Time allocation and diving behaviour of harbour porpoises (*Phocoena phocoena*) in Danish and adjacent waters

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ABSTRACT

To gain insight into the time allocation and diving behaviour of harbour porpoises in Danish and adjacent waters, satellite linked dive recorders were mounted on 14 harbour porpoises. The animals were incidentally caught alive by fishermen using pound nets during 1997-99 in the Danish Belt seas. Information on diving behaviour was collected from April to November. Contact with individual porpoises remained for up to 130 days. The average number of dives per hour was 29 during April-August and 43 during October-November. Daily maximum dive depth corresponds to the depth of the Belt seas and Kattegat where depth generally does not exceed 50m. Maximum dive depth recorded was 132m from animals moving north into Skagerrak. Dives were frequently recorded in the category 10-15min, but could potentially be an artefact of the sampling regime. The diurnal pattern shows that harbour porpoises dive continuously both day and night, but with peak activity during daylight hours. On average they spent 55% of their time in the upper 2m during April-August. These values have implications for aerial abundance surveys when correcting for animals not visible. A mature female and its approximately 10 months old calf were both tagged and swam together for 43 days until contact was lost. The calf made more frequent but shorter dives than the mature female. The number of dives per hour decreased, while the dive depth and duration increased for both animals from May to June, suggesting a change in feeding behaviour. It is not known whether the female and calf synchronised their dives, but the diurnal dive pattern shows a correlated dive rhythm in May, but not in June. This change in mother-calf behaviour suggests that the calf foraged more independently, corresponding to the time of year when porpoise calves leave their mother.

KEYWORDS: SATELLITE TAGGING; TELEMETRY, DIURNAL; BEHAVIOUR; DIVING; HARBOUR PORPOISE; NORTHERN HEMISPHERE; ATLANTIC OCEAN

INTRODUCTION

The diving behaviour of cetaceans is almost impossible to study without the aid of electronic devices. Compared to other marine endotherms like seals and birds, for which the fur and feathers can be used as a base for attachment, the skin of cetaceans consist of live cells that are constantly being replaced, making gluing impossible. For short-term deployments (up to two days) suction cup tags have been used (e.g. Schneider *et al*., 1998) but to follow animals for days or months the tag needs to be attached more permanently to the animal. On large cetaceans this is done by shooting the tag into the tissue (e.g. Heide-Jørgensen *et al*., 2001). For small cetaceans, the animals may be caught and the tag attached by means of pins through the dorsal fin or dorsal ridge (e.g. Read and Westgate, 1997; Wells *et al*., 1999). The latter method has proven to be the most successful in terms of contact duration, with contact remaining for up to 349 days for a harbour porpoise (Teilmann *et al*., 2004).

Two different approaches for gathering dive data have been used in previous studies, one which requires recovery of the device and one in which data are transmitted electronically. Data loggers (e.g. Time-Depth-Recorders, TDRs), which store high resolution data, have only been used to a limited extent on free-living cetaceans. These instruments need to be recovered, as the quantity of data is too large to transmit via satellite and is thus stored in the memory onboard the tag. Difficulties in retrieving the tag have prevented the wide use of this technique. In order to circumvent this, satellite transmitters that store and transmit information have been developed (Satellite-Dive-Recorders, SDRs). This method secures long-term data retrieval as long as contact remains with the satellite. However, the method is limited by the data receiving capacity of the satellite, with the result being lower resolution data organised in bins over several hours unlike the individual readings every few seconds yielded by TDRs. Burns and Castellini (1998) monitored the behaviour of individual Weddell seal pups using both TDRs and SDRs. They found that although the data loggers gave a full record of all dives, while only half of the dives were represented in the data received by the satellite, on average the data from the SDRs gave an accurate representation of the diving behaviour.

The high mortality of harbour porpoises (*Phocoena phocoena*) taken as bycatch in gillnet fisheries throughout the Northern Hemisphere requires mitigation and management (e.g. Lowry and Teilmann, 1994; Vinther, 1999). Better guidance may be given if knowledge on the diurnal and seasonal movements and diving behaviour of these animals is taken into account.

The diving behaviour of harbour porpoises has previously been studied by Westgate *et al*. (1995), Otani *et al*. (2000; 1998) and Teilmann (2000). These studies all used data loggers deployed for up to 12 days.

The present study describes the diurnal and seasonal time allocation and diving behaviour of harbour porpoises over much longer periods than previously. Data are presented on 14 harbour porpoises monitored by SDRs for up to 130 days in Danish and adjacent waters.

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MATERIALS AND METHODS

The area

The tagged harbour porpoises remained primarily in the relatively shallow waters around the islands of Denmark (Fig. 1). The water depth only exceeds 50m along the Swedish west coast north of about 57°N. The bottom is generally comprised of sand, gravel or stone reefs, except for the Swedish westcoast where a rock bottom is found. These waters connect the Baltic to the ocean and have a very complex oceanography with low saline Baltic surface water (<10 psu) and heavy North Sea bottom water (about 30 psu) often forming a pronounced halocline. Although the tide is limited (<0.5m), strong currents are found in the narrow straits between the islands due to fresh water from the Baltic rivers and wind moving the water around.

Availability of the harbour porpoises

The porpoises tagged in this study were all incidentally trapped in pound nets in the Danish Belts (Fig. 1). Pound nets are used all around Denmark (except for the North Sea) in the spring to catch primarily herring (*Clupea harengus*), mackerel (*Scomber scombrus*) and garfish (*Belone belone*) and in autumn to catch eel (*Anguilla anguilla*). Often the porpoises are caught in nets together with herring. Herring may therefore 'guide' the porpoises along the pound net, into the trap. A pound net consists of a lead net that extends from the beach up to 1km ending in a trap. Several traps may follow spaced with another lead net. The trap consists of a wide opening that guide the fish into the final trap, which is a bag net open at the surface. The circumference of the bag is 40-80m with a mesh size of about 2cm. The meshes are too small for entanglement and the harbour porpoises are rarely injured and can swim around freely and dive to depths of 5-10m.

A network of pound net fishermen was established who reported when they observed a live porpoise in their nets. The fishermen were instructed to close the entrance to the net when a porpoise was found, to prevent the animal from escaping before the field team arrived, normally within a few hours. Compensation was paid to the fishermen for assistance with animal handling and for keeping the net closed until the porpoise was tagged and released.

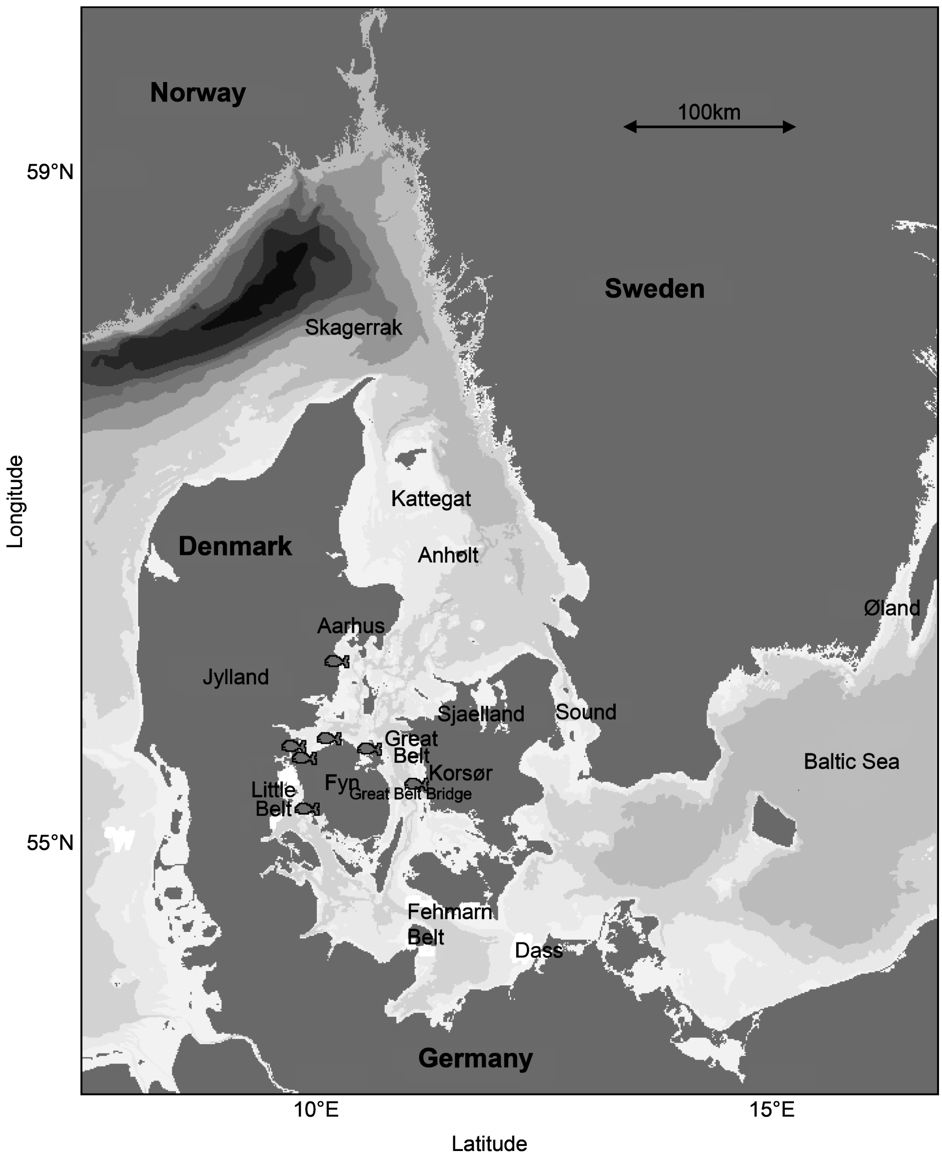

Fig. 1. Map of the study area with bathymetry and names mentioned in the text indicated. The locations of the pound nets where the harbour porpoises were caught are indicated with 'fish' symbols.

Handling and tag attachment

Fourteen harbour porpoises (Table 1) were equipped with SDRs (SDR-T10 with two 2/3 A-cells or two flat 3V lithium batteries (Wildlife Computers, Seattle, USA)). The SDR-T10 transmitters, which were cast in epoxy, weighed 130-240g in air and 10-20g in seawater. Each unit had a transmission power output of 0.25-0.5W, and a potential of around 12,500 transmissions. The transmitters were programmed to give a maximum of 100-500 transmissions per day depending on tag programming (see Table 1) giving an expected battery life of 25-125 days. All tags had a transmission repetition rate of 45s. A saltwater switch (SWS) ensured that transmissions would occur only when the animal was at the surface. Three front-mount and one side-mount designs were used (Table 1). The front-mount transmitters were glued (Flexane or Loctite 414) onto a saddle made from 2mm conveyor belt rubber material, which wrapped around the leading edge of the dorsal fin and was cut into shape for each individual animal to fit the dorsal fin. Side-mount transmitters were also glued (Loctite 414) onto a piece of conveyor belt somewhat larger than the transmitter housing, allowing the belt material to be cut into shape to fit the individual dorsal fin. A backing plate of the same material and shape was made for the side-mount tags. The inside of all 'saddles' was lined with 3mm neoprene to reduce abrasion of the skin of the dorsal fin. For all attachments three holes, forming a triangle, were used. Two holes about 2cm from the leading edge of the dorsal fin and one near the trailing edge.

Only animals considered to be in good health (no abnormalities and with a normal blubber layer, see Lockyer *et al*., 2003) were equipped with a satellite tag. After application of local anaesthesia (Lidocain 5% ointment), three holes were made in the dorsal fin by means of a 5mm stainless steel cork borer-type utensil. The best result was obtained if the cork borer was freshly sharpened around the inside of the hole, that the steel wall was as thin as possible and that a slow speed battery drill was used. Five millimetre threaded POM (polyoxymethylen or polyacetal) pins coated with polyester tubing (Sulzer Vascutek, Renfrewshire, Scotland) or silicone tubes as used in human surgery, to protect the tissue, were fitted through the saddle and the dorsal fin and fastened using nylon or iron nuts in both ends. Before inserting the pins they were coated with antiseptic ointment (Betadine). The manufacturer of the pins specified that POM, would degrade under UV light and detach the tag from the animal after some months, similarly the iron nuts would rust away and the tag fall off within an estimated one year period. The tissue samples inside the cork borer were saved for genetic analyses. Full data and sample sets for health check, body condition and reproductive status were taken when possible, including total length, girths, blubber thickness, full blood, serum and plasma, blood cytology, vaginal and blow cytology and bacteriology (Teilmann *et al*., 2004). The animals were handled on the boat for about 20-30 minutes until release.

Time and pressure (depth) were sampled at a default rate of every 10s. These data were stored in three types of 6hr summary histograms and then relayed to the satellite during the following 24hr (see below). In addition, status messages (every 15th transmission) and timelines (every 48th transmission) were transmitted in separate messages. The status messages included the maximum dive depth during the previous 24hr; status of the sensors, total number of transmissions and battery voltage. Timelines were recorded over 24hr and divided into 72 20min periods. Based on the depth sampled every 10s, the tag records whether the animal spends the majority of time (>50%) above or below 1m depth for each 20min period.

Three types of 6hr histograms were sampled: (1) maximum depth for each dive (limit of tags was 250m); (2) duration of each dive; and (3) time spent in each depth interval (TAD). Data from these three categories were sampled and stored in 14 user-defined intervals. Intervals for type 1 were set to 25m, then 5m bins up to 30m, 10m bins up to 100m and then >100m. Intervals for type 2 were one minute up to 10 minutes, 5 minute bins up to 25 minutes and then >25 minutes. Intervals for type 3 were 0-2m, 35m, then 5m bins up to 30m, 10m bins up to 90m and >90m (except for 6172_97, 6173_97, 6171_98 and 6173_98 for which the first bin was 0-5m). The pressure transducer had a resolution of ±1m and an accuracy of ±1% of the depth reading.

Data analysis

Data on movements, diving behaviour and transmitter status were collected via the Argos Location Service Plus system and received online over the Internet and on CD-ROMs. The software program *Satpak* 3.0 (Wildlife Computers) was used for validating dive data received from Argos and transforming data into an ASCII format. *Excel* and *SAS* were used for data analysis.

Table 1

Basic data for the tagged harbour porpoises.

ID no.	Sex	STD length (cm)	Body mass (kg)	Deployment period	Days of contact	Expected lifetime	No. of daily uplinks	Tag configuration
6171_97	F	110	27	14 Apr.-9 May 1997	26	25	500	SDR-T10 frontmount type 1
6170_97	F**	164	63	16 Apr.-23 May 1997	38	25	500	SDR-T10 frontmount type 1
6172_97	M	138	37	27 Oct.-6 Dec. 1997	41	31	400	SDR-T10 frontmount type 2
6173_97	M	114	24	1 Nov.-14 Nov. 1997	14	31	400	SDR-T10 frontmount type 2
6171_98	F**	166	58	11 May-24 Jun. 1998	45	50	250	SDR-T10 frontmount type 3
6173_98	F#	110	26	11 May-22 Jun. 1998	43	50	250	SDR-T10 frontmount type 3
6420_98	M	116	32	19 May-14 Jul. 1998	57	50	250	SDR-T10 frontmount type 3
6172_99	F*	138	45	30 Mar.-16 Jul. 1999	109	125	100	SDR-T10 frontmount type 3
6421_99	F	127	37	13 Apr.-20 Jul. 1999	99	125	100	SDR-T10 frontmount type 3
6422_99	M	120	31	13 Apr.-2 Aug. 1999	112	125	100	SDR-T10 frontmount type 3
6174_99	F'	112	30	25 Apr.-17 Aug. 1999	115	125	100	SDR-T10 sidemount type 2
6173_99	F#	144	65	25 Apr.-17 Aug. 1999	115	125	100	SDR-T10 sidemount type 2
6171_99	F	116	30	26 Apr.-4 Aug. 1999	101	125	100	SDR-T10 sidemount type 2
6170_99	M	118	37	27 Apr.-3 Sep. 1999	130	125	100	SDR-T10 sidemount type 2

**=Lactating female accompanied by calf. *=Female accompanied by calf. #=Calf accompanied by large female.

A dive was defined as deeper than 2m and lasting at least 10s. Surface time (breathing, resting or swimming at the surface), based on the timelines, was defined as the time spent above 1m depth. For each hour of the day, a monthly average value was used for comparison between months. Only for April-August and November were enough data available for this exercise.

RESULTS

System performance

From the 14 porpoises, 7,210 histograms were received (depth=2,341, duration=2,697, TAD=2,172), each representing a complete record of the diving behaviour during a 6hr period. This corresponds to 543-674 days of diving behaviour from each of the three histogram types received. The dive data collected represents on average 58% of the contact duration with the porpoises. The contact duration lasted from 14-130 days, depending on the daily allowance of transmission. On average the contact duration was within 96% of the expected lifetime based on battery capacity, indicating that the battery was the limiting factor in contact duration rather than tag attachment.

Frequency of dives

The overall average number of dives below 2m hr^{-1} was 34, with monthly means from 28 to 46 dives hr^{-1} (April-August, October-November, Fig. 2). The dive rate was not significantly different from April to August (mean=29 dives hr^{-1}, Analysis of Variance (ANOVA), $p>0.05$). Dive rates in October and November (mean=43 dives hr^{-1}) were significantly higher than in the April-August (ANOVA, $p<0.05$).

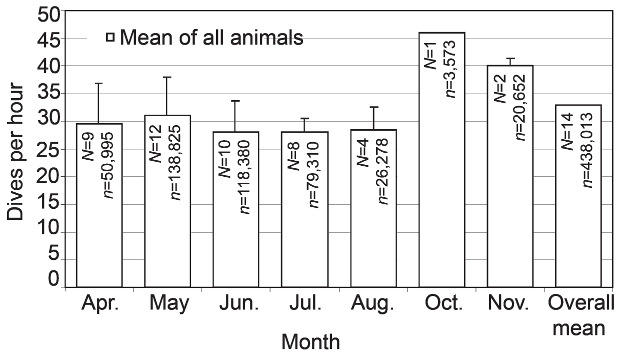

Fig. 2. Number of dives per hour by month. Bars indicate the average of individual means in the particular month and overall mean of animal means. Standard deviation is given above the bars for months where data from more than one animal exists. *N*=number of animals, *n*=number of dives.

Maximum dive depth

The status messages provided a daily exact maximum dive depth and 450 such values were received from the 14 animals (Fig. 3). They ranged from 6-132m, with median and mean values of 26m and 30m (Standard Deviation (SD)=17.8), respectively. The most frequent depths were 14-32m and represented 64% of all daily maximum dive depth values.

Diurnal and seasonal dive patterns

The time spent at the surface varied from 45-63% (mean 55%) in the 0-2m interval depending on the time of the day and month (Fig. 4). Although there was 18% difference in surface time during evening (15:00-21:00) from April to August, no significant differences were found between months or time of day (ANOVA, $p>0.05$).

As seen in Fig. 5, the time spent diving during May, June and July showed a similar pattern. The dive time was rather stable for most of the day, except between 15:00-20:00 when diving activity increase dramatically with peaks between 16:00-17:00. The same general pattern was seen for April and August, however, in April the dive time was lower than in May-July. In August, there was lower activity during 1:00-2:00 and a peak around 7:00 in the morning. In November a different pattern was seen with increased activity from 5:00 to 16:00, followed by a decrease over two hours where it remained until the morning. In early April and late August the sun rises at 6:00 and goes down around 20:00 in the study area. During the longest day (21 June) the sun is up from 4:30-22:00. In mid-November, the sun is up from about 7:30-16:00. There is no obvious correlation between daylight and diving activity during April-August, but in November the peak diving activity corresponds with daylight hours. Statistical correlation showed that May had the same diurnal fluctuations as April, August and November, while June correlated with November and August correlated significantly with July and November (Spearman Rank correlation, $p<0.05$). These correlations show that the diurnal dive patterns for all months correlate with other months, suggesting that abiotic parameters such as light may control the diurnal dive intensity. All the peak activity fell within the daylight hours. No obvious resting periods were found and a high level of diving activity was found throughout day and night in all months.

Time at depth

Generally, the majority of time was spent in the uppermost 5m with progressively less time spent in the deeper intervals. In October-November more time was spend at depths below 10m, compared to the spring and summer months. The overall TAD average for the whole study period shows that harbour porpoises in Danish waters spend about 68% of their time at 0-5m depth, 17% at 5-10m, 8% at 10-15m, 5% at 15-20m and 2% at depths deeper than 20m (Fig. 6).

Female/calf pair

The four adult females tagged in this study were all accompanied by a young animal and in two of the pairs both the female and calf were tagged (Table 1). The relationships between these two pairs were tested genetically (17 DNA microsatellite makers, see Teilmann *et al*. (2004) for details) and the results showed that one pair was a mother and calf (6171_98 and 6173_98) while the other was closely related as half siblings or cousins (6173_99 and 6174_99). In the latter case, the animals were seen swimming away close together after tagging, but the tracks separated the following day. The mother and calf swam close together until contact was lost after 45 (female) and 43 days (calf) due to low battery voltage (Fig. 7). Dive data were collected for 66% (female) and 52% (calf) of the total contact time. The time spent in the first 10m of the surface by the calf was 7% and 6% more than for the female in May and June, respectively (Table 2). From May to June there was an increase of 7% for the female and 4% for the calf in the time spent at greater depth than 10m (Table 2). At the same time the percentage of dives below 10m decreased by 3% and 9% for the female and calf, respectively. Thus, both animals made relatively fewer but longer duration dives from May to June (Fig. 8).

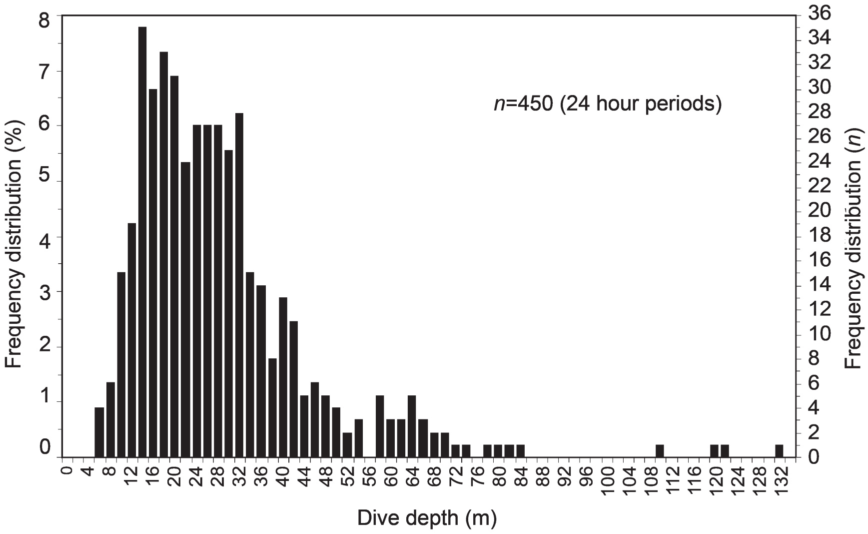

Fig. 3. Maximum dive depth for all animals recorded over 24hr periods. Note that both frequency in percent (left *y*-axis) and frequency in numbers (right *y*-axis) is given. *n*=number of 24-hour periods included.

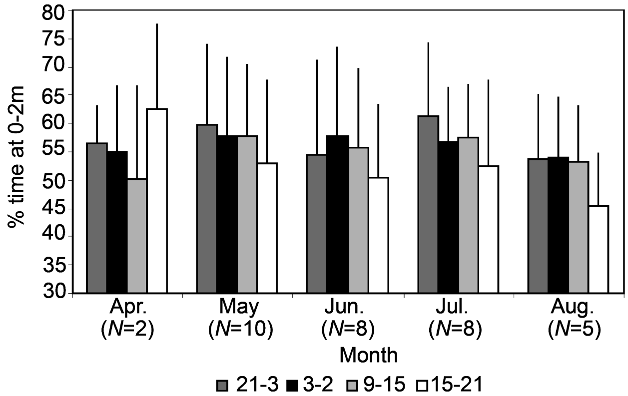

Fig. 4. Average time spent near the surface (0-2m) by month and time of day (night=21-3, morning=3-9, day=9-15, evening=15-21). Data obtained from the first histogram bin in TAD. *N*=number of animals included.

Dive durations up to 5min were recorded daily for both animals, while longer duration dives were recorded occasionally.

The diurnal dive patterns of the two animals, as expressed by the timeline data, were significantly correlated in May (Spearman Rank correlation, $p<0.05$), but not in June ($p>0.05$, Fig. 9). The calf spent significantly less time diving than the adult female during almost any time of the day in May (t-test, $p<0.05$), while this was less pronounced in June. In May, higher diving activity was seen around 4:00 in the morning and between 9:00 and 22:00. This period is mainly within daylight hours as the sun comes up around 5:00 and goes down around 21:15 in mid-May. The dive time below 1m based on timelines increased significantly from May to June for the adult female and the calf, respectively (*t*-test, $p>0.0001$). In June, both animals showed high diving activity in the early morning hours and

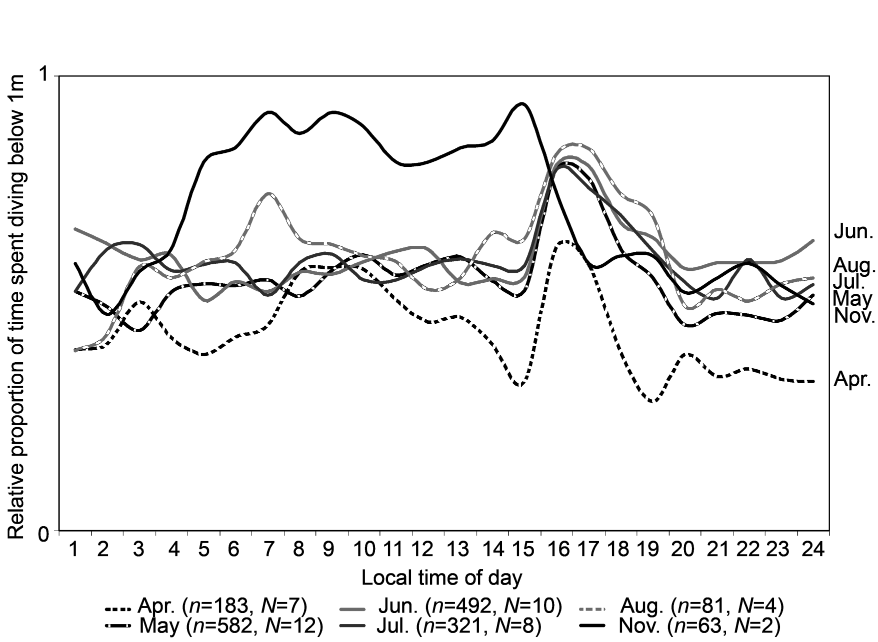

Fig. 5. Relative diving activity below 1m during the day (1 hour increments). *N*=number of animals, *n*=number of 20-minute 'timeline' periods included for each hour per month.

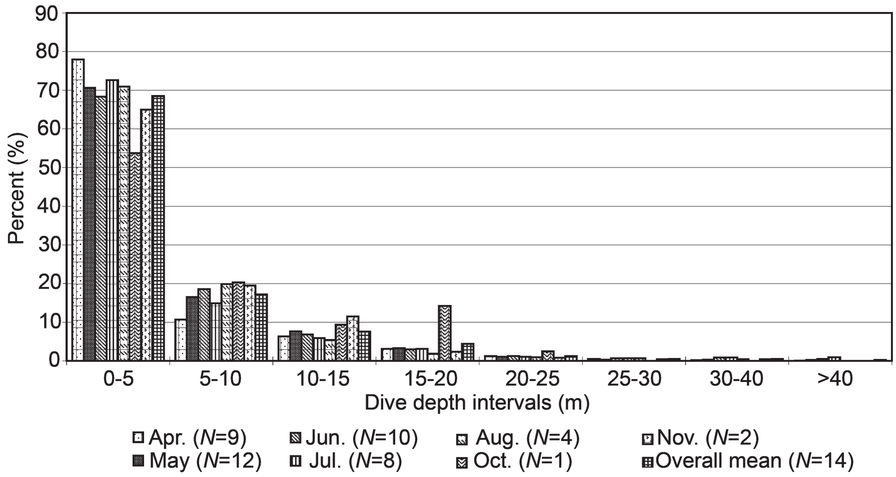

Fig. 6. Average time spent at the different depth intervals for all animals grouped by month. *N*=the number of animals.

from 15:00 to 21:00. Although less pronounced, the latter generally corresponds to the overall peak diving activity in Fig. 5.

The dive depth by the female-calf pair shows that 2-5m and 5-10m were about equally often used, followed by dives to 10-15m and 15-20m (Table 2). The total number of dives per hour decreased significantly for both the female (38 to 34) and the calf (42 to 38) from May to June (t-test, p>0.01). The deepest dives were recorded in the 30-40m category, which is consistent with the water depths of the geographical area utilised, which do not exceed 50m (Fig. 7).

DISCUSSION

Effect of tagging

In the present study dive data were collected from 14 harbour porpoises providing dive information for seven months of the year. Following tagged animals for longer periods such as this has the advantage of providing information well past the stressful experience of the tagging situation, thereby providing more reliable data on natural diving behaviour. A study on the effect of a captive porpoise carrying a satellite tag identical to those used in the present study (Geertsen *et al*., 2004) showed a significant behavioural response during the first day after tagging but thereafter no alteration in behaviour was detected during the following month. However, this porpoise was sedated with valium before tagging which may have caused the observed behavioural change during the first day rather than the handling procedure or the tag itself.

The increase in drag due to tag attachment has been measured on porpoise models in wind and water tunnels and these experiments indicate that a tag may substantially increase drag (Bannasch *et al*., 1994; Hanson, 2001). Therefore the possibility cannot be excluded that drag from tags may have a long-term effect by causing an increase in the energetic cost of swimming and diving, as was indicated for fur seals by Walker and Boveng (1995). However, the fact that two harbour porpoises carrying satellite tags caught by fishermen after 3 and 11 months, had full stomachs and their length and weight corresponded to natural growth suggests no strong influence from the tags on the behaviour of harbour porpoises (Teilman, unpubl. data).

Dive frequency

Three studies have described the diving behaviour of harbour porpoises using TDRs over a few hours or days. Westgate *et al*. (1995) recorded diving behaviour of seven harbour porpoises in the western Atlantic at the border between Canada and USA (animal lengths: 114-161cm; deployment duration 10-106 hours in August/September); Otani *et al*. (2000; 1998) presented diving data on three harbour porpoises in Japanese waters (animal lengths: 134-166cm; deployment duration 23-100 hours in April, May, and July); and Teilmann (2000) provided dive data on an immature harbour porpoise followed for 12 days in May in Danish waters. These studies yielded detailed data on individual dives but the duration of the recordings and the small sample size preclude general conclusions being made on diurnal, seasonal and individual variation in harbour porpoise diving behaviour.

In the present study a mean dive rate was found of 29 dives hr^{-1} in April-August and 43 dives hr^{-1} in October-November. The average number of dives per hour was 48 in May in Denmark (Teilmann, 2000), 28-35 in April-July in Japan (Otani *et al*., 1998), and an average of 30 (range=12-109) in eastern USA in August-September (Westgate *et al*., 1995). Although some variations occur between animals, it seems that independent of area, the average dive rate for harbour porpoises during the spring and summer months is around 30 dives hr^{-1} below 2m. The higher dive rate found during October-November may reflect an increased foraging activity, compensating for higher energy requirements as the water temperature decreases at this time of year. This is supported by the fact that the weight of captive harbour porpoises kept under semi-natural conditions has been shown to increase dramatically in October, peaking in January and decreasing again in the spring, with increase in food intake preceding the increase in weight of one-two months (Lockyer *et al*., 2003).

Maximum dive depth

All of the tagged animals dived to 30-50m, resembling the depths in the Danish Belt seas, suggesting that the porpoises regularly explore the seafloor (Figs 7 and 10). Two animals (6171_97 and 6421_99) swam north along the Swedish west coast to Southeast Norway, where water depths of several hundred meters occur. The deepest dives (84 and 132m) were recorded from these two animals. The maximum dive

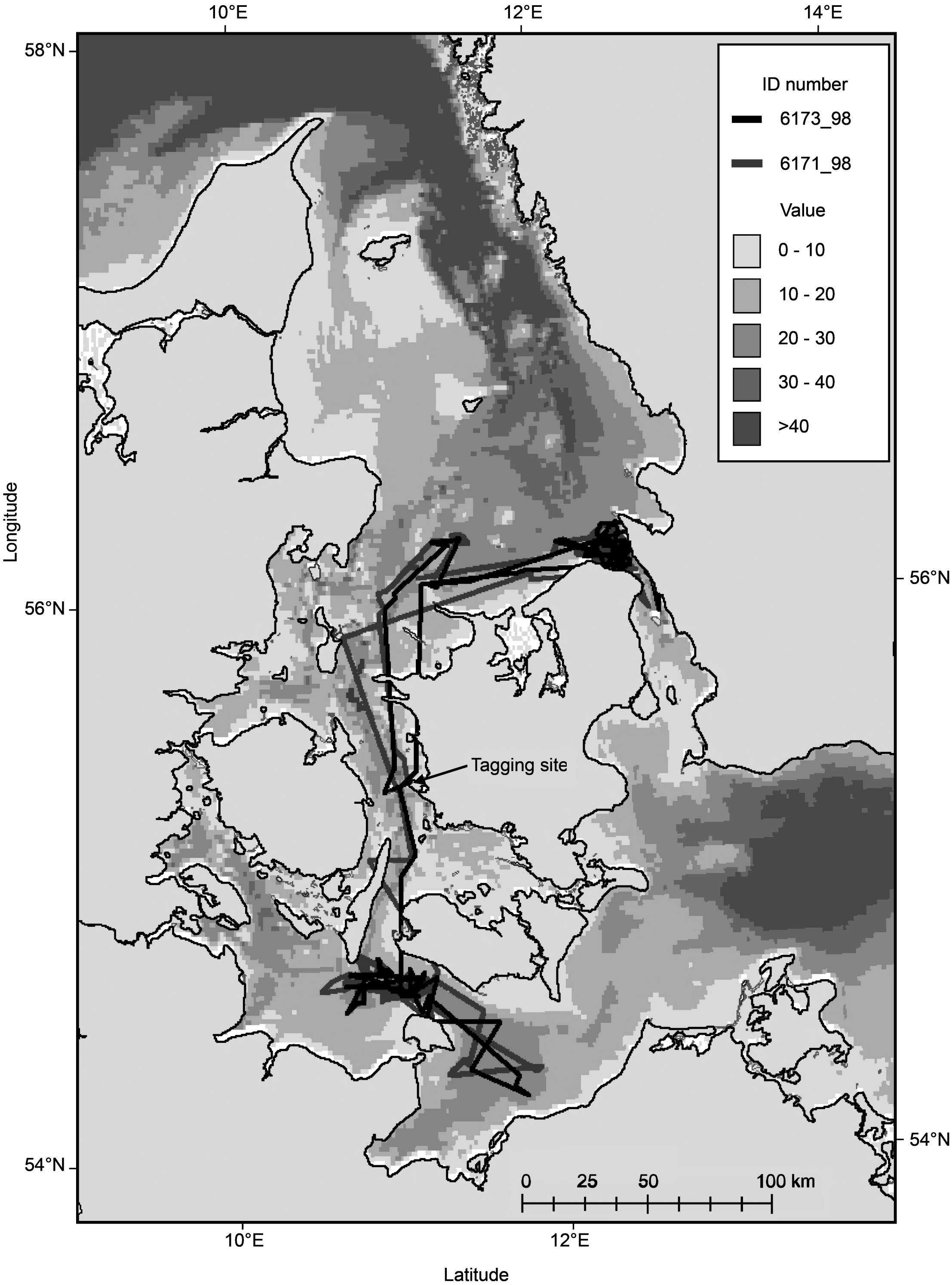

Fig. 7. Movements of mother (6171_98) and calf (6173_98) pair tracked for 45 and 43 days, respectively. The two animals were incidentally caught in the same pound net 11 May 1998 and contact was lost with the mother 24 June 1998 and two days later with the calf.

depths recorded for seven porpoises in the northwest Atlantic were 83, 119, 131, 136, 152, 207 and 226m, respectively (Westgate *et al*., 1995), whereas the three porpoises tagged in the eastern Pacific attained maximum dive depths of 65, 71 and 99m, respectively (Otani *et al*., 2000; 1998). This shows that harbour porpoises are capable of diving to depths of more than 200m and that water depth rather than diving ability is the limiting factor in dive depth within the continental shelf waters where harbour porpoises are mostly found.

An average dive depth represents both shallow resting and travelling dives, deep exploratory dives and feeding dives at various depths. Although deeper water was available in the northwest Atlantic and in the

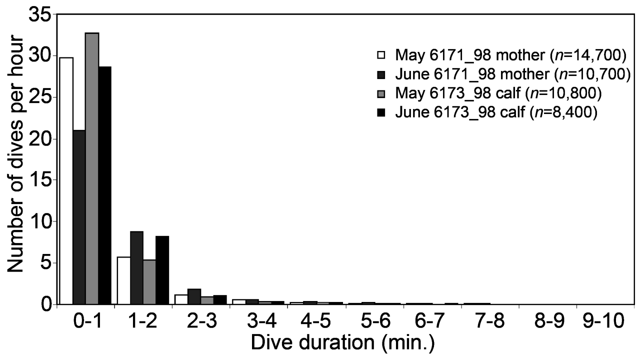

Fig. 8. Duration of dives in 1min intervals and number of dives per hour within each duration interval is indicated for the female (6171_98) and the calf (6173_98) in May and June 1998. *n*=total number of dives recorded by month for each animal.

Table 2

Time spent at depth intervals and the depth of dives for mother-calf pair (6171_98 and 6173_98). Note that the first interval is different between time at depth (0-5m) and depth of dives (2-5m). *n*=the number of hours where 'time at depth' was recorded. *N*=the total number of dives recorded for each animal.

	May		June	
Diving interval (m)	Mother	Calf	Mother	Calf
Time at depth (%) *n*=540 *n*=678				
0-5	52.9	60.6	46.7	50.6
5-10	19.7	19.0	17.7	19.6
10-15	20.5	16.6	23.2	22.0
15-20	6.0	3.3	10.3	6.7
20-25	0.8	0.4	1.7	1.0
25-30	0.0	0.1	0.0	0.2
30-40	0.0	0.1	0.0	0.0
>40	0.0	0.0	0.0	0.0
Depth of dives (%) *N*=27,100 *N*=28,800				
2-5	40.4	33.1	43.9	38.7
5-10	44.2	40.4	43.6	43.8
10-15	13.5	20.9	11.3	14.0
15-20	1.8	4.4	1.1	3.0
20-25	0.1	1.0	0.1	0.5
25-30	0.0	0.2	0.0	0.1
30-40	0.0	0.1	0.0	0.1
>40	0.0	0.0	0.0	0.0

eastern Pacific, the average depth of dives was 25m (Westgate *et al.*, 1995) and 12m (Otani *et al.*, 2000; 1998), respectively. Teilmann (2000) also found a mean dive depth of 12m. These values are similar to the findings in the present study. The shallow waters around Denmark may therefore represent an ideal habitat for harbour porpoises; high abundance of harbour porpoises is found in most areas around Denmark (Hammond *et al.*, 2002; Teilmann, 2003).

Diurnal dive patterns

Westgate *et al.* (1995) found that the proportion of time spent in the upper 2m varied from 33% to 60%, with a mean of 43% for the seven animals in their study. The range found in the present study is averaged over seven months and 14 animals and varied between 45% and 63% with an average of 55%. The lower proportion of time spent at the surface by the western Atlantic porpoises is probably due to the deeper water depth for this area and the deeper dive depth for these animals. Seasonal energetic requirements, depth dependent food availability and dive depth probably control the time spent at the surface layer.

The proportion of time when animals are visible to aerial observers is an important factor for correcting abundance estimates based on aerial surveys (e.g. Heide-Jørgensen *et al.*, 1992). The depth at which harbour porpoises can be seen depends on several factors including sea state, glare and clarity of the water. This study provides estimates of the proportion of time spent by porpoises in 0-2m by month from April to August. From 9:00-21:00 when most surveys are conducted, the time that porpoises are present at 0-2m varies from 50% during 9:00-15:00 to 63% during 15:00-21:00 in April, with less variation and the opposite dive pattern (more surface time during the morning-midday hours) for May-August. The availability of harbour porpoises to visual observers is therefore an important issue both diurnally and seasonally and may bias abundance estimates significantly if not taken into account.

The present and previous studies demonstrate that harbour porpoises dive continuously, both day and night (Otani *et al.*, 2000; Otani *et al.*, 1998; Teilmann, 2000; Westgate *et al.*, 1995). In the present study, porpoises were

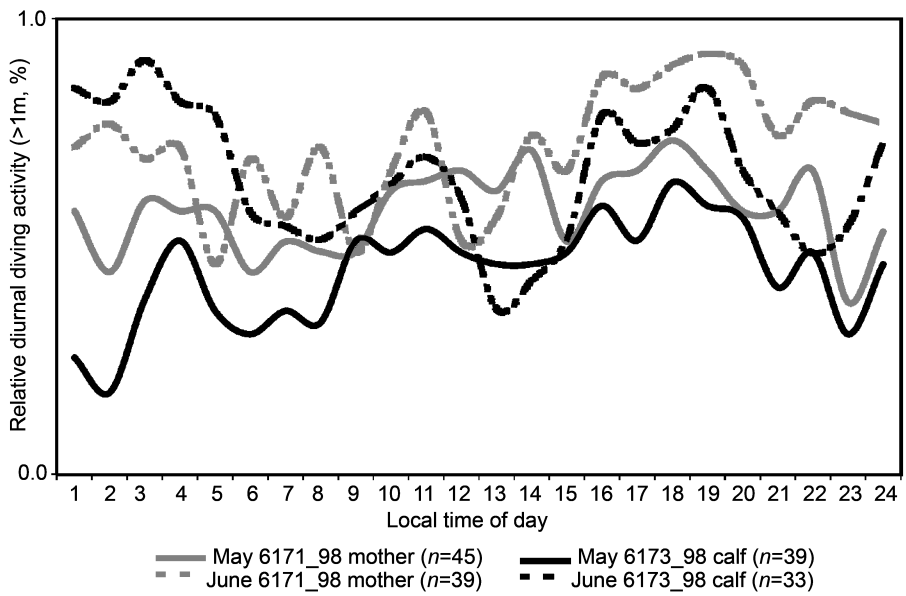

Fig. 9. Relative diving activity below 1m during the day (1 hour increments) for the female (light lines) and the calf (dark lines) in May (solid lines) and June (broken lines). *n*=number of 20-minute 'timeline' periods included for each hour per month.

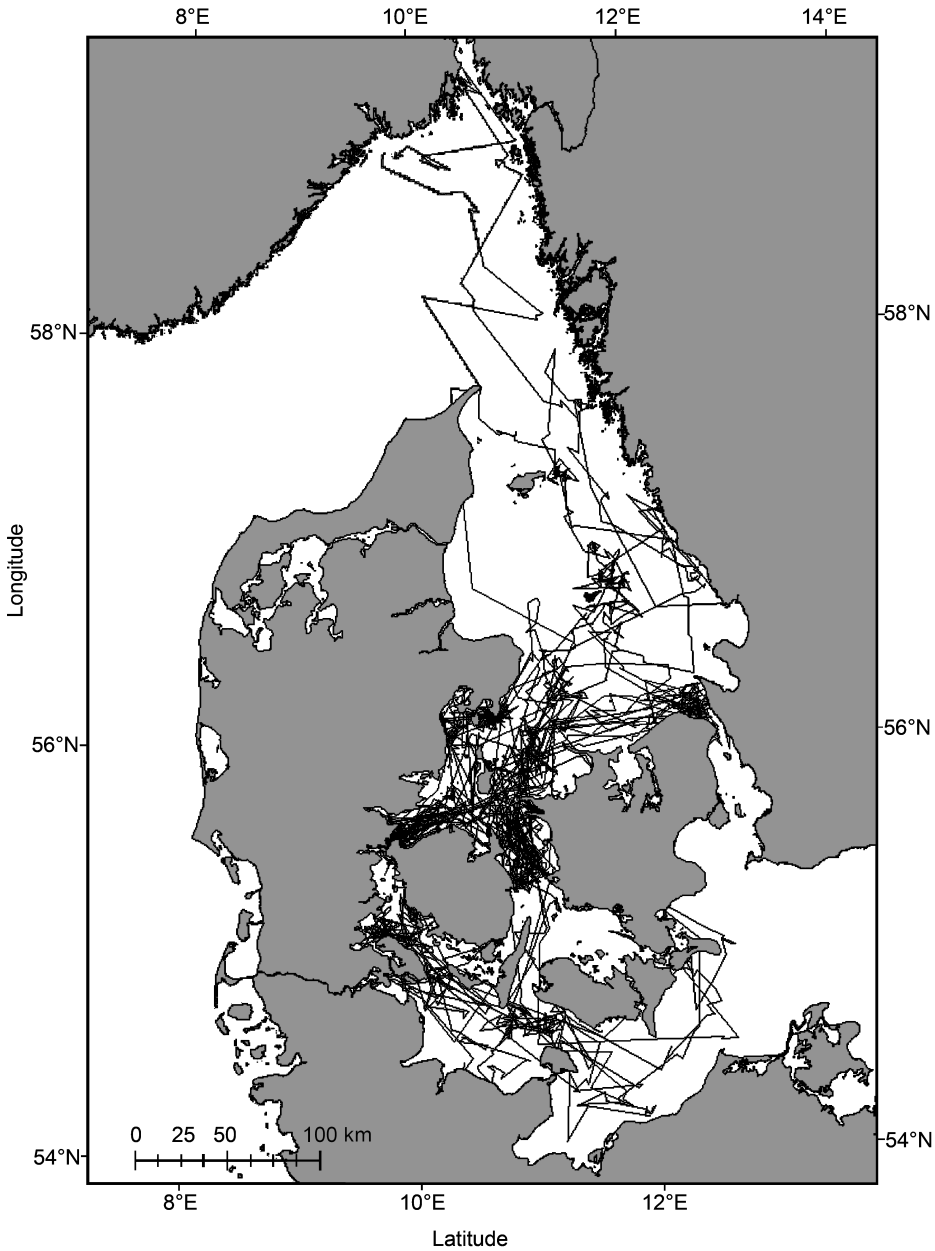

Fig. 10. Movements of 14 harbour porpoises tracked for 14-130 days.

found to dive more within daylight hours, in particular, in November. This is probably linked to prey behaviour or the use of vision to catch prey.

Female-calf pair

Following the movements and diving behaviour of a female-calf pair provided a unique insight into the behaviour of two closely related animals of different sizes, exploiting the same waters and food resources. Harbour porpoises give birth around July in Danish waters (Sørensen and Kinze, 1994), therefore the calf would have been some 10 months old when it was tagged in May and 11 months old when contact was lost. With a pregnancy rate of 0.61-0.73, most females give birth every year (Sørensen and Kinze, 1994). If females abandon their calves before giving birth to the next, these porpoises may have been tracked in the final stage of their time together.

The female spent more time diving than the calf, which made more frequent but shorter duration dives. This probably reflects size-related physiological constraints in breath-holding capacity (Schreer and Kovacs, 1997). Larger body size (both within and between species) generally allows longer and deeper dives due to the increase in the aerobic dive limit. This has for example been shown for white whales of various sizes (Martin and Smith, 1999). The female probably also had higher energy needs as she was lactating and possibly also pregnant. The number of dives per hour decreased for both animals from May to June and both animals dived deeper and for longer in June. This corresponds to the animals staying at the entrance of the Sound in May and moving to the Fehmarn Belt in June (Fig. 7). As the depths in the two areas exploited in May and June were similar, it could indicate that both animals increased their foraging time by 8-10%, as a response to sparse food resources, a change in prey species or increased energy requirements. Lockyer *et al.* (2003) showed that two porpoises kept in an outdoor enclosure lost up to 20% of their weight every summer, which correlated with a rise in water temperature. This however does not support an increase in energy requirements from May to June in the tagged porpoises.

It is not known whether the female and calf synchronised their dives, but the diurnal dive pattern showed a correlated dive rhythm in May. In June there were some similarities in the dive pattern during the day, but the diurnal dive pattern in June was not significantly correlated. This change in diurnal diving behaviour could indicate that the calf gradually became more independent, possibly foraging for its own food and also corresponding to the time of year when it leaves its mother.

Dive duration

The dive duration of the female-calf pair seems to fall within previously reported average dive durations (26-103s) given for harbour porpoises (Otani *et al*., 2000; Otani *et al*., 1998; Westgate *et al*., 1995), although the exact value cannot be calculated in the present study as the resolution of the duration intervals were 1min. The longest dive duration reported previously is 6.3min (Teilmann, 2000). Westgate *et al*. (1995) found dive durations up to 5.4min and Otani *et al*. (1998) recorded dive durations up to 4.7min. In this study significantly longer dive durations were recorded, with dives in the interval 10-15min, from both the female and its calf. An error in the dive duration data could arise if an animal, after a dive, swims to the surface breathes and dives again (to >2m) within 10s (sampling rate of the satellite transmitter), and thereby adding the dive durations of two or more dives together. To avoid this problem the depth limit for dive/surface separation was increased to 4m for some tags; this did not change the distribution of dive duration. In theory a harbour porpoise may still be able to move from 4m depth to the surface, take a breath and move down below 4m again within 10s. Since this cannot be ruled out, it still remains uncertain if harbour porpoises really are capable of diving for more than 10min.

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