

## Feeding kinematics, suction and hydraulic jetting capabilities in bearded seals (*Erignathus barbatus*)

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### SUMMARY

Feeding kinematics, suction and hydraulic jetting capabilities of bearded seals (*Erignathus barbatus*) were characterized during controlled feeding trials. Feeding trials were conducted both on land and in water, and allowed a choice between suction and biting, but food was also presented that could be ingested by suction alone. Four feeding phases, preparatory, jaw opening, hyoid depression and jaw closing were observed; the mean feeding cycle duration was  $0.54 \pm 0.22$  s, regardless of feeding mode ( $P > 0.05$ ). Subjects feeding on land used biting and suction 89.3% and 10.7% of the time, respectively. Subjects feeding in water used suction and hydraulic jetting 96.3% and 3.7% of the time, respectively. No biting behavior was observed underwater. Suction feeding was characterized by a small gape ( $2.7 \pm 0.85$  cm), small gape angle ( $24.4 \pm 8.13^\circ$ ), pursing of the rostral lips to form a circular aperture, and pursing of the lateral lips to occlude lateral gape. Biting was characterized by large gape ( $7.3 \pm 2.2$  cm), large gape angle ( $41.7 \pm 15.2^\circ$ ), and lip curling to expose the teeth. An excavation behavior in which suction and hydraulic jetting were alternated was used to extract food from recessed wells. The maximum subambient and suprambient pressures recorded were 91.2 and 53.4 kPa, respectively. The inclusion of suction data for phocids broadens the principle that suction feeding kinematics is conserved among aquatic vertebrates. Furthermore, bearded seals support predictions that mouth size, fluid flow speed, and elusiveness of prey consumed are among a suite of traits that determine the specific nature of suction feeding among species.

Key words: pinnipeds, feeding kinematics, suction feeding.

### INTRODUCTION

Inertial suction feeding is a common feeding mode among aquatic vertebrates of diverse lineages (Lauder, 1980; Muller et al., 1982; Lauder, 1985; Deban and Wake, 2000; Wainwright et al., 2007; Wilga et al., 2007). Prey is ingested from a distance by inducing water flow into the oral cavity through rapid jaw opening and buccal cavity expansion. Our knowledge of the detailed hydrodynamics of suction feeding has recently been advanced greatly for ray-finned fishes (e.g. Sanford and Wainwright, 2002; Svanback et al., 2002; Ferry-Graham et al., 2003; Carroll, 2004; Carroll et al., 2004; Day et al., 2005; Higham et al., 2005; Van Wassenbergh et al., 2005; Van Wassenbergh et al., 2006; Higham et al., 2006a; Higham et al., 2006b; Holzman et al., 2007; Wainwright and Day, 2007; Wainwright et al., 2007) and for chondrichthyans (e.g. Motta et al., 2002; Matott et al., 2005; Sasko et al., 2006; Dean et al., 2007; Nauwelaerts et al., 2007; Wilga et al., 2007). Significant work has been conducted for salamanders, which exhibit a diversity of intermediate stages between unidirectional and bidirectional suction feeding (Lauder and Shaffer, 1986; Shaffer and Lauder, 1985; Lauder and Reilly, 1988; Reilly and Lauder, 1988; Shaffer and Lauder, 1988; Miller and Larsen, 1989; Reilly and Lauder, 1990; Reilly and Lauder, 1992; Lauder and Shaffer, 1993; Deban and Wake, 2000), and for turtles and anurans (Lauder and Prendergast, 1992; Bels et al., 1997; Summers et al., 1997; Van Damme and Aerts, 1997; Deban and Olsen, 2002; Mason, 2003). This body of work has demonstrated that aquatic prey capture using inertial suction is conserved in the sequence and timing of events over a wide range of taxa. These similarities in kinematic patterns are

thought to be a result of life in an aquatic medium; the density and viscosity of water imparts strong selection pressures for inertial suction feeding (Lauder, 1985). However, among secondarily derived tetrapods, particularly aquatic mammals, few investigations of suction feeding have been conducted. Although anatomical data for the feeding apparatus among aquatic mammals are numerous, only a few experimental investigations of feeding behavior have been conducted (Kastelein and Mosterd, 1989; Kastelein et al., 1994; Kastelein et al., 1997; Marshall et al., 1998; Werth, 2000a; Marshall et al., 2003; Bloodworth and Marshall, 2005; Werth 2006a). Among pinnipeds, experimental feeding data are available only for walruses (*Odobenus rosmarus*), which are known to excel at suction feeding and demonstrate an effective excavation technique involving the alternation of suction and hydraulic jetting (forceful ejection of water out of the mouth; the opposite behavior to suction) to consume bivalves (Fay, 1982; Kastelein and Mosterd, 1989; Kastelein et al., 1994).

The feeding behavior and trophic ecology of bearded seals (*Erignathus barbatus* Erxleben 1777) are thought to be similar to walruses, and suction is presumed to be the primary feeding mode in this species (King, 1983), although there are no data to support or refute this statement. Bearded seals are the largest of the arctic phocids, and their biology was poorly known until recently because they are pagophilic, inhabit remote regions where the ice is in constant motion, and they occur at low densities (Burns, 1981). However, during the past decade concerted efforts have greatly increased our knowledge of bearded seal natural history, and their importance to arctic ecosystems (e.g. Hammill et al., 1994; Lydersen

et al., 1994; Kovacs et al., 1996; Lydersen et al., 1996; Andersen et al., 1999; Lydersen and Kovacs, 1999; Gjertz et al., 2000; Krafft et al., 2000; Lydersen et al., 2001; Marshall et al., 2001; Van Parijs et al., 2001; Lydersen et al., 2002; Van Parijs et al., 2003; Van Parijs et al., 2004; Davies et al., 2006; Marshall et al., 2006; Van Parijs and Clark, 2006; Dehn et al., 2007; Risch et al., 2007). Analyses of stomach contents and recent stable isotope analyses demonstrate that bearded seals are generalist foragers (e.g. Hjelset et al., 1999; Dehn, 2007), and are the only northern phocid that feeds predominantly on benthic prey, including crustaceans, mollusks, infaunal worms and benthic fish; the importance of each group varies regionally (Chapksii, 1938; Pikharev, 1940; Vibe, 1950; Kenyon, 1962; Johnson et al., 1966; Kosygin, 1966; Burns, 1967; Kosygin, 1971; Lowry et al., 1980; Burns, 1981; Finley and Evans, 1983; Hjelset et al., 1999).

Owing to their size and suction feeding capability, bearded seals are excellent subjects to investigate suction performance in phocids. However, to date, suction feeding in this species has not been studied. Additionally, pinniped suction feeding has not been characterized within the context of vertebrate evolution. Bearded seals are probably important ecological components of arctic benthic ecosystems because of their potential for causing substantial bioturbation during foraging, similar to walruses, and hence this feeding modality warrants investigation in a broad ecological context. Therefore, the objectives of this study were to (1) investigate feeding behavior in bearded seals to determine the range of their behavioral repertoire for capturing prey and to determine if suction feeding is the primary feeding mode in this species, as opposed to biting, (2) determine if bearded seal suction performance is similar to values reported for walruses, and (3) compare suction feeding in bearded seals with other vertebrates.

## MATERIALS AND METHODS

### Subjects

This study was conducted at *Polaria*, a public aquarium in Tromsø, Norway, which is the only facility globally that holds bearded seals in captivity. Two subadult male bearded seals *Erignathus barbatus* Erxleben 1777 were used in this study. Both subjects were 4 years old during the first year of the study,

approaching sexual maturity, and of similar body mass. Subjects were trained using operant conditioning for normal husbandry care, and thus were easily trained to feed from the feeding apparatuses used in this study. Uniformly sized, cross-sectional pieces (~4 cm long and 2 cm wide) of herring were used in the study because this was the food that the subjects consume on a daily basis. Prior to the study all subjects were individually fed a ration of cut herring by hand. All work was conducted under Texas A&M University's Institute of Animal Care and Use Committee Animal Use Protocol #2003-89 and in accordance with animal care guidelines within Norway.

### Feeding platforms

Three feeding apparatuses were constructed to present food items to subjects in a controlled manner. The primary feeding apparatus was constructed from wood and Plexiglas™. A mirror, sandwiched between Plexiglas™ and plywood, was placed behind the feeding surface at a 45° angle to provide simultaneous frontal and lateral views of the muzzle, jaw, and vibrissae during feeding events. The subjects were presented with food items using a sheet of Plexiglas™ that was inserted vertically into the feeding platform with the face parallel to the camera's perspective (Fig. 1). Cut fish pieces were presented to the subjects in two ways, simultaneously. Thirty holes, 2.5 cm in diameter, were drilled through the Plexiglas™ in six rows and five columns, approximately 2 cm apart. Cut fish pieces were pushed through the holes such that portions of the fish projected ~3 cm from the feeding surface, and were accessible to the subjects. In addition, cut fish pieces were placed within eight recessed Plexiglas™ wells (cylinders) that were positioned behind several of the holes through the Plexiglas™. Holes of 1 cm diameter were drilled through the back of the Plexiglas™ wells to allow water to flow through. The feeding apparatus was suspended in the pool approximately 1 m below the surface of the water, with the Plexiglas™ in the vertical plane. A halogen light (500 W) was suspended over the feeding apparatus to illuminate the feeding surface and the subject's face. Feeding trials were also conducted with the feeding platform on land. Subjects hauled out pool-side to feed from the apparatus in the same manner as during the in-water trials.

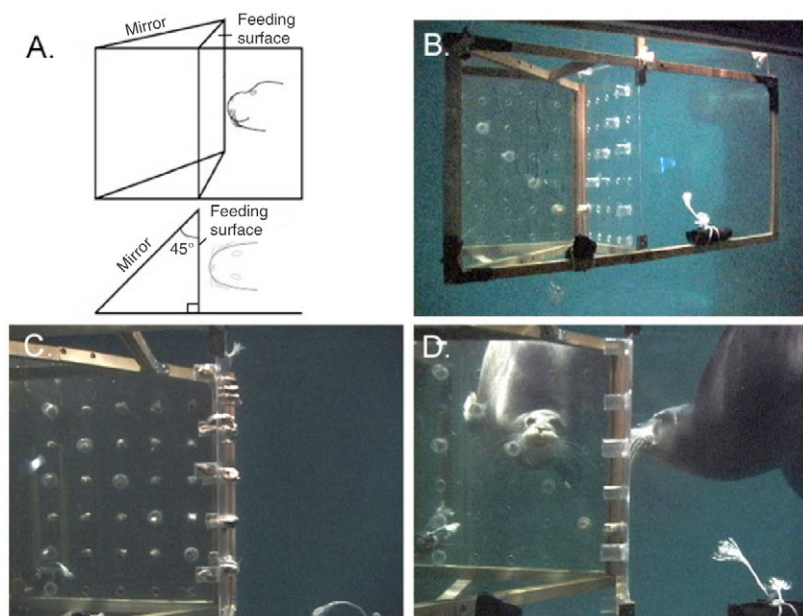


Fig. 1. Primary feeding platform. (A) Schematic from (top) the video camera's perspective and (bottom) above the platform. A mirror was placed at a 45° angle behind the Plexiglas™ feeding surface to allow for simultaneous frontal and lateral view of the muzzle during feeding trials. (B) Feeding platform in place in the pool. (C) Feeding platform with fish pieces in place. (D) Subject feeding from the platform (note the simultaneous lateral and frontal view).

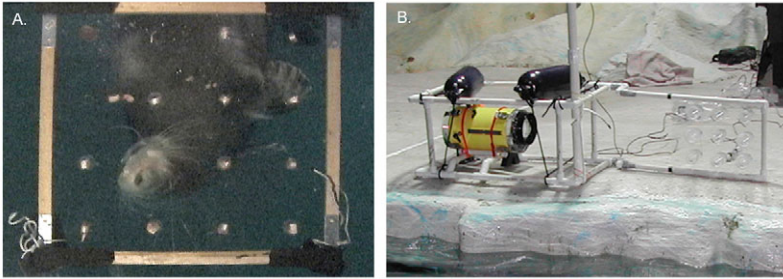


Fig. 2. Additional feeding platforms. (A) Frontal platform for gape and gape velocity verification. (B) Pressure recording platform.

A second, simpler square feeding apparatus was also constructed of wood and Plexiglas™ (Fig. 2A). The feeding surface in this feeding apparatus also had holes and recessed wells, and was similar to the primary feeding apparatus, but without the mirror. This apparatus was used to record subjects feeding in the frontal position to verify gape, and gape velocity, and to investigate potential shape changes of the muzzle during underwater feeding events. A third feeding apparatus was constructed from PVC and Plexiglas™ to measure pressure forces generated by feeding seals (Fig. 2B). This apparatus was constructed to hold a video camera within an underwater housing. The camera also recorded the lateral side of seals feeding from a Plexiglas™ feeding surface in which nine 2.5 cm holes were drilled. In this situation, recessed wells, with holes drilled in the back as described above, were placed behind every hole, and the subjects could only use suction to remove the food item. This apparatus was suspended into the water poolside, and facilitated the use of the electrophysiological recording equipment.

By presenting food items projecting from holes in the feeding surface and within the recessed wells during feeding trials using the primary feeding apparatus, subjects were forced to make several choices when presented with food. Upon encountering food items, their first choice was whether to consume fish projecting from the holes or fish residing within the recessed wells. If seals chose to consume fish projecting from holes in the Plexiglas™ feeding surface, then they had to choose whether to consume the piece of fish by biting and removing the fish with their teeth, or to use suction. If a subject chose to consume a piece of fish in the recessed well, then its only option was to use suction to obtain the food item. In this way it was possible to determine whether subjects used biting or suction as their primary feeding mode. In addition, food was presented to the subjects in the feeding apparatus such that the feeding surface was vertical, or horizontal; the latter most closely mimicked benthic foraging. Plastic tubing was attached to the back of one of the recessed wells so that dark green food coloring could be injected into the cylinder to visualize water flow generated by the subjects.

#### Feeding trials, kinematic variables and analyses

A feeding trial was defined as a single presentation to a subject of food items inserted into the Plexiglas™ feeding surface. Several trials were conducted each day, and feeding trials spanned a 2 week period, in each of the 2 years; pressure measurements were made only in year 2 of the experiment. A feeding event was defined as a single measurable ingestion of a food item. Therefore, a single feeding trial could produce numerous feeding events. A total of 133 feeding trials were analyzed to assess preferred feeding mode. Among these trials, 42 feeding events (14 lateral on-land trials,  $N=7$  per subject; 14 lateral in-water trials,  $N=7$  per subject, and 14 frontal in-water trials,  $N=7$  per subject) were chosen for kinematic analyses based on the criteria that both subject and prey were visible in the

video frame, all landmarks were visible during the trial, and rotation of the body was minimal (less than 15°). Subjects were videotaped (30 frames per second) using a Sony TRV 900 or 950 camcorder. Prior to feeding trials, zinc oxide was placed on the subject's lips, jaws and head to provide high contrast landmarks for digitizing. Landmarks were digitized frame-by-frame for motion analysis using Vicon Motus 9.0 motion analysis software system (Denver, CO, USA), which separates frames into individual fields to provide a 60 Hz record. Kinematic variables measured were: (1) maximum gape, the maximum distance from upper jaw tip to lower jaw tip; (2) time to maximum gape, the time from when the lower jaw began to open until maximum gape; (3) maximum gape angle, the maximum angle from the maxillary tip to corner of the mouth to mandibular tip; (4) time to maximum gape angle; the time from when the lower jaw began to open until maximum gape angle; (5) maximum opening gape angle velocity, the greatest angular rate of lower jaw opening; (6) time to opening gape angle velocity, the time from when the lower jaw began to open until maximum gape angle velocity was achieved; (7) maximum closing gape angle velocity, the greatest angular velocity during lower jaw closure; (8) time to maximum closing gape angle velocity, the time from when the lower jaw began to close until maximum gape angle velocity was achieved; (9) maximum hyoid depression, the greatest increase in distance from the eye to external rostral border of the hyoid apparatus visible externally; (10) time to maximum hyoid depression, the time from the start of hyoid depression to maximum hyoid depression relative to the eye; (11) velocity of food transport, and (12) gape cycle duration.

#### Pressure measurements

A total of 363 suction and 42 hydraulic jetting events generated by subjects were characterized using a Millar MPC-500 catheter pressure transducer connected to a transducer control box (TCB-600; Houston, TX, USA) and a Biopac MP150 portable electrophysiological recording system (Oleta, CA, USA). Electrophysiological data were saved to a MacIntosh iBook hard-drive. The pressure transducer was calibrated by inserting the distal end into a sealed flask and varying the pressure from -80 kPa to 0 kPa using a certified vacuum hand pump. Voltage output of the pressure transducer was linear across the entire pressure range ( $r^2=0.99$ ). Differential values of pressure traces from feeding trials were inspected through time, and analyzed using Acknowledge software (Oleta, CA, USA). Inspection of pressure traces prior to analysis ensured that noise artifacts were avoided. Furthermore, only pressure measurements that exceeded 0.1 V in magnitude were included in the data analysis.

Pressure measurements were collected using the smallest feeding apparatus; pressure was measured only underwater. A pressure transducer was placed through the back of a recessed well (that contained the food) so that the tip of the transducer, where the

recording element was located, projected approximately 2 cm beyond the Plexiglas™ feeding surface. This allowed the pressure sensor to be just at the seal's lips, or slightly within the oral cavity, during feeding. Control over the distance between the pressure transducer element and the lips of the subject was important since suction forces are inversely proportional to distance (Svanback et al., 2002; Ferry-Graham et al., 2003). This distance was verified visually during all feeding trials, and verified on the video footage. Only suction data from feeding trials in which the tip of the transducer was in contact with the lips of the subject, or within the oral cavity, were used in this study. Suction measurements collected in these feeding trials were: (1) the duration of the preparatory phase, a short suprambient pressure trace prior to a suction event verified by video (2) the maximum suprambient pressure during the preparatory phase, (3) duration of the subambient pressure drop, (4) the maximum subambient pressure, (5) duration of the change from maximum subambient pressure to ambient pressure, and (6) entire duration of the suction profile. Hydraulic jetting measurements collected were: (1) duration of the superambient pressure increase, (2) the maximum suprambient pressure, (3) duration of the change from maximum suprambient pressure to ambient pressure, (4) entire duration of the hydraulic jetting pressure profile.

### Statistics

Normality of data was tested using a Kolmogorov–Smirnov test. Levene's test was used to test the assumption of homogeneity of variances. All kinematic and pressure data were  $\log_{10}$  transformed to normalize variances.  $\log_{10}$ -transformed kinematic variables were used in a one-way analysis of variance (ANOVA), with the kinematic variables as the dependent factors and location (on land vs in water) as the independent factor, to determine the differences between kinematic profiles of suction vs biting. Pearson's 'r' correlation analyses assessed the positive or negative relatedness of the timing and displacement variables of feeding events. All statistical tests were conducted using SPSS 14.0 for the PC.

## RESULTS

### Biting vs suction behavior

During on-land feeding trials subjects used their teeth to grasp and bite the fish pieces projecting from the holes in the Plexiglas™ feeding surface. Biting was clearly evident by the large gape of the subjects, with curling of the lips to expose the teeth. Subjects would often bite the fish pieces in half, clearly leaving pieces behind in the apparatus. Subjects used suction successfully only on projecting pieces of fish; fish that were not in recessed wells. This was possible in the air because subjects could grasp the end of a fish piece with their mouths, sealing their lips around it, and use suction to ingest the fish. Attempts to use suction when food items were placed in the recessed wells were unsuccessful. On land, feeding behavior comprised 89.3% biting and 10.7% sucking ( $N=49$  trials).

In-water feeding trials yielded markedly different results from on-land feeding trials. Underwater, the subjects used suction exclusively whether or not food was projecting from a hole, or located within a recessed well. When food items within recessed wells were difficult to extract, subjects would employ suction, and alternate this behavior with hydraulic jetting. This behavior was evident when pieces of fish would oscillate back-and-forth within the recessed well until enough force was employed to remove it. The fact that suction, and not biting, was being used, even when feeding from the recessed wells, was clearly evident from the reduced gape (confirmed by kinematics, see below), pursing of the lips to form a circular aperture, sealing of the lips to occlude lateral

gape, and the lack of lip curling and observation of teeth. Alternating suction with hydraulic jetting was successful for extracting difficult-to-get food because holes in the Plexiglas™ were slightly narrower than the diameter of the Plexiglas™ cylinder, which created a small bottleneck (~2 mm). The alternation of suction with hydraulic jetting resulted in small changes in the position of fish pieces within the cylinder that allowed food to be extracted through this small bottleneck. Further evidence that suction and hydraulic jetting were being used alternately was the appearance of air bubbles from turbulence flowing from the back of the recessed wells toward the subject's lips during suction events, alternating with cloudy plumes of minute fish particles and scales exiting the back of the recessed wells during hydraulic jetting events. Also, during experiments in which food color was injected into a recessed well to visualize water, water flow clearly alternated in direction, depending upon whether suction or hydraulic jetting was being employed. Lastly, these suction and hydraulic jetting behaviors were confirmed during the pressure transducer experiments (see below).

During in-water feeding trials, suction behavior dominated, constituting 96.3% of feeding behaviors; no biting behavior was observed underwater ( $N=17$  trials). The remaining 3.7% of behaviors were hydraulic jetting events. During analyses of the first year's data, it became evident that the frequency of hydraulic jetting behaviors depended on the number of fish pieces inserted per recessed well. Therefore, during the second year, a series of feeding trials ( $N=30$ ) in which only recessed wells were used was conducted. Each recessed well was filled with a minimum of two pieces of fish, with the intent of making the extraction of fish as difficult as possible. Placing fish in the recessed wells in this manner increased the frequency of hydraulic jetting behaviors. Since all fish items were placed within the recessed wells, biting was not an option for subjects to obtain food items during these trials. These feeding trials resulted in suction and hydraulic behavior frequencies of 86% and 14%, respectively.

### Use of vibrissae

Mystacial vibrissae were used during both on-land and underwater feeding trials. On land, subjects appeared to use vision to search and find food items, but always resorted to using vibrissae to center the mouth over the food. Subjects closed their eyes during this last centering step. Underwater, vision appeared to be used little if at all at close range; the vibrissae were used to search for food and center the mouth over the food item. Once the seals were searching for food on the feeding apparatuses, their eyes were always closed and their vibrissae were everted. The vibrissae were brought from a state of relaxation to an active state in which they were spread apart, directed forward of the rostrum, and used to scan the Plexiglas™ feeding surface. Although it is difficult to ascertain conclusively, it appeared the seals were able to use vibrissae to detect either the opening of a recessed well or a small piece of fish protruding from the well. Individual and multiple vibrissal deflections were often observed as the whiskers moved over, or into, a recessed opening. Subjects usually moved immediately in the direction of these vibrissal deflections.

### Feeding kinematics

Four feeding phases: (I) preparatory, (II) jaw opening, (III) hyoid depression and (IV) jaw closing were observed regardless of the feeding mode. During suction feeding (in-water trials) the mean durations for phase I–IV were, 0.06 s (s.d.  $\pm 0.06$ ), 0.21 $\pm$ 0.09 s, 0.16 $\pm$ 0.05 s and 0.11 $\pm$ 0.05 s, respectively. During biting (on-land trials), the mean duration for phases I–IV were 0.06 $\pm$ 0.03 s,

Table 1. Summary of kinematic variables

Kinematic variable	Suction	N	Biting	N	P
Gape cycle (s)	0.53±0.25	26	0.52±0.1	13	0.51
Max. gape (cm)	2.70±0.85	28	7.3±2.2	14	<b>0.001*</b>
Time to max. gape (s)	0.17±0.1	28	0.17±0.08	14	0.949
Max. hyoid depression (cm)	1.8±0.66	14	0.85±0.49	14	<b>0.001*</b>
Time to max. hyoid depression (s)	0.30±0.15	14	0.31±0.12	14	0.694
Maximum gape angle (degrees)	24.4±8.13	14	41.7±15.2	14	<b>0.002*</b>
Time to max. gape angle (s)	0.20±0.13	14	0.18±0.08	14	0.745
Max. opening gape angle velocity (deg. s <sup>-1</sup> )	204.8±92.4	14	328±176	14	<b>0.040*</b>
Time to max open. gape angle velocity (s)	0.10±0.04	14	0.17±0.07	14	<b>0.006*</b>
Max. closing gape angle velocity (deg. s <sup>-1</sup> )	289.8±198.1	14	234.6±145.3	14	0.582
Time to closing gape angle velocity (s)	0.08±0.03	14	0.16±0.10	14	<b>0.008*</b>

Values are means ± s.d.; significant values are shown in bold type. \* $P < 0.05$ .

0.13±0.06 s, 0.18±0.08 s and 0.15±0.05 s, respectively. The preparatory phase involved closing of the mouth prior to jaw opening, and adduction of the hyoid. The duration of hyoid depression overlapped with phases II and IV. The mean feeding cycle duration was 0.53±0.21 s, and was not significantly different between suction and biting feeding modes ( $P > 0.05$ , ANOVA). However, motion analysis data strongly supported differences in the kinematics of suction *versus* biting feeding (Table 1, Fig. 3), and supported the behavioral data on suction and biting feeding behavior. In general, suction was characterized by a small gape (2.7±0.85 cm) and gape angle (24.4±8.13°), whereas biting was characterized by a large gape (7.3±2.2 cm) and gape angle (41.7±15.2°). Both gape and gape angle were significantly different between suction and biting ( $P < 0.01$  and 0.01, respectively, ANOVA). Time to maximum gape and time to maximum gape angle were not significantly different between suction and biting ( $P > 0.05$ ; *t*-test). Displacement and temporal measures of maximum gape and maximum gape angle during in-water feeding trials were not significantly different between frontal and lateral feeding trials ( $P > 0.05$ ; *t*-test), and these data were pooled with similar measurements from the lateral perspective ( $N = 28$ ). During all feeding trials, maximum hyoid depression always occurred after maximum gape; maximum hyoid depression was significantly greater during suction than biting ( $P < 0.01$ , ANOVA). Not surprisingly, maximum opening gape angle velocity was significantly different between suction and biting (204.76±92.4 deg. s<sup>-1</sup> and 328±176 deg. s<sup>-1</sup>, respectively;  $P < 0.05$ , ANOVA), as were time to maximum opening gape angle velocity (0.10±0.04 s and 0.17±0.07 s;  $P < 0.01$ , ANOVA) and time to closing gape angle velocity (0.08±0.03 s and 0.16±0.10 s;  $P < 0.01$ , ANOVA). Kinematic variables of biting and suction feeding are summarized in Table 1.

A Pearson's correlation analysis further supported these differences between suction and biting feeding kinematics (Table 2). Feeding site (feeding mode) was significantly correlated with maximum hyoid depression (negatively), maximum gape, maximum gape angle, maximum opening gape angle velocity, time to opening gape angle velocity, and time to closing gape angle velocity. Maximum hyoid depression was negatively correlated with maximum gape. Smaller hyoid depression and greater gape resulted in biting, whereas greater hyoid depression and small gape resulted in suction feeding. Time to maximum hyoid depression was correlated with time to maximum gape, and time to maximum gape angle highlighting the synchronization of these movements. Time to maximum hyoid depression was also negatively correlated with maximum closing gape angle velocity. Food velocity was

significantly correlated to time to maximum opening gape angle velocity.

#### Suction and hydraulic jetting pressures

Bearded seals used both suction and hydraulic jetting when feeding from any of the feeding platforms during in-water trials. The electrophysiological data (Fig. 4A) demonstrated that suction events comprised three phases: a preparatory phase, an expansive phase (during which maximum subambient pressure occurred) and a compressive phase. The preparatory phase was always characterized by a small suprambient pulse in pressure. The mean magnitude and duration of preparatory phases were 3.78±2.58 kPa and 0.10±0.04 s, respectively. The expansive phase was characterized by a rapid (0.15±0.085 s) subambient drop in pressure. The maximum subambient measurement recorded was 91.2 kPa. The compressive phase was characterized by a rapid (0.12±0.096 s) return of pressure to the baseline values. The duration of the expansion phase was significantly longer than the duration of the compression phase ( $P < 0.01$ , *t*-test). Pressure traces of hydraulic jetting (Fig. 4B) demonstrated only a rapid compressive phase (0.055±0.034 s) and expansive phase (0.051±0.028 s); a preparatory phase was never observed. The mean durations of the compressive and expansive phases during hydraulic jetting were not significantly different ( $P > 0.05$ , *t*-test); the maximum suprambient measurement recorded during hydraulic jetting was 54 kPa. Mean hydraulic jetting duration (0.11±0.055 s) was significantly shorter than the mean suction duration (0.26±0.11 s;  $P < 0.01$ , *t*-test).

#### DISCUSSION

Underwater, bearded seals approached the feeding apparatus, everted their vibrissae to search the feeding surface, oriented their lips over a food item, pursed their lips to form a circular aperture, and rapidly opened their lower jaw. After the initiation of jaw opening, the hyoid apparatus was rapidly depressed, which resulted in the flow of water and fish into the oral cavity. This sequence of events was similar when feeding on land, except that seals primarily bit and grabbed the fish with their teeth, using a greater gape, gape angle, opening gape angle velocity, but reduced hyoid depression. Occasionally, seals feeding on land would place protruding fish between their lips, and use suction to remove it from the feeding apparatus. Although some attempts were made by seals on land to obtain fish in wells using suction these were not successful. During all feeding trials the bearded seals closed their eyes. This behavior has been observed in other aquatic feeding mammals (e.g. Marshall et al., 1998; Marshall et al., 2003; Bloodworth and Marshall, 2005). Eye closure may serve to increase the tactile sensory modality, by closing down

their visual sense. Psychophysical data suggests that increased direction of attention within a particular sensory modality enhances that sense, but can result in a decrease in stimulus processing of other modalities (Kawashima et al., 1995; Spence, 2002; Marx et al., 2003). Alternatively, eye closure may be a protective function for bearded seals feeding in the wild in substrates that are potentially abrasive to the eye.

The suction generation mechanism in bearded seals, and probably all aquatic mammals, is limited to rapid jaw opening and depression of the hyolingual complex (Werth, 2000a; Werth, 2000b; Bloodworth and Marshall, 2005; Bloodworth and Marshall, 2007; Werth, 2007). This mechanism differs considerably from cranial

elevation observed in ray-finned fishes in which the amount of force from the epaxial musculature is correlated with the magnitude of the pressure produced [as well as other parameters (Carroll, 2004; Wainwright et al., 2007)]. Rapid jaw opening, and hyolingual depression, is probably widespread among suction feeding aquatic mammals, but few comparative data are available. The maximum opening gape angle velocity for bearded seals ( $204 \text{ deg. s}^{-1}$ ) is similar to values reported for pygmy and dwarf sperm whales (*Kogia* spp.;  $293 \text{ deg. s}^{-1}$ ), the latter a known suction feeder (Bloodworth and Marshall, 2005). By contrast, the maximum opening gape angle velocity in bottlenose dolphins (*Tursiops truncatus*), a known ram feeder, was reported to be  $84 \text{ deg. s}^{-1}$  (Bloodworth and Marshall,

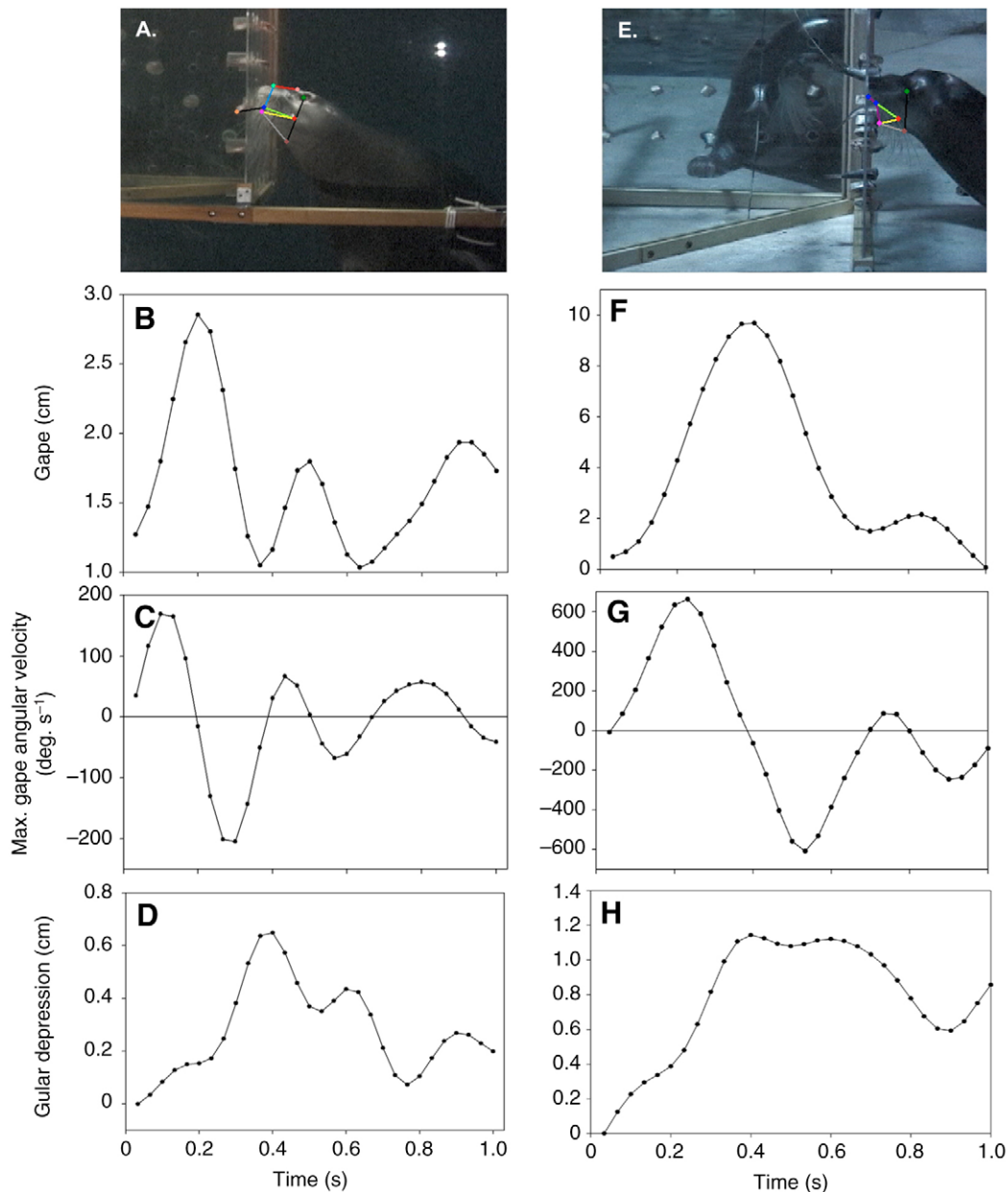


Fig. 3. Kinematic profiles of suction vs biting. (A) Frame from video during an in-water feeding (suction) trial with overlaid spatial model stick figure. (B) Plot of gape (cm) for a single suction feeding trial. (C) Plot of maximum gape angle velocity ( $\text{deg. s}^{-1}$ ) for a single suction feeding trial. (D) Plot of hyoid depression (cm) for a single suction feeding trial. (E) Frame from video during on-land feeding (biting) trial with overlaid spatial model stick figure. (F) Plot of gape (cm) for a single biting feeding trial. (G) Plot of maximum gape angle velocity ( $\text{deg. s}^{-1}$ ) for a single biting feeding trial. (H) Plot of hyoid depression (cm) for a single biting feeding trial.

2005). In aquatic mammals that presumably use suction extensively, the tongue functions as a cylindrical piston that is rapidly depressed and retracted to produce subambient pressures (Werth, 2000b; Werth, 2006a; Werth, 2007). Interestingly, the use of the tongue in hyolingual depression in aquatic mammals is a departure from the presence of tongues in adult postmetamorphic salamanders, which usually signifies a terrestrial feeding mode (Lauder and Shaffer, 1993; Deban and Wake, 2000). Time to maximum hyoid depression for bearded seals (0.3 s) is similar to values reported for pygmy and dwarf sperm whales [0.28 s (Bloodworth and Marshall, 2005)], and pilot whales [*Globicephala melas*; ~0.45 s (Werth, 2000a)]. Conversely, time to maximum hyoid (gular) depression for bottlenose dolphins was reported to be 0.62 s [pooled data (Bloodworth and Marshall, 2005)]. Although the function of the hyolingual complex in pinnipeds has not received much attention, the hyolingual apparatuses of presumed suction feeding odontocetes (toothed whales) are robust, and hyolingual muscles have relatively large cross-sectional areas (Reidenberg and Laitman, 1994; Werth, 2007). However, among marine mammals the orofacial morphology, tongue morphology, and the rapidity of hyolingual depression may be more important in generating suction than the force produced by hyolingual muscles (Bloodworth and Marshall, 2005; Bloodworth and Marshall, 2007). Several modifications of the orofacial morphology (e.g. short blunt rostra and mandible, reduced dentition) and hyolingual complex (short, broad tongues) are hypothesized to enhance suction performance in odontocetes (Reidenberg and Laitman, 1994; Marshall et al., 2001; Werth, 2000a; Werth, 2000b; Bloodworth and Marshall, 2005; Werth, 2006b; Bloodworth and

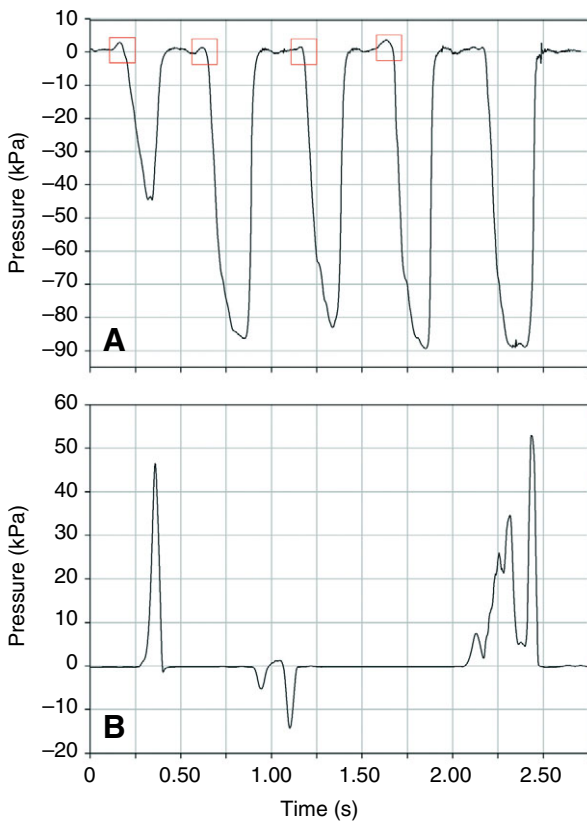


Fig. 4. Electrophysiological traces of pressure data. (A) A series of five suction events of varying magnitude. Red squares indicate prominent preparatory phases just prior to suction. (B) A series of two hydraulic jetting events (and one suction event).

Table 2. Pearson correlation analysis

	Site	Max. hyoid depression	Time max. hyoid depression	Food velocity	Max. gape	Time max. gape	Max. open. gape angle	Time max. open. gape angle velocity	Time max. close. gape angle velocity	Gape cycle	Max. close. gape angle velocity
Site	1										
Max. hyoid depression	<b>-0.7**</b>	1									
Time max. hyoid depression	0.078	0.181	1								
Food velocity	0.357	0.140	-0.140	1							
Max. gape	<b>0.81**</b>	<b>-0.5**</b>	0.268	0.304	1						
Time max. gape	0.010	0.295	<b>0.72**</b>	0.094	0.242	1					
Max. gape angle	<b>0.5**</b>	-0.301	0.176	<b>0.78**</b>	0.242	0.267	1				
Time max. gape angle	-0.064	0.349	<b>0.72**</b>	0.124	0.267	0.267	0.267	1			
Max. open. gape angle velocity	<b>0.39*</b>	-0.299	0.124	<b>0.463*</b>	0.267	0.267	0.267	-0.112	1		
Time max. open. gape angle velocity	<b>0.51**</b>	-0.144	0.024	<b>0.48**</b>	0.318	0.318	0.318	0.105	0.105	1	
Time max. close. gape angle velocity	<b>0.49**</b>	<b>-0.4*</b>	0.227	0.280	0.357	0.357	0.357	<b>0.424*</b>	1	0.005	1
Gape cycle	0.110	0.039	0.371	0.225	0.041	0.211	-0.363	0.005	0.055	1	0.165
Max. close. Gape angle velocity	-0.109	-0.013	<b>-0.46*</b>	0.137	-0.148	-0.169	0.190	0.143	0.154	-0.17	1

Log<sub>10</sub> transformed data; significant values are shown in bold type. \* P<0.05, \*\* P<0.01, N=28.

Marshall, 2007; Werth, 2007). Bearded seals, and possibly all pinnipeds that use suction to feed, also have short, broad snouts and jaws that presumably increase suction performance. The mobile and muscular muzzle and lips of bearded seals occlude the sides of the mouth, blocking lateral gape, and direct water flow toward the rostral lips. The rostral lips simultaneously purse to form a circular aperture through which water flows. The function of the lateral lips is analogous to the membranous labial lips that span the jaws in suction feeding ray-finned fishes (Lauder, 1979), the labial lobes of suction feeding salamanders (Lauder and Shaffer, 1986; Lauder and Reilly, 1988; Miller and Larsen, 1989; Deban and Wake, 2000), and the labial cartilages of suction feeding elasmobranchs (Motta et al., 2002; Matott et al., 2005; Wilga et al., 2007). The pursing of the rostral lips is convergent with the shape of the mouths of suction feeding fishes, and salamanders (Deban and Wake, 2000; Wainwright et al., 2007). Modifications of the orofacial morphology in bearded seals (and odontocetes) supports the general premise that differences in peripheral morphology are correlated with increased suction performance among aquatic vertebrates (Lauder and Shaffer, 1986; Lauder and Shaffer, 1993).

Bearded seals modulated their feeding kinematics between aquatic and terrestrial environments, mainly through differences in gape, gape angle, hyoid depression, and maximum opening gape angle velocity. Cryptodire turtles (Summers et al., 1997) and adult tiger salamanders [*Ambystoma tigrinum* (Lauder and Shaffer, 1986; Shaffer and Lauder, 1988)] also exhibit a reduction in hyoid depression when feeding in a terrestrial environment. Although, bearded seal gape cycle and time to maximum gape did not differ significantly between aquatic and terrestrial environments, gape during biting was greater than during suction, which explains the increased opening gape angle velocity on land vs in water. The differing density and viscosity of the two environments also probably influences this variable.

Pressure traces of the preparatory phase were usually characterized by a small suprambient pulse in pressure, which suggests that subjects were pushing their tongues up to the hard palate to expel any intraoral water. The adduction of the hyolingual complex would increase intraoral volume displacement during hyoid depression, thus increasing suction capability. Ray-finned fishes are also known to exhibit hyoid adduction, and a super-ambient pulse in pressure, during a preparatory phase (Lauder, 1980; Lauder, 1985; Nemeth, 1997). As in other suction feeding vertebrates, depression of the hyoid apparatus in bearded seals is important in generating subambient pressures. The maximum subambient pressure measured in bearded seals (91.9 kPa) is comparable to data collected from walruses by Fay [91.2 kPa (Fay, 1982)] and Kastelein et al. [51–118 kPa (Kastelein et al., 1994)], and higher than odontocetes (Kastelein et al., 1997; Werth, 2006a), all of which are more massive than bearded seals.

A significant finding of this study was that bearded seals exhibited an excavation behavior (alternation of suction and hydraulic jetting) similar to walruses (Fay, 1982; Kastelein and Mosterd, 1989; Born et al., 2003; Levermann et al., 2003). On average, the duration of bearded seal suction events was rapid relative to walruses (0.27 s vs 0.77–1.06 s, respectively), which probably reflect differences in maximum subambient pressures between the two pinnipeds. Longer durations of suction and hydraulic jetting events in bearded seals resulted in greater sub- or suprambient pressures recorded. A similar relationship between duration and maximum sub- and suprambient pressures was also reported in tiger salamanders (Lauder and Shaffer, 1986). Different durations of suction events in bearded seals and walruses probably reflect real differences in foraging ecology.

Most bearded seal prey are epibenthic, or shallow infaunal species, whereas walruses are specialized infaunal molluscivores that target mature, large, deeply burrowing bivalves [e.g. *Mya* spp. (Fay, 1982)]. It is probable that large bivalves resist being preyed upon by walruses, and require a longer handling (suction duration) time. However, generally speaking, feeding data presented in this study support the claim that bearded seal feeding and foraging is similar to that of walruses (King, 1983).

Investigations of suction feeding in bearded seals provide new data for a previously undocumented vertebrate group, the Phocidae, regarding the convergence evolution of suction feeding behavior by vertebrates. In general, the kinematics of suction feeding in bearded seals is similar to other suction feeders across a diverse array of lineages. The bidirectional flow of water during suction feeding in bearded seals (and probably all aquatic mammals), is most similar to postmetamorphic salamanders that have lost their gills, and gill slits (Lauder and Shaffer, 1986; Shaffer and Lauder, 1988; Deban and Wake, 2000). Unlike fish, the volume of the buccal cavity in bearded seals is limited, and the ingested volume of water should equal the ejected volume of water. Seals differ from other bidirectional suction feeders (inertial or compensatory) in that they are not known to exhibit behaviors that are analogous to buccopharyngeal expansion as observed in turtles (Van Damme and Aerts, 1997; Lemell et al., 2002), nor are they known to possess structures similar to a postglottal pharynx in pipid frogs (Mason, 2003). Although, it is generally thought that suction feeding in bidirectional systems is less efficient than unidirectional systems (Lauder and Shaffer, 1986; Shaffer and Lauder, 1988; Reilly and Lauder, 1988) (but see Miller and Larsen, 1989), inertial suction feeding by bearded seals demonstrates that mammalian bidirectional suction feeders can generate substantial subambient pressures. However, this may be simply due to relative species size, and a correspondingly large, buccal volume.

Despite differences in the mechanisms of suction generation among aquatic animals, the hydrodynamics of suction should be similar across all vertebrates, including seals. Suction hydrodynamics are best known among ray-finned fishes (e.g. Sanford and Wainwright, 2002; Ferry-Graham et al., 2003; Carroll et al., 2004; Day et al., 2005; Higham et al., 2005; Van Wassenbergh et al., 2005; Van Wassenbergh et al., 2006; Higham et al., 2006a; Higham et al., 2006b; Holzman et al., 2007; Wainwright and Day, 2007; Wainwright et al., 2007). In ray-finned fishes, the size and shape of the buccal cavity influence the relationship between peak pressure and fluid velocity (Van Wassenbergh et al., 2006), but peak pressure drop is usually in close agreement with peak fluid velocity (Higham et al., 2006b). The velocity, acceleration of fluid flow, pressure gradient and effective distance of fluid flow are related to the size of the mouth aperture (Ferry-Graham et al., 2003; Higham et al., 2006a; Higham et al., 2006b; Wainwright and Day, 2007; Wainwright et al., 2007). Suction feeding imparts three forces on the prey: drag, pressure gradient and acceleration reaction. Pressure gradient is the largest of these forces (Wainwright and Day, 2007), and prey capture is more successful when the pressure gradient is steeper. Steep pressure gradients can be accomplished by either increasing the rate of fluid velocity, or by restricting the size of the mouth aperture (Wainwright and Day, 2007). The large and rapid maximum subambient pressures, and the relatively small aperture of bearded seals, should result in a steep gradient in pressure that imparts sizeable forces on their prey items. Suction feeding performance of bearded seals is analogous to that of bluegill sunfish (*Lepomis macrochirus*). Bluegill sunfishes generate a higher fluid speed and higher fluid acceleration than largemouth bass



(*Micropterus salmoides*), in the earthbound reference, whereas largemouth bass generate a higher volume flow and higher volume flow rate (Higham et al., 2006b). The higher fluid speed and acceleration in bluegill sunfishes is related to their narrow mouth aperture, and their ability to focus their suction generation more in front of the mouth, resulting in greater accuracy. Bearded seals probably share these characteristics. A trade-off probably exists between the ability to generate higher fluid speeds and higher volumetric flow rate [without taking ram feeding into account (Higham et al., 2006b)]. Vertebrates that generate high fluid speed should also possess small mouths, with an ability to deliver high force to buccal expansion (Higham et al., 2006b). Suction performance data of bearded seals presented here supports this prediction. Their mouth aperture is relatively small and directed forward, the rapid depression of the hyolingual apparatus delivers force for buccal expansion, and the intraoral pressures measured were high relatively to other aquatic mammals. Furthermore, bearded seals target relatively non-elusive prey, most of which are benthic and epibenthic. Bearded seals probably exhibit high fluid flow and a steep pressure gradient, which are advantageous for feeding upon benthic prey.

Bearded seals feeding on marine worms within infaunal tubes could use the substrate and the cylindrical geometry of the worm tubes to passively increase suction distance. The positive effect of the substrate passively increasing the suction distance of benthic foragers has been documented in both ray-finned and chondrichthyan fishes (Carroll et al., 2004; Nauwelaerts et al., 2007). Although significant fluid velocities during suction events in ray-finned fishes are usually confined to a region within one mouth width from the mouth (Ferry-Graham et al., 2003; Day et al., 2005), visualization of water flow around the mouth of benthic foraging bamboo sharks (*Chiloscyllium plagiosum*) demonstrated that the boundary of the flow field can be passively increased up to 2.5 times the mouth width distance, because of the effect of the substrate (Nauwelaerts et al., 2007). Bearded seals feeding on marine tube worms may benefit not only from the effect of the substrate on fluid flow into the mouth during suction, but may be able to further extend the boundary of the flow field beyond the effect of the substrate due to the cylindrical geometry of infaunal tubes.

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