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# Functional Ecology

MISS JULIE MARIE VAN DER HOOP (Orcid ID : 0000-0003-2327-9000)

DR SUSAN E. PARKS (Orcid ID : 0000-0001-6663-627X)

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## Foraging rates of ram-filtering North Atlantic right whales

van der Hoop, J.M.<sup>1</sup>; Nousek-McGregor, A.E.<sup>2</sup>; Nowacek, D.P.<sup>3</sup>; Parks, S.E.<sup>4</sup>; Tyack P.<sup>5</sup>; Madsen, P.T.<sup>1,6</sup>

<sup>1</sup> *Department of Bioscience, Aarhus University, 8000 Aarhus C, Denmark (jvanderhoop@bios.au.dk)*

<sup>2</sup> *School of Life Sciences, University of Glasgow, Glasgow, UK*

<sup>3</sup> *Nicholas School of the Environment & Pratt School of Engineering, Duke University, Beaufort NC 28156 USA*

<sup>4</sup> *Biology Department, Syracuse University, Syracuse NY 13244 USA*

<sup>5</sup> *Sea Mammal Research Unit, Scottish Oceans Institute, University of St. Andrews, St. Andrews, Fife, UK*

<sup>6</sup> *Aarhus Institute of Advanced Studies, Aarhus University, 8000 Aarhus C, Denmark*

### Abstract

1. North Atlantic right whales spend their summer months foraging primarily in American and Canadian Atlantic waters on high-energy-density prey. Here they rapidly accumulate and store energy obtained within a few months to support future migrations and reproduction while fasting. High drag from their ram-filter foraging strategy places a limit on what prey densities will be energetically efficient to target.
2. Our understanding of the volume of prey-laden water filtered by right whales during a dive or foraging bout, and what information they use to decide to forage or not, has been limited

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by the difficulties of measuring when they feed at depth, how fast they swim during continuous ram filtration, and how often they might swallow accumulated prey.

3. We used 10 DTAG deployments from right whales in the Bay of Fundy, Canada, to quantify swimming speeds and estimate the volume of prey-laden water filtered per dive. We used the tag's inertial sensors to evaluate the timing of frequent biomechanical changes that indicate the truncation of continuous filtration, and whether the number or timing of these fluking bouts relate to longer feeding dives or other foraging decisions.
4. During foraging dives, right whales descended at  $1.4 (\pm 0.2)$  m/s and slowed to swim at  $1.1 (\pm 0.3)$  m/s while filtering. We found consistent pauses in the fluking behaviour of foraging right whales, every  $56 (\pm 22 \text{ SD})$  seconds. Whales filtered on average  $78 (\pm 30)$  m<sup>3</sup> of water per fluking bout, and on average filtered  $673 (\pm 201)$  m<sup>3</sup> per dive.
5. Right whales filter large volumes of water at low speeds with a high duty cycle, but require sufficiently high prey energy densities to compensate for a high-drag foraging strategy. Closely related bowhead whales have a larger gape but swim more slowly, filtering greater volumes with lower drag. Our findings highlight that these endangered balaenids acquire their energy in a relatively short period of intense foraging; even moderate changes in their feeding behaviour or their prey energy density are likely to negatively impact their yearly energy budgets and therefore reduce fitness substantially.

#### Second-Language Abstract

1. Les baleines noires de l'Atlantique du Nord passent les mois d'été à se nourrir principalement de proies à haute densité énergétique dans les eaux américaines et canadiennes de l'Atlantique. Dans ces régions, elles accumulent et emmagasinent rapidement l'énergie obtenue en quelques mois afin de supporter les migrations futures et la reproduction alors qu'elles jeûnent. La forte traînée découlant de leur stratégie de recherche de nourriture utilisant une filtration continue impose une limite aux densités de proies qu'il leur sera énergétiquement efficace de cibler.
2. Notre compréhension du volume d'eau chargée de proies filtrées par les baleines noires lors d'une plongée ou d'un épisode de recherche de nourriture, et des informations qu'ils utilisent pour décider de se nourrir ou non, a été limitée par les difficultés de mesurer le moment où elles se nourrissent en profondeur, la vitesse à laquelle elles nagent lors de la filtration en continu, et la fréquence à laquelle elles peuvent avaler les proies accumulées.
3. Nous avons utilisé 10 déploiements de DTAG sur des baleines noires dans la baie de Fundy, au Canada, pour quantifier la vitesse de nage et estimer le volume d'eau rempli de proies qui est filtré par plongée. Nous avons utilisé les senseurs inertiels des balises pour évaluer le moment des fréquents changements biomécaniques indiquant une interruption de la filtration en continu, et pour déterminer si le nombre ou le moment de ces efforts de propulsion sont liés à des plongées plus longues ou à d'autres décisions alimentaires.
4. Pendant les plongées de quête alimentaire, les baleines noires sont descendues à  $1.4 (\pm 0.2)$  m/s et ont ralenti pour nager à  $1.1 (\pm 0.3)$  m/s en filtrant. Nous avons trouvé des pauses régulières à chaque 56 secondes ( $\pm 22 \text{ SD}$ ) dans le comportement de propulsion des baleines

en quête de nourriture. Les baleines filtraient en moyenne  $78 (\pm 30) \text{ m}^3$  d'eau par séance de propulsion, et en moyenne  $673 (\pm 201) \text{ m}^3$  par plongée.

5. Les baleines noires filtrent de grands volumes d'eau à basse vitesse de façon hautement récurrente, mais requièrent des proies dont la densité énergétique est suffisamment élevée pour compenser une stratégie d'alimentation à forte traînée. De proches voisins comme les baleines boréales ont une gueule plus grande mais nagent plus lentement, ce qui leur permet de filtrer de plus grands volumes avec moins de traînée. Nos résultats soulignent que ces balaenidés en voie de disparition acquièrent leur énergie sur une période relativement courte et intense de recherche de nourriture; même des changements modérés dans leur comportement alimentaire ou la densité énergétique de leurs proies sont susceptibles d'avoir un impact négatif sur leur budget énergétique annuel et donc de réduire considérablement leur aptitude à survivre et se reproduire.

**Keywords:** biomechanics, drag, filter-feeding, foraging, ram filtration, right whale

## Introduction

Endangered North Atlantic right whales (*Eubalaena glacialis*, hereafter right whales) are capital breeders that spend their summer months foraging on planktonic prey, primarily lipid-rich copepods (including *Calanus* spp.) in American and Canadian Atlantic waters. Here, they obtain food with high energy density (Michaud & Taggart 2007; Davies *et al.* 2015), which allows rapid accumulation of energy over a short period of time. The energy acquired during a foraging season facilitates the growth of dependent calves, the energetic recovery of lactating females (Miller *et al.* 2011; Miller *et al.* 2012; Christiansen *et al.* 2018), and the storage of energy for future demands. Accumulated lipid stores are required to sustain individuals during prolonged fasting migrations, are critical for successful calving and nurture (Christiansen *et al.* 2018), and can buffer against effects from human stressors, including unanticipated energetically costly life-history events such as entanglement (van der Hoop, Corkeron & Moore 2016).

The abundance and distribution of prey in right whale foraging habitats is known to vary year-to-year and in multi-year regime shifts (Patrician & Kenney 2010; Greene *et al.* 2013). Prey availability has been linked to changes in population health (Rolland *et al.* 2016), reproduction (Hlista *et al.* 2009; Miller *et al.* 2011; Meyer-Gutbrod & Greene 2014), and distribution (Davies *et al.* 2015), and recent observations suggest that declines in the occurrence of whales in the Bay of Fundy since 2010 have coincided with changes in food supply (Davies *et al.* In Review). Quantification of the rates and dynamics of food acquisition in this endangered, capital breeding species is therefore

critical to evaluate the energetic consequences of changing habitats and human stressors (Harcourt *et al.* 2019)

Right whales target prey patches above  $10^3$  copepods/m<sup>3</sup> (Murison & Gaskin 1989) and up to  $10^5$  copepods/m<sup>3</sup> (Mayo & Marx 1990; Baumgartner & Mate 2003; Baumgartner *et al.* 2017). In the Grand Manan Basin in the Bay of Fundy, a right whale Critical Habitat and summer foraging area (Brown *et al.* 2009), individual diving behaviour is strongly correlated with the depth of maximum *Calanus* abundance between 100 and 150 m (Baumgartner & Mate 2003; Baumgartner *et al.* 2017). There, 4 - 8 km patches of copepods with energy densities above 15 J/m<sup>3</sup> develop; within the large patch, concentration and energy density can vary on scales of 500 m (Michaud & Taggart 2011). To target these high densities of small prey, right whales ram filter feed as they propel themselves forward with their mouths agape (Watkins & Schevill 1976; Werth 2001; Lambertsen *et al.* 2005; Goldbogen *et al.* 2016; Potvin & Werth 2017). Through cross-flow filtration, water moves parallel along the inner surface of the baleen plates, rather than perpendicular; this concentrates small (1-3 mm) copepods while slowing the overall flow of prey-laden water through the mouth, to then be swallowed (Potvin & Werth 2017).

Right whales show morphological adaptations to their high-drag foraging mode, with fused vertebrae to maintain rigidity when swimming with an open mouth (Sanderson & Wassersug 1993). Similarly, one would expect biomechanical adaptations, such as the low-speed, continuous swimming adopted by other ram-filter feeders (Sims 2000b; Simon *et al.* 2009). Simon *et al.* (2009) noted consistent, brief pauses in the swimming behaviour of bowhead whales (*Balaena mysticetus*), and proposed these pauses likely indicate the truncation of a continuous filtration event and the processing (swallowing) of accumulated prey. It would therefore be expected that with their shared foraging strategy, right whales would show similar biomechanical patterns that may relate to the rate of prey acquisition.

However, we still know very little about how a gigantic filter feeder with one of the highest predator-prey size ratios survives on a very specific resource that is constrained in both space and time. This lack of understanding primarily stems from the difficulties of measuring when right whales feed at depth, how fast they move during continuous ram filtration and how often they might swallow accumulated prey. Subsurface behaviour of right whales is difficult to observe, but the analysis of high-resolution acoustic bio-logging tag data has provided insights on the fine-scale movement and behaviour (Nowacek *et al.* 2001; van der Hoop *et al.* 2017), body condition (Nousek-McGregor *et al.* 2013), acoustic ecology (Parks *et al.* 2011) and foraging of right whales (Parks *et al.* 2012).

Here, we harness the rich potential of multisensor biologging DTAGs to quantify swimming speeds and test hypotheses related to the detailed foraging behaviour and biomechanics in right whales. Specifically, we use 10 DTAG deployments from right whales feeding in the Bay of Fundy, Canada, to address the following questions: 1) How fast do right whales filter? Optimal diving behaviour would maximize the time spent foraging on high-energy-density prey, while staying within oxygen requirements (Thompson & Fedak 2001). This can be accomplished by minimizing the proportion of time spent traveling to and from the resource at depth and also recovering at the surface, or by reducing oxygen consumption at depth. To reduce the energetic demands of a high-drag feeding strategy (and therefore increasing time in the prey layer), we hypothesized that right whales would adopt a slow filtering speed, similar to bowhead whales. However, given their relatively small mouth apertures compared to bowhead whales, do right whales swim and therefore filter water faster than bowheads? We investigate how the factors of gape, speed, and foraging time affect the volumes of water filtered across different species and groups of ram filter feeders.

We expected biomechanical adaptations to a high-drag foraging strategy: 2) Do right whales show the same characteristic gait patterns as other ram filter feeders during foraging dives? 3) If so, are pauses in fluking consistent in their timing (i.e., a biomechanical pattern; intrinsic) or are they variable in duration and filtered volume (i.e., related to prey processing/density/patch structure; extrinsic)? If biomechanically driven, we would expect low variation in bout duration. If extrinsically driven, we would expect fluking bouts to be variable in duration and filtered volume. Further, 4) are these diving behaviours and foraging biomechanics linked? We hypothesized that if fluking bout duration is inversely related to prey density, and if right whales maximize their diving behaviour to forage within high-quality patches, dives with shorter bouts would be longer (i.e., if pauses are linked to prey processing, and if that processing is linked to accumulated prey mass, then shorter fluking bouts would reflect more dense prey, and longer or more tortuous dives would maximize time spent in a high-quality prey patch).

## Methods

We used archival digital acoustic recording tags (DTAGs) to record the acoustic environment and locomotor behaviour of right whales in the Bay of Fundy, Canada, in the late-summer foraging season, July and August 2001, 2002, and 2005 (Table 1; Nowacek *et al.* 2001; Nowacek, Johnson & Tyack 2004; Parks *et al.* 2011). The tags recorded sound at 32 kHz (2001 and 2002) and 96 kHz (2005). The DTAG includes a pressure sensor and 3-axis accelerometers and magnetometers; sensor

data were recorded at 23.5 Hz (2001, 2002) and 50 Hz (2005) and were decimated to ~5 Hz for analysis. We used a combination of existing bio-logging tag analysis tools (animaltags.org) and additional software, custom written in MATLAB 2015b (Mathworks, Natick, MA, U.S.A.) for all analyses.

DTAGs were initially deployed on right whales in the Bay of Fundy to test for whales' responses to sounds, including vessels and alerting stimuli, following a playback protocol (Nowacek, Johnson & Tyack 2004). We made use of this existing tag library and selected deployments where no playbacks occurred (tags 01\_214a, 01\_221a, 02\_233a, 05\_219a; Table 1). Additionally, we analyzed data from deployments where >2 h of data were available 2h after the end of the final sound exposure to the animal (Table 1). For one whale, we used the 2h preceding the playback (02\_221d). We chose a 2h wait from the end of the last playback to be cautious, though exposed whales were reported to return to normal activity within minutes (Nowacek, Johnson & Tyack 2004). For transparency, we show the full depth record of all deployments and the temporal extent of the playbacks in Fig. 3 and S1, and mark the timeframe of our analysis for each deployment.

**Table 1. Information on tag deployments, analysed tag data, and tagged whales.** Total duration refers to the total duration of recorded data, versus the analyzed data that were selected 2h following the end of the last acoustic playback to the animal. Acoustic playbacks were either None, or were Alarm (A), high-frequency sounds (H), or silence (S), as described in Nowacek, Johnson and Tyack (2004). Additional aspects and portions of the dataset are described in (Table 1; Nowacek *et al.* 2001; Nowacek, Johnson & Tyack 2004; Parks *et al.* 2011). The number of foraging and non-foraging dives (to > 50 m) reflect only those in the analyzed time periods. EgNO refers to the individual identifiers in the New England Aquarium North Atlantic right whale catalog. Length ( $\pm 95\%$  prediction interval) was estimated from age following Moore *et al.* (2004) or measured by aerial photogrammetry (M; W. Perryman Pers Comm), and gape area estimates ( $\pm 95\%$  prediction interval) are described in the manuscript text.

| Deployment ID | EgNO | Acoustic Playback | Total Duration (h:m) | Analyzed Duration (h:m) | N Foraging dives | N Non-foraging dives | Sex | Age | Length (m) | Estimated gape area (m <sup>2</sup> ) |
|---------------|------|-------------------|----------------------|-------------------------|------------------|----------------------|-----|-----|------------|---------------------------------------|
| 01_214a       | 2790 | None              | 2:26:00              | 2:26:00                 | 6                | 0                    | F   | >4  | 11.9 (M)   | 1.3±0.1                               |
| 01_221a       | 2830 | None              | 1:43:03              | 1:43:03                 | 8                | 0                    | M   | >3  | 12.1 (M)   | 1.4±0.1                               |
| 02_233a       | 1409 | None              | 1:48:00              | 1:18:54                 | 5                | 0                    | M   | 18  | 12.5 (M)   | 1.5±0.1                               |
| 05_219a       | 3108 | None              | 11:32:46             | 11:32:46                | 39               | 1                    | F   | 4   | 12.0±0.2   | 1.3±0.1                               |
| 02_221d       | 2350 | A                 | 7:54:00              | 2:14:21                 | 7                | 1                    | M   | >11 | 13.4±0.2   | 1.8±0.2                               |
| 05_210b       | 3323 | A, H, S           | 10:48:00             | 8:31:51                 | 8                | 4                    | M   | 2   | 11.1±0.3   | 1.0±0.1                               |
| 05_215a       | 2413 | A, H, S           | 13:57:11             | 11:34:41                | 22               | 2                    | F   | 11  | 12.5 (M)   | 1.5±0.1                               |
| 05_224a       | 3208 | A, H, S           | 8:37:00              | 5:35:38                 | 12               | 0                    | M   | 3   | 11.6±0.3   | 1.2±0.1                               |
| 05_226b       | 3360 | H                 | 9:00:00              | 7:57:22                 | 18               | 0                    | F   | >3  | 11.6±0.3   | 1.2±0.1                               |
| 05_230a       | 3142 | A, H, S           | 6:20:26              | 4:09:34                 | 7                | 0                    | F   | 4   | 12.0±0.2   | 1.3±0.1                               |

Balaenid whales show characteristic U-shaped foraging dives and V-shaped non-foraging dives (Nowacek *et al.* 2001; Baumgartner & Mate 2003; Simon *et al.* 2009). We distinguished between U- and V-shaped dives based on bottom phase duration: the bottom phase of dives began the first time the pitch angle became positive after the whale left the surface, and ended when the pitch was last negative. U-shaped foraging dives had a clear bottom phase with only slightly variable depth, whereas V-shaped dives had bottom phases <5 s (Fig. 1). We defined dives as departures from the surface >50 m as has been the convention for characterizing diving behaviour of right



whales in deep-water foraging habitats (Nowacek et al. 2001; Baumgartner & Mate 2003). There were no instances of shallow feeding excluded from the analysis; shallow feeding was not expected or observed as most *Calanus* were in diapause and concentrated at depth (Baumgartner et al. 2003, 2017; Michaud & Taggart 2007). We checked the sensitivity of the dive depth threshold based on the breakpoint in the cumulative distribution function of all dive depths >5 m. Setting the depth threshold at 50 m rather than 10 m did not lead to a difference in the number of estimated foraging or non-foraging dives: the shallowest foraging dive was 100 m, no matter the threshold used. Incomplete dive cycles due to tag release were not included in the analysis.

### *Speed estimation*

For applications where animal speed is used to test ecological and physiological hypotheses, many biologging tags have introduced external sensors to measure passing flow. Many have calibrated measured speed with the rotation rate of external impellers (Burgess et al. 1998; Blackwell et al. 1999; Watanabe et al. 2012) and micro-turbines (Gabaldon et al. Submitted), as well as the amplitude of vibrations as measured by the tag's accelerometers (Cade et al. 2018). Absolute speed estimates are sensitive to stalling at high and low speeds, tag shape and placement on the body, orientation with respect to the flow, and calibration technique, as well as to the estimation errors in the analytical techniques (e.g. reviewed in Cade et al. 2018). Another method is to use the relationship between the amplitude of low-frequency (50-500 Hz) flow noise recorded on the tag's hydrophones, which is approximately cubic with speed (Finger, Abbagnaro & Bauer 1979). This method has proven useful in estimating speed by calibrating measured flow noise *in situ* to the vertical speed of a tagged animal when it is oriented at sufficiently high pitch angles (Sato et al. 2003; Miller et al. 2004; Goldbogen et al. 2006; Simon et al. 2009; von Benda-Beckmann et al. 2016).

We estimated the vertical swimming speed as the change in depth divided by the sine of the pitch angle, when the absolute pitch angle exceeded 30 degrees to ensure reliable speed estimation (*sensu* Simon, Johnson & Madsen 2012). To estimate swimming speed for times when the pitch angle was low (e.g. the bottom phase of foraging dives), we used the low-frequency flow noise as recorded on each tag as a proxy for speed (following e.g., Burgess et al. 1998; Goldbogen et al. 2008; Simon et al. 2009). We computed flow noise as the noise power centered at 500 Hz, band-pass filtered with a 2-pole Butterworth filter, and subsequently decimated a resolution of 25 Hz (Simon et al. 2009). For each tag and all dives, we then computed the mean noise power in 5 s bins and the mean vertical speed in the same 5 s bins. We ignored the first and last 5 seconds of each dive as air

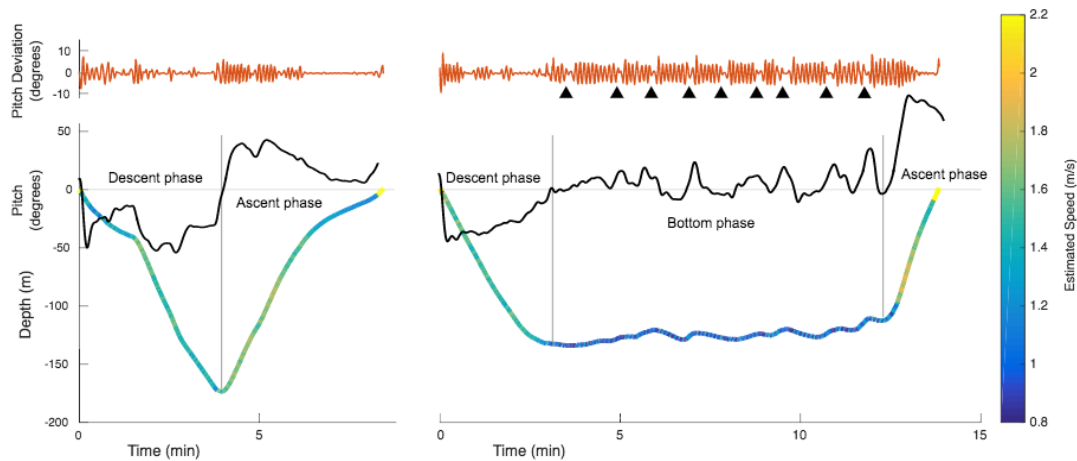
bubbles could often be heard escaping the plastic housing of the tag at these times. We obtained a flow-noise calibration by fitting a second-order polynomial to the relationship between the  $\log_{10}(\text{noise power})$  and vertical speed (as in Goldbogen *et al.* 2006; Goldbogen *et al.* 2008) for each deployment, and applied this relationship to estimate speeds from flow noise when the pitch angle was low.

### *Inertial sensor analysis*

We derived pitch, roll, and heading from the accelerometer and magnetometer signals after correcting for the orientation of the tags on the whales by rotating each three-element vector (Johnson & Tyack 2003; Johnson 2015). We calculated the pitch deviation as the difference between the instantaneous and mean body posture orientation (following e.g., Simon, Johnson & Madsen 2012; van der Hoop *et al.* 2017). This cyclic pattern in pitch deviation is reflective of fluking behaviour as swimming motion is along the pitch axis (Fig. 1). We detected pauses in fluking behaviour by detecting instances where the Hilbert-transformed pitch deviation signal was lower than its 10% value for that deployment  $>2$  s. This 10% cutoff is similar to the  $<0.04$  radian Hilbert transform threshold previously used for glide detection (Woodward 2006; Nousek-McGregor *et al.* 2013; van der Hoop *et al.* 2017) but allows for differences in tag placement between deployments which can lead to different measured pitch values. The 2-s detection threshold was set specifically to distinguish between pauses in fluking behaviour and prolonged gliding behaviours previously described in right whales (Nowacek *et al.* 2001; Nousek-McGregor 2010; Nousek-McGregor *et al.* 2013). Detected pauses were checked for each dive and manually confirmed. We detected pauses only during the bottom phase of U-shaped dives and only when body pitch was  $<30$  degrees, i.e., when the whale was not orienting upwards or downwards or changing depth (Fig. 1).

We computed the duration of each bout of active fluking between consecutive pauses. We expected that if short bouts (i.e., frequent pauses) indicated higher prey densities, then longer U-shaped foraging dives would be associated with shorter fluking bouts, to maximize the time at depth in a good prey patch; to test this hypothesis we used a linear model for the effect of foraging bout duration on dive duration. We calculated the instantaneous fluke stroke rate (Hz) over the deployment as the time between successive peaks in the pitch deviation signal. We calculated the mean instantaneous fluke stroke rate over (1) the descent, bottom, and ascent portions of each dive; and (2) each fluking bout.

We constructed dead-reckoned pseudo-tracks of each whale within each dive from the accelerometer, magnetometer and depth sensors, and the estimated speed within each dive. We used the derived northings and eastings (m) to calculate the tortuosity of the whales' paths in the horizontal plane at 10-s intervals within each dive. The tortuosity metric here was computed as 1 minus the estimated distance covered/the stretched-out track length over the time interval; the index therefore ranges from 0 for straight-line movement to 1 for extreme circular movement (Wilson *et al.* 2007).



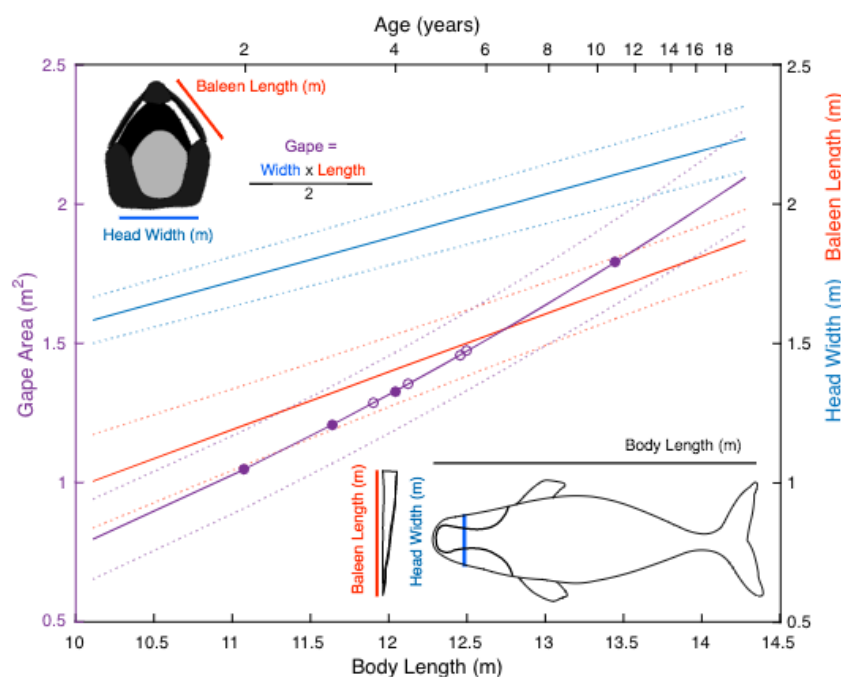
**Figure 1. Example V-shaped non-foraging (left) and U-shaped foraging (right) dive profiles of North Atlantic right whales.** Diving depth is coloured by estimated speed (m/s), overlaid with body pitch (degrees; black). Pitch deviation (degrees, orange) is plotted above each dive, with triangles indicating the start of pauses between fluking bouts detected in the foraging dive. Dive phases of descent, bottom and ascent, as determined from the pitch record, are also noted.

#### Filtered volume estimation

We obtained the ID number and age at tagging from the North Atlantic Right Whale Consortium Catalog (2006). Length measurements from aerial photogrammetry were available for 4 individuals (W. Perryman Pers. Comm.; Table 1, Fig. 2) and for all other individuals, we estimated body length from the length-at-age curve in Moore *et al.* (2004). Only minimum age was available from the catalog for two individuals that were not measured (02\_221d, Eg 2350; 05\_226b, Eg 3360), so we used these available ages to obtain conservative length estimates for these individuals. To estimate gape, we fit a linear model to aerial photogrammetry measurements of North Atlantic and Southern right whale (*E. australis*) calves and adults ( $n = 56$ ) from Miller (2005) and Miller *et al.* (2012) to estimate the mouth width (width at 10% of the body length; m) from total body length (m). We estimated the length of the longest baleen plate (m) for each individual from body length (m) based on values reported for North Pacific (*E. japonica*,  $n = 21$ ) and Southern right whales ( $n = 14$ ; Fig. S2;

Omura *et al.* 1969; Best & Schell 1996). We were unable to find similar measurements for North Atlantic right whales in the literature or in the North Atlantic Right Whale Consortium Necropsy Database. Following previous work (Watkins & Schevill 1976; Kenney *et al.* 1986), we estimated the gape area as the (mouth width x longest baleen plate length)/2 (Figs. 2, S2), and propagated errors from the age-length, length-width and length-baleen length estimates. The volumetric filtration rate was estimated by integrating the estimated swimming speed (m/s) and the estimated gape of each tagged whale (m<sup>2</sup>) over bout durations and dive durations (*sensu* Simon *et al.*, 2009).

We used a linear model to assess the effect of estimated swimming speed, gape area, and bottom time on the total volume filtered per dive. We used linear models to test whether the proportion of time spent foraging per dive differed with dive depth, with the expectation that if dive duration was aerobically limited, then deeper dives would have significantly shorter bottom times due to transit to and from the foraging depth. We computed these statistics for foraging dives only.

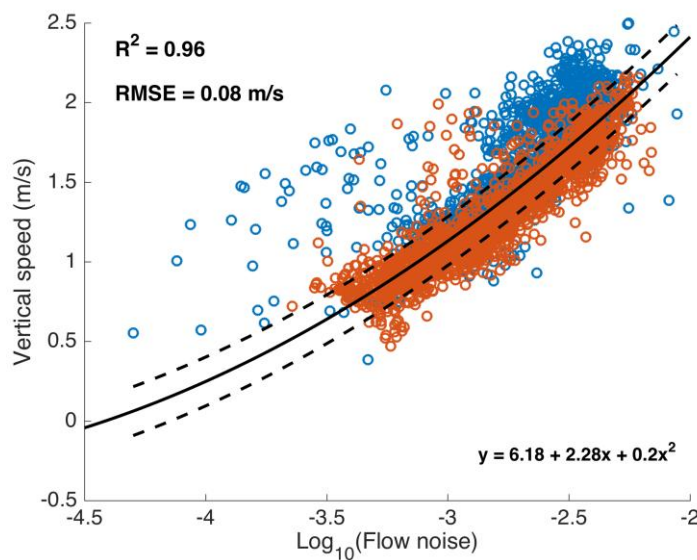


**Figure 2.** Estimated gape area (m<sup>2</sup>, purple), head width (m, blue) and baleen length (m, orange) with body length (m) and age of North Atlantic right whales. Dotted lines represent 95% CI. Circles represent estimated gape for individuals with measured (open) and estimated (closed) body lengths in this study. Baleen lengths are from North Pacific (Omura *et al.* 1969) and Southern right whales (Best & Schell 1996), head width from Miller (2005) and Miller *et al.* (2012), and length-at-age curve for North Atlantic right whales from Moore *et al.* (2004).

## Results

For 10 whales tagged for longer than 74:06 h:m, we analyzed a total of 57:04 h:m of tag data (range 1:18-11:34 h:m per whale; Table 1, Fig. 3) during which individuals completed a total of 140 dives >50 m. Of these, 132 were categorized as U-shaped (foraging) dives and 8 as V-shaped (non-foraging) dives. The mean depth of U-shaped foraging dives was 138 ( $\pm 25$ ) m, and the shallowest foraging dive was 89 m (tag 02\_221d; Table 1). The mean depth of V-shaped dives was 124 ( $\pm 25$ ) m.

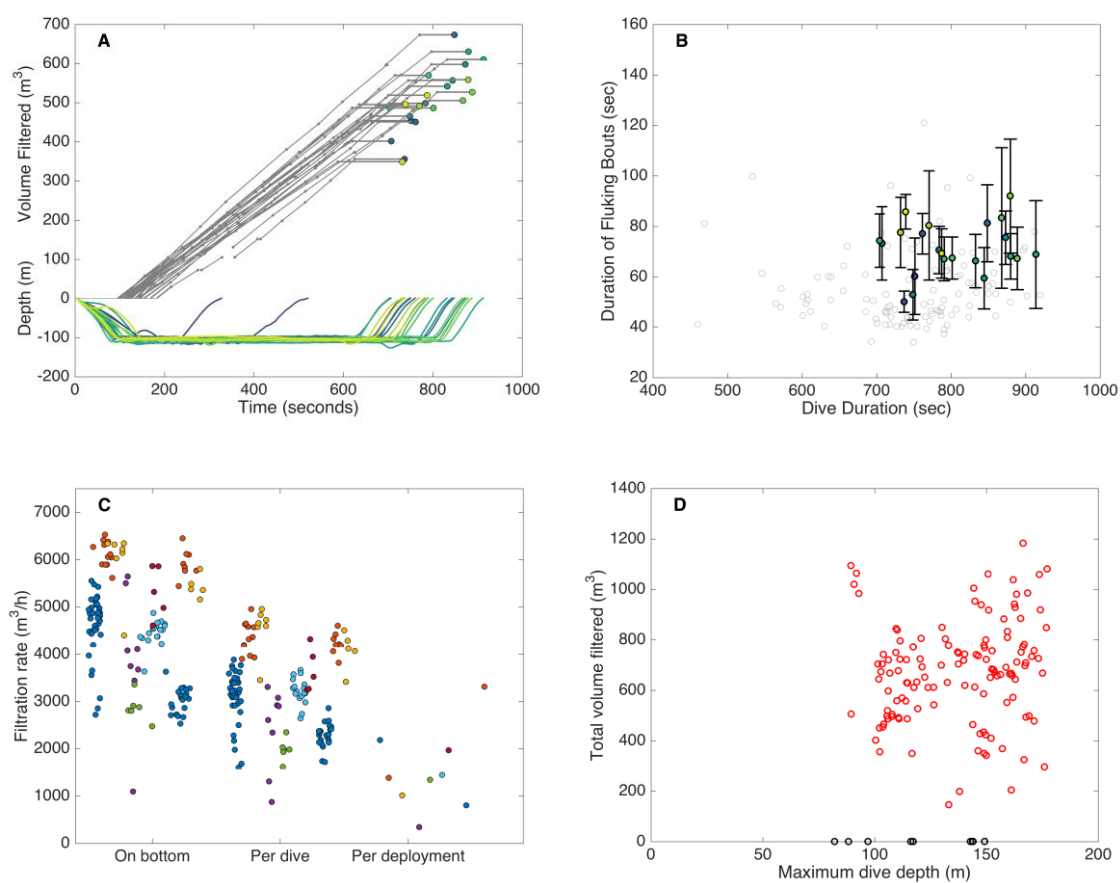
For the 10 tag records, the  $R^2$  for the flow-speed correlations averaged 0.76 ( $\pm$ SD 0.19), with an RMSE of 0.13 m/s ( $\pm 0.05$ ; Fig. 3). For U-shaped foraging dives, right whales descended at mean ( $\pm$ SD) pitch angles of  $-58$  ( $\pm 9$ ) degrees, at speeds of on average 1.4 ( $\pm 0.2$ ) m/s with fluke stroke rates of 0.07 ( $\pm 0.04$ ) Hz (Fig. 1). Ascents were similar, with mean pitch angles of  $54$  ( $\pm 10$ ) degrees and speeds of 1.5 ( $\pm 0.2$ ) m/s, with fluke stroke rates of 0.14 ( $\pm 0.02$ ) Hz. At the bottom of U-shaped foraging dives, right whales on average slowed to 1.1 ( $\pm 0.3$ ) m/s while actively swimming with fluke stroke rates of 0.16 ( $\pm 0.2$ ) Hz. In contrast, during V-shaped dives, pitch angles on descent and ascent were  $-5$  ( $\pm 5$ ) and  $23$  ( $\pm 14$ ) degrees, respectively, at speeds of 1.5 ( $\pm 0.2$ ) and 1.3 ( $\pm 0.2$ ) m/s.



**Figure 3.** The relationship between flow noise and vertical speed on ascents (blue) and descents (orange)  $\geq \pm 30$  degrees body pitch. Black line is the fitted relationship with dashed lines as prediction intervals.

We detected pauses in consistent fluking behaviour at the bottom of foraging dives, every 56 ( $\pm 22$  SD) seconds (Fig. 1, 4B). The median duration of these pauses was 3.5 s. These pauses did not appear to be a consequence orientation in a different axis: within 20 seconds preceding and

following a pause in continuous fluking, rolls were occasional, and heading was often continuously changing; the change in depth ranged  $\pm 10$  m (Fig. S3). We hypothesized that if bout duration was inversely related to prey density, and if right whales maximized their diving behaviour to forage within high-quality patches, dives with shorter bouts would be longer. We found no relationship between dive duration and the duration of fluking bouts within each dive ( $R^2 = 0.001$ ; Fig. 4B). The number of fluking bouts increased with dive duration, as expected as both are related to time; however, the number of bouts within a dive ranged from 0-14 (mean  $8.2 \pm 3.1$ ). During these bouts, estimated swimming speed was  $1.1 (\pm 0.3)$  m/s.



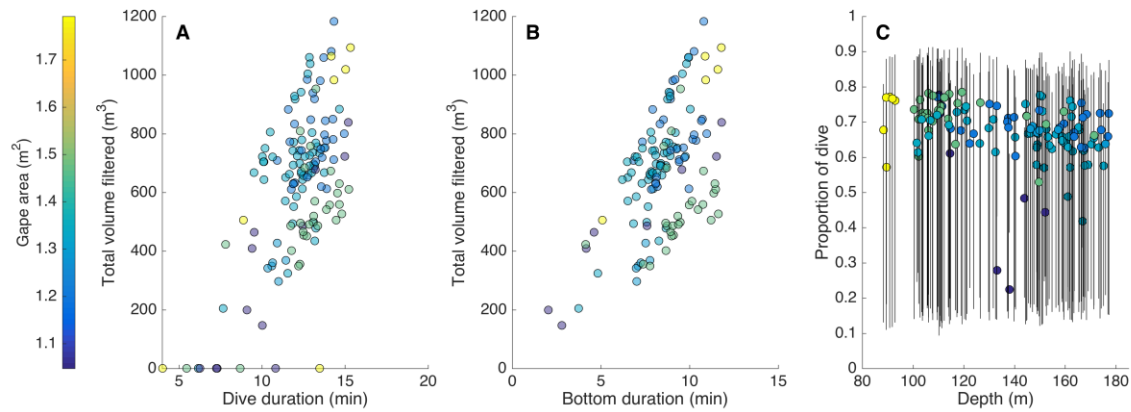
**Figure 4.** A: The total volume of water filtered per dive ( $m^3$ , circles), coloured to match each dive profile for a representative North Atlantic right whale (05\_215a). The grey line shows the rate at which the volume is filtered (i.e., the filtration rate through time for each dive). Small points along the grey line note the timing of pauses in fluking. B: The mean (error bar SD) duration of fluking bouts (sec) during each dive versus the duration of those dives (sec). The coloured circles match the same dives in panel A. Grey points are data for the other tag. C: Estimated filtration rate ( $m^3/h$ ) calculated during the bottom phase, per entire dive cycle, and throughout the tag deployment;

colours represent different individuals. D: The estimated total volume of water filtered ( $\text{m}^3$ ) compared to the maximum depth of each foraging (red) and non-foraging dive (black; m).

Whales filtered on average  $78 (\pm 30) \text{ m}^3$  of water per fluking bout, but fluking bouts did not end after a fixed volume of water had been filtered (range 10 –  $328 \text{ m}^3$ ). Per dive, whales filtered a mean of  $673 (\pm 201) \text{ m}^3$  of water total (Fig. 4A), and dives were not terminated at a fixed volume of water filtered per dive (Figures 4A, 5, 6). At the bottom of foraging dives, the mean filtration rate was  $1.4 (\pm 0.3) \text{ m}^3/\text{s}$ ; however, including transit time, mean filtration rates per complete foraging dive were  $0.9 (\pm 0.2) \text{ m}^3/\text{s}$ , or  $3210 (\pm 870) \text{ m}^3/\text{h}$ . The total volume filtered over the course of a tag deployment varied from  $342 \text{ m}^3/\text{h}$  (01\_214a) to  $3315 \text{ m}^3/\text{h}$  (05\_219a), primarily driven by activity budgets, as whales exhibit other (e.g. non-foraging) behaviours (Fig 4C).

In foraging dives, whales descended to the foraging depth within the first  $17 (\pm 5)\%$  of the dive duration ( $2.0 \pm 0.4 \text{ min}$ ) and foraged until  $85 (\pm 5)\%$  of the dive duration ( $10.9 \pm 1.5 \text{ min}$ ) before ascending (Fig. 5C). We detected a significant relationship between dive depth and the proportional time of onset of foraging ( $F_{1,129} = 5.71$ ,  $p_{\text{slope}} = 0.0184$ ), but the effect size was  $3 (\pm 3)\%$ ; this means the onset of foraging varied from 14% (SE 13-17%) into the dive cycle for a 82-m dive compared to 19% (SE 17-20%) for a 177-m dive. Further, depth of dive explained little to no variance in the proportional time to onset of feeding ( $R^2 = 0.035$ ). Similarly, the proportional time of the end of foraging decreased significantly with depth ( $F_{1,129} = 16.9$ ,  $p_{\text{slope}} < 0.0001$ ), with a similarly small effect size of  $-6 (\pm 3)\%$  and  $R^2 = 0.119$  (Fig. 5C). The total proportion of the dive spent foraging decreased with depth by a total of 10% (73% to 63%) across the range of dive depths (82-177 m;  $R^2 = 0.088$ ). There was no significant relationship between the depth of each dive and the total volume filtered ( $R^2 = 0.001$ ,  $F_{1,115} = 0.212$ ,  $p = 0.884$ ; Fig. 4D). Even in the shortest dives with  $<5 \text{ min}$  and  $<50\%$  of bottom time (Figures 4A, 5 B, C), whales performed fluking bouts.

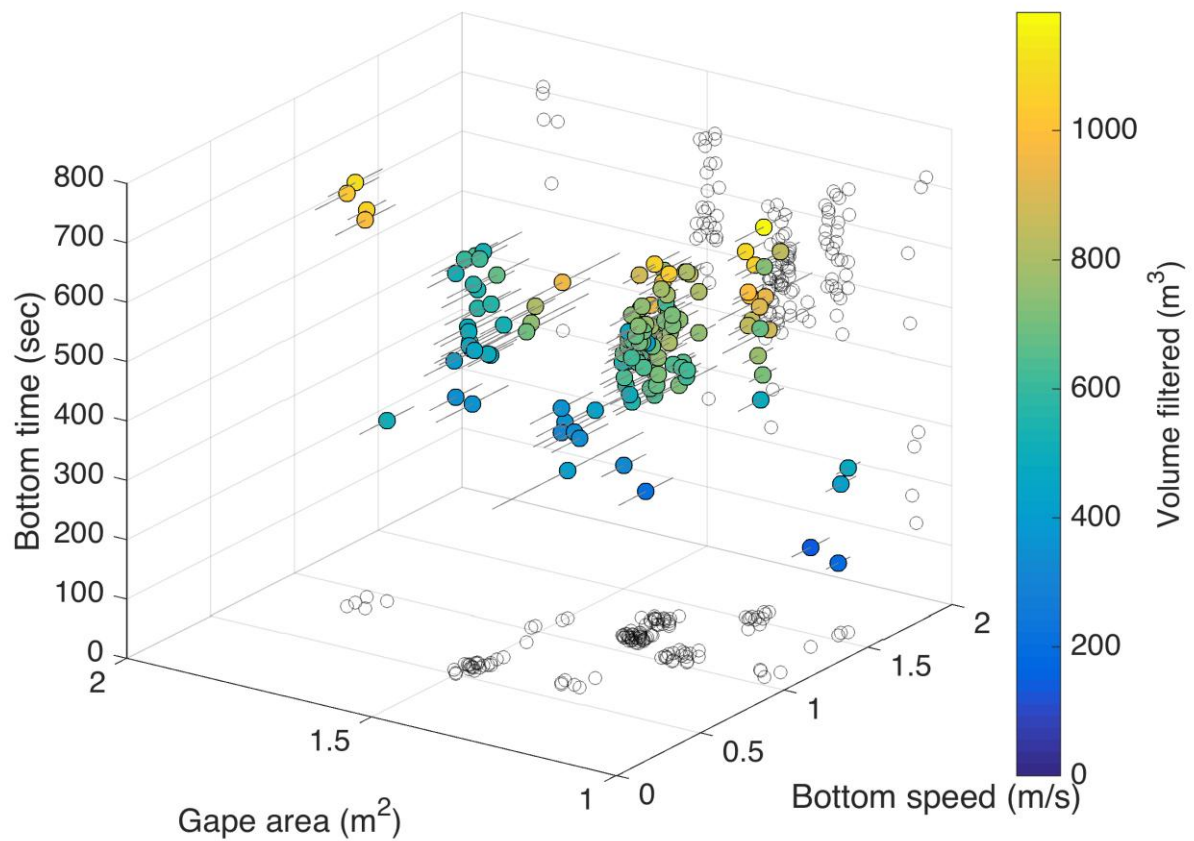




**Figure 5.** Total volume of water filtered per dive ( $\text{m}^3$ ) versus dive duration (min; A) and bottom foraging duration (min; B) for 10 North Atlantic right whales. The vertical bars in C show the proportional time of onset of foraging to the end of foraging, at the foraging depth of each dive; circles represent the total proportion of each dive spent foraging. In all panels, colours indicate the gape area size ( $\text{m}^2$ ) of different whales.

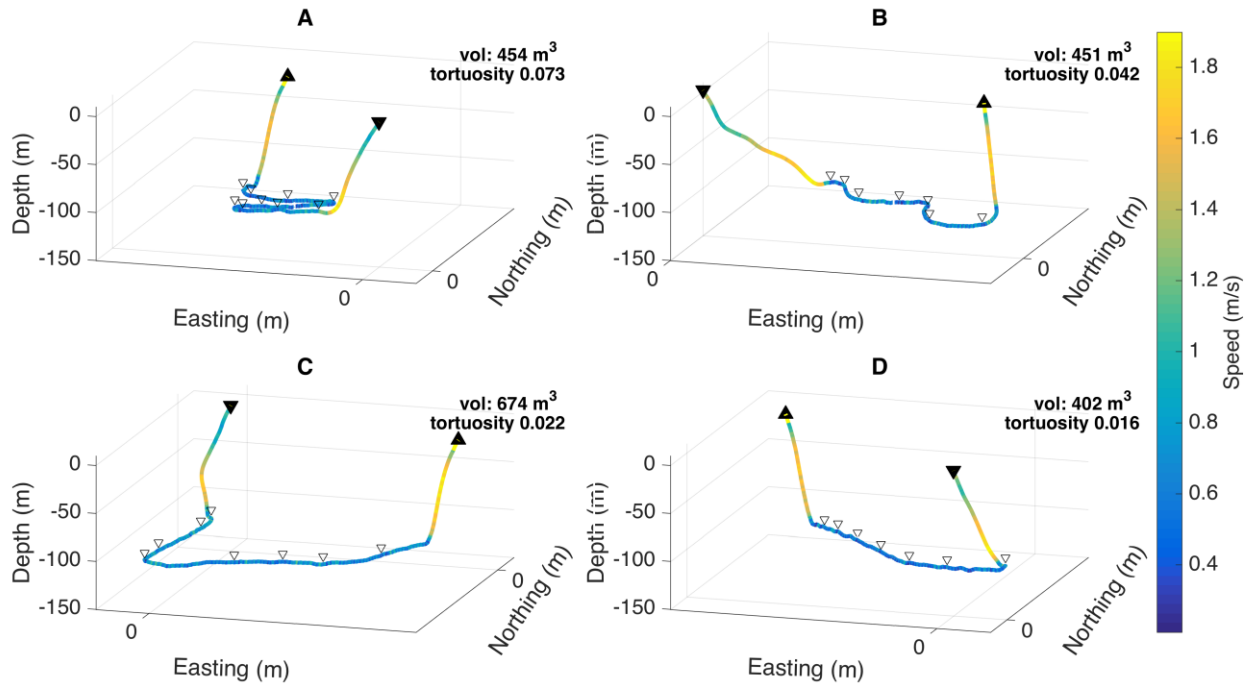
Three variables contribute to the total filtered volume per dive: swimming speed (estimated from flow noise), gape (estimated from age and morphometrics) and time per dive spent foraging (bottom time, estimated from tag data). We used a linear model to assess the effect of each of these variables on the total volume filtered per dive. The three factors explained 89.5% of the variability in filtered volume ( $F_{3,126} = 357$ ,  $p < 0.0001$ ). The dive bottom time had the greatest effect size ( $875 \pm 71 \text{ m}^3$ ), followed by swimming speed ( $704 \pm 53 \text{ m}^3$ ). Gape had the lowest effect size of  $349 \pm 67 \text{ m}^3$  across the range of 1-1.8  $\text{m}^2$ .





**Figure 6.** The estimated bottom speed (m/s;  $\pm$  prediction error in grey), gape area (m<sup>2</sup>) and bottom time (sec) of the dives of 10 North Atlantic right whales, coloured by the estimated total volume of water filtered (m<sup>3</sup>) per dive. The 2D projections are shown in grey circles; gape is jittered randomly up to 0.05 m<sup>2</sup> to see overlapping points.

Based on the dead-reckoned tracks of individuals, whales exhibited a variety of subsurface foraging behaviours (Fig. 7). The tortuosity of horizontal movement within dives was on average 0.022 ( $\pm 0.025$ ), up to 0.117 and varied even between sequential dives (Fig. 7). We expected tortuosity to reflect animals ‘working a patch’, maintaining residence in an area, and therefore hypothesized that dives with higher filtered volumes, or more or shorter fluking bouts, would have more tortuous paths. We found no relationship between the total volume filtered per dive and the mean tortuosity within that dive ( $F_{1,128} = 0.793$ ,  $p = 0.375$ ,  $R^2 = -0.002$ ) nor the bout duration (inter-pause interval) and the tortuosity of the dive ( $F_{1,128} = 0.003$ ,  $p = 0.958$ ).



**Figure 7.** Subsurface foraging behaviour (pseudo-tracks) of four sequential dives (A, B, C, and D) of one example North Atlantic right whale (05\_215a) foraging in the Bay of Fundy, Canada. The estimated volume of water filtered per dive is printed on each panel. Filled black triangles indicate position of dive initiation (downwards-facing) and surfacing (upwards-facing); white triangles at depth indicate pauses in fluking behaviour. The colour along the track indicates estimated swimming speed.

## Discussion

Balaenid whales acquire their food in a short period in the spring and summer, putting a premium on understanding where, how and how much prey-laden water these ram filter feeders process to fuel their capital-breeding lifestyle. We employed pressure, inertial, and acoustic sensors on bio-logging tags to estimate the filtration rates of right whales and the biomechanics relevant to their foraging behaviours: 1) How fast do right whales filter? 2) Do right whales show the same characteristic gait patterns as other ram filter feeders during foraging dives? 3) If so, are pauses in fluking a biomechanical pattern or related to prey processing/density/patch structure?

We found that right whales made repeated foraging dives to depths where they slowed to  $1.1 (\pm 0.3)$  m/s, or  $0.09 (\pm 0.03)$  body lengths/s. At depth, they carried out a repetitive gait with short,  $\sim 2$  second pauses between bouts of higher frequency fluking behaviour. We suggest that, similar to observations in bowhead whales, right whales swim at consistently low speeds when foraging to

reduce the drag of their open mouths. However, right whales only slow down by 26% (compared to 40% for bowhead whales; Simon *et al.* 2009), likely due to the smaller cross-sectional mouth area per body size; the faster swimming speed of right whales provides a higher filtration rate, but only partially compensates for the smaller mouth area. To acquire similar prey resources as bowheads, right whales must feed on higher density prey aggregations, on prey with higher energy density, and (or) for longer periods of time.

Based on in-situ speed estimates, measured diving behaviour and individual-specific gape measurements, the right whales in this study filtered on average 3211 ( $\pm 874$ ) m<sup>3</sup> of water per hour during complete foraging dives (i.e., a round-trip from the surface, including time of descent and ascent). Over the course of deployments, filtration rates varied from 342 m<sup>3</sup>/h to >3300 m<sup>3</sup>/h depending on individual behaviour and size. During active foraging at the bottom of U-shaped dives, the whales filtered 4520 ( $\pm 1230$ ) m<sup>3</sup>/h, which is ~30% lower than the estimates of 6250 m<sup>3</sup>/h by Kenney *et al.* (1986) and 6534 m<sup>3</sup>/h by Baumgartner and Mate (2003). This difference is primarily due to explicitly including variation in mouth gape with age (determined from body size and baleen length, Fig. 2), as well as *in situ* estimates of swimming speed as these individuals forage at depth with their mouths agape (Fig. 1).

Previous models of foraging in right whales assume a constant mouth area of 1-1.2 m<sup>2</sup> and speeds of 1.5 m/s (Kenney *et al.* 1986; Baumgartner & Mate 2003), whereas our gape estimates account for changes with age for the first time (1-2 m<sup>2</sup>, a doubling over the lifespan). Not including this variation would lead to considerable underestimates of the volumes filtered and subsequent prey consumed by adult right whales. This study included many sub-adult individuals, aged 2-4 years, with estimated gape areas of 1.1-1.3 m<sup>2</sup> (Table 1). The difference in estimated filtered volumes for these animals, using age-specific gape versus a constant gape of 1.2 m<sup>2</sup> (Kenney *et al.* 1986; Baumgartner & Mate 2003), is negligible at ~4%. However, the underestimate of filtered volume is considerable in older and larger individuals with estimated gape areas of up to 1.8 m<sup>2</sup> (Fig. 2). We estimated a gape of 1.8 m<sup>2</sup> for an >11-year old male (02\_221d) in this study. This individual filtered an average of 760 ( $\pm 400$ ) m<sup>3</sup> of water per dive. Per-dive volume estimates would have been 530 ( $\pm 270$ ) m<sup>3</sup>, 230 m<sup>3</sup> or 30% less than if we had assumed a non-age adjusted gape of 1.2 m<sup>2</sup>.

Second, previous studies used higher fixed values for swimming speed, or at least minimum swimming speeds of 1.5 m/s (Watkins & Schevill 1976; Watkins & Schevill 1979; Kenney *et al.* 1986; Baumgartner & Mate 2003). We estimated swimming speeds of 1.1 ( $\pm 0.3$ ) m/s for whales when foraging. Though this difference may seem minimal, it translates to considerable differences in volume filtered: an 8-m whale with a gape of 1.6 m<sup>2</sup> would filter 8640 m<sup>3</sup>/h swimming at 1.5 m/s,

compared to 5760 m<sup>3</sup>/h (33% less) swimming at 1.0 m/s. Considering the error in our speed estimation (mean RMSE = 0.13 m/s), filtered volume estimates are likely within  $\pm 10\%$ , still less than the difference between assuming a constant speed versus an estimate from flow noise. Speed estimates from flow noise do have a low-speed limitation because 1) flow noise must be higher than background noise and self-noise of the recorder so will be more challenging to detect at slow speeds, 2) the regression relationships induce errors at either end of the measured speeds (Figure 3; Burgess *et al.* 1998; Blackwell *et al.* 1999; von Benda-Beckmann *et al.* 2016; Cade *et al.* 2018). We measured vertical speeds in the range of 0.4-3.5 m/s (Fig. 3). Though there are limitations in the flow-noise approach, they provide estimates of variation in swimming speed critical to addressing our main hypotheses. Including morphological variation and tag-derived estimates of swimming speed through water with the time spent foraging during the bottom phase of U-shaped dives refined the estimates of filtration and therefore hourly prey ingestion during foraging with variable behaviour over the course of a day.

We found a marked stereotypy in the diving behaviour of right whales in deep-water foraging habitats: individuals performed repeated foraging dives to consistent depth and duration for periods of >10 hours (34 dives, Fig. 3). Right whales are able to rapidly descend to foraging depth at high pitch angles, and similarly return to the surface quickly after foraging, optimizing their time at depth (Nowacek *et al.* 2001; Baumgartner & Mate 2003). We hypothesized that if whales were consistently diving to their aerobic dive limit, they would have filtered lower total volumes of water in deeper dives, due to the time required to transit to the foraging patch (Thompson & Fedak 2001). However, the lack of a significant effect of dive depth on the total volume filtered per dive and the low explanatory power of depth on foraging duration emphasizes that by completing many shorter, aerobic dives with steep ascents and descents and short surface intervals right whales maximize the time spent foraging in a consistent prey patch, regardless of its depth (Baumgartner *et al.* 2017). While individuals are able to optimize their time foraging in high-density prey layers, they apparently will also go without foraging for extended periods of time (2+ hours; Fig. S1) in this otherwise rich environment. Understanding why individuals do or do not forage should be explored with future prey-density measurements simultaneous with tag deployments (Baumgartner & Mate 2003; Parks *et al.* 2012); this may improve our understanding the effects of physiological mechanisms such as digestion and prey processing that may limit the duration of productive foraging bouts (Horning 2012).

Previous descriptions of right whale diving behaviour in deep-water foraging habitats categorized three types of dives based on *k*-means clustering: foraging dives, V-shaped dives and 'other' or 'Type 2' dives (Baumgartner & Mate 2003; Nousek-McGregor 2010). These 'Type 2' dives are often to depths just above of the bottom mixed layer and even to the seafloor (Baumgartner & Mate 2003). These dives have previously been described as intermediate between foraging and V-shaped dives: they do not maximize the time spent at depth, with longer ascents compared to typical foraging dives (Baumgartner & Mate 2003; Nousek-McGregor 2010). However, the reduction in speed in the clear bottom phase of these dives is consistent with foraging (Nousek-McGregor 2010). In this analysis, we separated deep dives into foraging and non-foraging categories based only on a clear bottom phase and found that shorter dives with a lower proportion of time spent on the bottom (fitting the description of 'Type 2' dives) do show clear fluking bouts at low speeds (Figures 4A; 5 B,C). The 'Type 2' or 'other' dives therefore may be those where foraging was terminated, perhaps due to inadequate prey densities (Thompson & Fedak 2001; Stephens 2008; Hazen, Friedlaender & Goldbogen 2015). The deep non-foraging dives may serve to locate and/or judge prey patches. The diverse suite of sensors in these DTAGs is therefore useful to further elucidate behaviours previously inferred from time-depth recorders, without inertial sensors.

Presenting dive behaviour through time can be misunderstood to suggest that a submerged animal's path is straight in the horizontal dimension. The incorporation of inertial sensors in tags enables the estimation of a dead-reckoned track, though these are also imperfect due to additive error in the sensors and ignorance to external forces, e.g., currents (Johnson & Tyack 2003; Schmidt *et al.* 2007; Shiomi *et al.* 2010; Liu *et al.* 2015). Irrespective of these errors, *pseudo*-tracks do, however, capture the qualitative nature of animal movement and can be useful in inferring how animals move, rather than where they go; for our purpose, these tracks illustrate the degree to which right whales move horizontally within dives (Fig. 7). The variation in the horizontal movement patterns of whales foraging at depth (Fig. 7) as well as small-scale changes in the vertical dimension between dives (Fig. S3) further suggest that right whales are capable of detecting fine-scale variations in prey density and adjusting their foraging behaviour accordingly (Mayo & Marx 1990; Mayo & Goldman 1992; Kenney, Mayo & Winn 2001; Baumgartner *et al.* 2017). Simultaneous measurements of the vertical distribution of prey and right whale diving behaviour made in foraging habitats have shown how right whales are able to repeatedly target the depth of maximum copepod concentrations (Baumgartner & Mate 2003; Parks *et al.* 2012). By making fine-scale adjustments in the vertical dimension (~20 cm), right whales can increase energy intake by as much as 20% (Mayo & Goldman 1992). In the horizontal plane, copepod energy density can vary by a factor of 3.5 over a horizontal distance of 2 km in the Bay of Fundy (Michaud & Taggart 2011), and high energy (10-30

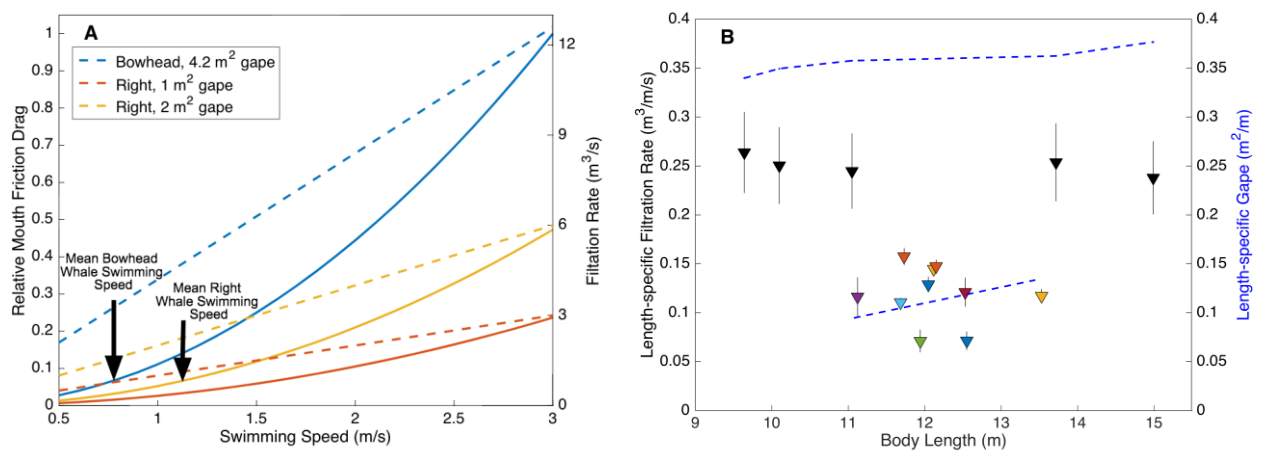
kJ/m<sup>3</sup>) patches ~1km in length and 1-10 m thick can form in similar deep-water foraging habitats of right whales (Davies, Taggart & Smedbol 2014); variations in C5 concentration, lipid content and energy density are considerable at horizontal scales of 500 m (Michaud & Taggart 2011). Further study to map the fine-scale horizontal distribution of copepod layers, and their nutritional value, especially relative to surface-corrected 3-D movements of foraging whales could further elucidate how right whales exploit and detect patches of different energy densities and dimensions.

The bowhead whale is a closely related balaenid species with similar foraging ecology and behaviour to right whales; both target calanoid copepod prey by continuous ram filtration (Laidre, Heide-Jørgensen & Nielsen 2007; Pomerleau *et al.* 2011; Walkusz *et al.* 2012). Bowhead and right whales share similar morphology (Figures 8, 9) but differ considerably in the magnitude of their gape area, as well as their baleen areas, widths and lengths for a similar body size (Omura *et al.* 1969; Werth 2004; Lambertsen *et al.* 2005; George *et al.* 2016; Werth *et al.* 2018). We have shown that right whales slow to 1.1 ( $\pm 0.3$ ) m/s during presumed foraging bouts, faster than the estimate by Simon *et al.* (2009) of 0.7 ( $\pm 0.1$ ) m/s for foraging bowhead whales. The slow foraging speed of balaenids has been linked to their ram-filtering strategy that incurs high drag, the level of which is a function of the frontal area of the whale, i.e., its gape and the square of the forward speed. The estimated gape sizes for right whales in this study were 1.1-1.8 m<sup>2</sup>; a 12-m right whale would have a gape of 1.3 m<sup>2</sup>, compared to the 4.2 m<sup>2</sup> gape of a 12-m adult bowhead (Werth 2004; Simon *et al.* 2009). Due to their smaller gape per body size compared to bowheads (Fig. 8B), right whales have a lower frontal area and therefore can forage at higher swimming speeds while likely incurring similar levels of drag and energetic cost as bowheads. Within the tagged right whales in our study, this is illustrated in the inverse relationship between gape and foraging speed (Fig. 6 projected on bottom). However, foraging at higher speeds only partially compensates for a smaller gape and still does not achieve the same filtration rate.

Drag increases linearly with area, but with the square of velocity (Vogel 1994). While the baleen area primarily affects drag forces and the outflow speed after water is filtered through the baleen (Werth & Potvin 2016; Potvin & Werth 2017; Werth *et al.* 2018), the mouth opening area affects the inflow volume of prey-laden water. The tradeoffs in the relationship between mouth friction drag, area, and speed have been illustrated by Potvin *et al.* (2017); we present the estimated open-mouth friction drag relative to bowhead whales (i.e. scaled by gape area) and put these values in context with their resulting filtration rates (Fig. 8A). When foraging at higher speeds, right whales incur similar drag forces to bowhead whales, due to their smaller gape area; however, even at these speeds their filtration rate remains lower. At 1.1 m/s, an 11-m right whale filters at a rate of 1.1



$\text{m}^3/\text{s}$ ; a bowhead of the same length with a gape of  $4.2 \text{ m}^2$  filters nearly  $3 \text{ m}^3/\text{s}$  of water at its preferred speed (Fig. 8). That same right whale, with a gape of  $1 \text{ m}^2$ , would achieve a filtration rate of  $3 \text{ m}^3/\text{s}$  only by swimming at  $3 \text{ m/s}$ , where its drag force would be roughly 4x greater than the bowhead filtering at the same rate swimming at  $0.7 \text{ m/s}$ . A larger (14 m) right whale with a gape of  $2 \text{ m}^2$  could filter  $3 \text{ m}^3/\text{s}$  swimming at  $1.5 \text{ m/s}$ , but would incur twice the drag cost doing so. While the filtration of ram feeding vs. intermittent lunge/suction feeding has been often contrasted in cetaceans (Goldbogen *et al.* 2016; Werth *et al.* 2018), there has been little discussion of the drag and size tradeoffs in filtration efficiency within balaenids.



**Figure 8.** A: Filtration rates (dashed lines) and relative mouth friction drag (solid lines, relative to bowhead) across swimming speeds for a 12-m bowhead whale with an estimated gape area of  $4.2 \text{ m}^2$  and two right whales (body lengths 11 m and 14 m) with gape areas of  $1 \text{ m}^2$  and  $2 \text{ m}^2$ . Average speeds of filtering bowhead (Simon *et al.*, 2009) and right whales (this study) are marked with arrows. B: Length-specific filtration rate of bowheads (black triangles; Simon *et al.*, 2009) and right whales (coloured triangles; this study) and length-specific gape of bowhead (blue dot-dash; data from Werth 2004) and right (blue dash) whales. Error bars are  $\pm 1\text{SD}$ .

With a smaller gape than bowhead whales, and with greater drag-induced costs and pressures, right whales have been predicted to target higher densities of prey when foraging. Prey-field sampling in areas around right whales when foraging or not have suggested density thresholds of  $800\text{-}1000 \text{ copepods}/\text{m}^3$ , below which right whales will stop feeding (Murison & Gaskin 1989; Mayo & Marx 1990; Beardsley *et al.* 1996). At those thresholds, right whales in this study, which filtered  $1.4 \text{ m}^3/\text{s}$  at the bottom of foraging dives, would be concentrating  $>60,000$  copepods per minute in their mouths. *In situ* measurements of the prey field in the vicinity of whales tagged with time-depth recorders suggest that right whales target prey patches of  $10^3\text{-}10^5 \text{ copepods}/\text{m}^3$  (Baumgartner & Mate 2003). By selectively targeting high-density prey patches, right whales are

likely able to obtain sufficient energy to offset their high-drag foraging strategy. There are few estimates of prey densities selected by foraging bowhead whales, especially around tagged individuals. Laidre, Heide-Jørgensen and Nielsen (2007) report densities of  $1 \text{ g/m}^3$  in surface waters but do not provide densities at depths where bowhead whales spend the majority of their time feeding (Simon *et al.* 2009). Such densities appear low; even assuming prey densities around bowhead whales are an order of magnitude higher ( $10 \text{ g/m}^3$ ), right whale energy acquisition considerably outpaces that of bowheads.

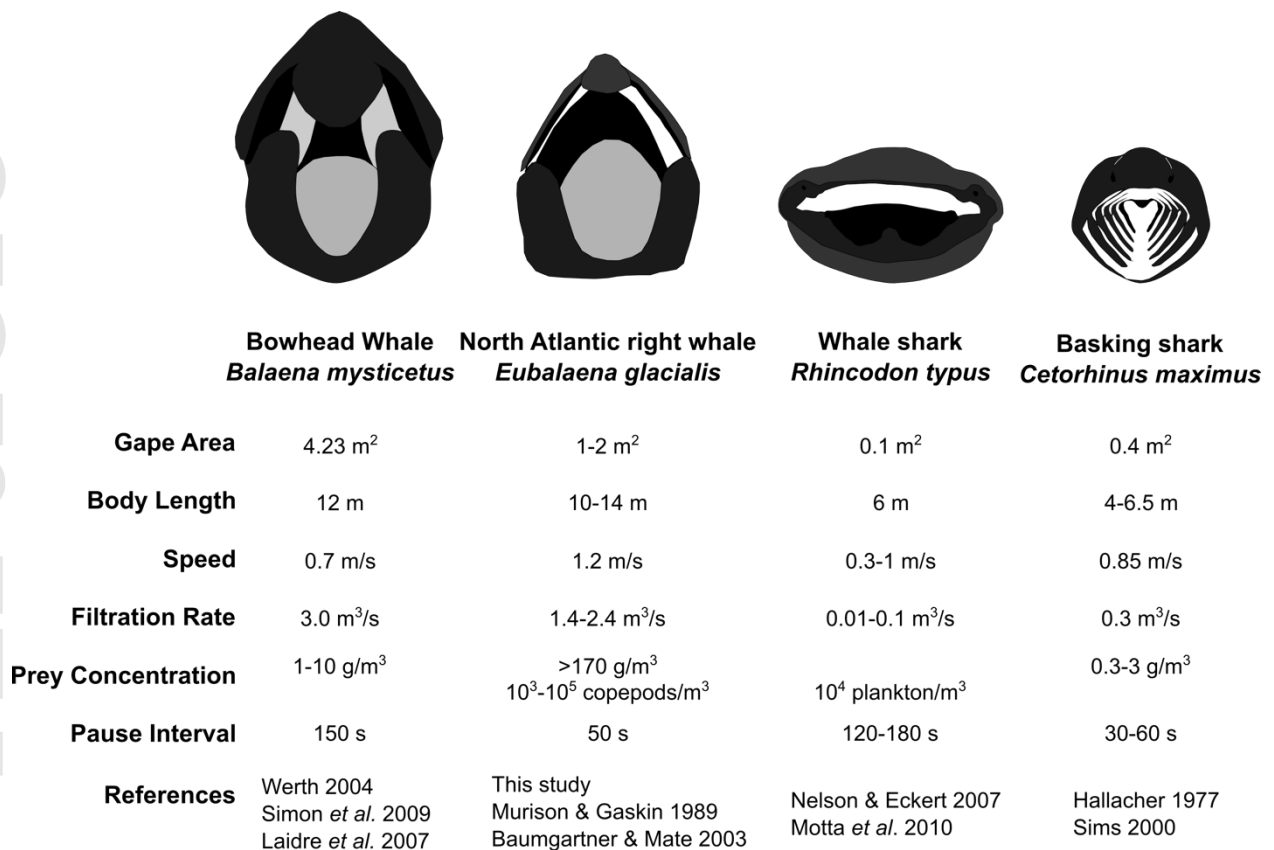
If right whales waited until the end of a dive to process or swallow prey, a massive accumulation of material would occur in the mouth (Werth 2001; Werth *et al.* 2018). We estimated that right whales filtered  $670 \text{ m}^3$  of water per foraging dive (mean body length =  $12.1 \pm 0.6 \text{ m}$ ). Even assuming the lowest threshold of copepod density measured in the Bay of Fundy ( $800 \text{ copepods/m}^3$ ; Murison & Gaskin 1989), and with a capture efficiency of 95% (Mayo, Letcher & Scott 2001), a 12-m right whale would accumulate  $5 \times 10^5$  copepods in their mouth by the end of a dive (1.7 MJ based on the lower individual energy content of 3.4 J; Michaud & Taggart 2007). At the highest measured copepod densities of  $15000 \text{ copepods/m}^3$  (Baumgartner & Mate 2003), this would translate to as many as 9 million copepods per dive (18-36 L, 45 MJ based on the upper individual energy content of 5 J; Michaud & Taggart 2007). Such high maximum feeding rates highlight why right whales may be able to acquire a large proportion of their total annual energy intake in the months when copepods are at their highest energy densities and when and where they maximally aggregate. It also highlights that taking brief pauses from foraging to swallow prey throughout the dive is therefore likely to be necessary.

Simon *et al.* (2009) reported a characteristic swimming gait in bowhead whales, where periods of high-amplitude and high-frequency (0.12 Hz) fluking were interrupted by consistent pauses, half a fluke stroke in duration, occurring every 2.4 minutes, or  $\sim 480 \text{ m}^3$  of water filtered. They suggested these pauses may be related to prey handling and that the consistency of the behaviour may be due to exploitation of continuous prey patches. In balaenids, the prey slurry likely accumulates in the postlingual recess just before the esophagus, prior to swallowing (Lambertsen *et al.* 2005). If pauses in fluking are linked to prey processing, and if that processing is linked to accumulated prey mass (i.e. if it is limited by pharynx/esophagus size, 3-10 cm; Albert 1981; Lowry & Frost 1984), then the timing of the pauses should be a function of swimming speed and prey density. We detected similar pauses,  $\sim 3 \text{ sec}$  long, between  $\sim 50$  second bouts of fluking behaviour. We found that the timing of pauses did not occur at completely fixed time intervals (SD 22 s) or after specific volumes of water were filtered (SD  $30 \text{ m}^3$ ), which is consistent with the alternative hypothesis that



the rate of prey acquisition or bolus formation may instead be the driver of these intervals. These pauses lasted less than half a full fluke stroke cycle (~6.25 sec) and therefore differ from prolonged glides (>5 sec) employed in burst-and-coast swimming (Weihs 1974; Videler & Weihs 1982; Williams 1999). These pauses are also consistent with observations of right whales 'nodding' at the surface while skim feeding (Mayo & Marx 1990). Further, the more frequent timing of these pauses in right whales compared to bowheads is consistent with filtering much more dense concentrations of prey, in concert with the morphological differences described above.

After obtaining prey via an efficient cross-flow filtration system (Sanderson *et al.* 2016; Potvin & Werth 2017), accumulated prey must be swallowed; pausing filtration to swallow has been observed in other ram-filter feeders ranging in size from basking and whale sharks (Fig. 9; Sims 2000b; Nelson & Eckert 2007; Motta *et al.* 2010) to paddlefish (Sanderson, Cech & Cheer 1994) and herring, shad, sardines, menhaden, and alewife (Sanderson & Wassersug 1990). Hallacher (1977) and later Sims (2000) noted pauses in the open-mouth feeding behaviours of basking sharks, with ~3 s interruptions to swallow prey. The rates of prey-handling pauses may therefore be additional density-mediated foraging behaviours (Hallacher 1977; Runge, Pepin & Silvert 1987). The differences in gape areas, body size, filtration rate, and prey density between balaenids and large fishes (Fig. 9) illustrate how continuous ram filtration in large fishes is much less efficient per unit time, though they often forage on similar prey species. Basking sharks often forage on calanoid copepods though in different habitats they will forage on larger zooplankton prey (Baduini 1995; Sims & Merrett 1997; Sims 2008). The much longer feeding season and an order of magnitude lower metabolic rate in large ram-filter-feeding fish (Sims 2000a; Motta *et al.* 2010; Watanabe *et al.* 2015) likely allows for much lower acquisition rates. Additionally, fish are able to forage continuously, as they do not have the same time restriction of returning to the surface to breathe as whales do; the oxygen demands of filter-feeding fish are met within the medium and by the same water flow through the gills as is used to filter prey (Sanderson, Cech & Cheer 1994; Sanderson *et al.* 2001; Sims 2008). Still, ram-feeding fish show evidence for threshold feeding behaviours, leaving patches when prey densities are <0.5-0.7 g/m<sup>3</sup> (Sims 1999). Specific models to incorporate metabolic rate and oxygen demand versus drag, speed, and filter area of ram-filter feeding marine animals may elucidate how different species and groups address these tradeoffs in morphology, movement, and energetics.



**Figure 9.** Comparative morphometrics, swimming speed during filtering, filtration rate, prey concentration and inter-pause interval for four species of large ram-filter feeders. The four buccal cavity outlines shown are colour-coded: white represents baleen or gill racks, grey the tongue (mysticetes), black and dark grey for the overall shape of the head.

Some of the parameters used to estimate filtration rates of swimming animals could incorporate improved measures in future studies. For example, changes in mouth aperture or gape are hard to measure, especially at depth. At the surface, aerial footage from surface-feeding whales may be useful to quantify rates of mouth closure or small changes in gape or mouth position through time, but how these movements translate from surface-feeding to depth would be unknown. Use of sensors on tags to measure gape would help refine these estimates (Liebsch *et al.* 2007; Robson *et al.* 2009). Prey density and energy content are important to inform the optimal filtering speed for trade-offs between energy expenditure and acquisition. Attempts to co-locate zooplankton sampling with time-depth recorders have led to estimates of energy acquisition (Baumgartner & Mate 2003), but there is always some degree of spatial and temporal decoupling that may lead to substantial errors in these estimates. In-situ prey-field measurements from onboard sonar tags would address many of the temporal and spatial decoupling problems between tag data and ship-based echosounders (Lawson *et al.* 2015; Goulet *et al.* In Press). These, in concert with the speed estimates

and biomechanics, could help elucidate individual foraging decisions, fluking behaviours and how they directly relate to measured prey densities.

Short-duration, minimally invasive acoustic bio-logging tags provide short glimpses into the foraging behaviours of right whales at depth. These technologies can be combined with repeated aerial photogrammetry or photographs over time to estimate changes in body shape and condition (Pettis *et al.* 2004; Miller *et al.* 2011; Nousek-McGregor *et al.* 2013; Pettis *et al.* 2017), as well as over what time periods and in what areas right whales may be obtaining sufficient energy resources. With the recent observed changes in distribution, body condition, and prey availability (Angell *et al.* 2004; Greene *et al.* 2013; Meyer-Gutbrod & Greene 2014; Davis *et al.* 2017), it is critical to further understand the energetic tradeoffs between filtration and acquisition in right whales. If prey densities or energy content decrease (DFO 2018), the energy gained per energetic cost incurred will not balance and could result in an energy deficit and poor body condition (Fortune *et al.* 2013). Comparative studies that integrate prey measurements, filtration and biomechanics could further quantify how foraging in different habitats directly contributes to individual health, nutritive status, and the fitness necessary for the survival and recovery of the species.

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## Author Contributions

JVDH and PTM conceived the ideas and designed methodology with input from the other authors; DPN, SEP, PLT designed the initial experiments; DPN, SEP collected the data; JVDH and AENM analysed the data; JVDH led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

## Data Availability

Code and data associated with the manuscript are available at  
<https://doi.org/10.5281/zenodo.2660074>.

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