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Diving behaviour of long-finned pilot whales *Globicephala melas* around the Faroe Islands

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Three long-finned pilot whales *Globicephala melas* were equipped with satellite-linked time-depth recorders on the Faroe Islands on 15 July 2000. The purpose was to study the diving behaviour and habitat use of free-ranging pilot whales in the northeast Atlantic. Summarised data on the diving behaviour of the whales were collected for up to 129 6-hour periods. The maximum depth of dives was 828 m and the mean number of dives below 12 m was 12.2/hour (SD = 8.2). On average, the whales spent 60% of their time above 7 m depth. All three whales had significantly longer surface times when they were outside the continental shelf than when they were on the shelf. The mean vertical speeds ranged from 0.9 m/second for dives to 150 m to 2.3 m/second for dives to 600 m. No dives below 12 m lasted longer than 18 minutes, and more than 60% of dives lasted less than three minutes. The mean number of dives that lasted less than one minute was significantly higher in offshore areas than on the continental slope for all three whales. Compared to other odontocetes of similar size, long-finned pilot whales apparently either have a lower dive capacity or utilise a niche in the water column that requires less diving activity.

Key words: diving behaviour, Faroe Islands, Globicephala melas, pilot whale, satellite tracking

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Long-finned pilot whales *Globicephala melas* (hereafter referred to as pilot whales) inhabit the deep waters of the North Atlantic (Buckland, Bloch, Cattanach, Gunnlaugsson, Hoydal, Lens & Sigurjónsson 1993, Bloch, Heide-Jørgensen, Stefansson, Mikkelsen, Ofstad, Dietz & Andersen in press) and are known to feed on squid and other prey usually found at relatively deep depths (Desportes & Mouritsen 1993). Other odontocetes that prey on bathypelagic food items have been found to have extraordinary diving capacities, not only in terms of the time they remain submerged and the depths they reach, but also in the number of repeated deep dives they make (*cf.* Hooker & Baird 1999, Heide-Jørgensen & Dietz 1995, Heide-Jørgensen, Richard & Rosing-Asvid 1998). It is, therefore, anticipated that pilot whales would have similar capacities for deep as well as long-duration dives.

The elucidation of the diving capabilities and surfacing behaviour of pilot whales is not only of interest for a physiological comparison with similar species, but also for an enhanced understanding of the ecology of this numerous and wide-roaming species. In purely practical terms, the evaluation of the time spent at the surface by pilot whales greatly impacts the interpretation of visual surveys that attempt to estimate the abundance of pilot whales. Ship-based line transect surveys are commonly used to estimate the offshore abundance of cetaceans (e.g. Hammond, Benke, Berggren, Borchers, Buckland, Collet, Heide-Jørgensen, Heimlich-Boran, Hiby, Leopold & Øien 1995), and one basic assumption of line transect theory is that all animals on the trackline are detected during the passage of the survey platform. An obvious problem with whales is that they can only be detected when at the surface and this 'availability bias' (Marsh & Sinclair 1989) needs to be estimated to convert line transect estimates of relative abundance into total abundance estimates. To estimate the discrete availability of individual whales it is necessary to observe their diving habits and the time they spend at the surface. This is most efficiently done by equipping whales with dive depth recorders.

Our study evaluates the characteristics of the diving behaviour of free-ranging pilot whales in the waters surrounding the Faroe Islands. We developed estimates of the time they spent at the surface and compared their diving capabilities to those of other odontocetes with similar offshore occurrence and feedings habits.

Methods

One female and two male pilot whales were selected from a pod of about 80 pilot whales, and subsequently beached and equipped with satellite-linked time-depth recorders at Sandavagur (62.05°EN, 7.154°W) on 15 July 2000. When this was completed, the three whales were reunited with their pod and all were driven back to sea. Bloch et al. (in press) provide details on the capturing operation, as well as the configuration and attachment of the UHF transmitters.

We used Telonics (Mesa, AZ) ST-10 transmitter units with controller board, pressure transducer and dive data collection software provided by Wildlife Computers (Woodinville, WA). Data on diving behaviour were collected and compressed before transmission to the Argos Data Collection and Location Service.

The recorders were equipped with a salt-water conductivity switch that allowed transmissions when dry for more than 250 milliseconds. On the surface, the salt-water switch would recalibrate the pressure transducer, which measured the depth of the instrument every 10 seconds. The range of the pressure transducer was 0-1,500 m and the resolution of the readings was 6 m. Data were collected in four 6-hour periods that covered the following hours: 02:00-07:59, 08:00-13:59, 14:00-19:59 and 20:00-01:59 local time (= GMT - 1 hour).

Only compressed and summarised dive information was transmitted to the satellite. Dives where defined as submergence below 12 m. For each dive the maximum depth (or the 'destination depth') was recorded into one of 14 categories or bins: 12-17 m, 18-35 m, 36-53 m, 54-101 m, 102-149 m, 150-197 m, 198-299 m, 300-401 m, 402-599 m, 600-797 m, 798-1,001 m, 1,002-1,199 m, 1,200-1,398 m and >1,398 m. Except for the first bin (0 - <18 m), the same bins were used for collecting the time spent at depth, which was also sampled by incrementing the appropriate depth bin after each 10-second reading. The duration of dives deeper than 12 m were binned in the following categories: 0 - <1 minute, 1 - <3 minutes and increments of 3-minute bins up to a duration of 36 minutes. The time spent at surface was defined to be less than 7 minutes. Finally, the actual reading of the maximum depth of dives was assessed for each 24-hour period.

The positions of the whales were used to distinguish between diving over the continental shelf (depth less than ca 200 m) and diving outside the shelf. Since the dive data were collected in 6-hour intervals (and 24-hour periods for maximum depth measurements) some of the intervals include data from both on and off the continental shelf.

Vertical speeds could be calculated when the destination depth bin (i.e. the bin with the deepest dives) was isolated from the previous bin by at least one transit bin without dives. The vertical speed of the whales through the segments of the water column to different destination depths was estimated using the formula by Heide-Jørgensen et al. (1998):

$$\text{Vertical speed } (ms^{-1}) = N * D/(\sum TAD/2),$$

Table 1. Data on the three pilot whales equipped with time-depth recorders including their sex, length, estimated body mass, sample size, surface time and dive rate measured during 6-hour periods with standard deviation given in parentheses.

Whale IDNO	Sex	Body length (cm)	Body mass (kg)	No. of 6-hour periods with data	Mean proportion of time at surface (0-6 m) %	Mean dive rate (dives/hour)
20167	♂	585	1916	63	60.5 (16)	7.2 (3.8)
20693	♀	420	837	78	56.3 (14.4)	23.0 (7.2)
20696	♂	450	994	129	62.1 (15.0)	8.6 (3.3)
ALL				270	60.0 (15.2)	12.2 (8.2)

where N is the number of dives to the isolated destination depth, D is the vertical distance (in metres) through the transit dive bin to the bin with the dive destinations and TAD (time-at-depth) is the time spent (transit time) in the transit dive bins. The instruments measure the total time spent in each bin based on the number of 10-second increments recorded. A whale may enter a new bin after ≤9 seconds in the previous bin, after which it will be assigned a full 10-second period in the new bin. The whale may also exit the bin after ≤9 seconds and get the 10-second period assigned to the preceding bin. Since this is a completely erratic process, the probabilities of each event are considered equal. Therefore the transit time may be over- or underestimated with up to 9 seconds (cases where the transit bins can be passed in less than 10 seconds were excluded). This unbiased error will not exceed a maximum of 10%, and when using averages the error will be reduced with sample size.

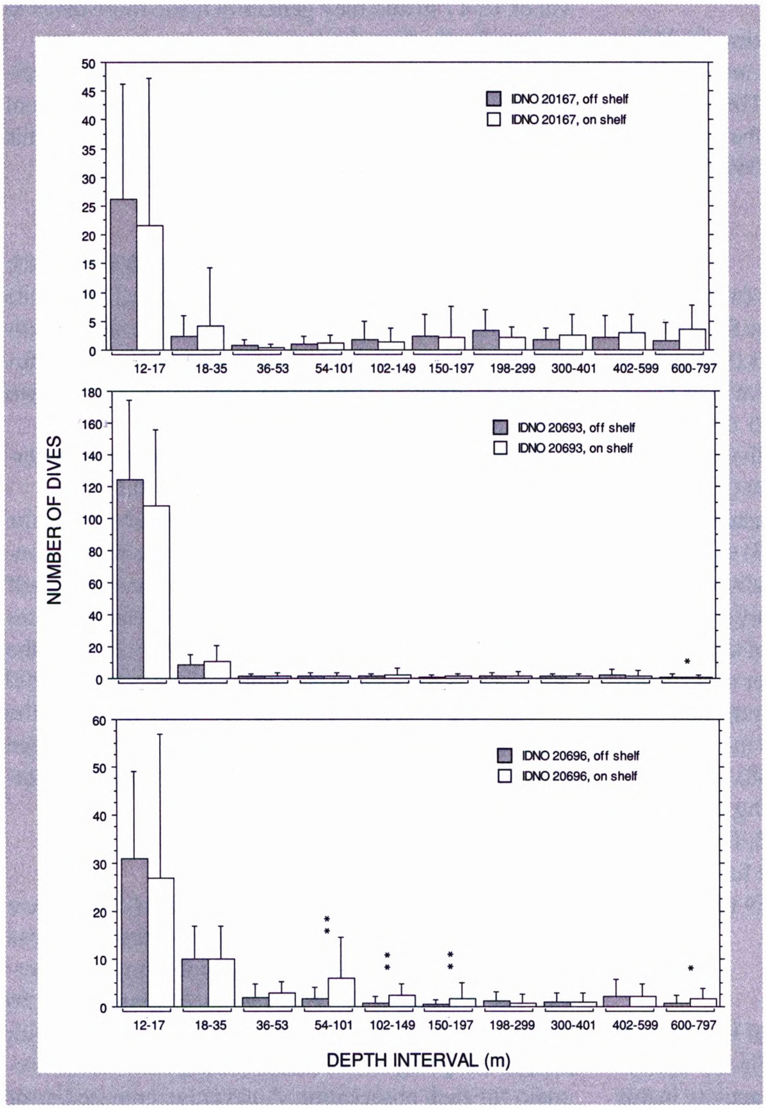

Figure 1. Distribution of mean number (+ SD) of dives to 10 depth intervals per 6-hour period for the three pilot whales according to whether the whales were on or off the shelf when diving. The significance of the difference between on and off the shelf values are shown as *: 0.01<α<0.05 and **: α< 0.01.

Body mass (in kg) of the whales was estimated from body length (in cm) using the power function given in Lockyer (1993):

$$\text{Body mass} = 0.00023 * \text{body length}^{2.501}$$

The whales were captured on day 197 after 1 January and this enumeration was used for the regression on time. Standard descriptive statistical methods, regressions and ANOVA and ANCOVA models were employed to test hypotheses and characterise dive patterns. A standard level of significance of 0.05 was chosen.

Results

The three pilot whales equipped with satellite-linked time-depth recorders were estimated to weigh between 800 and almost 2,000 kg (Table 1). Data on diving patterns were collected for 378-774 hours.

Table 2. Proportion of time (in % of 6-hour samples) spent at the surface (<7 m) and at different depth intervals for the three pilot whales when they were outside the continental shelf (off) and over the shelf (on). Standard deviations are given in parentheses. The significance of the difference between on and off the shelf values (actual readings of seconds for each cell) are shown as *: 0.01< α <0.05, and **: α <0.01.

Depth interval (m)	Female (IDNO 20693)		Large male (IDNO 20167)		Small male (IDNO 20696)	
	Off	On	Off	On	Off	On
<7	52.4 (13.9)	58.3 (14.4)	52.2 (17.2)	64.5 (14.1)	52.0 (22.5)	64.1 (12.0)
0-17	80.6 (14.5)	79.3 (17.4)	73.7 (13.9)	65.7 (17.6)	78.1 (15.3)	67.6 (24.7)
18-35	3.9 (4.0)	5.5 (5.7)	2.3 (1.5)	3.0 (3.4)	6.2 (6.0) **	10.1 (7.6)**
36-53	1.4 (1.4)	1.8 (1.6)	1.4 (0.9)	1.4 (0.8)	1.9 (2.3) **	5.2 (6.0)**
54-101	2.5 (1.8)	3.0 (3.3)	3.8 (2.9)	4.3 (2.9)	2.8 (3.0) **	6.6 (7.0)**
102-149	2.0 (1.8)	2.6 (4.3)	4.0 (3.2)	3.8 (2.8)	1.7 (1.7)	2.4 (2.7)
150-197	1.6 (1.5)	1.6 (1.8)	3.1 (2.2)	1.6 (1.5)	1.5 (1.5)	1.4 (1.6)
198-299	2.8 (3.1)	1.8 (2.5)	4.3 (3.3)*	6.6 (4.7)*	2.8 (3.2)	1.8 (2.5)
300-401	2.0 (2.8)	1.7 (2.8)	3.0 (3.4)	4.9 (4.9)	2.0 (2.4)	1.7 (3.0)
402-599	2.6 (4.4)	1.8 (3.6)	3.4 (4.6)	4.9 (5.0)	2.5 (4.3)	2.3 (3.2)
600-797	0.6 (1.5)	0.2 (0.8)	1.1 (2.4)	2.2 (3.0)	0.4 (1.0)*	1.0 (1.8)*

Maximum depths of dives

All three whales had a mean daily maximum diving depth of around 600 m. The deepest dive recorded was 828 m for the small male (IDNO 20696). The maximum dive depth increased slightly with time for the larger male (IDNO 20167) and the female (IDNO 20693), but not for the small male (IDNO 20696).

Dive rate

The three whales had different dive rates (measured as the number of dives below 8 m/hour). The female pilot whale (IDNO 20693) had a dive rate of 23.0 dives/hour which was significantly higher than the dive rates measured for the two other whales (7.2-8.6 dives/hour; ANOVA: $P < 0.0001$; see Table 1). The dive rate of the two males were not significantly different ($P = 0.054$).

With regard to the number of dives measured over 24 hours, the female pilot whale (IDNO 20693) significantly increased her dive rate ($P < 0.005$) from about 18 to 27 dives/24-hour period from day 197 (15 July) to day 216 (3 August). The male pilot whales did not show a similar increase (ANCOVA with day number as a covariate: $P > 0.10$). No difference in dive rate could be detected when the whales were on (<200 m) or outside the continental shelf (ANOVA: $P = 0.468$).

The dive rate varied significantly during the four 6-hour periods for the female (IDNO 20693; $P = 0.0203$), but not for the two males ($P > 0.60$). The female made more dives during the period 08:00-13:59 than during any other quarter of the day.

Depth of dives and time at depths

Most diving activity occurred at depths of less than 36 m with >90% of dives within 12-17 m (Fig. 1). The female (IDNO 20693) had the highest dive activity in this interval with an average of 124.3 dives per 6-hour period off the shelf and 108.1 dives on the shelf. The two males also made more dives off the shelf within the interval of 12-17 m and they generally made more dives to greater depths than the female.

Analysis of the proportion of the time spent at various depths indicates that >65% of their time was spent above 18 m, and that, again, more time was spent at this depth off the shelf than on the shelf (Table 2).

Time at surface

The three pilot whales spent, on average, 60% (95% CI: 57.9-62.0) of their time above 7 m depth. The female (IDNO 20693) increased her surface time significantly with time ($P < 0.0001$) from around 40 to 65% during the 17 days for which data were collected. The two males did not show a similar pattern.

The length of the surface time did not seem to be correlated with the dive rate (ANOVA: $P = 0.12$).

All three whales spent significantly more time at the surface (above 7 m) when they were outside the continental shelf than they did when they were on the shelf (ANOVA: $P < 0.0001$; see Table 2). For all three whales combined, the difference was 62.7% (SD = 13.4) of the time spent at the surface when in waters deeper than 200 m and 52.2% (SD = 17.4) of the time when on the shelf. There was no effect of time of day on the surface time for any of the whales (ANCOVA with day number as a covariate: $P > 0.21$).

Vertical speed

Dives within the first three depth categories (<54 m) were excluded because the whales may pass through these depth categories within the 10-second sampling interval. The remaining 50 observations (representing 156 dives) of vertical speeds covered 37,393 seconds with a mean sampling of 747 seconds (range: 80-4,269 seconds) for each observation. An average unbiased error of ± 2.7% (10/(747/2)) was caused by the 10-second increments of the time-at-depth readings, however, larger errors may be anticipated at shorter sampling peri-

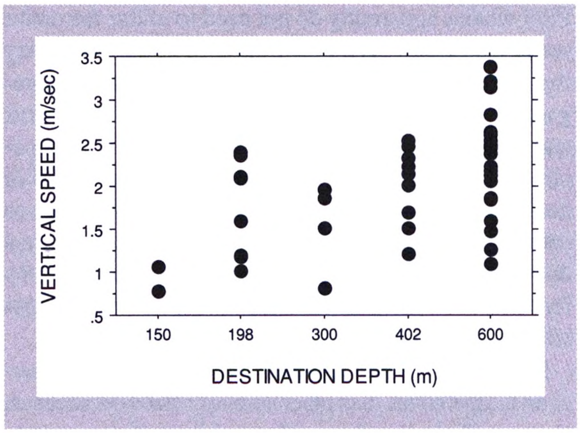

Figure 2. Vertical speed of dives according to destination depth for the three pilot whales.

ods. When averaging over several observations this unbiased error will be ignorable. The vertical speeds ranged from 0.79 to 3.38 m/second with a mean of 1.99 ± 0.6 m/second (N = 50), and the means ranged from 0.9 m/second for dives to 150 m and 2.3 m/second for dives to 600 m. Clearly, the vertical speeds, increased with increasing destination depth of the dives (ANOVA: P < 0.0001; Fig. 2). There was no difference between the vertical speeds exhibited by the three whales (ANCOVA with destination depth as a covariate: P = 0.78).

Duration of dives

No dives below 12 m lasted longer than 18 minutes, and more than 60% of dives lasted less than three minutes (Fig. 3). The female pilot whale clearly made the greatest number of dives of the shortest duration, as 88.4% (± 11.1) of her dives lasted less than three minutes, as compared to the two males for which 65.2% (± 22.8) of their combined dives lasted three minutes or less.

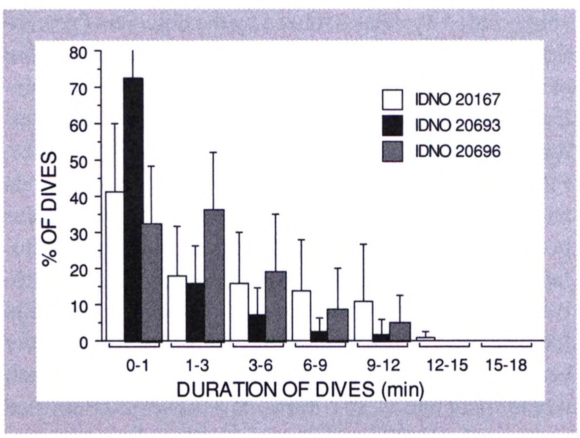

Figure 3. Distribution (in %) of the duration of dives (+SD) in seven time categories for the three pilot whales.

The number of dives that lasted less than one minute was significantly higher in offshore areas than on the continental slope for all three whales (ANOVA: P = 0.0163). No significant difference was evident for dives with durations of 1-3 minutes. The whales, however, made significantly more dives that lasted 3-6 minutes on the continental shelf than outside the shelf (ANOVA: P < 0.0001), but no difference could be detected for dives of longer duration.

Discussion

The female and one of the males used in our study were adult animals and the second male was in puberty, judged by their relative body length (Bloch, Lockyer & Zachariassen 1993b). Body size is important in determining dive capabilities. Because the whales were mature or in puberty, it can be assumed that the animals were capable of exhibiting the maximum diving performance of the species. Furthermore, the whales travelled over deep-water areas beyond the continental shelf where they had access to water depths exceeding 1,500 m (Bloch et al. in press).

Data on dive capacity from captive pilot whales are restricted to a trained, immature, male short-finned pilot whale *Globicephala macrorhynchus* weighing 545 kg diving for targets in the open ocean (Bowers & Henderson 1972). During training, the whale was capable of making frequent dives to 500 m and once to 610 m, but the dive duration never exceeding 15 minutes. Attempts to make the whale go even deeper were not successful.

Diving behaviour of free ranging pilot whales has only been studied in the Mediterranean Sea, where five whales equipped with retrievable time-depth recorders provided dive data for a total of 25 hours (Baird, Borsani, Hanson & Tyack 2002). The results are in good agreement with our findings; maximum dive depth was 648 m despite water depths exceeding 2,000 m, no dives lasted more than 13 minutes, the mean duration of the dives was about eight minutes and the mean of descent and ascent rates on deep dives were 1.75 and 2.02 m second^{-1}, respectively.

Data on the diving capacity of other free-ranging odontocetes are restricted to a few species of which four inhabit waters of similar depths and have comparable feeding habits. Northern bottlenose whale *Hyperodoon ampullatus* make some of the longest and deepest dives recorded for a mammal. The maximum depth recorded is 1,453 m with a duration of 70.5 minutes (Hooker & Baird 1999). Ascent and descent rates for deep dives

(>800 m) ranged from 0.46 to 1.93 m $second^{-1}$ and thus appear slower than the vertical speeds recorded for pilot whales. Narwhals *Monodon monoceros* have been reported to make frequent dives to depths exceeding 1,000 m (Heide-Jørgensen & Dietz 1995), and more recent studies have shown that the maximum dive depth is in excess of 1,500 m (Heide-Jørgensen, Dietz, Laidre & Richard 2002). However, the maximum duration of dives by narwhals only occasionally exceeded 25 minutes, thus allowing relatively short times at the bottom (Heide-Jørgensen & Dietz 1995). The vertical speeds for narwhals ranged from 1.09 m $second^{-1}$ for dives to 100 m and 2.08 m $second^{-1}$ for dives to 900 m when calculated using the methods we used in our study. Time-depth recorder measurements of ascent and descent for narwhals diving in shallow areas (<300 m) ranged between 0.6 and 1.5 m $second^{-1}$, with no significant differences between the two rates (Laidre, Heide-Jørgensen & Dietz 2002).

The maximum dive depth of sperm whales *Physeter macrocephalus* is uncertain, but frequent dives to depths of 400-1,300 m and possibly 2,000 m by sperm whales tagged with acoustic transponders have been recorded (Watkins, Daher, Fristrup, Howald & Notarbartola di Sciara 1993, Watkins, Daher, DiMarzio, Samuels, Wartzok, Fristrup, Howey & Maiefski 2002). The duration of the dives ranged from 18 to 73 minutes, the latter definitely being the record for cetaceans. Ascent and descent rates ranged from 0.74 to 1.52 m $second^{-1}$. Belugas or white whales *Delphinapterus leucas* have been reported to make dives to a maximum depth of 862 m (Heide-Jørgensen et al. 1998), but the data were collected from whales found in relatively shallow waters where no deeper dives could be anticipated. Less than one percent of the dives lasted more than 18 minutes. The majority of the dives (>50%) lasted either less than three minutes or between nine and 18 minutes. Vertical speeds for belugas ranged from 0.50 m $second^{-1}$ for dives to 52 m to 1.90 m $second^{-1}$ for dives to 800 m (Heide-Jørgensen et al. 1998).

Pilot whales are intermediate in body size between narwhals/belugas and sperm whales/bottlenose whales. Diving capacity depends on body volume or mass (e.g. Kooyman 1988), and it is thus expected that pilot whales would exhibit a dive capacity of at least the same magnitude as the Monodontids. The limited sample of three pilot whales monitored for 270 6-hour periods does not suggest that these pilot whales exhausted their diving capabilities, at least not around the continental shelf off the Faroe Islands.

Pilot whales, narwhals, belugas, sperm whales and bottlenose whales all partly or entirely feed on squid. Pilot whales apparently do not need to utilise the entire water column to find a prey column in the areas they frequent. Around the Faroe Islands, pilot whales eat gregarious squid species, such as *Todarodes sagittatus* and *Gonatus* sp. All are neritic and oceanic squid species most common at depths between 100 and 500 m and with vertical movements that allow the whales to catch the squid at night in the surface layers (Desportes & Mouritsen 1993). They also prey at unknown depths for some fish species such as greater argentine *Argentina silus* and blue whiting *Micromesistius poutassou*.

Our study suggests that pilot whales either have lower dive capabilities than other similarly-sized odontocetes or, more likely, that they utilise a niche in the water column that requires less extreme diving in terms of duration of dives and maximum depth of dives.

The reduced diving activity is also obvious from the longer surface time of the three pilot whales (mean = 60.0%) than of belugas (mean of six whales = 39.1%; Heide-Jørgensen et al. 1998) and narwhals (mean of seven whales = 39.3%; Heide-Jørgensen & Dietz 1995). The results of our study indicate that the three pilot whales spend a considerable amount of time at the surface, in fact, considerably more time than reported for other odontocetes, and that they preferred particularly short dive durations (see also Baird et al. 2002).

There is no obvious explanation of why the female pilot whale made many more short dives (especially during the morning) compared to the males. Genetic studies suggest that the female might be the mother of the small male (IDNO 20696), but they were not swimming together (Bloch et al. in press) and they certainly did not follow the same diving schedule.

When analysing ship-based line-transect sighting surveys of pilot whales it is often assumed that all pods on the transect line are detected by the observers (Buckland et al. 1993). Violation of this assumption is either caused by whales missed by the observers ('perception bias') or by whales diving during the passage of the survey platform ('availability bias'). The dive information from the three pilot whales is useful for elucidating the problems associated with the availability bias. Pilot whales are usually found in relatively large pods around the Faroe Islands (on average around 150 whales per pod; Bloch, Desportes, Mouritsen, Skaaning & Stefansson 1993a). The large pod sizes make it more likely that some of the whales in the pods will be available for detection at the surface during the passage of the vessel. According to the results from this study each whale spent almost two thirds of its time at the surface and not all whales in a large pod will be diving in synchrony. One of the whales in our study did have a dive rate almost three times higher than those observed for the other two whales. The combined probability of long surface time and whales diving out of synchrony will give a high probability of detecting large pods during the passage of the vessel. Our study provides the first verification that it might indeed be possible that all large pods of pilot whales can be expected to be seen on the transect line of a ship-based sighting survey.

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