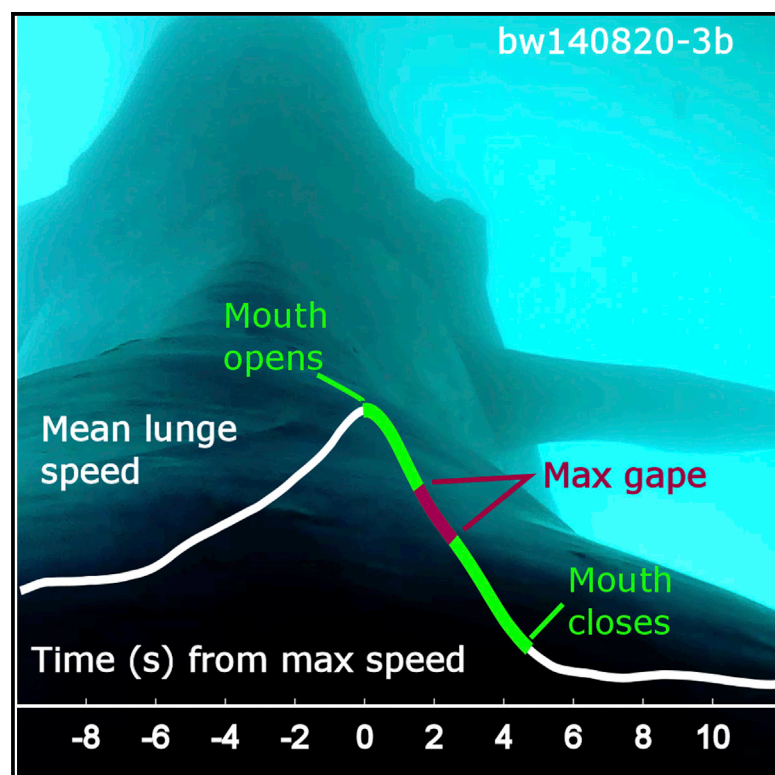# Current Biology

Kinematic Diversity in Rorqual Whale Feeding Mechanisms

Graphical Abstract

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In Brief

Rorqual lunge feeding has been assumed to be kinematically similar across species. Cade et al. use new video and accelerometry tags to show that blue whales, krill specialists, and humpback whales, foraging generalists, have similarly stereotypical lunges on krill—but humpbacks feeding on fish demonstrate kinematic diversity in lunge timing.

Highlights

- Tags with both video and 3D accelerometry were deployed on feeding rorquals

- Skull movement could be observed in concert with animal orientation and motion

- Lunging whales displayed prey-dependent inter- and intra-species kinematic diversity

- Humpback whales most likely sacrifice energy efficiency to increase foraging flexibility

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Report

Kinematic Diversity in Rorqual Whale Feeding Mechanisms

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SUMMARY

Rorqual whales exhibit an extreme lunge filter-feeding strategy characterized by acceleration to high speed and engulfment of a large volume of prey-laden water [1–4]. Although tagging studies have quantified the kinematics of lunge feeding, the timing of engulfment relative to body acceleration has been modeled conflictingly because it could never be directly measured [5–7]. The temporal coordination of these processes has a major impact on the hydrodynamics and energetics of this high-cost feeding strategy [5–9]. If engulfment and body acceleration are temporally distinct, the overall cost of this dynamic feeding event would be minimized. However, greater temporal overlap of these two phases would theoretically result in higher drag and greater energetic costs. To address this discrepancy, we used animal-borne synchronized video and 3D movement sensors to quantify the kinematics of both the skull and body during feeding events. Krill-feeding blue and humpback whales exhibited temporally distinct acceleration and engulfment phases, with humpback whales reaching maximum gape earlier than blue whales. In these whales, engulfment coincided largely with body deceleration; however, humpback whales pursuing more agile fish demonstrated highly variable coordination of skull and body kinematics in the context of complex prey-herding techniques. These data suggest that rorquals modulate the coordination of acceleration and engulfment to optimize foraging efficiency by minimizing locomotor costs and maximizing prey capture. Moreover, this newfound kinematic diversity observed among rorquals indicates that the energetic efficiency of foraging is driven both by the whale's engulfment capacity and the comparative locomotor capabilities of predator and prey.

RESULTS

Lunge feeding in rorqual whales (Balaenopteridae) is characterized by the rapid engulfment and subsequent filtration of large volumes—up to 160% of body mass [1]—of prey-laden water, but the precise mechanisms underlying this dynamic process remain poorly understood. The long-standing paradigm of lunge feeding consists of three discrete phases (Movies S1 and S2): (1) acceleration to high speed, (2) engulfment (Figures 1 and 2), and (3) filtration [5]. Lunge feeding at high speed generates dynamic pressure that is required to expand the ventral feeding pouch during engulfment [10, 11]. Quantification of the timing of the gape cycle relative to whale speed is critical for estimating the forces at play during lunge feeding and thus the energetic costs of foraging, yet to date this timing could only be assumed from indirect kinematic signatures [6–8, 12]. The kinematic signature of a rorqual lunge includes an increase in speed and overall body acceleration followed by a rapid deceleration [2, 7, 13, 14]. However, all prior studies either lacked direct observation of skull and jaw kinematics (e.g., [5–7]) or did not have kinematic sensors (e.g., [15]), and this led to conflicting hypotheses about the temporal relationship between the acceleration and engulfment phases: a peak speed mouth opening hypothesis [5, 6] and an early mouth opening hypothesis [7].

Using low-resolution (1 Hz) tag data from three rorqual species feeding on krill (Euphausiids) [2, 13, 14], Goldbogen et al. [5] and Potvin et al. [6] predicted that rorqual mouths open at maximum swim speed, followed by a discrete engulfment phase during deceleration. Hydrodynamic models of engulfment suggest that this decoupling of body acceleration and engulfment would increase the efficiency of lunge feeding with respect to prey capture but at a cost of increased drag from the acceleration of the water inside the mouth [6]. In contrast, higher-resolution (25 Hz) tag data from humpback whales feeding on an unknown prey type led Simon et al. [7] to the hypothesis that peaks in rate of acceleration (i.e., jerk) and minimum specific acceleration (MSA) during the acceleration phase implied higher than normal drag forces and thus that the mouth must open several seconds before maximum speed [7]. This hypothesis implied that rorquals continue accelerating during the mouth-opening phase, yielding a higher cost of transport during engulfment and a greater degree of forward momentum after mouth closure [7].
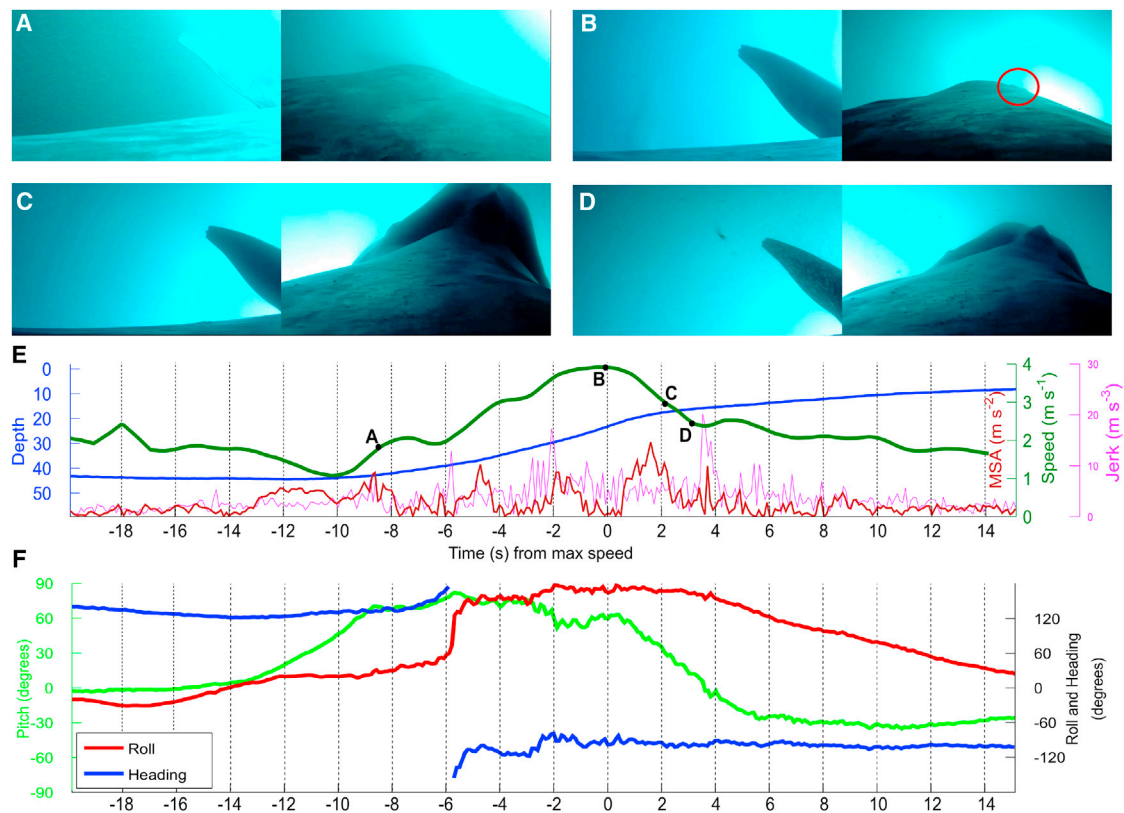
Figure 1. Visualization of a Blue Whale Feeding Event Using a CATS Tag that Integrates Dual, Forward-Facing Video Cameras with Orientation and Motion Sensors

(A) The whale is pitched upward at 70° at the start of the acceleration phase. The left flipper is visible in the left panel.

(B) At peak speed, the blow holes (homologous to the nostrils) are just visible above the back (red circle), signifying the start of upper-jaw lift.

(C) Maximum gape. At this moment, the whale is ventral side up, angled at a pitch of 32°.

(D) The upper jaw before complete mouth closure and before the animal spins to its left to return to normal position. The target prey (a krill swarm) can be seen in the left panel.

(E) Animal speed (derived from flow noise and smoothed with a 0.5 s running mean), depth, minimum specific acceleration (MSA), and jerk (calculated from 10 Hz accelerometry data). Letters correspond to the images above.

(F) Animal orientation described using the Euler angles pitch (green), roll (red), and heading (blue).

See Movie S1. This tag (bw140820-3b; Figure S1A; Table S1) was placed on the left side of the animal facing forward. Axis conventions are as in Figure S2.

To resolve this ambiguity, we developed a novel tag sensor suite including video cameras and high sample rate movement sensors (Figure S1; http://www.cats.is) that provide information on body kinematics not just at the location of tag attachment on the animal but also at points observable by the cameras, thus enabling measurements of how the engulfment phase overlaps with the acceleration phase in lunge-feeding rorquals. Data were obtained for krill-feeding blue whales (*Balaenoptera musculus*; six whales, 25 lunge-feeding events) off of California and Chile; krill-feeding humpback whales (*Megaptera novaeangliae*; four whales, 20 lunges) off of western South Africa and Monterey, CA; sand-lance-feeding humpback whales (three whales, 13 lunges) near Cape Cod, MA; and an anchovy-feeding humpback whale (one whale, 19 lunges) in Monterey Bay, CA.

Tag data and our kinematic analyses demonstrated that lunging blue whales opened their mouths 0.0 ± 1.0 s (mean ± SD) after peak speed, started closing their mouths 2.6 ± 1.3 s after peak speed, and had engulfment cycles totaling 4.9 ± 0.8 s (Table 1; Figures 1 and 3A). Krill-feeding humpback whales

(Table 1; Figure 3B) had shorter engulfment cycles (2.0 ± 0.5 s) but similar timing in relation to peak speed (opening: 0.2 ± 0.7 s after peak; start closing: 1.3 ± 0.8 s after peak). Both groups closed their mouths very close to the inflection point when deceleration began to subside (Table 1; Figure 3), suggesting that peak speed and the inflection point may be good indicators of gape cycle for krill-feeding rorquals in the absence of video data. In contrast to the stereotypy exhibited by krill-feeding whales, humpback whales feeding on fish (Table 1; Figures 2 and 3C) had more variable engulfment durations (4.8 ± 3.0 s) and relationships of the engulfment cycle to speed (opening: 1.1 ± 2.8 s after peak; start closing: 4.4 ± 4.2 s after peak). When speed could be calculated from orientation-corrected depth rate (OCDR) [7], the timing of the peaks in speed was close to that for flow noise for all measured lunges (0.5 ± 0.5 s in absolute distance).

Our analyses were consistent with previous studies (e.g., [7, 16]) indicating higher MSA and jerk signals during lunge-feeding events compared to non-feeding swimming. Prior to
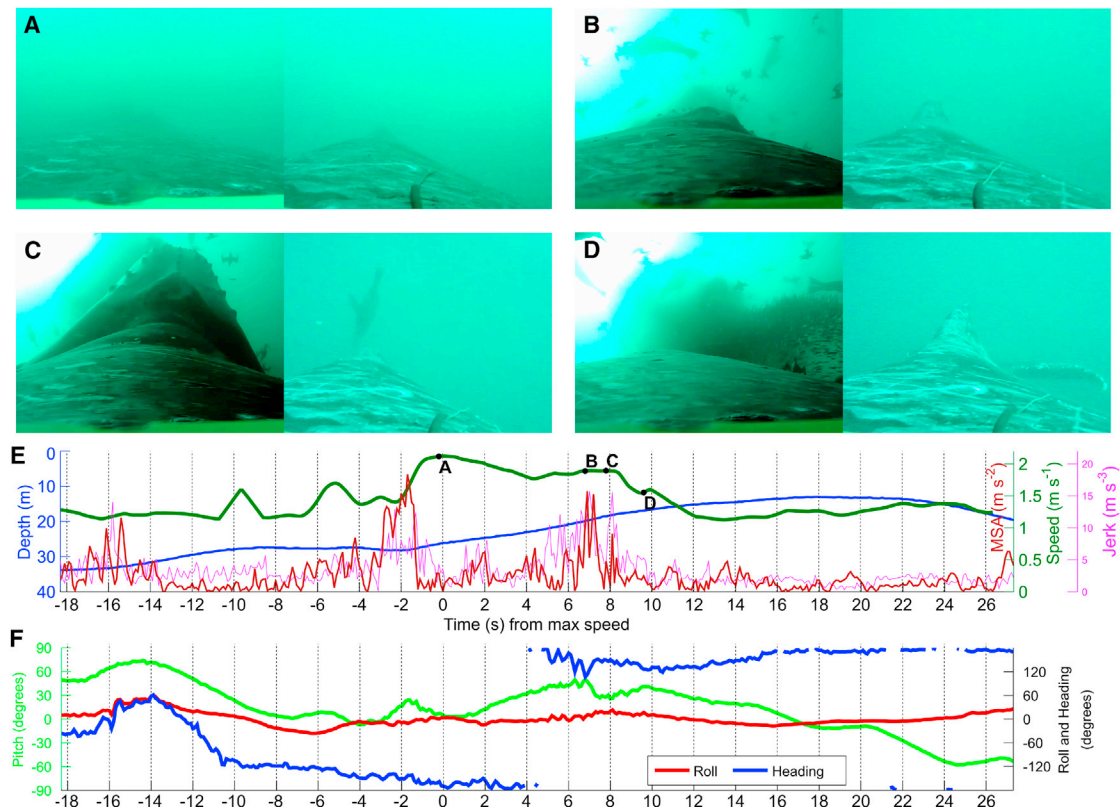
Figure 2. Visualization of a Humpback Whale Feeding on Anchovies

(A) At the peak in speed, the animal had not yet begun the lunge but was situated in a horizontal position 8 m below and to the left of a school of anchovies (*Engraulis mordax*).

(B) At a subsidiary peak, the mouth began to open with the whale pitched at 45° and moving to its left.

(C) Maximum gape directly before a steep deceleration.

(D) Evasive prey are seen attempting to avoid simultaneous predation by the tagged animal, Caliornia sea lions (*Zalophus californianus*), and diving sea birds.

(E) Animal speed (derived from flow noise and smoothed with a 0.5 s running mean), depth, MSA, and jerk (calculated from 10 Hz accelerometry data). Letters correspond to the images above.

(F) Animal orientation described using the Euler angles pitch (green), roll (red) and heading (blue).

See Movie S2. This tag (mn151012-7; Figure S1B; Table S1) was placed along the dorsal midline and had forward-facing (left) and rear-facing (right) cameras. Axis conventions are as in Figure S2.

confirmation with video, the peaks in jerk and MSA were suggested in the early mouth opening hypothesis to, respectively, be related to skull movement and indicative of working against maximum resistance from water entering the mouth [7]. However, we found that peaks in both MSA and jerk were highly variable in relation to mouth opening and averaged 1–2 s before that event (Table 1). It is thus unlikely that these peaks indicate mouth opening and closing events; instead the increased jerk and MSA signals are most likely related to fluking action and other body positioning in preparation for the lunge.

Blue whales had maximum speeds approximately 1.5 times higher than those of humpback whales (Table 1), largely in agreement with past studies [1], and had a gape cycle about 2.5 times as long as that of humpbacks feeding on krill, but the overall relationship of engulfment to maximum speed and the shape of the speed profile were similar (Figure 3) and consistent between lunges. Humpbacks feeding on fish exhibited more variable timing of engulfment relative to speed and more variable maneuvering during lunges. Although blue whale lunges

can vary with respect to approach mechanics (e.g., straight ahead, lateral, and 180° or 360° rolls) [17, 18], the pre-engulfment phase frequently involves acceleration from below the prey followed by an inversion (i.e., 180°) roll coincident with mouth opening. The blue whales in this study exhibited a flipping behavior (Movie S1) in which they approached prey with a near-vertical (rostrum-up) orientation, began engulfment, flipped ventral-side up (i.e., roll = 180°), and then rolled back to a dorsal-up orientation during filtration, and the kinematics of these maneuvers were consistent across lunges (Figure 3F). Similarly, humpback whales feeding on krill had consistent approach characteristics between lunges but did not exhibit large roll excursions (Figure 3G). In contrast, humpback whales feeding on fish had high variability in lunge approach orientation (Figures 3D–3H) and had approximately twice the cumulative heading changes on approach (95% confidence interval [CI] 1.5 to 2.5 times as much as krill-feeding humpbacks), signaling increased maneuvering in the horizontal plane (Figures 2 and 3D; Movie S2).

Table 1. Timing of Kinematic Events during Blue Whale and Humpback Whale Lunge Feeding

	Peak Speed to Mouth Open (s)	Speed Inflection to Mouth Close (s)	Mouth Open to Mouth Close (s)	Mouth Open to Maximum Gape (s)	Duration of Maximum Gape (s)	MSA Peak to Mouth Open (s)	First Jerk Peak to Mouth Open (s)	Maximum Speed (m/s)	Mean Speed (m/s) during Maximum Gape	Minimum Speed (m/s) during Filtration [a]
Blue Whales (Krill)										
Mean	0.0	0.7	4.9	1.6	1.0	2.0	1.7	3.9	2.9	1.1
SD	1.0	1.1	0.8	0.4	0.9	1.8	2.5	0.8	0.4	0.4
No.	25	24	24	25	24	25	25	25	24	25
Humpback Whales (Krill)										
Mean	0.2	−0.3	2.0	0.7	0.5	1.2	1.3	2.7	2.2	1.0
SD	0.7	0.8	0.5	0.2	0.6	0.9	0.9	0.7	0.3	0.3
No.	16	16	15	16	19	16	16	20	19	20
Humpback Whales (Fish)										
Mean	1.1	0.0	4.8	1.2	2.1	1.2	0.9	2.5	1.9	1.0
SD	2.8	3.3	3.0	0.6	2.9	2.1	2.0	0.4	0.5	0.2
No.	32	31	32	32	32	32	32	32	32	32

All times are in seconds. "No." is the number of lunges. See also Figure S3.

[a]The minimum speed attained within 20 s of mouth opening. Of these measurements, 17 out of 25 blue whale lunges, 17 out of 20 humpback whale lunges on krill, and 31 out of 32 humpback whale lunges on fish had minimum speeds at or below the minimum detectable speed.

Regardless of how much of the engulfment phase overlapped with the acceleration phase, all whales decelerated during a lunge-feeding event. The mean minimum forward speed attained within 20 s of mouth opening is reported in Table 1; however, for 65 of 77 whales this was within the lower bound of detectable speeds ($\sim$1 m s^{-1}), implying that the minimum speed could be lower than reported. Observations of feeding blue and humpback whales suggest that they maintain some momentum after engulfment, but the increase in bulk (more than doubling in size [1]) and associated increase in drag contribute to continued deceleration during the filtering phase. Thus, it appears that blue and humpback whales in this study did not completely stop, as proposed in the lunge-stop model associated with the peak speed mouth opening hypothesis [2], but did most likely slow down below the speeds proposed in the maintaining-momentum model that is associated with the early mouth opening hypothesis [7]. The momentum maintained after engulfment may be determined by the size of the engulfed water mass relative to the whale's body mass, a functional characteristic that exhibits positive allometry [1]. Blue whales have greater mass-specific engulfment capacity relative to humpback whales, so the amount of momentum transfer from the whale to the engulfed water may be relatively greater in blue whales; thus, blue whales would predictably conserve less momentum after engulfment than humpback whales [19].

DISCUSSION

Our analyses demonstrate a previously unrecognized level of prey-dependent kinematic diversity during rorqual lunge feeding. Specifically, we show that blue and humpback whales feeding on krill exhibit largely discrete engulfment and body acceleration phases, supporting the peak speed mouth opening hypothesis [5, 6]. However, some fine-scale kinematic differences were evident among krill-feeding whales. For example, the humpback whales that we observed feeding on krill off of South Africa demonstrated a small temporal overlap of body acceleration and engulfment, with mouth opening occurring 0.6 s prior (95% CI 0.4 to 0.9 s prior) to maximum speed. This 0.6 s overlap represents $\sim$25% of the engulfment phase, implying that these whales actively accelerated through the early part of engulfment. Therefore, data from these individuals also support some aspects of the early mouth opening hypothesis [7] that was first postulated from humpback whale data. Although fluctuations in prey density could drive some of the observed kinematic differences [18], all krill-feeding humpback whales opened their mouths much closer to the peak in speed than the 1.8 s temporal overlap predicted by the early mouth opening hypothesis [7].

The kinematic variability measured in fish-feeding humpback whales contrasts with the largely stereotypical profiles that characterize krill feeding (Figure 3). Although many rorqual species feed on both krill and other planktonic prey like forage fish and copepods, blue whales are unique in being mostly obligate krill feeders [20]. In contrast, humpback whales are well known for switching between krill and schooling fish as conditions vary [21]. Krill, though considered plankton, exhibit strong escape responses of up to 50 cm s^{-1} [22] that predators must overcome with fast approach speeds and rapid engulfment behaviors.
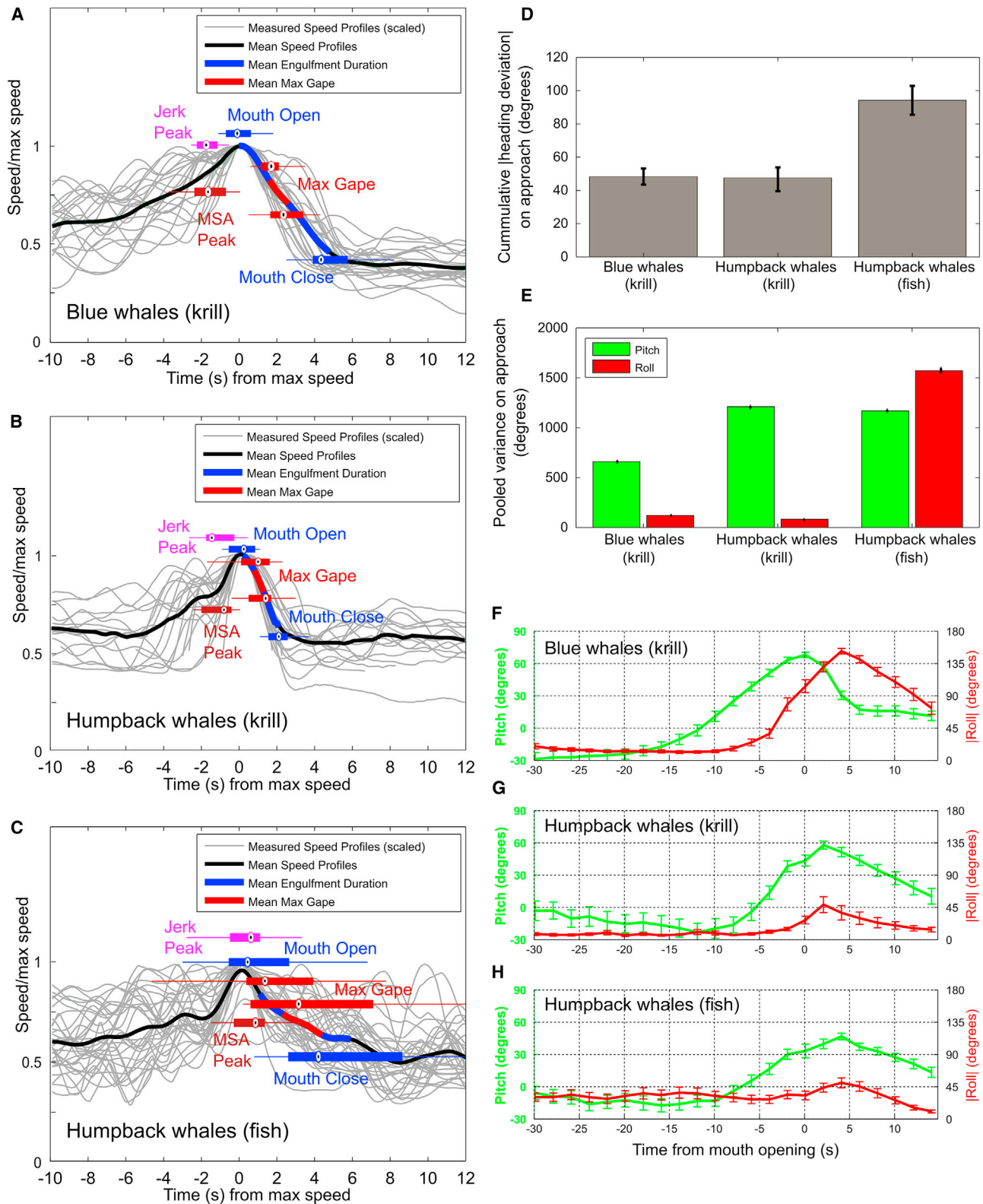
Figure 3. Observed Speed Profiles and Body Orientation during Lunges for Blue Whales Specializing on Krill and Humpback Whales Feeding on Krill or Fish

(A–C) Speed profiles. Thick lines are the mean speed values and a representation of the mean engulfment cycle for each set of lunges. The lengths of box whiskers represent the entire range of data, the central oval indicates the median value, and the edges of the box are the 25th and 75th percentiles.

(legend continued on next page)

Typical humpback ichthyoid prey, however, are even more evasive. Small fish (e.g., 10 cm in total length) have estimated maximum escape speeds ranging from 90 cm s^{-1} (*Engraulus japonicas*) to 2.5 m s^{-1} (*Sprattus sp.*) [23–25]; thus, humpback whales feeding on fish must account for the increased mobility of prey by utilizing more dynamic foraging strategies.

Although blue whales exhibit higher lunge speeds (Table 1) [1], humpback whales have relatively large flippers and flukes that enhance acceleration and maneuverability [26]. In other predators, turning capacity is inversely related to attack speed [27], and this trade-off is evident in the divergent foraging strategies between humpback and blue whales. As obligate krill feeders, blue whales have most likely adopted an optimal strategy for pursuing this specific prey type using extremely large mouths in concert with high-speed lunges to easily overcome krill escape responses [1]. Blue whales maneuver more when targeting lower-density krill patches [17, 18], presumably to access the best available patch in the local environment, yet these maneuvers still follow consistent trajectories (i.e., rolls are largely around the whale's longitudinal body axis) that suggest that the prey are not engaged in escape responses that require extensive pursuit. In contrast, our results demonstrate that humpback whales capture prey using slower lunge speeds, shorter duration gape cycles, and more variable attack angles (Table 1; Figure 3). To fully inflate the buccal cavity with short, low-speed lunges that produce lower stress on the buccal cavity (Table S1), humpback whales exhibit an engulfment apparatus that allows for full inflation with strains that are 75% of those in blue whale buccal cavities [10]. However, this morphology may then limit the ability of humpback whales to lunge at faster speeds when pursuing less agile prey.

An enhanced foraging efficiency has been predicted for blue whales due to their extremely high engulfment capacity [1], and the complex trade-off between maneuverability, lunge speed, and engulfment capacity noted in this study is further indication that humpback whales are less efficient when feeding on krill relative to blue whales. The flexibility of humpback whales as generalist predators to feed on diverse prey, however, may bolster foraging efficiency over broad spatial and temporal scales relative to blue whales.

The ability of different rorqual species to modulate the fine-scale kinematics of the skull and body suggests that high-cost foraging strategies (i.e., increased maneuvering and temporally coupled acceleration-engulfment phases) can be used to capture more agile but possibly higher-quality prey. Alternatively, low-cost foraging methods (i.e., decreased maneuvering and temporally decoupled acceleration-engulfment phases) could be employed by both study species when targeting less agile prey like krill. These trade-offs imply that

the prey density thresholds necessary to support these large predators [28] are not solely dependent on differences in body size and energetic requirements, but are also determined in part by the predator's foraging capability and the prey's escape performance. This observation is also supported by fundamental differences in behavior and ecological niche; although blue whales and humpback whales in pursuit of krill are generally solitary feeders, humpback whales feeding on fish may coordinate in groups of two to 15 to employ complex prey-aggregating strategies prior to lunges (e.g., blowing curtains of bubbles [3, 29]). The three western North Atlantic humpback whales in this study foraged on sand lance (~10 cm) that migrated into the water column [30] by producing bubble nets in groups of between one and five animals, whereas whales in Alaska feeding on larger and more mobile herring (~20–30 cm) sometimes feed in groups of up to 15 animals (e.g., [31]). These group behaviors, combined with the ability to modulate the coordination of body acceleration and engulfment timing, allow humpbacks to efficiently exploit different prey types and adapt to dynamic prey conditions in fluctuating climatic regimes [21]. Fin whales (*Balaenoptera physalus*), the second-largest cetacean, exhibit similar morphology to blue whales yet are not limited to krill feeding. Although fin whales are not known to implement complex prey-herding techniques, they have uniquely asymmetrical jaw pigmentation that may aid in corralling mobile prey [32]. Molecular evidence also suggests that fin whales may be more closely related to humpback whales than to blue whales [33, 34]. Fin whales thus represent a key target species for future work in order to refine our understanding of how biomechanical and behavioral processes influence the energetic consequences of predator-prey interactions (Figure S3).

In other aquatic vertebrates that exhibit an integration between locomotion and feeding, behavioral plasticity often reflects broad-scale functional and evolutionary responses to ecological dynamics that force optimization of maneuverability, accuracy, and prey capture speed [35]. The integration of video and movement sensors enables the quantification of locomotion in wild animals and allows for greater estimation of maneuverability parameters and energetic costs. In future work, data from these devices and advanced hydromechanical models should enable more accurate measurements of rorqual lunge-feeding performance and increase our understanding of the ecological role of rorquals as globally distributed apex predators. Rorquals include the largest animals ever and demonstrate both generalist and specialist foraging techniques; continued examination of cetacean predator-prey interactions should shed light on the role of prey specialization in driving predator evolution and foraging success.

(D) Cumulative absolute value of heading changes from 30 to 10 s before mouth opening.

(E) Pooled variance of approach orientation from 30 to 10 s before mouth opening. Error bars indicate the SE of that variation over time as the animal approaches the lunge.

(F–H) Mean pitch and absolute value of roll during lunging by species and prey type.

Error bars in (D) and (F)–(H) indicate the SE. Observe the high degree of stereotypy in the krill-feeding whales, with an acceleration phase always followed by rapid deceleration. Fish-feeding humpbacks show high diversity in feeding strategies, with large data ranges indicating diverse engulfment durations and timings in relation to speed. Although all three types have high orientation changes around the time of mouth opening, humpback whales feeding on fish are unique in having large changes in yaw during approach. See also Figure S3 and Table S1.

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