

Deep-diving behaviour of the northern bottlenose whale, *Hyperoodon ampullatus* (Cetacea: Ziphiidae)

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Using suction-cup attached time–depth recorder/VHF radio tags, we have obtained the first diving data on northern bottlenose whales (*Hyperoodon ampullatus*), the first such data on any species within the family Ziphiidae. Two deployments in 1997 on northern bottlenose whales in a submarine canyon off Nova Scotia demonstrated their exceptional diving ability, with dives approximately every 80 min to over 800 m (maximum 1453 m), and up to 70 min in duration. Sonar traces of non-tagged, diving bottlenose whales in 1996 and 1997 suggest that such deep dives are not unusual. This combined evidence leads us to hypothesize that these whales may make greater use of deep portions of the water column than any other mammal so far studied. Many of the recorded dives of the tagged animals were to, or close to, the sea floor, consistent with benthic or bathypelagic foraging. A lack of correlation between dive times and surface intervals suggests that the dives were predominately aerobic.

Keywords: northern bottlenose whale; *Hyperoodon ampullatus*; Ziphiidae; time–depth recorder; diving; foraging

1. INTRODUCTION

Beaked whales (the Ziphiidae) are one of the least known mammalian groups. All beaked whales are considered to be deep divers, based predominantly on their deep-water distribution and long dive times (Mead 1989*a*), but there is little direct evidence of dive depths to support this claim (Schreer & Kovacs 1997).

There has been some speculation that the northern bottlenose whale (*Hyperoodon ampullatus*) may be one of the deepest and longest-diving mammals (Benjaminsen & Christensen 1979; Gray 1882). Ohlin (1893) reported seeing 500 fathoms (900 m) of line taken out by a harpooned bottlenose whale in less than two minutes, while Gray (1882) reported that harpooned animals remained submerged for two hours and came to the surface ‘as fresh as if they had never been away’. Ohlin (1893) also reported the possibility of benthic feeding, based on the presence of sea stars (echinoderms) in the stomachs of some animals and mud on the beaks of others. However, dive profiles have not previously been obtained for this or any other species of beaked whale. Here we present the first detailed information on the diving behaviour of beaked whales, based primarily on deployments of time–depth recorders (TDRs) on two northern bottlenose whales in the Gully, a submarine canyon off the coast of Nova Scotia.

2. METHODS

Fieldwork was conducted between June and August in 1996–1998 from a 13 m auxiliary sailboat in the Gully, 370 km

east of Halifax, Nova Scotia (approximate position: 43° N, 59° W). Northern bottlenose whales are consistently found in this canyon and have been studied there since 1988 (Whitehead *et al.* 1997*a,b*). Differentiating adult males from adult females in the field was based on their sexual dimorphism in size and head shape (Gray 1882; Mead 1989*b*).

Suction-cup attached tags were deployed on free-swimming whales using a crossbow (Baird 1998). Each tag contained a TDR and a VHF radio transmitter, and floated upon release from the whale. TDRs were built by Wildlife Computers, Redmond, WA, USA (tag no. 1) and by AGO Environmental Electronics Ltd, Victoria, BC, Canada (tag no. 2). Tag no. 1 recorded depth (every 1 s at 4 m accuracy) and velocity (every 5 s), while tag no. 2 recorded only depth (every 15 s at 20 m accuracy). Upon recovery of the tags, data were downloaded into a PC for analysis. Depth sensors of tags were calibrated both before and after tag deployments. The velocity sensor of tag no. 1 was based on rotation of a paddle wheel.

Drift in the depth values for tag no. 1 was corrected using the software ‘Zero-Offset Correction v. 1.26’ (Wildlife Computers), and data were then processed using ‘Dive-Analysis v. 4.08’ (Wildlife Computers), to produce summary statistics for each dive. Depth values from tag no. 2 were imported into Excel (Microsoft®) and drift was corrected by eye and using surfacing data (the times when radio signals were audible). These data were then processed using macros written by S.K.H., adhering to the same principles as those used by ‘Dive-Analysis’.

In addition to the TDR study, we used a hull-mounted fish-finding sonar system (Furuno® model CH-14; 60 MHz) set at a range of 600 m to track non-tagged whales as they dived. Sonar recordings were taken when there were no other whales in the immediate area. The research vessel was manoeuvred above the position where the whale began its dive, approximating the

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whale's speed and heading. When speed and direction were judged correctly, an echo from the whale was received on the sonar, usually within a minute of the whale having left the surface. Once this was achieved, we would attempt to maintain the echo on screen during the whale's descent by observing changes in the sonar image and consequently manoeuvring the boat in that direction. When we lost the echo on screen, a still photograph was taken to record the trace. These photographs were later digitized (CalComp Drawing BoardTM) and the differences in depth and time between the start and end positions of the dive descent were used to calculate the descent rate of the whale.

One possible error affecting the measurement of dive depths using this method was caused by the 15° vertical beam width. This could cause an image to be displayed when the whale was at 7.5° off the vertical plane, i.e. not directly under the research vessel. The maximum error incurred by this is $((1 - \cos 7.5^\circ)/\cos 7.5^\circ) = 0.9\%$ (cf. Papastavrou *et al.* 1989). Depth values could therefore be slightly underestimated in some cases, resulting in a maximum of 0.8% underestimation in descent rate.

3. RESULTS

Attempts to deploy the tags were made 84 times during 30 days between 1996 and 1998, with five successful tag attachments. Tags were recovered in three of these attachments and the data from two were successfully downloaded. The deployment in 1996 of a 500 m TDR (rated for less than the diving capacity of these whales) resulted in TDR failure, and VHF transmitter failure was probably responsible for one or both of the losses at sea in 1998. The first successful data recovery was from a tag (no. 1) deployed at 15.41 on 9 July 1997, on an adult female-sized whale ('individual 1') in a group of five animals, including one infant and one juvenile-sized whale. Individual 1 was observed with the juvenile and infant during all of its surfacings. The tag fell off after 2 h 33 min during a bout of high-speed swimming, 20 min after two groups joined (a total of eight whales). The second successful data recovery was from a tag (no. 2) deployed at 14.56 on 24 August 1997 on a sub-adult-sized whale ('individual 2'), in a group of three animals. This tag fell off after 27 h 56 min, at which time individual 2 was in a group of five animals.

A total of 56 sonar recordings were obtained over 20 days during 1996 and 1997. Forty-seven of these contained a trace of a single whale; however, nine showed two whale traces, resulting in a total of 65 traces.

Reactions of the whales to tag deployment appeared to be minimal, generally consisting of a flinch and a fast but shallow dive. Velocity data from individual 1 were high for 2 min after tag deployment (although the same velocity was observed later during apparently normal behaviour), then dropped to levels maintained throughout the majority of the tag attachment (figure 1). In general, bottlenose whales showed no obvious reaction to the research vessel when under power beyond distances of 15–20 m, and distances greater than this were maintained for the majority of the tag attachments. There was also no apparent difference in the surface behaviour of whales when the sonar system was transmitting (S. Al-Omari, unpublished data).

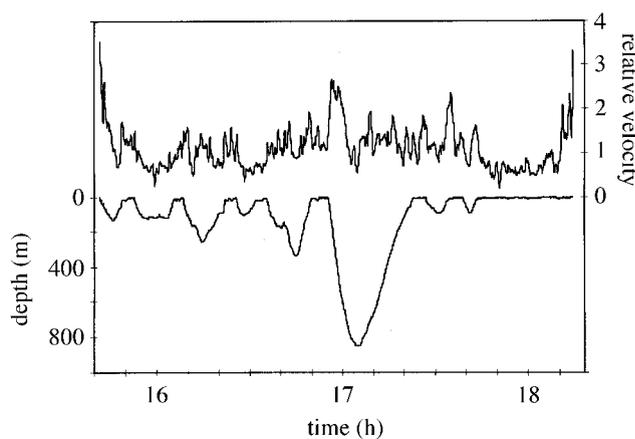


Figure 1. Dive and velocity profiles for individual 1. The lower graph shows depth while the upper graph shows relative velocity (uncalibrated) over the same time period.

We considered the whales to be 'diving' when the maximum dive depth was greater than 40 m (corresponding to twice the depth resolution of tag no. 2). Both tagged whales spent similar proportions of their time diving (70 and 62%, respectively, for individuals 1 and 2) and both spent similar proportions of dives at greater than 85% of maximum depth, indicating general consistency in dive shape (figure 2, table 1). Dives fell into two discrete types based on the bimodal distribution of the cumulative time spent in dives of different durations (not shown). A *k*-means cluster analysis of standardized variables (dive duration, maximum depth, bottom time, ascent and descent rates) also verified these groupings. These two types could generally be considered as 'short duration and shallow' and 'long duration and deep' (table 1).

The average depth of dives of individual 2 in the long-duration cluster was 1065 m ($n=22$, range 493–1453 m), while only one dive of individual 1 to 852 m was classified in this category (table 1). Using all dives, there was a strong relationship between the maximum depth of a dive and the duration of that dive (Pearson correlations: individual 1, $r=0.943$, $p<0.001$; individual 2, $r=0.930$, $p<0.001$). Dive duration was not significantly correlated with the following surface interval for either whale (Pearson correlations: individual 1, $r=-0.004$, $p=0.993$; individual 2, $r=-0.126$, $p=0.4$). Furthermore, even when recovery time is assumed to include all time between deep dives (including time spent on shallow dives), there was no significant relationship (Pearson correlation: individual 2, $r=0.134$, $p=0.572$).

Over all of the dives, average descent rates were not significantly different from average ascent rates (paired *t*-test, individual 1, $p=0.16$; individual 2, $p=0.38$). However, the long dives of individual 2 had significantly faster descent rates (mean 1.32 m s^{-1}) than ascent rates (mean 1.11 m s^{-1} ; paired *t*-test, $p=0.026$, table 1). Descent and ascent rates were found to vary with depth during deep dives ($>850 \text{ m}$, such that descent rates showed a general deceleration with depth (ANOVA, $p<0.001$), while ascent rates were relatively constant overall but appeared to show a slight (but non-significant) deceleration in the final 250 m before reaching the surface (figure 3). The difference between descent and ascent

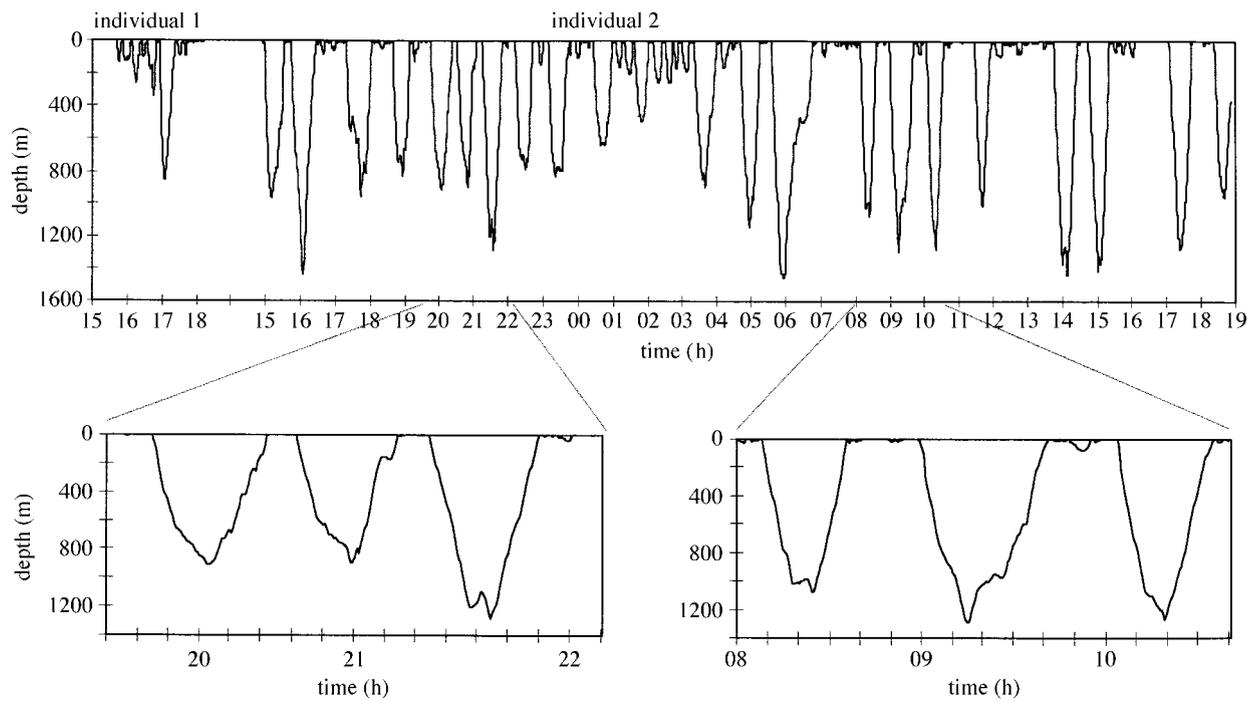


Figure 2. Dive profiles for individual 1 (2.5 h) and individual 2 (28 h) showing regular dives to depths exceeding 800 m. The time-scale is expanded for two sections of the dive profile of individual 2 in order to show dive shape in greater detail (to the same scale as shown in figure 1).

Table 1. Values of dive variables for short- and long-duration dives for each individual (mean (s.d.) and range are shown for all categories except the single deep dive of individual 1, for which the recorded values are shown)

dive type	individual	n	duration (min)	maximum depth (m)	time at depth >85%			percentage of dive at 85%
					maximum depth (min)	descent rate (m s ⁻¹)	ascent rate (m s ⁻¹)	maximum depth
short, shallow	1	7	11.17 (3.91)	166 (93)	3.16 (2.45)	0.73 (0.21)	0.56 (0.34)	27.5 (14.4)
	2	26	8.83 (3.40)	108 (65)	2.77 (1.85)	0.61 (0.43)	0.67 (0.36)	30.1 (13.2)
long, deep	1	1	29.48	852	7.02	1.93	0.80	23.8
	2	22	36.98 (9.4) ^a	1060 (273)	9.72 (3.10)	1.33 (0.32)	1.11 (0.36) ^a	27.4 (10.6)
			25.25–70.50	493–1453	5.00–17.00	0.60–1.93	0.46–1.78	11.6–50.8

^aAlthough there were 22 long-duration dives recorded for individual 2, the last dive has not been included in some calculations, since the tag fell off part way through the dive, while the animal was ascending.

rates was only found to be significant between the initial descent (mean 1.96 m s⁻¹) and the final ascent (mean 1.29 m s⁻¹) in the top 250 m (paired *t*-test, $p=0.005$, $n=16$; figure 3). Average descent rate and average ascent rate were found to be correlated with the depth of dive (Pearson correlations: individual 2, descent $r=0.72$, $p<0.001$, $n=48$, ascent $r=0.57$, $p<0.001$, $n=47$), with a trend for both to increase with increasing dive depth. When this analysis was restricted to deep dives, only descent rate was significantly correlated with depth of the dive (Pearson correlation: individual 2, $r=0.431$, $p=0.045$, $n=22$); neither overall ascent rate nor the final ascent rate (during the final 250 m) showed any correlation with dive depth.

The deepest sonar trace observed was to approximately 550 m, which was almost the limit of the sonar range used (600 m). Although most traces were lost before this

depth, no traces were observed to level out (suggesting that these represented the initial descent of deep dives). The sonar dive traces (of greater than 80 m descent) showed a mean descent rate of 1.87 m s⁻¹ (s.d. 0.35, range 1.12–3.03, $n=23$). The average start and end depths for these traces were 150 m and 340 m. This is comparable to the descent rates during the same depth range for long deep dives (individual 1: 2.45 m s⁻¹; individual 2: mean 2.04 m s⁻¹, s.d. 0.75), but is much greater than the descent rates observed for short, shallow dives (figure 4).

Accurate determination of sea-floor depths at locations of tagged whales was problematic, due to steep gradients in bottom depth in the submarine canyon. However, when the research vessel was close to the tagged animals, the maximum bottom depth was approximately 1500 m. Individual 1 was observed to move into shallower waters (750 m) just prior to the tag falling off and thus the final

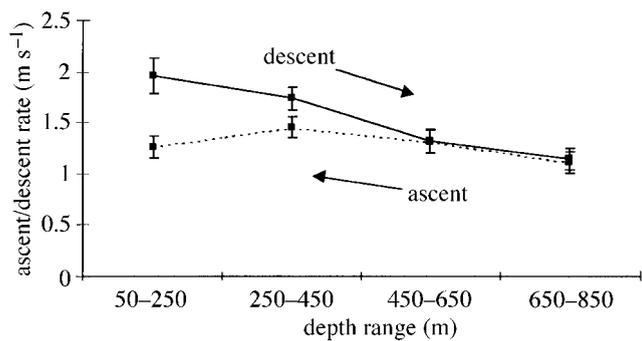


Figure 3. Variation in descent rate (solid line) and ascent rate (broken line) calculated over 200 m depth intervals during deep dives. Average descent and ascent rates (\pm s.e.) are shown for descents between 50 m and 850 m for dives to greater than 850 m.

dive of 852 m may have been to, or close to, the sea-floor (figure 1). The maximum depth of the canyon between the tag deployment and recovery site for individual 2 was also 1500 m. Given the dramatic changes in sea-floor depth changes over short horizontal distances, it seems likely that individual 2 was diving close to, or to, the sea-floor for many of the dives recorded (figure 2).

Eleven of the sonar recordings showed more than one trace of a whale within the same recording. Of these, two recordings showed one animal descending while another animal was stationary or moving slowly horizontally just under the water surface, five showed one animal descending and then approximately a minute 'behind' this, a second animal descending. Four of the sonar recordings showed two traces within 20 m or a few seconds of each other at depths of between 150 m and 300 m.

4. DISCUSSION

These results show that bottlenose whales are capable of diving to great depths and that they may do so on a regular basis. Individual 2 dived approximately every 80 min to depths of greater than 800 m and at times as deep as 1450 m; the dives of individual 1 showed a similar profile, with one dive to 852 m during the 153 min deployment (figure 2, table 1). Descent rates calculated from sonar dive traces of non-tagged whales appeared to be more similar to the descent rates of deep dives than those of shallow dives of the tagged animals (figure 4). This provides some support for the hypothesis that such deep diving recorded by the TDRs was not unusual, and that the dive parameters obtained using tag deployments are probably a reasonable representation of the diving behaviour of this species in the Gully region.

Other marine mammals have only occasionally been recorded to dive to similar depths. The deepest depths documented using TDRs or acoustic transponder tags have been from a northern elephant seal (*Mirounga angustirostris*) diving to 1500 m (DeLong & Stewart 1991), a southern elephant seal (*Mirounga leonina*) diving to 1200 m (Hindell *et al.* 1991), a sperm whale (*Physeter macrocephalus*) possibly diving to 2000 m (Watkins *et al.* 1993), and narwhals (*Monodon monoceros*) on occasion diving to depths greater than 1000 m (Heide-Jørgensen & Dietz 1995). Regardless of these, the maximum depths ever recorded are not good

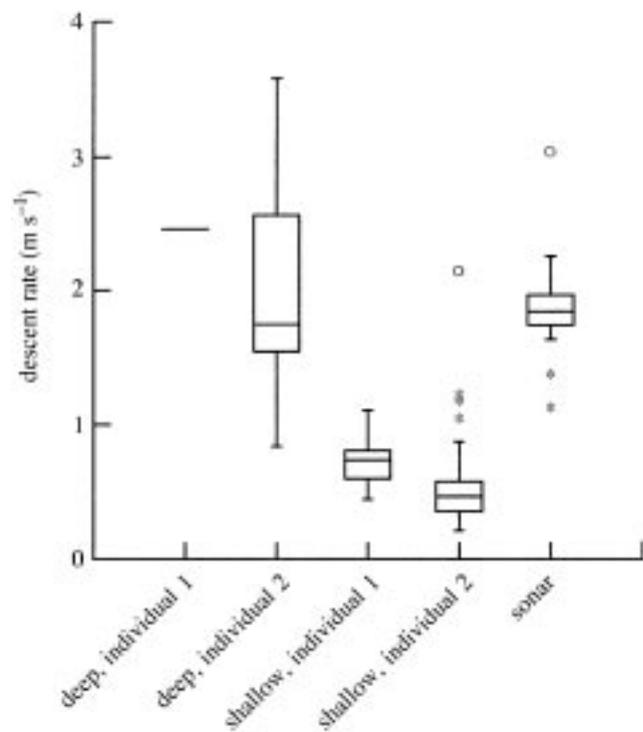


Figure 4. Box-plot comparison of the initial descent rates of dives. Long, deep dives and short, shallow dives are shown for individual 1 and individual 2. This shows that rates recorded for sonar dive traces of non-tagged whales are more comparable to the initial descent rates of deep dives than the descent rates of shallow dives. Box plot shows the median (centre line), the upper and lower quartiles (edges of the box), the range (ends of the bars or symbols); asterisks show outlier further than $1.5 \times$ interquartile range from either quartile, circles show outlier further than $3 \times$ interquartile range from either quartile.

representations of normal diving behaviour, and discussion of routine dive depths is more useful (Kooyman & Ponganis 1997; Schreer & Kovacs 1997). Routine dive depths for these deep-diving species have been reported as 400–600 m for sperm whales (Papastavrou *et al.* 1989; Watkins *et al.* 1993), and 350–700 m for northern and southern elephant seals (Le Boeuf *et al.* 1988; DeLong & Stewart 1991; Hindell *et al.* 1991). The regularity of dives of northern bottlenose whales to depths in excess of 800 m (figure 2) exceeds the recorded frequencies of dives to such depths for other mammals recorded thus far.

The area in which the whales were tagged is a submarine canyon, which varies in depth dramatically over a few kilometres (Hooker *et al.* 1999). It is likely that the deeper dives recorded were often to, or near to, the sea-floor. The diet of northern bottlenose whales is thought to be primarily the squid *Gonatus fabricii* (Benjaminsen & Christensen 1979; Clarke & Kristensen 1980; Lick & Piatkowski 1998), although its congener *Gonatus steenstrupi* is more likely to be found in the Gully (Kristensen 1981). Mature *Gonatus* in the North Atlantic live around the sea-floor on continental slopes (Kristensen 1984; Moiseev 1991) and have recently been observed to spawn at depths of approximately 1000 m (Bjørke *et al.* 1997). Unfortunately the squid biota of the Gully is not well-known, but the dive depths observed

here are consistent with what is known of the vertical distribution of the genus *Gonatus*. The lack of any distinct bursts of speed at depth (figure 1) tend to suggest that these whales may forage in a fairly passive manner, consistent with recent suggestions of suction feeding in beaked whales (Heyning & Mead 1996). The observation of more than one trace on some of the sonar images suggests that at least some of the spatial cohesion and coordination shown by groups at the surface (S. K. Hooker and R. W. Baird, personal observations) may be retained during dives.

The lack of correlation between dive duration and surface time suggests that these whales are not reaching their aerobic dive limit (Boyd 1997; Kooyman & Ponganis 1998; Kooyman *et al.* 1980). Based on their large body size and the low velocities exhibited during diving (figure 1), it seems likely that the aerobic dive limit for these whales is quite high (Kooyman & Ponganis 1998; Williams *et al.* 1991). It has been suggested that the shorter, shallower dives between long deep dives may also function for recovery (Castellini *et al.* 1988; Kooyman *et al.* 1992), but a relationship between dive duration and such an extended recovery period was not observed here, although small sample size may have prohibited the detection of such a relationship.

The effects of pressure on diving mammals are most dangerous during ascent, when the decrease in pressure may cause either decompression sickness (the bends), or shallow-water blackout, a reduced concentration of oxygen in the arteries resulting in a decrease in the amount of oxygen reaching the brain (Kooyman 1988, 1989; Kooyman & Ponganis 1997). Relative pressure changes are greatest near the surface and the slight decrease in ascent rate shown by northern bottlenose whales during the final phase of ascent could potentially be a response to this. Martin & Smith (1992) also observed a decrease in ascent rate of beluga whales (*Delphinapterus leucas*) within 140 m of the surface and suggested that this might serve a physiological function, reducing the rate at which gas bubbles appear in the blood or tissues. Deep-diving pinnipeds such as elephant seals show the opposite trend, i.e. an increase in ascent rates near the surface (e.g. Fletcher *et al.* 1996) although ascent rate was found to be less flexible than the descent rate to experimental changes in buoyancy (Webb *et al.* 1998).

Our data are based on only two TDR deployments and a small sample of sonar dive traces, and clearly more data are needed on the diving behaviour of this and other species of beaked whales to substantiate further these results. However, from the data presented here, it appears that bottlenose whales may make more regular dives to greater depths than any other diving mammal yet studied.

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