

VOLUME 51
PART 2

MEMOIRS

OF THE

QUEENSLAND MUSEUM

BRISBANE
31 DECEMBER 2005

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National Library of Australia card number
ISSN 0079-8835

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A Queensland Government Project
Typeset at the Queensland Museum

GULPING BEHAVIOUR IN RORQUAL WHALES: UNDERWATER OBSERVATIONS AND FUNCTIONAL INTERPRETATION

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MONIQUE MATTHEWS AND ANDY DUNSTAN

Arnold, P.W., Birtles, R.A., Soltzick, S., Matthews, M. & Dunstan, A. 2005 12 31: Gulping behaviour in rorqual whales: underwater observations and functional interpretation. *Memoirs of the Queensland Museum* 51(2): 309-332. Brisbane, ISSN 0079-8835.

Observations of non-feeding gulps in dwarf minke whales *Balaenoptera acutorostrata* sensu lato confirmed the axial rotation and lateral divergence (omega rotation) of the lower jaw suggested for rorquals. Gulps were either restricted to the inter-mandibular area or involved expansion of the whole ventral pouch; the extent of filling appears to be under voluntary control. Gulps may have different functions, e.g. feeding or display. Maximum gape (about 70°) occurred during inter-mandibular gulps, involving both depression of the lower jaw and elevation of the head and upper jaw. The lower jaw was depressed only to about 40°, much less than the 90° generally illustrated in the literature for rorquals. The mouth was closed as the ventral pouch was still filling; closure was rapid, associated with the moderate depression of the lower jaw. The whole ventral pouch contracted uniformly to expel water. The fibrocartilage skeleton of the ventral pouch was involved in outpocketing of the mental ("chin") region both at the beginning and end of gulps. During expulsion of water, partial axial rotation of the lower jaw maintained a groove just lateral to the baleen plates, opening as a vertical slit posteriorly. This would allow water expelled between the baleen plates to flow backwards, especially from the angle of the mouth. Incorporating these new observations, we discuss evolution of filter feeding and suggest that suction feeding was the primitive condition for baleen whales. □ *Minke whale*, *Balaenoptera*, *Mysticeti*, *feeding*, *evolution*, *functional morphology*

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The gulp feeding of rorqual whales, involving a massive expansion of the ventral pouch, is spectacular: the blue whale *Balaenoptera musculus* may envelop about 70 tons of water in a single gulp (Pivorunas, 1979). The anatomical specializations associated with such feeding attracted the attention of early anatomists (Hunter, 1787; Carte & Macalister, 1868; Lillie, 1915; Schulte, 1916) but analyses of the mechanisms have been much more recent (Pivorunas, 1976, 1977, 1979; Lambertsen, 1983; Orton & Brodie, 1987; Brodie, 1993; Lambertsen et al., 1995; Brodie, 2001; Arnold et al., 2002; Lambertsen & Hintz, 2004; Lambertsen, 2005).

Anatomical specializations include 1) a fibrocartilage articulation of the mandibular symphysis (Pivorunas, 1977); 2) a broad cranio-mandibular articulation in which the mandible rests on a fibrocartilage pad in the form of a truncated cone overlying the squamosal, replacing a ball and socket joint (Lambertsen et al., 1995, and references therein) and 3) a

possible further articulation between the suborbital plate of the maxilla and the coronoid process of the mandible (Lambertsen & Hintz, 2004; Lambertsen, 2005). The first two allow a medial to lateral (outward) rotation of the mandible around its longitudinal axis (alpha-rotation of Lambertsen et al., 1995); given the strong lateral curvature of the mandible such rotation increases the area of water and food capture. The loose cranio-mandibular articulation also allows a lateral displacement of the posterior ends of the mandibles, which swing outwards around a pivot point at the loose mandibular symphysis (omega-rotation of Lambertsen et al., 1995), further increasing capture area. The last, a possible cam articulation, was suggested as a means of countering negative lift on the large horizontal area of the mouth, especially at speed, and/or a means of initiating the gulp sequence to maximize prey capture.

The throat and ventral thorax are highly distensible. Muscles and connective tissue in the

ventral body wall have a high elastin content and can reversibly expand up to four times circumferentially, as well as 1.5 times along the body axis (Orton & Brodie, 1987). The oral lining can expand to a similar extent. Between the body wall and the oral lining plus tongue is a cleft called the *cavum ventrale* (Schulte, 1916; Pivorunas, 1979). It has been suggested that as water pours into the open oral cavity, the oral lining expands and the tongue falls back, everting into the *cavum ventrale* which expands to receive the water-filled sac formed by the oral lining and everted tongue. It was further suggested that the eversion of the tongue initiated expansion of the oral cavity (Lambertsen, 1983).

Muscle action (possibly the sterno-mandibularis: Lambertsen & Hintz, 2004) may open the mouth, which is assumed to be hydrostatically sealed for streamlining during normal swimming (Lambertsen & Hintz, 2004). Subsequent filling of the oral cavity has been considered essentially passive, powered by the kinetic energy of the whale's forward locomotion (Orton & Brodie, 1987). Lambertsen et al. (1995) suggested that the distension of the oral cavity creates a symmetrical medio-ventral torque which forces both alpha- and omega-rotation of the mandibles, initiating the rapid intake of water. As the mouth opens to angles above 70° the tendon of the temporal muscle, which inserts on the laterally directed coronoid process of the mandible, may act as a frontomandibular stay, limiting the opening of the lower jaw to around 90° (Lambertsen et al., 1995).

The base of a Y-shaped fibrocartilage skeleton extends backwards from the fibrocartilage joint of the mandibular symphysis, with the bifurcating branches of the Y running parallel to the mandibles (Pivorunas, 1997). Schulte (1916) suggested that the action of the mylohyoid muscles and ventral panniculus on the fibrocartilage skeleton would depress the anterior floor of the ventral pouch just behind the mandible (the mental or "chin" region). Lambertsen et al. (1995) and Lambertsen & Hintz (2004) suggested a similar outpocketing of the mental area could be created by a forward movement of the tongue; they considered this outpocketing of the mental area would "preload" the jaw structure before the mouth opens, ensuring the mouth opens more quickly, thus minimizing a bow wave effect.

It has been suggested that the lower jaw is brought back to its closed position through a

combination of muscle action and elastic recoil of the frontomandibular stay, possibly assisted by a forward rebound of the water mass enclosed within the ventral pouch (Lambertsen et al., 1995). The importance of preventing this rebound of water ("bounce phenomenon") while the mouth is still widely open was noted by Lambertsen & Hintz (2004), who envisioned this mechanism as part of developing a "rorqual adaptive zone", allowing gulp feeding at speed.

Muscle contraction and elastic recoil of the ventral pouch wall force water out of the oral cavity, and between the baleen plates.

The final element of the feeding sequence is manipulation of prey trapped by the bristles of the baleen plates and swallowing of the food. No direct observations of this process are available but Werth (2001) reviewed the evidence for prey removal through scraping by the tongue, head or lip shaking, or hydrodynamic flushing.

Such functional interpretations have been based primarily on manipulation of the jaw structure in whale carcasses, more recently supplemented by surface observations of feeding rorquals, especially humpback whales *Megaptera novaeangliae*. However, as noted by Werth (2000), "[much] of our understanding of the mechanical aspects of marine mammal feeding comes from speculative extension of anatomical knowledge...[this] information must be considered conjectural for in the absence of experimental evidence (or even underwater observations of animals in natural or captive conditions) there is no way to verify it directly."

As part of a study of dwarf minke whales *B. acutorostrata* sensu lato on the northern Great Barrier Reef, we have had the opportunity to observe and film non-feeding gulps underwater. We present these observations, based primarily on a detailed analysis of five gulp sequences, compare the new information with literature and footage of feeding rorquals, and discuss the new data in relation to mechanisms of gulp feeding proposed in the literature.

MATERIALS AND METHODS

Whales were observed from a commercial dive boat, *Undersea Explorer*, as part of a broader study of dwarf minke whales and whale-swimmer interactions during commercial swim-with-whale activities (Birtles et al., 2002; Valentine et al., 2004). Whales were observed in the vicinity of the Ribbon Reefs between Port Douglas and Lizard Island, Qld between

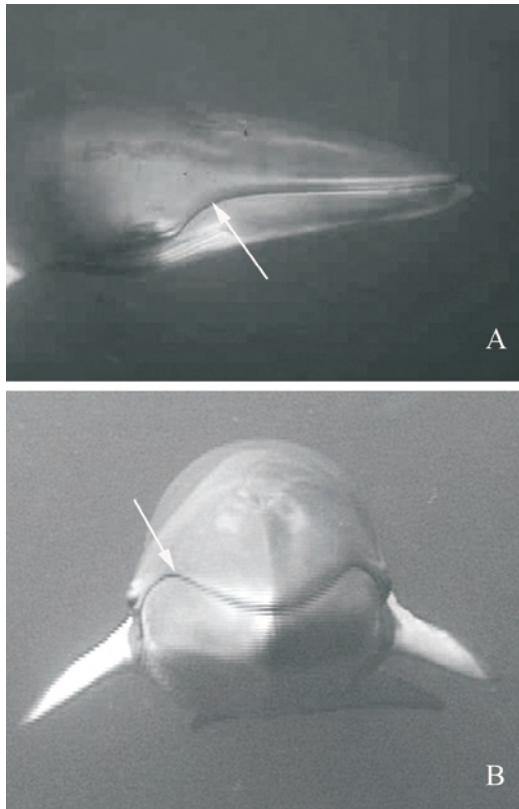


FIG. 1. Position of jaws during normal swimming. A, Lateral view showing the sharp ventral curvature of the lip of the mandible (arrow) just anterior to the eye. B, Anterior view of dwarf minke whale showing the medial curvature of the lip of the mandible (arrow). Also note the median ridge on the upper jaw which slopes down to either side of the upper jaw, giving a curved upper surface to the rostrum.

approximately 14° and 17°S (Arnold, 1997), primarily during June and July. During interactions, all swimmers used only mask, fins and snorkel and held onto a line, up to 50 m long, which was run out from the vessel. During open water encounters two lines were used, running from bow and stern, while usually only a single line was used when the vessel was moored at a reef; there were usually only 6 swimmers, including a researcher or videographer, per line. The length of the encounter and approach distances to the vessel and swimmers were under the control of the whales.

Digital video was taken with a Sony three-chip camera (DCR VX 1000E) in an Amphibico

VH-1000 waterproof housing. Still images were captured from video using DVD Tools. Using Adobe Photoshop version 8, the still images were converted to grayscale, brightness and contrast were individually adjusted to maximize resolution, and each image was then cropped.

Timing of events was by stopwatch. Angles of delta rotation (between the ventral margin of the upper jaw and the upper margin of the lip of the lower jaw) were measured by protractor from tracings of the images onto acetate sheets. Lateral displacement of the lower jaw (measured along the straight anterior margins of the lower lip) were similarly traced and measured.

Gulps were seen infrequently and even more rarely filmed. Thus observations were accumulated over field seasons 1999-2005. Analysis of gulps in this paper was based primarily on five video sequences, each of a different whale, recorded from 1999-2004; some of these sequences were included in the video *The Mystery of the Minkes* (New Zealand Natural History Unit). Incidental observations and photographs (digital and film) from six additional gulp events were also used. None of the gulping whales were measured, but a subsequent study (Sobczick, 2005) indicated a size range of 4.4 - 7.1 m ($n=81$ whales, from 33 encounters in 2003 and 2004).

The relatively clear water (usually >20 m horizontal visibility) and relatively small size of the whales (<8 m) allowed us to film whole gulp sequences, and to document behaviour before and after the gulp. This is rarely possible from shipboard observations although extended observations from an airplane may allow similar coverage of events, e.g. Watkins & Schevill (1979). The gulp sequences we filmed were not feeding events as no food was visible underwater. However we compared our observations and video with film of lunge feeding rorquals, such as Bryde's whale (*Balaenoptera edeni* species complex) contained on the BBC video *Blue Planet*, BBC/ABC video *Wild Australasia*, and private footage of Peter Constable) as well as photographs of lunge feeding blue (*Balaenoptera musculus*), fin (*Balaenoptera physalus*) and humpback (*Megaptera novaeangliae*) whales. Underwater video of feeding southern right whales (*Eubalaena australis*) and bowhead whales (*Balaena mysticetus*) were also available on commercial videos (*The Lost Whales*, New Zealand Natural History Unit and *Blue Planet*, BBC respectively)

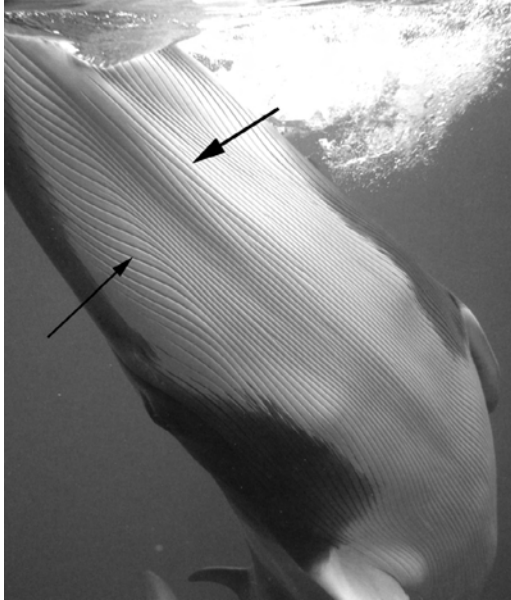


FIG. 2. Orientation of the grooves of the ventral pouch with the jaws adducted. As the whale's snout emerges from the water, the throat is taut; grooves under the mandible (thin arrow) are more vertically oriented and more widely spaced than the longitudinally oriented grooves medially on the ventral pouch. A median keel (thick arrow) on the ventral pouch is also visible.

for comparison of feeding activities, to complement recently published descriptions of balaenid feeding (Werth, 2004a; Lambertsen et al., 2005).

Our observations and filming of dwarf minke whales were carried out under permits from the Australian Department of Environment and Heritage (EA P1996/043, P1997/049, P1998/055, P1999/02, P2000/01, P2000/014 and E2004-51058) and from the Great Barrier Reef Marine Park Authority (G98/191, G99/169, G00/254, G01/248, G04/12096.1).

RESULTS

PROFILE OF HEAD AND LOWER JAW DURING NORMAL SWIMMING. Rorquals have the lower jaw tightly adducted to the rostrum during normal swimming, giving a streamlined head shape (Williamson, 1972). In lateral view, the lip of the lower jaw curves strongly ventrad just anterior to the eye (Fig. 1A), continuing posteriorly under and medial to the eye. In anterior view (Fig. 1B), it is also evident

that the lip of the lower jaw curves laterally from the base of the rostrum along the anterior margin overlying the supraorbital processes of the maxilla and frontal bones. The lower jaw is so tightly adducted to the upper jaw that the impression of the baleen plates can be seen on the oral lining covering the medial surface of the lower jaw (pers. Obs. on dwarf minke whale QM JM3861, dissected on 29-30 November, 1982 from photographs held in Great Barrier Reef Marine Park Authority library; Pivorunas, 1976, fig. 4). This lateral to medial curvature of the lip of the lower jaw indicates that the lip is at least partly directed medially, implying a more medial orientation of the mandibles when they are fully adducted.

Although the rostrum of the skull of the minke whale is almost flat (cf. arched rostrum of skull in pygmy right, right and bowhead whales, and to a lesser extent, gray whales; True, 1904), there is a strong median rostral ridge or crest overlying the skull in the living whale. This ridge slopes forward from the blowhole guard to the snout, as well as laterally from the median ridge toward the lateral margins of the upper jaw (Figs 1B, 4). The upper jaw is thus sloped or curved, as seen in anterior and lateral views, rather than flat. This curvature of the upper jaw and throat is more symmetrical when the whale is swimming (Fig. 1), than would be inferred from the shape of the skull alone.

When the lower jaw is tightly adducted to the upper jaw, the grooves of the ventral pouch are not uniformly spaced or oriented. The ventral most grooves in the inter-mandibular area and all the grooves in the thoracic area run longitudinally; they are closely spaced just behind the mandibular symphysis (Fig. 2) and may form a distinct median ventral keel (Fig. 2, thick arrow), especially evident as the head is raised above the longitudinal body axis or when the whale turns. Above these grooves, in the inter-mandibular area, are a series of more widely spaced, more vertically oriented grooves (Fig. 2, thin arrow).

TYPES OF GULPS

We recognize three types of gulps: 1) restricted to inter-mandibular area, 2) expanding the whole ventral pouch and 3) restricted to a narrow opening of the jaws, seen before the inter-mandibular or full ventral pouch gulps (Table 1).

Inter-mandibular gulp (IM). In four of the five gulps, distension was restricted to the

TABLE 1. Main characteristics of different types of gulp. Abbreviations. IM= distension restricted to inter-mandibular region; VP= whole ventral pouch is distended; Filtering gape= vertical angle between upper and lower jaw when water was being expelled through baleen plates; FCS= fibrocartilage skeleton of the ventral pouch, see text for further details; n.a.= not available, either because the full gulping sequence was not recorded or the angle of view did not allow observations to be made. The maximum opening of the mouth for IM4 was based on a second video sequence shot simultaneously from the side; the whale was distant and the image was indistinct, thus the angle could be measured only approximately.

Type and ID number of gulp	Figures of gulp herein	Time to fill (seconds)	Total time (seconds)	Maximum opening of mouth	Filtering gape	Depression of FCS at beginning of gulp	Depression of FCS at end of gulp
IM1	6	5.5	n.a.	~68°	~3°	yes	yes
IM2	7	5.7	8.6	~60°	n.a.	yes	n.a.
IM3	4a,5	2	6	~38°,42°	~2°- 3°	yes	yes
IM4	3	2.6	n.a.	~50°	n.a.	yes	n.a.
VP1	8	3.0	10.7	~40°	~3°- 5°	yes	yes

inter-mandibular region, although there appeared to be some re-distribution of water posteriorly after the mouth closed in gulp IM1 (Fig. 6D). Although the filling phase could be as short as 2 seconds (gulp IM3), in IM1 and IM2 it was 5.5 and 5.7 seconds respectively — almost twice as long as required to fill the ventral pouch in gulp VP1. Since the videographer was panning to maintain contact with the whale, it is not possible to determine relative swimming speeds during the different sequences. In the video of gulp IM1, however, it was possible to see the sweep of the caudal peduncle, indicating forward locomotion. It was during inter-mandibular gulps that the mouth opened most widely: 60°-70° in gulps IM1 and IM2. In both cases, this involved both a downward rotation of the lower jaw and a raising of the upper jaw (see Delta rotation). In gulp IM4, the rostrum was clearly raised as well (compare Fig. 3D-G). The rostrum was held almost horizontal in IM3 and the opening of the mouth was primarily due to depression of the lower jaw.

Full ventral pouch gulp (VP). Two ventral pouch gulps were recorded, one (VP1) in sufficient detail to summarize the main events (Table 1). The rostrum was held nearly horizontal, while the mandible was depressed to a maximum opening of about 40°. The ventral pouch was filled in 3 seconds, while the expulsion of water took place in 7.7 seconds.

“Preliminary” gulp. Before gulps IM 4 and VP1, the whale initially opened the mouth briefly (less than a second) and narrowly, exposing only the anterior-most plates in the baleen series. In IM4, the whale was turning on its side in the process of completing a 360° roll; fine debris was streaming from the baleen plates. In VP1, the initial gape

was as the whale approached the surface to breathe, while the full ventral pouch gulp was initiated as the whale was diving away from the surface after taking a breath.

MANDIBLE ROTATION: alpha rotation. Gulp IM4, seen in a dorso-lateral to dorsal view, showed the orientation of the jaw clearly. Initially, the jaw dropped with minimal rotation, however even in the first few images the lip of the mandible appeared to be vertically oriented, although it still remained medial to the external angle overlying the supraorbital process of the frontal bone (Fig. 3B-F). The head was raised (Fig. 3D-F), at which time the profile of the lower jaw became more distinctly bowed corresponding to the lateral curvature of the mandibles (Fig. 3F). Thus there was direct confirmation of alpha rotation, with each mandible swinging outwards around its axis. The lip of the mandible appeared to be just lateral to the supraorbital angle of the head (Fig. 3F) and the lateral angle of divergence of the mandibular lips increased to 48°. At this point, the floor of the oral cavity was stretched between the mandibles but there was no evidence of a distension of the ventral pouch lateral to the mandibles. Fig. 3G-I shows the closing of the mouth both by elevation and adduction of the lower jaw and the downwards movement of the rostrum. The ventral pouch just behind the symphysis was distinctly swollen lateral to the left mandible and the vertically oriented grooves curved around the distended throat (Fig. 3I-K). The mandibles remained partially abducted from the rostrum (Fig. 3I-L), providing a clear view of the baleen plates and creating a groove (orolabial sulcus) of the open vestibulum oris lateral to the baleen plates and at the gape (Fig. 3I-L). Thus a partial

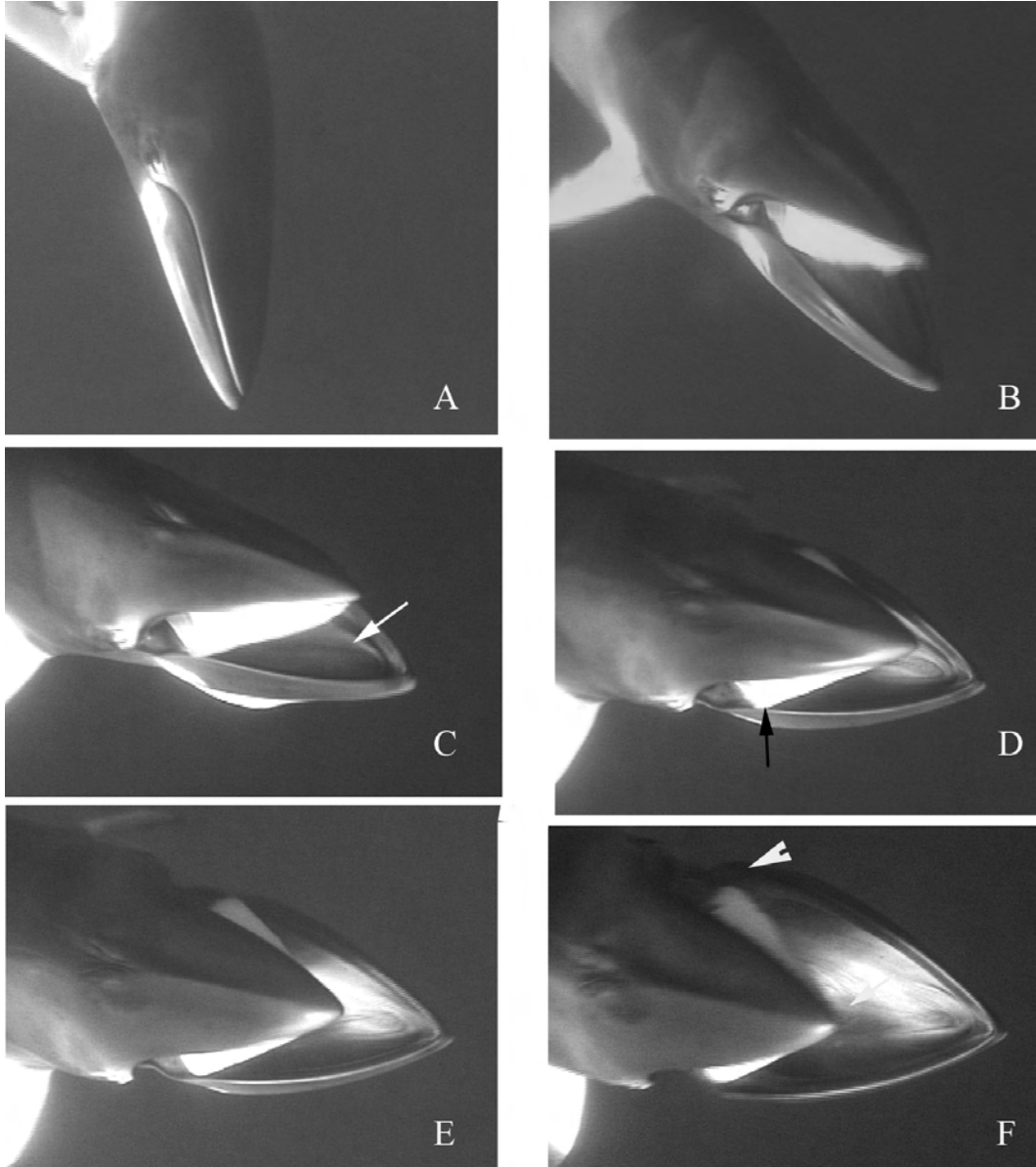


FIG. 3. Inter-mandibular gulp IM4. The mouth is just starting to open in A; baleen plates are visible in B, while the lip of the mandible appears to be oriented vertically. In C the mandible continues to drop and the rostrum is raised; the baleen plates are almost entirely exposed, revealing the dark plates at the posterior end of the baleen series; the lips of the mandibles are still vertical and form a sharp angle at the mandibular symphysis, thus showing minimal signs of alpha rotation and no lateral rotation. The curved structure just behind the mandibular symphysis (arrow) is the fibrocartilage skeleton of the ventral pouch. In D, the lips of the mandibles are still vertical and the mandibles still remain medial to the eye, again showing minimal signs of rotation. The white baleen plates are clearly visible and can be seen to protrude either side of the upper jaw, especially the longest plates which occur just before the angle of the gape (arrow). In E, the rostrum is raised, while the angle of lateral divergence of the mandibles has increased and the profile becomes increasingly bowed outwards, reaching a maximum in F. In F, the lip of the mandible (broad arrow) is just lateral to the profile of the head, so that a distinct gutter is formed lateral to, as well as just behind the baleen plate series.

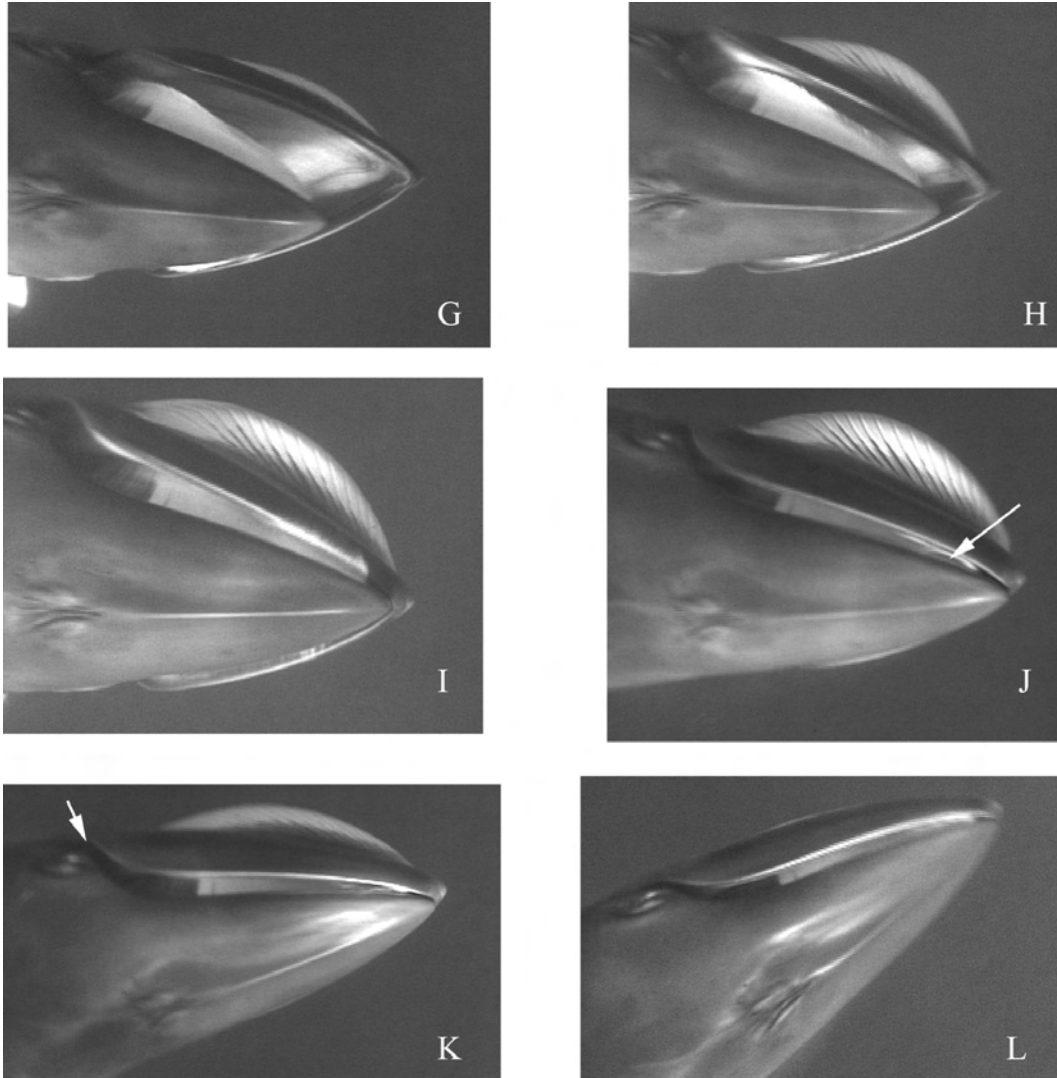


FIG. 3 (continued). This is consistent with full axial rotation of the mandible and also may indicate limited lateral (ω) rotation. A series of concentric wrinkles in the floor of the ventral pouch (thin arrow) denotes the anterior limit of the tongue. There is no sign of lateral distension of the pouch beyond the mandibles, although the floor of the oral cavity has been stretched outwards as the mandibles diverge. G, first signs of lateral swelling or distension of the ventral pouch are indicated as the white of the throat is seen beyond the left mandible. Note the upper and lower jaws are already closing. The lower jaw is still laterally displaced creating the gutter near the angle of the gape. H, swelling of the ventral pouch continues while the mouth closes; the gutter at the angle of the gape would allow displacement of water posterior to the baleen plates; the jaws have not been brought together closely enough for water to be filtered through the baleen plates. I. The mandibles are adducted towards the upper jaw, they already extend beyond the tip of the upper jaw. J, the ventral pouch reaches maximum expansion. The apparent whitish diffuse discolouration of the mandible (arrow) actually indicates fringes of baleen trapped as the lower jaws are brought back into position. K, L, mandibles are maintained at an angle to form a gutter just lateral to the baleen plates and opening as a posterior slit (K, arrow) through which water can exit to the rear. There is a steady expulsion of water, indicated by the deflation of the ventral pouch. Note the narrow vertical angle between the upper and lower jaws, leaving only a small portion of the base of the baleen plate series exposed- much of the water would exit along the gutter formed by the mandibles.

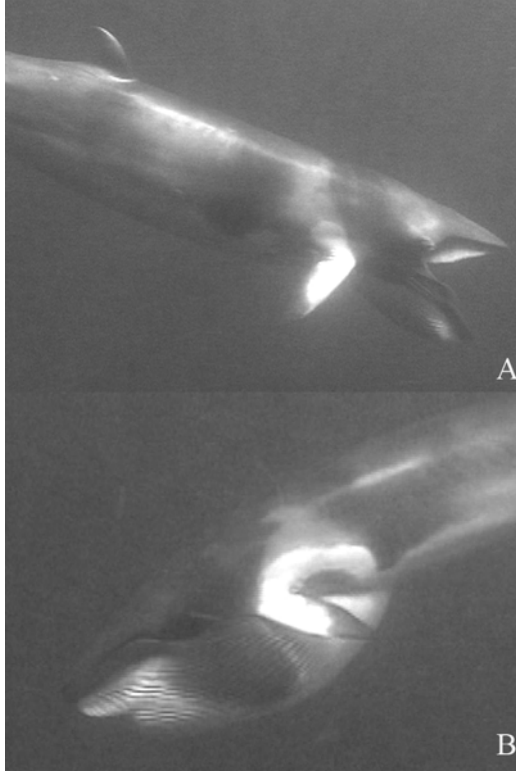


FIG. 4. A, Inter-mandibular pouch distension in gulp IM3. Expansion of the ventral pouch reaches its maximum about level with the eye; the body in the shoulder region remains unexpanded. B, Full ventral pouch gulp (VP1). The dark throat patch is obvious; also note that most of the pouch expansion occurs posterior to the inter-mandibular area.

alpha rotation of the mandible was maintained (compare Figs 1 and 3), providing a channel along which water could exit posteriorly after passing through the baleen plate series. The tongue was not seen at any stage of the opening of the jaw; concentric wrinkles just visible in the mid intermandibular region at the point of maximum opening of the mouth (Fig. 3F, arrow) probably indicate the anterior margin of the tongue which would have been in the posterior part of the throat at that stage.

Gulps IM1 (Fig. 6) and IM2 (Fig. 7A), as well as VP1 (Fig. 8A) also showed that the lower jaw may drop while still maintaining a low angle of lateral divergence of the mandibles –i.e. with only minimal evidence of alpha and no apparent omega rotation. It was only when the jaw was

depressed to about its maximum extent that there was a divergence of the mandibles, involving both alpha and omega rotation (see below).

Gulp IM3 showed a small distension of the ventral pouch as the jaw dropped, however it was only as the lower jaw was being closed that there was a distinct bulging of the ventral pouch (Fig. 4A) and substantial alpha rotation, as well as some lateral rotation (as indicated by the stretched frontomandibular stay and rotated lip of the lower jaw).

Gulps IM1 and IM3 included an oblique latero-posterior view of the whale as it swam away at the end of the gulp sequence. Gulp IM3 (Fig. 5) shows clearly that the mandible was held away from the upper jaw, not only leaving the baleen plates exposed but also forming a gutter between the baleen plates and the mandible which was open as a posterior slit at the gape, as also seen in IM4 (Fig. 3). The greatest abduction occurred at the rear of the channel, so that water could escape as the jaws were closing (Fig. 3H,I).

Omega rotation. Gulp IM2 (Fig. 7A) provided the best view of the angle of the mandibles at full divergence during a gulp. The posterior lip of the mandible was separated by a wide space from the external angle of the head, overlying the supraorbital process of the skull (Fig. 7A). This is a direct confirmation of lateral or omega rotation, spreading the mandibles widely to increase capture area. The angle of the mandibles (52° in oblique view, thus an underestimate) exceeded that associated with full alpha rotation in IM4 (see above). Although the lips of the mandibles formed an almost straight line, the anterior part of the frontomandibular stay could be seen diverging laterally from the gape to insert on the medial body of the mandible at the point of maximum curvature (IM1: Fig. 6, IM2: Fig. 7A). Thus the opening into the ventral pouch was an elongated ellipse, which was smaller in area than would be calculated from measuring the angle of the lips of the diverging lower jaws.

Gulp IM1 was videotaped from a more lateral aspect and thus it is difficult to assess the outward movement of the mandibles. However there was a wide separation of the lip of the mandible from the upper jaw and the frontomandibular stay could be seen stretched at the angle of the jaw (Fig. 6A). The extent of separation of the jaws would not occur solely through axial or alpha rotation and thus confirms omega rotation.

The temporal ridge formed by the frontomandibular stay may limit the extent of

separation of the jaws; on stranded specimens it can be seen as a thick column, strongly folded or pleated, which indicates the potential for considerable extension (e.g. figure of Antarctic minke whale *B. bonaerensis* in Baker, 1990: 10).

Delta rotation. Delta rotation involved not only depression of the lower jaw but also raising of the head and rostrum. This was particularly evident in inter-mandibular gulps IM1 (Fig. 6), IM2 (Fig. 7A) and IM4 (raising of rostrum seen in Fig. 3), although limited raising of the head was seen in other gulps, including VP1 (Fig. 8). Maximum vertical separation of the mandibles and upper jaw (delta rotation) occurred in sequences IM1 and IM2, with angles of 60–70°. This was due almost equally to raising the rostrum and dropping the mandibles. Other inter-mandibular gulps and the full ventral pouch gulp (VP1) had a maximum opening of about 40° which fully distended the ventral pouch (Fig. 8).

Once the rostrum was raised, there would be an upwards force on the palate as the whale moved forward, keeping the rostrum elevated. This may be partially compensated for by the forward rotation of the flippers (IM1, Fig. 6A,B). However, movement of the head was actively controlled and not simply a response to upward force of the water. In gulp IM4, for instance, the head was raised, briefly lowered, then raised further before being brought back towards the lower jaw.

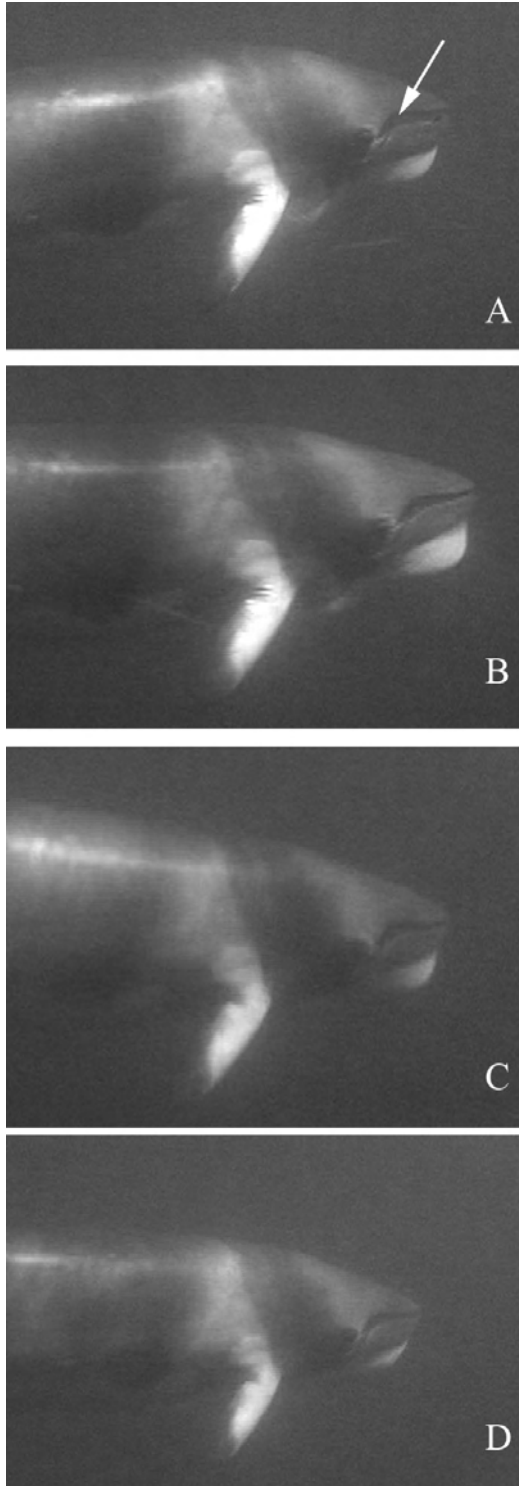
At the end of a gulp, the head was brought down to close the mouth. In gulps IM1 and VP1, where the sequence of events could be followed, the head was brought down only after the mandibles had returned to a horizontal position (VP1, Fig. 8). Timing of closure needs to be precise. Fig. 3D of gulp IM4 shows how far beyond the rostrum the baleen plates extended, especially the longest plates that occur about two-thirds of the way back in the series. As has been noted before (Lillie, 1915; Pivorunas, 1977), curvature of the mandible is needed to swing around these extended baleen plates. However, by the time the mouth was nearly closed, being open only at the anterior end, the mandibles had returned almost to the position they occupied when the whale was swimming normally (Fig. 3I, J). On two occasions we have seen and photographed the anterior-most baleen plates being trapped as the mandibles closed onto the rostrum (Fig. 3J).

ROLE OF THE FIBROCARILAGE SKELETON. In all the inter-mandibular gulps,

there was an initial distension or ballooning of the ventral pouch in the mental area just behind the symphysis (e.g. IM1, Fig. 6B). This could be followed by an expansion of the rest of the inter-mandibular area, but the mental swelling remained visible, defined by a ridge-like structure running posteriorly (IM1, Fig. 6; VP1, Fig. 8), around which the vertically oriented grooves curved. This ridge corresponds in position to one of the bifurcating branches of the fibrocartilage skeleton. In the ventral pouch gulp (VP1), initial bulging of the ventral pouch occurred more posteriorly (Fig. 8B), but this was immediately followed by a distension of the pouch in the mental region (Fig. 8C,D), just as in the inter-mandibular gulps. The vertically oriented grooves curved over a ridge-like structure as in the inter-mandibular gulps (Fig. 8D); this again is consistent with the position and structure of the fibrocartilage skeleton. In sequence VP1, as well as two other ventral pouch gulps photographed, maximum distension of the pouch occurred below the nape region, between the mouth and flipper, so that the ventral profile was of a parabola or smooth curve (Fig. 8F-K).

In gulp VP1, expulsion of water occurred in two stages. Initially the ventral pouch from the anterior ballooning of the mental region to its posterior insertion just in front of the umbilicus contracted as a unit, maintaining the smooth curve of the ventral profile, so that there was a less perceptible difference between the anterior ballooning of the mental region and the rest of the ventral pouch (Fig. 8F-K). Subsequently, the bulge in the ventral profile was restricted to the inter-mandibular area. Water within the ventral pouch appeared to be squeezed smoothly from the thoracic region towards the throat or inter-mandibular area, from which the last of the water was expelled after bulging in the mental region. In neither this sequence, nor in a second sequence (not illustrated) showing a full ventral pouch gulp, was there any indication of a forward movement of water in the ventral pouch as would be expected if there was a bounce mechanism assisting the closure of the lower jaw.

At the completion of the inter-mandibular gulps, the extent of white visible on the throat decreased as water was expelled through the baleen plates. In gulps IM1 and especially IM3, this was subsequently followed by a bulge in the throat which traveled forward to the mental region just behind the mandibular symphysis where it formed a distinct bulge over the fibrocartilage skeleton (IM3, Fig. 5B). This bulge



then decreased in size (IM3, Fig. 5C, D), bringing the inter-mandibular region back to its normal streamlined profile. Our interpretation of this forward traveling bulge is that it represents the last portion of water expelled, possibly forced forward by the tongue returning to its normal, more anterior position.

VERTICAL ANGLE OF JAWS DURING EXPULSION OF WATER. In lateral view, there was a narrow vertical separation of upper and lower jaws, giving a delta rotation of approximately 2° - 5° , which exposed the baleen plates to view (Figs 6D, 8K). Given the partial abduction of the lower jaw, a groove was formed outside the baleen plates into which water could be expelled (IM3, Fig. 5). The exposed portion of the baleen plates corresponded to the basal half of the plates. Thus, at least at the beginning of water expulsion, the area for egress of water (exposed baleen plates plus groove) was very much smaller than the surface area of the contracting ventral pouch.

LENGTH OF BALEEN PLATES. In dwarf minke whales, the baleen plates progressively increase in length to a maximum at about two-thirds of the way back, after which there is a sharp decrease in length. This profile is not only evident in lateral view but also dorsal view (IM4, Fig. 3D) where the longest plates extended furthest beyond the lateral borders of the rostrum. Gulp IM4 (Fig. 3H, I) shows the opening of the vestibulum oris at the gape. The longest plates are at the gape, with the forward extension of the frontomandibular stay crossing just lateral to the tips of the plates. These long plates would thus be the primary ones trapping food as water was expelled between the baleen plates into the posterior opening of the gutter at the gape.

DISCUSSION

The gulps which we filmed were not associated with feeding, as we never saw any food in the water. The two main types of gulps we documented (inter-mandibular, full ventral

FIG. 5. End of gulp IM3, showing beginning (A) of expansion of the ventral pouch in the mental region, which reaches its fullest extent in B and then begins to contract again in C and D. B shows the swelling of the mental region over the area covered by the fibrocartilage skeleton. Note in each image that the mandible is held out from the baleen plates through partial alpha rotation, creating a gutter (arrowed in A) and posterior slit for exit of the water.

pouch), may have different functions. The inter-mandibular gulps may be used as a display to swimmers (Birtles et al., 2002) and to other whales (unpublished observations). They showed a greater variability in duration than did the full ventral pouch gulps (Table 1). Whether or not these inter-mandibular gulps are also used in feeding, they do indicate the mechanics of oral cavity distension. The full ventral pouch gulps, in their duration and characteristics, are comparable to the lunge feeding seen in other rorquals (see comparisons below).

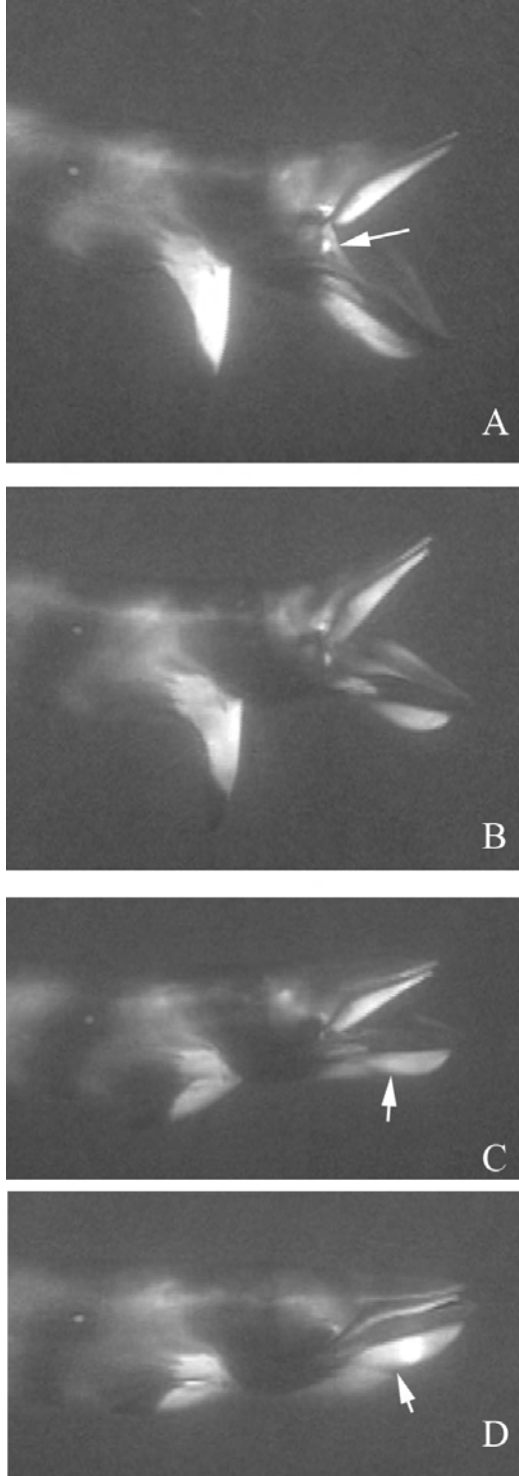
CHARACTERISTICS OF GULPS. The extent of pouch filling did not relate to the time the mouth was open; in inter-mandibular gulps IM1 and IM2 the maximum filling of the pouch took 5.5–5.7 seconds, while the full ventral pouch gulp VP1 lasted only 3.0 seconds. In all gulps which we observed underwater, the whale was progressing forward (pers. obs.; video of IM1). Thus whether only the inter-mandibular area or the whole pouch filled could be linked neither to the length of time that the mouth was open nor the occurrence of forward progression. Since the videographer followed the whale with the camera in open water, we could not assess the speed that the whale was traveling. Thus we can not check the relationship between the time taken to fill the ventral pouch and swimming speed.

Full alpha and omega rotation occurred in gulp IM2 but did not result in full expansion of the ventral pouch even in the inter-mandibular area; this contrasted with another sequence which had similar alpha and omega rotation but a fuller ventral pouch gulp. This difference suggests that expansion of the oral lining may not be entirely passive but under the control of the whale. Possible control mechanisms are discussed below.

In the sequences presented here, the whale could change the orientation of the head and travel of the body (either vertically or laterally) and thus the angle at which the water entered the mouth. However, in both IM1 and VP1, the whale was diving from the surface when the gulp began, so type of gulp was not directly related to the orientation of the whale as it traveled forward.

Initially, we thought that the rapid downward swing of the head could act as a lid on the still open ventral pouch but this downward sweep of the upper jaw occurred only after the mandibles had returned to a horizontal position and thus the opening of the ventral pouch was normal to the water flow (i.e., more water would not flow in).

We do not rule out the role of behavioural factors (e.g. length of time that the mouth is open, speed of travel, angle of travel of the body) in determining the extent to which the pouch fills; such factors could be particularly important in IM3 and IM4, which lasted for only 2.0 and 2.6 seconds respectively. However it does not explain the difference in filling of the pouch between IM1 and IM2 on the one hand and VP1 on the other. We suggest that there may be an anatomical basis as well. The ventral panniculus muscle extends for the whole length of the ventral pouch but the anterior and posterior portions of the muscles have different innervation: the facial nerve in the inter-mandibular area and the lateral thoracic nerve posteriorly (Schulte, 1916, based on observation of sei whale). In the humpback whale, Lillie (1915) illustrated two different sets of transverse muscles in the inter-mandibular area and thoracic area respectively. It thus seems possible that in an inter-mandibular gulp, the anterior inter-mandibular portion of the panniculus, as well as other transverse muscles such as the mylohyoid, relax while the posterior panniculus and thoracic muscles remain contracted. This would limit the backward movement of the tongue and the ability of the cavum ventrale to open up and receive the tongue. Relaxation of the posterior panniculus and transverse muscles in the thoracic region, as well as the inter-mandibular muscles, would allow full ventral pouch distension. One of the problems in testing this speculation is the poor documentation of baleen whale myology. Pivorunas (1977) and Lambertsen (1983) provided clear and well-illustrated re-descriptions of the inter-mandibular muscles. However, our Figs 4 and 8, in particular, show how great an area posterior to the inter-mandibular region is involved in a full distension of the ventral pouch. We are unaware of any detailed study on muscles which overlie this posterior region of the ventral pouch. The classic anatomical study on a common minke whale by Carte & Macalister (1868) was based on a single individual which had been dead for nearly two weeks before it was made available for dissection; similar constraints of limited sample size and extensive post-mortem times affected the description of a blue whale by Turner (1870), fin whale by Delage (1885) and humpback whale (Struthers, 1888). Lillie (1915) had access to fresh material. His observations, such as on axial rotation of the mandible, were astute and have been well supported by subsequent research, however his illustrations



were diagrammatic and his anatomical descriptions were very limited. The much quoted monograph by Schulte (1916), to which we refer above, was based on a sei whale foetus only 36 cm long. Thus there is a need for new, detailed anatomical descriptions of the whole ventral pouch before our suggestion of anatomical control of gulp feeding can be tested.

As pointed out by Brodie (2001) and Lambertsen & Hintz (2004), greatest resistance may occur at the beginning of opening of the jaws through frictional effects of the mandibles passing over the outwardly directed baleen plates and, perhaps more so, hydrostatic sealing of the mouth. Our observations of gulp IM4 show that the jaw is almost vertical as it drops initially so there would be some frictional resistance. In two of the sequences, where we saw what happened leading up to the gulp, there was a brief, narrow opening of the mouth ("preliminary" gulp). This may allow water into the oral cavity, breaking any hydrostatic seal; it may also clean the baleen plates.

JAW ROTATION: *delta rotation*. Images of feeding rorquals (Pivorunas, 1979; Lambertsen, 1983; Brodie, 1993; Berta & Sumich, 1999; Werth, 2000; Croll & Tershey, 2002; Heithaus & Dill, 2002; Hewitt & Lipsky, 2002; Bouetel, 2005) show a horizontal rostrum with the mandibles depressed at or almost at a right angle.

In our observations of dwarf minke whales, the opening of the mouth varied from about 40°-70°,

FIG. 6. Gulp IM1. A, As much of the delta rotation comes from raising of the upper jaw as depression of the lower jaw. The outward deflection of the lip of the lower jaw and the ventrally oriented, stretching frontomandibular stay of the jaw (arrow), indicates axial rotation of the lower jaw and, through the deflection of the lower lip and extension of the frontomandibular stay, probable partial omega rotation. B, the lower jaw is closing, while the upper jaw and head remain raised. In A and B, the swelling is predominantly in the mental region. C, the lower jaw has returned to a horizontal position while the upper jaw is still being brought down to its normal position; the bulge over the fibrocartilage skeleton (arrow) is clearly seen. D, there is an indication that water in the ventral pouch is being redistributed posteriorly, with distension of the ventral pouch behind the mental region. Note the position of the flippers, which are brought forward in A and B, then return to their more medial, more posteriorly oriented position (C, D) which is normal when swimming.

with the widest opening associated with inter-mandibular gulps. In the widest openings we observed, the rostrum was raised almost as much as the mandibles were depressed, presenting quite a different profile to that illustrated in the literature. Although we use the term “delta rotation” for such an opening of the mouth, the depression of the mandible itself was less than about 40° and thus much less than the delta rotation of 90° for the mandible which has been generally suggested in the literature quoted above.

Rapid (3 second) and full expansion of the ventral pouch could occur in non lunge-feeding dwarf minke whales with an opening of only 40° (Table 1:VP1). But is this also the case in feeding whales? Gaskin (1976) indicated that fin whales feeding at the surface on euphausiids opened their mouth to an angle of “45° or more”. Watkins & Schevill (1979), observing the same species feeding on fishes, noted maximum jaw openings estimated as 10°-20° and 30°, the latter when the jaw was closed more quickly. Further, feeding gulps did not always appear to be to capacity; Watkins & Schevill (1979) noted variable distension in feeding fin whales and noted that an individual might make a series of three to four gulps while feeding on fish. Mouth openings of at least 80° occur in video sequences of feeding Bryde’s whales (BBC: *Wild Australasia*), however this appeared to include raising the upper jaw as well as depressing the lower jaw. In blue whales observed feeding off southern Australia, gape varied from about 60° to 80°-85°, with the more usual gape estimated as about 70° (P. Gill, pers. comm.). Gill further noted that it “does seem that the wider [the blue whales] gape, the more the rostrum lifts back, as the mandible drops down”. Such records suggest that the images showing a right angle depression of the mandibles may represent an extreme case rather than the general condition in feeding rorquals. The ventral pouch structure must be able to withstand the maximum stress, such as would occur with an opening of 90°, and thus such angles are appropriate to consider in discussions on mechanics such as Lambertsen et al. (1995). However, a discussion of evolution of gulp feeding needs to consider the more general case, which appears regularly to be a mandibular delta rotation of <70°, perhaps considerably less.

Lambertsen & Hintz (2000) discussed the mechanisms for preventing water in the ventral pouch from bouncing forward and out of the still widely open oral cavity; they alluded to such

mechanisms as critical in developing a “rorqual adaptive zone”. Such a bounce mechanism seems very likely in a configuration of the ventral pouch such as shown in Pivorunas (1979) and elsewhere in the literature. It might also occur in the inter-mandibular gulps we document, if the whale is travelling quickly. However in full ventral pouch gulps, such as VP1, the lower jaw was already starting to close before maximum expansion of the ventral pouch occurred. This also happens in feeding whales, based on images of lunge feeding Bryde’s whales (e.g. BBC: *Wild Australasia*; images from Peter Constable). Water would thus still be flowing into the pouch as the mandibles were returning to their normal position. With water still being accommodated in the posterior portion of the ventral pouch as the mouth closes, water would not build up in the inter-mandibular area or bounce forward out of the still open oral cavity. With only the resistance of the mandibles, the lower jaw could return to the horizontal position relatively rapidly. This would be especially true in cases with a delta rotation of 40° or less for the mandibles, in which case there is less distance for the mandibles to be elevated before they are normal to the direction of travel and thus impede the inflow of more water. Minke whales (as well as sei whales) have a relatively short ventral pouch, with ventral grooves occupying about 47% of the body length (Nemoto, 1959). In blue, fin, Bryde’s and humpback whales, the ventral pouch is relatively longer, with ventral grooves occupying 58, 55, 58 & 58% of the body length respectively (Nemoto, 1959). The additional 11% in length of ventral pouch would translate into a significant increase in capacity; this can be seen in the almost cylindrical profiles of the full ventral pouch in blue whales (e.g. Grace, 1996; Clapham, 1997) rather than the semi-circular form of the ventral pouch shown in diagrams of feeding (Pivorunas, 1979 and others listed above). Thus the potential for rapid closure of the lower jaw while water is still filling the ventral pouch is even greater in species such as blue and fin whales, than has been demonstrated here for minke whales. This closing of the jaws while water is still filling the ventral pouch is central to the development of lunge feeding and the “rorqual adaptive zone”.

We saw no evidence of the bounce phenomenon after jaw elevation and adduction in the admittedly limited number of full ventral pouch gulps we have recorded. The bounce phenomenon might occur in true lunge feeding, however. One sequence of lunge feeding Bryde’s

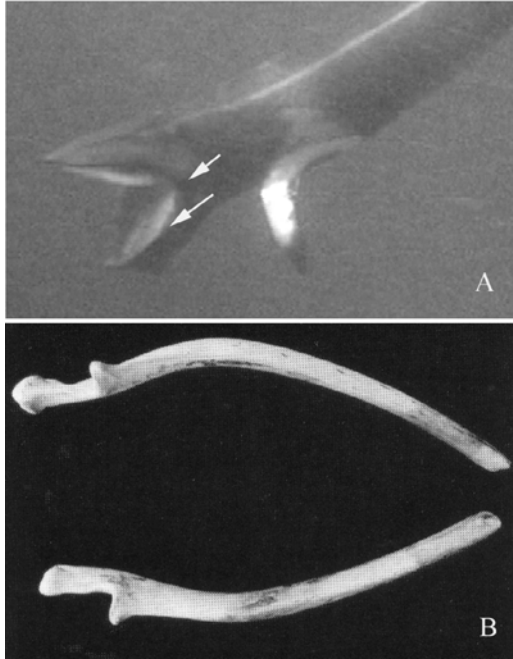


FIG. 7. A, Gulp IM2. Note the extensive lateral divergence of the mandibles, stretching the floor of the oral cavity. The upper arrow indicates the most lateral extension of the supra-orbital process of the head, at the base of the rostrum, while the lower arrow indicates the position of the lower lip. The wide gap between the arrows is greater than would be expected from axial rotation alone (Fig. 3) and indicates a lateral displacement of the lower jaw consistent with omega rotation. The angle of the mandibles exceeds that which would be consistent with full alpha rotation, as shown by the curvature of the upper mandible shown in B. B, Mandibles of a 7.1 m dwarf minke whale (QM JM3861) which are rotated laterally to different degrees. Upper mandible better illustrates the extensive lateral curvature.

whales (BBC: *Wild Australasia*) showed what appeared to be a forward movement of the water in the ventral pouch; it occurred well after the mouth had closed. It may have assisted in expulsion of water through the baleen plates but was only seen in one of the gulps. The control of a bounce phenomenon may thus be largely behavioural, i.e. closing the mouth before the ventral pouch has fully expanded to avoid a bow wave effect and rapidly closing the mouth to contain any movement of water later in the gulp. A further behavioural control would be in the timing of opening the jaws. This should occur only when the whale moves into the concentrated

prey, in order to maximize the density of food contained in the water pouring into the expanding ventral pouch. Such behavioural controls are essential to fully exploit any morphological specializations ("rorqual adaptive zone") for the capture of highly mobile prey.

Role of cranial movement in delta rotation. The mobility of the head and upper jaw was evident, especially in inter-mandibular gulps. Gulps IM1 and IM4 showed particularly well how raising the head and upper jaw could contribute to the extent of gape during a gulp. That this may also occur in full ventral pouch gulps of feeding whales is shown by the accounts and illustrations of elevated head and upper jaw in feeding fin whales (Gaskin, 1976, fig. 18), images of lunge feeding Bryde's whales (BBC: *Wild Australasia*) and the observations on blue whales by Gill, quoted above. Schulte (1916) noted the semispinalis capitis was the largest of the dorsal neck muscles; it has a "broad and deep" insertion on the supraoccipital. He also described "a great muscle complex" originating from the ribs and anterior spine and inserting on the base of the skull. Such muscles would be well placed for the respective elevation and depression of the head and upper jaw.

Alpha rotation. During normal swimming, the lower jaw is tightly adducted against the upper jaw and initially in the gulp only limited alpha rotation was seen. The lower jaws would thus have dragged over the baleen plates, with some frictional resistance (Brodie, 2001). At this stage, with only limited inflow of water, there would be no torque on the mandibles from filling of the ventral pouch (Lambertsen et al., 1995). In gulp IM4, as well as IM3, significant distension of the pouch in the mental region was seen only after the upper jaw was actively raised, at which point a clear lateral curvature of the mandibles was seen in IM4 associated with alpha rotation. The angle of divergence of the mandibles (Fig. 3F) and the position of the posterior portion of the lower jaw, level with or only slightly external to the frontal surface of the head, suggest that the movement of the mandible was predominantly, if not exclusively, due to rotation around its axis- i.e. the alpha rotation of Lambertsen et al. (1995). This would appear to be the maximum extent of alpha rotation as the curvature of the lower jaw in the images corresponded to the curvature of the mandible when it is allowed to fully rotate outwards (Fig. 7B). This was a particularly fast gulp (about 2.6 seconds) and it may not have been long enough to allow fuller expansion of the

ventral pouch leading to omega as well as alpha rotation. However, it is clear from this gulp and others (IM2, Fig. 7A; VP1, Fig. 8) that initial opening of the mouth may occur with only partial alpha rotation and no apparent omega rotation. This is also supported by video of a lunge feeding Bryde's whale (*Blue Planet: Open Seas*; identified as a sei whale) in which the lower jaw dropped with a dorsoventral curvature of the lower jaw, and thus mandible. This dorsoventral curvature occurs when the mandible is adducted against the rostrum (Tomilin, 1967, fig. 38). For the dorsoventral curvature to remain visible in lateral view, at most only partial alpha rotation must have occurred; moreover there was an inpocketing of the mental region which would not occur if water was pouring in at that stage. Lambertsen et al. (1995, table 2), in their model of passive filling envisioned almost immediate and complete alpha and omega rotation, with full alpha rotation from 45° to 0° as delta rotation increased to only 10°. Our sequence of gulp IM4 shows that a partial alpha rotation could occur at the beginning of the gulp sequence without any omega rotation, and that full alpha and omega rotation did appear to occur simultaneously but only when the jaw had reached full delta rotation (i.e. much greater than the 10° of Lambertsen et al., 1995). This sequence does not confirm the timing of mandible rotations postulated by Lambertsen et al. (1995).

The mandibles remained partially abducted at the end of gulps, forming a gutter (orolabial sulcus) leading to posterior vertical slit at the end of the open vestibulum oris (Fig. 3G-L). The widest expansion occurred at the rear of the channel, so that water could escape as the jaws were being closed (Fig. 3G, H); thus the term "spillwater groove" used by Struthers (1888) for this posterior opening is quite appropriate. That this is an important channel for the egress of water forced between the baleen plates is confirmed by underwater video of feeding Bryde's whales (*Blue Planet: Open Ocean*) in which contents of the ventral pouch could be seen streaming backwards not only from the anterior baleen plates but in a clear stream from the posterior opening of the groove formed by the partially abducted lip of the mandible.

The formation of the groove could occur only through a partial and actively controlled alpha rotation of the mandible and lower jaw. Lambertsen & Hintz (2004) noted the potential role of the superficial masseter muscle in tightly adducting the lower to the upper jaw. Relaxation

of the superficial masseter may be involved in the partial alpha rotation which we have documented as a regular feature of the gulp sequence in both inter-mandibular and full ventral pouch expansion. The major impediment to this process would be if there is a hydrostatic seal between the mandible and upper jaw. There is no question that the mandible and baleen plates are normally tightly opposed, to the extent that imprints of the lateral edges of the baleen plates are left on the medial surface of the mandible. However whether this is due to a hydrostatic seal or due to muscular contraction of ventral pouch, especially through longitudinal muscles (see below) can not be decided on available evidence. Lambertsen et al. (1995, fig. 12a) and Lambertsen & Hintz (2004, figs 2c, 3), show that the adducted mandible is rotated so that the lateral face of the neck of the mandible and the lateral face of the coronoid process are dorsal, while the medial face is ventrad. This would also follow from the statement in Lambertsen & Hintz (2004) that the lateral surface of the coronoid process just below its crest would provide the primary articulating surface with the maxilla, as well as the 45° angle of the mandibles in medial position in Lambertsen et al. (1995, fig. 12a). With such an orientation, the contraction of the pterygoid muscle, inserting on the medial surface of the angle of the mandible, would serve to rotate the mandible outwards. This may provide the initial power that overcomes frictional resistance and/or breaks the seal and allows the lower jaw to rotate outwards sufficient to allow inflow of water. Only a small deviation in the angle of the jaw would be needed. At the end of the gulp, there is a fine control of the angle of the lower jaw to form a groove where water exits. At this stage the lateral surface of the mandible would again be more dorsally directed and there could be an antagonistic action of the superficial masseter, rotating the lower jaw inwards and the combination of water mass and relaxation of the internal pterygoid rotating it outwards. The tendon of the contracted superficial masseter might act as a guide or cam mechanism in the rotation of the mandible at this stage (Lambertsen & Hintz, 2004).

Evidence for cam articulation is based on computer models and is still circumstantial. The partial alpha rotation documented here in minke whales is not evidence of the cam articulation. Equal degrees of alpha rotation are evident in dead right (Slijper, 1962; True, 1904) and bowhead (Lambertsen et al., 2005) whales, as

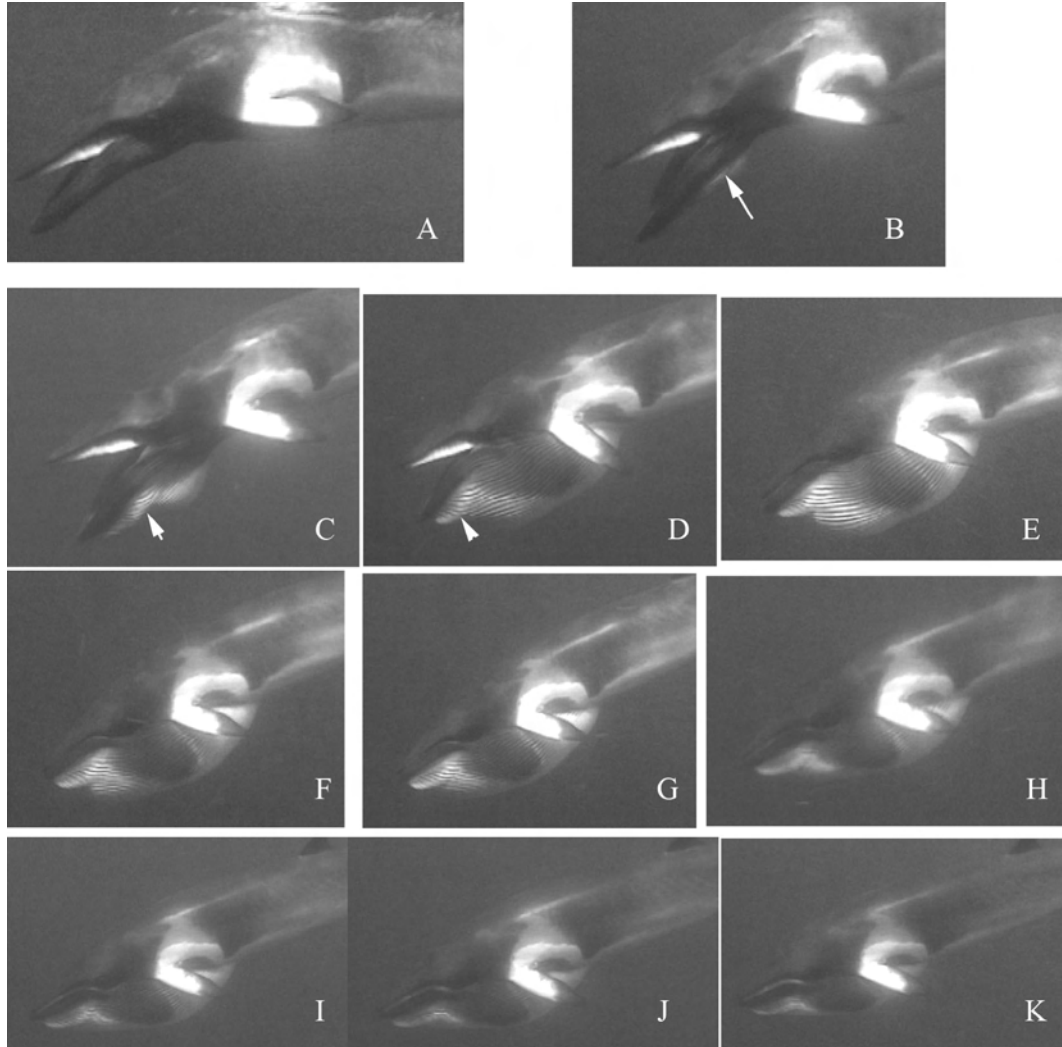


FIG. 8. Full ventral pouch gulp VP1. A, the narrow angle of lateral divergence of the mandibles as the jaw is lowered, indicates little α and no ω rotation. In B, the filling of the ventral pouch starts behind the mental region (arrow). C, the ventral pouch distends through continuation of the posterior swelling first seen in B, as well as expansion of the mental region overlying the fibrocartilage skeleton. The vertically oriented grooves are curved around the backwardly directed left arm of the fibrocartilage skeleton (arrow) and the ventral pouch seems to be divided into two discrete areas. The two areas remain distinct in 8Dd and 8Ee, as the ventral pouch reaches maximum expansion. Note also the smooth curvature of the ventral pouch as it is fully distended; the water may still be expanding the pouch as it is re-distributed posteriorly, but the mouth is closed at the point of maximum distension of the ventral pouch. F-K. This series of images shows expulsion of water. Note the small vertical angle between the upper and lower jaw, limiting exposure to the base of the baleen plates. Note also that the ventral profile of the pouch retains the smooth curve seen at the point of maximum expansion. There is thus no indication of a forward movement of water or "bounce phenomenon" envisioned in some models of water expulsion in rorquals.

well as video (*The Lost Whales*, New Zealand Natural History Unit) and studies of living balaenids (Werth, 2004a). Partial alpha rotation of the lower jaw is also evident in photographs of stranded pygmy right whales (Gaskin, 1972; Baker, 1990) and gray whales (Leatherwood et al., 1988). Balaenids, pygmy right whales and gray whales all appear to lack the skull structure needed for the cam articulation proposed to occur in rorquals (Lambertsen & Hintz, 2004).

A major difference between rorquals and other baleen whales is in the head profile (Lambertsen & Hintz, 2004; Lambertsen, 2005). In particular they suggested that the marked asymmetry between upper and lower jaws in rorquals would generate significant negative lift on the lower jaw that would need to be counteracted by a mechanism such as the cam articulation to prevent the lower jaw from opening, especially when the whale is swimming quickly. There appears, however, to be considerable variation in form of the upper jaw (as opposed to rostrum of the skull) in rorquals. While it is broad and flat in blue whales, it is highly sloped along the median ridge in minke whales (Fig. 1; see also Williamson (1972), pl. 3a,b). The profile of the head in minke whales, seen in lateral or anterior view, approximates a forwardly directed cone, with much less asymmetry between the upper and lower jaw than envisioned by Lambertsen & Hintz (2004). This would minimize the extent of negative lift they envision and thus the need for a mechanism such as the cam articulation. Moreover, the orientation of the head of a rorqual whale to the direction of water flow may vary considerably as it swims forward, especially in a highly manoeuvrable species such as minke whale. In dwarf minke whales, the head may pitch routinely as the whale swims (pers. obs.), presenting a continuously changing profile for water flow over the body. This creates a complex pattern of water flow which may not correspond to the simple hydraulic models for lift considered in discussions of gulp feeding and development of a "rorqual adaptive zone".

Omega rotation. Our underwater observations confirmed the lateral displacement of mandibles, or the omega rotation of Lambertsen et al. (1995). Gulp IM1 shows that the separation of the lower jaw may not be only lateral but also ventrad.

In gulp IM2 (Fig. 7A), the antero-lateral oblique orientation of the fronto-mandibular stay can be seen - this stay not only limits lateral displacement of the mandibles but also defines the postero-lateral boundary of the opening into

the oral cavity which is smaller than that which would be assumed based on lateral displacement of the mandibular lips. The lips of the mandible continue outwards, exposing a broad floor of the open vestibulum oris. The extent to which the vestibulum oris can expand, as well as the fronto-mandibular stay, may ultimately limit the lateral travel of the mandibles. Pivorunas (1977), in a dissection of *B. acutorostrata*, noted an intramuscular cleft, similar to the cavum ventrale, associated with the posterior face of the mandible. He suggested this could "aid the ventral pouch musculature in depressing the floor of the vestibulum oris that is located immediately dorsal to the mandibular furrows...". This might also allow a greater expansion of the vestibulum oris, accommodating the lateral movement of the mandibles.

Lambertsen et al. (1995) noted that as the lower jaws of humpback whales bowed out to maximum extent, the anterior tip of the lower jaw has to become displaced posteriorly to behind the rostrum; they illustrated the point (Lambertsen et al., 1995, fig. 8) with a lunge feeding humpback whale at the surface, which they used as evidence of omega rotation. While not disputing this as evidence of omega rotation, we note that this may be a feature peculiar to humpback whales, which have a particularly narrow rostrum for a rorqual and mandibles which are strongly curved laterally. In minke whales, by the time the upper and lower jaws were brought together, the mandibles had returned almost to their medial positions, to the extent that the anteriormost baleen plates could be trapped by the closing lower jaw. The tip of the lower jaw appeared to be anterior to the rostrum as in normal swimming (IM4, Fig. 3I-L).

ROLE OF THE FIBROCARILAGE SKELETON. Schulte (1916) suggested that deformation of the mental region would occur through the action of the mylohyoid and panniculus muscles on the fibrocartilage skeleton. In minke whales most of the spreading of the fibrocartilage skeleton occurred while the inter-mandibular area was expanded and thus the mylohyoid and panniculus muscles would be relaxed rather than contracted. Rather, we feel that the deformation of the mental region is a more passive process, driven by inflow of water at the beginning of the gulp. One line of evidence for this is that the fibrocartilage skeleton is clearly visible on carcasses, in which the muscles are flaccid (Pivorunas (1977) gave a long list of



FIG 9. Baleen flash in a dwarf minke whale, which has raised the upper jaw and baleen plate series out of water. The function of this behaviour is unknown (it may be associated with other behaviours such as bubble blasts or jaw clap and thus be a display) but it was not associated with feeding (i.e., no concentration of food was visible in the water). Similar behaviour has been described in sei whales, with the upper jaw and much of the baleen out of water; such behaviour has been attributed to feeding in sei whales but this may not always be the case.

published images; see also Clapham, 1997: 109). Pivorunas (1977) noted that the fibre structure of the fibrocartilage skeleton was not oriented in a single direction, as in a tendon, and thus referred to it as a “paratendinous” structure which could react to forces from several directions (i.e. as would occur with a distension of the mental region). Given the more vertical orientation of the grooves in the mental area, expansion would be confined primarily to that area and pooling of water would occur there. The fibrocartilage skeleton could reinforce the mental region against the stress of throat expansion in this region (Lambertsen & Hintz, 2004). We further envision the fibrocartilage skeleton as providing a flexible framework which could deform in a consistent, pre-determined way - the base of the skeleton swinging downwards and the branches outward. The ventral grooves which are crowded between the branches of the fibrocartilage skeleton in a swimming whale could open up freely as the branches diverged, allowing

swelling of the mental region initially, then the rest of the ventral pouch.

More vertically oriented grooves occur in other rorquals. Even in the humpback whale, where there are fewer grooves, there are more vertically oriented grooves in the mental region (e.g. Chadwick & Nicklin, 1999: 110) so the mechanism we propose is feasible in all the rorquals. Thus we suggest that the rorqual throat region consists of two functional areas: (1) anterior inter-mandibular region with more vertically oriented grooves, fibro-cartilage skeleton and a localized capacity for expansion, and (2) rest of throat and ventral pouch, with longitudinally oriented grooves, leading primarily to an increase in circumference of the rest of the ventral pouch.

Lambertsen et al. (1995) and Lambertsen & Hintz (2004) suggested that a similar ballooning of the mental region could occur before the gulp through bringing the tongue forward; the expansion of the mental region would change

water flow around the head acting to preload the jaw structure for rapid opening and thus minimization of a bow wave. This suggestion has been taken up as a feature of rorqual feeding in paleontological literature (Kimura, 2002). In those sequences in which we saw the lead up to the gulp, there was no evidence of such a deformation of the mental region. However the expansion of the mental region which we have observed at the beginning of the gulp sequence could serve at least some of the same functions as the preloading envisioned by Lambertsen et al. (1995). In particular, by providing a point of least resistance for inflow of water, it could minimize, and possibly eliminate, a bow wave effect at the beginning of the gulp.

At the beginning of the gulp, there was no evidence that the tongue was in the mental region; it would have been visible especially in gulp IM4. However, at the end of the gulp cycle, we noted a forward traveling bulge along the throat region, which ended as a swelling in the mental area (IM3, Fig. 5B) similar to that seen at the beginning of inter-mandibular gulps. This is consistent with the mechanism suggested by Lambertsen (1983), i.e. a movement of the tongue anteriorly, expelling the last water from the oral cavity, thus minimizing the swallowing of seawater. An additional function seems possible. The forward movement of water could create a wash effect against the bristles of the baleen plates, helping dislodge any trapped prey. Partial depression of the floor of the oral cavity (as shown by the forwardly traveling bulge in the inter-mandibular area) might also create a reduction in pressure within the oral cavity, further aiding dislodgement of prey from the baleen bristles (cf. Werth, 2001). Deformation of the mental area would be through the same mechanism as indicated above – deformation of the fibrocartilage skeleton allowing an expansion of the overlying ventral pouch wall.

Whereas we note that the distension or ballooning of the mental region is primarily passive (driven by kinetic energy of forward locomotion of the body or of the tongue), during normal swimming the fibrocartilage skeleton could act as an anterior insertion point for the contracted longitudinal muscles of the ventral pouch, maintaining a taut and streamlined form in the throat region. Orton & Brodie (1987) suggested that these longitudinal muscles have a postural role, based on their finding that Type I (slow, oxidative) type fibres were extremely dominant in the ventral pouch region.

Finally, we note that our observations do not support the role of the fibrocartilage skeleton as a clamp, trapping anterior baleen plates against the mandibles and thus preventing loss of water around the baleen plates (Pivorunas, 1977); the fibrocartilage skeleton was always well removed from the anterior baleen plates while water was being expelled from the ventral pouch.

VERTICAL ANGLE OF JAWS DURING EXPULSION OF WATER. One striking feature of the gulp cycle is the small vertical separation of upper and lower jaws and thus the small area through which expulsion of water may take place, even including the groove or orolabial sulcus formed by partial alpha rotation of the lower jaw. One implication of this is that the area for egress of water is much smaller than the area of the fully expanded ventral pouch over which contraction takes place. By hydraulic theory, a small force over a wide area can be translated to a larger force over a small area. By this line of reasoning, the elastic energy per unit area of the ventral pouch may not have to be particularly high to force water through the baleen plates. As pointed out by Orton & Brodie (1987) it is unknown to what extent the muscles in a fully expanded ventral pouch could contract – at this stage the elastic fibres may provide the primary, if not exclusive, driving force. As the pouch contracts, the hydraulic power differential decreases and at this point muscles may become the main driving force in water expulsion.

EVOLUTION OF FILTER FEEDING: *opening of vestibulum oris*. A characteristic mammalian feature is the cheek which encloses a space, the vestibulum oris, bounded internally by the oral arch [if you lick the outside of your teeth, your tongue is protruding into this space]. As recognized by anatomists (e.g. Schulte, 1916; Pivorunas, 1976) the cheek structure has been lost in whales, creating an open vestibulum oris. One result is the reptilian appearance of the head of baleen whales, with the gape extending well posterior to the eye. This is accentuated in mysticete whales, especially rorquals, by fibrocartilage articulations at the mandibular symphysis and, especially, with the skull. This allows rotation of the mandibles and a virtual dislocation of the mandibles, to give an almost snake-like appearance with the diverging and laterally displaced mandibles of a gulping whale (Figs 6A,7A).

The opening of the vestibulum oris was an essential feature in the development of the

continuous suspension feeding of balaenids. In the right whales, a secondary cheek structure was developed with the greatly enlarged lip of the mandible, arching upwards and meeting the strongly arched, narrow rostrum. The fibrocartilage joint at the mandibular symphysis allows for some axial rotation of the mandible and lip. Rotation of the lower jaw swings the secondary cheek structure outwards, forming a groove just lateral to the long baleen plates, which is open at the back. Thus there is a discrete channel (orolabial sulcus: Werth, 2004a) through which water can continuously pass through the baleen plates and posteriorly. Werth (2004a) clearly demonstrated how hydraulic effects from flow in the orolabial sulcus could assist in passage of water through the baleen plates.

The role of the vestibulum oris is quite different in rorquals. In modern rorquals, the open vestibulum oris allows for the lateral displacement of the mandibles (omega rotation), especially if there is a capacity for its floor to expand. Morphological specializations which could allow this include the facial cleft noted by Pivorunas (1977) in common minke whales and the associated grooves overlying the mandible, both allowing a greater capture area by the axial rotation and lateral displacement of the mandibles. Delta rotation may be limited by the frontomandibular stay but lateral displacement would be limited by the extent to which the floor of the vestibulum oris can expand laterally near the angle of the mouth.

During contraction of the ventral pouch, water can escape laterally in any direction through the basal portion of the baleen plates exposed by the narrow gape (2-5°); a photograph by Nicklin (in Darling, 1995) of a common minke whale showed water squirting out from all along the baleen series. However, partial alpha rotation of the mandible (IM4, Fig. 3; IM3, Fig. 5) would also form a channel open posteriorly, through which water could be directed rearwards after passing between the baleen plates. This would be assisted by the backwards orientation of the slits between the baleen plates (Pivorunas, 1976), possibly assisted by a drop in pressure as water is expelled through the posterior open slit formed by the partially rotated mandible (Figs 3, 5). Thus hydraulic assistance of water egress could occur in rorquals, through mechanisms similar to those operating in balaenids (Werth, 2004a; Lambertsen et al., 2005), with the difference that it occurs episodically at the end of a gulp in rorquals rather than continuously as in balaenids.

Such channeling of water is only possible due to the open vestibulum oris and loss of the classic mammalian cheek structure.

Sei whales are anomalous among the rorquals in that they have been described as both engulfment feeders and continuous skim feeders. Published direct observations of feeding are limited (Ingebrigtsen, 1929; Kawamura, 1974; Liouville in Andrews, 1914; Watkins & Schevill, 1979) and not always easy to interpret. Watkins & Schevill (1979) described sei whales as having their mouth wide open and closing slowly over a 20 second to 1 minute interval, which seems dysfunctional for engulfment feeding. Given the rapidity with which the oral cavity fills (even in non lunge-feeding events, see Table 1), keeping the mouth open for longer than a few seconds would result in a bow-wave effect. However, compared with other rorquals, the sei whale has a more strongly arched rostrum, down-turned at the tip (Leatherwood et al., 1988) and narrower, finely fringed baleen plates. It is possible that partial alpha rotation of the mandible and abduction of the lower jaw would form a channel more like that of the right whales, which would allow sufficient water to be ejected rearwards for continuous filtration. In this regard, Liouville noted that the sei whales he observed moved very slowly through the water, possibly allowing greater filtration of water through the finely fringed baleen plates. Ingebrigtsen, in contrast, noted that the sei whales moved quickly, with the baleen plates out of water. It is difficult to see how this could efficiently filter fine food, rather than creating a bow wave effect. Another possibility is that what Ingebrigtsen observed was not associated with feeding. We have seen dwarf minke whales with much of the rostrum and baleen plates free of the water (Fig. 9) when there was no concentration of food in the water and no evidence of feeding.

Suction feeding as the primitive state? Within mysticete lineages, the opening up of the vestibulum oris allowed for different developments, i.e. gulping of rorquals or the skimming of right whales. Gray whales represent a third development, suction feeding. Suction feeding involves expansion of the mouth volume, which can be accomplished by retraction of the tongue in a piston action and expansion of the throat, as by gular folds (Heyning & Mead, 1996). Suction feeding thus requires relatively little modification of the throat region.

Gular folds are found in at least some pygmy right whales and dwarf sperm whales, while they

are consistently present in the gray whale, the great sperm whale and most ziphiids. Suction feeding, at least for manipulation, if not capture, of food has been shown in gray whales (Ray & Schevill, 1974) and ziphiids (Heyning & Mead, 1996). A specialized form of suction feeding has been inferred for the sperm whale based on anatomy of the tongue and throat musculature: prey are sucked into the circular oropharyngeal opening, posterior to the oral cavity which is widely open through loss of cheeks and a closed vestibulum oris (Werth, 2004b). A form of suction feeding, at least in manipulating food, has also been demonstrated in delphinidan cetaceans – monodontids (beluga & narwhal), phocoenids (true porpoises) and delphinids (Werth, 2000). The widespread occurrence of gular folds and some form of suction feeding in such a range of extant odontocetes and baleen whales, representing diverse phylogenetic lineages (Messenger & McGuire, 1998; Nikaido et al., 2001), suggests that suction feeding occurred in earlier taxa of toothed whales, including those ancestral to baleen whales. Thus it would be the primitive condition for baleen whales.

The ventral grooves of rorquals are quite distinct from gular folds. As the foetus develop, one set of grooves appears under and posterior to the flipper, a second set develops at the throat and subsequently they coalesce (Ohsumi, 1960; Slijper, 1962). These grooves are distinct and more numerous than gular folds. For fossil mysticetes, it is impossible to determine if ventral grooves and associated elasticity of the throat and belly were present. However, two biomechanical analyses of feeding in the most derived fossil mysticetes (Bisconti & Varola, 2000; Kimura, 2002) suggested that jaw elevation and adduction were primarily through muscle action. An implication of that conclusion is that an elastic throat and ventral pouch, needed for gulp feeding, evolved more recently.

Reconstructions of early whales (e.g. Thewissen & Williams, 2002, fig. 2) show relatively little modification, however a form of suction feeding could exist as early as *Pakicetus* and certainly by the time of archaeocetes. Primitive baleen whales had a fibrous mandibular symphysis allowing axial rotation of the lower jaw, as required in all feeding types found in extant mysticetes. However, lateral mobility would be restricted by the high coronoid process which was still medial to the relatively well developed zygomatic arch (Fordyce & deMuizon, 2001, fig. 11). This, with the apparent

lack of baleen, suggests that suction feeding would be the most likely feeding mode, perhaps comparable to that developed in present day beaked whales (Heyning & Mead, 1996). The next stage could be as envisioned for aetiocetids by Deméré (2005), with baleen plates interspersed between widely spaced teeth. Either of the two other extant filtering modes (continuous filtration (skimming) of balaenids and neobalaenids; gulp feeding of balaenopterids) could have been derived from this suction feeding stage. However, in addition to axial rotation of the mandibles, gulp feeding requires additional specializations such as development of the elastic, highly distensible ventral pouch, specialized cranio-mandibular articulation, frontomandibular stay, possible re-orientation of mandibular condyles from dorsal to posterior position, lateral deflection of the coronoid process and capacity for extensive lateral displacement of the mandibles. Thus it represents the most derived form of suspension feeding seen in baleen whales.

FURTHER STUDIES. Our underwater observations have revealed two quite distinct types of gulps, inter-mandibular and full ventral pouch, which may have different functions. This flexibility in the form of gulps indicates a voluntary control of ventral pouch expansion which contrasts with previous models based on passive filling of the pouch. Further anatomical studies are needed on the myology of the entire ventral pouch to properly document the morphological specializations of gulp and lunge feeding. However more extensive studies on behaviour are also needed to document the extent to which the unique rorqual body plan has been exploited, not only for the high speed capture of prey but also for display and the social organisation of baleen whales.

ACKNOWLEDGEMENTS

First among the acknowledgements must be to John Rumney of *Undersea Explorer* who, since 1996, has provided the ship time and logistical support without which this project could not have been undertaken. We also thank all the passengers on board *Undersea Explorer* who have contributed to the project. We have received broad and much appreciated support from the Cod Hole and Ribbon Reef Operators Association and from individual operators, including Stan Kielbaska and staff of Mike Ball Dive Expeditions, Ian Stapleton and crew of

Nimrod Explorer; Chris Taylor and staff of *Taka*. While on *Undersea Explorer*, Tracey Chapman and Jenna Rumney also contributed some fine images. Peter Constable allowed use of his images of Brydes whales, which complement the commercially available images for this species complex. We also thank Peter Gill for providing us with his observations of gulp feeding in blue whales.

At James Cook University, we thank colleagues and postgraduate students past and present who have assisted in the Minke Whale Project, especially research team members Assoc. Professor Peter Valentine and Matt Curnock. At the Museum of Tropical Queensland, we thank Denise Seabright and Barbara Done. We thank the library staff at the Queensland Museum for supplying obscure references at short notice and Julie Jones, of the Great Barrier Reef Marine Park Authority library, who provided us with copies of the photographs documenting dissection of dwarf minke whale QM JM3861. We are also most grateful to two reviewers for their constructive suggestions. We thank the Institute of Cetacean Research for permission to use the photograph of dwarf minke whale mandibles (Fig. 7b) from Arnold et al. (1987).

Financial support was received from *Undersea Explorer*, Museum of Tropical Queensland, James Cook University and grants including Natural Heritage Trust (Australian Dept of Environment and Heritage) for 1999-2000, from CRC Reef Research Centre, Townsville for 2001-2005 and the Great Barrier Reef Marine Park Authority for 2003-2005.

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