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RESEARCH ARTICLE

Biomechanically distinct filter-feeding behaviors distinguish sei whales as a functional intermediate and ecologically flexible species

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ABSTRACT

With their ability to facultatively switch between filter-feeding modes, sei whales represent a functional and ecological intermediate in the transition between intermittent and continuous filter feeding. Morphologically resembling their lunge-feeding, rorqual relatives, sei whales have convergently evolved the ability to skim prey near the surface of the water, like the more distantly related balaenids. Because of their intermediate nature, understanding how sei whales switch between feeding behaviors may shed light on the rapid evolution and flexibility of filter-feeding strategies. We deployed multi-sensor bio-logging tags on two sei whales and measured the kinematics of feeding behaviors in this poorly understood and endangered species. To forage at the surface, sei whales used a unique combination of surface lunges and skim-feeding behaviors. The surface lunges were slow and stereotyped, and were unlike lunges performed by other rorqual species. The skim-feeding events featured a different filtration mechanism from the lunges and were kinematically different from the continuous filter feeding used by balaenids. While foraging below the surface, sei whales used faster and more variable lunges. The morphological characteristics that allow sei whales to effectively perform different feeding behaviors suggest that sei whales rapidly evolved their functionally intermediate and ecologically flexible form to compete with larger and more efficient rorqual species.

KEY WORDS: Filter feeding, Lunge feeding, Skim feeding, *Balaenoptera borealis*, Biomechanics

INTRODUCTION

Suspension filter-feeding strategies have evolved independently in multiple lineages of aquatic animals (Sanderson and Wassersug, 1993). By processing large volumes of water and filtering relatively small food items, filter feeders are able to exploit the tremendous amount of biomass found at lower trophic levels. The energetic efficiency afforded by filter feeding is also thought to be one of the drivers for the evolution of gigantism in several organisms

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including extinct teleost fishes (Friedman, 2012), elasmobranchs (McClain et al., 2015) and the largest animals that have ever lived: baleen whales (Goldbogen et al., 2019). The morphological diversity exhibited by aquatic filter feeders is accompanied by a wide range of prey preferences from small copepods to forage fish.

Large, filter-feeding whales fall into two broad categories. Lunge-feeding rorqual whales (Balaenopteridae) attack dense patches of prey by accelerating, engulfing large gulps of prey-laden water in their expandable buccal pouch, and filtering the water through relatively short, keratinous, brush-like baleen plates (Cade et al., 2016; Goldbogen et al., 2017a). This intermittent form of filter feeding allows rorquals to approach and catch their small, maneuverable prey (fish and krill). In contrast, continuous filter feeders, such as right whales and bowhead whales (Balaenidae), slowly swim through prey patches with their mouths open, using their wide gapes to maximize water intake ($1–3$ m^3 s^{-1}, northern Atlantic right whales; van der Hoop et al., 2019) while concurrently filtering prey through longer baleen plates (Goldbogen et al., 2017a; Simon et al., 2009). Because of the high drag and slow speeds associated with continuous filter feeding, balaenids primarily feed on slow-moving copepods (Werth, 2012).

Long, sleek and fast, sei whales (*Balaenoptera borealis*) outwardly resemble other rorqual species but have the ability to facultatively switch between feeding modes. Like their rorqual relatives, sei whales catch fish and krill by lunge feeding, but they can also skim plankton off the surface of the water using a behavior reminiscent of the more distantly related balaenids (Horwood, 2009; Ingebrigtsen, 1929). The oral morphology of sei whales reflects their generalist role (Baumgartner and Fratantoni, 2008): compared with most rorquals, sei whales have slightly longer baleen plates with finer fringes, denser fringe mats and larger gaps between the plates. However, sei whale baleen is not nearly as long as the baleen plates of balaenids, which have even finer fringes, denser fringe mats and even larger inter-plate gaps (Brodie and Vikingsson, 2009; Werth et al., 2018). Sei whales likely represent a functional and ecological intermediate in the transition between intermittent filter feeding and continuous filter feeding, and therefore understanding the tradeoffs between their lunge-feeding and skim-feeding behaviors may shed light on the evolution of cetacean feeding strategies.

Because of their elusive nature, heterogeneous distribution patterns and affinity for habitats that are difficult to work in, little is known about the feeding behaviors of sei whales, how and when skims and lunges are used, and how the intermediate morphology of sei whales affects their prey capturing ability. For the first time, we deployed suction-cup attached, multi-sensor video tags on two sei whales, with the aim of addressing three long-standing questions about the feeding ecology of this poorly understood species. (1) Are sei whale skim-feeding events mechanically similar to the continuous-feeding strategies used by balaenids, or are they

simply slow, extended lunges? In other words, given that the baleen plates of sei whales are more similar to those of other rorqual species (Jensen et al., 2017), can sei whales filter water continuously while swimming, or is skimming a different strategy for inflating the buccal cavity with water? (2) If sei whales can use their baleen to filter water continuously, does that mean that their ability to lunge feed is compromised? It has been suggested that as an ecological intermediate, sei whales sacrifice performance of both skimming and lunging (Baumgartner and Fratantoni, 2008; Brodie and Vikingsson, 2009). (3) If sei whale skims and lunges are biomechanically different, what are the advantages and disadvantages of each, and are they used in different behavioral contexts?

MATERIALS AND METHODS

In March 2019, we deployed suction-cup attached archival bio-loggers on two adult sei whales, *Balaenoptera borealis* Lesson 1828, foraging at the mouth of Berkeley Sound, in the Falkland Islands. The whales were tagged in separate groups that were surface feeding in shallow, coastal water (40–60 m depth). The tags (Customized Animal Tracking Solutions; Goldbogen et al., 2017b) were equipped with three-axis accelerometers (400 Hz), magnetometers (50 Hz), gyroscopes (50 Hz), pressure and temperature sensors (10 Hz), GPS, a video camera and a hydrophone. The whales were approached in a small boat and the tags were deployed using a carbon-fiber pole. For both deployments, the tag was attached to the dorsal surface, a few meters directly behind the blowhole (Figs 1 and 2). Immediately afterwards, a small unmanned aerial vehicle (DJI Phantom 4a) was launched to film feeding events and measure the body length of the animals (Johnston, 2019). This research was authorized by the Falklands Islands Government (permit #R11.2017) and approved by the Stanford and UC Santa Cruz IACUC committees. Once the tags were recovered, the accelerometer and magnetometer signals were aligned with the body axis of the whale (Johnson and Tyack, 2003), smoothed with a low-pass filter to remove sampling error and the fluctuations caused by the tail strokes (two-pass Butterworth, cutoff frequency 0.15 Hz; Segre et al., 2016), and used to calculate the pitch, roll and heading of the whale (Johnson and Tyack, 2003). A visual representation of the tail stroke was obtained by filtering an unsmoothed version of the pitch signal with a band-pass filter (cutoff frequencies 0.15 Hz, 0.40 Hz). Although the units of the tail-stroke signal are in degrees, the magnitude is non-intuitive and highly dependent on the placement of the tag. Therefore, we present this signal without dimensions as a guide to visually interpret when the tail strokes occur. Speed was obtained by calibrating the measurements of the background, high-frequency accelerometer vibrations with the orientation-corrected depth rate calculated during deeper dives (~30–40 m dives; minimum absolute pitch angle for calibration, 30 deg; program used for speed calculation from Cade et al., 2018). To groundtruth the velocities obtained from the accelerometers, we digitized the position of the tag in the aerial video of the lunge shown in Fig. 2 (DLTdv software; Hedrick, 2008). We found a difference of 0.1 m s^{-1} between the maximum lunging speed obtained from the accelerometers and the maximum lunging speed calculated from the aerial video. Finally, depth and speed were filtered with a low-pass filter (cutoff frequency 0.40 Hz) to remove sampling error.

Using a combination of whale-borne videos, aerial footage and kinematic data, we identified feeding lunges and bouts of skim feeding. Surface lunges were identified using changes in speed and

in the long axis roll (an important diagnostic feature revealed by the videos; see Movies 1 and 2). For each lunge, we measured the duration (from the start of the roll to maximum roll, which approximates the start of the acceleration to the end of the engulfment; Figs 1 and 2, left) and maximum speed. The exact time when the mouth opened was only visible in one aerial video of a tagged whale (Fig. 2, right); however, other aerial photos, aerial videos of untagged whales lunging, above-water photos and underwater footage suggest that the timing seen in the aerial video was representative (Fig. 3). We measured the maximum gape angle between the upper jaw and lower jaw using aerial videos of three lunges (from individual 2 and two untagged whales) with ImageJ software. Because the kinematics associated with rorqual skim feeding have never been described, skim-feeding events were initially identified using the whale-borne video and were clearly distinct from regular surfacing behavior used for breathing (Movie 1). Once we identified the diagnostic kinematics, we were able to find skim-feeding events that occurred when the cameras were not recording. Non-feeding surfacings were brief, with a sharp upwards pitch that quickly transitioned to a sharp downward pitch, and with no bubbles emerging from the mouth. In contrast, skims featured a shallow upward pitch maintained for several seconds (the diagnostic plateau shape visible in Fig. 1, cyan line), with the rostrum held above the water and with bubbles visibly emerging from the mouth during and afterwards (Movie 1). Because of the positive pitch angle, most of the body and the tags remained below the surface for the duration. We defined the start of the skim at the initial upward pitch, immediately before the whale reached the surface. The end of the skim was defined when the whale began its descent below the surface (Fig. 1). In some instances, the whale ended the skim by dipping its head below the water, and then re-emerged to take a breath before diving. For each skim, we measured duration and average speed. For both lunges and skims, we measured the duration of the filtering phase using the whale-borne videos as the time from the end of the feeding event to the time when bubbles were no longer emitted from the sides of the mouth, indicating that no more water was being processed. We only measured filtering duration if the bubbles were visible in the video and the whale did not break the surface to breathe during the filtering process.

RESULTS

We measured a total of 182 surface lunges, 70 skim-feeding events and 120 sub-surface lunges from two sei whales. The first whale (16.6 m long) performed 67 surface lunges, 30 skim-feedings and 120 sub-surface lunges. The deployment lasted 12 h, starting at 15:18 h local time. The whale performed a series of surface lunges and skims until 15:40 h, when it spent 76 min traveling to a new location before resuming its feeding. At 19:04 h, it transitioned from stereotypical surface lunges and skims to faster and more kinematically variable sub-surface lunges. At 20:29 h, it stopped feeding and spent the rest of the night traveling or resting (sunrise was at 07:00 h). Excluding periods of travel and rest, the whale fed at a rate of 56 events per hour. The second whale (15.7 m long) performed 115 surface lunges and 40 skims. The deployment lasted 11 h, starting at 17:32 h. The whale performed a series of lunges and skims until 19:14 h. Overnight, the whale traveled and rested until it began surface lunge feeding at 04:42 h, shortly before the tag fell off. The approximately 7 lunges performed in the morning were not included in the analysis, as the tag was poorly attached at that time. For the first evening of the deployment, the whale fed at a rate of 91 events per hour. Both whales were feeding on amphipods (*Themisto*
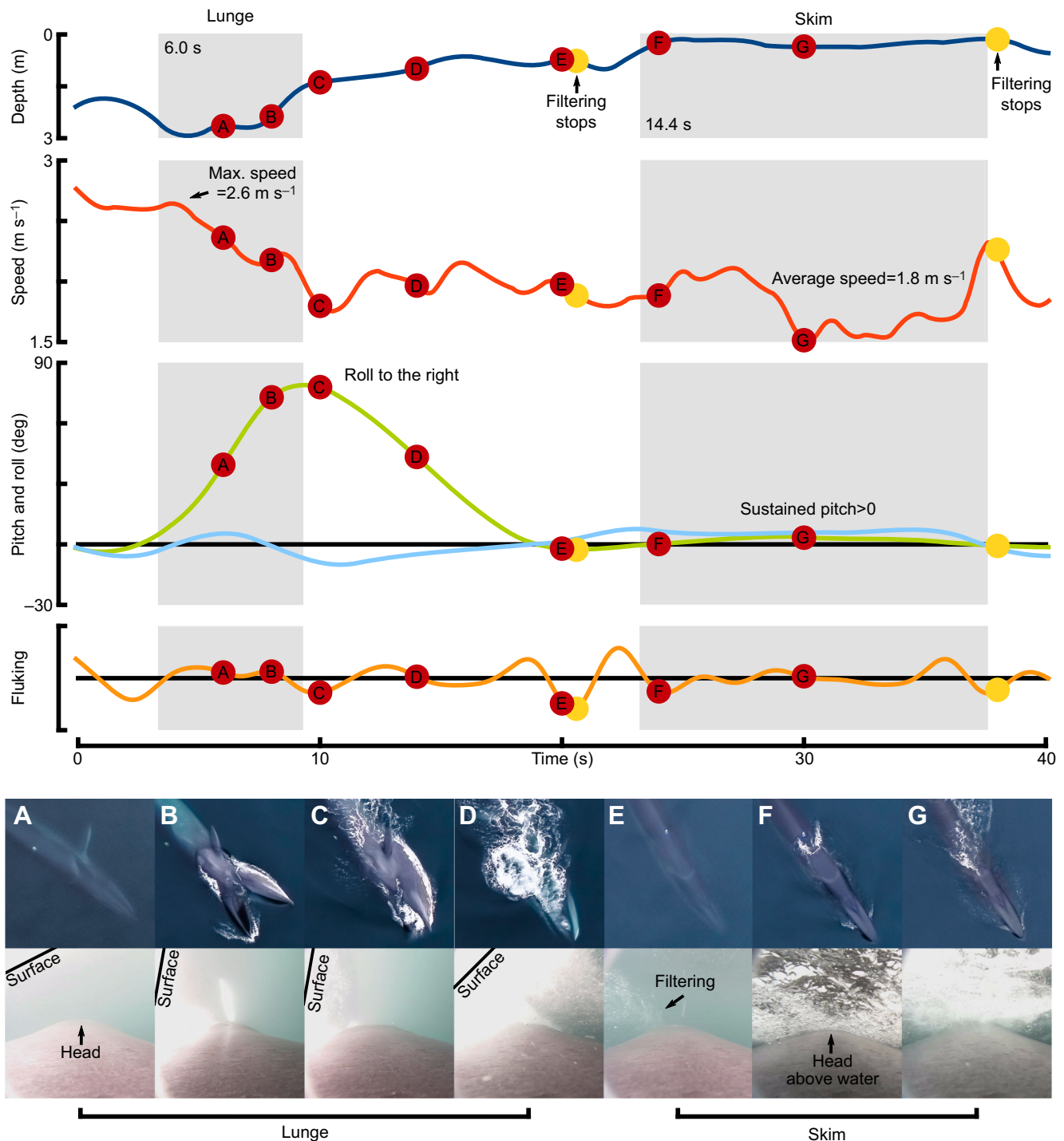
Fig. 1. Sei whales use combinations of slow surface lunges and skim feeding to forage continuously on amphipods. Surface lunges (left gray bar) were highly stereotypical events, characterized by slow speeds (red), rightward rolls (green), continuous fluking (orange; non-dimensional) and long filtration times (yellow dot; from underwater video). Skim-feeding events (right gray bar) were characterized by slow, constant speeds (red), extended periods at the surface (blue), slightly upward, sustained pitch angles (cyan) and short filtration times (yellow dot; from underwater video). Aerial and whale-borne photos of whale 1 show the whale (A) rolling and accelerating, (B) engulfing its prey, (C) closing its mouth, (D) rolling back to level while filtering, (E) filtering, (F) initiating a skim and (G) skimming (marked in the corresponding positions in the graphs above). Enlarged photographs are provided in Fig. S2.

gaudichaudii, visible in the video and observed from the tagging boat), and it is possible that in the evening the first whale switched to feeding on lobster krill (*Munida gregaria*, visible in the video).

The sei whale surface lunges were highly stereotyped, characterized by rightward rolls, slow speeds and little decrease in speed during filtration (Table 1, Fig. 2, left). A typical surface

lunge began with the whale initiating a rightward roll (Fig. 2, right), often immediately after filtration from the previous feeding event ended. The mouth opened shortly after the start of the roll (Fig. 2, right, photo A), and reached maximum gape approximately halfway through the rolling maneuver (Fig. 2, right, photo B). The maximum gape angle was small (57, 49,
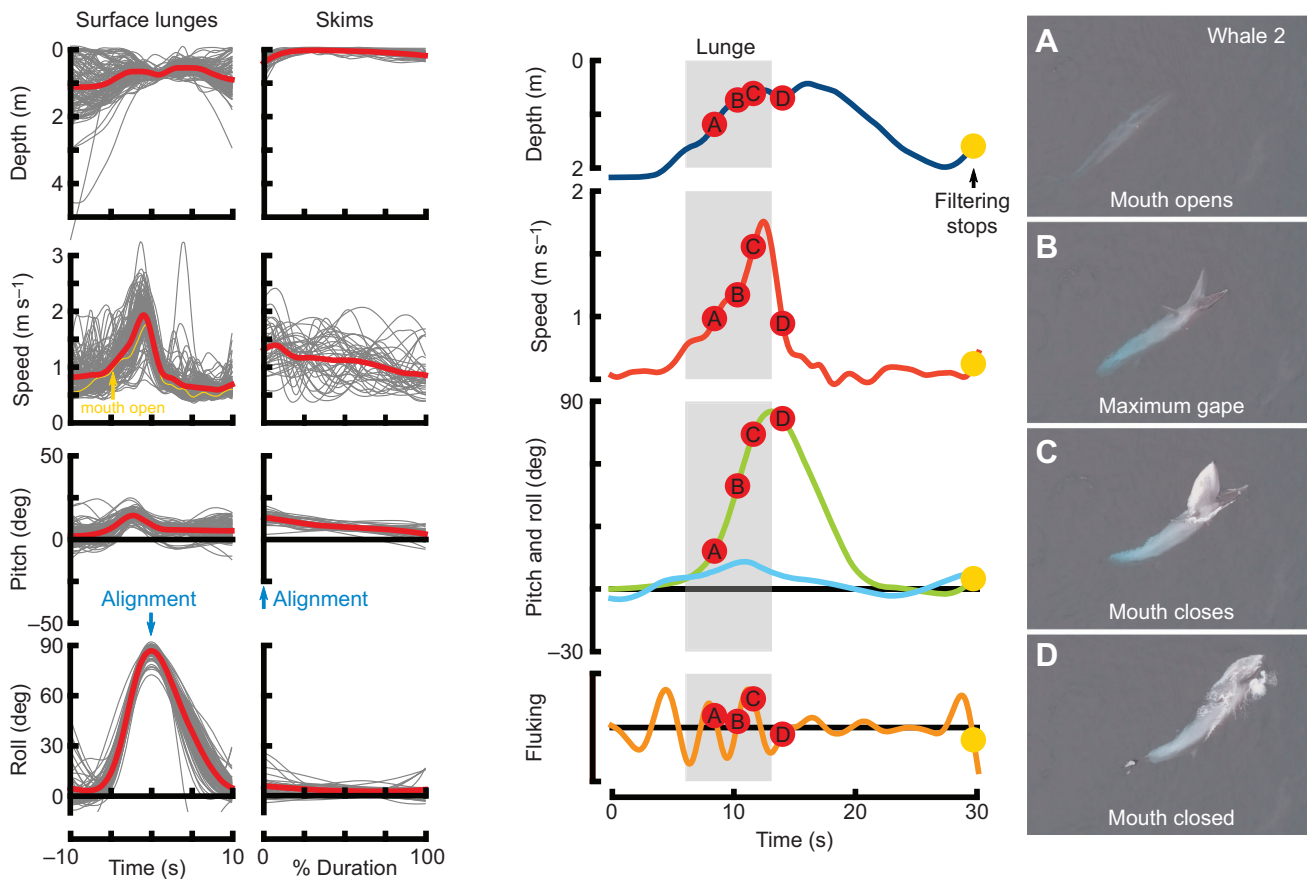
Fig. 2. Sei whale surface lunges were characterized by rightward rolls, slow speeds and little dropoff in speed during filtration. Left: 115 surface lunges performed by a single whale (whale 2) are shown, aligned at the time of maximum roll. Sei whale surface skim-feeding events were characterized by slow speeds, extended periods at the surface, and a slightly upward pitch angle. Forty skims performed by a single whale (whale 2) are shown, aligned to the time when the whale first broke the surface and scaled to a normalized duration. Right: surface-lunging sei whales opened their mouths at the start of the acceleration (red) and the initiation of the roll (green), such that the engulfment occurred when the whale was rolled on its side. Instead of accelerating before the mouth opens, like other rorquals, sei whales used tail strokes (orange; non-dimensional) to inflate their buccal cavity. The timing of the mouth opening for this lunge is shown on the left (yellow). Enlarged photographs are provided in Fig. S2.

60 deg) compared with mechanical tests of maximal gape angle in sei and fin whales (85–90 deg; Brodie, 2001) and photogrammetric measurements of Bryde's (80 deg; Goldbogen et al., 2007) and humpback (82.5 deg; Werth et al., 2019) whale gape angles. The whale continued to roll as the buccal cavity expanded and then the mouth began to close (Fig. 2, right, photo C). The mouth finished closing near the maximum roll excursion, when the whale was rolled approximately 90 deg on its side (Fig. 2, right, photo D). The whale fluked (used dorso-ventral tail strokes for propulsion) throughout the entire lunge, even after the mouth opened and as the buccal cavity expanded. In most cases, the fluking stopped as the filtration began. The surface lunges were slow (average maximum speed 2.1 m s^{-1}) with unpredictable speed profiles. Unlike most rorqual lunges, which feature a distinct acceleration followed by a rapid deceleration as the mouth opens, the peak speed of the sei whale surface lunges was highly variable in timing and the rapid deceleration occurred well after the mouth opened. The first whale maintained a higher velocity before initiating the lunges (Figs 1 and 3), while the second whale started slower with a more predictable acceleration profile (Fig. 2, left). Because of the variable acceleration profiles, we used the roll to determine the duration of the lunge from initiation to engulfment. Filtration during surface lunges lasted an average of 12.5±3.2 s (mean±s.d.).

The sei whale surface skim-feeding events were characterized by slow speeds, extended periods at the surface and a slightly upward pitch angle (Table 1, Fig. 2, left). A typical skim began with the whale arching upwards toward the surface, and maintaining a slightly upwards pitch angle for the duration of the event. Skim feeding was performed with slow, constant speeds (average 1.4 m s^{-1}), and was highly variable in duration (mean±s.d.: 12.6± 10.1 s; range: 3.0–49.1 s). After the skim-feeding events, filtration lasted an additional 2.9±1.2 s.

The sei whale sub-surface lunges were less stereotypical than the surface lunges, but featured higher maximum speeds (mean±s.d.: 2.9±0.4 m s^{-1}; maximum: 5.0 m s^{-1}) and a distinct acceleration and deceleration phase (Fig. S1), which made them similar to the feeding lunges used by most rorqual whales. Roll and pitch were more variable for the sub-surface lunges. Because of the variable nature of the sub-surface lunges, we were not able to measure the duration of the acceleration period, and the videos were too dark to measure filtration time. Only one whale performed sub-surface lunges: after spending most of the afternoon skimming and lunging at the surface, the whale began lunging a few meters below the surface and then switched to targeting a dense prey layer (visible in the videos) with multiple upward lunges performed during deeper dives (maximum 30 m depth; maximum 6 lunges per dive). We were not able to identify any skim-feeding events that were performed below the surface.
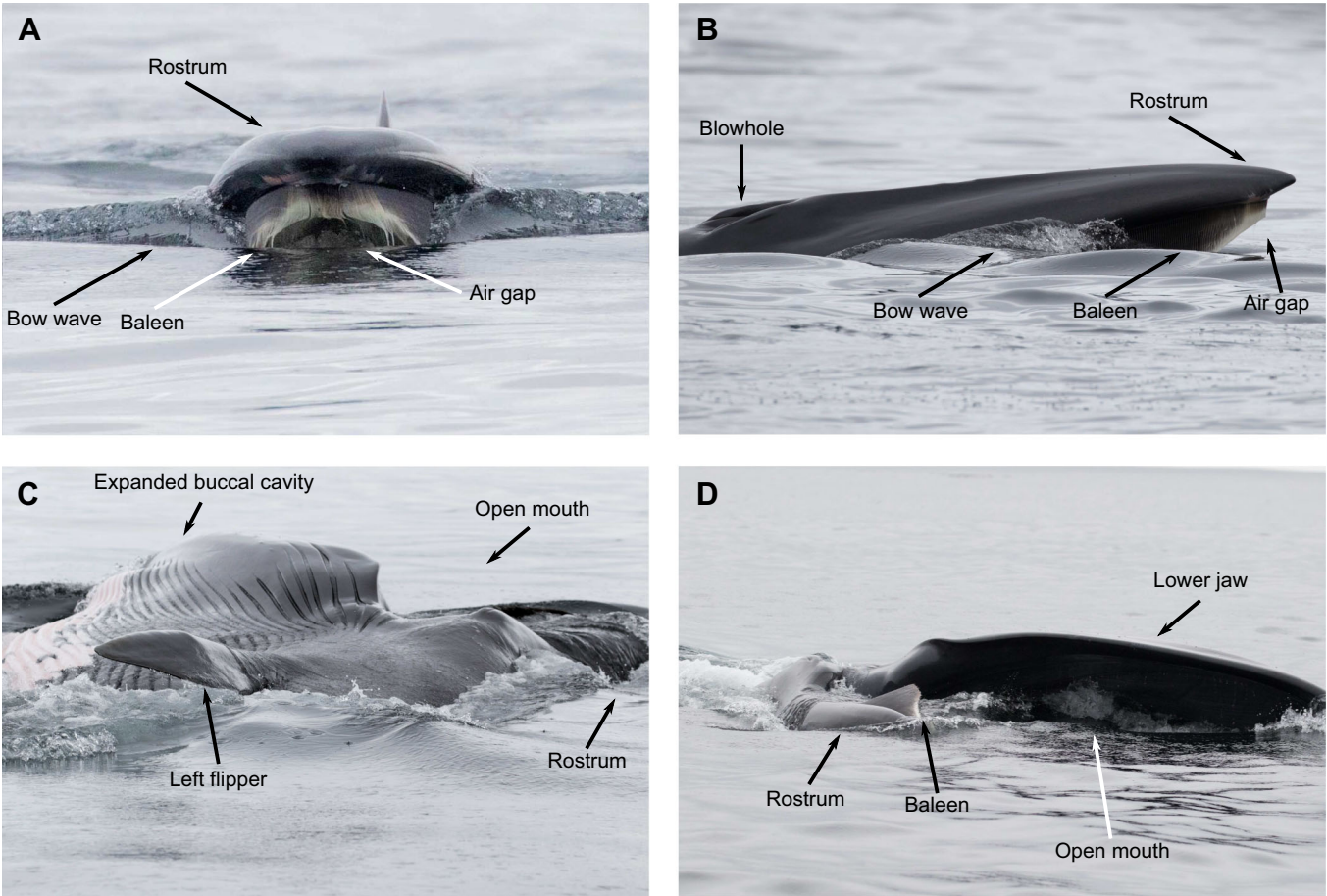
Fig. 3. Sei whales skim feeding and surface lunge feeding. (A) Anterior view of a sei whale skim feeding, showing the head held above the water, the gap between the anterior baleen and the water, and the bow waves forming on the sides of the mouth. (B) Lateral view (right side) of a sei whale skim feeding. (C) Posterior view (left side) of a surface lunge-feeding sei whale showing the rightward rolled body, the left flipper emerging from the water, the open mouth and the expanded buccal cavity. (D) Anterior view of a surface lunge-feeding sei whale, showing the inside of the mouth and the baleen.

DISCUSSION

Sei whales have the ability to switch between intermittent lunge-feeding and continuous ram-feeding strategies (Horwood, 2009; Ingebrigtsen, 1929). Although they outwardly resemble their rorqual relatives (long, sleek body shape), their feeding apparatus (baleen and jaw) has characteristics similar to both the lunge-feeding Balaenopteridae and the ram-feeding Balaenidae (Brodie and Vikingsson, 2009; Werth et al., 2018). By deploying multi-sensor bio-loggers on sei whales, we found that the skim-feeding behaviors of sei whales are indeed biomechanically distinct from their own lunging behaviors and those of other rorquals. Sei whale skims were long and slow (12.6 s, 1.4 m s^{-1}) compared with both their own surface (6.2 s, 2.2 m s^{-1}) and sub-surface lunges (2.9 m s^{-1}), and with the predatory strikes of other rorqual whales (blue whales: 3.9 m s^{-1}, krill-feeding humpbacks: 2.7 m s^{-1}, Cade

et al., 2016; fin whales: 3.0 m s^{-1}, Goldbogen et al., 2006). The skims featured a constant speed profile unlike the characteristic acceleration and deceleration that occurs during lunges (Fig. 2, left; Fig. S1), and there was no indication from the kinematics (specifically, the rapid deceleration caused by the engulfed water) or the drone footage that the buccal cavity was inflated during skim-feeding events (in other large rorqual species, the inflated pouch expands past the outline of the body and is visible from orthogonal aerial photographs). All of the skims were performed with an upright posture, different from the extremely stereotyped ∼90 deg rightward roll of the surface lunges and the highly variable body orientations of the sub-surface lunges (Fig. 2, left; Fig. S1). Finally, the duration of the filtration period was much longer for lunges than for skims (Fig. 1, Table 1) and the underwater footage shows bubbles coming out of the side of the mouth during the skims. This

Table 1. Kinematic properties of sei whale feeding behaviors

	Average/maximum speed (m s^{-1})	Duration (s)	Filter duration (s)
Skim feeding (n=30, 40)	1.4±0.4 (0.8–2.3)	12.6±10.1 (3.0–49.1)	2.9±1.2 (0.4–5.7) (n=36)
Surface lunges (n=67, 115)	2.1±0.4 (0.8–3.2)	6.2±1.1 (4.3–12.2)	12.5±3.2 (3.9–18.1) (n=50)
Sub-surface lunges (n=120, 0)	2.9±0.4 (2.0–5.0)	–	– (n=0)

Sample sizes are shown for each of the two individuals. For the skim feeding bouts, we report average speed over the duration of the skim. For lunge feeding events, we report the maximum speed during the lunge. Filtering duration was only measured if the bubbles were visible in the video and the whale did not break the surface to breathe during the filtering process. Data are means±s.d. with range in parentheses. Raw data are provided in Table S1.

suggests that filtration was indeed occurring concurrently with water intake during skimming, as occurs in continuous filter-feeding balaenids (Werth et al., 2018). Taken together, this evidence suggests that sei whale skims are biomechanically distinct from lunges, and that the baleen plates of sei whales can be used for both continuous filtration and intermittent lunge filtration, as inferred by previous anatomical studies (Brodie and Vikingsson, 2009; Werth et al., 2018).

However, there were some important differences between the skims performed by sei whales and the ram-feeding behaviors of balaenids. The sei whale skims were shorter in duration (12.6 s), compared with the 2.4 min feeding bouts of bowheads (Simon et al., 2009) and the 50 s bouts used by right whales (van der Hoop et al., 2019). Furthermore, the balaenids only paused briefly in-between feeding bouts, to swallow. In comparison, sei whale skims appeared to be discrete events which required additional filtration afterwards and with the whale often changing behavior once the skim was completed (Fig. 1). Additionally, all of the sei whale skims that we identified were performed at the surface with the rostrum lifted out of the water (Fig. 3A,B). We did not find any sub-surface skims in the onboard videos (raised rostrum, bubbles emerging from the mouth) or in the kinematic data (constant depth, sustained slightly positive pitch angle). It has been theorized that because their baleen lacks a subrostral gap (unlike that of balaenids), skimming sei whales need to keep their rostrum out of the water to facilitate the continuous laminar flow of the water into the mouth (Baumgartner and Fratantoni, 2008). This would mean that they can only skim feed at the surface. Although our dataset does not preclude the possibility, we did not find any examples of the sei whales skim feeding while completely submerged.

This brings up our second question: does the sei whale's ability to skim compromise its effectiveness at lunge-feeding? Our data suggest that sei whales use specialized lunges to feed at the surface, but switch to more typical rorqual lunging behavior underwater (Fig. S1). The surface lunges we recorded were slow and highly stereotyped, and the mouth opened shortly after the start of the acceleration. The sei whales fluked through the lunge, using their tail strokes and not their momentum to inflate the buccal pouch (Fig. 2, right). Because of the slow swimming speeds and small maximum gape angles, the ventral grooves did not appear to expand fully (Fig. 1, photo C, and Fig. 3C), and the relatively short filtration times (Table 1; relative to Kahane-Rapport et al., 2020) further suggest that the buccal cavity was not fully inflated. Other plankton-feeding rorqual species lunge at faster speeds, open their mouth at the fastest point in their trajectory, stop fluking, and use their momentum to inflate their buccal pouch while foraging at depth (Cade et al., 2016) and near the surface (movie 1 from Segre et al., 2016; Torres et al., 2020, but kinematic data from surface lunges is limited). Although some humpback whales that forage slowly on large schools of fish continue fluking after opening their mouths (Cade et al., 2020; Simon et al., 2012), this has not been demonstrated in krill-feeding whales. By opening their mouths immediately after starting the lunge, the sei whales spent little time accelerating and timed their maximum gape to occur when they were rolled on their sides (Fig. 2, right). Although drag forces become considerable when fluking with an open mouth, they are probably mitigated by the slow speeds (Potvin et al., 2009). This specialized style of surface lunging combines kinematic elements of continuous filter feeding (fluking with the mouth open) and intermittent filter feeding (post-engulfment filtering), and may in itself represent a functionally intermediate behavior. The benefits of this type of lunge are not immediately clear: it is possible that the

slow speeds help to both conserve energy (Potvin et al., 2012) and minimize the escape response of the prey (Werth, 2012).

However, sei whales also have the ability to lunge at faster speeds, as illustrated by the sub-surface lunges performed by one of the tagged individuals (Table 1; Fig. S1). These lunges featured variable body orientations during the approach and a prominent acceleration and deceleration phase (Fig. S1), similar to the typical lunges performed by other rorqual species. It is likely that when feeding on more elusive prey (i.e. fish: Baumgartner and Fratantoni, 2008; Ishii et al., 2017), sei whales use even higher performance maneuvers and accelerations during their lunges. When one of the tagged whales was traveling, it accelerated from 2.2 to 7.3 m s^{-1} over the course of a single tail stroke (acceleration: 1.2 m s^{-2}). This illustrates that the sei whales have large, latent power reserves, but they simply may not need to draw on them while targeting less mobile prey.

Surface-feeding sei whales captured amphipods using a combination of slow, stereotyped lunges and skims (Fig. 1), which allowed them to forage at high rates compared with other large rorqual species (Friedlaender et al., 2014, 2020; Goldbogen et al., 2015). Because of their biomechanical differences, it is likely that surface lunges and skims serve different purposes. The slow nature of both the lunges and the skims suggests a relatively low energetic cost of feeding (Potvin et al., 2012), and both lunges and skims began almost immediately after the filtration from the previous feeding event ended (Fig. 1). We counted 34 feeding events that began within 5 s of the previous filtration ending (out of 86 total), and many more that likely would have started earlier if the whale had not paused to breathe or reposition itself. However, because the skims had a shorter filtration time, the whale could begin the next feeding event sooner (Fig. 1, yellow circles; Table 1). Meanwhile, the lunges allowed the whale to roll on its side, possibly to present a larger gape area to the surface compared with the skims (Fig. 2, right). We did not discern any clear patterns in the sequencing of the feeding events, but on several occasions the whale transitioned directly from a skim to a lunge. This suggests that perhaps fine-scale variations in prey patch quality cause the whales to choose one feeding strategy over the other, in the moment. Because of their faster speeds and more complex maneuvers, sub-surface lunges are likely more energetically costly (Potvin et al., 2010) than both surface-feeding behaviors but are probably important for catching prey that is not trapped at the surface.

In this study, we used several different data streams to better understand the near-surface feeding biomechanics of sei whales. This approach has limitations that are worth acknowledging. First, with our small sample size, we likely captured only a subset of the full range of sei whale feeding behaviors. Future work can help to identify whether sei whales use faster and more variable lunges when feeding on different types of prey or at depth. Although we did not find evidence of sub-surface skim feeding in our data, we cannot rule out the possibility that skims can be performed at depth. It may be that sub-surface skims have unique kinematic signatures that look different from surface-skimming behaviors, and are therefore more difficult to detect (although, we did not see any evidence of this when the video cameras were recording). It is also possible that our data did not contain any sub-surface skims, but that sei whales can perform them in different behavioral contexts. A second limitation is that we were not able to directly observe the jaw and buccal cavity during skim-feeding events. Orthogonal, aerial photos of skim-feeding events suggest there was little buccal cavity inflation, and aerial photos and videos of surface lunges suggest that the buccal cavities were not fully inflated. However, little is known about the

shape and elastic limitations of an expanded sei whale buccal cavity and how it compares to the dynamic morphology of other species. Virtually nothing is known about the angle of the jaw during skims and how that affects hydrodynamics and inflation (see Brodie and Vikingsson, 2009, for one theory). More aerial and underwater images would help to resolve many of these open questions. Finally, although we have confidence in our estimation of speed (because of the digitized aerial video), it is important to acknowledge that speed calculated from accelerometer vibrations has limitations. Often, the speed is calibrated using deeper dives and steeper descents (which these sei whales did not perform), and it is not clear whether hydrodynamic effects near the surface affect the speed measurements. Furthermore, this method is more accurate when estimating higher speeds, and there is more variation in the measurements at slower speeds (which these sei whales used for their specialized feeding behaviors). There is little doubt that the foraging speeds of these sei whales are slow (Figs 1 and 2; Fig. S1), but the nuances of the speed profiles remain to be discovered. In spite of these limitations, accelerometer vibrations currently outperform mechanical speed sensors and other methods for determining swimming speed from bio-loggers (Cade et al., 2018). This study provides a good first step towards understanding the biomechanics of sei whale feeding behaviors, which appear to be unique among baleen whales. However, further research will help to better place these behaviors in a more robust comparative framework.

Sei whales represent a functional and ecological intermediate in the transition between intermittent and continuous filter feeding. Functionally, sei whales can lunge feed like other rorqual species, skim feed like balaenids, and perform distinctive surface lunges that may represent a biomechanical intermediate between the two behaviors. Ecologically, sei whales are flexible. When feeding below the surface, they use a cadence similar to that of other rorqual species: fast, variable lunges, performed multiple times per dive. At the surface, they use a combination of skims and surface lunges to forage with a style reminiscent of balaenids: featuring slow speeds, high feeding rates and short pauses between feeding events. However, sei whales are not an evolutionary intermediate between balaenids and rorqual whales. According to recent phylogenetic analyses, sei whales have only recently diverged from Bryde's whales (∼3 million years ago; Fig. 4; Slater et al., 2017), a species that primarily forages by lunge feeding (Nemoto, 1970). It is not

clear whether Bryde's whales have the ability to skim feed, but they lack the three-dimensional baleen morphology that is thought to make this behavior effective for sei whales (Werth et al., 2018). This suggests that sei whale skim-feeding behaviors and morphology are recently derived from the ancestral lunge-feeding mode, and thus evolutionarily convergent with the continuous feeding styles of balaenids (Werth et al., 2018). The unique morphological characteristics that allow sei whales to effectively perform different types of feeding behaviors (skim feeding, slow surface lunges, fast sub-surface lunges) further suggest the rapid evolution of their functionally intermediate and ecologically flexible form. This contrasts with gray whales that have recently (<10 million years ago) evolved a distinct morphology that allows them to suction feed on seafloor-dwelling invertebrates (Marx et al., 2016), but precludes them from lunge feeding (Fig. 4). Both species evolved within the Plio-Pleistocene transition when increasingly intensive upwelling regimes allowed for the rapid diversification of mysticetes and the evolution of gigantism (Slater et al., 2017). It is possible that sei whales and gray whales rapidly evolved their specialized feeding morphology to escape the increased competition with bigger rorqual species that are highly efficient when forging at depth (Goldbogen et al., 2019). While gray whales narrowed their ecological niche, sei whales became flexible generalists with a variety of prey capturing capabilities.

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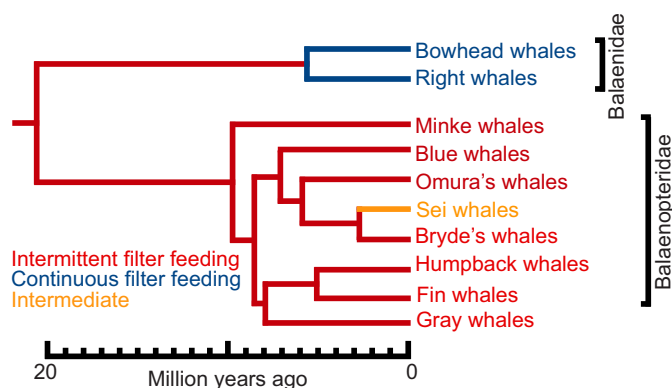

Fig. 4. Phylogenetic analysis. Morphologically resembling their lunge-feeding, rorqual relatives (Balaenopteridae), sei whales have convergently evolved the ability to skim prey near the surface of the water, like the more distantly related bowhead and right whales (Balaenidae). Sei whales represent an ecological and evolutionary intermediate in the transition between intermittent filter feeding and continuous filter feeding. Phylogeny adapted and simplified from Slater et al. (2017).

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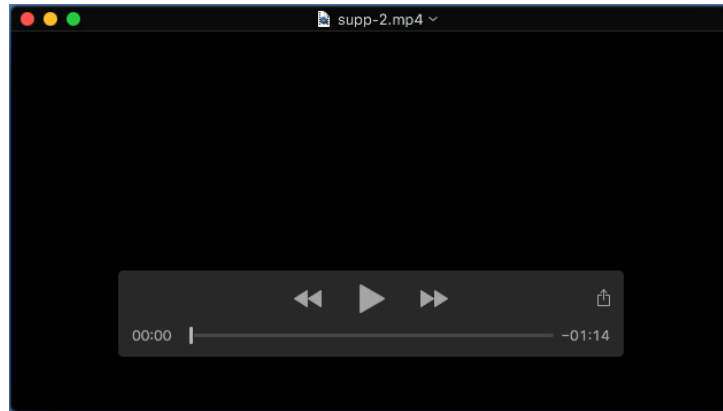
Movie 1: A sei whale performs a non-feeding surfacing, a surface lunge, and a skim-feeding event. The surface lunge and skim are the sequences shown in Figure 1.
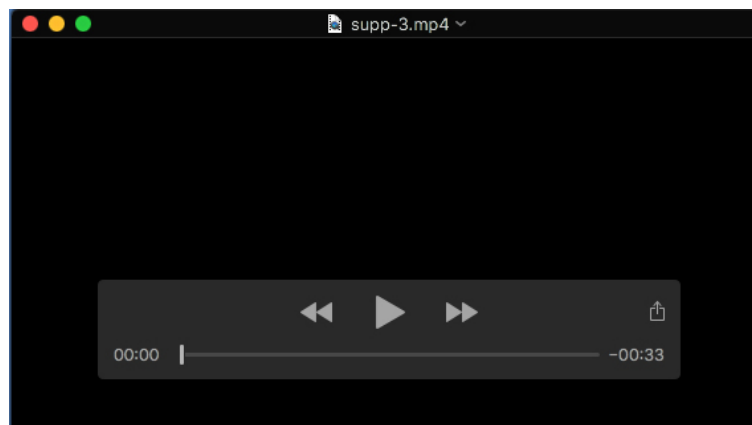
Movie 2: A sei whale performs a surface lunge. The surface lunge is the sequence shown in Figure 2.
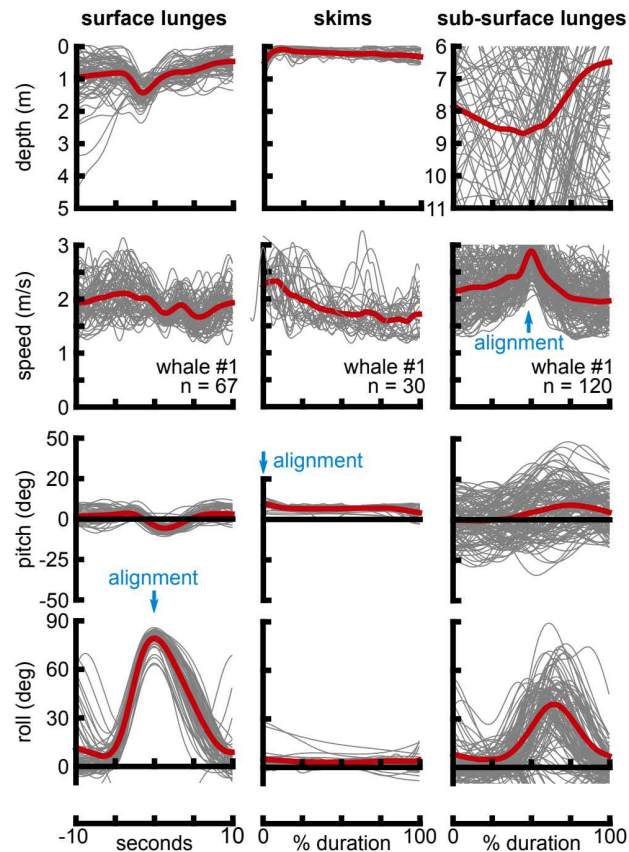
Figure S1. Sei whale surface lunges were characterized by rightward rolls, slow speeds, and little dropoff in speed during filtration. 67 surface lunges performed by a single whale (individual #1) are shown, aligned at the time of maximum roll. Sei whale surface skim-feeding events were characterized by slow speeds, extended periods at the surface, and a slightly upward pitch angle. 30 skims performed by a single whale are shown, aligned at the time when the whale first breaks the surface and scaled to a normalized duration. Sub-surface lunges are similar to lunges performed by other rorqual whales, with high speeds, a distinct acceleration and deceleration phase, and variable roll, pitch, and depth. 120 sub-surface lunges performed by a single whale are shown, aligned at the time of maximum speed.

Images from figure 1, whale #1, lunge
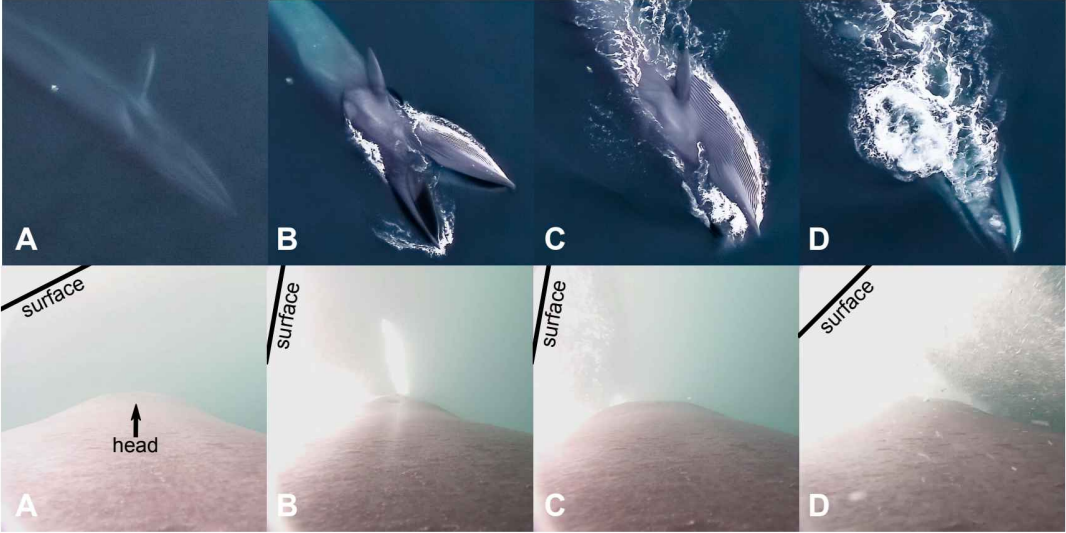
Images from figure 1, whale #1, skim
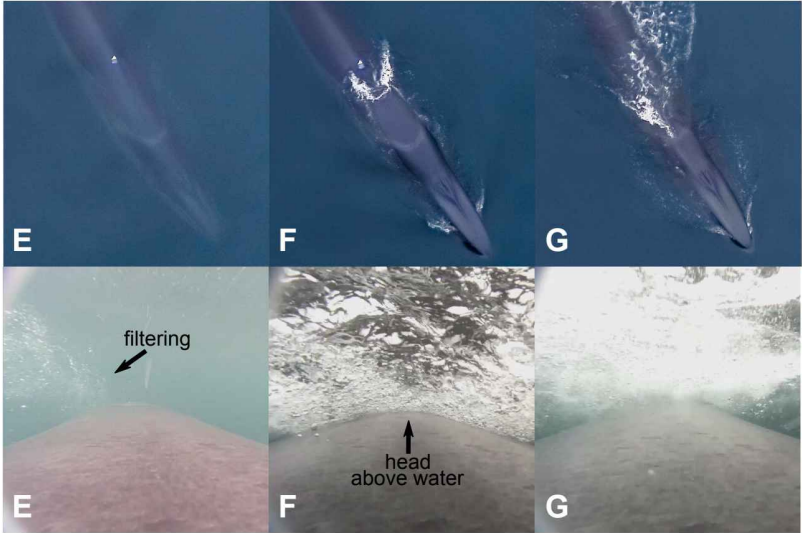
Images from figure 2, whale #2, lunge

B) maximum gape   C) mouth closes   D) mouth closed

Figure S2. Enlarged photographs from Figure 1 and Figure 2.

Table S1. Raw data used to create Table 1.

Click here to download Table S1