

Comparative feeding kinematics and performance of odontocetes: belugas, Pacific white-sided dolphins and long-finned pilot whales

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SUMMARY

Cetaceans are thought to display a diversity of feeding modes that are often described as convergent with other more basal aquatic vertebrates (i.e. actinopterygians). However, the biomechanics of feeding in cetaceans has been relatively ignored by functional biologists. This study investigated the feeding behavior, kinematics and pressure generation of three odontocetes with varying feeding modes (belugas, *Delphinapterus leucas*; Pacific white-sided dolphins, *Lagenorhynchus obliquidens*; and long-finned pilot whales, *Globicephala melas*). Four feeding phases were recognized in all odontocetes: (I) preparatory, (II) jaw opening, (III) gular depression, and (IV) jaw closing. Belugas relied on a feeding mode that was composed of discrete ram and suction components. Pacific white-sided dolphins fed using ram, with some suction for compensation or manipulation of prey. Pilot whales were kinematically similar to belugas but relied on a combination of ram and suction that was less discrete than belugas. Belugas were able to purse the anterior lips to occlude lateral gape and form a small, circular anterior aperture that is convergent with feeding behaviors observed in more basal vertebrates. Suction generation in odontocetes is a function of hyolingual displacement and rapid jaw opening, and is likely to be significantly enhanced by lip pursing behaviors. Some degree of subambient pressure was measured in all species, with belugas reaching 126 kPa. Functional variations of suction generation during feeding demonstrate a wider diversity of feeding behaviors in odontocetes than previously thought. However, odontocete suction generation is convergent with that of more basal aquatic vertebrates.

Key words: ram, suction, kinematics, subambient pressure, RSI, aperture shape.

INTRODUCTION

Approximately 550 million years of vertebrate evolution has resulted in a diversity of jaw functions, such as kinetic skull expansion using 4-bar linkages (Lauder, 1982; Westneat and Wainwright, 1989; Westneat, 1994), ballistic tongue projection (Deban et al., 1997; Deban et al., 2007), surface tension prey transport (Rubega and Obst, 1993; Rubega, 1997; Prakash et al., 2008) and mastication (Hiiemae and Crompton, 1985; Herring, 1993). Among aquatic vertebrates specifically, jaw function includes suction generation, and many aquatic taxa rely on some degree of suction to capture prey. Suction feeding is characterized by rapid buccal volume expansion that generates a pressure gradient and a flow of water and prey into the mouth (Muller et al., 1982; Wainwright and Day, 2007). While suction generation has been best studied among more basal vertebrates, suction performance data for secondarily aquatic vertebrates (such as marine mammals) are limited to only a few pinniped (Fay, 1982; Kastelein et al., 1994; Marshall et al., 2008) and cetacean taxa (Kastelein et al., 1997; Werth, 2000a; Bloodworth and Marshall, 2005; Werth, 2006b).

Some mammals returned to the aquatic environment as recently as 50 million years ago, resulting in the appearance of modern whales and dolphins of the order Cetacea (Rice, 1998; Thewissen and Williams, 2002). This transition resulted in a radiation of adaptations for feeding (O'Leary and Uhen, 1999; Uhen, 2007), and feeding modes that presumably converge with feeding modes of basal aquatic vertebrates. Among cetaceans, certain lineages have specialized for filter feeding (baleen whales, suborder Mysticeti), biting (killer whales, *Orcinus orca*), ram feeding (some delphinids)

and suction feeding (kogiids, porpoises, belugas and some delphinids) (Kastelein et al., 1997; Werth, 2000a; Bloodworth and Marshall, 2005). The feeding morphology of many extant odontocetes is often used to support these functional hypotheses regarding feeding mode, due to the limited availability of direct physiological and kinematic data. Presumed odontocete ram feeding piscivores exhibit long, narrow snapping jaws with many teeth that are characterized as convergent with other amniote ram feeding piscivores (Thorbjarnarson, 1990); presumed suction feeding odontocetes possess short, blunt rostra and few teeth, similar to other suction feeding actinopterygians (Werth, 2006a). However, among more basal suction feeding lineages, morphological diversity is not always indicative of functional diversity (Collar and Wainwright, 2006) and, until recently, functional hypotheses of odontocete feeding modes have rarely been tested directly. For example, beluga whales are anecdotally known to generate large suction forces. However, pressure generation has not been measured directly nor have the kinematics of suction generation been systematically investigated.

Therefore, the present study conducted controlled feeding trials to characterize the kinematics and behavioral performance among three presumed suction or ram feeding odontocetes. Additionally, direct measurements of *in vivo* pressure changes were recorded to characterize suction feeding capability and performance in each species. Comparisons were made among belugas (*Delphinapterus leucas* Pallas 1976; DL), Pacific white-sided dolphins, (*Lagenorhynchus obliquidens* Gill 1865; LO) and long-finned pilot whales (*Globicephala melas* Lesson 1828, referred to herein as pilot

whales; GM). Belugas, known for their suction capability (Ray, 1966; Brodie, 1989), belong to a more ancestral family within Odontoceti (Monodontidae) whereas Pacific white-sided dolphins and pilot whales belong to the most derived odontocete family (Delphinidae). However, whereas Pacific white-sided dolphins herd and consume individual prey using ram (Fiscus and Kajimura, 1980; Heise, 1997; Morton, 2000), pilot whales have been observed in captivity to capture prey using suction (Brown, 1962; Werth, 2000a). These odontocete species present a diversity of feeding modes that are apparent within multiple families.

MATERIALS AND METHODS

Subjects included seven beluga whales and seven Pacific white-sided dolphins, held at Sea World of Texas (San Antonio, TX, USA), as well as two pilot whales housed at Sea World of California (San Diego, CA, USA). All subjects were adults with mean total body lengths of 332 ± 43.9 cm (DL), 193 ± 27.8 cm (LO) and 450 ± 32.3 cm (GM) and mean masses of 577 ± 153 kg (DL), 108 ± 19.2 kg (LO) and 1081 ± 348 kg (GM). The use of all subjects was approved by Sea World, Inc. and the Institutional Animal Care and Use Committee of Texas A&M University (AUP 2006-237).

Kinematic analyses

In conjunction with trainers, controlled feeding trials were conducted for each individual. When cued, the subject was released from its station to freely capture the prey item *via* its preferred feeding mode (Fig. 1A,C,E). Frozen (non-mobile) herring (*Clupea harengus*), capelin (*Mallotus villosus*), mackerel (*Scomber japonicus*) and squid (*Loligo opalescens*) were presented to the subjects by hand following

Bloodworth and Marshall (Bloodworth and Marshall, 2005). The trainer gently held the prey item and presented it to the subject. On cue, the subject was free to approach (approximately 1 m distance) and ingest the prey item *via* its preferred feeding mode. Opportunistic video was also collected in which the trainer did not retain the prey but instead prey items were free-floating when the subject approached. In these situations, prey items were held 0.5 m below the water, and released when the subject was approximately 3 m from the prey. Prey items were distributed according to the daily regimen for each species and individual. Although mean prey length varied (herring: 24.2 ± 2.8 cm, capelin: 14.5 ± 1.2 cm, mackerel: 23.1 ± 0.8 cm, squid: 20.7 ± 2.3 cm; measured from 10 representative individuals of each species), no significant differences in kinematic variables were found for prey types among odontocete species (MANOVA, Wilks' λ , $F=1.21$, $P=0.18$) or within species (MANOVA, Wilks' λ , DL: $F=1.77$, $P=0.19$, LO: $F=1.85$, $P=0.19$, GM: $F=1.81$, $P=0.42$), and all prey types were pooled.

Feeding trials were recorded using a Sony TRV950 video camera (Sony Corp., New York, NY, USA) at 60 Hz. Immediately following each feeding trial, a calibration square of known dimensions was placed perpendicular to the video camera and in the plane of the subject. To characterize the movement of the jaws and hyolingual apparatus during feeding trials, seven homologous anatomical landmarks were digitized (Fig. 1A,C,E) and 17 lateral kinematic variables were calculated (Table 1) using the Peak Motus motion analysis system (v. 9; Vicon, Denver, CO, USA). Gape angle (GANG) refers only to the angle formed between the mandibular tips and the vertex of the jaw and not with landmark 3, which is prominent in belugas. Five additional lateral gape occlusion

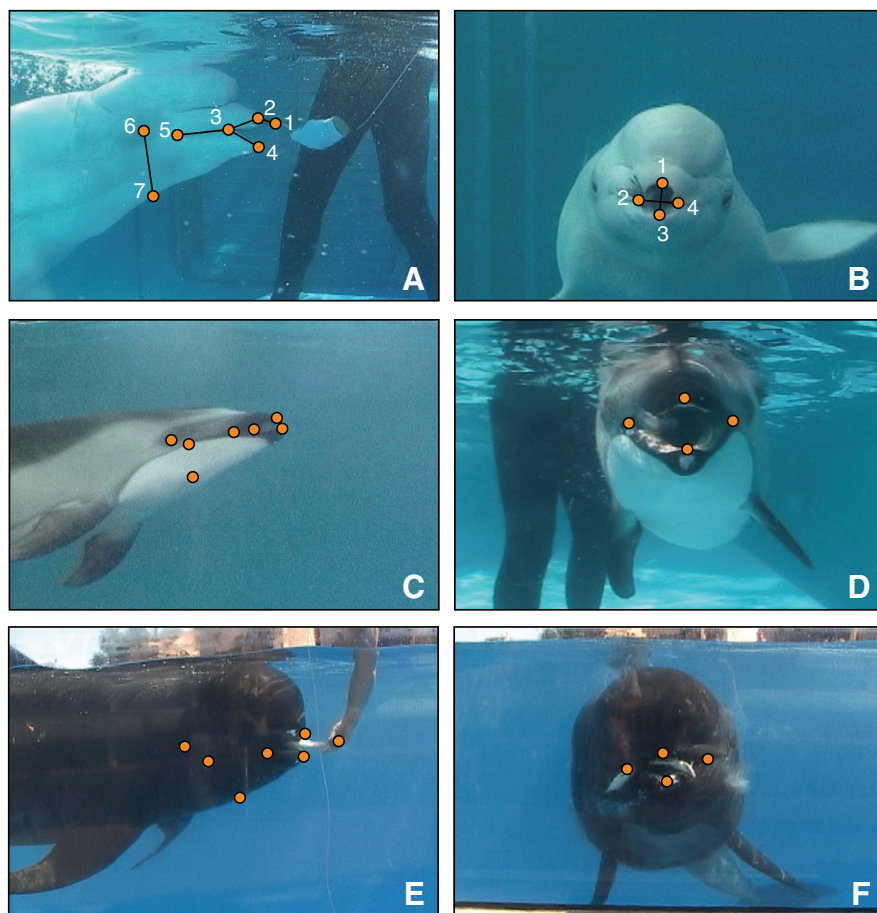


Fig. 1. Experimental setup as shown with video frames at maximum gape in lateral perspective (A,C,E) and frontal perspective (B,D,F) for (A,B) belugas, (C,D) Pacific white-sided dolphins and (E,F) pilot whales. Representative numbered lateral digitized landmarks and spatial model are shown for belugas (A,B). Lateral anatomical landmarks (orange dots) were: (1) point on the prey item furthest from the subject (tail), (2) tip of upper jaw, (3) most anterior extent of lateral gape occlusion, where the lips were occluded to form a pursed lateral gape, (4) mandibular tip, (5) corner of the mouth, (6) center of the subject's eye, and (7) rostral border of the externally apparent hyoid. Landmarks 3 and 5 overlapped when pursing was absent. Frontal perspective anatomical landmarks (orange dots) were: (1) center of the upper lip at the midsagittal plane, (2) right aperture commissure, (3) center of lower lip at the midsagittal plane, and (4) left aperture commissure. Belugas displayed a characteristic small circular aperture shape.

Table 1. Kinematic and pressure generation variables

| Variable | Abbreviation | Definition |
|--|------------------------------|--|
| Maximum gape | GAPE | Greatest distance of rostral tips of mandible and maxilla |
| Time to maximum gape | t_{GAPE} | 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 externally apparent vertex of the jaw to the mandibular tip |
| Time to maximum gape angle | t_{GANG} | 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 | t_{GAOV} | 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 | t_{GACV} | Elapsed time from the onset of gape opening to the frame of maximum gape angle closing velocity |
| Maximum subject velocity | v_{subject} | Greatest linear rate of subject movement toward the prey |
| Time to maximum subject velocity | t_{subject} | Elapsed time from the onset of gape opening to the frame of maximum subject velocity |
| Maximum prey velocity | v_{prey} | Greatest linear rate of prey movement toward the subject |
| Time to maximum prey velocity | t_{prey} | Elapsed time from the onset of gape opening to the frame of maximum prey velocity |
| Time to prey ingestion | t_{ING} | 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 | t_{MVT} | Elapsed time from the onset of gape opening to the first frame in which prey movement toward the subject's mouth is visible |
| Maximum hyolingual depression | GULD | Linear displacement of the hyoid from its resting position; taken at the frame of maximal distance between the eye and hyoid |
| Time to maximum hyolingual depression | t_{GULD} | Elapsed time from the onset of gape opening to the frame of maximum hyolingual depression |
| Percentage occlusion | OCC | Distance from the vertex of the jaw to most anterior extent of lateral gape occlusion, divided by the total length of the rostrum from the vertex to the rostral tips, multiplied by 100; taken at the frame of first visible prey movement toward the subject |
| Maximum posterior velocity of the pursed corner of the mouth | v_{post} | Greatest linear rate of posterior movement of the most anterior extent of lateral gape occlusion, corrected for subject velocity |
| Time to maximum posterior velocity of the pursed corner of the mouth | $t_{\text{v}_{\text{post}}}$ | 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 | v_{ant} | Greatest linear rate of anterior movement of the most anterior extent of lateral gape occlusion, corrected for subject velocity |
| Time to maximum anterior velocity of the pursed corner of the mouth | $t_{\text{v}_{\text{ant}}}$ | Elapsed time from the onset of gape opening to the frame of maximum anterior velocity of the pursed corner of the mouth |
| Total duration | t_{DUR} | Elapsed time from the onset of gape opening to the last frame of gape closing |
| Suction distance | D_{prey} | Net distance traveled by the prey item |
| Ram distance | D_{predator} | Net distance traveled by the subject |
| Ram–Suction Index | RSI | Mean Ram–Suction Index value for the species |
| Aperture width | Width | Horizontal distance between right and left aperture commissures (frontal); taken at the frame of maximum gape |
| Maximum subambient pressure | P_{sub} | Change in value from the baseline to the maximum subambient pressure recorded during the event |
| Maximum suprambient pressure | P_{supra} | Change in value from the baseline to the maximum suprambient pressure recorded during the event |
| Expansive phase duration | t_{EXP} | Elapsed time from the start, when the pressure increases or decreases from the baseline, to the maximum pressure |
| Rate of expansive phase pressure change | P_{EXP} | Maximum subambient or suprambient pressure divided by expansive phase duration |
| Compressive phase duration | t_{COMP} | Elapsed time from the maximum subambient or suprambient pressure back to the baseline |
| Rate of compressive phase pressure change | P_{COMP} | Maximum subambient or suprambient pressure divided by compressive phase duration |
| Total duration | t_{DUR} | Elapsed time from the onset of rapid pressure change until the return to baseline |

kinematic variables [percentage occlusion (OCC), maximum posterior velocity of the pursed corner of the mouth (v_{post}), time to maximum posterior velocity of the pursed corner of the mouth ($t_{\text{v}_{\text{post}}}$), maximum anterior velocity of the pursed corner of the mouth (v_{ant}) and time to maximum anterior velocity of the pursed corner

of the mouth ($t_{\text{v}_{\text{ant}}}$)] were calculated to characterize the lip pursing behavior that is common among belugas. Up to five feeding events per individual that best fit the following criteria were digitized and analyzed: (1) both the prey item and the subject were visible in the frame and in focus prior to jaw opening, (2) all anatomical

landmarks were visible in all frames, (3) the subject was perpendicular to the camera, and (4) ingestion was observed. For pilot whales, five feeding sequences for each prey type were analyzed (10–15 trials per individual), resulting in approximately the same number of trials for the species. Feeding event duration lasted from the first frame in which gape angle opening velocity increased from zero and gape began to increase ($t=0$) to the last frame in which gape angle closing velocity returned to zero and gape returned to the original closed position.

In addition to kinematic analyses, a Ram–Suction Index (RSI) was calculated, as well as measurements of maximum biological gape capabilities and oral aperture shape. RSI was calculated following Norton and Brainerd (Norton and Brainerd, 1993) for trials in which prey items were free-floating (not held by a trainer):

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

where D_{predator} is the net distance traveled by the subject (landmark 6, subject's eye) and D_{prey} is the net distance traveled by the food item (landmark 1, prey's head). Calculations were made at the onset of the feeding event and the frame of prey capture (when the prey crossed the boundary between the upper and lower jaws). Maximum biological gape and gape angle were calculated using Image J image analysis software (NIH, Bethesda, MD, USA) from digital photographs ($N=5$ photographs). These photographs were taken above water during a trained open gape husbandry behavior and when subjects opened their mouths to receive a food reward for the behavior; both behaviors resulted in maximal biological gape capability. These data were compared with corresponding kinematic data to determine what percentage of gape capability was utilized during feeding trials. To characterize the morphology influencing fluid mechanics of suction generation in odontocetes, the degree of circularity of the oral aperture at the anterior lips was calculated from additional feeding sequences that were recorded from the frontal perspective (Fig. 1B,D,F). Feeding event duration in the frontal perspective followed the lateral kinematic protocol (above) except linear velocity of the upper and lower jaws was used instead of gape angle opening velocity. Four frontal kinematic variables were measured (Table 1), and aperture area and circumference at maximum gape were measured using Image J (NIH). The ratio of vertical:horizontal diameter of the oral aperture (aperture ratio) was calculated as a measure of aperture circularity. Measurements of oral aperture stereotypy followed Wainwright et al. (Wainwright et al., 2008).

Pressure generation capability

Pressure generation was measured in conjunction with lateral kinematic feeding trials. A pressure transducer (MPC 500 MikroTip Pressure Catheter, Millar Instruments, Houston, TX, USA) was inserted through the prey item following Kastelein et al. (Kastelein et al., 1997) such that the sensor protruded approximately 2 cm from the head of the prey item and was oriented toward the subject (Fig. 1A,C,E). As the subject approached the prey item, the transducer measured changes in ambient pressure just prior to ingestion of prey. As the subject's lips closed on the prey (using suction or biting), the prey slid over the transducer into the subject's mouth while the transducer was retained by the trainer. Placement of the transducer sensor was verified from video, and confirmed that actual pressures changes were a result of feeding behaviors and not a bow wave. The transducer was connected to a poolside control box (TCB 600, Millar Instruments) and a portable electrophysiological recording system (Biopac MP150 System, Biopac Systems, Goleta, CA, USA), which continuously recorded

and saved the output (AcqKnowledge Software 3.9, Biopac Systems) to a laptop computer. AcqKnowledge was also used to analyze subambient and suprambient pressure traces for six pressure variables (Table 1). Prior to feeding trials, the transducer was independently calibrated in the lab. The transducer was inserted into a sealed flask and pressure was decreased to subambient pressure of 80 kPa using 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 to ensure linearity.

Statistics

Statistical tests were performed using JMP 7.0.1 (SAS Institute, Cary, NC, USA) to determine differences in kinematic and pressure profiles among species and to analyze correlation among variables. All data were \log_{10} -transformed and standardized for normalization and standard comparison among variables of different measurement types. Due to the absence of Phase I in many feeding trials, interspecific analyses of variance (ANOVA) were used to test for species differences within each kinematic phase. An interspecific constrained ordination nested MANOVA and a canonical centroid plot of least squares means (Mardia et al., 1979) 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. *Post hoc* tests determined if species differences existed within each variable and in which species differences occurred. Differences among kinematic and biological maximum gape capability were determined using Student's *t*-tests. Pressure variables were analyzed using the same constrained MANOVA technique, followed with *post hoc* tests. A separate MANOVA was used to determine if significant differences occurred between subambient and suprambient pressure profiles, and Student's *t*-tests were used to compare durations and rates between expansive and compressive pressure phases. Correlation within species for kinematic and pressure generation variables was determined using a Pearson's *R* test for correlation.

RESULTS

Kinematics

Overall, feeding events of odontocetes in this study consisted of four phases, similar to those observed in Werth (Werth, 2000a) and Bloodworth and Marshall (Bloodworth and Marshall, 2005): (I) preparatory, (II) jaw opening, (III) hyolingual depression, and (IV) jaw closing (Table 2). Phase I began at the onset of jaw opening and ended when gape increased by greater than $0.2 \text{ cm field}^{-1}$ and the jaws rapidly opened. Phase I was observed in 32% of all trials and was marked by the occurrence of hyolingual adduction (in some cases), small gape and slow gape angle opening velocity, as well as movement of the subject toward the prey. The absence of phase I was observed during both ram and suction feeding mode trials. When present, no significant differences in duration of phase I were found among species (ANOVA, $F=1.30$, $P=0.29$). Phase II began when gape increased by $\geq 0.2 \text{ cm field}^{-1}$ and persisted until maximum gape. Phase III began when hyolingual depression increased by $\geq 0.2 \text{ cm field}^{-1}$ and concluded when hyolingual depression returned to its original position or at the end of the feeding event. Phase IV began at maximum gape and concluded when the jaws closed and gape decreased by $\leq 0.2 \text{ cm field}^{-1}$. Phase III persisted the longest in all three species and overlapped with phases II and IV. Significant differences were observed in phase II, III and IV durations among species (ANOVA, phase II: $F=17.4$, $P<0.0001$; phase III: $F=11.4$,

Table 2. Summary of kinematic variables for odontocetes

| | Belugas | Pacific white-sided dolphins | Pilot whales | <i>P</i> |
|---|-----------------------------|------------------------------|------------------------------|----------|
| Lateral perspective variables | | | | |
| Phase I | 0.205±0.096 ^A | 0.038±0.026 ^A | 0.2±0.038 ^A | 0.29 |
| Phase II | 0.214±0.026 ^B | 0.102±0.01 ^C | 0.282±0.025 ^A | <0.0001* |
| Phase III | 0.425±0.052 ^A | 0.196±0.013 ^B | 0.334±0.024 ^A | <0.0001* |
| Phase IV | 0.37±0.053 ^A | 0.14±0.01 ^B | 0.241±0.02 ^B | <0.0001* |
| GAPE (cm) | 6.346±0.356 ^B | 6.451±0.462 ^B | 7.974±0.465 ^A | 0.0025* |
| <i>t</i> _{GAPE} (s) | 0.277±0.038 ^A | 0.14±0.016 ^B | 0.314±0.031 ^A | <0.0001* |
| GANG (deg.) | 16.381±0.811 ^A | 16.812±1.239 ^A | 14.13±0.825 ^A | 0.25 |
| <i>t</i> _{GANG} (s) | 0.3±0.038 ^A | 0.139±0.016 ^B | 0.307±0.027 ^A | <0.0001* |
| GAOV (deg. s ⁻¹) | 119.715±8.079 ^B | 248.383±22.062 ^A | 94.887±6.413 ^C | <0.0001* |
| <i>t</i> _{GAOV} (s) | 0.175±0.039 ^A | 0.092±0.013 ^B | 0.213±0.024 ^A | 0.0027* |
| GACV (deg. s ⁻¹) | 115.225±8.863 ^B | 226.019±26.033 ^A | 89.62±6.566 ^B | <0.0001* |
| <i>t</i> _{GACV} (s) | 0.387±0.04 ^A | 0.179±0.017 ^B | 0.417±0.036 ^A | <0.0001* |
| <i>v</i> _{post} (cm s ⁻¹) | 256.481±28.422 ^A | 175.115±11.903 ^A | 124.027±14.832 ^B | 0.0094* |
| <i>t</i> _{post} (s) | 0.37±0.045 ^A | 0.095±0.015 ^C | 0.196±0.023 ^B | <0.0001* |
| <i>v</i> _{ant} (cm s ⁻¹) | 166.27±20.025 ^A | 92.32±13.288 ^B | 113.242±10.65 ^{A,B} | 0.0066* |
| <i>t</i> _{ant} (s) | 0.491±0.057 ^A | 0.248±0.021 ^B | 0.437±0.035 ^A | 0.0002* |
| <i>v</i> _{subject} (cm s ⁻¹) | 49.164±6.585 ^B | 81.466±8.507 ^A | 84.76±4.314 ^A | <0.0001* |
| <i>t</i> _{subject} (s) | 0.234±0.049 ^A | 0.16±0.019 ^A | 0.23±0.038 ^A | 0.3278 |
| <i>v</i> _{prey} (cm s ⁻¹) | 219.064±18.737 ^A | 89.295±14.539 ^B | 119.961±16.335 ^B | <0.0001* |
| <i>t</i> _{prey} (s) | 0.339±0.117 ^A | 0.149±0.021 ^B | 0.319±0.028 ^A | <0.0001* |
| OCC (%) | 78.764±2.877 ^A | 41.103±4.465 ^B | 65.556±2.234 ^A | <0.0001* |
| <i>t</i> _{MVT} (s) | 0.254±0.049 ^A | 0.104±0.014 ^B | 0.188±0.024 ^A | 0.0089* |
| GULD (cm) | 2.675±0.240 ^{A,B} | 3.377±0.317 ^A | 2.357±0.27 ^B | 0.0503 |
| <i>t</i> _{GULD} (s) | 0.4±0.05 ^A | 0.186±0.019 ^B | 0.435±0.041 ^A | <0.0001* |
| <i>t</i> _{ING} (s) | 0.377±0.049 ^A | 0.189±0.018 ^B | 0.387±0.039 ^A | <0.0001* |
| <i>t</i> _{DUR} (s) | 0.684±0.07 ^A | 0.279±0.02 ^B | 0.555±0.041 ^A | <0.0001* |
| <i>D</i> _{prey} | 3.71±0.59 ^A | 2.776±0.435 ^A | 4.119±0.607 ^A | 0.215 |
| <i>D</i> _{predator} | 8.705±1.477 ^A | 6.978±0.872 ^A | 8.68±1.086 ^A | 0.676 |
| RSI | 0.329±0.072 ^A | 0.416 ±0.064 ^A | 0.367±0.052 ^A | 0.433 |
| Frontal perspective variables | | | | |
| GAPE (cm) | 7.732±0.495 ^A | 8.275±0.61 ^A | 8.012±2.28 ^A | 0.747 |
| <i>t</i> _{GAPE} (s) | 0.26±0.023 ^A | 0.169±0.025 ^B | 0.225±0.155 ^{A,B} | 0.005* |
| Width (cm) | 7.535±0.395 ^C | 11.321±0.575 ^B | 21.313±6.542 ^A | <0.0001* |
| <i>t</i> _{DUR} (s) | 0.548±0.077 ^A | 0.392±0.049 ^A | 0.421±0.205 ^A | 0.108 |
| Aperture ratio | 1.046±0.072 ^A | 0.736±0.047 ^B | 0.385±0.074 ^C | <0.0001* |
| Aperture area (cm ²) | 42.15±4.449 ^B | 57.25±6.46 ^B | 102.96±50.621 ^A | <0.0001* |
| Aperture circumference (cm) | 24.187±1.273 ^C | 31.382±1.754 ^B | 48.678±13.839 ^A | <0.0001* |

Values are means±s.e.m. with associated significance values. Different letters indicate significant differences among species (*post hoc* tests). *Significant differences ($\alpha=0.05$) among species (ANOVA). See Table 1 for definitions of abbreviations.

$P<0.0001$; phase IV: $F=11.5$, $P<0.0001$). Total duration of feeding events was significantly shorter (ANOVA, $F=22.0$, $P<0.0001$) in Pacific white-sided dolphins (0.28 ± 0.02 s) than belugas (0.68 ± 0.07 s) or pilot whales (0.56 ± 0.04 s).

Feeding behaviors

Belugas were the most versatile at modulating their feeding behavior. They were able to capture prey using pure suction, pure ram and a combination of both (ram–suction). The ram–suction feeding mode was observed most frequently (Fig. 1A, Table 2). Belugas approached prey at low velocity (mean v_{subject} : 49.2 ± 6.6 cm s⁻¹, maximum v_{subject} : 168.4 cm s⁻¹). When phase I was observed (31.2% of trials), it occurred as the subject approached the prey (ram component) and included hyolingual adduction. During phase I, bubbles expelled from the lateral lip margins indicated hydraulic jetting, which was supported by suprambient pressure recordings (see below). Supination of the flippers (flares) reduced forward velocity to near zero as subjects approached the prey. At this point, the lips were within one mouth diameter (mean GAPE: 6.3 ± 0.4 cm) from the prey, and the jaws opened rapidly [Fig. 2; mean gape angle opening velocity (GAOV): 119.7 ± 8.1 deg. s⁻¹, range: 60.3 – 234.3 deg. s⁻¹]. In addition, the mobile lateral lips pursed to occlude lateral gape (mean OCC: $78.8\pm2.9\%$)

and the anterior lips created a characteristic small, circular oral aperture that coincided with maximum gape (Fig. 1B, see below). This pursing behavior effectively increased gape angle at the anterior lips. Maximum gape angle (maximum GANG: 25.7 deg.) was 45.6% of the biological capability. Hyolingual depression created subambient pressure and a flow of water and 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 v_{prey} : 219.1 ± 18.7 cm s⁻¹, maximum v_{prey} : 555.4 cm s⁻¹) 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 (hydraulic jetting) until the lips returned to their resting position and the mouth was closed. For this ram–suction feeding mode, the ram approach component and the suction ingestion component both occurred within one gape cycle and were not separate events. Pure suction and pure ram feeding trials occurred infrequently ($N=4$ trials). Kinematics were not significantly different from the ram–suction mode (MANOVA, Wilks' λ , $F=2.05$, $P=0.06$), although these trials tended to differ in subject and prey velocities, and ram trials tended to display larger gapes (mean GAPE: 10.02 ± 0.87 cm) with faster angular velocities [mean GAOV: 189.12 ± 35.01 deg. s⁻¹, mean gape

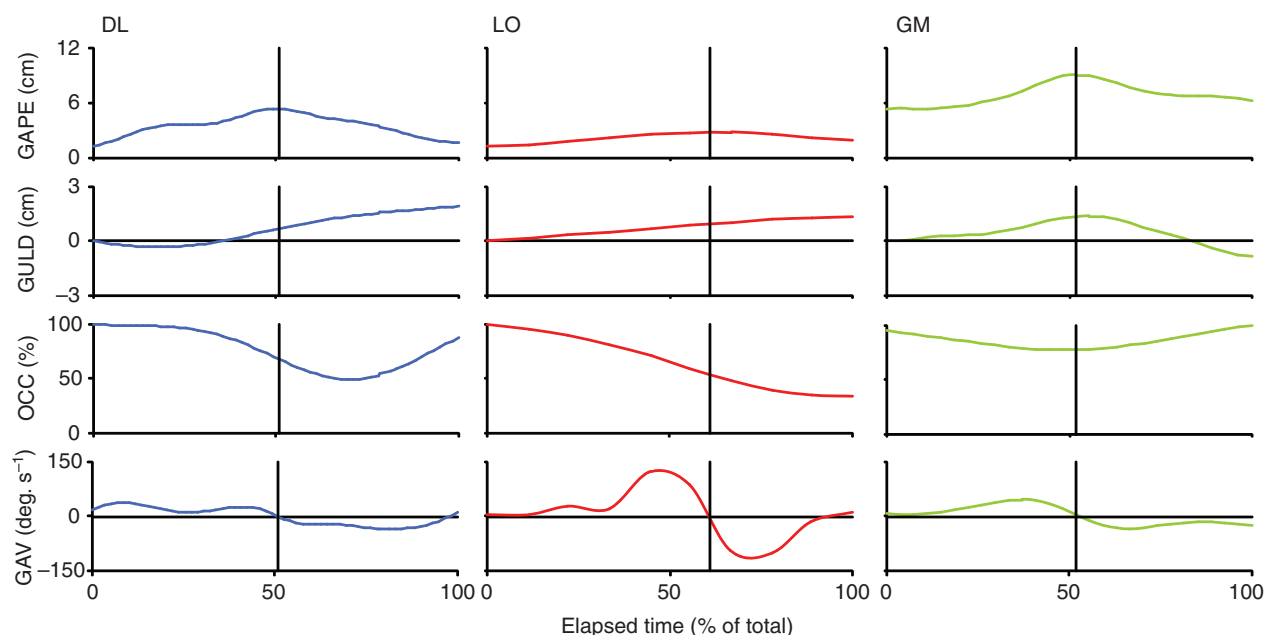


Fig. 2. Kinematic profiles from representative feeding trials of belugas (DL; blue), Pacific white-sided dolphins (LO; red) and pilot whales (GM; green). Elapsed time is scaled to percentage of total feeding event duration, and a black vertical line represents maximum gape. Variable abbreviations follow Table 1; GAV=gape angle velocity (opening and closing combined).

angle closing velocity (GACV): $175.79 \pm 42.42 \text{ deg. s}^{-1}$]. No preparatory phase was apparent in either ram or suction feeding modes, resulting in shorter duration of feeding events ($<0.5 \text{ s}$).

Lateral feeding trials for Pacific white-sided dolphins demonstrated that this species captured prey using ram and a small degree of suction (Fig. 1C, Table 2). Pacific white-sided dolphins were frequently observed to utilize more than one gape cycle to fully ingest prey (48.4% of trials), which represented ram capture, followed by additional gape cycles that incorporated suction, in which prey was manipulated. Only the first gape cycle (prey capture) was used in this analysis. Feeding was characterized by high approach velocity (mean v_{subject} : $81.5 \pm 8.5 \text{ cm s}^{-1}$, maximum v_{subject} : 218.5 cm s^{-1}). A preparatory phase without hyolingual adduction, as opposed to belugas, was observed in 45% of trials. During phase I, the jaws opened slowly, and after maneuvering for orientation, the jaws began to open rapidly (Fig. 2; mean GAOV: $248.4 \pm 22.1 \text{ deg. s}^{-1}$, maximum GAOV: $713.0 \text{ deg. s}^{-1}$). At this time, the anterior lips were slightly pursed, and the lateral lips occluded approximately 50% of the total jaw length. This is a surprising finding given that long-snouted dolphins are typically not thought to possess this ability. Maximum gape angle (maximum GANG: 36.5 deg.) was approximately 97.2% of the biological maximum. Rapid jaw movement appeared to create a slight flow of water into the mouth that resulted in some movement of the prey toward the mouth (mean v_{prey} : $89.3 \pm 14.5 \text{ cm s}^{-1}$). An oral aperture at the anterior lips was not clearly defined as in belugas (Fig. 1D). Maximum gape was followed by maximum hyolingual depression (mean GULD: $3.4 \pm 0.3 \text{ cm}$), maximum prey velocity (range of v_{prey} : $9.6\text{--}298.0 \text{ cm s}^{-1}$) 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. Limited suction capability during prey capture was confirmed with direct pressure recordings (see below). After prey moved into the mouth, the jaws closed rapidly (mean GACV: $226.0 \pm 26.0 \text{ deg. s}^{-1}$, maximum GACV: $690.1 \text{ deg. s}^{-1}$) 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 (hydraulic jetting) as indicated by bubbles. The lateral lips did not return to their resting position until after this time.

Pilot whales captured prey with a combination of ram and suction feeding modes only (Fig. 1E, Table 2) and did not capture prey using pure ram or suction feeding modes. Phase I was infrequently observed (16% of trials) and included hyolingual abduction followed by hyolingual adduction. Also during this phase, bubbles were expelled from the lateral lip margins, and hydraulic jetting was confirmed by direct measurement (see below). Pilot whales approached prey at a high velocity (mean v_{subject} : $84.8 \pm 4.3 \text{ cm s}^{-1}$, range: $41.8\text{--}121.3 \text{ cm s}^{-1}$). In some trials, pectoral flares were used to reduce velocity (but not stop) and maneuver as the subject approached the prey. The jaws opened slowly (mean GAOV: $94.9 \pm 6.4 \text{ deg. s}^{-1}$, range: $50.2\text{--}162.2 \text{ deg. s}^{-1}$) at the onset of phase II (Fig. 2). Hyolingual depression began after jaw opening and appeared to generate a flow of water that slightly drew the prey toward the mouth. The lateral lips occluded lateral gape by more than 50% of the total jaw length (mean OCC: $65.6 \pm 2.2\%$, range: $34.2\text{--}91.2\%$) and reached its minimum at maximum gape; the lateral lips rarely opened along the entire margin of the jaw. Maximum gape angle (maximum GANG: 24.2 deg.) was 61.3% of maximum biological capability, intermediate between belugas and Pacific white-sided dolphins. Synchronous opening of gape and lateral occlusion indicated that the lips were not engaged in an active pursing behavior, to seal the lateral gape for a prolonged duration, and that the proximity of the upper and lower jaws contributed solely to lateral lip occlusion. Pilot whales were the most limited in lip mobility; anterior lip pursing and an anterior oral aperture were not observed (Fig. 1F). Maximum hyolingual depression (mean GULD: $2.4 \pm 0.3 \text{ cm}$) occurred after maximum gape (during phase IV) and was concurrent with rapid prey movement into the mouth

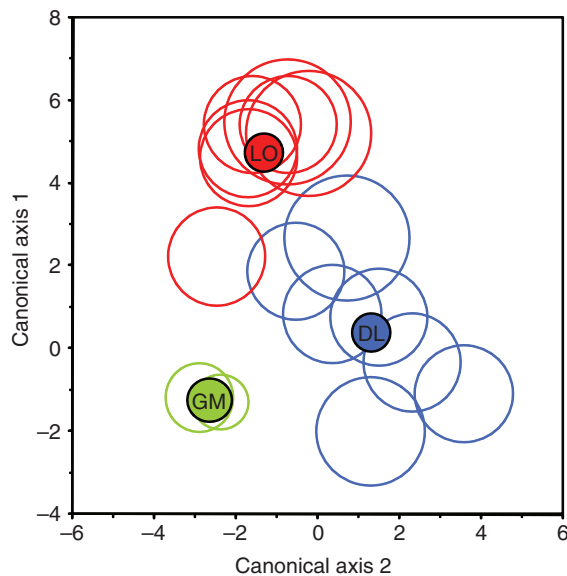


Fig. 3. Canonical centroid plot of lateral kinematic variables. Centroids were plotted for each species (filled circles; blue: belugas, DL, red: Pacific white-sided dolphins, LO, green: pilot whales, GM) and individual within species (unfilled circles). Circle size represents the 95% confidence level for each point (Mardia et al., 1979); large overlap between circles indicates insignificant differences between points. For definitions of abbreviations see Table 1. Variables t_{GAPE} , GAOV and $t_{\text{v}_{\text{ant}}}$ loaded positively and GAPE and t_{GANG} loaded negatively onto the first canonical axis; variables t_{GAPE} , GANG and $t_{\text{v}_{\text{post}}}$ loaded positively and GAPE, t_{GANG} and t_{GAOV} loaded negatively onto the second canonical axis. Together, these axes explained 93.8% of the variance among species.

(mean v_{prey} : $120.0 \pm 16.3 \text{ cm s}^{-1}$, maximum v_{prey} : 324.9 cm s^{-1}). 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 (hydraulic jetting). Duration of feeding events was relatively long (mean t_{DUR} : $0.555 \pm 0.041 \text{ s}$).

Comparative kinematic analyses

Beluga ($N=33$ trials), Pacific white-sided dolphin ($N=31$ trials) and pilot whale ($N=25$ trials) feeding kinematics differed significantly from each other in lateral kinematics (MANOVA, Wilks' λ , $F=2.35$, $P<0.0001$). Gape angle (ANOVA, $F=1.41$, $P=0.25$), $t_{\text{v}_{\text{subject}}}$ (ANOVA, $F=1.13$, $P=0.33$) and GULD (ANOVA, $F=3.12$, $P=0.0503$) were the only variables that did not differ significantly among species. For the remaining 20 variables, belugas and pilot whales were more similar overall in their kinematic profile than Pacific white-sided dolphins were to either of the two other species (*post hoc* tests, $P \leq 0.05$). Exceptions included GAOV and $t_{\text{v}_{\text{post}}}$, for which all species were significantly different from each other (Table 2; *post hoc* tests, $P \leq 0.05$). Additionally, GAPE and v_{post} were similar between belugas and Pacific white-sided dolphins but significantly different from pilot whales, and v_{subject} and v_{prey} were similar between Pacific white-sided dolphins and pilot whales and significantly different from belugas.

Species kinematic differences were also demonstrated through a canonical centroid plot (Fig. 3). Variables t_{GAPE} , GAOV and $t_{\text{v}_{\text{ant}}}$ loaded positively and GAPE and t_{GANG} loaded negatively onto the first canonical axis; variables t_{GAPE} , GANG and $t_{\text{v}_{\text{post}}}$ loaded positively and GAPE, t_{GANG} and t_{GAOV} loaded negatively onto the second canonical axis. Together, these axes explained 93.8% of the

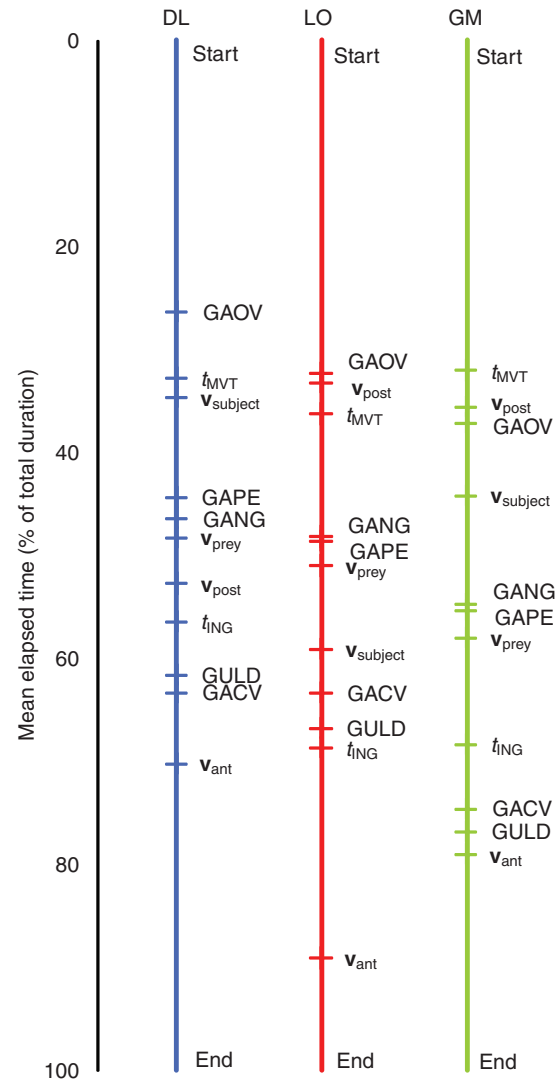


Fig. 4. Timeline of kinematic events for belugas (DL), Pacific white-sided dolphins (LO) and pilot whales (GM). Abbreviations follow Table 2. Markers represent mean percentage of total duration for each variable. The kinematic sequence was conserved: gape and angular velocity increased, maximum gape and gape angle occurred simultaneously, hyolingual depression reached its maximum after maximum gape, prey reached its maximum velocity toward the subject and was ingested, and the gape closed rapidly.

variance among species. Species means (represented by centroids) did not overlap, and further supports the conclusion that feeding kinematics among species were significantly different. In addition, individuals within species occupied distinct kinematic space, with negligible overlap between a few beluga and Pacific white-sided dolphin individuals. Pacific white-sided dolphin and pilot whale individuals displayed heavy overlap within their respective species, indicating that these individuals generally did not vary in their lateral kinematics. Belugas were more variable among individuals, which reinforces the observed variation in feeding behaviors.

Several analyses support the conservation and coordination of a posteriorly directed 'wave of buccal expansion' among odontocetes (Summers et al., 1998; Wainwright et al., 2008). The sequence and timing of kinematics appear conserved among odontocetes (Fig. 4), with a posteriorly directed wave of expansion from the tips of the jaws through the hyolingual apparatus.

Multiple variables loaded onto canonical axes (above) and provided further evidence of kinematic synchrony. Additionally, many variables were correlated (DL: 33.8%, LO: 27.3%, GM: 35.9% of possible correlations) within each species (Pearson R correlation, $P \leq 0.05$), which indicates coordination of kinematics. All timing variables were positively correlated to each other in belugas ($R \geq 0.47$, $P \leq 0.006$); timing variables were also highly correlated, although to a lesser degree in Pacific white-sided dolphins and pilot whales. Gape, gape angle, angular opening and angular closing velocities were positively correlated to each other in all species (DL: $R \geq 0.47$, $P \leq 0.007$; LO: $R \geq 0.70$, $P \leq 0.0001$; GM: $R \geq 0.38$, $P \leq 0.021$). Lateral occlusion was correlated to maximum prey velocity for belugas ($R = 0.47$, $P = 0.007$) but to no other variables in Pacific white-sided dolphins or pilot whales ($P \geq 0.08$). Significant correlation with GULD was observed singly with v_{ant} in belugas ($R = -0.41$, $P = 0.021$), $v_{subject}$ in Pacific white-sided dolphins ($R = 0.54$, $P = 0.002$) and tv_{post} in pilot whales ($R = 0.40$, $P = 0.048$). For pilot whales, correlations between timing variables and magnitude variables were more numerous than either other species. This high degree of correlation contributed to the greater amount of overall correlation present among kinematic variables in pilot whales, and indicates that kinematic magnitude variables were more strongly dependent on timing in pilot whales than for either other species.

A RSI was calculated for belugas ($N=21$ trials), Pacific white-sided dolphins ($N=20$ trials) and pilot whales ($N=24$ trials; Table 2, Fig. 5). All species displayed mean suction distances that were less than mean ram distances. These distances resulted in a majority of positive RSI values that indicated a general reliance on ram feeding in all species. Five trials resulted in negative RSI values (beluga RSI: -0.181 and -0.27 ; Pacific white-sided dolphin RSI: -0.267 ; pilot whale RSI: -0.111 and -0.113). However, kinematics (see above) and direct measurements (see below) confirmed stronger suction generation in belugas than that indicated by mean RSI. Maximum suction distance (DL: 8.96 cm, LO: 7.87 cm, GM: 11.54 cm) was approximately one mouth diameter of each species. The range of ram distances varied (DL: 0.86–25.6 cm, LO: 1.78–16.85 cm, GM: 1.84–19.0 cm). No significant differences were found in mean RSI values among species (MANOVA, Wilks' λ , $F=1.29$, $P=0.14$).

A clearly defined circular oral aperture formed consistently at maximum gape for belugas (Fig. 1B) but not for Pacific white-sided dolphins or pilot whales (Table 3, Fig. 1D,F). Lateral lip occlusion in belugas allowed an oral aperture to form and dictated its size and shape. Significant differences in anterior lip shape among species were found (MANOVA, Wilks' λ , $F=2.14$, $P<0.0001$). Belugas and Pacific white-sided dolphins achieved aperture ratios ≥ 1.0 (circular to tall and narrow shapes) whereas pilot whales did not. Aperture ratios <1.0 were more common for Pacific white-sided dolphins (78.3% of trials) and were more representative of the typical aperture shape. Aperture width, ratio, area and circumference were significantly different among all species (*post hoc* tests, $P \leq 0.05$) whereas GAPE was not (*post hoc* tests, $P=0.766$), although trends were similar to those observed during lateral analyses. Therefore, variance in aperture shape (ratio, area and perimeter) probably reflected differences in pursing capability. The high degree of stereotypy displayed among frontal aperture shape variables in belugas (Table 3) suggests that aperture area and perimeter may be tightly regulated in this species. However, stereotypy was not significantly different among species (MANOVA, Wilks' λ , $F=0.65$, $P=0.75$), although belugas were the only species capable of a true pursed aperture.

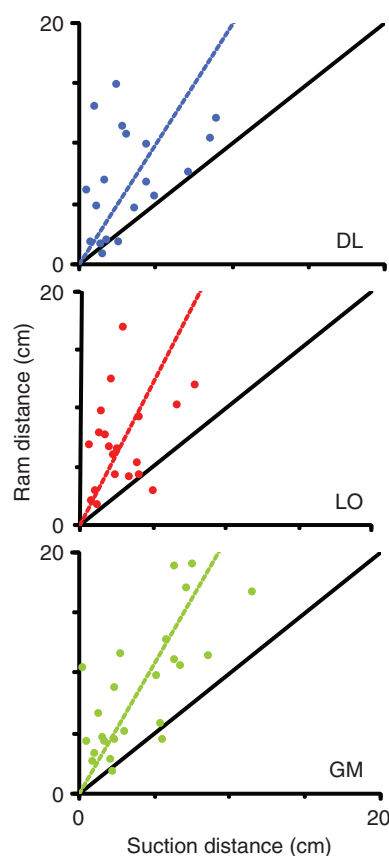


Fig. 5. Ram and suction distances in two-dimensional space for belugas (DL), Pacific white-sided dolphins (LO) and pilot whales (GM). A black solid line indicates the 0 Ram–Suction Index (RSI) isocline; points above the line represent ram feeding and points below the line represent suction feeding. Mean RSI was plotted as an isocline (colored line).

Intraoral pressure generation

Suction (subambient pressure, $N=412$ traces) occurred more frequently than hydraulic jetting (suprambient pressure, $N=75$), and was observed to some degree in all species (Table 4, Fig. 6). Belugas generated the greatest subambient pressures (126 kPa). Although total duration was longest in belugas (0.356 ± 0.01 s), rates of pressure change were greater than either other species. Pilot whale suction performance (22.9 kPa) was similar to Pacific white-sided dolphins (26.4 kPa). However, suction durations of pilot whales were intermediate to belugas and Pacific white-sided dolphins. Species were significantly different among suction variables (MANOVA, Wilks' λ , $F=6.86$, $P<0.0001$) but not hydraulic jetting variables (MANOVA, Wilks' λ , $F=1.09$, $P=0.35$). For suction timing variables, all species were significantly different from each other (*post hoc* tests, $P<0.0001$), and Pacific white-sided dolphins displayed the shortest mean total duration of events (0.146 ± 0.008 s), with the shortest mean expansive (0.076 ± 0.006 s) and compressive (0.070 ± 0.004 s) durations.

A high degree of correlation was observed among pressure generation variables in all species (80% of subambient and 71% of suprambient variables; Pearson correlation, $P \leq 0.038$). Subambient pressure generation was significantly correlated to expansive phase duration in belugas ($R = -0.16$, $P = 0.023$) and pilot whales ($R = -0.24$, $P = 0.005$) but not in Pacific white-sided dolphins ($R = 0.08$, $P = 0.451$). Total duration was only correlated to subambient pressure generation

Table 3. Degree of stereotypy in aperture shape among odontocetes

| | Belugas | Pacific white-sided dolphins | Pilot whales | <i>P</i> |
|------------------------|---------|------------------------------|--------------|----------|
| GAPE | 0.24 | 0.31 | 0.26 | 0.766 |
| t_{GAPE} | 0.30 | 0.46 | 0.50 | 0.513 |
| Width | 0.19 | 0.23 | 0.30 | 0.296 |
| t_{DUR} | 0.52 | 0.53 | 0.29 | 0.318 |
| Aperture ratio | 0.22 | 0.22 | 0.18 | 0.934 |
| Aperture area | 0.37 | 0.48 | 0.45 | 0.391 |
| Aperture circumference | 0.20 | 0.28 | 0.27 | 0.260 |

Values are mean coefficient of variation calculated for each species with associated significance values. No significant differences ($\alpha=0.05$) were found among species (ANOVA). See Table 1 for definitions of abbreviations.

in pilot whales ($R=-0.19$, $P=0.025$). Suprambient pressure generation displayed a similar pattern in correlations, except that expansive phase duration was not significantly correlated to pressure generation ($R=-0.13$, $P=0.692$), and pressure generation was significantly correlated to total duration in belugas ($R=-0.54$, $P=0.02$) and not in pilot whales ($R=-0.33$, $P=0.302$).

DISCUSSION

The use of ram and suction in odontocetes

Belugas

Suction is an important component of beluga feeding behavior. When approaching prey items, belugas maintained a slow approach velocity less than 50 cm s^{-1} and were able to ingest prey with greater velocity than other odontocete species in this study (over 500 cm s^{-1}). Behavioral adaptations that allow belugas to create a pursed circular aperture are clearly integral to prey capture and suction capability in belugas. This was evidenced by suction pressures similar to other mammals capable of some of the greatest subambient pressures known among vertebrates (walrus: 91.4–118.8 kPa, bearded seal: 91.2 kPa) (Fay, 1982; Kastelein et al., 1994; Marshall et al., 2008). In conjunction with the contribution of orofacial morphology, it is possible that hyolingual adduction and hydraulic jetting observed at the onset of the feeding event may also enhance suction generation by enhancing intraoral volume displacement. The strong suction

generation of belugas is convergent with suction feeding actinopterygian fishes where the shape and size of the aperture regulates the velocity of water flow into the mouth, and determines the magnitude of suction generation (Wainwright and Day, 2007). The relatively small aperture area and circumference, coupled with aperture pursing ratios that indicated a circular shape, provided evidence that belugas presumably use similar mechanisms as actinopterygian fishes to modulate hydrodynamic parameters to increase suction performance.

Although belugas displayed strong evidence for the use of suction during prey capture, the importance of suction may have been underestimated by RSI measurements in this study. Beluga feeding behavior may not always have a suction component, as indicated by the presence of pure ram feeding trials; ram feeding was also supported by RSI. However, suction is effective over limited distances (Svanback et al., 2002; Wainwright and Day, 2007), which results in prey movement due to suction that is limited and less variable (Wainwright et al., 2001). Kinematic analyses confirmed that the highest velocity prey movements were observed after belugas slowed forward velocity to near zero. Additionally, feeding events with varying ram distances can have the same RSI with proportional suction, resulting in RSI values that are incapable of describing true suction and ram performance (Wainwright et al., 2001). Ram in belugas was probably utilized to bring the subject

Table 4. Pressure generation performance values

| | Belugas | Pacific white-sided dolphins | Pilot whales | <i>P</i> |
|---|--------------------------------|--------------------------------|--------------------------------|----------|
| | Means \pm s.e.m. | Means \pm s.e.m. | Means \pm s.e.m. | |
| Subambient pressure | | | | |
| Expansive duration (s) | 0.156 \pm 0.005 ^A | 0.076 \pm 0.006 ^C | 0.127 \pm 0.009 ^B | <0.0001* |
| Compressive duration (s) | 0.2 \pm 0.007 ^A | 0.07 \pm 0.004 ^C | 0.174 \pm 0.009 ^B | <0.0001* |
| Total duration (s) | 0.356 \pm 0.01 ^A | 0.146 \pm 0.008 ^C | 0.299 \pm 0.015 ^B | <0.0001* |
| Suprambient pressure | | | | |
| Expansive duration (s) | 0.141 \pm 0.034 ^A | 0.096 \pm 0.013 ^A | 0.104 \pm 0.01 ^A | 0.073 |
| Compressive duration (s) | 0.157 \pm 0.032 ^A | 0.112 \pm 0.015 ^A | 0.191 \pm 0.104 ^A | 0.520 |
| Total duration (s) | 0.299 \pm 0.063 ^A | 0.208 \pm 0.022 ^A | 0.295 \pm 0.108 ^A | 0.115 |
| | Maximum | Maximum | Maximum | |
| Subambient pressure | | | | |
| Expansive rate (kPa s ⁻¹) | 2563.78 | 1288.3 | 427.827 | |
| Compressive rate (kPa s ⁻¹) | 975.236 | 661.918 | 430.108 | |
| Subambient pressure (kPa) | 126.123 | 26.442 | 22.931 | |
| Suprambient pressure | | | | |
| Expansive rate (kPa s ⁻¹) | 4355.49 | 2498.9 | 279.137 | |
| Compressive rate (kPa s ⁻¹) | 1298.6 | 2047.57 | 2245.42 | |
| Suprambient pressure (kPa) | 87.11 | 82.527 | 19.819 | |

Values are means \pm s.e.m., associated significance values (for timing variables) and maximum performance values. Different letters indicate significant differences among species (*post hoc* tests). *Significant differences ($\alpha=0.05$) among species (ANOVA).

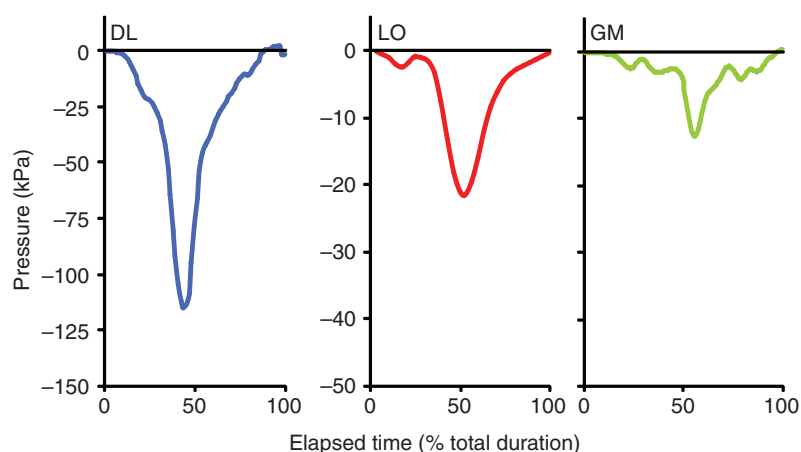


Fig. 6. Representative pressure traces from belugas (DL), Pacific white-sided dolphins (LO) and pilot whales (GM). Traces are shown as kPa vs time scaled to percentage of total duration. Note the scale of each trace.

closer to the prey, at which point direct pressure measurements indicated that prey were exposed to substantial suction forces. Evidence suggests that in the wild, belugas frequently consume benthic or concealed prey (Seaman et al., 1982; Dahl et al., 2000; Barros and Clarke, 2002) and, in this circumstance, suction performance may be of great importance. The presence of the substrate can enhance the distance across which suction is effective (Nauwelaerts et al., 2008). It is possible that suction feeding may be of consistently greater importance during benthic prey capture in belugas than indicated in this study.

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 high velocity (up to 220 cm s^{-1}) with a large gape angle that was $\sim 100\%$ of maximum capability. While a large gape may increase drag exerted on the subject and affect feeding performance, delayed jaw opening in Pacific white-sided dolphins may limit this effect. Additionally, fast approach velocities indicate that this potential increase in drag does not affect their ability to maintain high speed during prey capture. Feeding events were rapid and may reflect a need to rapidly herd and capture elusive schooling prey in natural environments, as demonstrated in some actinopterygian fishes (Wainwright et al., 2001). The low anterior lip aperture ratios of Pacific white-sided dolphins demonstrate that they do not purse their lips as well as belugas, although some lip pursing was observed from the lateral perspective. In some trials, prey was captured before maximum gape occurred, indicating that Pacific white-sided dolphins did not always rely on jaw closure to capture prey. Surprisingly, the lip margins did not fully open until after maximum gape, a behavior that indicated a limited capability to purse the anterior and lateral lips, which partially occluded lateral gape. This was an unexpected finding in a presumed ram feeding odontocete and underscores the need for direct kinematic and physiological measurements of feeding modes. This ability is evidence that Pacific white-sided dolphins are capable of limited suction capability, which was confirmed by the maximum *in vivo* subambient pressure measurement of 26 kPa; a harbor porpoise generated up to 40 kPa of subambient pressure (Kastelein et al., 1997). In contrast to belugas, the evidence from this study suggests that rapid gape opening is likely to be the primary mechanism by which Pacific white-sided dolphins can generate suction. 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 oropharynx.

Pilot whales

Pilot whales in this study utilized a combination of suction and ram feeding modes with indistinct components, as opposed to belugas. Some adaptations for suction generation were observed, which are supported by direct observations of suction use by pilot whales in captivity (Brown, 1962; Werth, 2000a). The hyolingual preparatory phase was similar to that observed in belugas. During phase I, water was often expelled at the lip margins, a hydraulic jetting behavior thought to enhance suction generation. Although approach velocity was similar to Pacific white-sided dolphins (85 cm s^{-1}), pilot whales were also able to slow their forward velocity with pectoral flippers, similar to belugas. Gape was limited to $\sim 60\%$ of the maximum capability, which effectively occluded some lateral gape and probably compensated for a lack of anterior lip pursing capability. Unlike Pacific white-sided dolphins, gape and lateral occlusion opened in synchrony, and no changes in morphology (pursing) occurred. Pilot whales in this study performed similarly to previously published pilot whale kinematics (Werth, 2000a).

Despite evidence for suction generation, pilot whales in this study relied more heavily on ram than belugas. Slow prey velocity (half that of belugas) and fast approach velocity contributed to an RSI indicative of ram. Although lateral gape was partially occluded, pilot whales were the least able to create a circular anterior mouth aperture, which may influence their dependence on ram. However, pilot whales were more similar to suction specialized belugas in kinematics, and were capable of generating a slight degree of subambient pressure. Due to low angular opening velocities observed in pilot whales, this suction capability is likely to be a result of hyolingual depression and not rapid jaw opening. However, hyolingual depression did not differ among belugas, Pacific white-sided dolphins or pilot whales, which reinforces the importance of orofacial morphology to suction generation (Bloodworth and Marshall, 2007; Werth, 2007). Maximum subambient pressure values of pilot whales (23 kPa) resembled Pacific white-sided dolphins, and was also less than a harbor porpoise (Kastelein et al., 1997), although kinematics indicated that pilot whales were more similar to belugas in feeding mode. However, in retrospect, pilot whale pressure traces may be misleading. Werth noted that food items were captured by means of laterally directed suction in rehabilitating pilot whales (Werth, 2000a). Furthermore, in the wild pilot whales primarily consume squid (Gannon et al., 1997b; Gannon et al., 1997a), and teuthophagy in odontocetes is presumed to be related to suction feeding behavior (Werth, 2000b). It is possible that if pressure measurements had been collected at the lateral sides of the mouth, this study might have measured greater

subambient pressures. Future studies of pilot whale feeding performance should test this functional hypothesis.

Comparisons with other vertebrates

A major finding of this study is that a greater diversity in suction generation mechanisms exists among odontocetes than previously thought. Based on the kinematic data, belugas generate subambient pressure through increased intraoral volume coupled with hyolingual depression and retraction and not by rapid jaw movements. Additionally, belugas adducted the hyoid (and presumably the tongue) just prior to the onset of feeding events (Phase I), which probably functions to remove residual water from the oral cavity and maximize the volume change at the onset of hyolingual depression. Similar behaviors reported in other suction feeding specialists (Lauder, 1980b; Marshall et al., 2008) support this hypothesis. Results from previous mammalian suction performance studies indicate that faster hyolingual and jaw kinematics are associated with suction (Kastelein et al., 1997; Werth, 2000a; Bloodworth and Marshall, 2005; Marshall et al., 2008). This relationship is also prominent among teleosts, with an extreme case represented by syngnathids (de Lussanet and Muller, 2007; Van Wassenbergh et al., 2008; Van Wassenbergh et al., 2009). However, in this study, belugas exhibited some kinematics that were more similar to ram feeding bottlenose dolphins, and that may result from a suite of varied morphological and behavioral specializations for suction generation in belugas. Lateral occlusion and pursing behaviors of belugas are likely to be as important as hyolingual depression and fast jaw movements to generate suction, and may contribute to a broader repertoire of feeding behaviors in odontocetes than previously thought.

Suction generation is tightly coupled with the physical properties of the medium, resulting in conservation of kinematics among elasmobranchs (Wilga and Motta, 1998), actinopterygians (Lauder, 1980a; Lauder, 1982), salamanders (Reilly and Lauder, 1990; Deban and Wake, 2000) and aquatic turtles (Lauder and Prendergast, 1992). 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, and all species utilized a posteriorly directed 'wave of buccal expansion' that has been observed in all suction feeding vertebrate lineages (Lauder and Shaffer, 1985; 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 expansion from the anterior jaws to the gills coordinates maximum flow velocity with maximum gape (Bishop et al., 2008). This pattern may be especially beneficial to obligate bidirectional flow suction feeders, including odontocetes. Lateral gape occlusion is a common behavioral adaptation of suction feeders, including odontocetes and pinnipeds (Werth, 2000a; Bloodworth and Marshall, 2005; Marshall et al., 2008). The non-kinetic mammalian skull constrains lateral occlusion but this function can be taken on by the oral lips in a behavior analogous to 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 in odontocetes, particularly in belugas, probably functions to create a small, circular anterior aperture to increase the flow of water into the mouth, as in teleosts (Wainwright and Day, 2007).

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). This dichotomy is exemplified by bluegill sunfish

(*Lepomis macrochirus*), with high velocity water flow and greater accuracy, and largemouth bass (*Micropterus salmoides*), which ingest a larger volume of water and have a greater ram component to their feeding mode (Higham et al., 2006a). Suction generation by belugas was analogous to bluegill suction feeding. Both exhibit a relatively small gape and high subambient pressure values that indicated a high velocity water flow (Higham et al., 2006b; Wainwright and Day, 2007). The capability to restrict gape indicates not only that belugas can generate a higher velocity flow of water into the mouth but that belugas probably direct suction force toward the prey for greater accuracy. Alternatively, ram feeding by Pacific white-sided dolphins was 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, direct comparisons of intraoral volume change to teleosts with unidirectional suction flow should be made with caution.

CONCLUSIONS

Belugas, Pacific white-sided dolphins and pilot whales employ varying degrees of suction and ram to capture prey that result from kinematic differences among species. Belugas generated suction pressures in excess of 100 kPa and were also able to purse their anterior lips to occlude lateral gape and create a small, circular anterior aperture, a behavior that was not performed as efficiently or consistently in the other species. Both Pacific white-sided dolphins and pilot whales were able to generate a slight degree of suction, which was probably compensatory or used during prey manipulation. The suction generation mechanism of marine mammals appears to result from hyolingual displacement or rapid jaw movement, and may also benefit from lip pursing behaviors. Odontocete feeding behaviors are more diverse than previously thought. However, kinematics are conserved and converge on the high velocity vs high volume paradigm apparent in other suction feeding vertebrates. Other behaviors, such as lateral gape occlusion and utilization of a posteriorly directed 'wave of buccal expansion', are also convergent with more basal vertebrate taxa, and further demonstrate the ubiquity of suction feeding across aquatic vertebrates.

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