



Published in final edited form as:

. 2019 October ; 35(4): 1556–1578. doi:10.1111/mms.12614.

New views of humpback whale flow dynamics and oral morphology during prey engulfment

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Abstract

The rise of inexpensive, user-friendly cameras and editing software promises to revolutionize data collection with minimal disturbance to marine mammals. Video sequences recorded by aerial drones and GoPro cameras provided close-up views and unique perspectives of humpback whales engulfing juvenile salmon at or just below the water surface in Southeast Alaska and Prince William Sound. Although humpback feeding is famous for its flexibility, several stereotyped events were noted in the 47 lunges we analyzed. Engulfment was rapid (mean 2.07 s), and the entrance through which the tongue inverts into the ventral pouch was seen as water rushes in. Cranial elevation was a major contributor to gape, and pouch contraction sometimes began before full gape closure, with reverberating waves indicating rebounding flow of water within the expanded pouch. Expulsion of filtered water began with a small splash at the anterior of the mouth, followed by sustained excurrent flow in the mouth's central or posterior regions. Apart from a splash of rebounding water, water within the mouth was surprisingly turbulence-free during engulfment, but submersion of the whale's head created visible surface whirlpools and vortices which may aggregate prey for subsequent engulfment.

Keywords

mysticete; rorqual; humpback whale; *Megaptera novaeangliae*; feeding; anatomy; baleen; tongue

The resourceful and highly acrobatic foraging behaviors of humpback whales (*Megaptera novaeangliae*) are widely known, both during typical surface and subsurface lunge feeding (Hain et al. 1981; Weinrich et al. 1992; Goldbogen et al. 2008; Hazen et al. 2009;

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Friedlaender et al. 2009, 2013; Ware et al. 2010; Simon et al. 2012) and particularly when using bubbles to corral prey into densely packed balls for more efficient engulfment (Gormley 1983, Leighton et al. 2007, Wiley et al. 2011). Bubble-related behaviors have frequently been observed and recorded, especially in the coastal waters of Southeast Alaska (Jurasz and Jurasz 1979, D'Vincent et al. 1985, Winn and Winn 1985), where humpback whales have recently learned to capture juvenile salmon released from hatchery sites (Chenoweth et al. 2017).

The study of feeding in humpback whales and other mysticetes has been revolutionized by digital tagging (Goldbogen et al. 2013, Goldbogen and Meir 2014, Kirchner et al. 2018). Small, unobtrusive devices temporarily affixed to a whale's body by suction cups measure a whale's acceleration, depth, and body position/motion in various directions while cameras record close-up features. Together these instruments provide precisely quantified data revealing a whale's movements as it approaches and ingests prey, as well as its activities between feeding bouts. A flurry of biologging studies continues to reveal intricate details of ecology, physiology, morphology, biomechanics, and behavior in humpback and other whale species (Goldbogen et al. 2006, 2007; Simon et al. 2012; Cade et al. 2016). Unfortunately, some of the most relevant phenomena of whale feeding—indeed, the most pertinent aspects of filtration, including directions, quantities, and timing of intraoral current flow and their relation to intraoral morphology—can be surmised only indirectly given the inability, at present, of placing a tag and recording directly within a whale's mouth. Nonetheless, tag data or calculations from related mathematical modeling have substantially clarified diverse intraoral events (Goldbogen et al. 2012, 2015, 2017a, b). Although video footage from whale-mounted cameras reveals valuable findings directly from foraging animals, often at depths or positions otherwise unavailable to human researchers (Cade et al. 2016, Goldbogen et al. 2017a), they are somewhat constrained by the limited vantage points they provide from their affixed location on the backs or flanks of whales. Importantly, these cameras can only provide views within the mouth or show a whole whale interacting with its environment when a second whale serendipitously enters the frame of a tagged whale (Segre et al. 2017).

Fortunately, just as digital tags have gained new capabilities while decreasing in size and cost (Goldbogen et al. 2013, 2017a; Goldbogen and Meir 2014), other recent technological advances have made it easier to capture and analyze video recordings of marine mammal behavior (Nowacek et al. 2001, 2016; Anderson and Gaston 2013; Hunt et al. 2013; Karnowski et al. 2016; Pirotta et al. 2017, 2019; Johnston 2019), and particularly of humpback whales (Ware et al. 2006, Christiansen et al. 2016a, Kirchner et al. 2018). Simple, user-friendly, and inexpensive video cameras and editing software enable researchers to document feeding and other activities (Letessier et al. 2015, Raoult et al. 2016, Brooks 2017). Advantages include great clarity due to high pixel resolution, zoom lenses, and swivel capability, and the ability to record video in previously limited settings, such as underwater or from high vantage points, as with unmanned aerial systems (UAS, commonly called drones). Aerial and underwater drones can be remotely operated or autonomous (Schiffman 2014). Other miniature, highly mobile video cameras, such as GoPro cameras, can be quickly affixed to people and poles or other objects (Raoult et al. 2016).

There are several obvious advantages to collecting data with drones and GoPro cameras. First, these tools can generally be set up and used by a single operator, or at most by just a few people. Second, these tools can be used proficiently with minimal training. Third, reliable data can be obtained and immediately analyzed with little or no postcollection data processing. Fourth and perhaps most important, drone and GoPro camera systems can be used under a wide range of field conditions, even those that would normally prohibit traditional vessel-based observation, although they are generally unsuitable for use in high wind speeds or water currents, or for conditions with low visibility in air or water.

These new technologies are rapidly changing the study of wildlife (Bevan et al. 2016, Rümmler et al. 2016, Schofield et al. 2017, Sykora-Bodie et al. 2017, Rees et al. 2018, Rieucou et al. 2018, Weimerskirch et al. 2018, Verfuss et al. 2019), especially in marine settings where observation had been mostly limited to vessel-based or airborne observers. Because new camera systems allow more rapid (near instantaneous) changes in orientation than most boats and manned aircraft can achieve, animals can be followed and stable vantage points maintained or switched very quickly (Hodgson et al. 2013, 2017; Goebel et al. 2015; Koski et al. 2015; Durban et al. 2016; Fiori et al. 2017; Johnston et al. 2017; Krause et al. 2017; Torres 2017; Burnett et al. 2018; Torres et al. 2018). Not only have these video recording systems become less expensive and more readily available (Goldbogen and Meir 2014, Nowacek et al. 2016, Dawson et al. 2017), they are also less noisy and less dangerous to operate (Christiansen et al. 2016b), so that they pose fewer risks to animals and likely cause fewer changes in wild animals' natural behavior (Ditmer 2015 et al., Dominguez-Sanchez et al. 2018). Nonetheless, risks remain when these systems are used in close proximity to marine mammals or other threatened wildlife (Pomeroy et al. 2015, Hodgson and Koh 2016, Smith et al. 2016, Sullivan and Torres 2018). As is often the case, technology can evolve faster than rules governing its use (Vas et al. 2015).

During long-term studies of humpback whale foraging behavior and ecology, we analyzed video sequences of surface and near-surface lunge feeding. Many observed behaviors (and much video footage) of our study involved humpback whales feeding on juvenile salmon immediately after the fish were released from net pens at hatcheries located in coastal fjords of Southeast Alaska and Prince William Sound.

Our findings encompass diverse yet interrelated aspects of humpback whale anatomy and biomechanics with behavioral ecology, many of which we presume apply to feeding in other rorquals (Balaenopteridae). This makes it difficult to organize them into discrete categories, although all findings focus more on the morphology than the behavior of feeding. Close-up drone and GoPro videos reveal hidden details when played back at real-time speed or frame-by-frame. Thus the “new views” of this paper's title include both novel vantage points affording new visual perspectives as well as new insights about humpback (and possibly general rorqual) feeding ecology, oral morphology, and biomechanics.

Methods

We analyzed 36 min of video footage that included 47 humpback whale engulfment events. In nearshore waters of the Gulf of Alaska during 2014–2018, footage was captured with

three sources: hand-held cameras, a drone, and a GoPro Hero5 Black camera affixed to a 3.5 m pole. Videos were captured near hatchery release sites and whales were likely feeding on yearling or young-of-the-year coho salmon or young-of-the-year chum salmon recently released from the hatcheries, although whales could have been feeding on some wild fish as well.

In Southeast Alaska we recorded feeding bouts of at least five individual humpback whales (average body length in North Pacific 12.3 m; Nichol and Heise 1992) engaged in bubble net-related or other lunge feeding at or just below the surface within small fjord inlets around Baranof Island in the eastern Gulf of Alaska, in water ~40 m deep. Typically these involved feeding on schools of small (4–20 g, or 4–14 cm) yearling coho and young-of-the-year chum salmon just released from floating net pens (Chenoweth et al. 2017). Floating walkway platforms around net pens provide a unique and exceptionally close-up vantage point, typically directly above and *within* a circular bubble net/ring released by the whales to corral prey.

The 2017 GoPro-recorded MP4 sequences were shot with the camera mounted on a pole held straight up or at an angle over the water, so as to be as close as possible to the feeding whales without disturbing them (often within 2–4 m; NOAA NMFS permits 14122, 18529), and to record their feeding behaviors in multiple views. It is important to note that the whales approached the observers who recorded whale behaviors while the observers were standing on the floating net-pen walkways; there was no need for people to approach whales. In this fortuitous setting (with floating net pens above 25-m-deep water) a pole-mounted camera is quieter than a drone and easier to control and move rapidly into proper position, including underwater (see Video S1 for this study and from Chenoweth et al. 2017).

In Prince William Sound in 2016 and 2017, underwater and drone videos were obtained of humpback whales feeding, presumably on young-of-the-year chum salmon and pink salmon recently released from hatcheries. Drone video (DJI Phantom 3 Professional, shooting 23 frames/s at 8,300 kbps and 1,280 × 720 pixel resolution) was recorded in May 2017 near Evans Island, above the Armin F. Koernig Hatchery at Port San Juan, after a release of chum salmon. Underwater video was recorded in April 2016 with a GoPro Hero4 Silver at Wally Noerenberg hatchery and release site in Lake Bay on the southern end of Esther Island in Prince William Sound after a release of pink salmon. The underwater videos display direct anterior views (*i.e.*, looking into the mouth) prior to engulfment (Fig. 1), continuing to full lateral and ventral views as whales turn and sweep by the camera (Fig. 2). Underwater footage provided valuable information but poor water clarity limited the image resolution. Water in these protected inlets has limited visibility (1–4 m; better on sunny days) but few or no surface waves except for small, wind-driven ripples (capillary waves), promoting excellent aerial views of whales and their feeding behavior. These opportunistic videos were donated to our study by the Prince William Sound Aquaculture Corporation.

Video sequences were analyzed with VLC Media Player 3.0.3. Because the GoPro camera has a wide-angle fisheye lens that can distort images, postproduction lens correction was used to create a linear field of view. The rolling shutter of GoPro and other CMOS-based

cameras can cause blurring if the camera is unsteady; postproduction image correction *via* GoPro Studio v.2.5.7 software can improve clarity and contrast. Frame-by-frame video analysis was also done using GoPro Studio, with digitization of landmarks and kinematic analysis using Tracker v.4.92 and angle measurement *via* MB-Ruler 5.3.

Whales were observed/recorded swimming and feeding in many different body positions and rotatory orientations, including lateral (side) swimming and partially or wholly inverted (upside-down) body posture (Kot et al. 2014), with frequent but not exclusive use of bubble netting and engulfment upward through or parallel to the sea surface. Because the 47 engulfment events we recorded involved differing body positions, some sequences yielded less information than others and could not be used in all analyses. Also, we hesitate to use the term “lunge feeding” (Pivorunas 1979, Werth 2000, Goldbogen 2010) for all sequences; about 64% (30 of 47) of sequences demonstrate “classic” rapid rostral lunges, whereas the rest involve humpback whales gently rising through the surface (~1.0–<2.0 m/s swim speed, estimated by body length as determined when in proximity to objects of known proportions), following a similarly slow approach—possibly to avoid alarming or otherwise scattering aggregated prey.

Results

Among the highlights of our analysis (elaborated upon in correspondingly numbered sections that follow):

1. Cranial elevation (up to 54°) is a major contributor to gape.
2. The entrance through which the tongue inverts into the ventral pouch (Lambertsen 1983, Werth et al. 2018) can be seen.
3. Engulfment is rapid (mean 2.07 s, $n = 24$).
4. Expulsion of filtered water lasts 10 times longer than engulfment (mean 22.3 s, $n = 24$).
5. Pouch contraction (and some expulsion of filtered water) begins before full gape closure.
6. Reverberating waves along the gular region indicate rebounding water within the pouch.
7. Expelled water begins with a small splash at the anterior of the mouth, followed by more sustained flow in the mouth’s central or posterior regions.
8. Apart from a splash of rebounding water, water within the mouth is surprisingly turbulence-free during engulfment.
9. Submersion of the whale’s head creates visible surface whirlpools and vortices.

Although humpback whales rotate into varied body orientations when engulfing prey, there is little variation in the timing or kinematics of engulfment or expulsion by body position.

1. Gape Angle and Cranial Elevation

We recorded widely varying foraging behaviors including presence or absence of bubble netting, rapid lunges with forward locomotion but no change in depth, slow or quick vertical ascent from directly below the surface with no horizontal movement, and engulfment in varied body orientations. Despite this variation, our recorded engulfment sequences display remarkably stereotyped events. Total gape angle (*i.e.*, between upper and lower jaws, including both cranial elevation and mandibular depression) averaged 82.5° (SD = 5.89, range 70°–94°, $n = 20$). Previous studies (Arnold et al. 2005, Goldbogen et al. 2017b) mentioned the role of cranial elevation in rorqual feeding but perhaps underestimated its ubiquity and contribution to gape. Our kinematic analysis revealed substantial cranial elevation (mean 39.5°, SD = 8.5, range 24°–54°, $n = 20$).

2. Tongue Inversion and Water Entry into the Ventral Pouch

Lambertsen (1983) initially proposed, based on ideas of Pivorunas (1979), the anatomical mechanism whereby the vast quantity of prey-laden water engulfed by rorquals (Fig. 2) fills a massive, balloon-like pouch temporarily created by inversion of the tongue and invaginated oral floor into an intermuscular gular space: the ventral (oral) pouch, AKA *cavum ventrale*. This space extends from the oral (buccal) cavity to the umbilicus and is externally demarcated by the accordion-like throat pleats and associated ventral groove blubber (VGB) and its musculature (Shadwick et al. 2013). Lambertsen (1983) demonstrated the tongue inversion phenomenon *via* post mortem manipulation of a suspended minke whale (*Balaenoptera acutorostrata*) body: *viz.*, suturing the esophagus and filling the mouth with flowing water from a hose. Although this process is externally observable *in vivo via* extensive gular expansion, actual infolding and translocation of the inverted tongue and influx of water into the opening of the pouch have not heretofore been seen—and precise anatomical details remain vague—because these actions occur rapidly and on the floor of the mouth, in a location briefly visible only from within or directly above the oral cavity. We have captured what we believe to be the first *in vivo* views recording the moments of tongue inversion and water flow into the rapidly filling ventral pouch.

Lingual inversion was recorded in dorsal (Fig. 3) and lateral view (Fig. 4), whereas the opening into the ventral pouch (created during lingual inversion), and water flow into this opening, can be seen only from directly above the whale's open gape in the early phase of engulfment (Fig. 3). As the grayish tongue folds inward and the oral floor slides backward into the expanding pouch during rapid water influx, a dark opening is briefly visible (Fig. 3), for only about 0.2 s, after which the oral floor drops away and all that can be seen in the open mouth is deep (>3 m, based on water clarity), prey-laden seawater. Seen from above, the initial opening is a dark, oval-shaped hole, longer anteroposteriorly than mediolaterally, before it almost immediately (in about 0.05 s) becomes a long slit about 1.5–2.5 × 0.5 m. (These measurements refer to the fleeting moment before the rapidly sliding oral floor gives way and drops out of sight.) The briefly observable dark, midline opening in the ventral oral floor is surrounded by lighter white tissue of the tongue on both sides (Fig. 3). This white tissue lies an estimated >1–1.5 m away from the dark lips at the dorsum of the mandibles; it is distinguishable from the light gray baleen plates and the expansive gray connective tissue

at the angle of the jaws (which is farther posteriorly and darker in coloration), and this white tissue does not represent the rotating mandibles themselves.

As water streams through this channel—due to the combined influence of gravity and the ram mechanism provided by the whale’s forward locomotion—the ventral pouch is filled like a water balloon. Kinematic analysis confirms that fish within the oral cavity move downward and toward the opening (caudoventrally, relative to the whale), presumably caught in the powerful current flowing into the expanding pouch. In our video sequences, this motion is somewhat difficult to discern (looking down into murky green water from the camera’s vantage point several meters above the surface), but water/prey influx is clearly detectable *via* displacement of individual fish. As the pouch fully inflates, the oral floor tissue is deeper (*i.e.*, farther from the surface of the water) and instantly disappears from view. Then gape closes as the depressed lower jaws are elevated and the elevated upper jaw is depressed. The true muscular “tongue proper” (aside from a flaccid, floppy mass on the oral floor) can best be seen in lateral view (Figs. 1A, 4), although the genioglossal tubercle, immediately posterior to the mandibular symphysis, is evident in several recorded sequences (described below).

3. Oral Extension and Anatomy (Mandibular Tendons, Genioglossal Tubercle, Baleen)

At the moment of peak gape (Fig. 4), a whitish gray band can be seen between the upper and lower jaws at the angle of the mouth. This band presumably shows stretched tendons of jaw adductor musculature (mainly *m. temporalis*, it appears, but also possibly *m. masseter*), which controls gape closure as well as mandibular rotation (Lambertsen et al. 1995).

Another briefly glimpsed “internal” anatomical structure that is momentarily seen but readily identifiable is the prominent tubercle of the *m. genioglossus*, the large muscle that originates along the mandibular symphysis (Fig. 4H) and controls tongue protraction to its normal position (Werth and Ito 2017). This tubercle is visible just as the mouth opens (when the tongue is in its resting position, prior to inversion), but it can no longer be seen as gape increases to $> \sim 30^\circ$ and the oral floor drops away. We noticed nothing notable (that has not previously been reported) about the baleen filtering apparatus, with the sole exception being that the most distal (= ventral) tips of the plates bend laterally (labially) during engulfment (Fig. 3). Externally visible features associated with engulfment, including the Y-shaped fibrocartilage just under the mandibles at the front of the pouch (Pivorunas 1977), can also be seen in several of our recorded sequences.

4. Timing of Engulfment and Expulsion

Engulfment occurs rapidly, with a mean time of 2.07 s (SD 0.19, range 1.72–2.48, $n = 24$), measured from the start of water influx and gular expansion (even before peak gape) until the pouch is fully expanded. Expulsion (purging) of engulfed water—at which time filtration occurs, separating retained prey from expelled water—is also a rapid event, occurring in ~ 20 s (mean 22.3 s, SD = 5.15, range 14.2–36.1, $n = 24$). Depending on the whale’s orientation and depth it is often easy to visualize excurrent water flow (from bubbles, streams, and surface disruption) during expulsion; whales expelled water with the head above or underwater and the body partially or completely on its side (90° rotation) or in normal,

dorsal-up position. Specific observations about degrees and directions of excurrent flow are outlined below.

5. Timing of Gape Closure and VGB Contraction

In about 65% of recorded engulfments (17 of 26), gape begins closing before the pouch is fully expanded. Our video sequences reveal that contraction of VGB musculature (to expel engulfed water from the mouth) typically and unexpectedly begins well before full gape closure (mean 0.34 s, SD = 0.06, range 0.24–0.49, $n = 17$).

6. Reverberating Waves Rebounding Through Filled Ventral Pouch

It is often possible (in about 40% or 10 of 26 recorded engulfment events where the expanded gular region is fully or largely visible) to see one or more waves moving rapidly over the external surface of the VGB and inflated oral pouch (Fig. 5). In most instances, a single wave is visible; this wave appears to represent completed filling of the pouch, as the wave originates at the posterior-most point of the pouch and “bounces” (reflects) anteriorly, rebounding toward the mouth opening just as gape begins to close and expulsion begins. This would be a simple phenomenon resulting from reversing longitudinal fluid flow, as inflowing water “hits” the posterior wall of the fully expanded pouch and reverses course. This splash can be seen from inside an open whale mouth (Fig. 5C).

7. Excurrent Flow of Engulfed Then Expelled Water

The location/direction of excurrent flow (due to postengulfment expulsion/purging during filtration) varies according to a whale’s body orientation, forward swimming speed, and whether the head is at, above, or below the sea surface, and—if above—whether the head is pointed upward (Fig. 6) or held parallel to the surface (Fig. 7). Thus unlike other aspects of engulfment, where there was little observed variation, there was far less stereotypy of excurrent flow.

If the head is pointed upward (Fig. 6), water first exits through the posterior portion of the baleen racks, probably assisted by gravity, then in most cases after a slight (0.4–0.5 s) delay a second surge of water abruptly flows through the anterior-most baleen plates. This break in water flow, in which water does not flow gradually from the posterior toward the anterior of the mouth but indeed skips the middle baleen plates as it takes a sharp jump and surges directly to the anterior of the racks, is highly suggestive of a rebound phenomenon. If the whale surfaces with its head pointed straight upward, two major excurrent flows can be seen pouring out of each angle of the mouth well before gape closure (presumably due to gravity’s influence).

However, with whales swimming forward at or just below the sea surface prior to and during engulfment (in all body orientations; Fig. 7), the first flow of excurrent water is not observed at the angle of the mouth, but instead close to the anterior of the mouth—whether from simple reversed/rebounded flow or contraction of VGB musculature and return of the tongue to its original position, it is impossible to determine from our video sequences. In such cases, a second, larger excurrent flow carrying most (perhaps 60%–80%) of the expelled water is later visible (from bubbles or streaming water; Fig. 7) more posteriorly. In summary,

the portion of the baleen racks that commence the filtration process (Werth 2013) seems to depend on a whale's orientation, forward locomotion, and related aspects of engulfment, particularly its position above or below the water's surface.

8. Wave Propagation or Other Water Motion Around and Within Mouth

It is striking how calm and smooth the water level in the mouth is during engulfment relative to the water outside the mouth (Fig. 8), which often shows waves or chop due to wind or the motion of the whale (particularly its emergence above the surface). This is true no matter the whale's body orientation; even whales turned nearly upside-down show calm water in the mouth (Fig. 8A). In many recorded sequences there are no turbulent, disruptive currents within or immediately adjacent to the mouth.

9. Vortical Flow from Head Depression

In multiple sequences (distant aerial plus close-up GoPro), large (2–4 m diameter) whirlpools are visible on the water's surface at the point where the head, following engulfment and water expulsion, sinks underwater (Fig. 5C, 8D-F). In multiple instances a pair of whirlpools swiftly rotating in opposite directions (clockwise and counterclockwise, presumably linked by a submerged semitoroidal vortex) are clearly evident, persisting for >30 s. These whirlpools apparently form from vortices shed as the depressed head entrains air from above the surface into a collapsing bowl-like cavity.

10. Influence of Body Position on Engulfment

Earlier we alluded to the stereotyped nature of humpback whale feeding in our recorded sequences: despite a wide range of body positions/orientation, swim speeds, and behaviors (especially flipper motion), there is little variation in kinematic events of water engulfment and expulsion, especially in terms of timing. Minor exceptions found in whales rotated from the normal dorsal-up orientation include slightly lower gape angles and cranial elevations. As noted above, excurrent flow also varies with body position: water normally exits at the angle of the mouth (instead of anteriorly or all along the jaws) when a whale surfaces from straight below and rises in a chin-up posture. The opening to the oral pouch can be seen only when looking straight down into the mouth, but VGB contractions and waves rebounding along the pouch are best observed in rotated whales.

Discussion

The speed of the engulfment events analyzed here (mean 2.07 ± 0.19 s) is in line with previously published data that used biologging tags to measure (Goldbogen et al. 2008, Simon et al. 2012) or mathematical modeling to estimate (Potvin et al. 2010) engulfment timing in humpback whale lunge feeding. Cade et al. (2016) reported similar (2.0 ± 0.5 s) tag-based engulfment times for humpbacks engulfing krill, but longer (4.8 ± 3.0 s) tag-based times for humpbacks engulfing fish. Based on our finding that the mouth often (in 65% of recorded engulfments) begins closing before full pouch expansion, we conclude that the pouch does not always completely expand prior to initiation of gape closure; this has been previously suggested (Arnold et al. 2005). The reason for this is uncertain. It may be that earlier gape closure (before peak pouch expansion) helps to (1) minimize drag, (2) maintain

forward momentum, (3) control water influx, and (4) filter/retain elusive prey before they have an opportunity to swim from the engulfed water mass. Alternatively, the whales recorded for our study may have engulfed nonmaximal volumes. This would minimize filtering time, expend less energy, and allow for more engulfments overall. As long as nonmaximal engulfment could still capture the bulk of a whale's intended schooling prey, this would prove beneficial.

Cranial elevation appears to peak before maximal gape (Fig. 1), possibly because the water mass entering the oral pouch or the influence of fluking or pectoral braking (Edel and Winn 1978, Fish and Battle 1995) generate forces that pull the head downward, thereby lessening cranial elevation during peak gape. With regard to tongue inversion and water entry into the pouch, some of our recorded sequences involved inverted or otherwise rotated lunging whales, where the expanding pouch must be filled solely by ram-driven engulfment forces (Goldbogen et al. 2006, 2007) with no assist from gravity.

It is unlikely that the externally visible reverberations along the inflated pouch of postengulfment whales are powered by VGB musculature or otherwise represent an active process, although this phenomenon might also be attributed to passive elastic rebound from stretchy tissues within the VGB (Orton and Brodie 1987, Shadwick et al. 2013). Propagation of such elastic waves is most likely when two waves are evident (Fig. 5B), the first probably stemming from simple reversed flow and the second (which also originates posteriorly but reaches the mouth later) probably due to highly elastic tissues that permit remarkably rapid and extensive gular expansion. However, most of these reverberations are unlikely to be caused by tissue elasticity because maximum tissue deformation (*i.e.*, strain) during engulfment, as determined by Shadwick et al. (2013), are within the compliant, near zero-stress range of the VGB stress-strain curve measured by Orton and Brodie (1987). Based on studies by Potvin et al. (2009, 2010, 2012), larger (15+ m) rorquals may have insufficient VGB-induced elastic potential energy to generate the kinetic energy needed to expel engulfed water masses, so a combination of elastic rebound of the VGB tissue and passive rebounding (reflected) flow of engulfed water may both aid excurrent (filtering) flow in large whales.

The externally visible pouch reverberations and the rebounding flow they represent may aid humpback (and other rorqual) whales in expelling large volumes of engulfed water, but their consequences for oral filtration are unclear. Provided this unsteady flow affects baleen porosity, the reverberations may have an adverse impact; alternatively, they might speed up or otherwise aid filtration, but our study found no evidence to support these speculative inferences.

It was easy to observe excurrent flow of filtered water exiting the mouth when whales were at or just above the surface (Fig. 6), but streams of expelled bubbles could be seen in whales below the surface (Fig. 7). Unfortunately, we cannot tell from our results if or how excurrent flow might differ in subsurface expulsion, although it does appear to be at least partly affected by gravity when a whale's head is out of water (Fig. 6).

Other flow phenomena may also be noteworthy, including the calmness of water around and within the mouth immediately prior to and during engulfment (Fig. 8). This is potentially important given that nonlaminar flow might scatter or disperse prey items directly, or startle or alarm prey (as by vibrations or currents) and thereby indirectly lead to decreased prey density (Werth 2012). This is not mere speculation: video sequences provided direct evidence of preengulfment bubble netting and post-engulfment whirlpools and vortices (created by rapid head/body depression through the air-water interface at the surface) resulting in more tightly aggregated prey (Fig. 8), although it is uncertain whether this response was active (from fish swimming away from the phenomena) or passive, with currents alone aggregating the prey. Although our video analysis suggests such hydrodynamic effects, further study is needed to resolve the precise mechanisms involved, and to determine their relative importance.

Vortical flows from head depression are potentially significant in that they presumably occur to substantial depths, perhaps ~3–5 m, and hence might further aggregate small schooling prey, either passively, by creating a low-pressure zone in which prey become concentrated (as in the humpback feeding described by Hays et al. 1985), or due to prey items' active behavioral response to moving water currents (Werth 2012). We observed humpbacks repeatedly engulfing prey in the same approximate surface location (within ~4 m) after short intervals (<30 s), and it is possible that hydrodynamic effects of previous engulfments might aid further feeding bouts. It is possible that subsurface vortical flow continues to aggregate prey for future ingestion, especially in the case of small or weakly swimming prey. It must be noted that all of our recorded engulfments were at or just below the surface. An obvious benefit of tags affixed to whales is the possibility of recording data (including video) from depths where cameras attached to drones or held by observers cannot penetrate.

With regard to overall body position and orientation, humpback whale feeding is famous for its behavioral flexibility (*e.g.*, McMillan et al. 2018). There are many humpback foraging behaviors that were not observed in our study. Nonetheless we have found—throughout all the sequences we analyzed, and relative to other published accounts of humpback feeding behavior (Jurasz and Jurasz 1979; Hain et al. 1981; D'Vincent et al. 1985; Hays et al. 1985; Goldbogen et al. 2008; Friedlaender et al. 2009, 2013; Hazen et al. 2009; Ware et al. 2010; Simon et al. 2012; Kirchner et al. 2018)—certain common aspects that appear to be largely or entirely invariant. These include high (>80°) gape angle with a large contribution from cranial elevation, rapid (within 2 s) filling of the oral (ventral) pouch, and initial expulsion of excurrent water from the anterior-most baleen (unless the whale's head is raised at an angle above the water surface, when water pours out closer to the angle of the mouth).

From this kinematic conservatism, we conclude that mechanisms of engulfment, including precise timing of events and involvement of anatomical structures, are physically constrained relative to other aspects of feeding. Although humpback whale foraging is remarkable among cetaceans for encompassing a greatly varied behavioral repertoire, the morphology and biomechanics of feeding are likely curbed by brute limitations of tissues and the environment.

Supplementary Material

Refer to Web version on PubMed Central for supplementary material.

Acknowledgments

We thank the Northern Southeast Regional Aquaculture Association for assistance and access to their facilities. Geoff Clark and the Prince William Sound Aquaculture Corporation provided drone and GoPro footage of their facilities captured by Klint Hischke and Dan Orlando. We are grateful for field support provided by the Alaska Whale Foundation and to Mark Kelley Photography which generously donated a percentage from book sales to support this study. We thank scientists who have aided our understanding of orqual engulfment, especially Rick Lambertsen, Jeremy Goldbogen, Bob Shadwick, Jean Potvin, Nick Pyenson, Brian Kot, Haruka Ito, and Frank Fish. Research in Southeast Alaska was authorized under NOAA Fisheries permits 14122 and 18529. Research reported in this publication was supported by the National Institute of General Medical Sciences of the National Institutes of Health under Award Numbers UL1GM118991, TL4GM118992, or RL5GM118990. The content is solely the responsibility of the authors and does not necessarily represent the official views of the National Institutes of Health.

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Figure 1. Aerial view (A) showing measurement of gape angle (here 44°) prior to engulfment and mandibular depression, with left flipper sweeping anteriorly and retracted tongue (arrow) just before it inverts and translocates into inflated ventral pouch. Inset (B) shows underwater head-on view of approaching whale in GoPro video frame just after tongue inversion (start of engulfment).

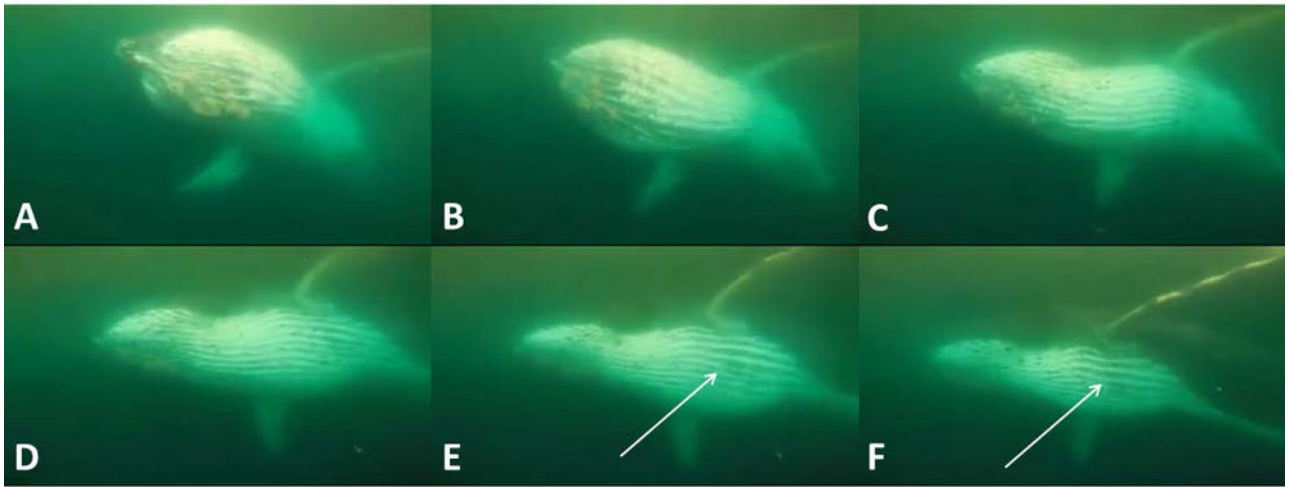


Figure 2. Expulsion of engulfed water usually begins with contraction of posterior-most ventral groove blubber (VGB) musculature, resulting in water-filled expansion mainly of the anterior of the pouch, as at the start of this sequence (frames A→F = 3.38 s). Toward the end of this sequence the pouch’s expanded posterior region (arrows) probably represents mainly engulfed prey, although there may also be more water still to be expelled.

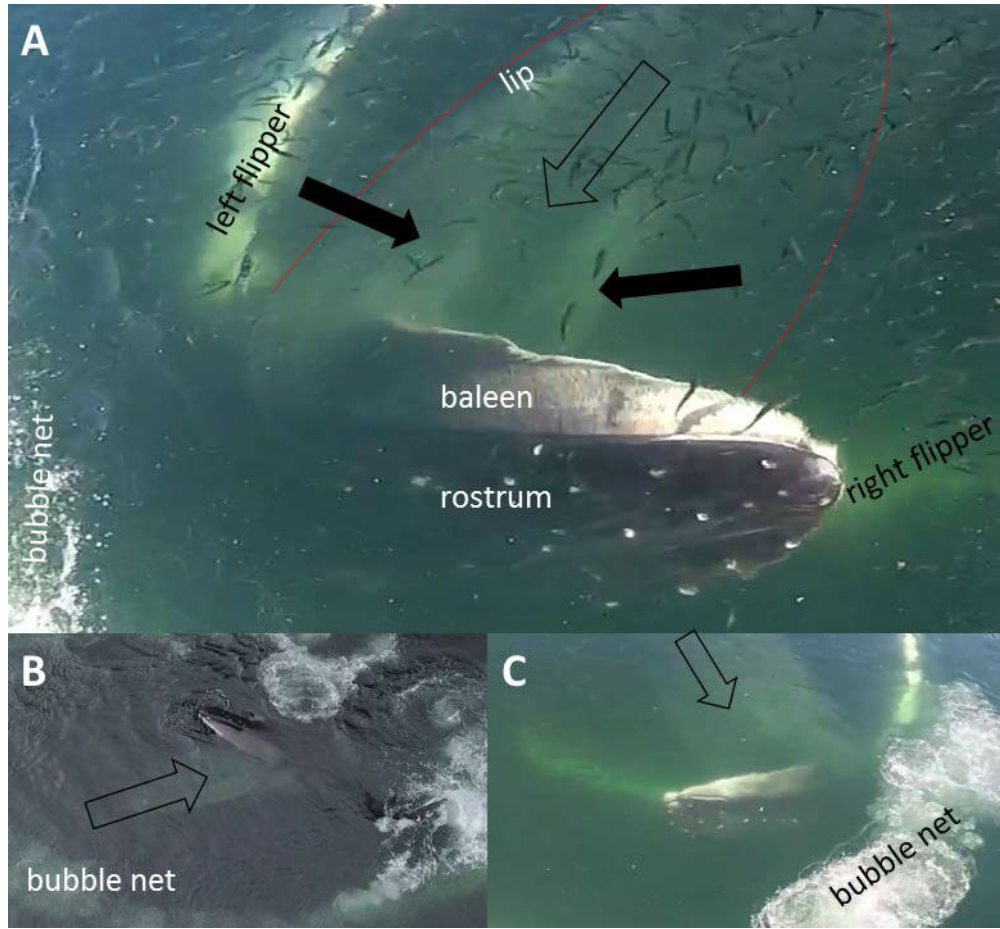


Figure 3. Outlined arrows show patent opening from buccal cavity into filling ventral pouch created by infolding of tongue (black arrows) in these dorsal views of whales ascending within circular bubble nets. Red arc indicates extent of lower jaws (*i.e.*, boundary of the buccal cavity); note also juvenile salmon being engulfed and swept into expanding pouch, and slight lateral (outward) bending of the tips of baleen plates.

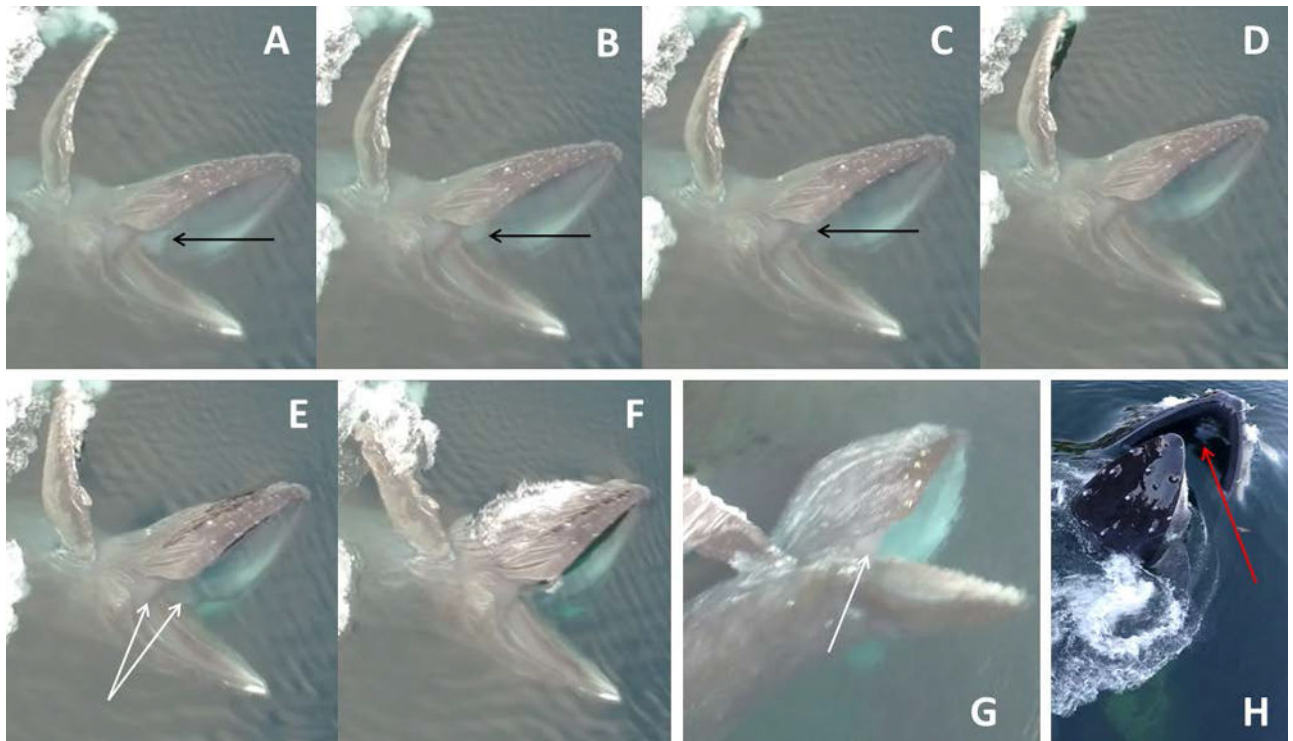


Figure 4. Interior anatomical features (*i.e.*, within the humpback mouth) are observable during these dorsolateral views of engulfment. In sequence A→F (total 0.24 s), the infolding tongue is visible in frames A-C (black arrows) just before it inverts and disappears into the expanded ventral pouch; white arrows indicate mandibular tendons, best seen with full pouch inflation (photo G, of the same whale during a different engulfment event). Red arrow in frame H (different whale during different engulfment event) indicates genioglossal tubercle at origin, by mandibular symphysis, of genioglossus tongue muscle.

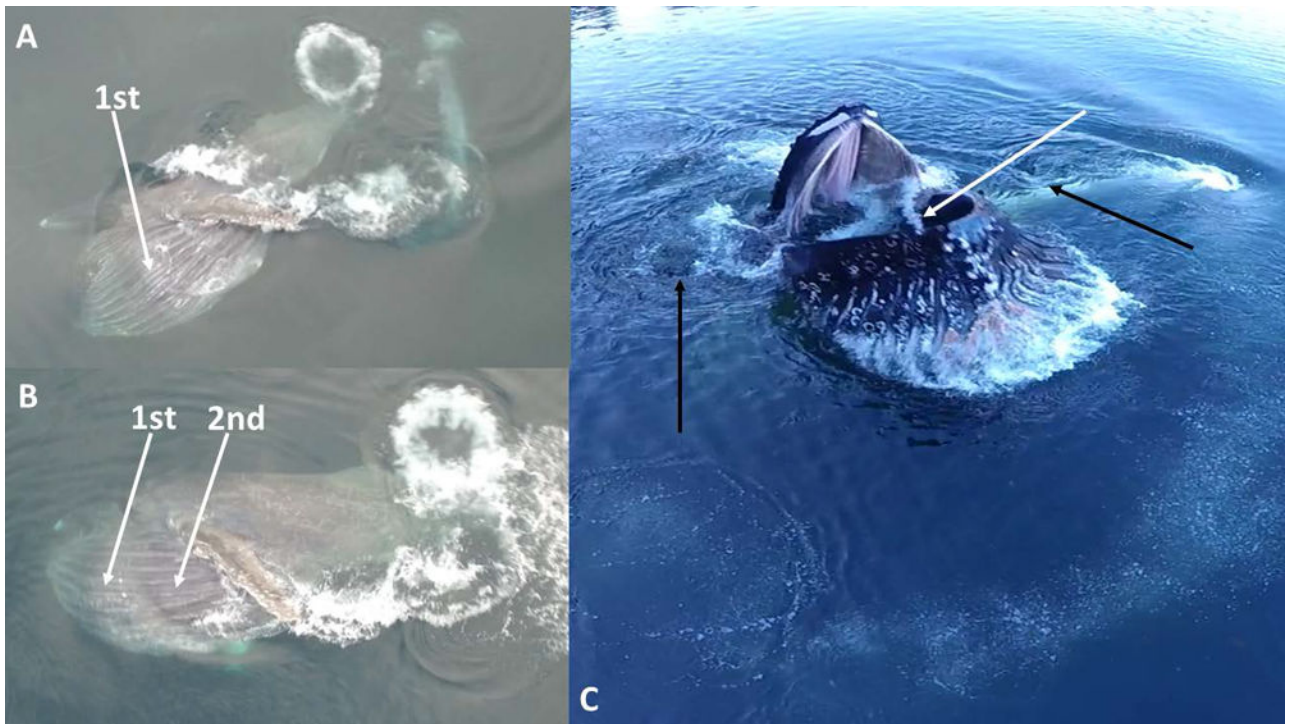


Figure 5. Rebounding waves (white arrows) can be seen reverberating through the expanded ventral pouch, initially (A) after the pouch is fully filled and water reverses flow as it “bounces” off the filled chamber’s posterior limit, then (B, 0.12 s later) as the first wave travels anteriorly (toward the mouth) over the still-opened pouch, a second wave arises posteriorly, most likely from contracting VGB musculature. Occasionally (C) a sharp splash of water can be seen emerging from the open mouth, above and distinct from the volume of water filling the pouch; this splash probably arises *via* rebounding wave energy. Also note (black arrows in C) paired, oppositely flowing whirlpools created by the whale’s (and flippers’) rapid descent after rising up to engulf prey in the middle of a bubble net the whale created.

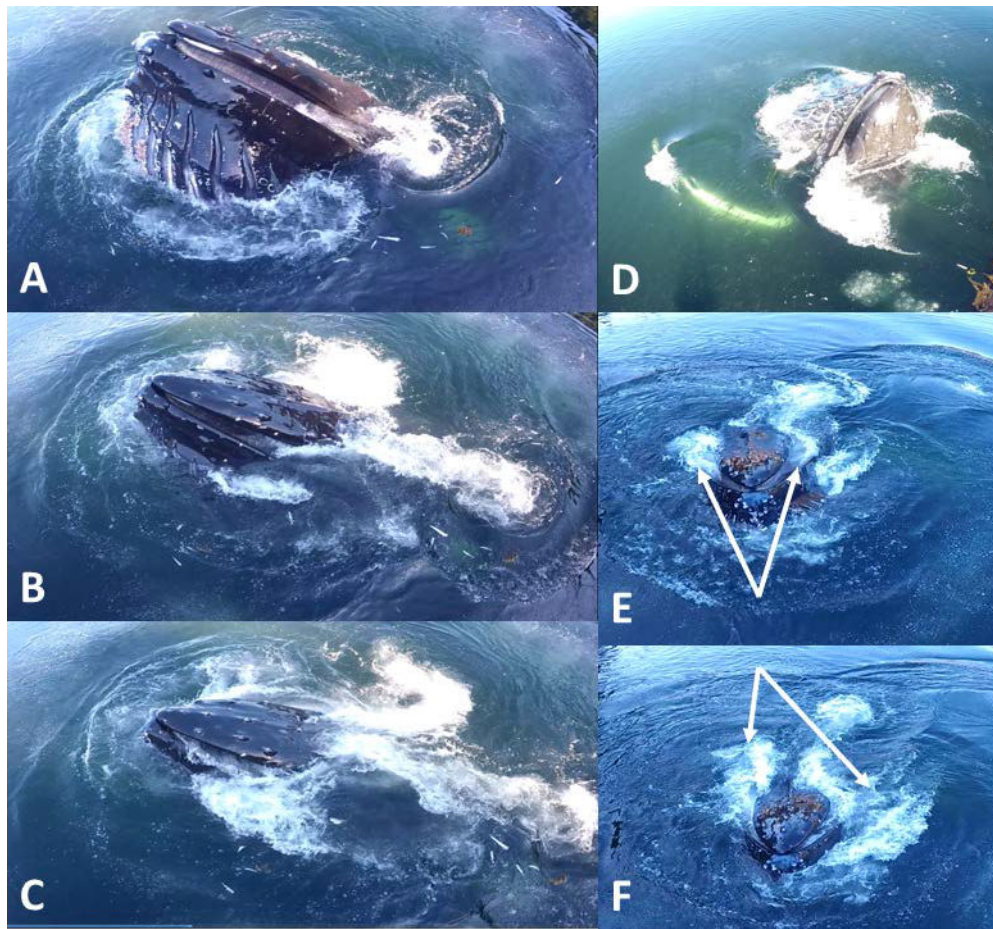


Figure 6. Expulsion of filtered water in whales slowly rising vertically through the water surface is complicated by the fact that flow is initially or mainly governed by gravity, particularly if the whale is wholly vertical (D). Otherwise the excurrent flow begins posteriorly before being overtaken by stronger flow at the center of the mouth (sequence A→C = 1.34 s total). However, this central expulsion (arrows in E) is itself replaced by sustained expulsion from the posterior of the mouth (F, 0.66 s after E).

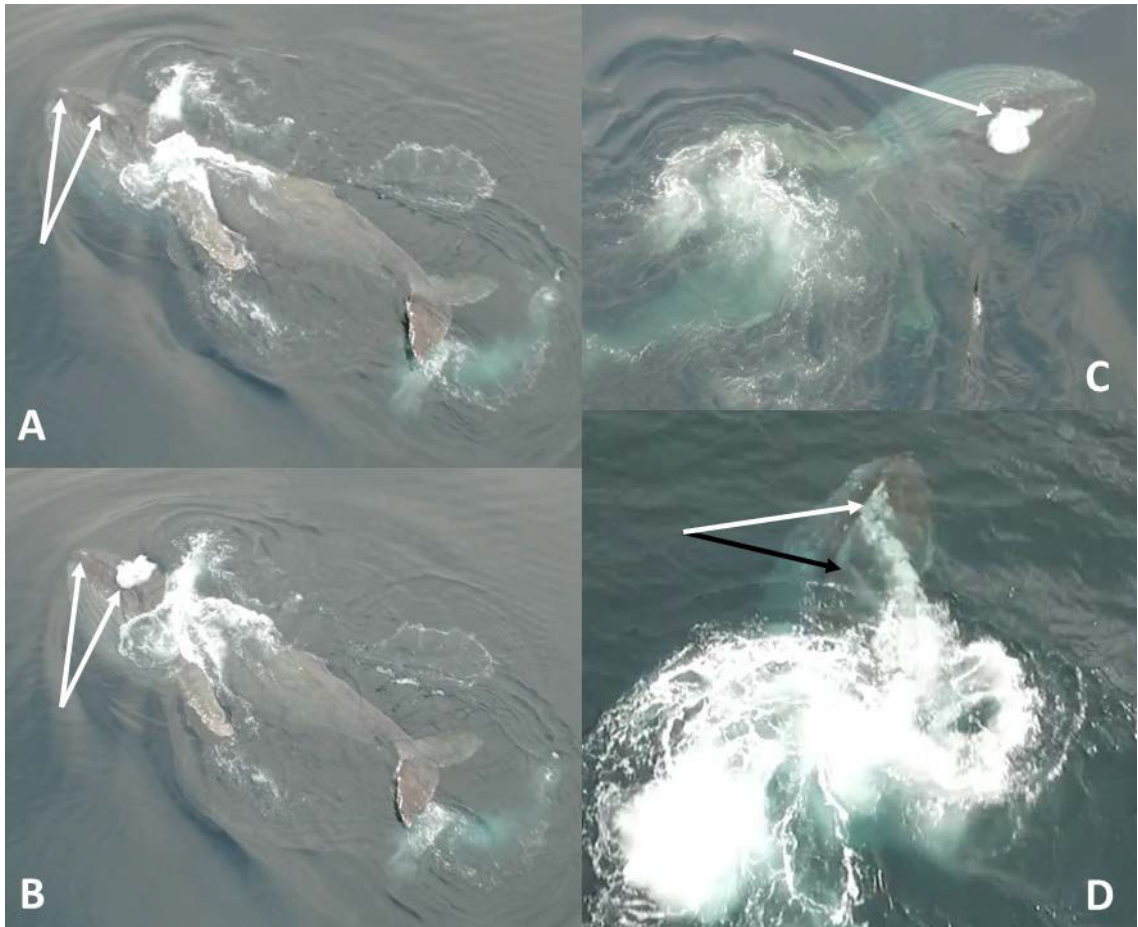


Figure 7. For a lunge-feeding humpback whale (*i.e.*, with rapid horizontal locomotion), excurrent flow of filtered (purged) water initially (A) appears at the anterior of the mouth (perhaps from a rebounding wave within the ventral pouch), then almost immediately *via* a second distinct flow at the posterior end of the mouth. The posterior flow becomes larger (frame B, 0.07 s after A) as the anterior flow dissipates and disappears (C; different engulfment event). The posterior expulsion often decreases (black arrow in frame D, 0.18 s after C) and a large, sustained (10-20 s) flow emerges from the center of the mouth and baleen apparatus (white arrow).

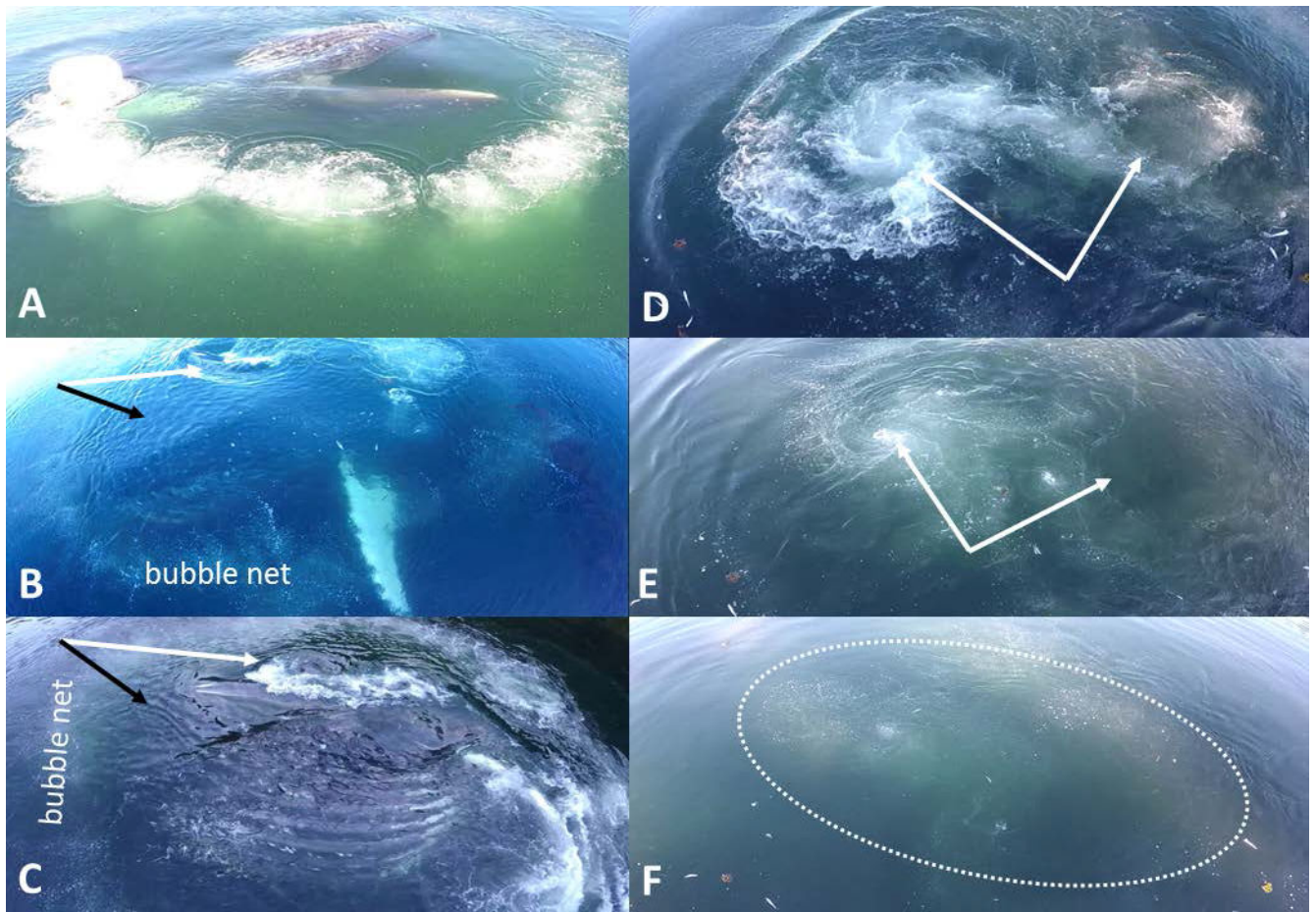


Figure 8.

Apart from the dynamic flows of engulfment and expulsion, water within the mouth is often calm, with no surface waves, even in postengulfment gape closure as in the inverted whale in frame A closing its mouth around fish within a bubble ring. In B and C (separate feeding events), water within the mouth shows only slight wind-generated capillary waves (black arrows) despite surface waves created by motion/depression of the upper jaw (white arrows). In sequence D→F (total 24.36 s) a whale has disappeared below the surface after engulfment, leaving two whirlpools on the surface (connected by a circulating underwater vortex). The vortex generates tiny bubbles (not directly produced by the whale) which rise to the surface and may continue to aggregate prey; some small fish are also shown with bubbles in the dotted oval.