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Bimodal vertical distribution of right whales *Eubalaena glacialis* in the Gulf of St. Lawrence

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ABSTRACT: Critically endangered North Atlantic right whales *Eubalaena glacialis* have recently shifted their summer distribution from the Bay of Fundy to the Gulf of St. Lawrence (GSL), Canada. Entanglement in fishing gear and vessel strikes remain the main lethal threats. Foraging on deep aggregations of *Calanus* prey in the Bay of Fundy involves stereotyped deep 'flat-bottom' (U-shaped) dives, while foraging on sub-surface *Calanus* aggregations on the winter feeding grounds of Cape Cod Bay involves surface feeding. To explore North Atlantic right whale feeding behaviour in the GSL, 5 acoustic and biologging tags (DTAGs) were deployed using suction cups in 2019 and 2020. One whale knocked off the tag after 14 min. Diving behaviour of the other 4 whales with 2.0 to 4.7 h of data was mostly split between flat-bottom foraging dives at, or very close to, the sea floor, and near-surface activities, including logging, respirations, and potentially also sleeping. This biphasic vertical distribution not only places the whales at risk of being hit by vessels, but it may also put them at risk of coming into contact with groundlines used in various fishing industries in the GSL. Although additional research is needed as this limited dataset was restricted to hours of daylight, these results provide new information about right whale behaviour in the GSL that can help inform management actions to reduce human impacts on this endangered species.

KEY WORDS: North Atlantic right whale · Behaviour · Habitat use · Entanglement · Vessel strike risk · Ship strike · Human impacts

1. INTRODUCTION

The North Atlantic right whale *Eubalaena glacialis* (hereafter referred to as 'right whale') is a critically endangered large baleen whale found primarily along the east coast of North America. Hunted for centuries and protected since 1935, the numbers of this species have hovered between 300 and 500 individuals over the last 40 yr (Pace et al. 2017). From December through March, pregnant females, and some other adults and juveniles, are found in the waters off the southeastern USA where mothers birth and begin to nurse their young (Kraus et al. 1986b, Krzystan et al. 2018). After that, mothers and calves migrate north to feed and the pair remain together for about a year (Hamilton et al. 1995), though there is substantial variation in the timing of separation (Hamilton & Cooper 2010, Hamilton et al. 2022). The active feeding grounds off New England, USA, and eastern Canada are mostly utilised from March through October. Right whales engage in surface active behaviour (often including copulatory behaviour) year-round (Parks et al. 2007), but conception is believed to take place in the late fall and early winter (Cole et al. 2013). Individuals of the species can be identified by photographs of natural markings on their heads (Payne et al. 1983) and much of what is known about their ecology comes from a detailed catalogue of repeated sightings

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of individuals throughout their range (Hamilton et al. 2007, https://rwcatalog.neaq.org). Right whales feed on a variety of zooplankton species and can do so anywhere in the water column (Baumgartner et al. 2017).

Recent climate-related changes in the oceanographic conditions of their feeding grounds have resulted in extensive, and potentially enduring, shifts in their use of certain habitats (Davis et al. 2017, Plourde et al. 2019, Record et al. 2019, Simard et al. 2019, Lehoux et al. 2020, Meyer-Gutbrod et al. 2021, Sorochan et al. 2021). These include an increase usage of Cape Cod Bay off Boston, MA, USA, in late winter and early spring (Pendleton et al. 2022), a near abandonment of the Great South Channel east of Cape Cod in late spring, and of the Bay of Fundy and Roseway Basin (Davies et al. 2019), west and south of Nova Scotia, Canada, respectively, in summer and fall. At the same time, right whales have moved into the Gulf of St Lawrence, Canada, where approximately 40% of the population now feeds from May through October (Crowe et al. 2021), and into the waters south of Cape Cod, where they are found year-round, though primarily in the spring (Quintana-Rizzo et al. 2021, O'Brien et al. 2022).

These shifts in distribution have resulted in an increase in right whale mortality and serious injury (Pace et al. 2017, Pettis et al. 2023). Lethal vessel strikes and entanglement in fishing gear (and other ropes) have replaced whaling as the main sources of mortality (Knowlton et al. 2012, Daoust et al. 2017, Corkeron et al. 2018, Sharp et al. 2019, Bourque et al. 2020, Wimmer & Maclean 2021), with all non-neonatal deaths attributed to these causes (Sharp et al. 2019). While right whales were relatively protected from these threats in the Bay of Fundy (due to the relocation of the shipping lanes and the mismatch in the timing of most fishing with right whale occurrence), there were initially no such protections in the Gulf of St. Lawrence when right whales first shifted there in 2015 (Crowe et al. 2021). The Gulf has an active snow crab and lobster fishery that spatially and temporally overlaps right whale occurrence, and it serves as the access point to the Great Lakes for all major shipping. A high death toll followed (at least 3 right whales in 2015, 12 in 2017, and 9 in 2019; Daoust et al. 2017, Sharp et al. 2019, Bourque et al. 2020). These numbers together with those from US waters led the National Oceanic and Atmospheric Administration to initiate an Unusual Mortality Event[1] in 2017, which remains open as of the date of this publication. In addition to high mortality, the species also contends with a number of sublethal threats that appear to be suppressing their reproductive potential (Stewart et al. 2022, Pirotta et al. 2023, T. Frasier et al. preprint doi:10.1101/2023.11.21.568115). These include the energetic consequences of prior acute injuries from non-lethal ship strikes or entanglement (Stewart et al. 2021), as well as any ongoing chronic entanglements (van der Hoop et al. 2017); chronic stress responses resulting from noise exposure (presumably in concert with all other stressors present; Rolland et al. 2012); and reduced prey availability and quality, likely as a consequence of climatic and oceanic changes (Record et al. 2019, Gavrilchuk et al. 2021, Meyer-Gutbrod et al. 2021, Pershing & Pendleton 2021). The population has thus been declining and currently numbers an estimated 356 (+7/−10) individuals as of October 2023 (Pettis et al. 2023).

Where and how right whales forage has a direct impact on the risks they face while feeding. Foraging behaviour seemed to target deep aggregations of *Calanus* spp. prey in the old summer habitat of the lower Bay of Fundy, with the whales employing deep 'flat-bottom' dives (Murison & Gaskin 1989, van der Hoop et al. 2019, Baumgartner & Mate 2003, Baumgartner et al. 2003) that are typical of foraging in marine mammals more broadly (e.g. Johnson et al. 2006, Heide-Jørgensen et al. 2013, Wright et al. 2017). However, this is not the only foraging behaviour known in this species, as they have also been observed to employ surface and near-surface skim-feeding on the winter feeding grounds of Cape Cod Bay to target sub-surface *Calanus* aggregations (Mayo & Marx 1990, Parks et al. 2012). Each of these behaviours results in a different exposure to human activities, and thus a different risk profile that must be mitigated (Baumgartner et al. 2017, Hamilton & Kraus 2019). For example, surface and near-surface skimming places the animals at great risk of being struck by vessels (Parks et al. 2012). Meanwhile, feeding at the bottom increases the likelihood of a whale coming into contact with fishing groundlines and becoming entangled (Hamilton & Kraus 2019). Although *Calanus* spp. copepod prey have been observed aggregating near the bottom in the southern Gulf of St. Lawrence in the summer (Sorochan et al. 2023), it is not yet known if *E. glacialis* in the Gulf target these aggregations for foraging. To better understand foraging behaviour of right whales in their new habitat of the Gulf of St. Lawrence, and the extent to which they face the various human threats present there, acoustic and biologging tags (DTAGs)

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[1] www.fisheries.noaa.gov/national/marine-life-distress/2017-2023-north-atlantic-right-whale-unusual-mortality-event. Last accessed 29 February 2024

were deployed on animals with the intention of undertaking a preliminary investigation of their diving behaviours.

2. MATERIALS AND METHODS

2.1. Field methods

Two cruises took place in the Gulf of St. Lawrence, Canada, from 6 to 19 August 2019 and 1 to 15 August 2020 on the RV 'Coriolis II', a 50 m long research vessel with a draught of 5.2 m and a crane capable of deploying a smaller vessel for tagging. In 2019, the majority of the cruise was in the Shediac Valley and Banc-des-Américains Marine Protected Area in the Southern Gulf of St. Lawrence. In 2020, the cruise spanned the area from the Shediac Valley and surrounding area in the south, across the Honguedo Strait and to the west of Anticosti Island in the north (Fig. 1).

During most hours of daylight and in Beaufort sea states of 5 or less (acknowledging that sighting rates decline sharply beyond sea state 1, 2, or 3, depending on the species), 1 to 3 (most typically 2) observers were on the bridge of the vessel to detect and record marine life, particularly cetaceans and specifically right whales.

DTAGs are acoustic and biologging suction-cup-attached tags designed for use on marine animals, particularly cetaceans (Johnson & Tyack 2003). This project used DTAG-3 units, which contain a depth (pressure) sensor, a temperature sensor, a saltwater switch, a complete acoustic recording system (stereo hydrophones, board, preamplifier, etc.), 3D accelerometers and magnetometers, and a VHF transmitter to allow for recovery, all powered by a rechargeable lithium-ion battery and run by an on-board processor. Data are stored to 64 GB flash memory.

For these deployments, the tags were sampling all sensors (except acoustics) at a rate of 250 Hz. The DTAGs were typically set to release from the animals after 5 h, although in 2019, the first deployment was set for 2 h and the second for 3 h to accommodate additional small-vessel activities.

When attempting tagging, the 5.4 to 7.3 m rigid-hull inflatable boat approached the whale to collect images and assess the health of the animal following standard protocol (Pettis et al. 2004), and identify the individual using callosities and other identifying markings (Kraus et al. 1986a, Hamilton et al. 2007). Tagging was attempted only on animals deemed to be in relatively good health.

Three DTAGs were deployed in 2019, and 2 were deployed in 2020 (see Table 1 & Fig. 1). The tags were attached using a 10 to 12 m handheld carbon-fibre pole, in line with the methods outlined by Johnson & Tyack (2003). The whales were approached obliquely from the side and at slow speed, avoiding approaching the animals from the head or the tail. Only minor force was needed to ensure that the suction cups would engage and the release mechanism would disengage the tag from the pole to deploy the DTAG. As the whale made its first dive, the saltwater switch started the electronic timer that would ultimately release the negative pressure in the suction cups and allow the tag to float free for recovery. Once the tag had been released, radio receivers with Yagi antenna were used to bring the researchers to the exact location of the tag.

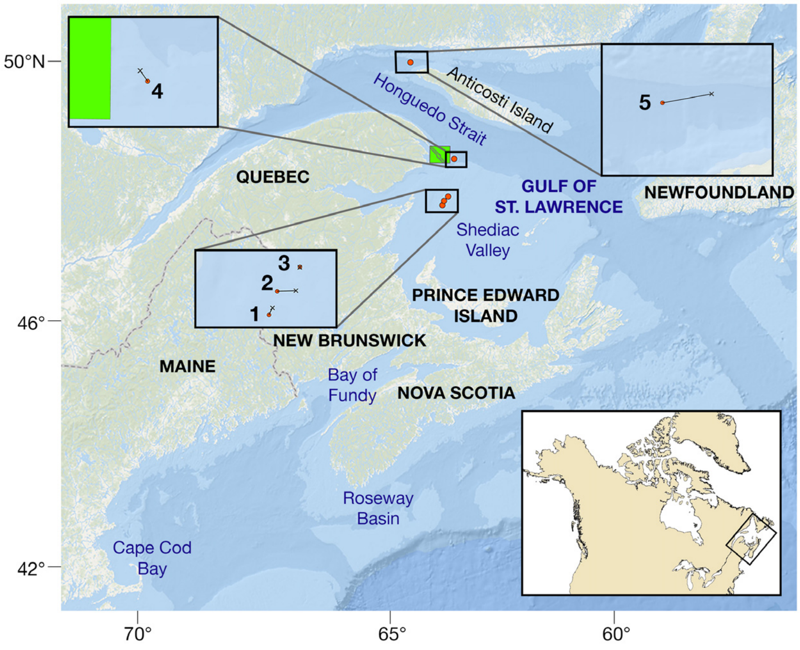

Fig. 1. The Northwestern Atlantic from Cape Cod Bay to the Gulf of St. Lawrence (sources: Canadian Hydrographic Service, General Bathymetric Chart of the Oceans [GEBCO], DeLorne, NaturalVue, Province of Nova Scotia, HERE map data, Garmin, Food and Agriculture Organization, National Oceanic and Atmospheric Administration, United States Geological Survey, Natural Resources Canada, Parks Canada). DTAG deployments on North Atlantic right whales *Eubalaena glacialis* are marked by a straight-line track between the deployment locations (●) and recovery locations (×). The Banc-des-Américains Marine Protected Area is highlighted in green

Table 1. Details of DTAG deployments on North Atlantic right whales *Eubalaena glacialis* including attachment time and location in decimal degrees (DD), the time and location where the tag was recovered (rec'd), the water depth where the tag was deployed and where it was recovered, and the setting of the timer for tag release. Atlantic Daylight Time (for Nova Scotia and New Brunswick) is UTC −3 h (acknowledging that some individuals were in Quebec waters, in this case to the north of those tagged in the Atlantic time zone), meaning all data were collected during daylight

Date	Tag on (UTC)	Lat. (DD)	Long. (DD)	Tag rec'd (UTC)	Lat. (DD)	Long. (DD)	Water depth (m)	Intended duration (h)
10 Aug 2019	19:29	47.8367	−63.8355	21:50	47.8567	−63.8203	84–81	2
14 Aug 2019	17:14	47.9048	−63.8013	14:08[a] (+1)	47.9069	−63.7207	92–75	3
15 Aug 2019	18:00	47.9757	−63.7039	18:45	47.9745	−63.7048	78–79	5
10 Aug 2020	17:45	48.5551	−63.5758	22:13	48.5730	−63.5952	123–124	5
12 Aug 2020	12:30	50.0338	−64.6387	17:38	50.0521	−64.4989	179–158	5

[a] Note that the tag deployed on 14 August 2019 was recovered on the subsequent day (15 August) and thus recovery provides no information on potential detachment time

2.2. Analyses

The DTAGs were programmed and the data downloaded using host software provided by Mark Johnson (Johnson & Tyack 2003). The data were unpacked, calibrated, and corrected for depth-drift using MATLAB (2020a, MathWorks) scripts adapted from those originally used by Johnson & Tyack (2003), and user-defined temperature-depth data point pairs associated with the time the animal spent at the surface.

Accelerometer and magnetometer data were converted to pitch, roll, and yaw through a naïve filter-based approach. This operates by first isolating the gravitational component of the accelerometer signal, A_g, by applying a one-half fluking period moving average filter to the acceleration data, which rejects the dynamic fluctuations induced by animal fluking. The vectorial components of A_g were then decomposed into tag (and therefore whale) pitch and roll with respect to gravity using inverse trigonometric calculations. The pitch and roll estimates were used to rotate the magnetometer signal into a gravitationally aligned reference frame, allowing yaw to be computed using the x and y components of the rotated magnetometer signal.

Accelerometer data were also used to determine likely tag slippage by employing an automated bidirectional sliding-window analysis of animal gait patterns. As the animals exhibit consistent and periodic fluking behaviours during propulsion, pattern shifts in the accelerometer data were assumed to be tag slippage incidences (Zhang et al. 2022). The data were analysed both forward-in-time and backward-in-time to ensure slippages were correctly and confidently identified.

Once the depth data were calibrated and corrected, dive profiles were analysed using a custom-made script (adapted from Wright et al. 2017) in Igor Pro (Version 6.3.4.1, Wavemetrics). The period of the analyses was limited to the beginning of the second dive until the beginning of the last descent in the data set. This was done to eliminate the dive immediately following the tagging, as well as the last dive, in case it was truncated by the release of the tag. Any data at depths of 5 m or less was deemed to be surface activity, as were any dives of 15 s or less in duration. Bottom time was defined as the period between first arrival at 85% of the maximum depth of the dive, and the last moment the animal passes 85% of maximum depth on the way back to the surface. Dives were initially assigned to 1 of 2 groups: even dives, with similar descent and ascent times; and uneven dives, with an ascent 75% longer than a descent, or vice versa. Even dives were then further separated into 3 categories: parabolic dives, which were characterised by descents with a declining vertical speed (i.e. 50% of the maximum depth was achieved in the first 35% of the duration of the descent, with the remaining 50% of the depth taking 65% of the duration of the descent to achieve); U-shaped dives, where 55% or more of the total dive time was spent at the bottom; and V-shaped dives, which had even ascent and descents and less than 55% of the total dive time spent in the bottom phase.

Similarly, dives were categorised into 'shallow,' 'bottom,' and 'midwater' groupings based on the depth of the water over straight-line track of the animal during the deployment. The depth at the deployment and recovery locations were taken from the GEBCO Grid (GEBCO Bathymetric Compilation Group 2023), which provides bathymetry data, in m, on a 15 arc-second interval grid. If the straight-line track crossed lines of bathymetry at 10 m intervals, these locations and depths were also extracted. Water depths for the beginning of each dive were then approximated by extrapolating from these points, assuming a constant horizontal movement of the whales. Dive categories were determined by the maximum depth of the dive: shallow dives were those within the 15 m (approximately 1 whale length) closest to the surface (creating an effective category of dives to between 5 and 15 m); bottom dives were those where the whales reached within 15 m of the approximate bottom depth in the area; and midwater dives were those to the remaining intermediate depths in the water column.

Every deployment suffered from repeated tag slippage. In most cases, larger slips appear to have arisen from a series of smaller slips that were not individually identifiable. As a result, the 3D orientation of the tag at any given time could not be fully resolved. This meant that a variable, but non-negligible, amount of pitch could be seen to be reflected in roll and orientation (and vice versa), preventing an in-depth analysis of these aspects of diving behaviour. However, even if all of the fluking energy was not contained within the axis of pitch (see Fig. 2), the fluking frequency was still accurately captured. Accordingly, the tagged animal's fluking frequency was used as a proxy for comparing propulsive effort, which has been shown to be strongly correlated in other cetaceans during accelerative and steady-state fluking (Zhang et al. 2022). More commonly used dynamic body acceleration proxies for propulsive effort (e.g. ODBA, VeDBA; Wilson et al. 2006, Gleiss et al. 2011) are not appropriate for animals of this physical size, as effects from body rotations can overwhelm the specific accelerations generated by the animal's motion, leading to inconsistent results (Martín López et al. 2022). As there are multiple tag slippages for each deployment and the tag position cannot be exactly resolved after each slippage, intra-deployment comparisons would lead to additional inconsistencies between slippages. An alternative magnitude-based proxy such as minimum specific acceleration is less sensitive to body rotations (Simon et al. 2012); however, it is still sensitive to on-animal tag positioning (e.g. near centre-of-mass versus on the tail) and only represents a minimum bound rather than a direct estimate of specific acceleration. In contrast, fluking frequency is not affected by body roll or tag position as it does not rely on acceleration magnitudes, and because of this it is sufficient as a proxy for inter- and intra-deployment relative comparisons of animal propulsive effort. Fluking frequency was thus calculated over running time windows the size of the median fluking period (obtained by computing the inverse of the median of the non-zero fluking frequencies for deployment) for each individual (1: 6.84 s; 2: 6.10 s; 3: 2.81 s; 4: 7.15 s; 5: 8.40 s). Acoustic data on the DTAGs were not analysed beyond a cursory review as animals were not alone in the area and thus, it was not possible to distinguish the origins of the few calls recorded on the tags. The acoustic data are not discussed further here.

2.3. Whales with mud

To further explore the possibility that right whales have been feeding at or near the bottom in the Gulf of St. Lawrence, images stored in the North Atlantic Right Whale Consortium (NARWC 2022) and taken in the Gulf of St. Lawrence were explored for whales with mud on their head, in a way similar (albeit more simplistic) to Hamilton & Kraus (2019). The proportion of sightings where mud was recorded on the heads of 1 or more whales was estimated each year for the 2010—2020 period.

3. RESULTS

3.1. Diving behaviour

Just over 13.5 hours (0.22 to 4.75 h per tag) of diving behaviour were recorded from 5 individuals, generating a dataset containing 94 dives in total (4 to 43 dives per whale) at maximum depths varying from 37 to 175 m depending on the animal (see Table 2). Dive times ranged from the defined minimum of 15 s to 16 min 18 s, with an overall mean of 4 min 31 s (individual means ranging from 1 min 20 s to 9 min 41 s). One whale (No. 3) entered into a surface active group (SAG) almost immediately after tagging, and the tag was knocked off after 14 min. This animal spent most of the deployment period at depths less than 15 m, with 1 dive to around 37 m, which would be expected given the involvement in the SAG. This tag was not considered further in quantitative analyses (i.e. all results subsequently reported are with n = 4). The other 4 tags stayed on for periods close to (or at) their intended durations (i.e. 2 to 4.5 h) and displayed a range of dive types and depths (see Fig. S1 in the Supplement at www.int-res.com/articles/suppl/n054p155_supp.pdf).

Of these 4 animals, 2 were male and 2 were female, with 1 of each being a younger individual, under 10 yr old, and the other being in their early 30s (Table 2).

Table 2. Summary of the results from DTAG data from North Atlantic right whales *Eubalaena glacialis*. NARWC ID: numbers and names assigned by the North Atlantic Right Whale Consortium (NARWC) and which were provided as part of the extracted data (NARWC 2022). Note that deployment duration was calculated from the beginning of the first full dive to the beginning of the start of the last 'dive', but the usable data starts at the beginning of the second dive as the first dive (immediately after tagging) was discarded. Shallow transit time consists of ascents and descents to and from shallow dives only. Midwater transit time consists of ascents and descents to and from midwater and bottom dives. Duration metrics are presented as hh:mm:ss

Tag deployment	1	2	3	4	5
Tag date	10 Aug 2019	14 Aug 2019	15 Aug 2019	10 Aug 2020	12 Aug 2020
NARWC ID	4140 (Casper)	1934	1419	1720 (Galileo)	4190 (Curlew)
Sex	M	F	M	M	F
Min. age at tagging (yr)	7	30	34	33	8
Bottom depth of deployment (m)	84–81	92–75	78–79	123–124	179–158
Deployment duration	02:02:43	02:32:20	00:13:59	04:18:46	04:46:57
Usable data (from start dive 2)	01:52:28	02:26:15	00:12:58	04:15:42	04:44:15
Max. depth (m)	80.2	86.1	37.3	123.0	174.7
Total surface time	00:41:37	01:43:10	00:07:36	01:11:39	02:41:36
Total shallow bottom time	00:00:00	00:05:02	00:00:27	00:01:38	00:09:21
Total midwater bottom time	00:00:00	00:01:11	00:01:20	00:00:52	00:11:38
Total bottom bottom time	00:54:54	00:23:20	00:00:00	02:27:27	00:38:14
Shallow transit time	00:00:00	00:02:21	00:00:22	00:01:06	00:08:08
Midwater transit time	00:15:56	00:11:09	00:03:11	00:32:57	00:55:15
% Surface time	37.0	70.5	58.6	28.0	56.9
% Shallow bottom time	0.0	3.4	3.5	0.6	3.3
% Midwater bottom time	0.0	0.8	10.3	0.3	4.1
% Bottom bottom time	48.8	16.0	0.0	57.7	13.5
% Shallow transit time	0.0	1.6	2.8	0.4	2.9
% Midwater transit time	14.2	7.6	24.6	12.9	19.4
Combined surface and shallow	00:41:37	01:50:34	00:08:26	01:14:25	02:59:06
Combined midwater	00:15:56	00:12:21	00:04:32	00:33:49	01:06:54
Combined bottom	00:54:54	00:23:20	00:00:00	02:27:27	00:38:14
% Combined surface and shallow	37.0	75.6	65.0	29.1	63.0
% Combined midwater	14.2	8.4	35.0	13.2	23.5
% Combined bottom	48.8	16.0	0.0	57.7	13.5

Collectively, these 4 animals performed more U-shaped dives than any other type during the deployments (mean of individual proportions was 50%; range 12–92%). Qualitatively, the higher activity levels within this dive type in terms of both high fluking frequency and the frequent, abrupt changes in roll and orientation (see Fig. 2, Table 3) suggest that these dives were likely related to foraging. Despite this, brief periods of inactivity can be seen in many U-shaped dives during ascent and descent (see Fig. 2). These U-shaped dives were also the deepest dives in general, almost exclusively reaching the bottom (see Table 4).

In contrast, the parabolic dives had some of the lowest level of activity (see Table 3). In some cases, fluking frequency was not just low, but absent entirely for much of the dives (see Fig. 3, but also noting that an above-zero fluking rate is artificially extended into the beginning of the dive due to the use of the calculation window of the median fluking period for the whole deployment). They were most prevalent in the shallowest of dives (grand mean of individual proportions was 66%; range 40–100%) and all but 2 of those recorded went to a maximum depth around 10 m, with the remaining 2 reaching the midwater (see Table 4).

Uneven dives were the most prevalent of all dive types in midwater depths (grand mean 82%; range 46–100%) and were also quite numerous in the shallow depth range (see Table 4). Activity levels were inconsistent from one dive to the next, both in extent and distribution throughout the elements of the dive. Finally, V-shaped dives were only recorded for a single animal (Tag 5) at midwater and near-bottom depths. The activity levels for the V-shaped dives were somewhere between the high levels of the U-shaped dives, and the low levels of the parabolic dives (Table 3).

Despite the limited qualitative analysis of the 3D movement data, it was clear that *Eubalaena glacialis* tended to approach (or sometimes exceed) a vertical position in the water column (i.e. ±90°) while descending to, or ascending from, U-shaped dives (see Fig. 2),

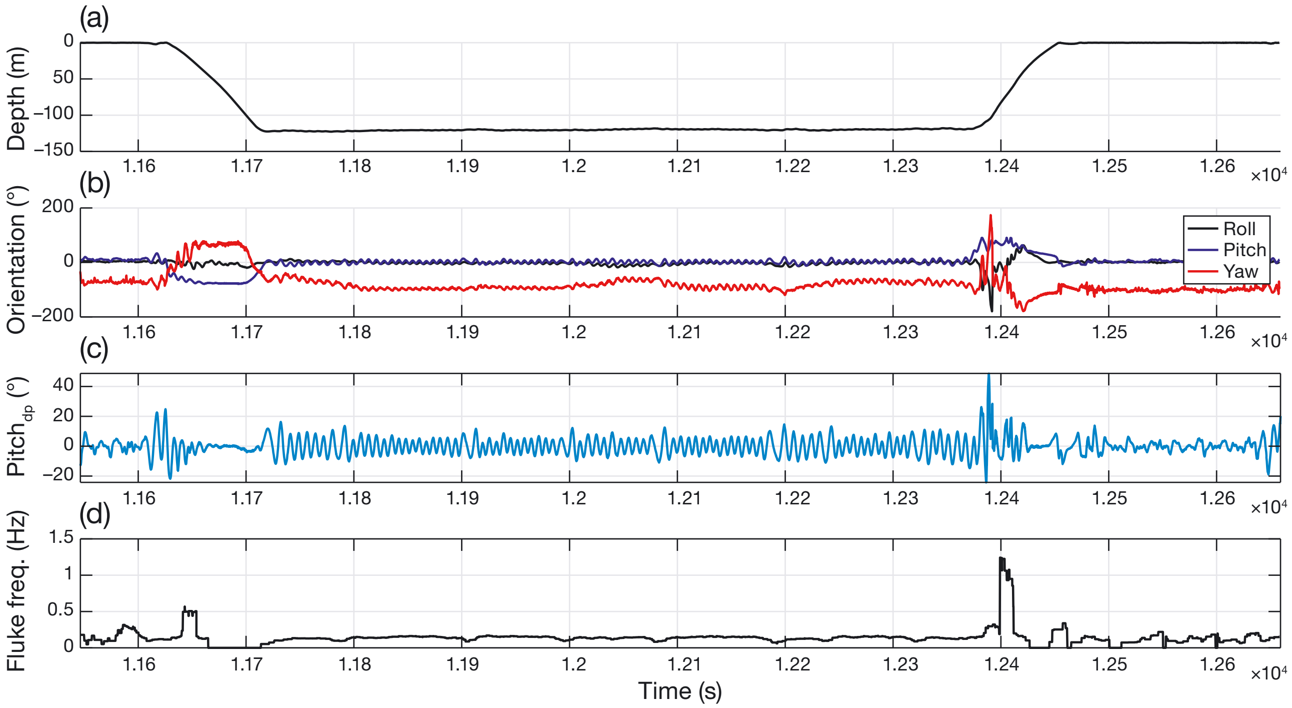

Fig. 2. Foraging dive example from North Atlantic right whale *Eubalaena glacialis* Tag 4 over time (s) showing (a) depth profile; (b) approximate pitch, roll and heading (yaw); (c) approximate relative pitch (i.e. high-pass filtered to remove the overall angle of the whale in the water column); and (d) fluking frequency. Note that in the pitch and yaw traces the sinusoidal fluking signal is present in the yaw (heading), despite the fact the animal is at (or near) 0 roll (i.e. vertically upright), which indicates that the tag orientation has not been fully resolved

Table 3. Indications of energy expended by North Atlantic right whales *Eubalaena glacialis* during the different dive types provided as a mean (with range) across individuals (except for Tag 3, i.e. n = 4). Vertical descent and ascent speeds are provided, representing minimum values for actual angular velocities, given the near-vertical orientation of the animals observed during these dive phases. Fluking rates were calculated over a running time window the size of each animals' median fluking period. Note that between-individual ranges are not provided for V-shaped dives as they were only observed on Tag 5

Dive type	Mean bottom time (s)	Mean transit time (s)	Mean descent velocity (minimum) (m s^{-1})	Mean ascent velocity (minimum) (m s^{-1})	Mean of mean fluking frequency (Hz)
V-shaped	93.0	194.1	1.22	1.12	0.16
U-shaped	355.2 (155.0–632.0)	106.1 (49.0–170.0)	1.77 (1.72–1.87)	1.93 (1.62–2.11)	0.30 (0.12–0.57)
Parabolic	26.2 (14.9–32.8)	21.0 (12.4–28.2)	0.58 (0.40–0.70)	0.54 (0.52–0.56)	0.09 (0.03–0.14)
Uneven	123.2 (26.0–297.9)	80.9 (54.2–106.7)	0.84 (0.47–1.26)	1.12 (0.49–2.29)	0.18 (0.10–0.39)

while achieving much more shallow angles for the same segments of the parabolic dives (see Fig. 3). This position means that the descent speed for the U-shaped dives to the bottom approaches the vertical speed (i.e. dive depth less 5 m divided by time, as 5 m is the threshold for being at the 'surface') for both descent (grand mean 1.77 m s^{-1}; range 1.72–1.87 m s^{-1}, excluding Tag 3) and ascent (grand mean 1.93 m s^{-1}; range 1.62–2.11 m s^{-1}, excluding Tag 3), as very little is unaccounted for in the horizontal direction (although it will still marginally underestimate the true speed of the animal as some horizontal movement will be lost, especially at the beginning and end of the transits). However, this position also means that all data in the other axes become suspect as neither roll nor orientation can be resolved at all when the animal is in the vertical plane. The vertical speeds for the descents and ascents of U-shaped dives are in stark contrast to those of parabolic dives to all depths (descents: grand mean 0.58 m s^{-1}; range 0.4–0.7 m s^{-1}; accents: grand mean 0.54 m s^{-1}; range 0.52–0.56 m s^{-1}, excluding Tag 3) — although these cannot be taken to represent the full animal speeds as the whales were also moving horizontally during these periods.

Table 4. Distribution of dive types throughout the water column for the different North Atlantic right whales *Eubalaena glacialis* that were tagged. Dive types not observed in a given data set (or all data sets) within a given depth category are shaded grey. The most prevalent dive type at each depth is shown in **bold and underlined**

Dive type	Tag 1 No. dives	Tag 1 Mean depth (range)	Tag 2 No. dives	Tag 2 Mean depth (range)	Tag 3 No. dives	Tag 3 Mean depth (range)	Tag 4 No. dives	Tag 4 Mean depth (range)	Tag 5 No. dives	Tag 5 Mean depth (range)
Shallow										
V-shaped										
U-shaped			2	5.8 (5.7–5.9)						
Parabolic			**4**	**8.0 (6.4–8.7)**	**1**	**10.5**	**3**	**10.0 (8.5–11.7)**	**12**	**9.0 (6.3–14.1)**
Uneven			4	7.1 (5.9–8.6)					9	9.6 (6.6–12.1)
Midwater										
V-shaped									5	88.1 (18.7–142.6)
U-shaped										
Parabolic									2	27.0 (25.9–28.0)
Uneven			**1**	**73.7**	**3**	**24.9 (15.4–37.3)**	**2**	**27.0 (19.7–34.3)**	**6**	**22.9 (16.1–28.8)**
Bottom										
V-shaped									4	162.3 (153.6–173.4)
U-shaped	**11**	**77.4 (73.9–80.3)**	**2**	**85.1 (84.1–86.1)**			**14**	**120.6 (115.3–123.0)**	**5**	**169.2 (164.9–174.7)**
Parabolic										
Uneven	1	79.2	3	79.5 (77.6–81.4)						

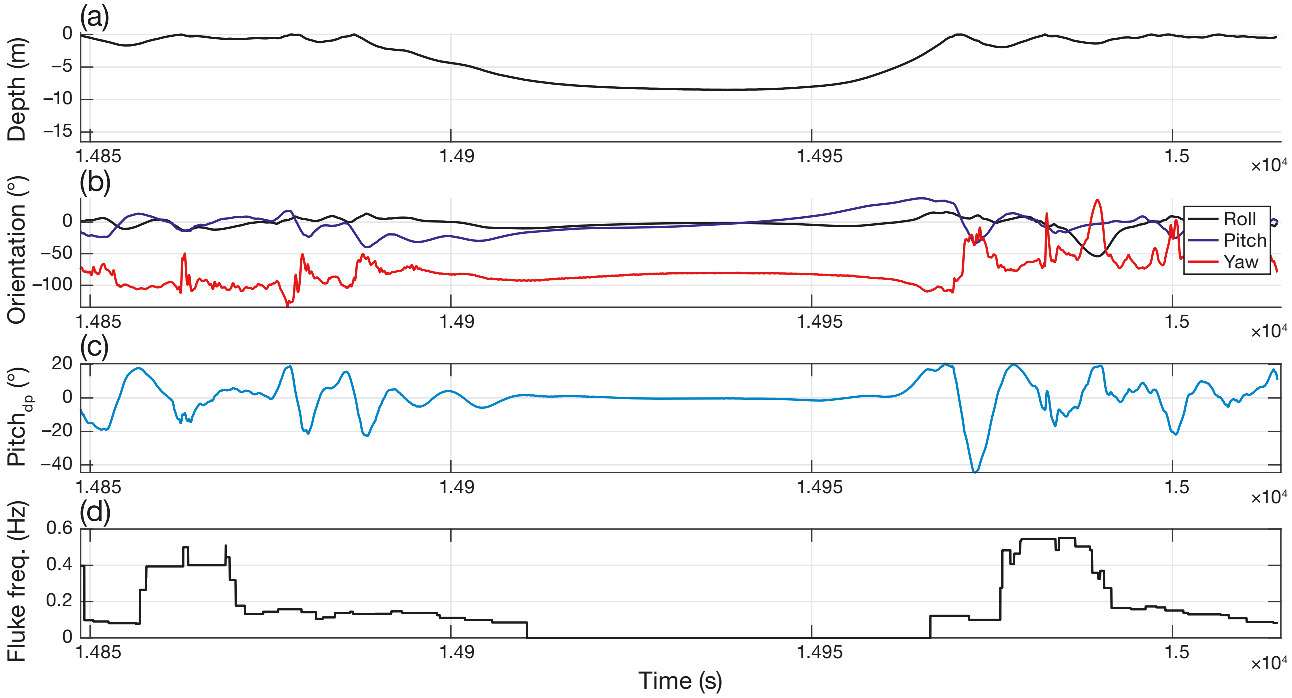

Fig. 3. Parabolic (sleeping) dive example from North Atlantic right whale *Eubalaena glacialis* Tag 4 over time (s) showing (a) depth profile; (b) approximate pitch, roll and heading (yaw); (c) relative pitch (i.e. high-pass filtered to remove the overall angle of the whale in the water column); and (d) approximate fluking frequency. Note that in the pitch and yaw trace there is obvious interaction between all 3 axes (particularly pitch and yaw), indicating that the tag orientation has not been fully resolved. However, this would not influence the periods of complete fluking inactivity shown in pitch or fluking rate that extend from descent to ascent in both dives shown

When rolling could be resolved with reasonable accuracy (i.e. at points away from the near-vertical), it was found to be uncommon in the data across all dive types, with animals typically remaining within 20° of upright at all times. On only 2 occasions (both during U-shaped dives) were animals observed to turn upside-down (or close to it): once on a descent and once at the end of a bottom phase. Finally, the horizontal re-orientation of animals (e.g. turning from a northward direction to an eastward direction) tended to occur quite slowly throughout the tag records. Nonetheless, whales were occasionally observed to turn horizontally throughout a full 360° (or more) within the course of 1 dive.

In terms of time spent in the different segments of the water column, the whales (with the exception of Tag 3) spent between 13.5 and 57.7% of the time during the deployments within 15 m of the sea floor (Table 2), primarily engaged in U-shaped dives. Individuals spent 29.1 to 75.6% of their time within 15 m of the surface, primarily at (or very close to) the surface, but also engaging in shallows dives that were most often parabolic. However, shallow dives constituted less than 4% of each deployment (Table 2), partly due to the short nature of the predominant parabolic dives. Time spent in the midwater between these 2 segments was generally quite limited, ranging from 8.4 to 23.5% of the deployment durations (grand mean 18.5%). Most of this time was spent transiting the water column during dives into the bottom segment (see Table 2).

3.2. Whales with mud

As shown in Table 5, of the 5724 sightings exported from the NARWC catalogue (NARWC 2022), 65 included animals observed with mud on their heads (representing 1.1%). For the complete years 2017–2019 where whales were known to be more common in the GSL, 59 of the 4596 sightings (or 1.3%) included observations of whales with mud on their heads.

Table 5. Sightings of North Atlantic right whales *Eubalaena glacialis* with mud on their heads in the Gulf of St. Lawrence. Data as of 1 July 2022 (NARWC 2022). Data is not effort-corrected

Year	Count of sightings	Count of unique IDs	Images with mudded whales (%)
2010	2	1	0 (0)
2011	3	3	0 (0)
2012	10	8	0 (0)
2013	8	4	0 (0)
2014	43	21	0 (0)
2015	97	51	1 (1.0)
2016	136	50	3 (2.2)
2017	767	134	8 (1.0)
2018	1377	132	46 (3.3)
2019	2452	134	5 (0.2)
2020[a]	829	89	2 (0.2)
Total	5724		65 (1.1)
2017–2019	4596		59 (1.3)

[a] Analysis of 2020 data was incomplete at the time of the data request of the North Atlantic Right Whale Consortium

4. DISCUSSION

This is the first tagging study conducted on right whales in the Gulf of St. Lawrence and it provides critical insight into their particular foraging behaviour in this new habitat. Despite the low sample size, our dataset covers a range of individuals from the population, as it included both adult and younger males and females. Although the short deployments and small sample size prevents any separation of possible annual variability from geographical, age, or sexual differences, or even individual variation, the results strongly suggest that, at least during the daytime, right whales in the Gulf do not regularly feed at or near the surface. The majority of all foraging activity (i.e. U-shaped dives) observed across all deployments occurred at, or very close to, the bottom. Foraging was the primary activity for the 2 longer-duration tags placed on males (Tags 1 and 4), as U-shaped dives made up the majority of those in the dataset. U-shaped dives were less prevalent for the 2 females tagged (Tags 2 and 5), but the resulting bottom time still made up 16.0 and 13.5% of the deployment periods. These results are consistent with the finding that *Calanus* spp. are present in larger numbers near the seafloor (acknowledging that the plankton sampler was unable to sample right to the bottom) during the day in areas of the Gulf where *Eubalaena glacialis* have been observed most commonly (Sorochan et al. 2023). In particular, the 2 tags lasting for more than 30 min from 2019 (Tags 1 and 2) were deployed within 24 h of a plankton tow at the same location (reported in Sorochan et al. 2023), where *Calanus* spp. were found in larger numbers near the seafloor and both whales dove near to, if not to, the bottom (given the approximated depth, based on the depths at the locations of deployment and release of the tags).

The analysis of images of mud on the heads of whales in the Gulf also provides some support for at-or-near-bottom foraging. The 1.3% of sightings with observations of mud in the 2017–2019 catalogue is consistent with the findings of Hamilton & Kraus (2019), who reported seafloor encounter rates (i.e. occasions where mud was observed on the whale heads) in the Gulf of at least 1.2% (1980–2016). These proportions are substantially lower than those observed in the Bay of Fundy (7.3%; Hamilton & Kraus 2019). However, the substrate in the Shediac Valley area, where the whales were mostly observed from 2017 to 2019, is not just made up of soft material, but is hard or mixed across large areas.[2] This would certainly reduce observations of whales with mud on their heads in the Gulf. In combination, these results suggest that the whales are utilising the Gulf in a very similar way to their previous summer use of the lower Bay of Fundy, instead of like their winter feeding strategy in Cape Cod Bay. This adds further credence to the idea that climate-related shifts in prey distribution and quality are causing changes in the distribution of right whales during the summer.

All the whales spent the majority of their time at either the surface or near the bottom. Even Whale 5, who undertook a large number of V-shaped dives (often believed to be associated with travel or searching; e.g. Baumgartner & Mate 2003), spent the majority of the time within 15 m of the surface. The resulting bi-phasic use of the water column means that whales also spent the majority of their time exposed to the risk of entanglement in groundlines near the bottom or vessel strikes at or near the surface. The near-vertical descents and ascents also suggest they are wasting as little time as possible in-between the surface and bottom. The use of midwater depths for transit only does somewhat limit vertical overlap with the end lines of fishing gear in the water column. However it is important to note that this does not eliminate the risks presented by those ropes as they may be slack in midwater creating obstacles across 3 dimensions. It would also not prevent whales from encountering end lines 'spaghetti-ing' (i.e. loose excess rope looping around chaotically) at the surface during slack water.

One additional consideration for ship strike risk is the possibility that right whales may be sleeping during parabolic dives to around 10 m, given the similarities with the sleeping dives found in porpoises (Wright et al. 2017). Specifically, the stereotypical parabolic shape of the dive, the very low activity levels, and relatively low vertical velocities (if not overall whale speeds) are consistent across both species. The low activity levels also indicate their purpose is not skim feeding, due to the need for a certain level of fluking to propel the whale's open mouth through the water (van der Hoop et al. 2019). Similarly, the gradual depth changes to around 10 m of the parabolic dives are also inconsistent with the skim-feeding behaviour reported by Parks et al. (2012) for tagged whales in Cape Cod Bay. There the whales spent 84% (62–98%) of their time with their dorsal surface between 0.5 and 2.5 m deep and moved for periods consistently at the depth of greatest prey concentration. Parks et al. (2012) also reported a complete lack of U-shaped dives, which is also inconsistent with our finding in the Gulf. However, it must be noted that these results do not exclude the possibility that *E. glacialis* may occasionally engage in skim feeding in the Gulf, particularly given our small sample size.

The parabolic dives were the most prevalent dive type in shallow waters, although they only represented a small proportion of the total dive time recorded for each animal (less than 4% of the deployment period). Even if the parabolic dives are not all connected with sleeping behaviour (or even not at all), they still place the whales away from the surface and out of sight, but within the draft depth of many commercial shipping vessels for the duration of these dives. Additionally, if the animals are indeed sleeping, then they would be less aware of their surroundings and likely also less responsive (Miller et al. 2008), leaving them less likely to react appropriately to an approaching ship.

Finally, the distribution of the whales in the water column also has implications for the total amount of anthropogenic noise to which they are exposed. The vertical proximity to a nearby source (e.g. a ship) will clearly influence the level of noise received by an animal. However, sound propagation is heavily dependent on the variation of sound speed with depth and temperature, meaning that the depth of the whale greatly influences the received level from a more distant source of noise (Urick 1983).

The results presented here are preliminary, and only represent the daytime activity of 5 whales sampled in 2 years. However, they are highly suggestive that right whales spend the majority of their time in the locations where they are at greatest risk of human interactions: at the surface or at the bottom. Additional deployments of biologging tags are needed, especially overnight, to confirm this bi-phasic distribution of right whales in the water column. In particular, complete records of the activity and full dive profiles of the whales over the full diel cycle would provide information about any temporal trends that might inform strategies to mitigate risks. It may also reveal the full suite of whale behaviours at depth, which may support more innovative engineering-based solutions to improve human–whale coexistence in the Gulf of St Lawrence.

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[2] www150.statcan.gc.ca/n1/pub/38-20-0001/2021001/m04-eng.htm

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