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Drift Dives in a Bowhead Whale (*Balaena mysticetus*)

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During so-called drift dives, an animal spends a proportion of the dive not moving, suspended in the water column while drifting up- or downwards, depending on its buoyancy. Roles of drift dives are believed to include resting, sleeping, or digesting food (e.g., Crocker et al., 1997; Miller et al., 2004; Andersen et al., 2014), which are important components in at least some species' activity cycles. Drift diving was first documented in both species of elephant seals, *Mirounga angustirostris* and *M. leonina* (e.g., Hindell et al., 1991; Le Boeuf et al., 1992), and later other pinnipeds such as New Zealand fur seals (*Arctocephalus forsteri*; Page et al., 2005) and hooded seals (*Cystophora cristata*; Andersen et al., 2014). Drift dives also occur in cetaceans such as sperm whales (*Physeter macrocephalus*; Miller et al., 2008) and humpback whales (*Megaptera novaeangliae*; Zoidis et al., 2014). Herein, we describe the presence of drift dives in a bowhead whale (*Balaena mysticetus*) and hypothesize about their role.

In mid-April 2013, four bowhead whales in Disko Bay, West Greenland, were instrumented with Acousonde™ sound and movement tags (www.Acousonde.com) in a tag-retention study carried out by the Greenland Institute of Natural Resources. Tags were connected to a stainless steel or Kevlar tether, 0.5 to 1 m long, and then to a 4-cm stainless steel spear, which was implanted 10 cm under the skin on the whale's dorsal side as described in Heide-Jørgensen et al. (2013). A magnesium link, connected to the tether right above the skin, corroded in the presence of saltwater and detached the tag from the insertion point. While multi-day deployments were sought, all tags detached prematurely within 8 to 25 h. Retrieval was enabled by the ARGOS transmitter (SPOT5; Wildlife Computers, Redmond, WA, USA) and VHF transmitter (ATS Telemetry, Isanti, MN, USA) that were attached to the Acousonde™.

The tags recorded various data streams on nine different channels. Those relevant to this paper are water depth (10 Hz sampling rate), the x-axis of the 3-D accelerometer (10 Hz sampling rate), and acoustic sampling (HTI-96-MIN hydrophone with nominal sensitivity of -201 dB re 1 V/µPa, preamp gain 14 dB, anti-alias filter with 3-dB reduction at 9.2 kHz and 22-dB reduction at 11.1 kHz, 25,811 Hz sampling rate).

While investigating the data, we found that one of the whales' records included dives during which the accelerometer's x-axis ($accel_x$) remained near -1 g for extended periods while the whale was at depth. The front of the Acousonde™ is heaviest as it contains the battery and the electronics, whereas the distal end is made of syntactic foam. Therefore, when free-floating, the Acousonde™ assumes a position near vertical in the water column, and the tag's $accel_x$ channel reports a value near -1 g (see illustration in Figure 1C, inset). Such a position can only be obtained by a tethered tag if a whale is motionless in water with little or no current, or if it is descending vertically on a dive, in which case the depth values would change accordingly. In the cases described here, the value of $accel_x$ remained near -1 g for periods of up to ~48 min while the whale's change in depth over the same period was small, on average a few mm/s. Basically, the Acousonde™ indicated that the whale was immobile at depth while slowly drifting and ascending.

Depth and $accel_x$ values were averaged over 3-s samples (no overlap) throughout each of the four tagged whales' records. The first 1.5 h of data, during which the whales showed behavioral effects of tagging (S. B. Blackwell, unpub. data, 2013-2015; Quakenbush et al., 2015), were excluded from all analyses. In addition, surface intervals were removed by ignoring data collected within 5 m of the surface. All 3-s samples with $accel_x$ values between -1.02 and -0.98 g and a change in depth of less than 20 cm/s were flagged—such samples will hereafter be called "drift samples." One whale (S1, a male as determined by genetics

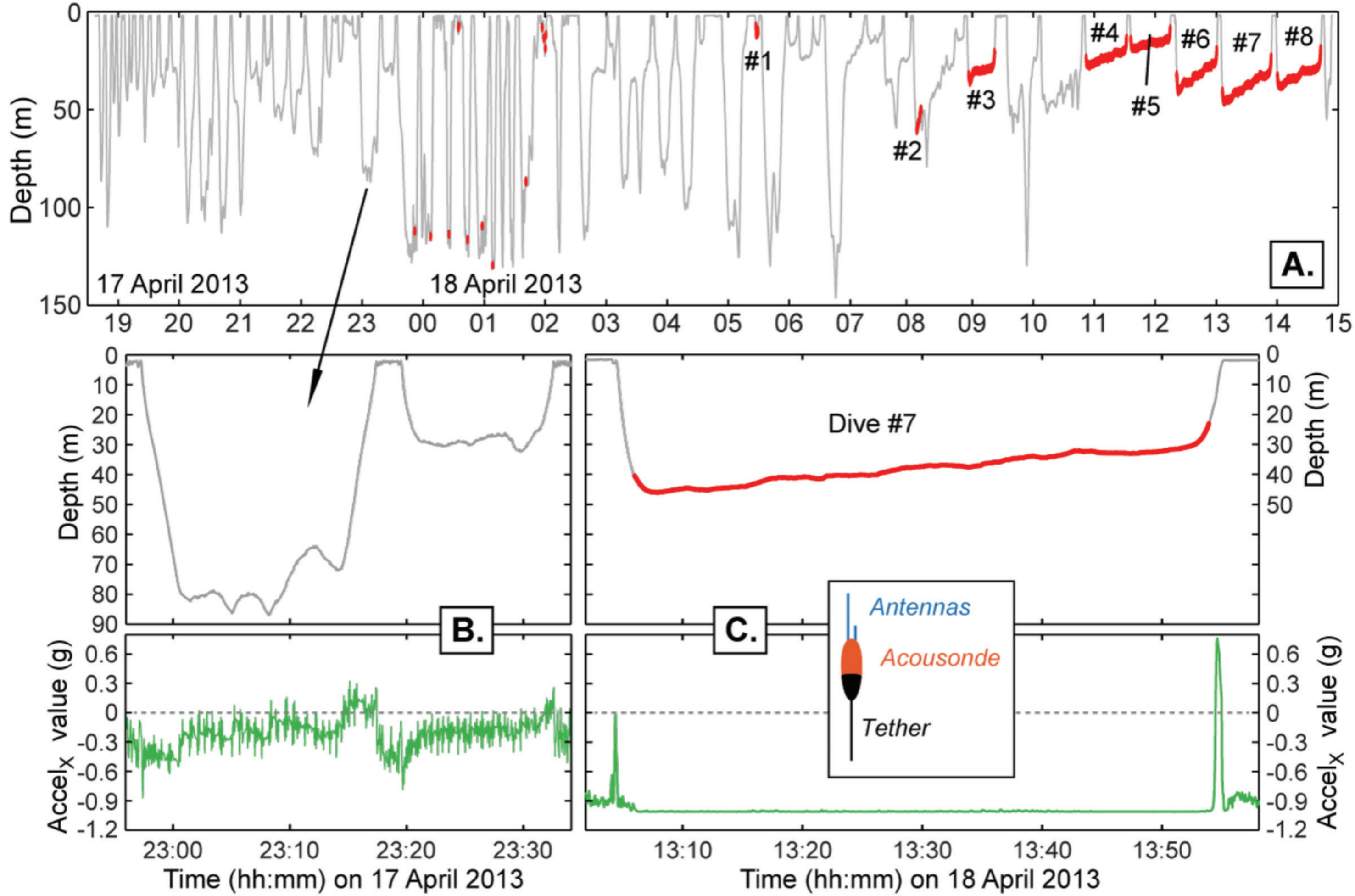

Figure 1. (A) Entire 20-h dive record of whale S1, 17-18 April 2013—red dots show all detected drift samples; (B) two example dives without drifting—with the exception of the sections highlighted in red in (A), dives showed regular stroking by the whale (lower panel), generally of the burst-and-glide type; and (C) drift dive #7 (see Table 1), showing how the accel$_x$ value quickly stabilized at ~-1 g (position of Acousonde™ shown in inset) and stayed there for the dive's entire bottom time of ~48 min.

Table 1. Characteristics of S1's drift periods, and the dives containing those periods, numbered 1 through 8 (see Figure 1). The "Start time" and "Dive duration" pertain to the entire dive. The "Duration of drift" is the time between the first and last drift sample. "% still" indicates the percentage of the drift duration made up by drift samples. "Mean depth" is calculated over the entire drifting duration, while "Mean $accel_x$" and "Mean depth change" are calculated using only drift samples—that is, 3-s samples that met the $accel_x$ and depth change criteria. See text for information on the "Slope of regression on drift." Because depth is a positive value, the negative slopes represent ascent in the water column. S1 was tagged at 1841 h on 17 April 2013.

Dive (and drift) #	Start time of dive (18 April 2013)	Dive duration (mm:ss)	Duration of drift (mm:ss)	% of dive in drift	% still	Mean depth (m)	Mean ± SD $accel_x$ value (milli-g)	Mean ± SD depth change (cm/s)	Slope of regression on drift (mm/s)
1	5:26:32	3:44	2:18	61.6	87.0	10.1	-1,003 ± 7	8.8 ± 4.6	--
2	8:01:58	49:52	4:12	8.4	88.1	55.0	-1,006 ± 5	4.3 ± 2.3	--
3	8:54:50	28:11	25:33	90.7	100.0	30.1	-1,005 ± 5	1.8 ± 2.3	-1.7
4	10:50:44	41:43	39:48	95.4	98.9	23.4	-1,008 ± 5	1.4 ± 2.1	-3.6
5	11:34:57	40:19	38:51	96.4	98.7	16.2	-1,006 ± 6	1.4 ± 2.0	-2.1
6	12:19:06	42:16	39:24	93.2	96.2	32.6	-1,005 ± 7	1.8 ± 2.8	-6.4
7	13:04:32	50:29	47:57	95.0	100.0	38.0	-1,009 ± 3	1.5 ± 2.1	-5.7
8	13:58:28	45:19	42:36	94.0	97.3	32.4	-1,007 ± 6	1.4 ± 2.2	-5.8

from a skin sample obtained during tagging), the subject of this paper, had a total of 4,742 drift samples. The other three whales (T1, T2, and T3) did not demonstrate drift periods of any substantial length: they had 2, 34, and 43 drift samples, respectively, 85% of which were grouped into durations of less than 15 s, and the longest of which lasted 21 s.

In contrast, all but 17 of S1's drift samples occurred during eight different dives (Table 1). Six of those dives (#s 3 through 8 in Table 1) included longer drift periods lasting 25.5 to 48 min, during which the whale was immobile in the water column ($accel_x$ near -1 g) and slowly ascending. More than 96% of 3-s samples included in those periods satisfied the conditions for a drift sample ("% still" column in Table 1). Two shorter periods (#s 1 and 2 in Table 1), less than 4.2 min long, preceded these longer periods but showed similar behavior. Whale S1's 20-h dive record is shown in Figure 1A, together with a comparison of $accel_x$ values during regular dives (Figure 1B) vs drift dives (Figure 1C). All of S1's drift dives were in the second half of his dive record, and five of the eight drift periods (#s 4 through 8) occurred in a continuous bout lasting nearly 4 h, interrupted only by active ascents to the surface to breathe (Figure 1A). Regular fluke stroking resumed during the short dive following dive #8, during which the tag detached.

The average slope of the longer drift periods (#s 3 through 8 in Table 1) was estimated by fitting a linear regression to the drift samples as a function of time while omitting the end of the descent and the start of the ascent. Regression slopes (all ascending) were in the range of 1.7 to 6.4 mm/s (Table 1). These vertical drift rates are remarkably close to neutral buoyancy, a point at which slight changes in buoyancy lead to larger changes in the rate of movement (Aleyev, 1977; Webb et al., 1998). At the generally shallow depths of S1's drift dives (< 50 m), the influence of gas (through the amount of air taken on a dive) is critical. Sperm whales have been observed releasing air to adjust their buoyancy during drift dives (Miller et al., 2004, 2008). Similarly, bubble releases were heard more than a dozen times on S1's acoustic record; such behavior may explain the "bumpiness" in the drift dives' bottom time.

Low levels of flow noise in S1's acoustic record provided further evidence for the lack of movement during drifting at depth as flow noise can be used as a proxy for swim speed (e.g., Simon et al., 2009). Sound pressure levels (SPLs) in the one-third octave band centered at 25 Hz were plotted as a function of depth for 1-s non-overlapping samples taken throughout S1's record (Figure 2). Received levels during the eight drift periods had a median value of 75.6 dB re 1 μPa compared to 117.3 dB for the non-drift samples of the record, a difference of > 40 dB (Figure 2). Note that S1's acoustic record was not otherwise quiet during drift periods, with continuous song by bowhead whales and bearded

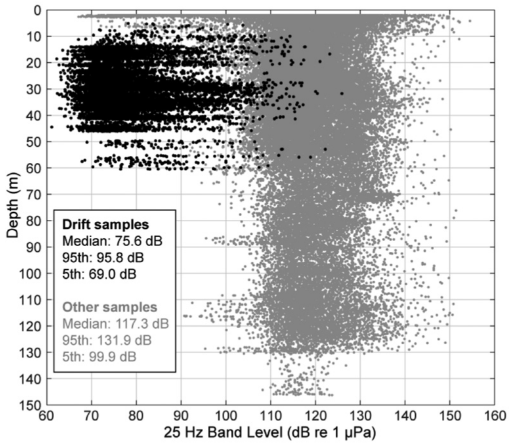

Figure 2. Received sound pressure level in the one-third octave band centered at 25 Hz as a function of depth for 1-s non-overlapping samples taken throughout the record of S1. Black dots denote sound levels taken during times of drifting while gray dots denote sound levels during all other activities. The median, 5th, and 95th percentiles are given for each cloud of points.

seals (*Erignathus barbatus*), occasional calls by beluga (*Delphinapterus leucas*), and numerous cracking icebergs. Median received broadband SPLs during drifting was 107 dB re 1 μPa (10 Hz to 9.3 kHz, n = 14,479 1-s samples, 5th to 95th percentile, 103 to 115 dB).

Mean dive durations for bowhead whales are relatively short, generally between 8 and 18 min (Krutzikowsky & Mate, 2000; Laidre et al., 2007; Heide-Jørgensen et al., 2013; Citta et al., 2021). Meanwhile, reported maximum dive durations are more variable, from less than 30 min for some individuals (Laidre et al., 2007) to more than an hour (Krutzikowsky & Mate, 2000). S1's dive durations were within these ranges: 41.4 min (± SD 7.4 min) for the six dives that included a high percentage of drifting (#s 3 through 8 in Table 1), and 16.4 min (± SD 10.5 min) for the remaining 42 dives of his record.

The function of the dives described here may be for rest or sleep as such is the function usually ascribed to drift dives (e.g., Miller et al., 2008; Meir et al., 2013). The lack of movement (Figure 1), low received levels of sound (Figure 2), and long dive durations all support this assertion. Researchers studying bowhead whales in the field have seen them rest at the surface (e.g., J. C. George, W. R. Koski, & W. J. Richardson, pers. comm., 29 April 2022) and so have fishermen (Christiansen, 1962). Carroll & Smithhisler (1980) also mention cases in which bowheads that were apparently resting were startled when approached by a vessel. Resting underwater has been described in humpback whales (Cartwright & Sullivan, 2009; Bejder et al., 2019) and sperm whales (Miller et al., 2008) but not yet, to our knowledge, in bowhead whales. This may be in part because time-depth information alone, which constitutes the majority of bowhead dive records collected to date, makes it difficult to distinguish drift dives from active foraging dives. This problem has also been reported with other diving marine mammals—for example, distinguishing benthic feeding vs benthic resting dives in elephant seals (Hassrick et al., 2007). An examination of time-depth recorder data from past studies (i.e., Heide-Jørgensen et al., 2013), including manual evaluation of candidate dives, confirmed these difficulties.

The tagging procedure is likely stressful for a bowhead whale, but we have no evidence that S1 reacted differently to tagging than the other three whales in 2013, or the nine whales tagged similarly (with retrievable Fastloc GPS tags) in 2008 through 2011 (Heide-Jørgensen et al., 2013). Effects of tagging were examined for the 2013 whales by quantifying their fluke stroke rate, flow noise, and vertical displacement during surface intervals, all of which returned to baseline 0.5 to 1.5 h after tagging (S. B. Blackwell, unpub. data, 2013-2015; Quakenbush et al., 2015). Meanwhile, S1's first long drift (#3) took place more than 14 h after tagging.

In summary, this paper has shown the presence of drift dives in a bowhead whale dive record. A larger sample size of long-duration records that include accelerometer information will be necessary to determine the importance and purpose of drift dives to bowhead whales.

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Literature Cited

Aleyev, Y. G. (1977). *Nekton*. Dr. W. Junk b.v., The Hague. https://doi.org/10.1007/978-94-010-1324-6

Andersen, J. M., Stenson, G. B., Skern-Maurizen, M., Wiersma, Y. F., Rosing-Asvid, A., Hammill, M. O., & Boehme, L. (2014). Drift diving by hooded seals (*Cystophora cristata*) in the Northwest Atlantic Ocean. *PLOS ONE*, *9*(7), e103072. https://doi.org/10.1371/journal.pone.0103072

Bejder, L., Videsen, S., Hermannsen, L., Simon, M., Hanf, D., & Madsen, P. T. (2019). Low energy expenditure and resting behaviour of humpback whale mother-calf pairs highlights conservation importance of sheltered breeding areas. *Scientific Reports*, *9*, 771. https://doi.org/10.1038/s41598-018-36870-7

Carroll, G. M., & Smithhisler, J. R. (1980). Observations of bowhead whales during spring migration. *Marine Fisheries Review*, *42*(9-10), 80-85.

Cartwright, R., & Sullivan, M. (2009). Behavioral ontogeny in humpback whale (*Megaptera novaeangliae*) calves during their residence in Hawaiian waters. *Marine Mammal Science*, *25*(3), 659-680. https://doi.org/10.1111/j.1748-7692.2009.00286.x

Christiansen, B. (1962). *Grønlandshval, og hval som sover* [The Greenland right whale, and whales which sleep]. *Norsk Hvalfangst-tidende*, *51*(2), 55-56.

Citta, J. J., Quakenbush, L., & George, J. C. (2021). Distribution and behavior of Bering-Chukchi-Beaufort bowhead whales as inferred by telemetry. In J. C. George & J. G. M. Thewissen (Eds.), *The bowhead whale,* Balaena mysticetus*: Biology and human interactions* (pp. 31-56). Academic Press. https://doi.org/10.1016/B978-0-12-818969-6.00004-2

Crocker, D. E., Le Boeuf, B. J., & Costa, D. P. (1997). Drift diving in female northern elephant seals: Implications for food processing. *Canadian Journal of Zoology*, *75*(1), 27-39. https://doi.org/10.1139/z97-004

Hassrick, J. L., Crocker, D. E., Zeno, R. L., Blackwell, S. B., Costa, D. P., & Le Boeuf, B. J. (2007). Swimming speed and foraging strategies of northern elephant seals. *Deep-Sea Research II*, *54*, 369-383. https://doi.org/10.1016/j.dsr2.2006.12.001

Heide-Jørgensen, M. P., Laidre, K. L., Nielsen, N. H., Hansen, R. G., & Røstad, A. (2013). Winter and spring diving behavior of bowhead whales relative to prey. *Animal Biotelemetry*, *1*, 15. https://doi.org/10.1186/2050-3385-1-15

Hindell, M. A., Slip, D. J., & Burton, H. R. (1991). The diving behaviour of adult male and female southern elephant seals, *Mirounga leonina* (Pinnipedia: Phocidae). *Australian Journal of Zoology*, *39*, 595-619. https://doi.org/10.1071/ZO9910595

Krutzikowsky, G. K., & Mate, B. R. (2000). Dive and surfacing characteristics of bowhead whales (*Balaena mysticetus*) in the Beaufort and Chukchi Seas. *Canadian Journal of Zoology*, *78*, 1182-1198. https://doi.org/10.1139/z00-046

Laidre, K. L., Heide-Jørgensen, M. P., & Nielsen, T. G. (2007). Role of the bowhead whale as a predator in West Greenland. *Marine Ecology Progress Series*, *346*, 285-297. https://doi.org/10.3354/meps06995

Le Boeuf, B. J., Naito, Y., Asaga, T., Crocker, D., & Costa, D. P. (1992). Swim speed in a female northern elephant seal: Metabolic and foraging implications. *Canadian Journal of Zoology*, *70*, 786-795. https://doi.org/10.1139/z92-111

Meir, J. U., Robinson, P. W., Vilchis, L. I., Kooyman, G. L., Costa, D. P., & Ponganis, P. J. (2013). Blood oxygen depletion is independent of dive function in a deep diving vertebrate, the northern elephant seal. *PLOS ONE*, *8*(12), e83248. https://doi.org/10.1371/journal.pone.0083248

Miller, P. J. O., Aoki, K., Rendell, L. E., & Amano, M. (2008). Stereotypical resting behavior of the sperm whale. *Current Biology*, *18*(1), R22. https://doi.org/10.1016/j.cub.2007.11.003

Miller, P. J. O., Johnson, M. P., Tyack, P. L., & Terray, E. A. (2004). Swimming gaits, passive drag and buoyancy of diving sperm whales, *Physeter macrocephalus*. *Journal of Experimental Biology*, *207*, 1953-1967. https://doi.org/10.1242/jeb.00993

Page, B., McKenzie, J., & Goldsworthy, S. D. (2005). Inter-sexual differences in New Zealand fur seal diving behaviour. *Marine Ecology Progress Series*, *304*, 249-264. https://doi.org/10.3354/meps304249

Quakenbush, L., Delnavaz, V., Heide-Jørgensen, M. P., Kauffman, M., Rekdal, S. L., Nielsen, N. H., & Blackwell, S. B. (2015, December). Short-term effects of tagging on West Greenland bowhead whales (*Balaena mysticetus*). *Proceedings of the 21st Biennial Conference on the Biology of Marine Mammals*, San Francisco, CA.

Simon, M., Johnson, M., Tyack, P., & Madsen, P. T. (2009). Behaviour and kinematics of continuous ram filtration in bowhead whales (*Balaena mysticetus*). *Proceedings of the Royal Society B: Biological Sciences*, *276*(1674). https://doi.org/10.1098/rspb.2009.1135

Webb, P. M., Crocker, D. E., Blackwell, S. B., Costa, D. P., & Le Boeuf, B. J. (1998). Effects of buoyancy on the diving behavior of northern elephant seals. *Journal of Experimental Biology*, *201*, 2349-2358. https://doi.org/10.1242/jeb.201.16.2349

Zoidis, A. M., Lomac-MacNair, K. S., Chomos-Betz, A. E., Day, A. J., & McFarland, A. S. (2014). Effects of sex, seasonal period, and sea state on calf behavior in Hawaiian humpback whales (*Megaptera novaeangliae*). *Aquatic Mammals*, *40*(1), 44-58. https://doi.org/10.1578/AM.40.1.2014.44