarks include: (1) center of the upper lip at the midsagittal plane, (2) right corner of the mouth, (3) center of lower lip at the midsagittal plane, and (4) left corner of the mouth.

2.3 Pressure generation capability

The same controlled feeding trials used to collect lateral kinematic data were also used to measure the subambient and suprambient pressure generated by presumed suction and ram feeding odontocetes. A pressure transducer (MPC 500 MikroTip Pressure Catheter, Millar Instruments, Houston, TX, USA), modified to a length of 3 m, was inserted through the prey item (Fig. 2) so that approximately 2 cm protruded from the fish's mouth. The transducer was connected to a control box (TCB 600, Millar Instruments, Houston, TX, USA) and a portable electrophysiological recording system (Biopac MP150 System, BIOPAC systems, Inc., Goleta, CA), which continuously recorded and saved transducer output as volts (v) vs. time (s) at a sampling rate of 500 Hz (AcqKnowledge Software 3.9, BIOPAC systems, Inc., Goleta, CA, USA). To ensure accurate conversion of volts to kPa of pressure, the transducer was calibrated in the lab. It was inserted into a sealed flask and subambient pressure was decreased to -80 kPa with a certified vacuum hand pump. Pressure was released in a controlled manner, and readings from the transducer at several intervals were recorded. Known pressure readings from the pump were regressed with corresponding transducer output to obtain a transducer-specific conversion factor and ensure linearity. Transducer diameter was minimal and the influence on water flow parameters was negligible. Acqknowledge 3.9 (BIOPAC systems, Inc., Goleta, CA, USA) was also used to analyze the data for subambient and suprambient pressure spikes. The seven pressure variables measured, their abbreviations, and definitions, are listed in Table 3.

2.4 Statistics

Statistical tests were performed using JMP 7.0.1 (SAS Institute, Inc., Cary, NC, USA) to determine differences in kinematic and pressure profiles among species and to determine correlation among variables. Normality was tested using a Shipiro-Wilks test, and all lateral and frontal kinematic data were subsequently log-transformed and standardized for comparison. An interspecific analysis of variance (ANOVA) was used to test for species differences within each kinematic phase. Differences among

Table 3 Definitions and abbreviations for pressure generation variables.

Pressure change variable	Abbreviation	Definition
Maximum subambient pressure	Psub	change in value from the baseline to the maximum subambient pressure recorded during the event
Maximum supra-ambient pressure	Psupra	change in value from the baseline to the maximum suprambient pressure recorded during the event
Expansive phase duration	tEXP	elapsed time from the start, when the pressure increases or decreases from the baseline, to the maximum pressure
Rate of expansive phase pressure change	PEXP	maximum subambient or suprambient pressure divided by expansive phase duration
Compressive phase duration	tCOMP	elapsed time from the maximum subambient or suprambient pressure back to the baseline
Rate of compressive phase pressure change	PCOMP	maximum subambient or suprambient pressure divided by compressive phase duration
Total duration	tDUR	elapsed time from the onset of rapid pressure change until the return to baseline

kinematic variables across prey types among species and within species were determined with a multivariate analysis of variance (MANOVA) followed by an intraspecific ANOVA for each species. An interspecific constrained ordination nested MANOVA and a canonical centroid plot of least squares means tested for significant differences among subjects nested within species for kinematic and pressure variables; tests for lateral kinematics, frontal kinematics, and RSI were performed separately. In all cases, *post hoc* tests on least squares means were used to determine in which species differences occurred. Linear regression (with intercept constrained to zero) was performed to determine two dimensional RSI isoclines. Differences among kinematic and biological maximum gape capability were determined using student's t-tests to compare gape and gape angle calculated using both measurements. Correlation among kinematic and pressure generation variables was determined for the transformed lateral and frontal kinematic data, as well as pressure data, using a Pearson's r test for correlation.

2.5 Evolutionary analysis of feeding characters

Species mean data from this study, as well as kinematic data for pygmy and dwarf sperm whales (*Kogia* spp.) and bottlenose dolphins (*Tursiops truncatus*, Bloodworth and Marshall, 2005) and pressure data for a harbor porpoise (*Phocoena phocoena*, Kastelein et al., 1997), were used to conduct a preliminary evolutionary analysis of feeding in the suborder Odontoceti. Comparative data were available for: GAPE, tGAPE, GANG, GAOV, Vprey, GULD, tGULD, Dprey, Dpredator, tDUR, RSI, and Psub. In addition, several comparative morphological characters were analyzed to increase Odontoceti ancestral state resolution and robustness. These included: mandibular bluntness index ratios (MBI; Werth, 2006), tongue and hyoid morphometrics (A. Werth, unpublished data), and maximum total tooth counts (Minasian et al., 1984). Tongue ratios (width:length) and hyoid ratios (length:width; from the anterior tip of the basihyal to the posterior tip of the thyrohyal, and from tip of the left to tip of the right thyrohyal) were used to control for variation due to species size.

Mean values for each character were transformed into discrete character states by simple gap coding (Riska, 1979; Thorpe, 1984; Archie, 1985). The difference between subsequent ordered means (a gap) was calculated and compared to the pooled among-species standard deviation times a constant of 1, and integers were assigned to groups of means falling between gaps. To prevent the exclusion of data from the analysis, if gaps were not found, the constant was decreased in increments of 0.1 until at least two discrete character states were coded (Thorpe, 1984). Three discrete character states were more biologically meaningful for RSI, tooth counts, and MBI. Therefore, these characters were coded until 3 states were determined.

Discrete character states were mapped onto an accepted odontocete phylogeny (Fig. 1) using Mesquite 2.5 (Maddison and Maddison, 2008). Ancestral states were reconstructed using a one parameter Markov k-state maximum likelihood model (Maddison and Maddison, 2006). The most likely hypothesis of odontocete ancestral state was determined for each character, and a composite map of state changes was determined. Equivocal ancestral states were reconstructed subjectively based on the most common state present in extant taxa. If no most common state was found, the state present in the most basal clade was assumed to be ancestral. The composite map was then used to determine in which taxa changes in characters took place, and decipher which characters were plesiomorphic, apomorphic, and synapomorphic within suborder Odontoceti as well as within Families of odontocete taxa.

3. RESULTS

3.1 Kinematic analyses

Eleven hours of video were recorded to obtain over 1300 feeding trials. Of these, 89 were used for lateral kinematic analyses, 64 were used for RSI calculations, and 49 were used for frontal kinematic analyses. Overall, feeding events of odontocetes in this study consisted of four phases: (I) preparatory, (II) jaw opening, (III) hyolingual depression, and (IV) jaw closing. Phase I began at the onset of jaw opening and ended when gape increased by greater than 0.2 cm/field and the jaws rapidly opened. Phase I was observed in 32% of all trials and consisted of hyolingual adduction, small gape, and slow gape angle opening velocity, as well as movement of the subject toward the prey. Phase II overlapped with phases II and IV. It began when gape increased rapidly and lasted until maximum gape. Phase III began when hyolingual depression increased by greater than 0.2 cm/field and lasted until hyolingual depression returned to its original position, or until the end of the feeding event. The longest duration in all species was observed for phase III. Phase IV began at maximum gape and concluded when the jaws closed and gape decreased by less than 0.2 cm/field.

Belugas, Pacific white-sided dolphins, and pilot whales differed in mean phase durations. Mean durations of phases I, II, III, and IV for belugas were 0.205 ± 0.096 s, 0.214 ± 0.026 s, 0.425 ± 0.052 s, and 0.370 ± 0.053 s, respectively. Pacific white sided dolphin phase durations were 0.038 ± 0.026 s, 0.102 ± 0.01 s, 0.196 ± 0.013 s, and 0.140 ± 0.01, respectively. Pilot whale phase durations were 0.200 ± 0.038 s, 0.282 ± 0.025 s, 0.334 ± 0.024 s, and 0.241 ± 0.02 s, respectively. Duration of phase I was not significantly different for any species (ANOVA, F=1.30, P=0.29). However, duration of phase II (ANOVA, F=17.4, P<0.0001), phase III (ANOVA, F=11.4, P<0.0001), and phase IV (ANOVA, F=11.5, P<0.0001) were significantly different. Phase II and III durations were longer in belugas and pilot whales, and duration of phase IV was longer in belugas than either other species (Fig. 4, *post hoc* tests, P<0.05). Total duration of feeding events was short in Pacific white-sided dolphins (0.279 ± 0.02 s) and long in belugas (0.684 ± 0.07) and pilot whales (0.583 ± 0.05 s).

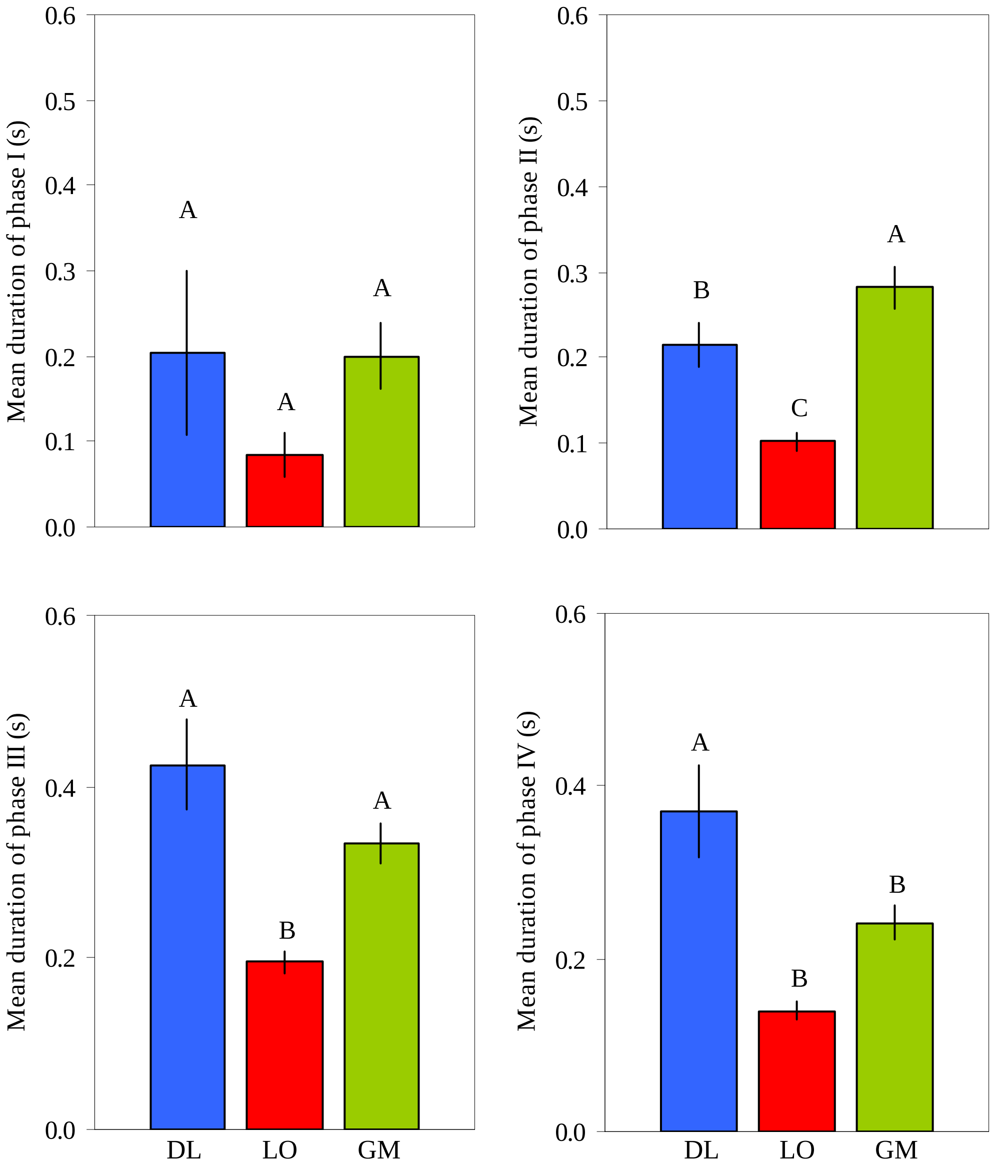

Fig. 4 Kinematic phase mean (± SEM) durations. Different letters indicate significant differences at P<0.05.

3.1.1 Feeding behaviors

Analysis of 33 beluga feeding trials demonstrated that belugas were able to capture prey by using suction, ram and a combination of both (combination: Figs. 5 and 6). During suction feeding events, belugas approached the prey at low velocity (mean: 49.2 ± 6.6 cm/s, maximum: 168.4 cm/s). When phase I was observed (31.2% of trials), it occurred as the subject approached the prey (ram component), and included hyolingual adduction and slow gape opening. Bubbles expelled from the lateral lip margins indicated hydraulic jetting, which was supported by suprambient pressure recordings (see below). Supination of the pectoral flippers (flares) reduced forward velocity to near zero as subjects approached the prey. At this point, the lips were within one mouth diameter (mean: 6.3 ± 0.6 cm) from the prey, and the jaws began to open more rapidly than during Phase I (mean: 119.7 ± 8.1°/s, range: 60.3-234.3°/s). However, unlike other odontocetes (Bloodworth and Marshall, 2005), the mobile lateral lips occluded lateral gape (mean: 78.8 ± 2.9%) and the anterior lips were pursed, a behavior that resulted in a small, circular oral aperture that coincided with maximum gape (see below). Hyolingual depression overlapped with phase II and appeared to create subambient pressure and a flow of water into the mouth, which was evidenced by movement of prey into the mouth. This observation was also supported by direct pressure measurements (see below). Prey moved into the mouth at a high velocity (suction component, mean: 219.1 ± 18.7 cm/s, maximum: 555.4 cm/s) after maximum gape and before maximum hyolingual depression. Rapid opening of the lateral lips was observed after prey capture, and bubbles were again expelled from the entire length of the lateral lip margin, until the lips rapidly returned to their resting position and the mouth was closed.

Ram feeding was also employed by belugas (6% of trials) to capture prey. Ram kinematic events were similar to suction events, except for differences in velocity and timing. No preparatory phase was observed for these trials. The subject approached the prey at high velocity (maximum: 140 cm/s), which was maintained throughout the feeding trial. Gape began to open when the subject was within one mouth diameter from

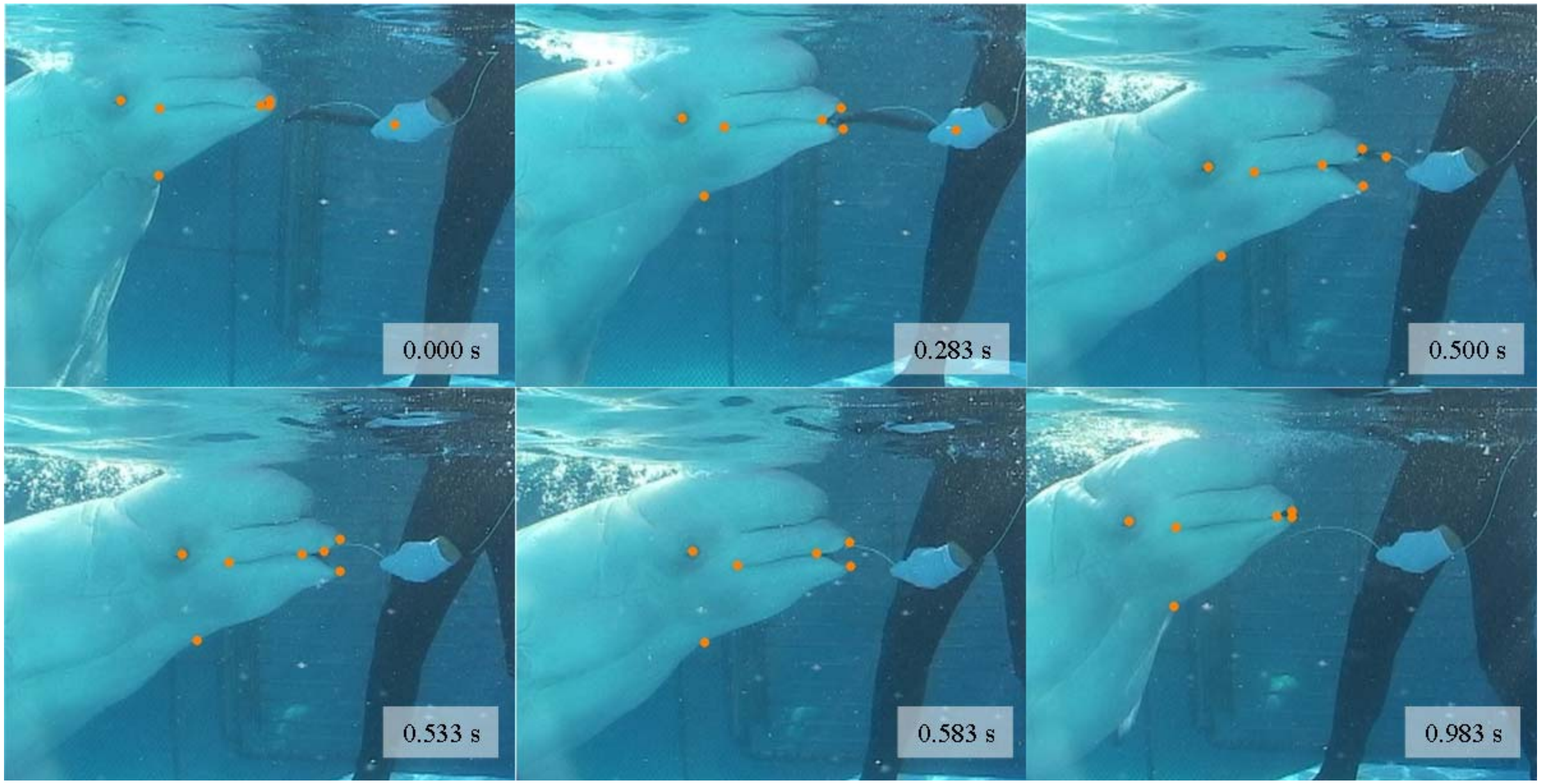

Fig. 5 Video frames from a representative beluga feeding trial. Frames were taken at the start of the sequence, the frame of first visible prey movement, maximum gape, the last frame that the prey was visible in the mouth, maximum hyolingual depression, and the end of the feeding trial. Anatomical landmarks are displayed as orange points and elapsed time of each event is indicated.

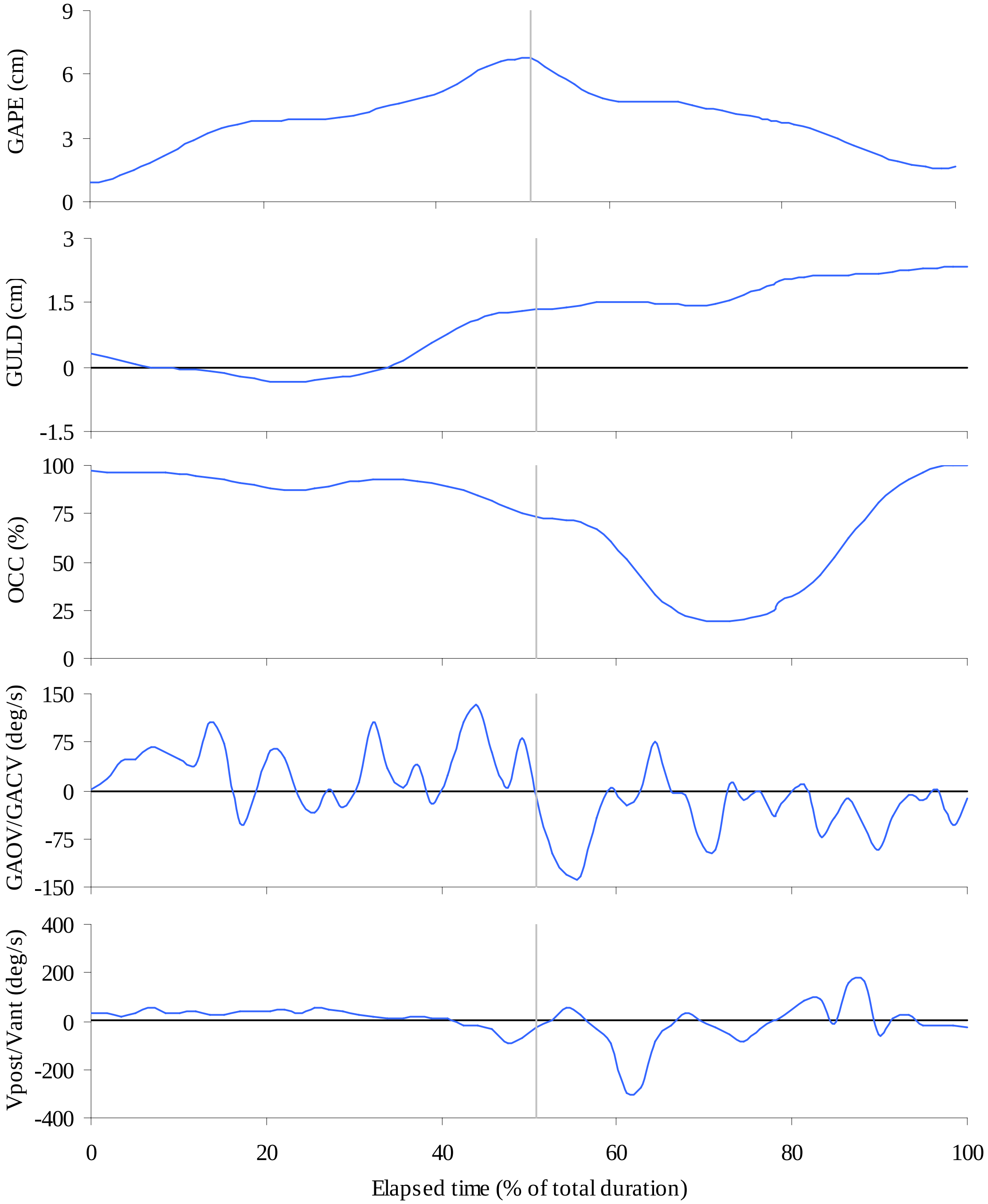

Fig. 6 Lateral kinematic profile of selected variables for a representative beluga feeding trial (Fig. 5). Elapsed time is scaled to percent of total duration. A gray vertical line represents maximum gape.

the prey (mean: 6.3 ± 0.6 cm) and was more rapid than during suction trials (maximum GAOV: 234.3°/s, maximum GACV: 293.8°/s). However, occlusion of the lateral lips and pursing of the anterior lips was also observed in ram feeding trials and indicated a combined use of suction and ram. Maximum gape occurred as the prey item was captured, followed by maximum hyolingual depression. The lateral lips opened directly after maximum gape and the jaws began to close. The prey item was fully ingested when the lateral lips returned to their resting position. Mean total duration of ram feeding events (mean: 0.342 ± 0.03 s) was shorter than suction feeding events (mean: 0.684 ± 0.07 s).

Analysis of 31 Pacific white-sided dolphin lateral feeding trials demonstrated that this species captured prey using ram, and a small degree of suction (Figs. 7 and 8). Ram feeding was characterized by high approach velocity (mean: 81.5 ± 8.5 cm/s, maximum: 218.5 cm/s). A preparatory phase occurred in 45% of trials but no hyolingual adduction was observed. During phase I, the jaws opened slowly and Pacific white-sided dolphins maneuvered so the prey was oriented head-first for ingestion. After orientation, the jaws began to open rapidly (mean: 248.4 ± 22.1°/s, maximum: 713.0°/s). As the jaws opened, Pacific white-sided dolphins slightly pursed their anterior lips, and prey was observed to move toward the mouth. At this time, lateral gape occlusion was approximately 50% of total jaw length, and gape was approximately 75% of the maximum. Rapid jaw and lateral lip movement appeared to create a slight flow of water into the mouth that resulted in some movement of the prey toward the mouth (mean: 89.3 cm/s). Hyolingual depression was clearly visible in Pacific white-sided dolphins, and overlapped with phase II as gape opened and prey began to move into the mouth. An oral aperture at the anterior lips was not as clearly defined for Pacific white-sided dolphins as that observed in belugas. Maximum gape was followed by maximum hyolingual depression (mean: 3.4 ± 0.3 cm), maximum prey velocity (range: 9.6-298.0 cm/s), and fully opened lateral lips. High prey velocity was observed in some trials and indicated that some degree of suction may have been used to ingest prey. Some suction capability was also confirmed with direct pressure recordings (see below). After prey

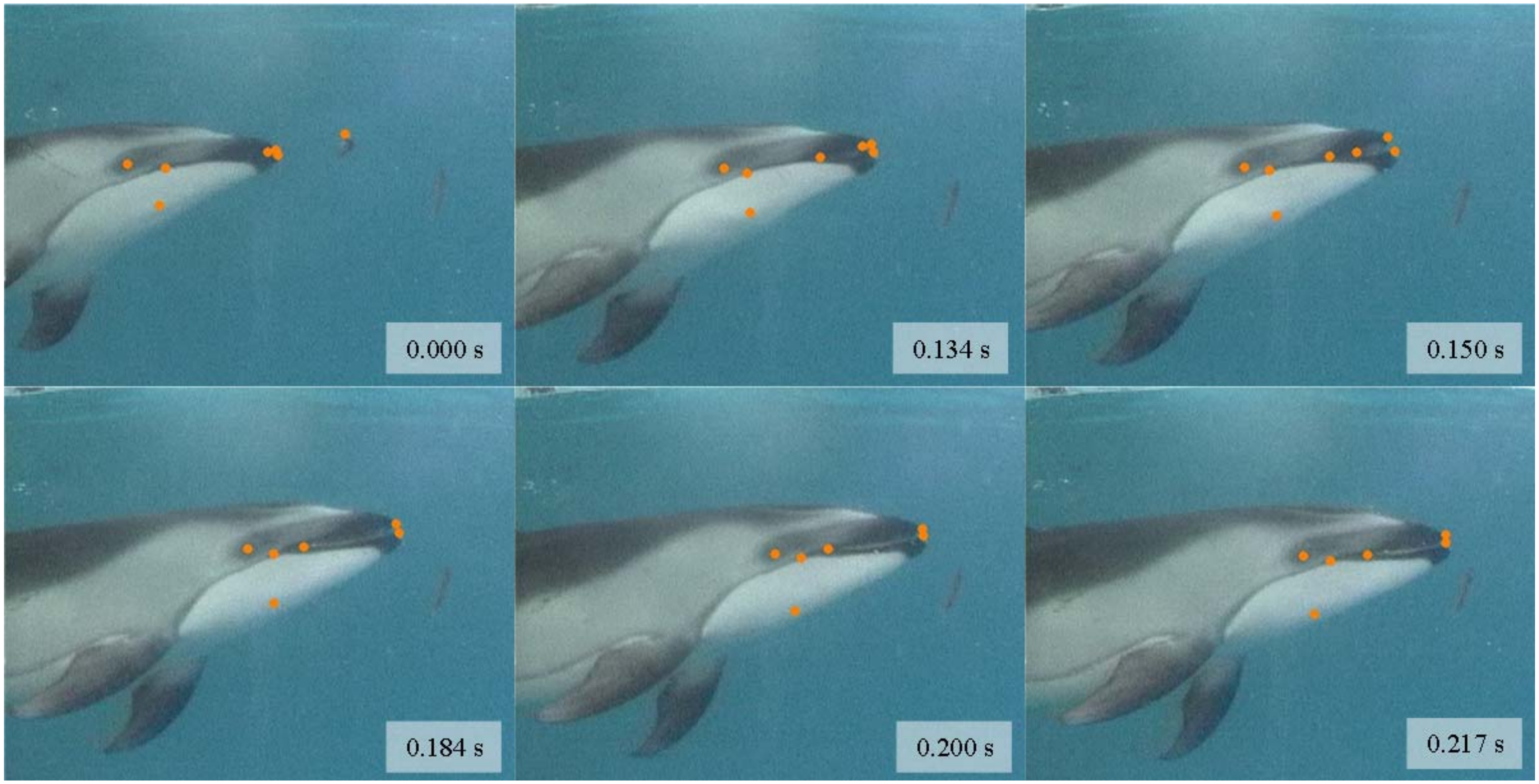

Fig. 7 Video frames from a representative Pacific white-sided dolphin feeding trial. Frames were taken at the start of the sequence, the frame of first visible prey movement, maximum gape, the last frame that the prey was visible in the mouth, maximum hyolingual depression, and the end of the feeding event. Anatomical landmarks are displayed as orange points and elapsed time of each event is indicated.

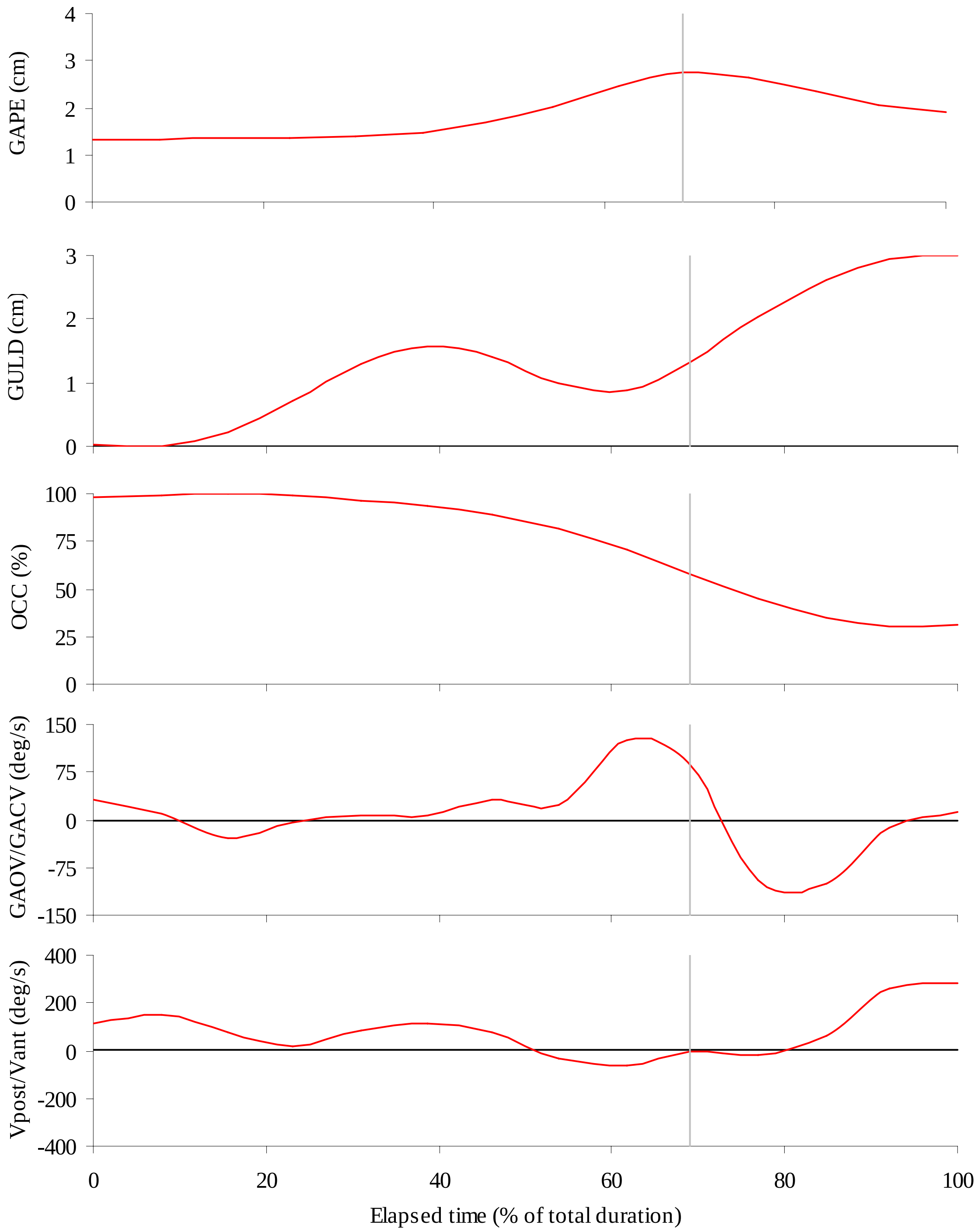

Fig. 8 Lateral kinematic profile of selected variables for a representative Pacific white-sided dolphin feeding trial (Fig. 7). Elapsed time is scaled to percent of total duration. A gray vertical line represents maximum gape.

moved into the mouth, the jaws closed rapidly (mean: 226.0 ± 26.0°/s, maximum: 690.1°/s) and the hyolingual apparatus returned to its resting position. In some trials, the hyolingual apparatus was adducted farther during phase IV than its starting position during phase II. Once the anterior tips of the jaws were within a few centimeters of each other, water was expelled from the lateral margins of the mouth. The lateral lips did not return to their resting position until after this time. The entire feeding sequence was more rapid (mean: 0.279 ± 0.02 s, range: 0.116-0.600 s) than in the other species.

Fifteen lateral kinematic pilot whale trials were analyzed and demonstrated that pilot whales captured prey with a mixture of ram and suction feeding modes (Figs. 9 and 10). When phase I was observed (16% of trials), hyolingual abduction was followed by hyolingual adduction. Also during this phase, bubbles were expelled from the lateral lip margins and gape slowly increased. Hydraulic jetting capability was confirmed with direct pressure measurements (see below). Pilot whales approached prey at a high velocity (mean: 85.5 ± 8.5 cm/s, range: 41.8-121.3 cm/s). In some trials, pectoral fin flares were used to reduce velocity (but not stop) as the prey was approached. The jaws opened slowly (mean: 107.5 ± 7.6°/s, range: 60.6-162.2°/s) at the onset of phase II and lateral gape opened synchronously. Hyolingual depression began after jaw opening and appeared to generate a flow of water that drew the prey toward the mouth. At this time, the lateral lips occluded lateral gape by more than 50% of the total jaw length (63.6 ± 2.8%, range: 34.2-81.7%). Lateral gape occlusion reached its minimum at maximum gape and the lateral lips never opened along the entire margin of the jaw. Proximity of the upper and lower jaws likely contributed to lateral lip occlusion. Anterior lip pursing and an anterior oral aperture were not observed. Maximum hyolingual depression (mean: 2.674 ± 0.4 cm) occurred after maximum gape (during phase IV) was concurrent with rapid prey movement into the mouth (mean: 114.5 ± 23.6 cm/s, maximum: 324.9 cm/s). Some suction generation was indicated by rapid prey velocity and was confirmed with direct pressure measurements (see below). After maximum gape, water was expelled from the lateral lip margins as the jaws closed. Duration of feeding events was relatively slow (mean: 0.583 ± 0.1 s).

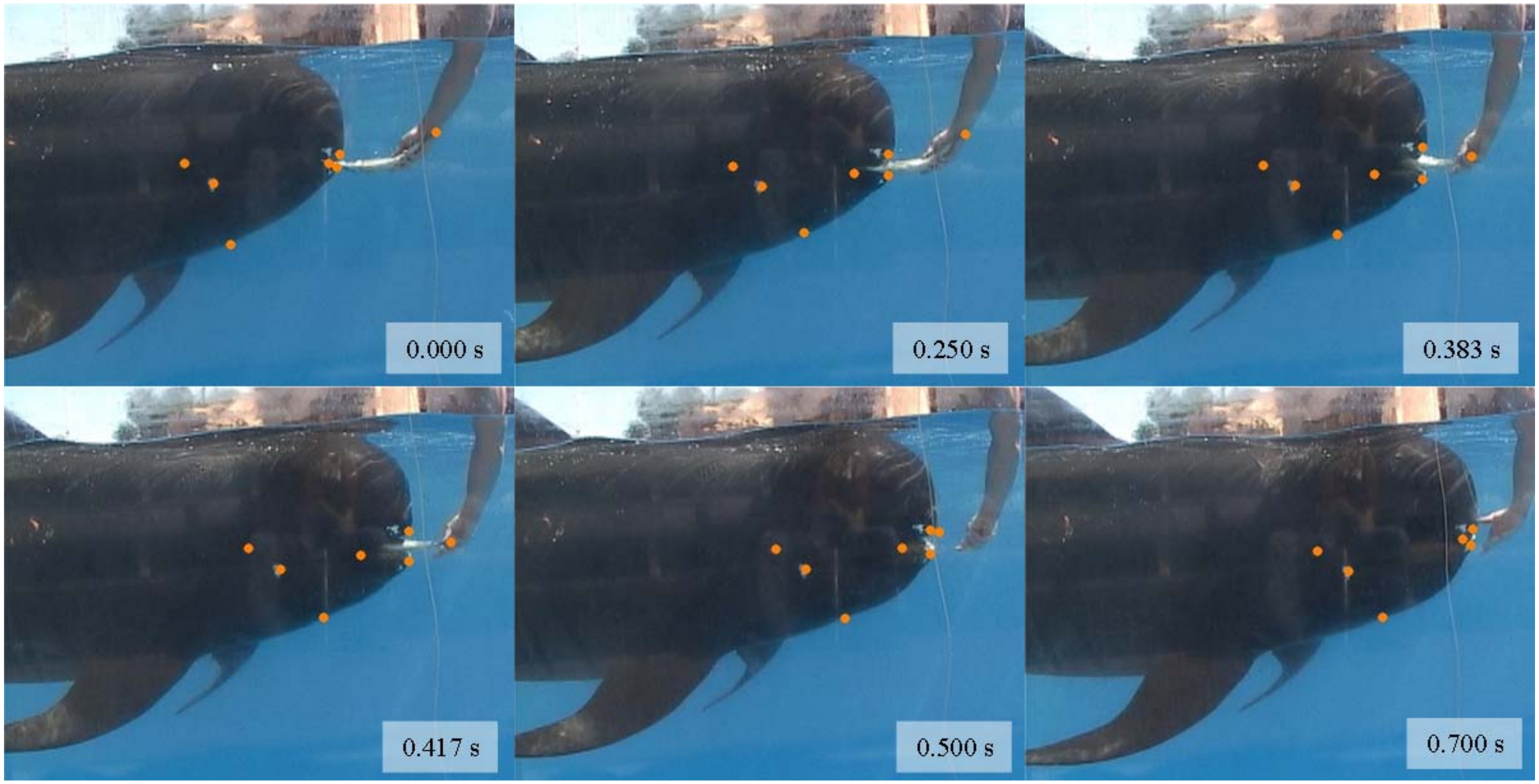

Fig. 9 Video frames from a representative pilot whale feeding trial. Frames were taken at the start of the sequence, the frame of first visible prey movement, maximum gape, maximum hyolingual depression, the last frame that the prey was visible in the mouth, and the end of the feeding event. Anatomical landmarks are displayed as orange points and elapsed time of each event is indicated.

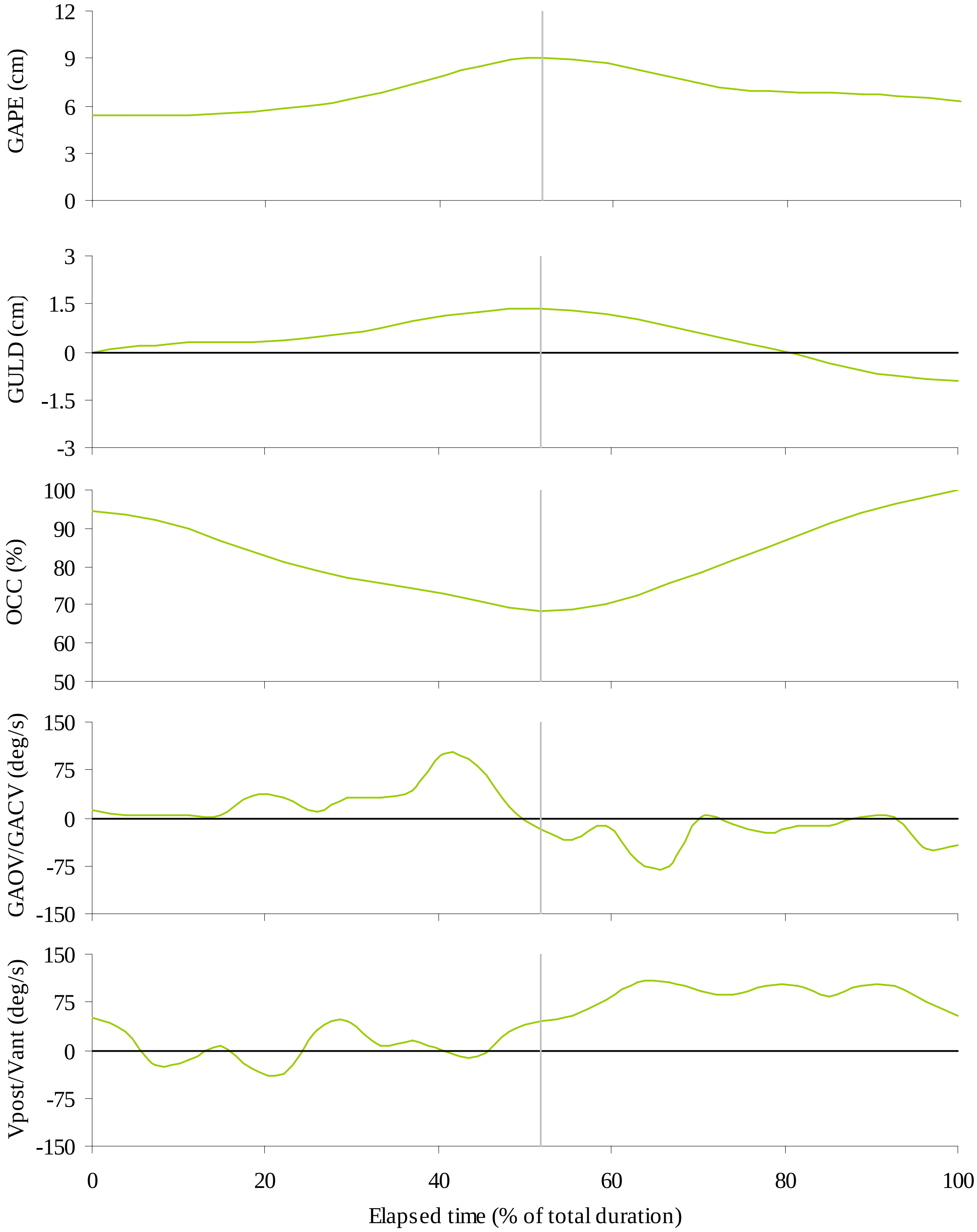

Fig. 10 Lateral kinematic profile of selected variables for a representative pilot whale feeding trial (Fig. 9). Elapsed time is scaled to percent of total duration. A gray vertical line represents maximum gape.

3.1.2 Lateral kinematic analyses

At the time of video collection, 10 randomly chosen prey of each prey type were measured to determine mean prey length (herring: 24.2 ± 2.78 cm, capelin: 14.5 ± 1.16 cm, mackerel: 23.1 ± 0.843 cm, squid: 20.7 ± 2.28 cm). Belugas fed primarily on herring for 87.9% of trials and on capelin for the rest. Pacific white-sided dolphins fed on capelin for 90.3% of trials and on herring for the remainder. Pilot whales fed on herring for 40% of trials, mackerel for 20% of trials, and squid for the remaining 40% of trials. No significant differences in kinematic variables were found for prey types among odontocete species (MANOVA, Wilks' lambda, F=1.19, P=0.19) or within species (ANOVA, beluga: F=1.77, P=0.19, Pacific white-sided dolphins: F=1.18, P=0.43, pilot whales: MANOVA, Wilks' Lambda, F=2.17, P=0.37). However, for consistency among fish prey types, pilot whale trials that utilized squid prey were excluded from analyses.

Twenty-three lateral kinematic variables were analyzed from each beluga, Pacific white-sided dolphin, and pilot whale feeding trial (Table 4). Species differed from each other in most lateral kinematics (Figs. 11 and 12, MANOVA, Wilks' Lambda, F=2.18, P<0.0001). *Post hoc* tests on least squares means demonstrated that overall, belugas and pilot whales were more similar in their kinematic profile than Pacific white-sided dolphins were to either of the two other species (*post hoc* tests, P<0.05). Maximum gape, maximum gape angle, maximum hyolingual depression, and maximum posterior opening velocity of the laterally occluded lips, were not significantly different among species. Gape angle velocity was greater for Pacific white sided dolphins than either belugas or pilot whales. Belugas exhibited the greatest maximum anterior closing velocity of the laterally occluded lips, the greatest prey velocity, and the greatest percent of lateral gape occlusion at the time of initial prey movement. For these same variables, pilot whales were not significantly different than either belugas or Pacific white-sided dolphins. Subject velocity was similar for Pacific white-sided dolphins and pilot whales, and both species approached prey at significantly higher velocities than belugas. No species difference in time to maximum gape angle opening velocity or time to maximum

Table 4 Mean values ± SEM for lateral kinematic variables.

Variables	DL	LO	GM
GAPE (cm)	6.346 ± 0.356	6.451 ± 0.462	8.997 ± 0.56
tGAPE (s)	0.277 ± 0.038	0.140 ± 0.016	0.327 ± 0.046
GANG (°)	16.381 ± 0.811	16.812 ± 1.239	15.878 ± 1.003
tGANG (s)	0.300 ± 0.038	0.139 ± 0.016	0.316 ± 0.039
GAOV (°/s)	119.715 ± 8.079	248.383 ± 22.062	107.473 ± 7.612
tGAOV (s)	0.175 ± 0.039	0.092 ± 0.013	0.212 ± 0.033
GACV (°/s)	115.225 ± 8.863	226.019 ± 26.033	85.868 ± 5.856
tGACV (s)	0.387 ± 0.04	0.179 ± 0.017	0.422 ± 0.046
Vpost (cm/s)	256.481 ± 28.422	175.115 ± 11.903	149.378 ± 21.576
tVpost (s)	0.370 ± 0.045	0.095 ± 0.015	0.220 ± 0.028
Vant (cm/s)	166.270 ± 20.025	92.320 ± 13.288	122.483 ± 14.192
tVant (s)	0.491 ± 0.057	0.248 ± 0.021	0.459 ± 0.051
Vpred (cm/s)	49.164 ± 6.585	81.466 ± 8.507	85.522 ± 5.65
tVpred (s)	0.234 ± 0.049	0.160 ± 0.019	0.241 ± 0.031
Vprey (cm/s)	219.064 ± 18.737	89.295 ± 14.539	114.471 ± 23.59
tVprey (s)	0.339 ± 0.117	0.149 ± 0.021	0.320 ± 0.037
OCC (%)	78.764 ± 2.877	41.103 ± 4.465	63.587 ± 2.787
tMVT (s)	0.254 ± 0.049	0.104 ± 0.014	0.189 ± 0.029
GULD (cm)	2.675 ± 0.240	3.377 ± 0.317	2.674 ± 0.364
tGULD (s)	0.400 ± 0.05	0.186 ± 0.019	0.430 ± 0.056
tING (s)	0.377 ± 0.049	0.189 ± 0.018	0.422 ± 0.057
tDUR (s)	0.684 ± 0.07	0.279 ± 0.02	0.583 ± 0.053

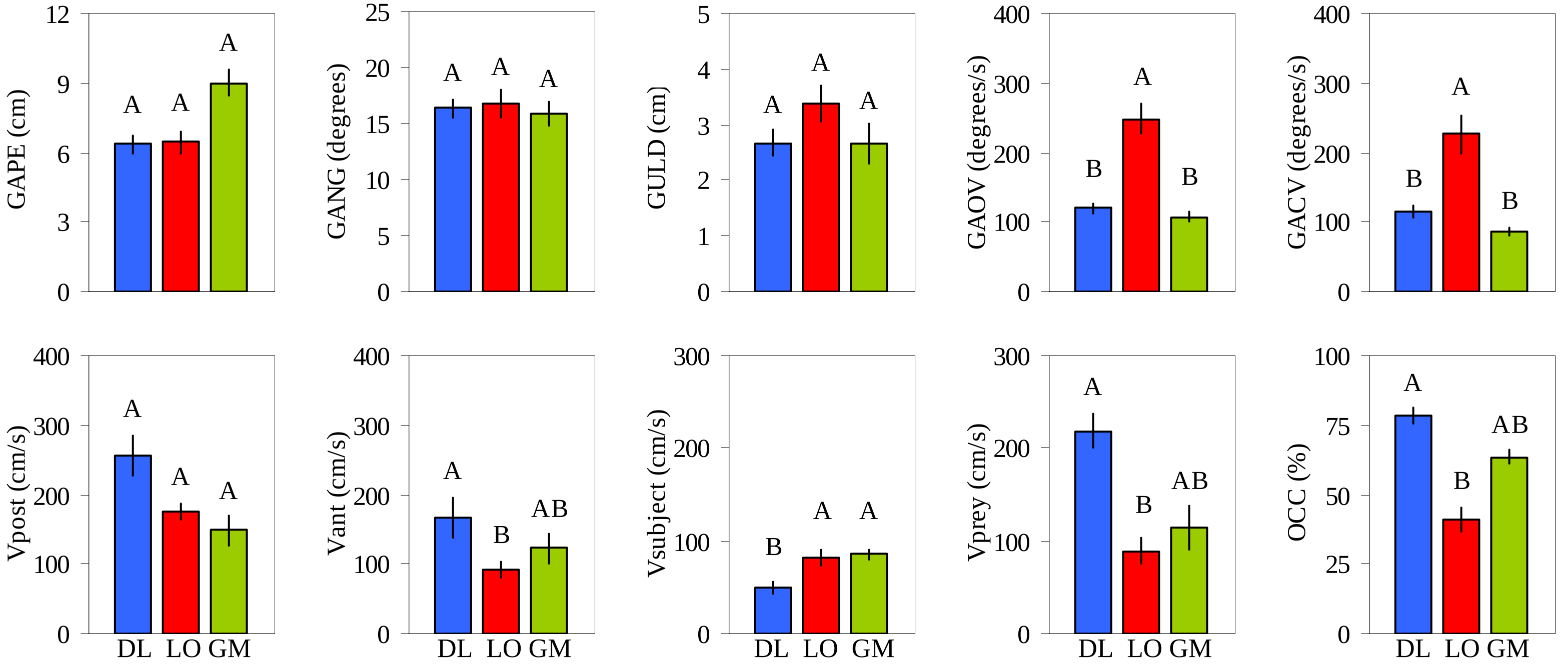

Fig. 11 Mean values ± SEM of lateral kinematic magnitude variables. Different letters indicate significant differences at the $P<0.05$ level.

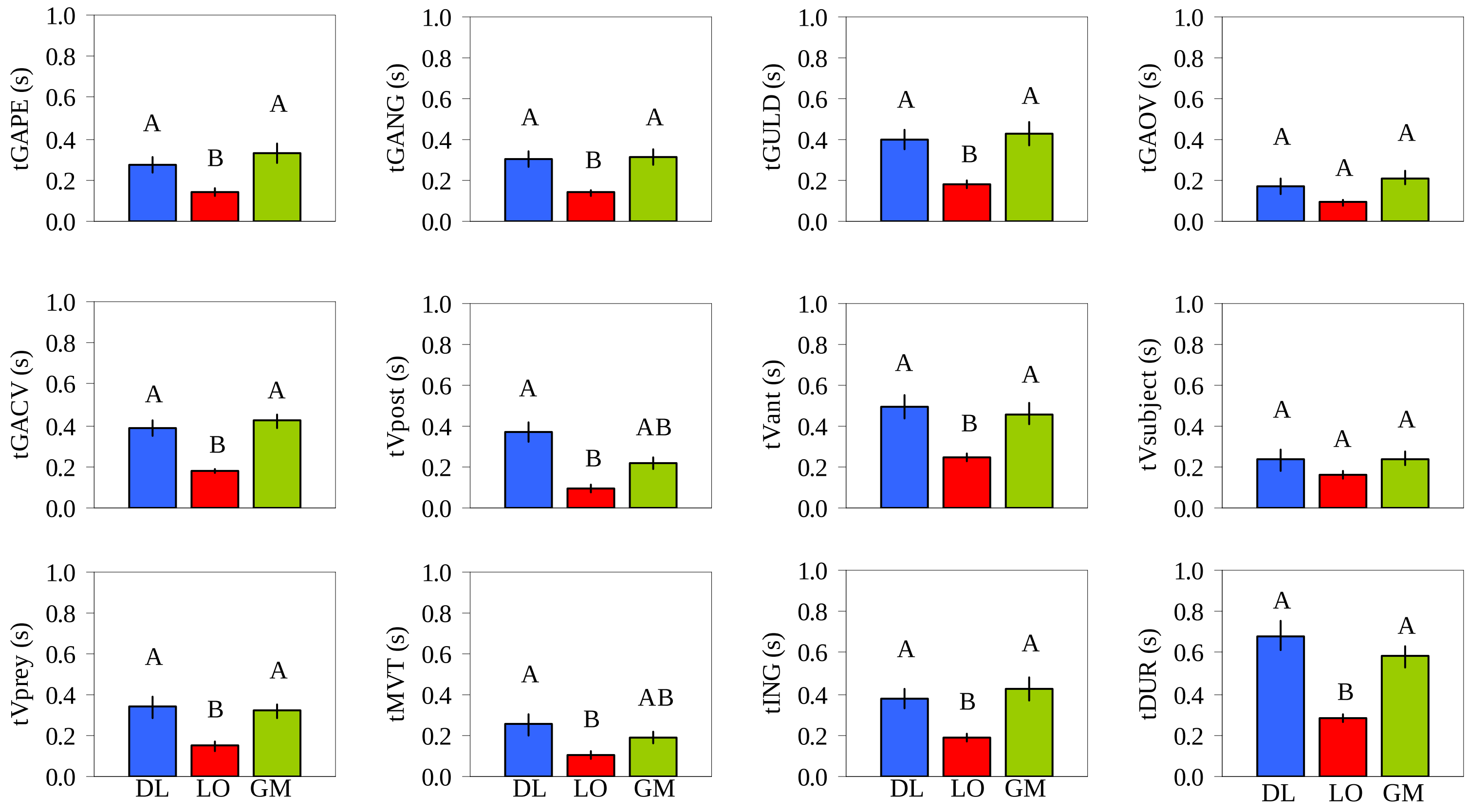

Fig. 12 Mean values ± SEM of lateral kinematic timing variables. Different letters indicate significant differences at the $P<0.05$ level.

subject velocity was found. For all remaining timing variables, belugas and pilot whales were similar, and significantly longer in duration than for Pacific white-sided dolphins. Pilot whales were not significantly different than belugas or Pacific white-sided dolphins for time to maximum posterior lateral occlusion velocity and time to initial movement of prey. Least squares means were also used to construct a canonical centroid plot for beluga, Pacific white-sided dolphin, and pilot whale feeding kinematics (Fig. 13). Variables GAOV, GACV, and tVant loaded strongly onto canonical axis one; variables GAPE, GANG, and tVpost loaded strongly onto canonical axis two. Together, these axes explained 94.3% of the variance among species. An overlap of more than 50% indicated that means (represented by centroids) were similar. Species means did not overlap and indicated a significant difference among all three species. Six out of 7 Pacific white-sided dolphin individuals overlapped (four with each other and two with each other) and suggested that individuals generally did not vary in lateral kinematics. Belugas were highly variable (3 out of 7 individuals overlapped by more than 50%) and suggested that complete feeding repertoire of belugas was not fully captured. Only two pilot whales were used in this study, and these individuals were also highly variable.

Coordination of kinematic sequence and timing is critical for maximum suction generation in teleosts (Holzman et al., 2007). Similar coordination was also observed in all species in this study (Fig. 14). Although the magnitude of kinematic variables differed substantially, the kinematic sequence was conserved: gape and angular velocity increased, maximum gape and gape angle occurred simultaneously, prey reached its maximum velocity toward the subject as hyolingual depression reached its maximum, prey was ingested, and the gape rapidly closed. A posteriorly directed “wave of buccal expansion” was observed in all species, beginning as the anterior jaws opened and progressed posteriorly through hyolingual depression.

Significant correlation was observed in 49.8% of possible combinations of lateral kinematic variables pooled across belugas, Pacific white-sided dolphins, and pilot whales (Table 5, Pearson r correlation, $P<0.05$). For all variables, at least one correlation was significant. All timing variables were significantly correlated to each

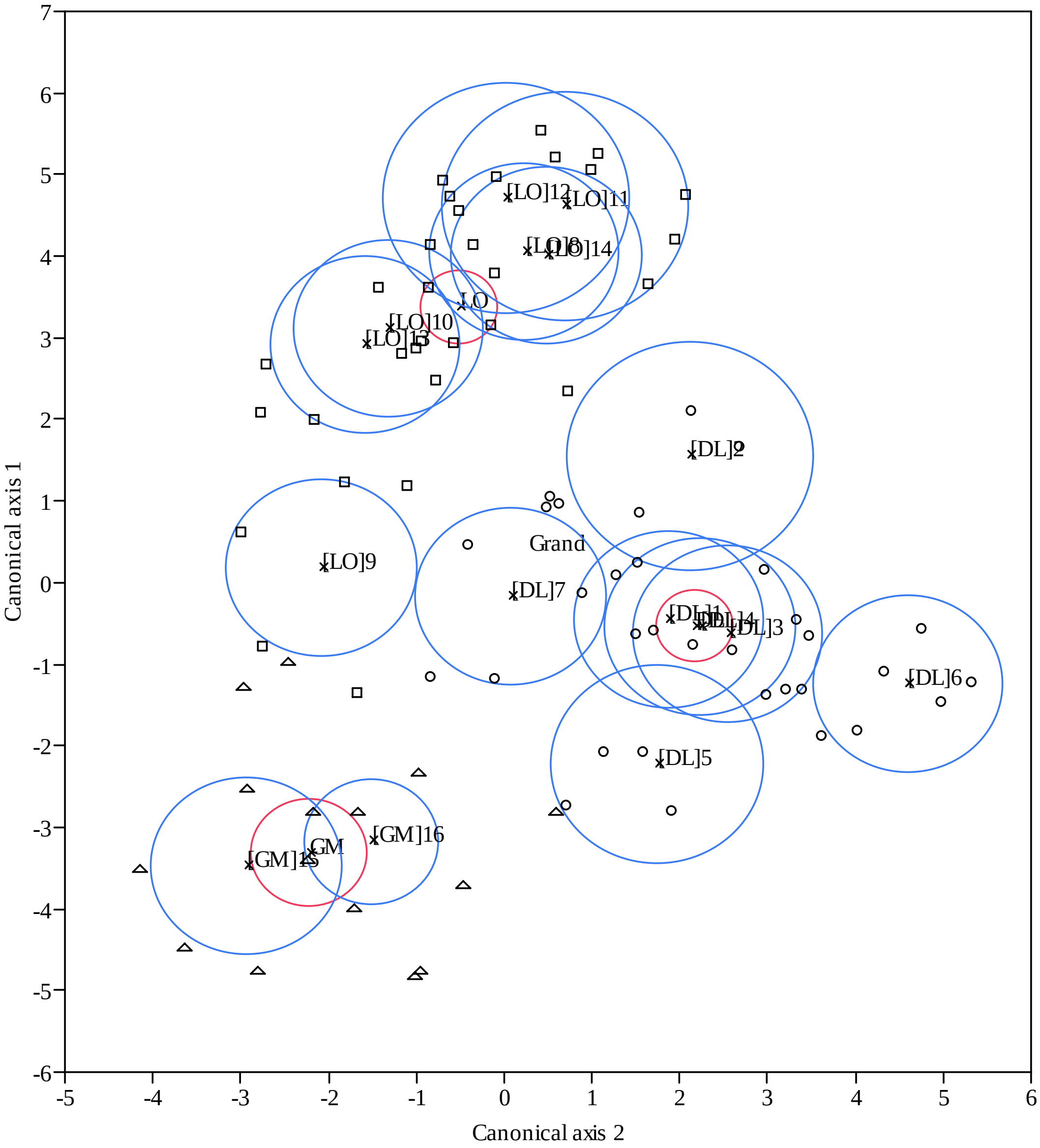

Fig. 13 Canonical centroid plot of lateral kinematic variables. Canonical scores for each trial were plotted (belugas: circles, Pacific white-sided dolphins: squares, pilot whales: triangles). Centroids were also plotted for each species (red) and individual (blue). Species and individual codes are marked for each centroid and follow Table 1.

other. Gape, gape angle, and gape angle velocities were positively correlated to each other, and faster velocities occurred when feeding events were shorter. Lateral gape occlusion was greater and hyolingual depression was shorter when subject velocity was slower. Similarly, prey velocity was greater when lateral occlusion was greater. Hyolingual depression was positively correlated to gape angle opening velocity and subject velocity.

In all species, maximum gape and gape angle measured kinematically were significantly less than maximum gape and gape angle measured from still photos of a maximum gape behavior (referred to as biological maxima herein, t-tests, $P<0.0001$). Maximum biological gape was 17.0 ± 0.59 cm for belugas, 10.5 ± 0.50 cm for Pacific white-sided dolphins, and 19.3 ± 0.62 cm for pilot whales. Kinematic gape was 37.7% of maximum biological gape for belugas, 61.2% for Pacific white-sided dolphins, and 46.7% for pilot whales. Similarly, kinematic gape angle was 39.8%, 67.9%, and 47.3% of biological maximum gape angle for belugas, Pacific white-sided dolphins, and pilot whales, respectively.

Ram-suction index (RSI) was calculated for lateral trials in which the prey was not held by a trainer (free-floating), and resulted in a total of 20 trials each for belugas and Pacific white-sided dolphins, and 24 trials for pilot whales (Fig. 15). Squid-fed trials were included in pilot whale RSI analysis. All species displayed mean ram distances (belugas: 8.5 ± 1.5 cm, Pacific white-sided dolphins: 7.0 ± 0.9 cm, pilot whales: 8.7 ± 1.1 cm) that were greater than suction distances (belugas: 3.9 ± 0.6 cm, Pacific white-sided dolphins: 2.6 ± 0.3 cm, pilot whales: 4.9 ± 0.5 cm). These distances resulted in RSI values that were positive overall (belugas: 0.32 ± 0.07 cm, Pacific white-sided dolphins: 0.43 ± 0.05 cm, pilot whales: 0.26 ± 0.04 cm). Maximum suction distance for each species (belugas: 8.96, Pacific white-sided dolphins: 6.01, pilot whales: 9.04) was less than one mouth diameter, and the range of ram distances varied (belugas: 0.9-25.6 cm, Pacific white-sided dolphins: 1.8-16.9 cm, pilot whales: 1.8-19.0 cm).

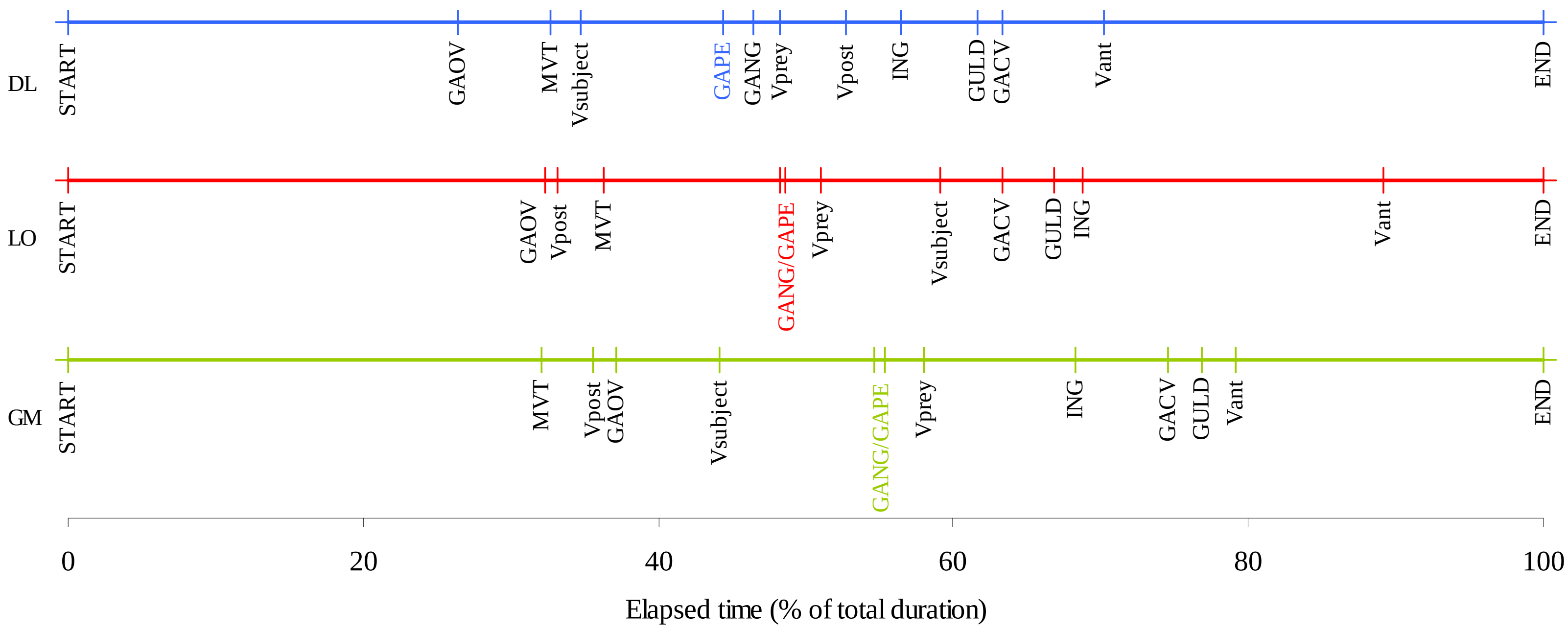

Fig. 14 Timeline of kinematic events. Abbreviations follow Table 2. Time of maximum gape is colored according to species; belugas (DL) are blue, Pacific white-sided dolphins (LO) are red, and pilot whales (GM) are green. Markers represent mean percent of total duration for each kinematic variable within each species.

Table 5 Pearson correlation among lateral kinematic variables. Bold indicates significance at the P<0.05 level.

Variable	GAPE	tGAPE	GANG	tGANG	GAOV	tGAOV	GACV	tGACV	Vpost	tVpost	Vant	tVant
GAPE		0.118	**0.820**	0.078	**0.313**	0.060	**0.287**	0.001	0.173	-0.041	0.090	0.116
tGAPE	0.118		0.050	**0.975**	**-0.460**	**0.884**	**-0.258**	**0.895**	-0.113	**0.706**	0.082	**0.781**
GANG	**0.820**	0.050		0.036	**0.535**	0.029	**0.555**	-0.088	**0.229**	-0.019	0.086	0.088
tGANG	0.078	**0.975**	0.036		**-0.490**	**0.871**	**-0.269**	**0.925**	-0.078	**0.789**	0.153	**0.802**
GAOV	**0.313**	**-0.460**	**0.535**	**-0.490**		**-0.316**	**0.837**	**-0.570**	0.026	**-0.514**	**-0.288**	**-0.444**
tGAOV	0.060	**0.884**	0.029	**0.871**	**-0.316**		-0.168	**0.801**	-0.143	**0.638**	-0.037	**0.650**
GACV	**0.287**	**-0.258**	**0.555**	**-0.269**	**0.837**	-0.168		**-0.385**	-0.052	**-0.325**	-0.093	**-0.293**
tGACV	0.001	**0.895**	-0.088	**0.925**	**-0.570**	**0.801**	**-0.385**		-0.112	**0.783**	0.198	**0.764**
Vpost	0.173	-0.113	**0.229**	-0.078	0.026	-0.143	-0.052	-0.112		0.178	0.180	0.155
tVpost	-0.041	**0.706**	-0.019	**0.789**	**-0.514**	**0.638**	**-0.325**	**0.783**	0.178		**0.338**	**0.799**
Vant	0.090	0.082	0.086	0.153	**-0.288**	-0.037	-0.093	0.198	0.180	**0.338**		**0.257**
tVant	0.116	**0.781**	0.088	**0.802**	**-0.444**	**0.650**	**-0.293**	**0.764**	0.155	**0.799**	**0.257**	
Vsubj	0.107	-0.159	-0.077	-0.175	0.168	-0.154	0.040	-0.183	0.056	**-0.237**	-0.022	-0.138
tVsubj	0.111	**0.553**	0.114	**0.573**	-0.080	**0.587**	0.085	**0.528**	-0.102	**0.410**	0.083	**0.409**
Vprey	0.005	-0.013	0.042	0.038	-0.125	0.025	-0.072	0.036	0.154	**0.325**	**0.275**	0.107
tVprey	0.030	**0.850**	0.013	**0.891**	**-0.434**	**0.790**	**-0.256**	**0.837**	-0.069	**0.777**	0.194	**0.783**
OCC	-0.129	**0.223**	-0.184	**0.268**	**-0.421**	**0.231**	**-0.421**	**0.334**	-0.065	**0.441**	0.149	0.207
tMVT	-0.079	**0.818**	-0.031	**0.865**	**-0.391**	**0.806**	-0.185	**0.757**	-0.051	**0.762**	0.135	**0.734**
tING	0.112	**0.886**	0.059	**0.913**	**-0.426**	**0.781**	**-0.267**	**0.870**	-0.089	**0.757**	0.169	**0.807**
GULD	0.062	0.049	0.149	0.020	**0.247**	0.010	0.190	-0.052	0.092	-0.036	-0.161	0.058
tGULD	0.013	**0.831**	-0.047	**0.847**	**-0.473**	**0.776**	**-0.308**	**0.827**	-0.100	**0.757**	0.100	**0.801**
tDUR	0.034	**0.732**	0.024	**0.799**	**-0.614**	**0.594**	**-0.411**	**0.787**	0.131	**0.862**	**0.388**	**0.881**

Table 5 continued.

Variable	Vsubj	tVsubj	Vprey	tVprey	OCC	tMVT	tING	GULD	tGULD	tDUR
GAPE	0.107	0.111	0.005	0.030	-0.129	-0.079	0.112	0.062	0.013	0.034
tGAPE	-0.159	**0.553**	-0.013	**0.850**	**0.223**	**0.818**	**0.886**	0.049	**0.831**	**0.732**
GANG	-0.077	0.114	0.042	0.013	-0.184	-0.031	0.059	0.149	-0.047	0.024
tGANG	-0.175	**0.573**	0.038	**0.891**	**0.268**	**0.865**	**0.913**	0.020	**0.847**	**0.799**
GAOV	0.168	-0.080	-0.125	**-0.434**	**-0.421**	**-0.391**	**-0.426**	**0.247**	**-0.473**	**-0.614**
tGAOV	-0.154	**0.587**	0.025	**0.790**	**0.231**	**0.806**	**0.781**	0.010	**0.776**	**0.594**
GACV	0.040	0.085	-0.072	**-0.256**	**-0.421**	-0.185	**-0.267**	0.190	**-0.308**	**-0.411**
tGACV	-0.183	**0.528**	0.036	**0.837**	**0.334**	**0.757**	**0.870**	-0.052	**0.827**	**0.787**
Vpost	0.056	-0.102	0.154	-0.069	-0.065	-0.051	-0.089	0.092	-0.100	0.131
tVpost	**-0.237**	**0.410**	**0.325**	**0.777**	**0.441**	**0.762**	**0.757**	-0.036	**0.757**	**0.862**
Vant	-0.022	0.083	**0.275**	0.194	0.149	0.135	0.169	-0.161	0.100	**0.388**
tVant	-0.138	**0.409**	0.107	**0.783**	0.207	**0.734**	**0.807**	0.058	**0.801**	**0.881**
Vsubj		-0.101	-0.218	-0.085	**-0.226**	-0.122	-0.070	**0.253**	-0.106	**-0.254**
tVsubj	-0.101		0.132	**0.563**	0.016	**0.591**	**0.519**	0.063	**0.478**	**0.407**
Vprey	-0.218	0.132		0.098	**0.461**	0.022	-0.048	-0.163	0.110	0.219
tVprey	-0.085	**0.563**	0.098		**0.256**	**0.914**	**0.938**	0.035	**0.857**	**0.798**
OCC	**-0.226**	0.016	**0.461**	**0.256**		0.116	0.213	-0.175	**0.295**	**0.400**
tMVT	-0.122	**0.591**	0.022	**0.914**	0.116		**0.887**	0.095	**0.796**	**0.730**
tING	-0.070	**0.519**	-0.048	**0.938**	0.213	**0.887**		0.070	**0.843**	**0.800**
GULD	**0.253**	0.063	-0.163	0.035	-0.175	0.095	0.070		0.137	-0.033
tGULD	-0.106	**0.478**	0.110	**0.857**	**0.295**	**0.796**	**0.843**	0.137		**0.782**
tDUR	**-0.254**	**0.407**	0.219	**0.798**	**0.400**	**0.730**	**0.800**	-0.033	**0.782**	

Significant differences in mean RSI variables were found among species (MANOVA, Wilks' Lambda, F=1.7, P=0.013). Pacific white-sided dolphin RSI was significantly greater than pilot whale RSI, and beluga RSI was not significantly different from either species (*post hoc* tests, P<0.05). The greatest mouth diameter was observed for pilot whales and may have led to greater suction distances and lower RSI values (Fig. 16). Suction distance of belugas was intermediate to pilot whales and Pacific white-sided dolphins, but was not significantly different. Pacific white-sided dolphin suction distance was significantly less than pilot whales (*post hoc* tests, P<0.05). No significant differences were found for ram distance among all species (*post hoc* tests, P>0.05).

3.1.3 Frontal kinematic analyses

Four kinematic variables were measured from 49 frontal perspective feeding events. Additionally, oral aperture ratio, area, and perimeter were calculated from frames of maximum gape for each trial (Fig. 17). Lateral lip occlusion of gape could be observed from the frontal perspective due to the extent to which this behavior is performed in belugas. This occlusion allowed an oral aperture to form and dictated its size and shape.

A circular anterior oral aperture formed consistently at maximum gape for belugas, unlike for the other odontocetes (Table 6, Fig. 18). Aperture formation by Pacific white-sided dolphins and pilot whales differed considerably from belugas (MANOVA, Wilks' Lambda, F= 2.28, P<0.0001). Aperture area and perimeter were greatest for pilot whales, and were not significantly different between Pacific white-sided dolphins and belugas (*post hoc* tests, P>0.05). The variables with the greatest difference among species were aperture width and aperture ratio (*post hoc* tests, P<0.05). In belugas, aperture ratio was closest to one and aperture width was the smallest of all three species; pilot whales exhibited the lowest aperture ratios and the greatest aperture widths. Mean maximum gape was similar across all species (*post hoc* tests, P>0.05). Therefore, variance in aperture shape (ratio, area, and perimeter) was due to differences in aperture width that reflected differences in pursing ability.

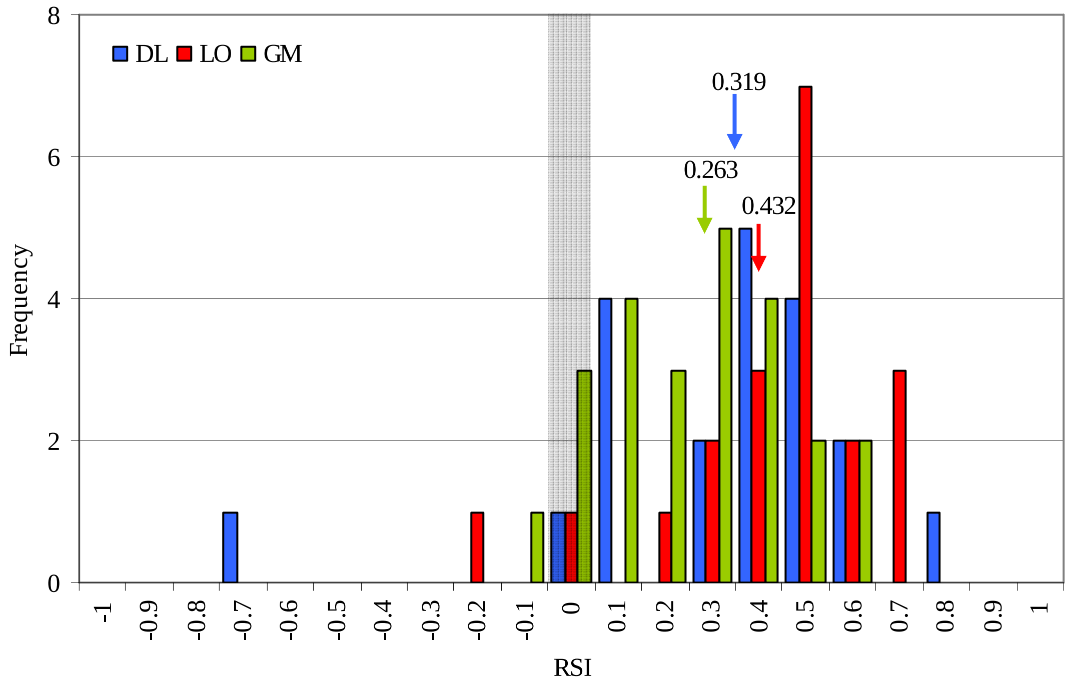

Fig. 15 Histogram of Ram-Suction Index (RSI) values. Gray shading indicates 0 RSI; negative values indicate suction and positive values indicate ram feeding modes. Arrows and values indicate means and are color coded for species.

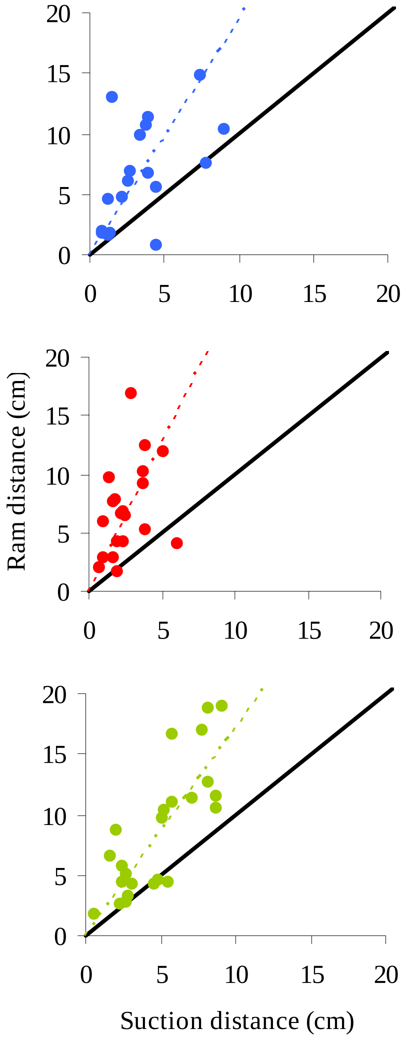

Fig. 16 Ram and suction distances in two dimensional kinematic space. A black solid line indicates the 0 RSI isocline; points above the line represent ram feeding and points below the line represent suction feeding RSI values calculated for each trial. Mean RSI was plotted as an isocline (dashed lines) and are color-coded by species (belugas: blue, Pacific white-sided dolphins: red, pilot whales: green).

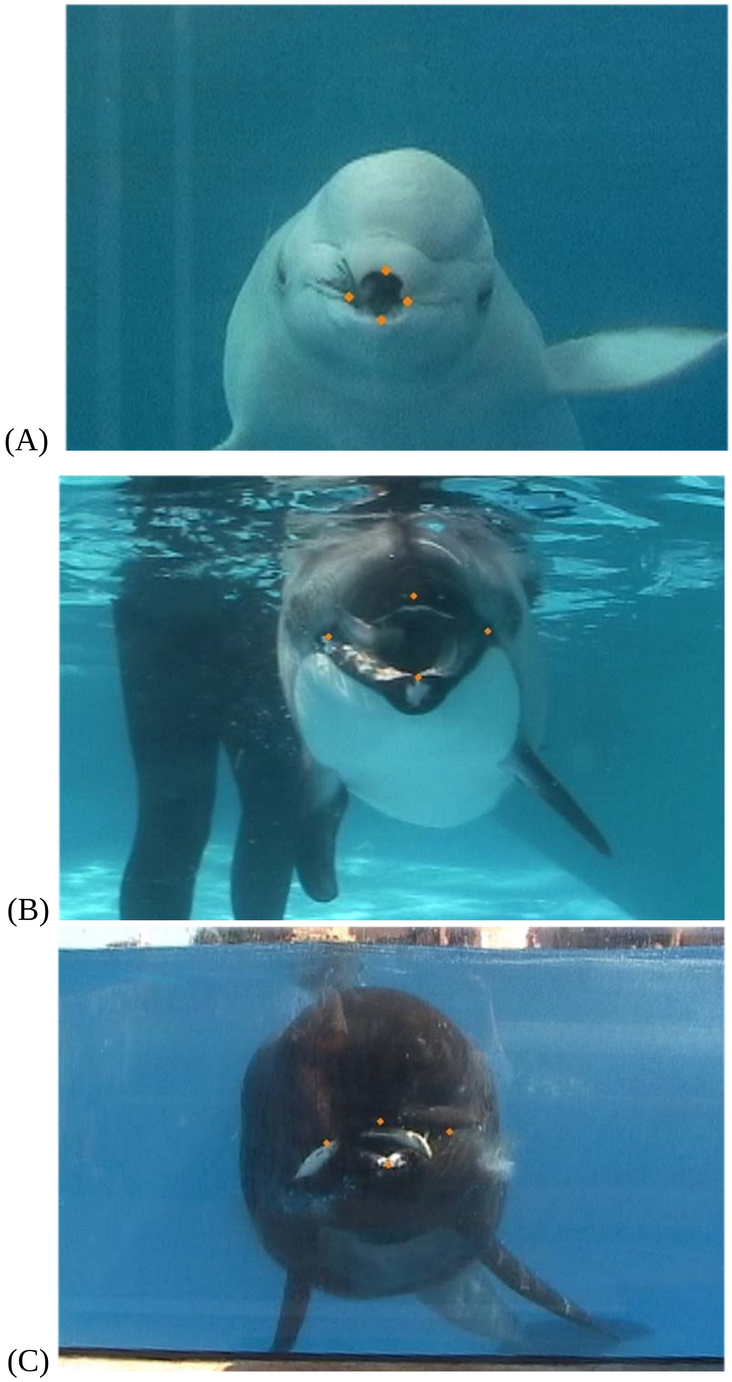

Fig. 17 Oral apertures at maximum gape. Representative still frames of maximum gape were extracted from frontal perspective videos for (A) a beluga, (B) a Pacific white-sided dolphin, and (C) a pilot whale. Points indicate anatomical landmarks used in the analysis. Belugas exhibited a distinctive circular aperture.

Belugas and Pacific white-sided dolphins achieved aperture ratios of one or greater (circular to tall and narrow), while pilot whales did not (Fig. 19). More than half (56.3%) of beluga frontal perspective trials resulted in aperture ratios greater or equal to one. In contrast, Pacific white-sided dolphins achieved ratios of one or greater for only 21.7% of trials. Aperture ratios less than one were more common for Pacific white-sided dolphins (78.3% of trials), and were more representative of the typical aperture shape. The narrow range of aperture ratios for pilot whales (0.27 to 0.55) suggests a stereotyped aperture shape, whereas the wide range observed in belugas (0.63 to 1.77) indicates a tighter control over aperture shape than the other two species.

For frontal kinematic variables, 47.6% of correlations were significant (Table 7, Pearson r correlation, $P<0.05$). Timing variables (time to maximum gape and feeding event duration) were correlated only with each other (0.68). Aperture area and perimeter were calculated variables and both increased when oral aperture gape and width increased; width increased with increased gape. Aperture ratios were greater when width was smaller and indicates that variation among aperture ratios in belugas, Pacific white-sided dolphins, and pilot whales is dependent on variation in aperture width.

3.2 Intraoral pressure generation

Maximum subambient (suction) and suprambient (hydraulic jetting) pressure peaks were analyzed for 368 pressure profiles. Suction profiles occurred more frequently than those for hydraulic jetting (belugas: 87% of traces, n=186, Pacific white-sided dolphins: 56% of traces, n=89, pilot whales: 89% of traces, n=93). When subambient and suprambient pressure were observed within the same feeding trial, both were analyzed. Some degree of subambient and suprambient pressure generation was observed in all species (Fig. 20). Belugas generated strong subambient pressure changes (maximum: -122.0 kPa) with fast expansive and compressive rates (mean PEXP: 18,243.9 kPa/s , mean PCOMP: 9,122.8 kPa/s) and a longer total duration (mean: 0.362 ± 0.01 s, Table 8, Fig. 21). Hydraulic jetting in belugas resulted in a similar profile except that mean duration was shorter (mean: 0.110 ± 0.03 s, Table 8, Fig. 22).

Table 6 Mean values ± SEM for frontal kinematic variables.

	DL	LO	GM
GAPE (cm)	7.732 ± 0.495	8.275 ± 0.61	8.012 ± 2.28
tGAPE (s)	0.260 ± 0.023	0.169 ± 0.025	0.225 ± 0.155
WIDTH (cm)	7.535 ± 0.395	11.321 ± 0.575	21.313 ± 6.542
tDUR (s)	0.548 ± 0.077	0.392 ± 0.049	0.421 ± 0.205
aperture ratio	1.046 ± 0.072	0.736 ± 0.047	0.385 ± 0.074
aperture area (cm^2)	42.150 ± 4.449	57.250 ± 6.46	102.960 ± 50.621
aperture perimeter (cm)	24.187 ± 1.273	31.382 ± 1.754	48.678 ± 13.839

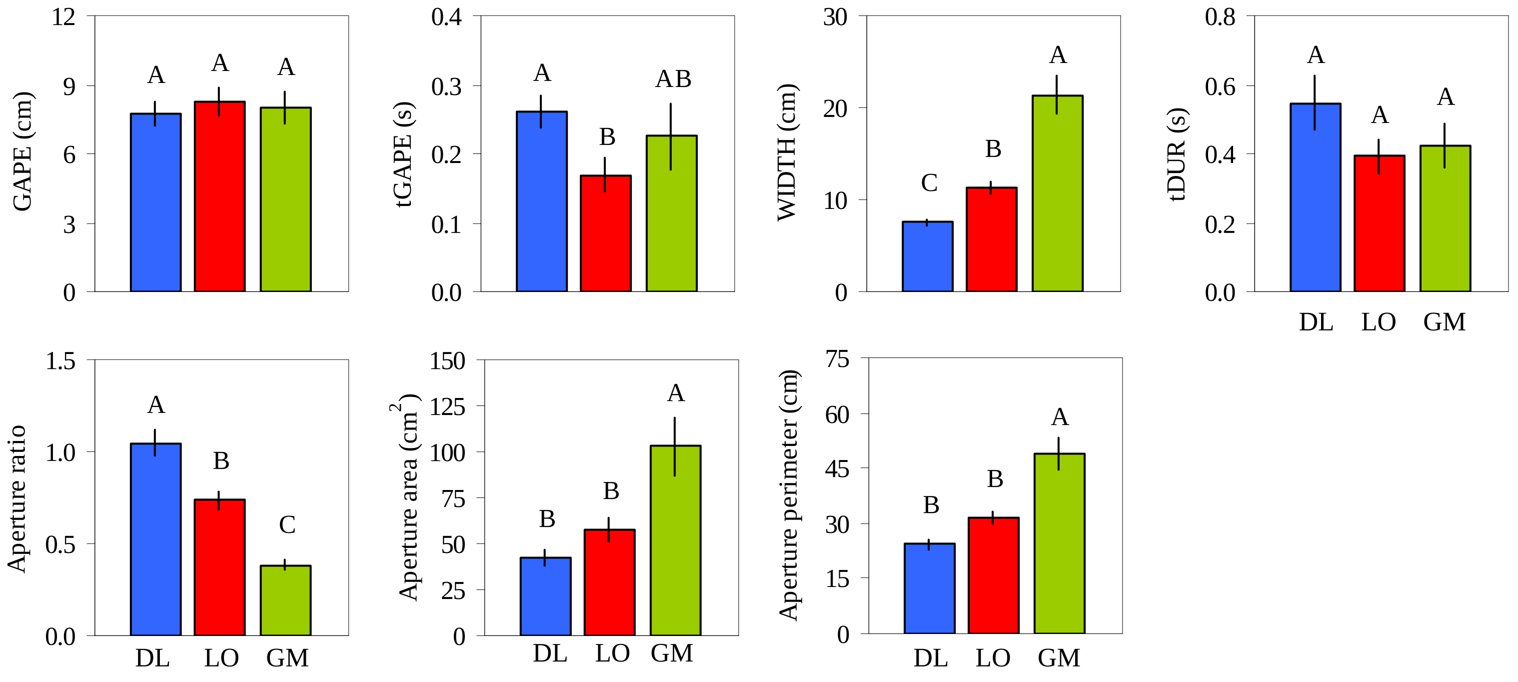

Fig. 18 Mean values ± SEM of frontal kinematic variables. Different letters indicate significant differences at the $P<0.05$ level.

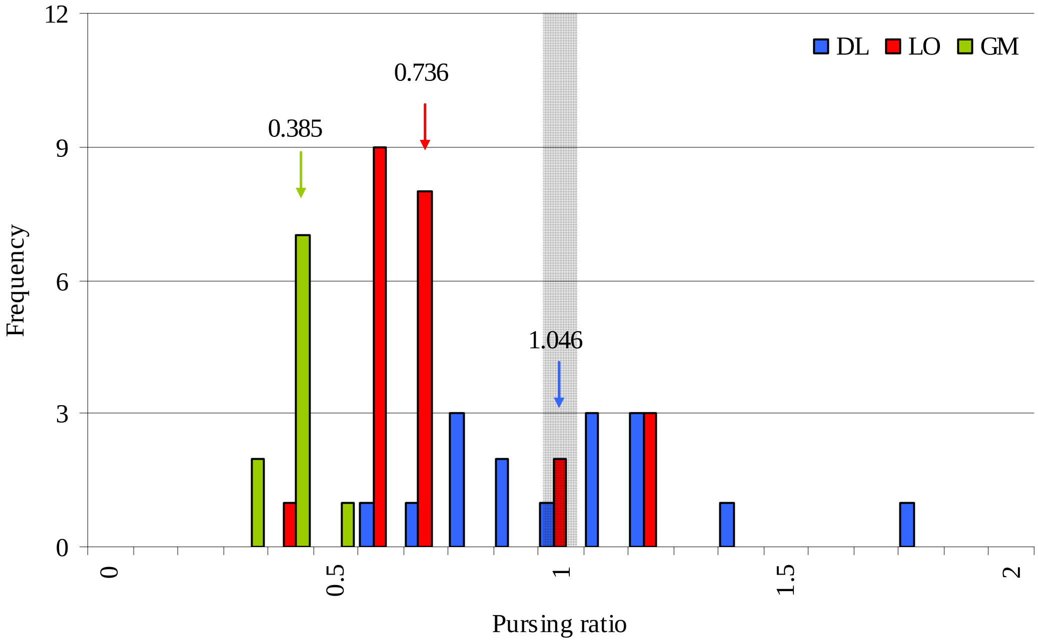

Fig. 19 Histogram of oral aperture ratios. Gray shading indicates a ratio of one; values less than one indicate horizontally elongated and values greater than one indicate vertically elongated aperture shapes. Arrows and values indicate means and are color coded for species.

Table 7 Pearson correlation among frontal kinematic variables. Bold indicates significance at the P<0.05 level.

Variable	GAPE	tGAPE	WIDTH	tDUR	aperture ratio	area	perimeter
GAPE		0.16	**0.37**	0.21	**0.35**	**0.76**	**0.607**
tGAPE	0.16		0.01	**0.68**	0.10	0.19	0.0676
WIDTH	**0.37**	0.01		-0.02	**-0.74**	**0.79**	**0.9157**
tDUR	0.21	**0.68**	-0.02		0.17	0.17	0.0829
aperture ratio	**0.35**	0.10	**-0.74**	0.17		-0.25	**-0.4838**
area	**0.76**	0.19	**0.79**	0.17	-0.25		**0.9429**
perimeter	**0.607**	0.0676	**0.9157**	0.0829	**-0.4838**	**0.9429**	

Pacific white-sided dolphins generated less subambient pressure than belugas (maximum: -27.1 kPa). Placement of the transducer was confirmed from video, and indicated that pressure generation resulted from subject feeding behavior and was not a bow wave. The rate of pressure change was slow (maximum PEXP: 2,569.8 kPa/s, maximum PCOMP: 4,889.7 kPa/s) and suction events were short (mean: 0.100 ± 0.01 s). Hydraulic jetting in Pacific white-sided dolphins produced pressure changes of a greater magnitude than suction (maximum: 100.1 kPa). Pressure change rates were much less during the expansive phase (maximum PEXP: 5,265.4 kPa/s, maximum PCOMP: 17,601.4 kPa/s) and duration was rapid (mean: 0.073 ± 0.01 s).

Subambient pressure generation was low in pilot whales (maximum: -19.6 kPa) and was reflected in low rates of pressure change (maximum PEXP: 593.9 kPa/s, maximum PCOMP: 430.1 kPa/s), as well as a long duration (mean: 0.284 ± 0.02 s). However, pilot whales generated strong suprambient pressure changes (+120.0 kPa) despite low rates (maximum PEXP: 1,442.4 kPa/s, maximum PCOMP: 9,797.0 kPa/s) and a long total duration similar to suction events (mean: 0.202 ± 0.04 s).

A significant species effect was found among subambient pressure generation timing variables (MANOVA, Wilks' Lambda, F=6.12, P<0.0001) but not for hydraulic jetting variables (MANOVA, Wilks' Lambda, F=0.93, P=0.59). Belugas, Pacific white-sided dolphins, and pilot whales were all significantly different from each other in expansive phase duration and total duration (*post hoc* tests, P<0.05). The longest duration was observed for belugas and the shortest duration was observed for Pacific white-sided dolphins. Compressive phase durations were similar between belugas and pilot whales and were longer than in Pacific white-sided dolphins (*post hoc* tests, P<0.05).

All subambient pressure generation variables were significantly correlated to each other, and 80% of suprambient pressure generation variables were significantly correlated to each other (Table 9, Pearson r correlation, P<0.05). The strongest correlations were observed between total duration and expansive and compressive phase durations for both types of events (suction: 0.81 and 0.92, hydraulic jetting: 0.91 and

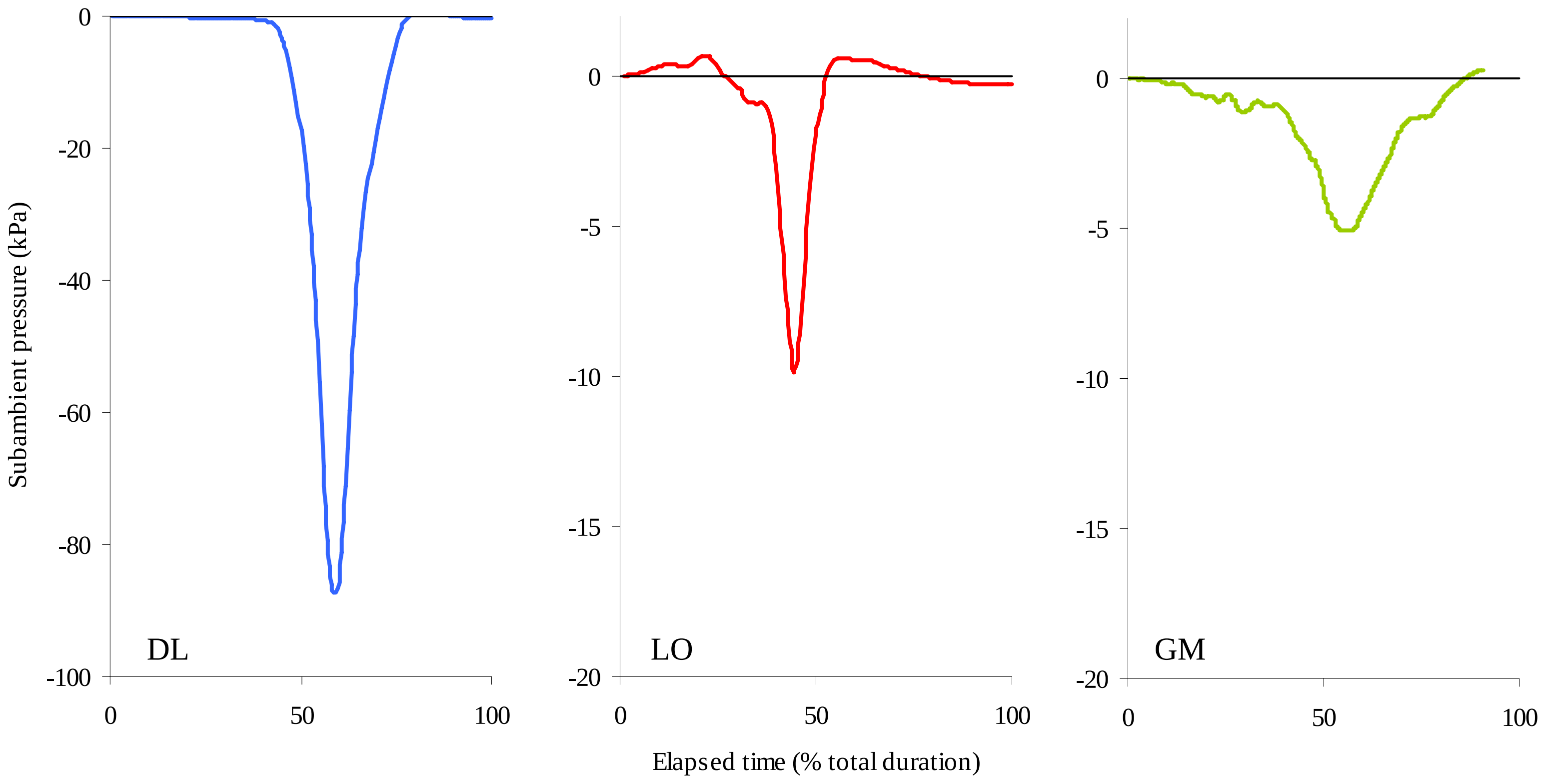

Fig. 20 Representative pressure traces from each species. Traces are shown for a beluga (blue), Pacific white-sided dolphin (red), and pilot whale (green) as kPa vs. time scaled to percent of total duration. Note the scale of each trace.

Table 8 Maximum pressure generation performance and mean event times ± SEM for pressure generation variables.

Subambient pressure generation	DL	LO	GM
Maximum Psub (kPa)	-121.961	-27.051	-19.551
Mean tEXP (s)	0.146 ± 0.006	0.046 ± 0.005	0.108 ± 0.009
Maximum PEXP (kPa/s)	18243.9	2569.77	593.892
Mean tCOMP (s)	0.216 ± 0.011	0.054 ± 0.006	0.176 ± 0.011
Maximum PCOMP (kPa/s)	9122.81	4889.66	430.108
Mean tDUR (s)	0.362 ± 0.014	0.100 ± 0.008	0.284 ±0.016
Suprambient pressure generation			
Maximum Psupra (kPa)	127.846	100.109	120.059
Mean tEXP (s)	0.052 ± 0.015	0.040 ± 0.009	0.1399 ± 0.038
Maximum PEXP (kPa/s)	14617.6	5265.42	1442.37
Mean tCOMP (s)	0.058 ± 0.018	0.034 ± 0.007	0.0624 ±0.016
Maximum PCOMP (kPa/s)	50051.6	17601.4	9797.02
Mean tDUR (s)	0.110 ± 0.029	0.073 ± 0.012	0.2023 ± 0.043

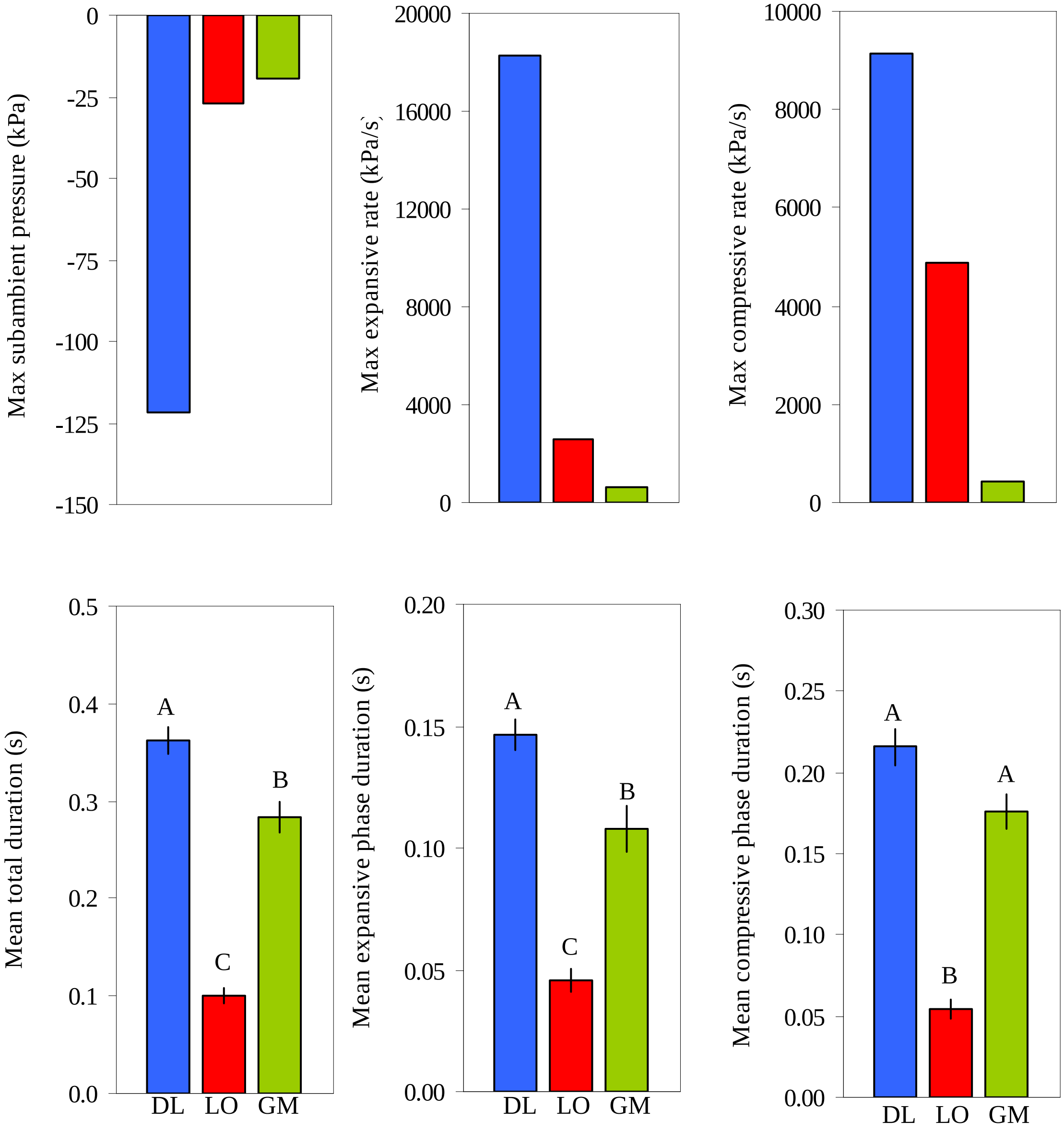

Fig. 21 Maximum performance values and mean timing values ± SEM for subambient pressure generation variables. Different letters indicate significant differences at the P<0.05 level.

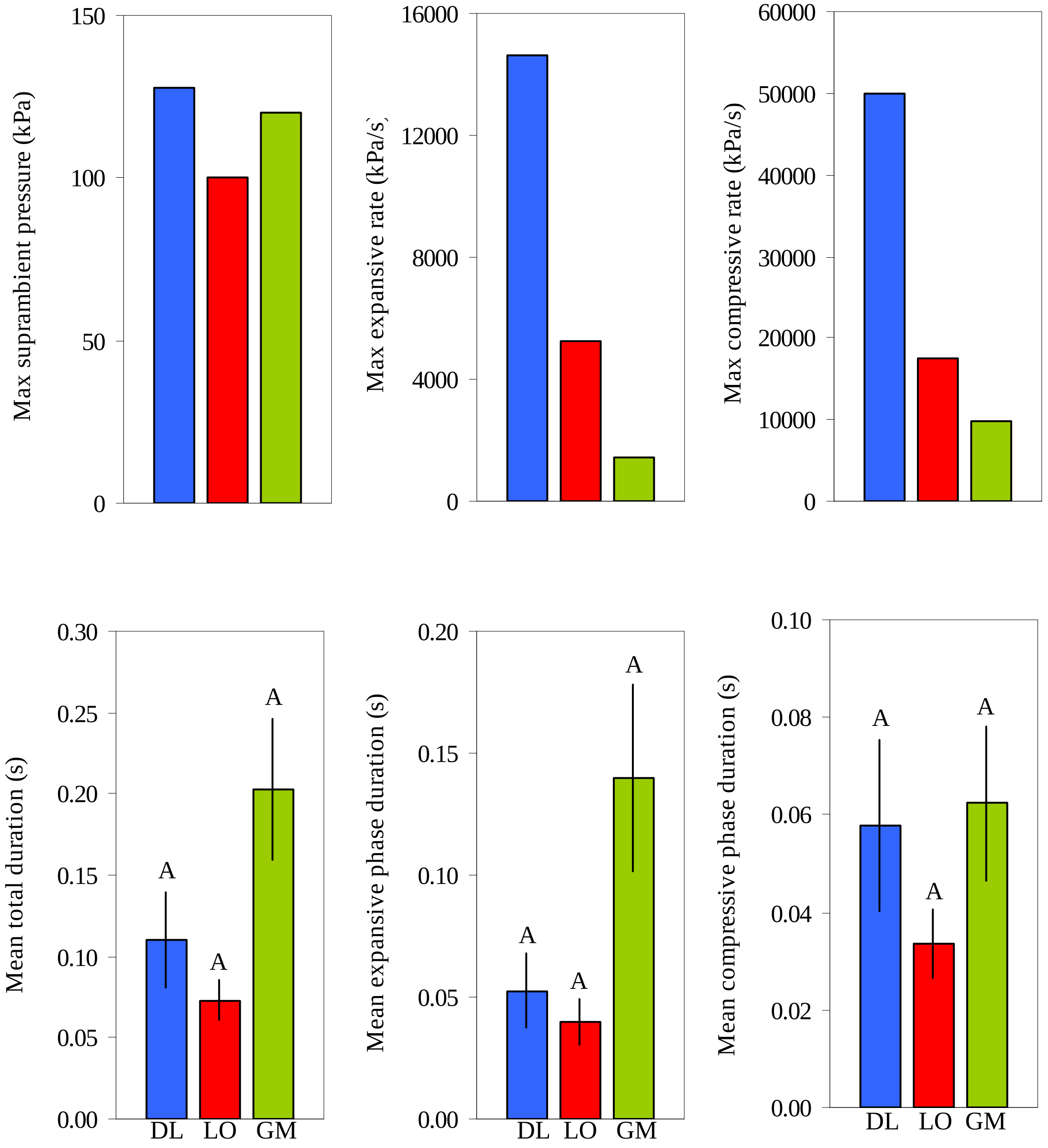

Fig. 22 Maximum performance values and mean timing values ± SEM for suprambient pressure generation variables. No statistically significant difference among species timing variable means was observed at the P<0.05 level.

0.80, respectively). Total duration was positively correlated to subambient pressure (0.20) but not suprambient pressure. The rates of pressure change during the expansive and compressive phases during both event types were negatively correlated to duration of the each phase as well as total duration, and indicate that larger rates occurred over a shorter duration. Both subambient and suprambient pressure were positively correlated to expansive and compressive phase rates of pressure change. The magnitude of suprambient pressure generation was not significantly correlated to any timing variables.

3.3 The evolution of suction feeding

Data from kinematic and biomechanical analyses were combined with published and unpublished data to explore the evolution of suction feeding in Odontoceti. Kinematic and biomechanical characters were available for fewer than 10% of species represented by the full phylogeny. For this reason, the phylogeny of Odontoceti (Fig. 1) was collapsed to condense species and provide a greater resolution of ancestral states. The genera of *Physeter* and *Kogia* were collapsed to their respective Families (Physeteridae and Kogiidae), as well as the genus *Platanista* (Platanistidae), beaked whales (Ziphiidae), belugas and narwhals (Monodontidae), and porpoises (Phocoenidae). The river dolphin Families of Lipotidae, Pontoporiidae, and Iniidae, were collapsed into a paraphyletic single branch based on similar available character state data. Family Delphinidae was divided into six polytomous sister clades of genera, based on Le Duc et al. (1999), to maintain resolution and are as follows: (1) *Sotalia* and *Steno*, (2) *Sousa*, *Stenella*, *Delphinus*, *Tursiops*, and *Lagenodelphis*, (3) *Lagenorhynchus acutus* and *L. albirostris* (paraphyletic), (4) *Orcaella* and *Orcinus*, (5) *Grampus*, *Pseudorca*, *Globicephala*, *Peponocephala*, and *Feresa*, and (6) *Lagenorhynchus* (with the exception species in clade 3), *Cephalorhynchus*, and *Lissodelphis*. Kinematic and biomechanical data were available for 46% of clades and morphological data were available for up to 100% of clades represented by this family level phylogeny of Odontoceti (Table 10). Tongue width:length ratios were the only data available for the Mysticete outgroup.

Table 9 Pearson correlation among pressure generation variables. Bold indicates significance at the P<0.05 level.

Subambient variables	Psub	tEXP	PEXP	tCOMP	PCOMP	tDUR
Psub		**0.21**	**0.62**	**0.16**	**0.56**	**0.20**
tEXP	**0.21**		**-0.64**	**0.54**	**-0.28**	**0.81**
PEXP	**0.62**	**-0.64**		**-0.31**	**0.66**	**-0.49**
tCOMP	**0.16**	**0.54**	**-0.31**		**-0.70**	**0.92**
PCOMP	**0.56**	**-0.28**	**0.66**	**-0.70**		**-0.60**
tDUR	**0.20**	**0.81**	**-0.49**	**0.92**	**-0.60**	
Suprambient variables	Psupra	tEXP	PEXP	tCOMP	PCOMP	tDUR
Psupra		0.05	**0.52**	0.00	**0.61**	0.06
tEXP	0.05		**-0.83**	**0.53**	**-0.39**	**0.91**
PEXP	**0.52**	**-0.83**		**-0.46**	**0.68**	**-0.75**
tCOMP	0.00	**0.53**	**-0.46**		**-0.79**	**0.80**
PCOMP	**0.61**	**-0.39**	**0.68**	**-0.79**		**-0.60**
tDUR	0.06	**0.91**	**-0.75**	**0.80**	**-0.60**	

Gap coding of biomechanical and morphological character states resulted in 16 characters with up to three character states (Appendix A) that were mapped onto an existing phylogenetic tree for Odontoceti. For family-level clades with multiple species represented, mean character values for the clade were used to code discrete character states. Gap coding with a criterion of one standard deviation usually coded binary discrete variables; however, three character states were coded for the following variables: total duration, RSI, tooth counts, tongue width:length ratios, MBI, and hyoid size ratios. If gap criteria were not lowered to enhance character state resolution for some variables, character states changes would not have occurred for total duration and tooth counts, and could not have been mapped onto the tree. Additionally, MBI and hyoid size would not have been informative, and only one species would have generated a gap. Standard deviation among family-level clades was usually high, and indicated a large variance in character states among families.

Character states from sixteen resulting characters were combined into a single character matrix (Table 10) that was plotted onto a family level phylogeny of Odontoceti (Fig. 23). Thirty four character state changes took place at 13 points along odontocete evolution. Four taxa did not display state changes on their respective terminal branches (Physeteridae, Delphinidae 3, Delphinidae 6, and Phocoenidae). Kinematics appeared to be conserved throughout the phylogeny, with few changes present; most state changes appeared to be morphological. These changes in feeding characters resulted in 7 terminal taxa with suction adaptations (Physeteridae, Kogiidae, Ziphiidae, Monodontidae, Phocoenidae, Delphinidae 4: *Orcaella* and *Orcinus*, and Delphinidae 5: *Grampus*, *Pseudorca*, *Globicephala*, *Peponocephala*, and *Feresa*) and 6 with ram adaptations (Platanistidae, the paraphyletic river dolphin clade: Lipotidae, Pontoporiidae, and Iniidae, Delphinidae 1: *Sotalia* and *Steno*, Delphinidae 2: *Sousa*, *Stenella*, *Delphinus*, *Tursiops*, and *Lagenodelphis*, Delphinidae 3: *Lagenorhynchus acutus* and *L. albirostris*, and Delphinidae 6: *Lagenorhynchus*, *Cephalorhynchus*, and *Lissodelphis*). The common delphinid ancestor was likely specialized for ram, and the presence of suction in clades 4 and 5 represent independent events of suction specialization.

Based on available evidence, the ancestral state for Odontoceti (Table 11) was most likely a ram feeding state. Morphological data were the most complete across the phylogeny and indicated that the odontocete common ancestor most likely had numerous teeth, a long narrow rostrum with a narrow tongue, and a medium size hyoid. This ancestor displayed a medial character state for 67% of characters with three coded states. The analysis tended to heavily weight characters if they were present in basal clades. Therefore, the ancestral state among Odontoceti resulted in suction feeding characters such as a small gape with a short duration, a long suction and short ram distance, and strong subambient pressure generation.

Table 10 Character matrix of gap coded character states. Missing values indicate unavailable data.

Family	GAPE	tGAPE	GANG	GAOV	Vprey	GULD	tGULD	tDUR	Dprey	Dpredator	RSI	Psub	Tooth count	MBI	Tongue W:L	Hyoid L1:W
Mysticeti															0	
Physeteridae													1	2	1	
Kogiidae	0	0	1	1	0	0	0	1	1	0	0		0	0		
Platanistidae													2	2		
Ziphiidae													0	2		2
Lipotidae, Pontoporiidae, Iniidae													2	2		1
Monodontidae	0	0	0	0	1	0	0	1	1	0	1	1	0	1	2	1
Delphinidae 1													2	2		0
Delphinidae 2	1	1	0	0		1	1	2	0	1	2		2	2	1	0
Delphinidae 3													2	2	1	1
Delphinidae 4													0	1		
Delphinidae 5	0	0	0	0	0	0	0	1	1	0	1	0	0	1	2	1
Delphinidae 6	0	0	0	1	0	0	0	0	1	0	1	0	2	2		1
Phocoenidae	0	0						0				0	1	1	1	1

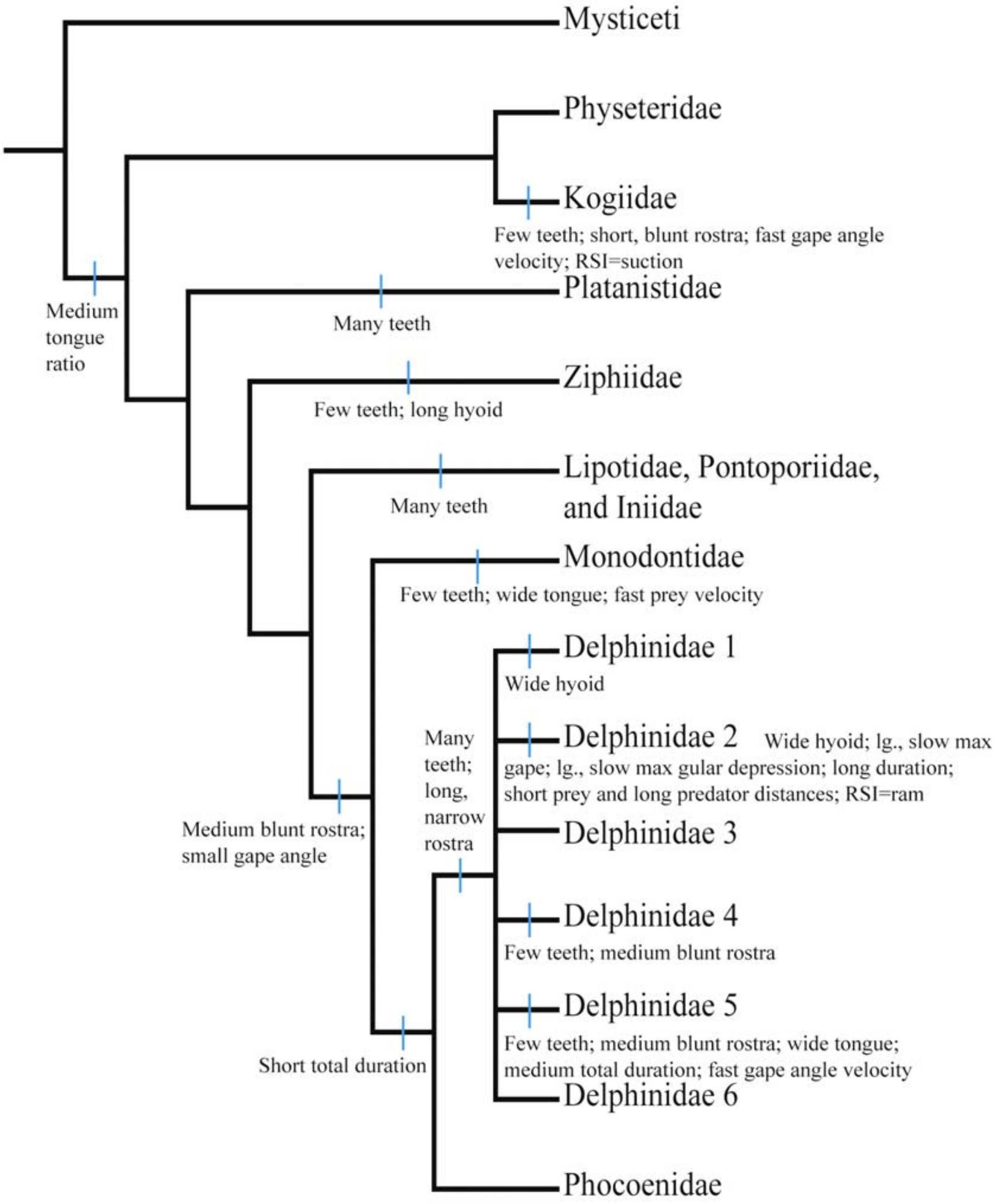

Fig. 23 Reconstruction of Odontoceti feeding character states. Blue bars indicate positions where at least one change in state occurred and were determined using maximum likelihood. Ancestral states (Table 11) are assumed unless otherwise noted.

Table 11 The most likely hypothesis of character states in the odontocete common ancestor. States were determined by maximum likelihood.

Variable	State
Total duration	Medium (0.47-0.68 s)
Gape	Small (<9 cm)
Time to gape	Short (<0.327 s)
Gape angle	Large (>40°)
Gape angle velocity	Slow (<120°/s)
Prey velocity	Slow (<115 cm/s)
Hyolingual depression	Short (<3.4 cm)
Time to hyolingual depression	Short (<0.43 s)
Suction distance	Long (>5 cm)
Ram distance	Short (<25 cm)
RSI	Suction/ram combination (-0.2<RSI<0.4)
Subambient pressure generation	Strong (>100 kPa)
Tooth counts	Medium (30-150 teeth)
MBI	Long/narrow rostra (MBI<0.57)
Tongue W:L	Narrow (<0.167)
Hyoid L1:W	Medium (0.57-0.67)

4. DISCUSSION

4.1 The use of ram and suction in odontocetes

4.1.1 Belugas

The results of the kinematic and pressure measurements demonstrate that suction is of great importance for belugas and suction feeding is likely their primary feeding mode. When approaching food items, belugas maintained an approach velocity less than 50 cm/s and were able to ingest prey with greater velocity than other odontocete species in this study (over 500 cm/s). Belugas also exhibited a limited gape and the ability to purse the anterior lips to create a circular aperture. This pursing behavior also functioned to occlude lateral gape. The shape and size of the oral aperture is an important component in vertebrate suction feeding, since it regulates the velocity of water flow into the mouth, and can determine the magnitude of suction generation (Wainwright and Day, 2007). Oral aperture surface area as small as 19 cm^2 and circumference as small as 18 cm provided evidence for high velocity of water flow in belugas. Therefore, it is likely that restricted gape capability and the ability to form a small, circular aperture contribute to well-developed suction capability in belugas.

Based on the kinematic data, belugas are able to increase intraoral volume through hyolingual depression and retraction. Belugas were observed to slightly adduct the hyoid (and presumably the tongue) just prior to the onset of a feeding event (Phase I). This behavior is a preparatory phase that likely functions to remove residual water from the oral cavity and maximize the volume change at the onset of hyolingual displacement. The observed expulsion of water from the mouth prior to some feeding event supports this hypothesis. Similar behaviors are reported in actinopterygian fishes (Lauder, 1980), and have been recently reported in bearded seals, which are also suction specialists (Marshall et al., 2008). Suction in marine mammals can be generated by rapid depression of the hyolingual apparatus or rapid opening of the jaws (Bloodworth and Marshall, 2005). Mean gape angle opening velocity of only 120°/s, a magnitude much smaller than that of ram feeding Pacific white-sided dolphins, indicated that hyolingual depression likely contributed more to suction generation in belugas than rapid jaw opening.

The importance of suction in the feeding mode of belugas was probably underestimated in this study. The animals used in this study were captive their entire lives and were habituated to receiving non-evasive prey. For this reason, they probably did not perform maximally in every feeding trial. In addition, evidence suggests that belugas frequently consume benthic prey (Finley and Gibb, 1982; Seaman et al., 1982; Dahl et al., 2000; Barros and Clarke, 2002; Laidre and Heide-Jorgensen, 2005). In elasmobranchs, benthic feeding enhances suction generation (Nauwelaerts et al., 2008). Belugas are capable of subambient pressure generation greater than -100 kPa in pelagic environments. If suction is enhanced during beluga benthic feeding, it is likely that the importance of benthic foraging in belugas may be greater than previously assumed. It is also likely that utilizing substrate-enhanced suction generation to capture benthic prey might be a primary feeding behavior in natural environments, and was not observed in this study.

4.1.2 Pacific white-sided dolphins

The primary feeding mode of Pacific white-sided dolphins in this study was definitively ram. Pacific white-sided dolphins approached prey items at up to 220 cm/s and did not ingest prey from a distance farther than 6 cm. Ram feeding behavior was characterized by a gape and gape angle that were greater than 60% of their maximum capabilities, and gape was not as limited as observed in belugas. Anterior lip aperture ratios of Pacific white-sided dolphins were generally less than one and represented a horizontally oblong aperture shape. The total mean feeding event lasted less than 0.3 s and was significantly shorter than for belugas or pilot whales. This greater ram component reflects the dependence on ram to rapidly capture elusive prey, a result that is not unusual (Wainwright et al., 2001). However, some indication of suction use was observed during kinematic feeding trials. In some trials, prey was captured before maximum gape occurred and Pacific white-sided dolphins did not rely on jaw closure and occlusion to retain prey. Surprisingly, the lip margins of Pacific white-sided dolphins did not fully open until after maximum gape. This behavior indicated a limited capability to purse the anterior and lateral lips, which partially occluded lateral gape. Based on known facial anatomy, this was an unexpected finding. Lateral gape was occluded by only 40% at the first frame of visible prey movement, and a lesser degree of occlusion persisted until after maximum gape.

The ability to occlude lateral gape and slightly purse the anterior lips indicated that Pacific white-sided dolphins may be capable of limited suction capability. This functional hypothesis was confirmed by the maximum *in vivo* subambient pressure measurement of -30 kPa. While this performance measure is not impressive for an animal this size, it does confirm a limited suction capability. In contrast to belugas, rapid gape opening may be the primary mechanism by which Pacific white-sided dolphins can generate suction, as evidenced by rapid gape angle velocities and minimal hyolingual depression, although some hyolingual contribution may also be present. This suction capability was most likely used to compensate for rapid approach velocities, to manipulate the orientation of prey within the mouth, or to transport prey from the jaws to the esophagus.

4.1.3 Pilot whales

Pilot whales in this study exemplified a mixture of suction and ram feeding modes that was intermediate to the feeding modes displayed by belugas and Pacific white-sided dolphins. Pilot whales can use suction to capture prey (Werth, 2000), and in this study, some adaptations for suction generation were observed. Pilot whales demonstrated a hyolingual preparatory phase similar to that observed in belugas. During phase I, water was often expelled at the lip margins, a behavior thought to increase the intraoral volume change and enhance suction generation. Although approach velocity was similar to Pacific white-sided dolphins (85 cm/s), pilot whales were also able to slow their velocity with their pectoral flippers in order to capture prey. Lateral gape occlusion greater than 60% of the total jaw length was observed in every trial for pilot whales, and the maximum observed gape was 45% of the maximum capability. However, this consistent capability was likely due to limited gape and not a pursing behavior. Unlike Pacific white-sided dolphins, gape and lateral occlusion opened in synchrony and indicated that no additional orofacial conformational change occurred. Gape did not open more than 50% of its capability and the lip margins remained in contact for approximately 50% of their length. It is possible that suction generated by rapid hyolingual depression and retraction in pilot whales is efficient enough to capture prey without the need for rapid jaw opening. The pilot whales in this study performed similarly to previously published pilot whale kinematics (Werth, 2000), and supported the assumption that kinematics measured in this study represent those of the population.

Although evidence suggested that pilot whales may rely on suction to acquire prey, other results suggested that ram was also a significant component of the feeding mode. Like Pacific white-sided dolphins, pilot whales rapidly approached their prey, which was then drawn into the mouth at over 100 cm/s, half the velocity of prey ingested by belugas. Movement of predator and prey can define suction and ram feeding modes (Norton and Brainerd, 1993), and the fast approach velocity of pilot whales indicated that they relied heavily on ram to capture prey. Pilot whales were unable to create a circular anterior mouth aperture, despite their ability to occlude lateral gape. Frontal aperture ratios ranged from 0.2 to 0.5 consistently, and minimum area and circumference were 35 cm^2 and 30 cm, respectively. This was the most horizontally oblong oral orifice of all three species, and pilot whales were the least able to form a small, circular anterior lip aperture.

Maximum subambient pressure values of pilot whales (-20 kPa) resembled Pacific white-sided dolphins. However, in retrospect, these results may be misleading. The individuals of these species, like belugas, were accustomed to receiving non-evasive prey and may not have performed maximally. Additionally, only two pilot whale individuals were sampled and may not have fully represented the feeding capabilities of pilot whales. High magnitude suprambient pressure generation also suggests that maximum capabilities may have been underestimated. Hydraulic jetting and suction are reciprocal behaviors of the same biomechanical mechanism that involves the hyolingual apparatus; where one behavior is observed, the other should also be present at a similar magnitude.

Belugas, Pacific white-sided dolphins, and pilot whales achieved suprambient pressure (hydraulic jetting) values greater than 100 kPa. Therefore, the maximum subambient intraoral pressure generation capability in pilot whales was likely underestimated. Behavioral anecdotes and kinematic data (Werth, 2000) suggest that pilot whales do indeed use suction. Werth noted that food items were pulled into the lateral sides of the mouth in rehabilitating pilot whales. If pressure measurements had been made at the lateral sides of the mouth, this study might have measured significantly greater subambient pressures. Future studies of pilot whale feeding performance should test this functional hypothesis.

Suction capability demonstrated in pilot whales in this study was likely a result of hyolingual displacement, and not rapid gape change. Like belugas, pilot whales exhibited a slow gape angle velocity. However, hyolingual displacement was similar to Pacific white-sided dolphins. Pilot whales and belugas possess a blunt rostrum (Werth, 2006) that is likely coupled with a short, wide tongue shape and a broad hyoid. This morphology may contribute more to suction generation than forceful hyolingual displacement (Bloodworth and Marshall, 2007). Jaw and hyolingual displacements in pilot whales were low. Therefore, the hyolingual contribution to suction generation may come from its shape and not necessarily forceful displacement, and this contribution may be greater than that of jaw displacement in pilot whales.

4.2 Comparisons with other vertebrates

4.2.1 Comparisons with marine mammal taxa

Few kinematic and pressure generation studies have been conducted for marine mammals, and comparative data are few (Table 12). Morphological and behavioral evidence supports the use of suction in beaked whales (Ziphiidae, Heyning and Mead, 1996), belugas (*Delphinapterus leucas*, Ray, 1966), pilot whales *(G. melas* and *G. macrorhynchus*, Brown, 1962; Werth, 2000), and killer whales (*Orcinus orca*, Donaldson, 1977). However, among marine mammals direct *in vivo* physiological data that demonstrate subambient intraoral pressure generation have only been collected for

Table 12 Summary of available feeding kinematic and biomechanical data for marine mammals.

Kinematic variables	Belugas[1]	Pacific white-sided dolphins[1]	Pilot whales[1]	Pygmy/dwarf sperm whales[2]	Bottlenose dolphins[2]	Pilot whales[3]	Harbor porpoises[4]	Bearded seals[5]	Pacific walrus[6]
Duration of gape cycle (s)	0.684	0.279	0.583	0.470	0.863	0.860	0.220	0.530	0.482
Max gape (cm)	6.346	6.451	8.997	8.54	12	10.6	4	2.70	---
Time to max gape (s)	0.277	0.140	0.327	0.282	0.564	---	0.280	0.170	---
Max hyolingual depression (cm)	2.675	3.377	2.674	2.25	4.75	2-6	---	1.8	---
Time to max hyolingual depression (s)	0.400	0.186	0.430	0.283	0.623	---	---	0.300	---
Max gape angle (°)	16.4	16.8	15.9	40	25	---	---	24.4	---
Time to max gape angle (s)	0.300	0.139	0.316	---	---	---	---	0.200	---
Max gape angle opening velocity (°/s)	119.7	248.4	107.5	293	84	---	---	204.8	---
Time to max gape angle opening velocity (ms)	0.175	0.092	0.212	---	---	---	---	0.100	---
Max gape angle closing velocity (°/s)	115.5	226.0	85.9	223	120	---	---	289.8	---
Time to max gape angle closing velocity (ms)	0.387	0.179	0.422	---	---	---	---	0.080	---
Ram-suction index	0.04	0.361	0.159	-0.67	+0.94	---	---	---	---
Max subambient pressure (kPa)	-122	-27	-20	---	---	---	~ -40	-91.2	-118.8
Max supra-ambient pressure (kPa)	+128	+100	+120	---	---	---	---	+54	---

[1]This study, [2]Bloodworth and Marshall (2005), [3]Werth (2000), [4]Kastelein et al. (1997), [5]Marshall et al. (2008), [6]Kastelein et al. (1994)

harbor porpoises (*Phocoena phocoena*, Kastelein et al., 1997), walruses (*Odobenus rosmarus divergens*, Kastelein et al., 1994), and bearded seals (*Erignathus barbatus*, Marshall et al., 2008). Additionally, feeding kinematics have been quantified for pilot whales (*G. melas*, Werth, 2000), pygmy and dwarf sperm whales, common bottlenose dolphins (*Kogia* spp. and *T. truncatus*, Bloodworth and Marshall, 2005), and bearded seals (*E. barbatus*, Marshall et al., 2008). These taxa represent both cetacean and pinniped mammalian radiations, and all are considered suction feeding specialists except bottlenose dolphins. The unshared ancestry of pinnipeds and cetaceans, and the presence of suction feeding capability in both lineages, further demonstrates the strong selection pressures of the aquatic environment, and the convergent evolution of mechanisms for suction generation.

The results of this study are evidence that a greater diversity in suction generation mechanisms exist among odontocetes than previously thought. Feeding kinematics of *Kogia* spp. were characterized by a large gape angle, fast gape angle velocities, short hyolingual depression, and a short total duration compared to bottlenose dolphins. These feeding characteristics indicated that *Kogia* spp. fed using suction (Bloodworth and Marshall, 2005). Gape angle was small for bearded seals, and their jaw opening and total duration of the feeding event were rapid (Marshall et al., 2008) compared to these two odontocetes. These results support the hypothesis that faster feeding kinematics are associated with suction feeding. However, in this study, belugas and Pacific white-sided dolphins did not differ in gape angle or hyolingual displacement. In addition, belugas exhibited gape angle velocities and a total feeding duration similar to ram feeding bottlenose dolphins. The discrepancies in kinematic patterns among suction feeding odontocetes may be due to the suite of varied morphological and behavior specializations for suction generation in belugas. The pursing behavior of belugas has never been described for odontocetes in the context of feeding kinematics. For this reason, lateral occlusion and pursing behaviors of belugas might be as important as hyolingual depression and fast jaw movements to generate suction, and may contribute to a broad repertoire of feeding modes in odontocetes.

This study measured intraoral pressure change of feeding Monodontids and Delphinids. Until now, some odontocetes were presumed to generate strong subambient pressures but none were quantified. Previous work suggested that porpoises could generate up to -40 kPa of pressure (Kastelein et al., 1997). However the pressure measured for belugas (-120 kPa) was more than double this quantity. Walrus and bearded seals are known benthic foragers that are also suction specialists. These species are capable of generating some of the greatest absolute suction values known among vertebrates (walrus: -120 kPa, bearded seal: -90 kPa) (Kastelein et al., 1994; Marshall et al., 2008). Suction generation in belugas resembled that of other suction feeding pinnipeds, rather than that of other odontocetes, which further reinforces the importance of suction in belugas. Alternatively, suction generation in Pacific white-sided dolphins and pilot whales was similar to harbor porpoises, and reflects a greater contribution of ram to the feeding mode and the possibility of suction use for compensation of ram speed or intraoral prey manipulation and transport.

4.2.2 Comparisons with more basal vertebrates

Suction generation is tightly associated with the physical properties of the medium. For this reason, the kinematics of suction feeding are conserved among basal aquatic vertebrates (Reilly and Lauder, 1990; Lauder and Prendergast, 1992; Wilga and Motta, 1998; Deban and Wake, 2000; Ferry-Graham et al., 2001; Gibb and Ferry-Graham, 2005). Furthermore, the coordination of kinematic sequence and timing is critical for maximum suction generation (Holzman et al., 2007). The kinematic events of odontocetes in this study were similarly conserved. All aquatic vertebrates, including mammals, can be characterized as utilizing a posteriorly directed “wave of buccal expansion” (Gillis and Lauder, 1994; Summers et al., 1998; Wilga and Motta, 1998; Sanford and Wainwright, 2001; Motta et al., 2002; Carroll and Wainwright, 2003). In teleosts, the progression of buccal expansion from the anterior jaws to the gills coordinates maximum flow velocity and maximum gape (Bishop et al., 2008). The same wave-like buccal expansion was demonstrated for odontocetes and has been observed in suction feeding salamanders (Lauder and Shaffer, 1985) and turtles (Summers et al., 1998). This pattern may be beneficial as a mechanism for generating a temporary unidirectional flow during feeding in obligate bidirectional flow suction feeders.

Lateral gape occlusion, as observed in odontocetes in this study, is a common behavioral adaptation of suction feeders. Lateral gape occlusion has also been reported for *Kogia* spp. (Bloodworth and Marshall, 2005), pilot whales (Werth, 2000), and bearded seals (Marshall et al., 2008). The capability to occlude lateral gape in odontocetes and other marine mammals is analogous to the lateral gape occlusion via labial cartilages of elasmobranchs (e.g. Motta and Wilga, 1999), lip membranes in teleost fishes (e.g. Ferry-Graham et al., 2008), and the labial lobes of aquatic salamanders (e.g. Deban and Wake, 2000). Lateral gape occlusion also functions to create a small, circular anterior aperture to increase the flow of water into the mouth (Wainwright and Day, 2007). In teleost fish, highly kinetic bones and ligaments protrude the jaws, which effectively occludes lateral gape (Motta, 1984). However, odontocetes are phylogenetically constrained to an autostylic jaw suspension and cannot protrude the maxilla and premaxilla. Therefore, the lateral lips of odontocetes are likely an analogous mechanism for lateral gape occlusion.

Typically, teleost suction feeders generate a flow of water in front of the mouth that is either high velocity or high volume (Holzman et al., 2008). Bluegill sunfish (*Lepomis macrochirus*) are specialized to generate high velocity water flow and strong subambient pressure during suction events. They have a smaller gape but greater accuracy than largemouth bass. However, prey size is limited by small gape. Alternatively, largemouth bass (*Micropterus salmoides*) exhibit a larger gape, ingest a larger volume of water at the expense of accuracy and flow velocity, and have a greater ram component to their feeding mode than bluegill sunfish (Higham et al., 2006a). The differences in suction generation between bluegill and largemouth bass are primarily due to differences in water flow speed and gape displacement speed (Holzman et al., 2008).

In this study, suction feeding by belugas is analogous to bluegill suction feeding. Belugas also exhibited a relatively small gape and high subambient pressure values that indicate a high velocity water flow; water velocity is positively correlated to subambient pressure generation (Higham et al., 2006b). In teleosts, smaller mouth diameters generally indicate greater subambient pressure capability (Wainwright and Day, 2007), which was also true for odontocetes. The capability to restrict gape indicates that belugas can direct suction force toward the prey for greater accuracy. It is possible that since beluga gape opening velocity was slow, belugas likely compensate with anterior lip pursing to create a smaller anterior aperture and increase strike efficiency, as well as a greater hyolingual displacement that increases flow velocity.

Alternatively, ram feeding by Pacific white-sided dolphins is analogous to feeding in largemouth bass. Pacific white-sided dolphins typically captured prey with a greater ram component although some suction was observed. The inability to form a small, restricted aperture, as well as the weak subambient pressure generated, indicate that Pacific white-sided dolphins probably displace a greater volume of water at a slower velocity and are not as accurate. However, odontocetes are constrained to a bidirectional suction flow, and direct comparisons of intraoral volume change to teleosts with unidirectional suction flow should be made with caution.

4.3 Evaluation of the ram-suction index

As evidenced by kinematic and pressure generation data, the use of ram and suction modes was common in belugas, Pacific white-sided dolphins, and pilot whales. However, these results were not necessarily reflected in RSI values. The RSI calculated by Norton and Brainerd’s index (Norton and Brainerd, 1993) suggested that all species relied heavily on ram to capture prey. The greatest mean RSI value was observed for Pacific white-sided dolphins and was probably the most accurate prediction of primary feeding mode. Kinematic and pressure analyses confirmed that Pacific white-sided dolphins relied heavily on ram and generated little suction. However, belugas generated the strongest suction pressures reported in vertebrates even though RSI values indicated a large ram component. This result indicates that mean RSI values did not capture the broad repertoire of feeding behavior in belugas.

Mean RSI values may have also been high (ram) due to the fluid dynamics and constraints of suction feeding. Suction is effective over limited distances (Svanback et al., 2002; Wainwright and Day, 2007). Therefore, prey movement due to suction is limited and less variable (Wainwright et al., 2001). Among teleosts, ram distance is often more variable than suction distance, and ram, often in the form of jaw protrusion, is used to bring the mouth closer to the prey so that suction can be effective (Norton and Brainerd, 1993; Ferry-Graham et al., 2001; Wainwright et al., 2001; Holzman et al., 2008b). For this reason, it is possible that the ram component of beluga feeding events detected by the RSI was due to the necessity for belugas to reduce the distance between the prey for suction to be effective; since jaw protrusion is not possible in odontocetes, predator movement (ram) would be necessary. Kinematic analyses confirmed that the highest velocity prey movements were observed after belugas slowed forward velocity to near zero.

The inherent complexities involved in using RSI have long been recognized. In a study comparing ram and suction distances among seven cichlid species, Wainwright et al. (2001) determined that species chosen based on presumed differences in ram and suction capabilities did not differ in suction distance. Additionally, Wainwright et al. (2001) suggested that strong suction not only draws the prey into the mouth of the predator, but that it may draw the predator toward the prey in a behavior that would be captured in RSI as ram distance, although this was unlikely in this study due to the size of the animals. RSI also obscures the contribution of ram and suction to the feeding mode (Wainwright et al., 2001). Feeding events with varying ram distances can have the same RSI as long as suction distance is proportional. Wainwright et al. (2001) concluded that RSI was not useful for the comparison of suction and ram feeding modes among species due to its bias toward ram distance and its inability to describe suction and ram performance.

Beluga kinematic and pressure generation data from this study further support these shortcomings of RSI analyses. Although significant differences were found among odontocetes, maximum suction distance for belugas was not as profound as the anticipated result. Belugas were chosen as a study species due to numerous anecdotal accounts of significant suction generation. In fact, trainers often noted that when they attempted to induce maximum suction with an increased grip on the prey, belugas could definitively use suction to remove the fish from the trainer's hand. Pressure generation analyses verified the capability for strong suction in belugas. However, ram and suction distances, and subsequently RSI, were not able to capture this suction component due to the limited distance across which suction is effective. Furthermore, RSI for belugas was calculated as a mean of RSI from all feeding trials. In a species with a wide feeding repertoire, such as belugas, means will likely not capture the full range of feeding behaviors.

4.4 Evolution of suction feeding in Odontoceti

4.4.1 Reconstructed ancestral feeding characteristics

The preliminary analysis of the evolution of suction feeding characters within Odontoceti conducted in this study indicated that the common ancestor of odontocetes was primarily a ram feeder. Six of 16 reconstructed ancestral character states were associated with a ram feeding mode and included: large gape angle with a slow velocity, weak hyolingual depression, slow prey velocity, and a long narrow rostrum with a narrow tongue. These predicted ancestral kinematic and morphological states coincide with the ram feeding behavior predicted by the archaeocete morphology; archaeocetes typically possessed 40-44 heterodont shearing teeth (O'Leary and Uhen, 1999; Thewissen and Williams, 2002), which indicate that the teeth were responsible for prey capture (ram and biting). However, some degree of subambient intraoral pressure generation may have been employed during feeding. Changes in feeding ecology occurred early in the Archaeocete radiation (Gingerich, 1998; Thewissen, 1998), and evidence suggests that members of Family Dorudontidae, the sister group to modern mysticetes and odontocetes, were feeding on marine prey exclusively (Thewissen et al., 1996; Roe et al., 1998; Thewissen and Williams, 2002). Suction is highly selected for in aquatic feeding vertebrates (Lauder, 1985), and may have been present in the fully aquatic, piscivorous Dorudontidae. However, any subambient pressure that was generated was likely only used during prey manipulation or transport to the esophagus, and was not likely used to capture prey (Werth, 2006).

The reconstruction of ancestral feeding states performed in this study supports the hypothesis of suction-enhanced intraoral transport in an ancestral odontocete. Ten feeding characters did not fully support a ram feeding mode, and four of these were intermediate between ram and suction: total duration of the feeding event, ram-suction index, tooth counts, and hyoid size. The remaining six reconstructed ancestral state variables supported a suction feeding mode: limited but fast gape, rapid hyolingual depression, large suction and small ram distance, and strong subambient pressure generation; although, these characters were not represented well over the phylogeny, and their predicted ancestral states may not be accurate. However, since several character states associated with suction were present, the reconstruction supports the hypothesis that limited subambient pressure generation capability may have been used for prey manipulation and intraoral transport in Archaeoceti, and might represent the transition from a ram to a suction prey capture method in some taxa (Werth, 2006). Therefore, suction generation capability likely evolved by the time of the dorudontines, though it was not a specialized behavior.

4.4.2 Plesiomorphies, apomorphies, and synapomorphies

Within suborder Odontoceti, characteristics of suction feeding appear to have evolved in almost every clade, suggesting that while some taxa are suction feeding specialists (belugas), other ram feeding delphinids (Delphinidae 2: *Sousa*, *Stenella*, *Delphinus*, *Tursiops*, and *Lagenodelphis* genera) may only have a limited use of suction during feeding. Based on the characters determined for the common ancestor, all characters used in this analysis underwent some degree of evolutionary change in at least one lineage, and no character was entirely plesiomorphic (unchanged from the ancestral condition) within Odontoceti. Similarly, no character was entirely apomorphic (a derived condition) within Odontoceti. However, this result was due to the method of gap coding that was used; characters that did not code at least two character states were re-coded until at least two states were determined. Therefore, synapomorphies of odontocetes could not be determined.

Instead, plesiomorphy, apomorphy, and synapomorphy should be used to describe character states within familial clades. The ancestral character of relatively long, narrow rostra is maintained in five of 13 terminal taxa and in these taxa, a long rostrum is plesiomorphic. Apomorphies, or states different than those in the predicted ancestor, were observed in every terminal taxa, though the number of apomorphies within a taxa ranged from one to nine. Delphinidae 5 (*Grampus*, *Pseudorca*, *Globicephala*, *Peponocephala*, and *Feresa*), Kogiidae, and Monodontidae display the most (3-5) changes from the ancestral state to derived character states associated with suction feeding capability. The feeding mode changes that have taken place in these taxa were not identical, and it is likely that specialization for suction generation was independently derived from a ram feeding ancestor numerous times. In total, at least six independent events of suction generation specialization were determined from the analysis (Fig. 24).

Although some extant members of Odontoceti are specialized for suction generation, the common ancestor of Family Delphinidae was likely more specialized for ram feeding than the odontocete ancestor. This delphinid ancestor was polydont with a long narrow rostrum, fast total feeding event duration and a large ram distance. These kinematic and morphological characters represent shared characters common within Family Delphinidae that are derived in relation to the odontocete ancestor (synapomorphic). However, clade 4 (*Orcaella* and *Orcinus*) and clade 5 (*Grampus*, *Pseudorca*, *Globicephala*, *Peponocephala*, and *Feresa*) have diverged from the common Delphinid ancestor to independently specialize for suction (apomorphic). This relationship among apomorphic feeding specializations is significant in that it occurs within the most diverse and most recently derived family within Odontoceti. For this reason, a study of transitions in feeding mode within Delphinidae might provide insight into the mechanism for the evolution of suction specialists.

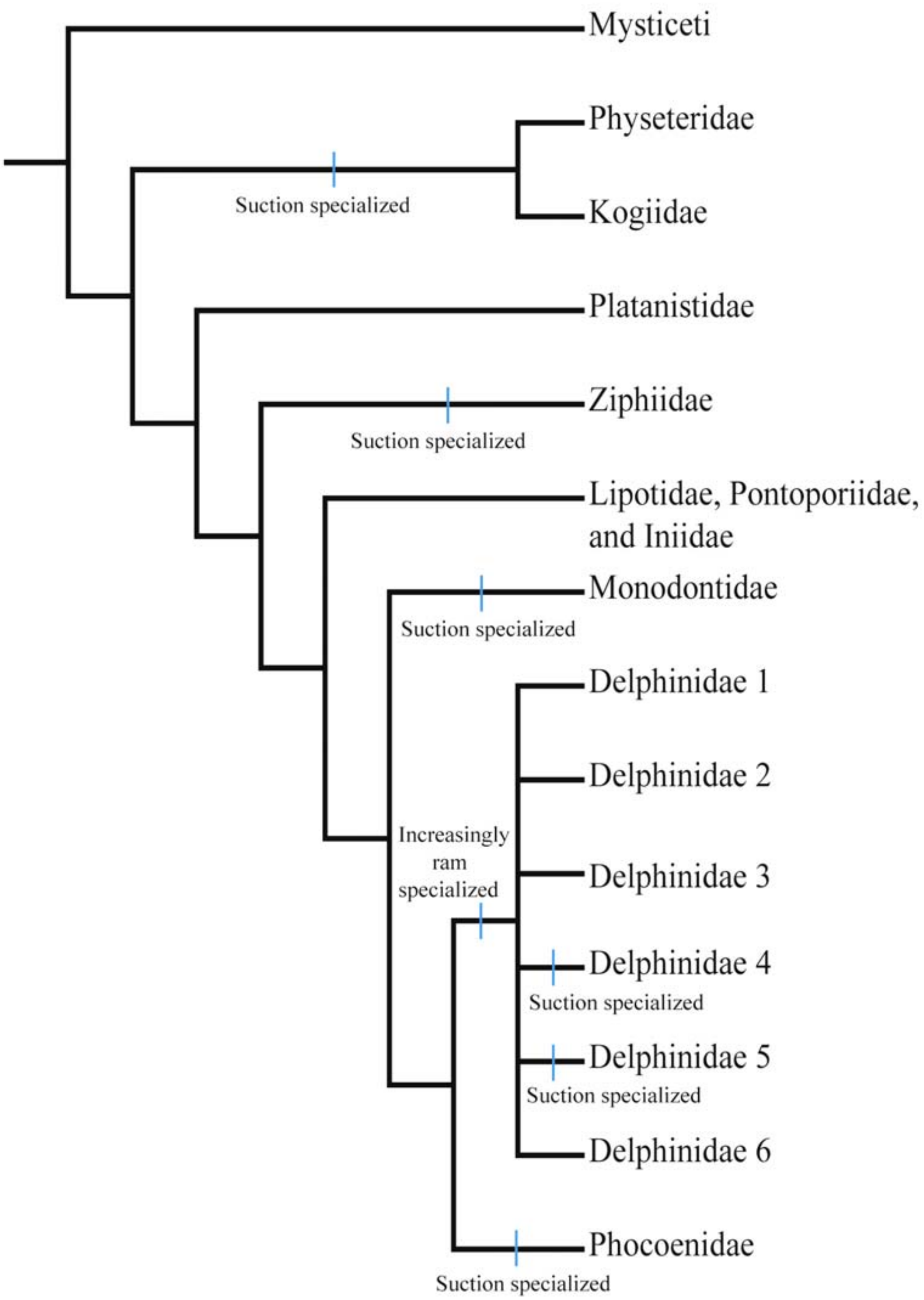

Fig. 24 The evolution of suction generation specialization within Odontoceti. Blue bars indicate changes in feeding modes.

These analyses suggest that feeding characters within each familial clade are a composite of both ancestral and derived character states. Such results are not unusual, and were found for the evolution of extreme jaw protrusion in the sling-jaw wrasse, *Epibulus insidiator* (Westneat and Wainwright, 1985), for example. Additionally, among ray-finned fishes, functionally convergent premaxillary protrusion has independently evolved several times, although the underlying mechanisms of protrusion are divergent (Westneat, 2004). The evolution of protrusion is analogous to the evolution of suction generation in odontocetes, as several clades functionally use some degree of suction generation to capture prey; however the mechanism underlying suction generation varies among taxa. This emergent property of functional systems has been termed “many-to-one mapping” (Wainwright et al., 2005; Alfaro et al., 2006). It appears that since suction feeding has independently evolved at least six times within Odontoceti, “many-to-one mapping” of biomechanics contributes to the variation in suction feeding performance observed in odontocetes.

5. CONCLUSIONS

This study combined kinematic and direct pressure generation measurements for odontocetes, and increased the comparative kinematic data for odontocetes. In addition, this study provided *in vivo* pressure data for odontocetes that can be used in comparison to other suction feeding vertebrates. A new feeding behavior was defined for odontocetes that included occlusion of the lateral lips and anterior pursing to form a small circular anterior aperture. This behavior was specialized in belugas and occurred to a lesser degree in Pacific white-sided dolphins and pilot whales. Additionally, suction feeding belugas appeared to employ less of their maximum gape capability during kinematic feeding events. The limited use of maximum gape appears to be an adaptation for suction feeding where hyolingual displacement is more important than rapid jaw opening, and was observed to a greater degree in belugas and pilot whales.

In this study, belugas were the most specialized for suction generation, but employed a wide repertoire of feeding behaviors that also included ram. Belugas were able to generate strong subambient pressures that were comparable to the strongest pressures known among vertebrates. Alternatively, Pacific white-sided dolphins relied on ram to capture prey. Feeding events occurred rapidly and little suction generation was observed. Some degree of lateral occlusion occurred in Pacific white-sided dolphins, but to a lesser degree than for belugas. The capability to occlude lateral gape, as well as direct measurement of suction generation, indicated that suction was likely compensatory or was utilized to transport or manipulate prey intraorally. Pilot whales exemplified a mixed use of ram and suction that was intermediate to belugas and Pacific white-sided dolphins. Although the lateral gape was occluded in all trials, pilot whales maintained a high approach velocity indicative of ram. Pilot whales were also incapable of generating strong subambient pressures. The mechanism for suction generation in odontocetes is an integration of hyolingual displacement, rapid jaw opening, and lateral gape occlusion. The results from this study help to establish a baseline for the diversity of feeding behaviors and kinematics in odontocetes, and provide data for comparison with other primarily and secondarily aquatic vertebrate taxa.

This study systematically examined the evolution of feeding modes within odontocetes. The preliminary analysis of suction feeding evolution indicated that suction feeding capability evolved independently at least five times within Odontoceti. Hypotheses of likely feeding mode character states were generated for odontocete taxa in which kinematic data are sparse. These data are able to provide direction for future studies on the diversity of feeding in odontocetes. A more detailed comparison of feeding modes within Family Delphinidae may be able to provide insight into the mechanism for suction evolution in Odontocetes.

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APPENDIX A

Table of gap coded characters. Each species that was used for the respective variable is listed, along with species means. The bold value in this column is group standard deviation. Coded character states are also listed, along with the constant (bold) used to calculate significant gaps.

Variable	SD	Gap criteria
Species	**Mean**	**Code**
duration of event	**0.244**	**0.70**
Phocoena phocoena	0.22	0
Lagenorhynchus obliquidens	0.28	0
Kogia spp.	0.47	1
Globicephala melas	0.58	1
Delphinapterus leucas	0.68	1
Tursiops truncatus	0.86	2
max gape	**2.755**	**1.00**
P. phocoena	4.00	0
D. leucas	6.35	0
L. obliquidens	6.45	0
Kogia spp.	8.54	0
G. melas	9.00	0
T. truncatus	12.00	1
time to max gape	**0.139**	**1.00**
L. obliquidens	0.14	0
D. leucas	0.28	0
P. phocoena	0.28	0
Kogia spp.	0.28	0
G. melas	0.33	0
T. truncatus	0.56	1
max gape angle	**10.316**	**1.00**
G. melas	15.88	0
D. leucas	16.38	0
L. obliquidens	16.81	0
T. truncatus	25.00	0
Kogia spp.	40.00	1

Variable	SD	Gap criteria
Species	**Mean**	**Code**
gape angle opening velocity	**93.683**	**1.00**
T. truncatus	84.00	0
G. melas	107.47	0
D. leucas	119.72	0
L. obliquidens	248.38	1
Kogia spp.	293.00	1
velocity of prey	**75.195**	**1.00**
Kogia spp.	41.00	0
L. obliquidens	89.30	0
G. melas	114.47	0
D. leucas	219.06	1
hyolingual depression	**0.984**	**1.00**
Kogia spp.	2.25	0
G. melas	2.67	0
D. leucas	2.68	0
L. obliquidens	3.38	0
T. truncatus	4.75	1
time to hyolingual depression	**0.165**	**1.00**
L. obliquidens	0.19	0
Kogia spp.	0.28	0
D. leucas	0.40	0
G. melas	0.43	0
T. truncatus	0.62	1
suction distance	**4.689**	**1.00**
T. truncatus	-2.45	0
Kogia spp.	5.19	1
L. obliquidens	6.01	1
G. melas	9.04	1
D. leucas	8.96	1

Variable Species	SD Mean	Gap criteria Code
ram distance	**16.267**	**1.00**
Kogia spp.	1.16	0
L. obliquidens	16.85	0
G. melas	18.99	0
D. leucas	25.60	0
T. truncatus	46.00	1
RSI	**0.577**	**0.80**
Kogia spp.	-0.66	0
G. melas	0.26	1
D. leucas	0.32	1
L. obliquidens	0.43	1
T. truncatus	0.94	2
subambient pressure	**48.030**	**1.00**
G. melas	-19.55	0
L. obliquidens	-27.05	0
P. phocoena	-33.00	0
D. leucas	-121.96	1
total tooth counts	**54.742**	**0.400**
Ziphiidae	8	0
Monodontidae	21	0
Kogiidae	32	0
Delphinidae 5	48	0
Delphinidae 4	55	0
Physeteridae	82	1
Phocoenidae	84	1
Delphinidae 1	124	2
Delphinidae 3	124	2
Delphinidae 6	137	2
Platanistidae	148	2
Lipotidae, Pontoporiidae, Iniidae	155	2
Delphinidae 2	167	2

Variable Species	SD Mean	Gap criteria Code
Tongue width:length	**0.100**	**1.00**
Mysticeti	0.17	0
Phocoenidae	0.31	1
Physeteridae	0.35	1
Delphinidae 3	0.35	1
Delphinidae 2	0.37	1
Delphinidae 5	0.48	2
Monodontidae	0.51	2
MBI	**0.170**	**0.50**
Kogiidae	0.92	0
Delphinidae 5	0.72	1
Monodontidae	0.69	1
Delphinidae 4	0.68	1
Phocoenidae	0.67	4
Physeteridae	0.57	2
Delphinidae 3	0.52	2
Delphinidae 6	0.48	2
Ziphiidae	0.46	2
Delphinidae 2	0.43	2
Delphinidae 1	0.42	
Lipotidae, Pontoporiidae, Iniidae	0.38	2
Platanistidae	0.32	2
Hyoid L1:W	**0.085**	**0.60**
Delphinidae 2	0.50	0
Delphinidae 1	0.52	0
Delphinidae 6	0.57	1
Delphinidae 3	0.59	1
Delphinidae 5	0.62	1
Lipotidae, Pontoporiidae, Iniidae	0.65	1
Phocoenidae	0.66	1
Monodontidae	0.67	1
Ziphiidae	0.78	2

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