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Dive form and function in belugas *Delphinapterus leucas* of the eastern Canadian High Arctic

Received: 8 January 1998 / Accepted: 27 April 1998

Abstract The underwater behaviour of 11 belugas or white whales was examined during summer using time-at-depth records relayed by satellite-linked data-loggers. Simultaneous tracking information was obtained for each whale. Eight distinct dive profiles were identified in submergences made to depths of >40 m. Four of these, together comprising 84% of these “deep” dives, were of a square profile. They were characterised by a continuous descent to a particular depth (usually the sea bed), a “bottom phase” at or near that depth, and a direct ascent to the surface. These dives are presumed to be made for benthic foraging. Other, much less common, dive shapes were “V”-shaped, parabolic and trapezoidal. “Shallow” dives (15–40 m depth) were of a variety of shapes, short duration and high average horizontal speeds. Many probably occurred during periods of directed travel. This population of belugas treats most of the water column as dead space separating resources of oxygen and nutrition.

Introduction

Until recently we had little understanding of what marine mammals are doing when they are below the water surface, where they spend much or most of their lives. In

the 1970s, however, researchers began to attach miniature data recorders to these animals, and could subsequently reconstruct a detailed time-depth record (TDR) from the device when it was retrieved. Further technological advances allowed time-depth records to be transmitted by radio link to low-orbit satellites and thence to the researcher. For the first time, it was possible to visualise how diving animals behaved when they were beyond the range of our real vision.

For reasons of ease of capture, recapture and device attachment, most applications of the techniques have been to seals (see Kooyma 1981; Le Boeuf et al. 1986, 1988; Boyd and Croxall 1992; McConnell et al. 1992 for some notable examples). Cetaceans are harder to capture because they do not haul-out on land, and the probability of recapturing a specific individual in order to retrieve a data-logger is in most cases very small. Furthermore, attaching electronic devices to their smooth skin has proved very problematic, so the longevity of data records from cetaceans is usually shorter than those from pinnipeds. In consequence, while our understanding of the diving behaviour of most pinnipeds has grown dramatically in recent years, that of cetaceans has developed relatively slowly. To date, TDR-type information has been published for fewer than 10% of cetacean species, and in most cases the data are of poor resolution, from only one or two individuals and for short periods of time.

One of the first cetaceans to be studied with data-recording devices was the beluga *Delphinapterus leucas* (Martin and Smith 1992; Martin et al. 1993; Smith and Martin 1994). The species is suitable for this type of research because it enters shallow water predictably for brief periods each summer and adults are sufficiently small (typically 500–1500 kg and 3 to 4.5-m body length; Martin 1990) to permit capture and handling with a small team and one small boat. Early results demonstrated that belugas were capable of deep, prolonged dives (Martin and Smith 1992) and appeared to have a small repertoire of dive “shapes” as shown by a time-depth trace. The objective of this paper is to examine

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TDR data collected from a much larger sample of animals and to determine the number and possible function of the different dive types encountered.

The dive records that form the raw material for this study were collected from belugas being simultaneously tracked by satellite in the Somerset Island/Lancaster Sound region of the eastern Canadian high Arctic (Fig. 1). Data were collected during and immediately after the short arctic summer, when the sea ice that blankets the area for most of the year briefly recedes and allows this population of whales access to areas around Somerset Island for some 2 months. The diving capability of these belugas allows them potential access to the

sea bed throughout the region (Martin and Smith 1992). The whales' geographical movements during this time (Smith and Martin 1994) demonstrate that they closely follow the retreating ice edge, with the apparent objective of reaching a relatively deep trench off the southeast coast of Prince of Wales Island as soon as possible. Having reached this trench, they may remain there for several weeks, before returning north through Peel Sound and then eastwards along the southern coast of Devon Island. While waiting for the ice to break up, belugas occupy shallow bays and inlets around Somerset Island, often for several consecutive days. Time in these shallow areas may be interspersed with forays to deeper areas offshore (Smith and Martin 1994).

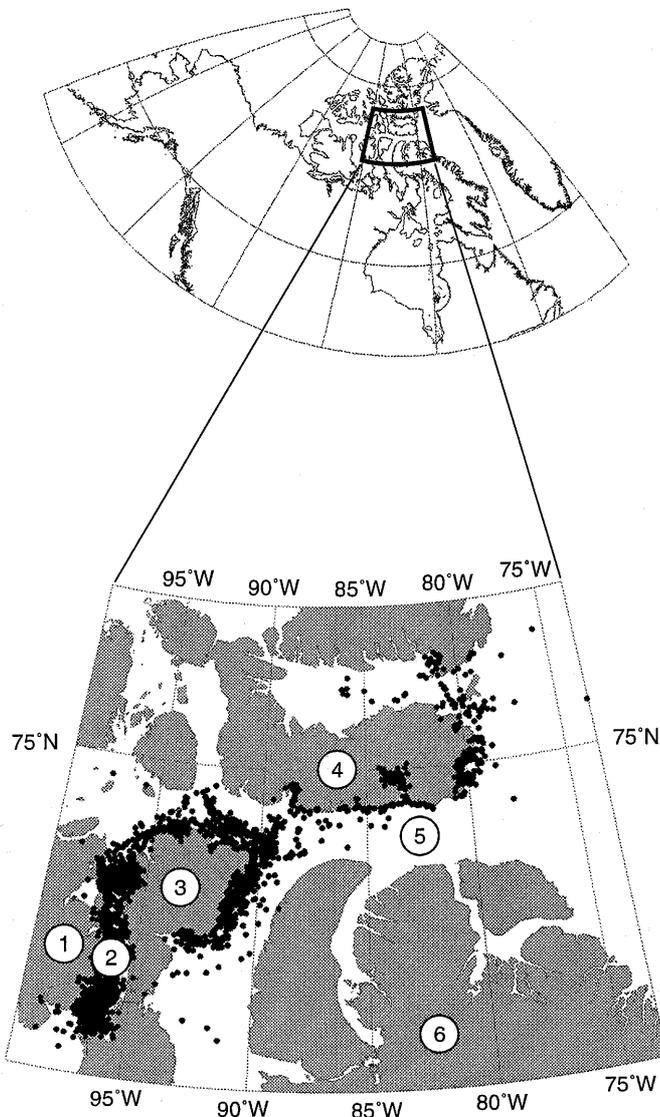


Fig. 1 Map of the region (Northwest Territories, Canada) where the study animals spent the summer and autumn (July–September) and from where the data considered in this paper were collected. *Dots* represent the approximate positions of the tagged whales every 6 h and give an impression of where the dive data were collected. *Circled numbers* refer to place names mentioned in the text: 1 Prince of Wales Island, 2 Peel Sound, 3 Somerset Island, 4 Devon Island, 5 Lancaster Sound, 6 Baffin Island

Materials and methods

Eleven adult or sub-adult belugas were captured at locations around Somerset Island in the Canadian Northwest Territories (Fig. 1) between 1990 and 1993. Details of the whales, their capture dates and the longevity of their data records are given in Table 1. Capture was effected individually in the shallow water of a bay or estuary using hoop-nets deployed by hand (see Martin and Smith 1992 for details). Whales were held at a convenient place nearby for 15–30 min for attachment of a satellite-linked data recorder to their dorsal ridge, and then released. The devices were constructed by the Sea Mammal Research Unit, housed in anodised aluminium tubes pressure-proofed to 1500-m water depth, and comprised a battery-pack, sensors, RF (radio frequency) stage (Toyocom, Tokyo or Microwave, Wash. USA) and a programmable controller unit. One sensor provided the controller with readings of ambient pressure every 4 s with an accuracy of ± 1 m, and a wet/dry sensor determined every 0.2 s whether the animal was at the surface. Transmitters functioned for periods of up to 75 days (average 46 days, Table 1) before falling away from the whale.

The transmitters sent data via, and were located by, polar-orbit satellites of System ARGOS (see Fancy et al. 1988). This study was carried out at high latitudes, so data could be received, and animal locations provided, up to 28 times a day. Transmitted data strings included error-checking code, and only error-free data were used for analysis. Due to ARGOS-imposed limitations on the rate at which data could be transmitted, information was summarised before transmission. The time-depth records (hereafter referred to as TDR data) on which the paper is based comprised depth readings recorded at intervals of either 20, 40 or 60 s, depending on year

Table 1 Details of the instrumented belugas. All were captured at sites around Somerset Island, Canadian Northwest Territories, and were tracked for varying periods during the summer and autumn (see Fig. 1)

Whale no.	Sex	Status	Date captured	No. days of transmission
5801_90	F	Sub-adult	17.07.90	11.0
5801_91	F	Adult	21.07.91	27.6
5805_91	F	Sub-adult	28.07.91	24.6
8750_91	F	Adult	31.07.91	47.2
8757_91	F	Adult	01.08.91	2.5
8752_92	F	Adult	26.07.92	75.0
8753_92	M	Adult	23.07.92	72.7
8754_92	F	Adult	23.07.92	69.8
8755_92	F	Adult	25.07.92	64.7
8750_93	F	Adult	13.08.93	58.9
8755_93	F	Adult	14.08.93	46.5

of deployment. Data were compiled into batches of 29–32 consecutive readings, and a batch was transmitted in a single 960-ms signal when the whale surfaced. Up to 16 such batches were stored by the logger simultaneously and transmitted in rotation, so data were dispatched up to 8 h after they were collected. Prior to analysis, sequential batches were concatenated to provide long time series of TDR data. Even with this level of data compaction, insufficient information could be transmitted to provide a continuous TDR record; the proportion of time covered varied from 5 to 30% per animal. When dives were obviously started between depth readings, the time of leaving the surface was estimated by extrapolating the rate of descent over the first complete inter-depth reading interval back to intercept the surface, then adding a correction for the fact that belugas accelerate slowly to their full descent speed. This correction was based on dives that happened to start just before a depth reading, and for which the rate of acceleration was therefore known. The same process was used for estimating the time that a dive ended.

From the 11 transmitter deployments detailed in Table 1, the profiles of 1112 dives were selected for analysis. All dives to depths greater than 40 m with complete TDR records were included, as were an arbitrary selection of the more numerous shallower dives, but subject to reaching a depth of at least 15 m. The 40-m threshold was chosen because some short submergences to depths less than this may not be adequately described by the coarsest (60-s interval) TDR data collected in this study. For these reasons the data set cannot be considered to be a random selection of dives from the tagged whales. Rather, it should contain all important dive types, allow an analysis of their context and, for those reaching depths greater than 40 m, demonstrate the relative frequency of occurrence of the various dive types.

The following definitions were adopted for various elements of the dive: *start of descent* (beginning of monotonic increase in depth resulting in submergence to at least 15 m); *end of descent/start of bottom phase of dive* (first distinct point of inflection or point where depth ceases to increase); *end of bottom phase of dive/beginning of ascent* (last distinct point of inflection preceding a monotonic and near-constant decrease in depth that leads to a surfacing); *end of ascent* (point at which the beluga reaches the surface after a submergence to at least 15 m); and *wiggle* (two consecutive intervals during the bottom phase of the dive with vertical travel in opposite directions; the first interval must be a deflection of 8 m or more, and the animal must restore at least 4 m of this within the next two TDR time intervals). These definitions were necessarily arbitrary, but were carefully chosen to permit the

repeatable and unambiguous discrimination of dive elements in this particular data set.

Each dive profile was examined by eye and allocated to a dive category by shape alone, using a multi-pass, iterative process and the characteristics of: (1) degree of continuity of descent and ascent, (2) rates of descent and ascent, (3) duration of bottom time, (4) profile of bottom time, and (5) the existence and number of wiggles. The objective was to identify the most important discrete and definable dive shapes that apparently represented distinct behaviours. The process allowed definitions to be modified as the dominant dive types, and the boundaries between them, became apparent. Once the definitions of the recognised dive profiles were finalised (Table 2), the entire sample was classified individually to one or other of these shapes, or marked as falling outside the definition of any shape (unclassifiable). The potential subjectivity of visual pattern recognition was removed from this process by ensuring that the definitions acted as a key and allowed for no ambiguity. Two observers classified each dive independently, and no discrepancy occurred. Each of the resultant groupings was then examined to look for multimodality in any other characteristic (mean descent rate, mean ascent rate, bottom time, duration, maximum depth, relative depth of dive, speed of horizontal movement) that might indicate that dives of more than one function had been artificially clustered together. All but the last two of these measures were calculated from the TDR profile, but “horizontal speed” and “relative depth” were contextual parameters determined as follows.

“Horizontal speed” was an estimate of the animal’s speed of horizontal movement when the dive was performed. It was determined from satellite-derived Lat/Lon locations of the whale before and after the dive, using only locations with a probable error of 350 m or less. The intention here was simply to obtain some broad indication of whether the whale was likely to be, for example, travelling or stationary when the dive was made.

“Relative depth” was the maximum depth of the dive divided by the estimated depth of water at the point where the dive was made, and had a value from zero (surface) to one (sea bed). Sea depths were derived from the most recent bathymetric charts of the Canadian Hydrographic Service, typically with a horizontal resolution of 500 m, using the nearest adequate satellite-derived whale location. The decision as to whether to estimate water depth for a particular dive was dependent on four factors: (1) location quality, (2) temporal separation between dive and location, (3) characteristics of local bathymetry, and (4) rate of horizontal animal movement. Thus a dive made by a whale moving rapidly

Table 2 Definitions of the eight dominant dive shapes recognised

Shape	Definition
‘Square’ dives (S1–S4)	(1) Continuous descent and ascent (2) At least three depth readings (covering a minimum of 40 s) within 10 m of maximum depth (3) Distinct bottom phase
S1	Continuous and constant descent and ascent other than when initiating and completing each of these phases. Bottom phase with no wiggles
S2	Continuous and constant descent and ascent other than when initiating and completing each of these phases. Bottom phase with one or more wiggles
S3	Continuous and constant descent and ascent other than when initiating and completing each of these phases. Bottom phase smoothly arched to produce shallow “W” shape
S4	Rate of depth change decreases with depth. Bottom phase “W” shaped
“V”-Shaped dives (V)	(1) Continuous or near-continuous descent and ascent (2) No more than two depth readings (covering a minimum of 40 s) within 10 m of maximum depth
Trapezoidal dives (T1 and T2)	(1) Distinct descent, intermediate and ascent phases of dive (2) Intermediate phase of at least 2 min in duration comprises a period of monotonic depth change, but with a distinctly lower rate of depth change than during either descent or ascent
T1	Increasing depth during intermediate phase
T2	Decreasing depth during intermediate phase
Parabolic dives (P)	(1) No distinct inflection point in rate of depth change during dive (2) Rates of depth change generally decrease with depth

over a steeply sloping sea bed would require a simultaneous $LQ = 3$ (lowest probability of error) location for the depth to be acceptable. In contrast, water depth for a whale moving little for days over a flat sea bed could be satisfactorily estimated with two or more clustered locations of $LQ = 0$ (highest probability of error) several hours apart. The purpose of estimating depth was to look for broad differences at the level of the dive type, so occasional errors at the level of the individual dive would not have been important.

One conclusion reached early in the process of dive categorisation was that the boundaries between the various dive shapes became less clear with decreasing maximum dive depth. The reason for this is transparent – a small difference of, e.g. 5 m in depth at a particular time would have little or no impact on perception of dive shape in a long dive reaching 300 m, but could radically change the profile of a short dive that took the whale only 25 m below the surface. It seemed likely that, if continued to shallow dives, the methodology would probably result in biologically artificial distinctions and the rejection of large numbers of “normal” dives as unclassifiable. In consequence, dives or less 40 m ($n = 331$) were considered independently from than 40 m or more ($n = 781$).

Mean values are shown ± 2 standard errors.

Results

Deep dives (> 40 m maximum depth)

Eight distinctive dive shapes, each represented by at least seven dives within the sample, were identified (Fig. 2, Tables 2, 3). These eight constituted 96% of dives reaching depths greater than 40 m and 97% of those to 100 m or more. The submergences that did not

conform to any of the eight shapes identified were a mixed bag of apparently truncated dives of recognisable shapes and a few erratic dives with no clear objective or definable shape.

“Square”dives

By far the most abundant dives, comprising 84% of the > 40 m sample and 94% of those to > 100 m, were of a “square” shape, with a continuous descent, a distinct “bottom” phase and a continuous ascent. Four shapes within this family were recognised, all of which were characteristic of deep, benthic dives (Table 2). S1 and S2 dives were carried out by all animals, usually in deep offshore areas and with, on average, medium rates of horizontal movement ($0.4\text{--}0.6\text{ m s}^{-1}$; see Table 3 for definitions of horizontal movement rate categories). In contrast, S3 and S4 dives were essentially restricted to two animals in 1992 (female 8752 and male 8753) and were seen only when the whales were resident in narrow, steep-sided fjords. They therefore had low rates of horizontal movement ($< 0.2\text{ m s}^{-1}$). The duration of square dives was usually long, means varying from 10.8 to 13.1 min. S1 dives had modal bottom times of 5–9 min, this representing some 40–70% of the time submerged (Fig. 3). Rates of descent and ascent were usually in the range $1.5\text{--}2.0\text{ m s}^{-1}$ (Fig. 3), and within dives these measures were not significantly different (paired t -test, $P = 0.84$).

Within the largest class S1 ($n = 401$), there was a small but non-trivial number of dives that appeared as possible separate groupings. Three modes of maximum dive depth occurred (Fig. 3): one of up to 100 m,

Fig. 2 Typical profiles of the eight dive shapes recognised. See Table 2 for defining characteristics

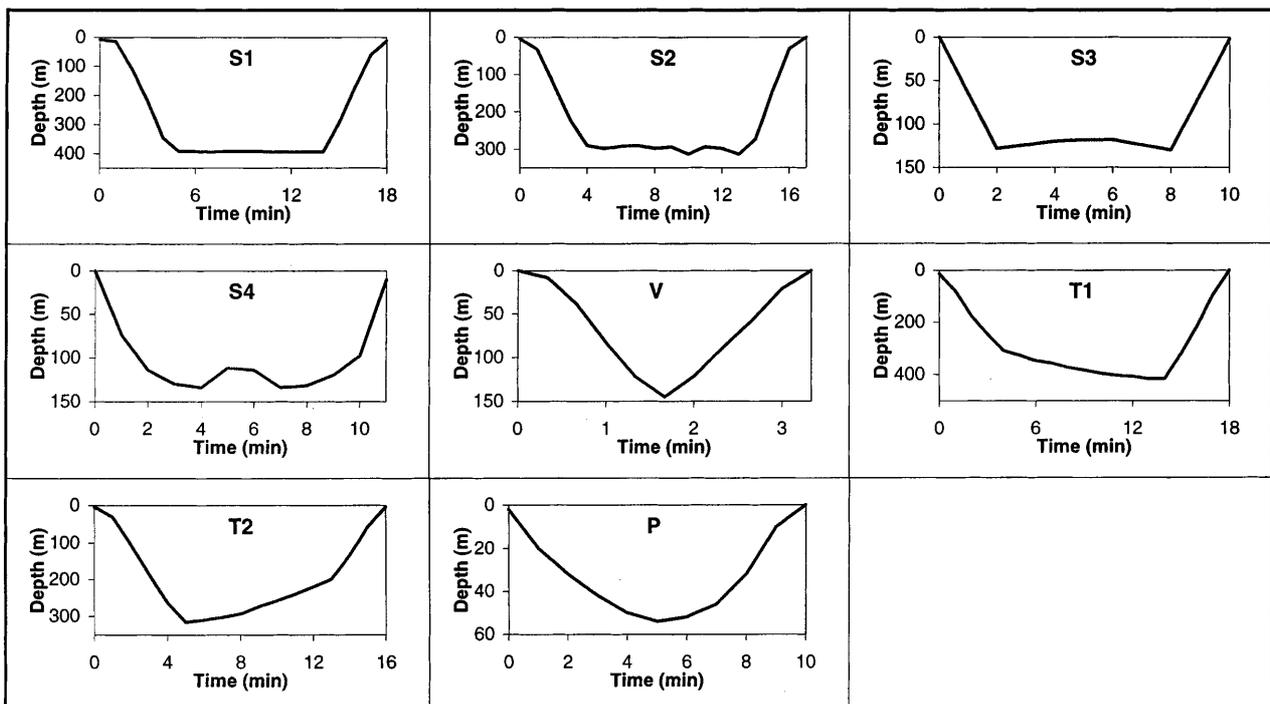


Table 3 Characteristics of the eight major dive shapes recognised in submergences to >40 m. For horizontal speed, *high* = mean >0.8 m s⁻¹, *medium-high* = 0.6–0.8 m s⁻¹, *Medium* = 0.4–0.6 m s⁻¹, *medium-low* = 0.2–0.4 m s⁻¹, *Low* = <0.2 m s⁻¹; relative depth and absolute depth indicate the nature of the great majority of dives of this shape, but some may differ from the norm (see Discussion)

Shape	Duration (min) (mean ± 2SE)	<i>n</i>	% dives >40 m	% dives >100 m	Relative depth (median)	Absolute depth (median)	Horizontal speed	Descent rate (m s ⁻¹) (mean ± 2SE)	Ascent rate (m s ⁻¹) (mean ± 2SE)
S1	13.1 ± 0.2	401	51.3	56.7	Benthic (0.95)	Deep (317 m)	Medium	1.70 ± 0.02	1.68 ± 0.04
S2	13.8 ± 0.5	106	13.6	15.4	Benthic (0.93)	Deep (307 m)	Medium	1.69 ± 0.04	1.76 ± 0.06
S3	10.8 ± 0.3	133	17.0	19.3	Benthic (1.0)	Deep (128 m)	Low	1.54 ± 0.12	1.49 ± 0.08
S4	12.1 ± 1.0	15	1.9	2.2	Benthic (1.0)	Deep (134 m)	Low	1.46 ± 0.38	1.39 ± 0.2
V	7.0 ± 1.7	56	7.2	1.5	All (0.24)	Shallow (57 m)	Medium-high	0.83 ± 0.36	0.59 ± 0.12
T1	13.6 ± 3.2	10	1.3	0.9	All (0.82)	Shallow/Deep (237 m)	Medium-low	1.40 ± 0.18	1.68 ± 0.2
T2	13.6 ± 1.5	7	0.9	0.6	All (0.82)	Shallow/Deep (250 m)	Medium	1.53 ± 0.2	1.37 ± 0.52
P	9.3 ± 1.5	20	2.6	0.4	Near-surface (0.22)	Top 75 m (54 m)	High	0.50 ± 0.24	0.45 ± 0.12
Not classified	12.2 ± 1.0	33	4.2	3.1	Near-surface (0.57)	All (130 m)	Medium-high	1.08 ± 0.2	0.90 ± 0.24
Σ		781	100.0	100.1					

another between 100 and 150 m, and the third for dives to depths greater than 150 m. Closer inspection showed that the first mode comprised ten benthic dives reaching 50–100 m by the adult male 8753_92 while it was in two relatively shallow inlets (Croker Bay and Bethune Inlet) in eastern Devon Island. The second mode (100–150 m) comprised 39 dives, of which 38 were also benthic dives by the same animal in these same inlets. The dives of 8753_92 therefore conform in nature with the vast bulk of the dives in this class, albeit at shallower depths consistent with the animal's location.

“V” dives

The second family of dives was very different from the first, comprising a descent followed immediately by an ascent, i.e. they had no “bottom” time. This type of dive accounted for 7% of all submergences to >40 m, but fewer than 25% of these exceeded 100 m. Most V-shaped dives had continuous descents and ascents, low rates of vertical travel, were of relatively short duration and reached their maximum depth in mid-water. However, some were briefly interrupted during ascent or descent and a few were carried out to the sea bed at vertical speeds characteristic of square dives. Of interest was that the deepest dive recorded during this study was a symmetrical V-shaped dive, the rates of descent and ascent being approximately equal. This dive reached a maximum depth of 528 m, lasted 12.7 min, and was carried out by adult female 8755_93 on 15 September 1993 off the northeast coast of Devon Island. The maximum water depth in the immediate area was 550 m, so the whale terminated the descent on, or very close to, the sea bed.

Trapezoidal dives

An uncommon (*n* = 17) but recognisable group of dives was one in which a whale descended at an approximately constant rate to a certain depth, then either descended further at a markedly slower rate (T1, = 1.3% of the >40-m sample) or ascended at a slow rate (T2, = 0.9%) before making a further transition to a normal ascent speed and subsequently surfacing. Some of these dives may have been simply benthic “square” dives made to a sloping sea bed, but a sufficient number appeared to reach their maximum depth in mid-water to suggest that they represented a distinct behavioural entity. Trapezoidal dives had medium or medium-low average horizontal speeds and rates of vertical movement similar to those of square dives (Table 3). Their maximum depths were bimodally distributed, one group of less than 65 m (*n* = 7) and another to more than 200 m (*n* = 10), perhaps indicating two different functions, but the sample size is

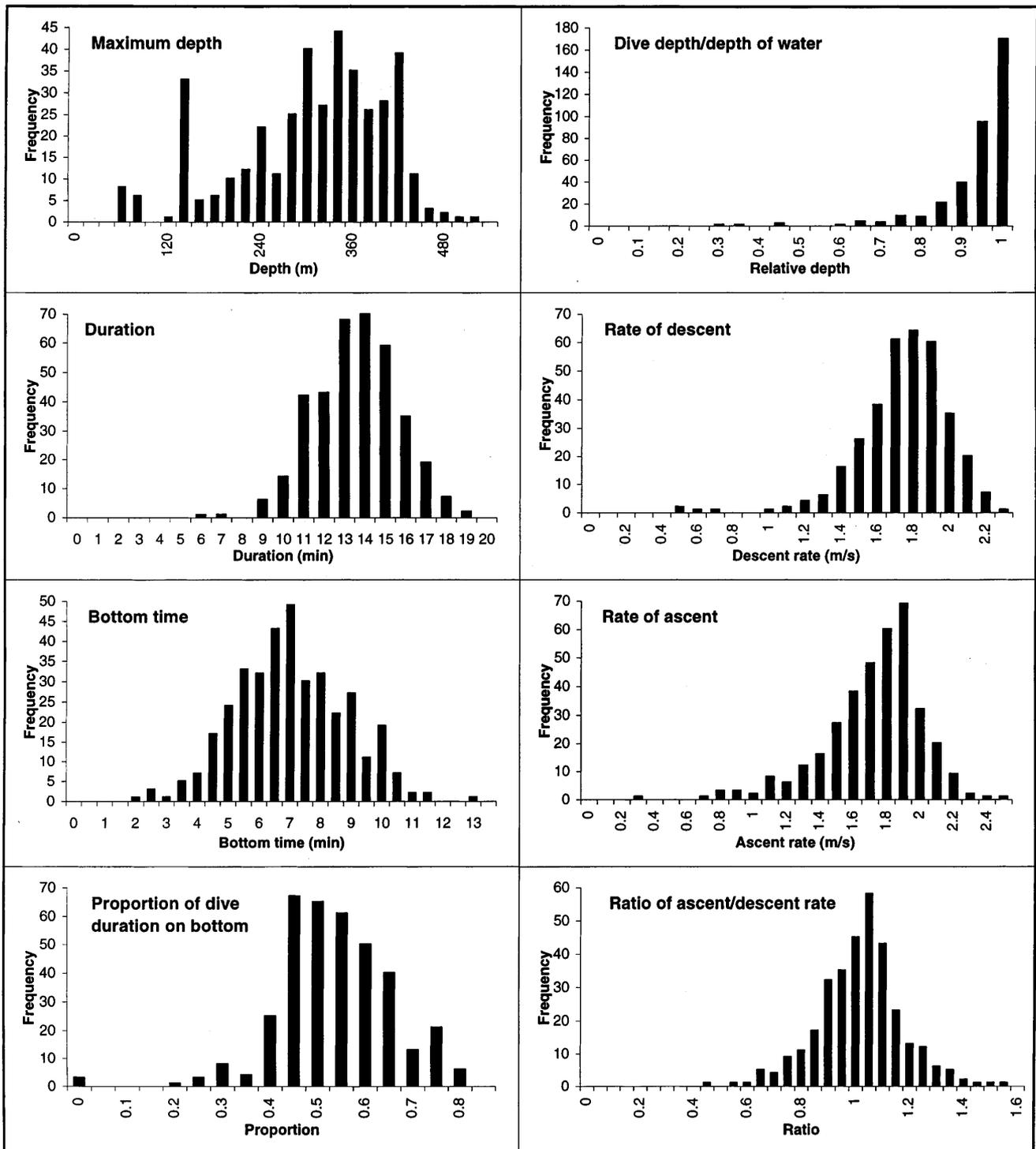
too small to allow confirmation of this (Table 3). Both T1 and T2 dives were normally of long duration (means of 13.6 ± 3.2 min and 13.6 ± 1.5 min respectively).

Parabolic dives

The final recognisable dive shape was that of a parabola, the dive profile having no inflection points. Only 20 dives to >40 m (2.6%) were of this shape, and only 3 were

made to depths greater than 75 m, the deepest being to 384 m. Horizontal speeds were on average high (mean 0.92 m s^{-1}) for parabolic dives reaching 41–74 m, suggesting that they were associated with periods of

Fig. 3 Frequency distributions of dive variables for S1 dives, the most common type of deep dive carried out by belugas in the eastern Canadian high Arctic



travel. Mean duration was 9.3 ± 1.5 min, falling to 8.5 ± 1.3 min for the 17 dives of < 75 m.

Shallow dives (15–40 m maximum depth)

For the reasons already given, all submergences reaching maximum depths of 40 m or less were considered separately. They numbered 331, or 30% of the total sample and were spread throughout the data record for each animal. The profile of almost half of these dives (142 or 43%) featured a flat bottom, and a further 88 (27%) were of a compressed parabolic shape. Others were of a shallow “V” profile. No clear line of distinction was apparent between these shapes, though, and they effectively formed parts of a continuum. The duration of shallow dives (mean 4.0 ± 1.8 min) was significantly shorter and much more variable than that of deep dives (mean 12.6 ± 0.2 min) (t -test: $T = 41.8$, $P < 0.0001$). Average horizontal speeds were in the high category (median 0.8 m s^{-1}), and significantly higher than for deep dives (Mann-Whitney test, $P < 0.0001$). Relative water depth was usually < 0.5 . Most of these dives were therefore not constrained by water depth, but the category certainly included dives made to the sea bed in coastal waters.

Discussion

Dive function

Square dives

Most square dives are carried out solely to enable the beluga to spend time on, or very close to, the sea bed. The evidence for this is twofold. Firstly, square dives comprise a continuous descent to a particular depth, a period of minutes remaining at or close to that depth, followed by an ascent directly to the surface. Secondly, where the depth of water at or near the location of the dive was known, we almost always found that it matched the maximum depth of the dive. Martin and Smith (1992) proposed that submergences of the S1 profile were foraging dives, and there is no other obvious function that can be ascribed to the square dive family, especially considering that collectively they comprise 84% of all submergences to > 40 m. Direct evidence of what belugas consume in the offshore regions of the study area is lacking, and almost nothing is known of what potential prey occurs at the depths reached by belugas during this study (H.E. Welch, personal communication). Nevertheless, information from elsewhere in the Arctic (Vladykov 1946; Tomilin 1967; Seaman et al. 1982; Brodie 1989; Welch et al. 1993) indicates that a broad range of benthopelagic fish and benthic invertebrates dominate this whale’s diet. Circumstantial evidence therefore

supports the hypothesis that square dives are primarily carried out for the purposes of foraging, and we subsequently make a working assumption that this is the case.

The variety of profiles at the bottom of the dive shown in the distinctive dive shapes S1-S4 likely reflect one or more influences on the whale at depth. The “standard” square dive profile is that of shape S1, which itself accounts for 51% of submergences to > 40 m and 55% of those to at least 100 m. The implication of these dives is that the whale is either near-motionless on the sea bed, or is actively swimming over very flat terrain.

The “wiggle” dive S2 could perhaps be the consequence of the whale either swimming closely above an uneven sea bed, or chasing prey that itself swims vertically for short distances in an effort to escape. “Wiggle” dives account for only about one in seven of > 40 -m dives, so if the wiggles do represent vertical pursuit of prey, this technique is apparently not a dominant one. Alternatively, and perhaps less likely, if wiggles indicate prey pursuit and lack of wiggles indicates no pursuit, then prey are encountered during very few submergences.

The remaining two “square” dive shapes S3 and S4 are particularly intriguing because, although abundant in the sample, they were exclusively carried out in narrow, steep-sided fjords or inlets on the southeastern coast of Devon Island (Fig. 1). A substantial proportion of these dives were made at the head of fjords with active glaciers, and may have been influenced by the shape of the ice wall underwater. Certainly, it should be expected that the dive profile might reflect the fact that such fjords have a “U”-shaped profile, little flat sea bed and mounds of morainic material. Shape S3 comprises a continuous descent to a certain depth, a “bottom” phase made up of a slow ascent and descent of a few metres (though whether the whale is travelling during this time we cannot discern), followed by the usual continuous ascent. The shape is common enough (133 examples) to suggest that it reflects deliberate and repetitive behaviour. One scenario that would fit this profile is the whale diving to the sea bed, then swimming or hovering some 8–30 metres above it for the duration of the “bottom” time before returning briefly to the sea bed and ascending normally. Another would be that the whale descends to a familiar spot, perhaps beside a mound of moraine, then forages on the mound before returning once more to the sea floor and then ascending. Why the animal should descend a few metres briefly before the ascent is perhaps the most puzzling aspect of this dive shape, but that is what it does uniformly.

The final dive shape in the “square” family is S4, which has the profile of a rounded “W”. The characteristics and possible interpretations of this shape are similar to those of S3, the chief differences being the lower rates of descent and ascent near the bottom of the dive and the greater amplitude of the “hump” in the middle of the bottom phase. The rates of descent and

ascent are consistent with the whale following the fjord wall down to its bottom at a constant swimming speed, and this is perhaps their most likely interpretation. The central hump may be due to exploration of a high mound of moraine, foraging 8–30 m off the sea bed, or perhaps simply returning some distance back up the fjord wall. Once again, the return to maximum dive depth before beginning the ascent is puzzling.

“V” dives

“V”-shaped dives were diverse, but none the less very different in character to all the other recognised dives. The essence of the dive shape was that the whale would descend to a particular depth, only to ascend immediately, although not usually rapidly, to the surface. The slow rates of descent and ascent characteristic of this group of dives indicate that either the whale was swimming very slowly at a steep angle or, conversely, was swimming at normal speeds at a shallower angle. The independent evidence of high average horizontal speeds during periods when “V” dives are made strongly supports the latter scenario. This, combined with the fact that the dives are usually made in the upper 100 m of the water column over deep water (many sub-40-m dives are also V-shaped), leads to the conclusion that they may represent an efficient mode of horizontal travel, perhaps with an additional element of exploration. If migratory travel speeds are typically, say, 1.4 m s^{-1} (Smith and Martin 1994), then a 5-min V-dive descending to 60 m would add only 4% to the horizontal distance travelled, yet may offer benefits of avoiding high near-surface drag (Hertel 1969) and the potential discovery of prey.

A small minority of V-dives was carried out to considerable depths, some to the sea bed, but there was no obvious discontinuity in this group to discriminate objectively two or more distinct dive types within the one profile shape. The deeper dives may have represented aborted square dives or were perhaps carried out specifically for exploration. It is possible to imagine that a whale would sometimes reach the sea bed and either satiate itself immediately by catching a large prey item, or perhaps decide that the area was unsuitable for prey. The 528-m submergence by whale # 8755_93 may have been such a dive.

Trapezoidal dives

These dives are clearly the same as those termed “drift” dives by Crocker et al. (1997), who found that they represented apparent periods of mid-water drifting in northern elephant seals. Unlike elephant seals, however, adult belugas are always negatively buoyant (Lønø and Øynes 1961; Fraker 1980; personal observation), so T2 dives must have been the result of active swimming. It was striking that the rate of descent (T1) or ascent (T2) during the bottom phase of the dive was usually re-

markably constant; in T1 dives this would be consistent with the whale simply stopping active locomotion at a particular depth. Some deep T1 dives reached the sea bed and the profile subsequently flattened off briefly before the animal returned to the surface. In such dives (a good example was carried out by whale 5801_91 on 3 August 1991 in 404 m of water) the dive profile does suggest that the animal actively swam to a certain depth in mid-water, then just drifted slowly down until it rested on the sea floor. Such deep dives were unusual in this category, however, and most were completed in mid-water at depths of less than 100 m.

Without knowledge of swimspeed, it is not possible to say what proportion of dives conforming to this characteristic shape do indeed involve periods of drift, glide or perhaps very leisurely swimming. Calculated horizontal speeds were similar to those of square dives, which probably involve little travel over the sea bed. Circumstantial evidence suggests that some “T” dives do involve an element of drifting, but the rarity of these dives also demonstrates that this behaviour is not a substantial element of the subsurface behaviour of these belugas.

Parabolic dives

Parabolic dives shared important characteristics with V-dives; they were rare beyond 100 m, of relatively short duration and were associated with high average horizontal speeds consistent with most of them being made during periods of travel. With the exception of accomplishing horizontal movement efficiently and away from the sea surface, there is no obvious function for a parabolic-shaped dive; it does not deliver the animal to a destination in the vertical plane in an efficient way, nor does it apparently involve an element of rest. All the evidence therefore seems to indicate that such dives are indeed carried out for travelling. Most “deep” parabolic dives reached maximum depths not much greater than the arbitrary 40-m threshold for deep dives. This, and the high number of similar-shaped dives in the “shallow” category, lends strong support to the idea that parabolic dives should be considered near-surface behaviour. The rare example carried out to substantial depths is likely to represent quite different activity; one of the three in this sample was made in a narrow U-shaped fjord and its profile was therefore more likely due to the whale following the sea bed than choosing a saucer-shaped path in mid-water.

Shallow dives

Dives that reached maximum depth at 40 m or less below the surface were generally characterised by having short submergence times, low rates of vertical movement and high rates of horizontal travel. Many were made in mid-water; others reached the sea bed. The natural conclusion is that most dives in this category occurred

during periods of directed travel. Nonetheless, other activities must also be involved. Belugas in this region are known to feed sometimes near the surface on arctic cod (*Boreogadus saida*) (Welch et al. 1993), and some of the short inter-breath submergences that occur in bouts between deep dives also reach 15 m or more.

Context

The analysis and interpretation of detailed marine mammal diving behaviour are still in their infancy. Even for pinnipeds, of which many species have now been examined in at least part of their range, no standard repertoire of dive types has been established. For cetaceans, the literature currently covers material only from narwhals (*Monodon monoceros*) (Martin et al. 1994), harbour porpoises (*Phocoena phocoena*) (Westgate et al. 1995) and some preliminary work on belugas (Martin and Smith 1992; Martin et al. 1993). The question of what constitutes a distinct dive type, and what is simply a variant of a previously recognised one, has not been satisfactorily resolved for any marine mammal, and certainly not for cetaceans. In this study we recognised a dive shape if it represented what appeared to be a distinctive behaviour. This criterion was necessarily subjective, and there were many dives that lay somewhere between the most obvious dive shapes when first examined. However, repeat examination of the dive profiles allowed dive-type definitions to be modified to reflect real discontinuities in the data set. In consequence, we are confident that the dive types presented in Fig. 2 represent the variety of dives in the data set with reasonable accuracy.

The decision here to rely on manual, rather than statistical, discriminatory techniques was based on the experience of those who have published similar work on pinnipeds. Hindell et al. (1991) found that statistical treatment alone was not adequate to satisfactorily determine the dive types extant in their southern elephant seal (*Mirounga leonina*) data sets. Schreer and Testa (1995, 1996), in the most thorough comparison of techniques to date, concluded that statistical techniques could sometimes reduce human subjectivity on Weddell seal (*Leptonychotes weddellii*) dive data, but more often than not performed apparently less well than the human eye. On balance, therefore, with no previous cetacean experience to use as guidance as to what number or range of dive types to expect, it seemed prudent to undertake the current analysis manually. Having done so, a comparative re-analysis using an array of statistical methods would be instructive. But the question would remain as to which of the manual or various automated methods can discriminate biologically meaningful differences in dive profiles most accurately.

The consideration of shallow (≤ 40 m) dives separately from those reaching greater maximum depths was necessitated by reasons of scale. Although belugas must undertake a range of behaviours in the top 40 m of the

water column, the ability of TDR data to differentiate between them (especially with measurement intervals of 20–60 s) is certainly less than for deeper dives. Even with higher resolution data the task would be problematical. As an example, take two shallow dives differing only by a few metres (a whale body length) in one or two particular depth readings. These dives could easily be perceived as having distinct shapes by either the human eye or a statistical program, and thus be interpreted differently, even if the difference to the whale was insignificant. Clearly, biologically relevant recognition and interpretation of dive shapes must take into account both relative and absolute measures of depth, as well as the size of the animal carrying out the dive.

This study has demonstrated that on their summer grounds in the Lancaster Sound Somerset Island region, where this population of belugas can easily reach the sea bed, their subsurface behaviour is overwhelmingly dominated by relatively shallow “travelling” dives and benthic “foraging” dives at depths of hundreds of metres. Travelling dives vary somewhat in profile, but they are consistently of short duration and relatively shallow maximum depth. Deep dives are invariably to the sea bed, and their profile demonstrates that the whale travels to and from the destination depth at a constant vertical speed that is usually in the range 1.5–2.0 m s⁻¹. More often than not, the bottom phase of the dive is flat, i.e. the whale remains at a constant depth, but whether the animal is travelling at this time, searching the mud for stationary prey such as benthic invertebrates, or waiting for active prey such as fish or squid, we cannot yet determine. Three variants of the “standard” square dive were identified: two (S3 and S4) appeared to be the result of the physical environment where the dive was made, and another (S2 = wiggle dive) may be the result of a different foraging behaviour – the vertical pursuit of prey. Wiggle dives are outnumbered 4:1 by flat-bottomed foraging dives, but they are common enough in the sample to suggest that this behaviour forms a significant part of the beluga repertoire in this region.

The two “W” - shaped dives S3 and S4 are intriguing because they represent behaviour specific to a particular habitat – narrow, steep-sided fjords. Some belugas in this population spend weeks in the fjords of southern and eastern Devon Island during the autumnal eastward migration (Smith and Martin 1994). As elsewhere, these whales are apparently foraging benthically in these areas, often at the head of the fjord against the glacier face, but as yet there is no clear indication of why the bottom phase of the dive so often involves a decrease and subsequent increase in depth.

Despite some diversity in time-depth profiles, the essential elements of diving behaviour in this population of whales can be simply described, and their function deduced with some confidence. Most of the dive shapes found here have also been described for pinnipeds (Le Boeuf et al. 1988; Asaga et al. 1989; Hindell et al. 1991; Schreer and Testa 1996), although the relative importance of the various dive types are different, especially

for those seals (e.g. elephant seals *Mirounga* spp.) that often forage in mid-water (Le Boeuf et al. 1988; Asaga et al. 1989; Hindell et al. 1991). One common characteristic of mid-water seal dives is totally missing from the beluga sample, however; that of multiple changes of direction during a deep descent. The fact that not one animal in the current sample broke its descent or ascent during a deep dive demonstrates that these belugas treat most of the water column merely as dead space separating resources of oxygen and nutrition.

The initial work on belugas of this same population (Martin et al. 1993) recognised S1 and V dives in submergences to below 50 m, and treated near-surface submergences as a separate group. Narwhals living in a fjord in northern Baffin Island carried out V-shaped and S2 = wiggle dives in addition to near-surface parabolic and square dives (Martin et al. 1994). The evidence indicated that, in this location at least, narwhals were routinely pursuing active prey in the vertical plane near the sea bed. The frequency and amplitude of the “wiggles” were greater than anything seen in the current beluga data set, indicating a different foraging strategy, and possibly different prey. These two species are taxonomically closely related, morphologically similar, and sympatric in many parts of their ranges. But their different feeding “equipment” (the narwhal has no functional teeth, no flexible lips, no neck flexibility and a much smaller gape), and the apparently different foraging strategies are at least circumstantial evidence for some degree of niche separation between the two. Studies of the food of the two species are equivocal on this point, indicating some overlap in the fish component, but that cephalopods and crustaceans are much more commonly taken by narwhals than by belugas (Vladykov 1946; Tomilin 1967; Finley and Gibb 1982; Seaman et al. 1982; Brodie 1989; Heide-Jørgensen et al. 1994). An unequivocal answer to the question of dietary overlap is likely to require further sampling and the deployment of both TDRs and video equipment on both species.

The only other cetacean for which similar data have been published is the harbour porpoise (Westgate et al. 1995). In this species “flat-bottomed” square dives (= S1 in this study) were the most common deep submergence type, but “wiggle” dives similar to our S2 category represented some 12% of dives. Although the water depth in which the flat-bottomed dives were made was not known precisely, porpoises are commonly entangled in bottom-set gillnets in this and other areas (Read et al. 1993; IWC 1996) and so, like belugas, presumably forage on or near the sea bed some of the time.

An outcome of this study has been the realisation that a distinct dive shape does not necessarily represent one distinct beluga behaviour; independent contextual information is needed to allow proper interpretation of what the animal is doing. Multimodality in characteristics other than shape (e.g. duration or relative depth) may indicate that two or more behaviours have been

artificially grouped. Equally, two or more apparently different dive shapes may represent the same whale behaviour, but appear distinct from one another. Trapezoidal dives of belugas fit the first scenario (the middle sloping element may be due to active swimming along a gradient or drifting in mid-water) and “travelling” dives (which may be square, V-shaped, parabolic or a mixture of these to our eyes) probably fit the latter. Concurrent information on swim-speed and ingestion events would greatly improve our ability to correctly distinguish and interpret dive behaviour. Sensors for both these variables are already in use on marine mammals and should therefore be readily adaptable for use in future studies of dive behaviour in cetaceans.

Information from TDRs is a powerful means of examining and interpreting cetacean behaviour during deep dives, when differences between dive profiles are large, but becomes less so in shallower submergences where the scale of such differences approaches the animal’s body size. Further progress will be dependent on the development of new sensors and visual imaging of underwater activity using miniature cameras attached to the animal. Only then can the effect of other important variables such as prey type and density, detailed bottom topography and interactions with other animals be taken into account when interpreting cetacean underwater behaviour.

Acknowledgements Thanks are due to the many Sea Mammal Research Unit and Cambridge University personnel who contributed to this project, among them Dustin Woods and Roland Bulkyn-Rackowe for help with data handling and filtering, and Colin Hunter, Bernie McConnell, Gilly banks and Phil Lovell for downloading and organising ARGOS data. Jack Orr, Hillary Adams, Haakon Hop, Gary Sleno and David St Aubin gave valuable assistance with fieldwork and logistics. The paper was improved by reviews from Andy Read, Andrew Westgate and two anonymous referees. The work was dependent on financial support from the Natural Environment Research Council, UK and the Canadian Department of Fisheries and Oceans. The Polar Continental Shelf Project (PCSP) of the Department of Energy, Mines and Resources, Resolute Bay, NWT provided expert and vital field support and transportation.

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