



## Biosonar, dive, and foraging activity of satellite tracked harbor porpoises (*Phocoena phocoena*)

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### ABSTRACT

This study presents bioacoustic recordings in combination with movements and diving behavior of three free-ranging harbor porpoises (a female and two males) in Danish waters. Each porpoise was equipped with an acoustic data logger (A-tag), a time-depth-recorder, a VHF radio transmitter, and a satellite transmitter. The units were programmed to release after 24 or 72 h. Possible foraging occurred mostly near the surface or at the bottom of a dive. The porpoises showed individual diversity in biosonar activity (<100 to >50,000 clicks per hour) and in dive frequency (6–179 dives per hour). We confirm that wild harbor porpoises use more intense clicks than captive animals. A positive tendency between number of dives and clicks per hour was found for a subadult male, which stayed near shore. It showed a distinct day-night cycle with low echolocation rates during the day, but five times higher rates and higher dive activity at night. A female traveling in open waters showed no diel rhythm, but its sonar activity was three times higher compared to the males'. Considerable individual differences in dive and echolocation activity could have been influenced by biological and physical factors, but also show behavioral adaptability necessary for survival in a complex coastal environment.

Key words: acoustic tag, TDR, biosonar, echolocation, diving, foraging, harbor porpoise, *Phocoena phocoena*, Danish waters, Kattegat, Great Belt, Argos.

Most of our knowledge concerning echolocation and acoustic communication stems from studies of harbor porpoises in captivity (Møhl and Andersen 1973; Kastelein *et al.* 1995; Goodson and Sturtivant 1996; Au *et al.* 1999; Teilmann *et al.* 2002; Verfuß *et al.* 2005, 2009; Atém *et al.* 2009; DeRuiter *et al.* 2009; Clausen *et al.* 2010; Miller 2010). However, there is one full bandwidth

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recording of echolocation by free ranging harbor porpoises where Villadsgaard *et al.* (2007) documented that animals in the wild use more intense clicks (178–205 dB re 1  $\mu$ Pa peak-to-peak) than those in captivity (129–174 dB re 1  $\mu$ Pa peak-to-peak, Linnenschmidt *et al.* 2012). There are also studies using stationary acoustic data loggers (like T-PODs) for long term monitoring of harbor porpoises (Carstensen *et al.* 2006). While such field studies document the presence and sonar signal characteristics of wild porpoises, they reveal little about the behavior of individual animals in their natural environment.

Gill net fishing is a major threat to harbor porpoises (*e.g.*, Vinther and Larsen 2004). Acoustic alarms (pingers) on fishing gear effectively reduce bycatch during experiments in commercial fisheries (Kastelein *et al.* 2001, Carlström *et al.* 2002). However, concern has been raised that extensive use of pingers may result in habitat exclusion. Gill nets with higher acoustic detectability would hopefully be the better choice to reduce bycatch in general (Teilmann *et al.* 2006). However, we lack detailed understanding about the natural bioacoustics and diving behavior of harbor porpoises and under which circumstances they are bycaught in nets. Such knowledge gathered from free ranging animals would improve mitigation of harbor porpoise bycatch.

For nearly 10 yr acoustic tags have been deployed on individual whales (*e.g.*, Madsen *et al.* 2002; Johnson *et al.* 2004, 2009; Akamatsu *et al.* 2005*a, b*; Goldbogen *et al.* 2006; Oleson *et al.* 2007). There are basically three types of acoustic tags; Bprobes (Acousonde), D-tags and A-tags. The Acousonde records dive and acoustic behavior. It has recently been deployed on pantropical spotted dolphins and short-finned pilot whales (<http://www.acousonde.com>). Due to the maximum recording frequency of 100 kHz it is inappropriate for recording the high frequency (120–140 kHz) echolocation and communication clicks of harbor porpoises. Its predecessor, the Bprobe, has been deployed on fin whales (Goldbogen *et al.* 2006) and blue whales (Oleson *et al.* 2007), among others. The D-tag provides short-term, but highly detailed information on the acoustic environment, the swimming and diving behavior and the acoustic performance of the host animal (Johnson and Tyack 2003). It records acoustic signals up to 96 kHz (Arranz *et al.* 2011). At its present stage it is deployed with suction cups that do not allow for observations over consecutive days. D-tags have been attached to several species of larger whales (Miller *et al.* 2004; Johnson *et al.* 2004, 2009, Shapiro 2006; Aguilar Soto *et al.* 2008; Arranz *et al.* 2011). The A-tag functions as an event recorder of short clicks up to more than 200 kHz and it registers time of occurrence, the amplitude and the bearing of signals within a defined bandwidth (Akamatsu *et al.* 2005*a*). The A-tag has been deployed on finless porpoises (*Neophocaena phocaenoides*) (Akamatsu *et al.* 2005*b*, 2010) and white-beaked dolphins (*Lagenorhynchus albirostris*).<sup>2</sup> In a pilot study the A-tag has been deployed on a harbor porpoise in Danish waters and recorded acoustic activity for 4.5 h (Akamatsu *et al.* 2007). The results showed the potential use of the A-tag combined with a satellite transmitter for studying the bioacoustics, dive behavior and movements of wild harbor porpoises.

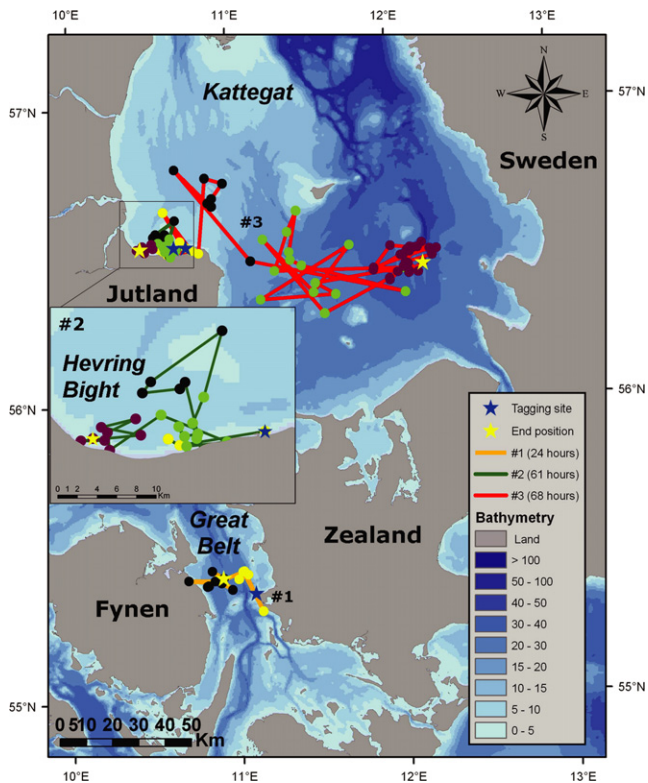
<sup>2</sup>Rasmussen, M. H., T. Akamatsu, J. Teilmann, G. A. Vikingsson and L. A. Miller. 2011. Biosonar, diving and movements of two tagged white-beaked dolphin in Icelandic waters. Deep-Sea Research II. (accepted for publication).

Here we present recordings over several days (22–67 h) of acoustic activity, dive profiles and movements of three free ranging harbor porpoises, each equipped with an A-tag, a dive recorder and a satellite transmitter.

## METHODS

### *Study Area, Subjects, and Capture Method*

In April 2006 and May 2007 three harbor porpoises, an adult male (#1), a subadult male (#2), and an adult female (#3) were captured in the Kattegat and Great Belt (Fig. 1) using pound nets (see Teilmann *et al.* 2007). The porpoises were tagged with several instruments and data collected for 23:40 h, 63:35 h, and 67:51 h, respectively.



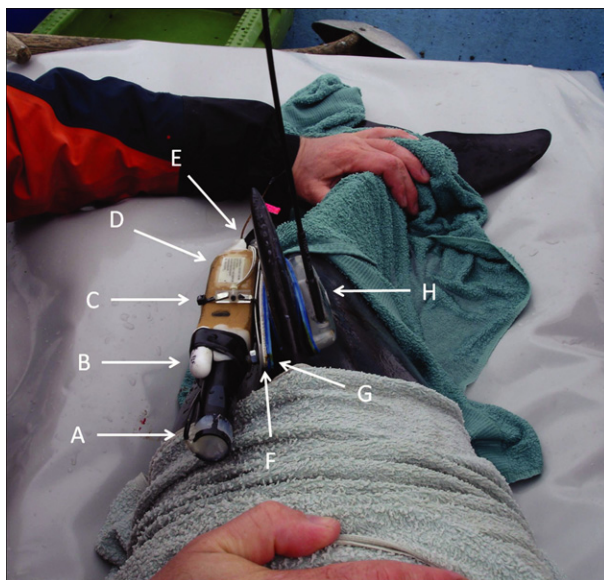
*Figure 1.* Satellite tracking map for the three porpoises in the present study. The area shown is the Inner Danish waters located between the mainland of Denmark (Jutland) to the west and southern Sweden to the east. Colored lines represent the movements of the animals during the tagging period. Yellow: porpoise #1. Green: porpoise #2. Red: porpoise #3. The colored dots represent locations for each day; yellow the day of tagging, black the second day (last day for #1), green the third day and purple the last (forth) day for #2 and #3. The blue stars show the position of tagging and the yellow stars show where the tags were released. (See Table 1 for information on the tagged animals).

The water depth in the study area is mostly less than 50 m except in the northeast where deeper waters occur. Water temperatures vary throughout the year between about 0°C and +20°C. The physical parameters of the region are dominated by an inflow of saline water from the North Sea and an outflow of estuarine water from the Baltic Sea making the Kattegat and Great Belt a complex oceanographic system (see Rheinheimer 1996 for details).

#### *Acoustic Data Logger and VHF Transmitter*

The porpoises were equipped with an A-tag W20-AS (stereo hydrophone, Little Leonardo, Tokyo, Japan, Fig. 2A). The tag functions like an ultrasonic event recorder and records the sound pressure along with the exact time of detection at each hydrophone (clock drift: 1 s/d). Signals were band pass filtered (55–235 kHz) and a hardware detection threshold was set at 142 dB (peak-to-peak re 1  $\mu$ Pa). The sampling frequency of 2 kHz for W20-AS provided a time resolution and shortest click interval of 0.5 ms. The total recording time is battery limited to 60–70 h. All components fit into a cylindrical waterproof housing measuring 21  $\times$  122 mm weighing 77 g.

The A-tag was imbedded in a float (Fig. 2D) for positive buoyancy after the detachment. Also embedded into the float was a VHF transmitter (MM130, ATS, Isanti, MN) for locating the data logging tags (Fig. 2E). Detailed information on the A-tag is available in Akamatsu *et al.* (2005a).



*Figure 2.* Dorsal fin of a harbor porpoise showing the tags: (A) stereo-acoustic A-tag, (B) time-depth recorder, (C) release device and cable tie, (D) float with data logging tags, (E) VHF radio transmitter, (F) aluminum backing plate with protecting closed cell neoprene (G), (H) satellite tag.

### *Diving Recorder*

A time and depth recorder (DST-milli; Star-Oddi, Reykjavik, Iceland) was attached to the float (Fig. 2B). According to the manufacturers specifications, the data resolution and accuracy of the depth recorder is 0.03% (12 bits) of full scale (900 m, *i.e.*,  $\pm 27$  cm) and  $\pm 0.4\%$  of depth reading, respectively. Both limit the minimum resolution of the data. The sampling rate for the three porpoises was chosen to be 1, 4, and 3 s for porpoises #1, #2, and #3, respectively. A dive was defined when the porpoise was below 2 m for at least 6 s.

### *Satellite Tag*

A satellite transmitter (SPOT5, Wildlife Computers, Redmond, WA) with an oval shape measuring  $10 \times 3.5 \times 1$  cm was attached to the dorsal fin opposite the acoustic package (Fig. 2H). The satellite transmitter was set to transmit every 45 s when at the surface. When the preset maximum (250 transmissions (equals 4–7 h/d) for the first two animals or 1,000 transmissions (equals 22–24 h/d) for the third animal) was reached no further positions were available for that day. Satellite positions were obtained from the ARGOS satellite system and had an accuracy of less than 100 m to a few kilometers. We used the satellite positions to link acoustic and dive behavior with the habitat as well as tracking the long-term movements after the acoustic package was detached.

### *Tagging Procedure*

Captive animals were slowly brought into reach by raising the pound net to the surface, carefully lifting the animal on board, and placing it on a soft pad on the deck of our boat. Only sub adult or adult animals without injuries and in good condition were selected for tagging. The satellite tag was mounted to the left side of the dorsal fin with two 5 mm silicone covered Delrin pins while the data logging tags and a release mechanism was placed on the right side. The hydrophones on the A-tag were 40–50 cm behind the blowhole (Fig. 2). During the tagging procedure (~30 min) the heart and respiration rates were continuously monitored. The float with the data logging tags, consisting of the A-tag, time-depth recorder, and VHF transmitter, (Fig. 2) was positively buoyant in water. The satellite-tag remained on the porpoise until the iron nuts corroded after about 1 yr. For more details on the tagging procedure and condition of the animals see Teilmann *et al.* (2007), Eskesen *et al.* (2009), and Sonne *et al.* (2012).

### *Release and Recovery of the Tag*

The release mechanism consisted of a plastic strip with a timer and a small detonator (Little Leonardo, Tokyo, Japan) connected to an aluminum back plate with a hook that kept the float with the data logging tags in place (Fig. 2C). The timer was programmed to release the float after 24 h, 72 h, and 72 h for porpoise #1, #2, and #3, respectively.

An ARGOS position of the animal at the time of detachment helped to locate the search area to within a radius of a few kilometers. A directional three or five element Yagi antenna and a VHF receiver (ICOM R10) were used to locate the VHF radio signal from the float with the data logging tags.

### *Data Analysis*

Data collected by the A-tag were processed in custom-made software in IGOR Pro 5 (WaveMetrics, Portland, OR). Two temporal filters were used before the majority of recordings were analyzed. First, splash noise from the animal breaking the surface was excluded by deleting data from 0 to 30 cm below the surface. The second filter reduced surface echoes that typically occurred at delays of about 0.5–2.5 ms after reception of the direct signal. In the following text we refer to detections as all acoustic triggerings of an A-tag before filtering. We refer to clicks as all detections after the data set has been filtered with the two temporal filters. However, no temporal filters were used when analyzing possible foraging sequences.

Owing to copious data and for comparing to previous studies, our results (clicks and dives) were pooled in 1 h time bins. Dives were manually counted and attributed to the time bin in which it started. Maximum dive depth was measured for each dive and averaged into 1 h time bins.

We used three criteria to define a possible foraging event. A click train had to include three parts: search, approach (initial and terminal part), and an indication of the buzz (see Fig. 7) to be defined as a possible prey capture sequence. In addition the click interval at the end of the approach had to be below 10 ms. These criteria were defined based on results of prey capture events by captive harbor porpoises in the facility at Fjord&Bælt, Kerteminde, Denmark (Atém *et al.* 2009, Verfuß *et al.* 2009). The levels of clicks recorded at the dorsal fin are 30 to 40 dB lower than the source level (1 m in front of the animal on the acoustic axis) (Hansen 2005). These attenuations have recently been verified with direct measurements using an A-tag attached with suction cups on a captive harbor porpoise approaching and echolocating on a hydrophone as a target at Fjord&Bælt (LAM, unpublished data). Since the threshold of the A-tag was 142 dB (peak-to-peak) re 1 $\mu$ Pa, low amplitude clicks were not recorded, especially those during the buzz just before and during prey capture (see Fig. 7 and Miller 2010). Thus the actual number of clicks produced by the animals and the maximum click rates are underestimated in this study.

We used parametric and nonparametric statistical tests according to Fowler *et al.* (1998) using Microsoft Office Excel 2007.

## RESULTS

There was considerable individual variation in biosonar, diving activity, and distance covered among the tagged animals. Porpoises #2 and #3 were tagged in Hevring Bight while porpoise #1 was tagged in the Great Belt (Fig. 1 and Table 1). Porpoise #1 swam off shore about 67 km while it carried the data logging tags. Porpoise #2 swam about 70 km with the tags attached and stayed near the coast for the full recording time (Fig. 1). Porpoise #3 spent most of its time in the open waters of the Kattegat and swam about 200 km with the data logging tags. We registered about four times the number of clicks per hour (24,227) for porpoise #3 compared to the other two porpoises (6,506 and 6,546; Table 1). Not surprisingly, the two porpoises in open waters (#1 and #3) dove deeper than the porpoise near the coast (#2). Periods without detection of clicks were evident for all tagged porpoises (Table 1). The coastal porpoise (#2) had the longest maximum period without click detections (1,300 s), while porpoise



Table 1. Data for three tagged harbor porpoises in the Kattegat and Great Belt. Positions separated by less than half an hour were deleted for distance and swimming speed calculations (See also Fig. 1),  $n$  gives the number of full hours of analyzed data.

Harbor porpoise ID	200606422 (2006 #1)	200606172 (2006 #2)	200706170 (2007 #3)
Location	Great Belt	Hevring Bight	Hevring Bight
Longitude, latitude	55.5°N, 11°E	56.5°N, 10.5°E	56.5°N, 10.5°E
Sex	M	M	F
Age group	Adult	Subadult	Adult
Standard length (cm)	149	111	166
Weight (kg)	53	-	62
Date and time of tagging	23 April 2006, 1110	26 April 2006, 1620	19 May 2007, 1240
A-tag type	W20-AS	W20-AS	W20-AS
Total attachment time (h:m)	23:40	63:35	67:51
Duration of satellite tracking (d)	202	201	27
Min. distance swam with float (km)	67	73	203
Min. average swim speed (km/h)	8.0	2.6	4.0
Total number of dives	906	2,659	2,815
Average number of dives per hour	41 ( $n = 23$ , SD = 14)	44 ( $n = 60$ , SD = 17)	47 ( $n = 60$ , SD = 45)
Average dives/hour during day	48 ( $n = 13$ , SD = 10)	33 ( $n = 31$ , SD = 9)	49 ( $n = 34$ , SD = 55)
Average dives/hour during night	32 ( $n = 10$ , SD = 14)	56 ( $n = 29$ , SD = 15)	44 ( $n = 26$ , SD = 27)
Max. dive duration (s)	94	138	213
Max. dive depth (m)	25	14	34
Total number of detections	467,380	622,467	2,831,044
Total number of clicks <sup>a</sup>	144,018	390,331	1,623,240
Average clicks/hour	6,546 ( $n = 22$ )	6,506 ( $n = 60$ )	24,227 ( $n = 67$ )
Average clicks/hour during day	5,370 ( $n = 12$ )	2,412 ( $n = 31$ )	23,625 ( $n = 36$ )
Average clicks/hour during night	7,958 ( $n = 10$ )	10,882 ( $n = 29$ )	24,927 ( $n = 31$ )
Max. period without any clicks (s)	236	1,300	99

<sup>a</sup>Residual detections (clicks) after noise filtering.

#1 and #2 had maximum periods without click detections of 236 s and 99 s, respectively. See Table 1 for more statistics.

#### *Temporal Changes in Biosonar Activity*

Porpoise #1 swam in the Great Baelt (Fig. 1). The biosonar activity of this porpoise increased from 3,000 clicks to over 12,500 per hour during the daytime and peaked to more than 19,000 clicks per hour around midnight. Hereafter the click activity dropped gradually to near zero during the morning hours before the float with the data logging tags was released (Fig. 3).

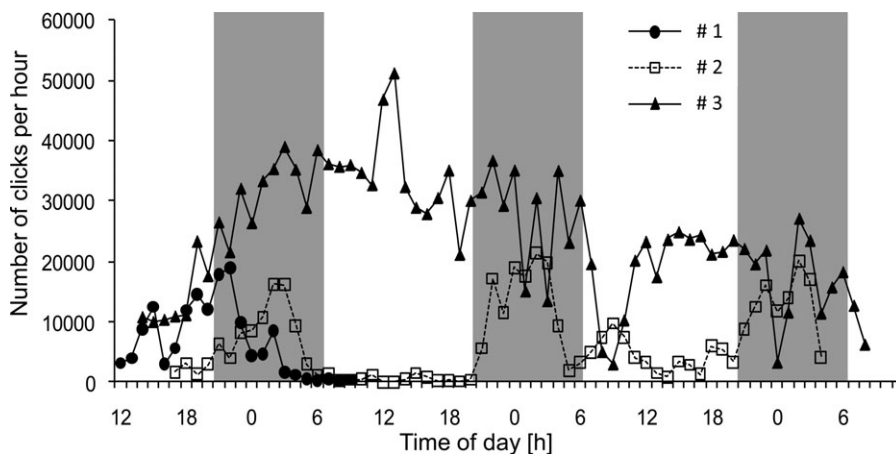
Porpoise #2 swam in coastal waters and showed clear diurnal patterns of biosonar activity (two-tailed  $t$ -test,  $P < 0.0001$ ) whereas porpoise #3 swam off shore in the Kattegat, and did not show such tendencies (Fig. 3). The biosonar activity of porpoise #2 was below 3,000 clicks per hour during the afternoon after tagging (Fig. 3). During the evening and early night the rate of clicks per hour increased gradually and peaked during the second part of the night with more than 16,000 registered clicks per hour. After two hours with intense echolocation a sharp decline in the clicking rate occurred from early morning and for the following 14 h ( $<1,000$  clicks per hour). The same general pattern was repeated the second and third night.

The adult female #3 showed a high rate of biosonar activity with more than three times the clicks recorded from the other two porpoises (Fig. 3, Table 1).

#### *Temporal Aspects of Diving Behavior*

The number of dives per hour varied from 6 to 179, but the overall average dive frequencies for the three animals were similar (41, 44, and 47 dives per hour; Table 1, Fig. 4), but significantly different ( $P < 0.01$ , Kruskal-Wallis test).

Porpoise #1 had the highest diving activity during the first hours after tagging with more than 50 dives per hour (Fig. 4). During the following evening and early night-time hours the dive activity gradually decreased to the minimum of nine dives per hour. In the second part of the night and during the morning hours, dive frequency increased and stabilized around 40 dives per hour before the data logging package was released (Fig. 4). Porpoise #1 dove deeper during the evening (14–18 m on average per hour) than during the night (7–11 m on average per hour) (Fig. 5). Porpoise #1, like porpoise #3, showed no correlation between its dive frequency and acoustic activity (Fig. 6B).



*Figure 3.* Changes in click rates with time. The figure shows all clicks recorded below a depth of 0.3 m with click intervals longer than 2.5 ms for the three tagged harbor porpoises. Data points indicate number of clicks emitted in 1 h time bins. Shading shows nighttime hours with dusk starting at 2000 and dawn at 0600. Note that porpoise #3 has no diel click rhythm in contrast to porpoise #2. These animals were captured in the same area (see Fig. 1).



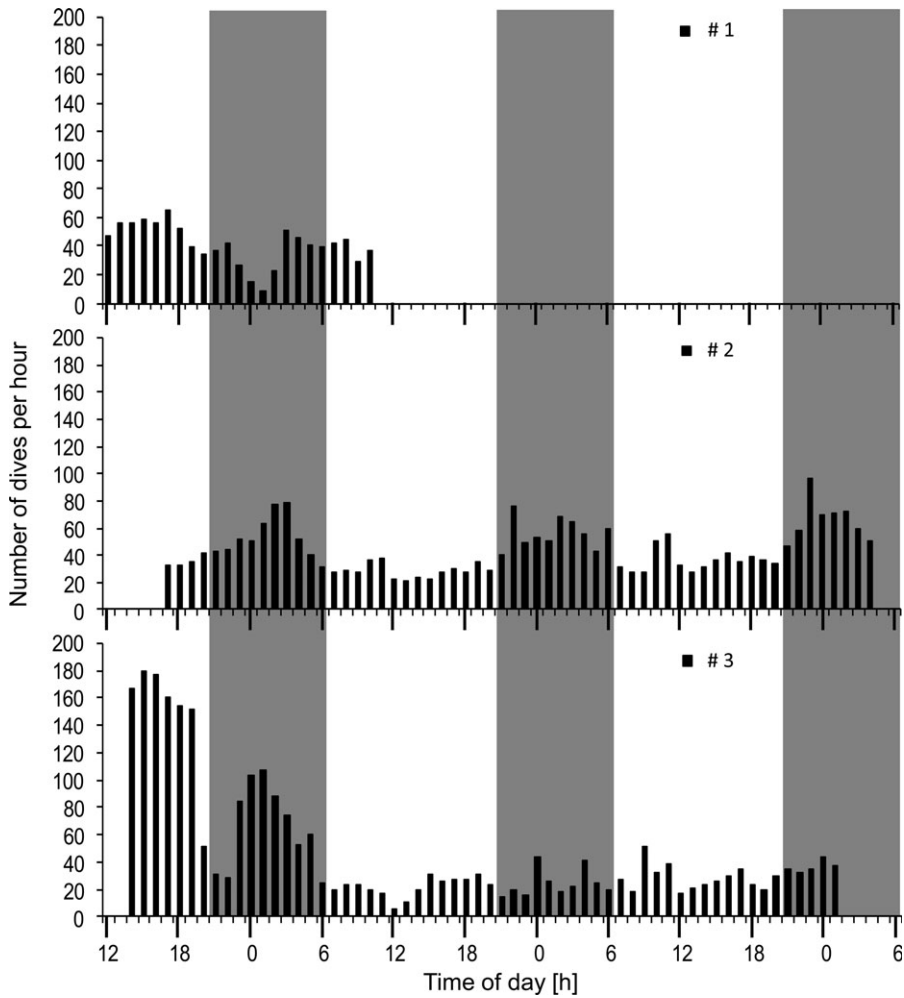


Figure 4. Changes in dive rates with time. The figure shows the number of dives in 1 h time bins for the three tagged harbor porpoises. A dive was tallied in the time bin in which it started. A dive was defined as having at least one data point below 2 m and lasting a minimum 6 s. Shading shows night-time hours with dusk starting at 2000 and dawn at 0600. Note that porpoise #2 shows a tendency for more dives at night than during the day (see Fig. 3 for click rates).

Porpoise #2 dove more at night than during the day (two-tailed  $t$ -test,  $P < 0.0001$ ). It remained in coastal waters for the entire tagging period (Fig. 1). Hence the dive depths were shallow, between 4 and 11 m on average (Fig. 5). We recorded lower dive frequencies (minimum 21 dives per hour) around noon and the highest dive activity at midnight with more than 50 dives per hour. Dive activity decreased towards dawn. The same pattern occurred during all three nights for porpoise #2 (Fig. 4). There was a positive correlation between dive and acoustic activity for this porpoise (Fig. 6A,  $r^2 = 0.66$ ,  $P < 0.0001$ ).

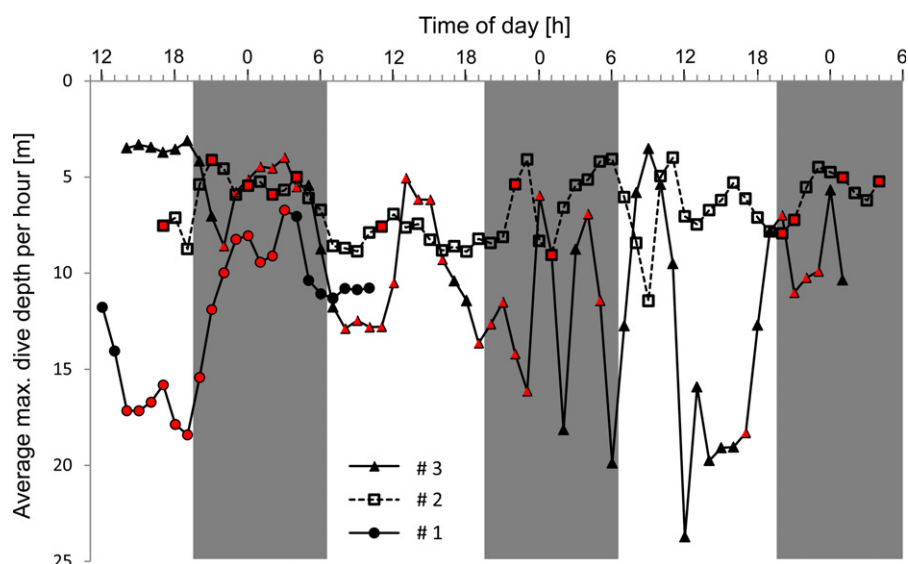


Figure 5. Average maximum dive depth in 1 h time bins during the time the three harbor porpoises carried the acoustic and dive tags. A dive was tallied in the hour in which it started. The red symbols represent possible foraging activity within that particular hour. Shading shows night-time hours with dusk starting at 2000 and dawn at 0600. See Table 1 for tagging dates and times and Figure 7 for illustrations of possible foraging events.

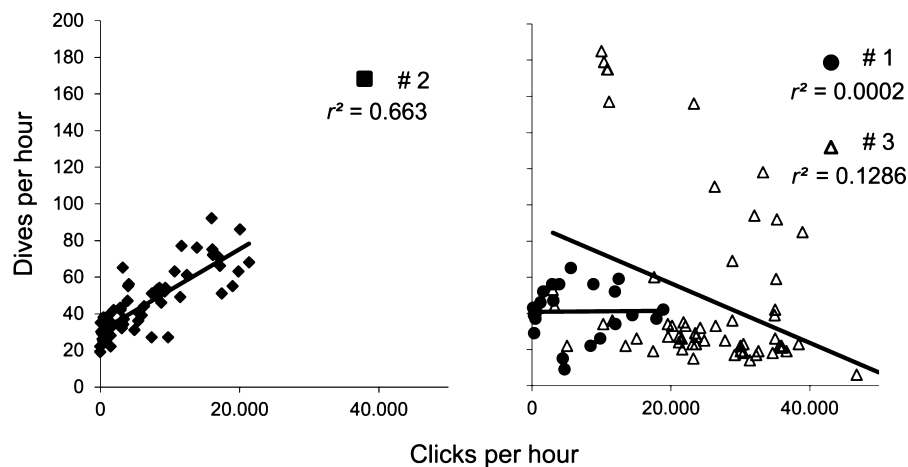


Figure 6. Relation between dive frequency and recorded clicks per hour for the three animals. The graph on the left for porpoise #2 shows a modest positive correlation between dive frequency and biosonar activity. This trend is not seen for porpoise #1 or #3.

Porpoise #3 had high dive activity (>160 dives per hour) for several hours after tagging (Fig. 4). After a short decrease in dive activity during the early evening her dive rate increased to between 60 and 120 dives per hour during the first night. Throughout the rest of the tag deployment the dive frequency stayed

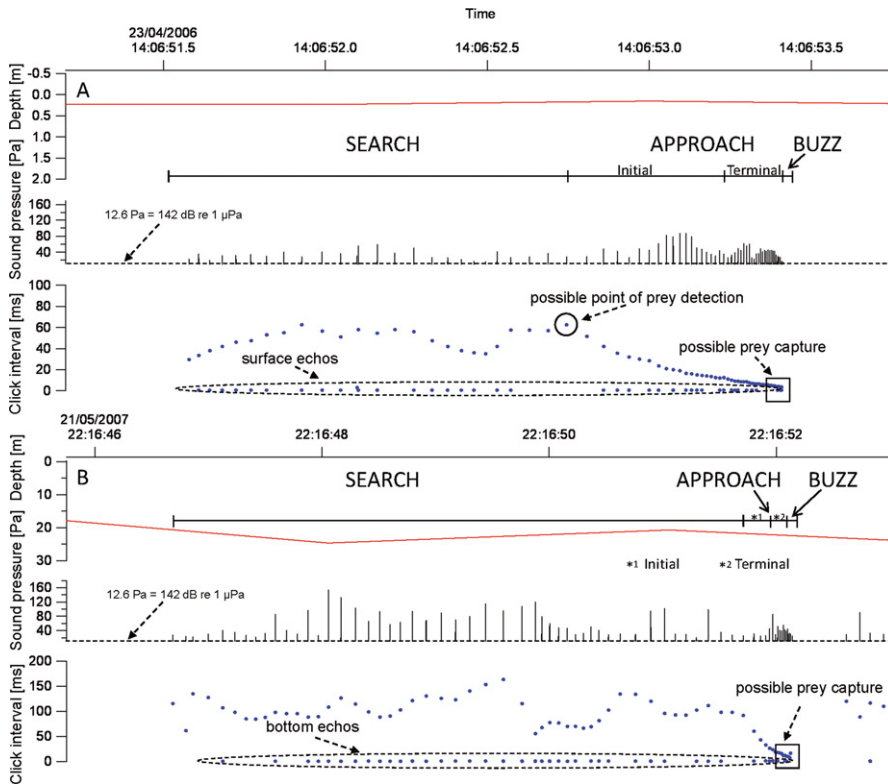


Figure 7. Possible foraging events from two free ranging harbor porpoises with acoustic tags. A is from porpoise #1 feeding near the surface (0–2 m) and B is from porpoise #3 feeding near or at the sea bottom (see also Fig. 5). Click trains are shown with arbitrary phases of search, approach, and buzz based on prey capture by captive harbor porpoises. The buzz is not resolved here. Also shown is a possible point of prey detection (circle in A) and possible points of prey captures (boxes). Surface and bottom echoes have click intervals on the order of 0.5 ms and are seen as horizontal lines of dots. No temporal filters were used here. Note that in B, estimated on axis source levels can be as high as 190 to 200 dB re 1  $\mu$ Pa peak-to-peak (see the Results and Discussion). Note also the different time axes and that the possible prey capture event occurs faster in B than in A.

around 30 dives per hour. The dive frequency and the biosonar activity showed no correlation (Fig. 3, 4, 6). Porpoise #3 had the greatest variation in average dive depth per hour. During the first day and night it did not dive deeper than 8 m on average (Fig. 5). As porpoise #3 moved into deeper waters of the Kattegat (Fig. 1), its average dive depth per hour increased gradually to a maximum of 24 m during day 3 (Fig. 5). There was no obvious correlation between diving and acoustic activity for porpoise #3 (Fig. 6B).

#### Possible Prey Capture Events

An example of possible foraging behavior from two of the tagged animals is shown in Figure 7. No temporal filtering was performed on the recordings of

possible foraging behavior. We illustrate one possible feeding event where porpoise #2 was within the surface layer (0–2 m depth) (Fig. 7A) and porpoise #3 was at the bottom of its dive, and may have been at or near the sea bottom (Fig. 7B). The changes in the click interval patterns were similar to those described by Verfuß *et al.* (2009) from the captive animals at Fjord&Bælt, and we therefore adopted their terminology. Three phases can be seen in Figure 7; search as well as initial and terminal parts of the approach. During the search phase click intervals varied between 30 and 150 ms. The initial part of the approach began with the possible point of prey detection and lasted for 0.5 s. During this time click intervals decreased rapidly from approximately 80 ms to 10 ms. The A-tag captured only a few clicks of the terminal part of the approach where the click intervals were below 10 ms and constantly decreasing to a minimum click interval of 3 ms. The terminal part presumably ended with a buzz (not recorded) and a possible prey capture (Fig. 7). Echoes reflecting from the surface and the bottom had intervals of about 0.5 ms (Fig. 7). The clicks of both animals varied in intensity from about 144 dB to about 163 dB re 1  $\mu$ Pa peak-to-peak (20 to 160 Pa) recorded by the A-tag near the dorsal fin, or 30 to 40 dB greater for source levels (Fig. 7).

Click trains that showed consecutive patterns of possible feeding events were tallied individually (Table 2). Porpoises #1 and #3 had the greatest number of possible feeding events near the surface (0–2 m depth). Porpoise #3 also foraged at the bottom of its dives, as did the other porpoises, except they showed fewer possible foraging events. Porpoise #1 showed most of its presumed foraging during the late afternoon and night while porpoise #2 showed almost all presumed foraging events during the night. Porpoise #3 had possible foraging events during the day and night (Fig. 5).

Figure 8 summarizes the occurrence of possible foraging, diving and biosonar activity on a 24 h cycle. Porpoise #1 had high foraging activity during the first part of the recording with 61 possible feeding events mostly in the afternoon and early evening hours. We found no foraging behavior during the second part of the recording for porpoise #1. Porpoise #2 showed only two possible feeding events during the day and 11 at night (Fig. 5, 8). Porpoise #3, however, showed foraging throughout the full recording time and we identified a total of 161 possible feeding events.

## DISCUSSION

To our knowledge these are the longest acoustic recordings from free-ranging cetaceans. In addition this is the first time geographical locations are associated

*Table 2.* Number of possible foraging events and where these occurred during each dive phase for each animal. Short click intervals indicating approach to the sea bottom or the surface were discarded in the analyses (see Methods). Porpoises #1 and #3 were swimming mostly in deeper waters while porpoise #2 stayed in shallow water with sand bottom near the coast (see Fig. 1).

Porpoise	Foraging events	Surface	Descending	Bottom	Ascending
#1	61	46	2	2	11
#2	13	3	0	7	3
#3	161	115	1	42	3

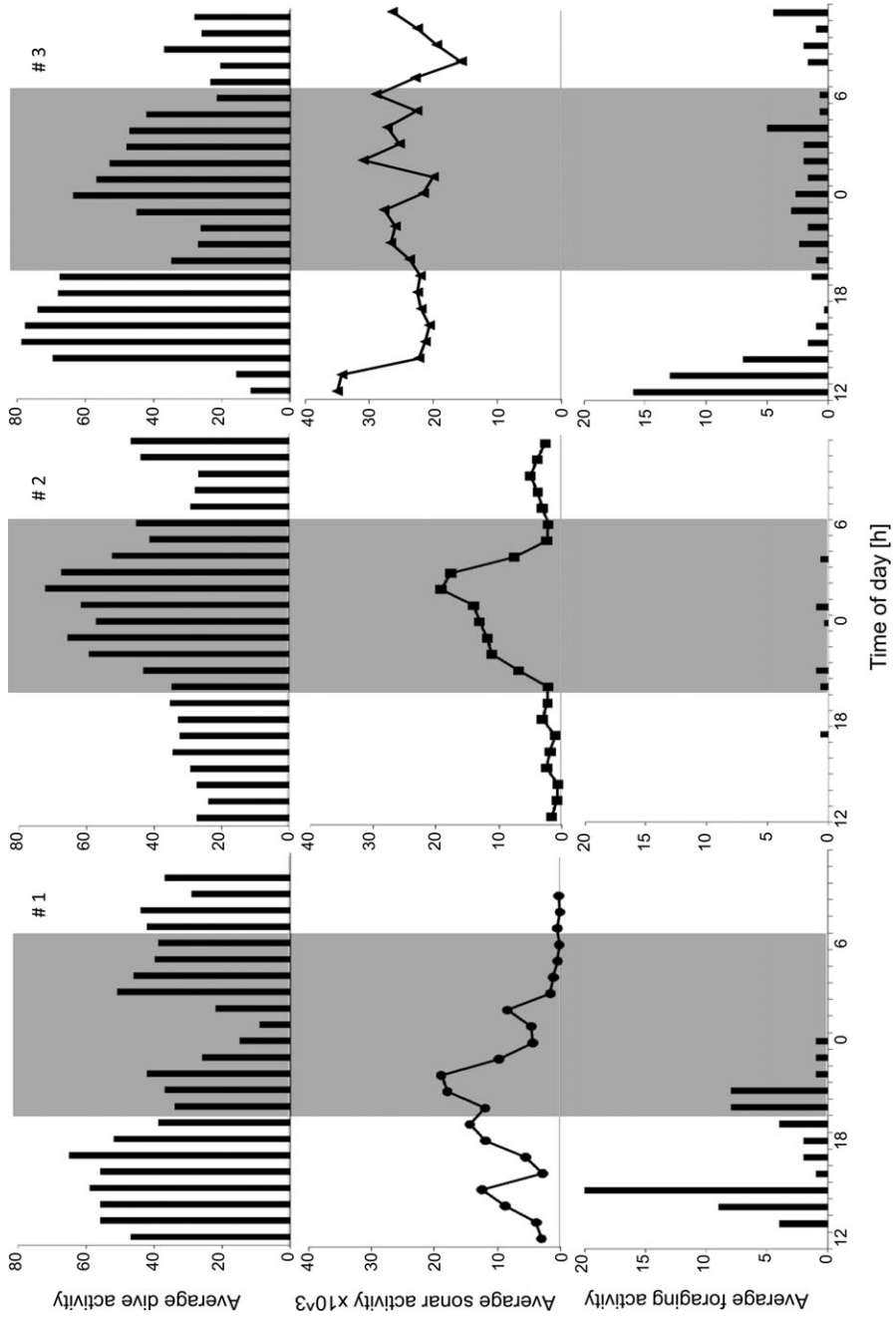


Figure 8. Summary of dive, biosonar and possible foraging activity for a 24 h cycle tallied in 1 h time bins. Note differences in the ordinate axes. Shading shows nighttime hours with dusk starting at 2000 and dawn at 0600.

with acoustic activity. The three tagged harbor porpoises utilized three different habitats; the Great Belt (#1), the coastal Kattegat (#2) and the central part of the Kattegat (#3) (see Fig. 1). Thus, it is not surprising that the porpoises exhibited different diving and biosonar behaviors even though all instruments had the same specifications and adjustments.

The A-tag had a threshold level of 142 dB re 1  $\mu$ Pa (peak-to-peak), which is not sensitive enough to register all of the animal's echolocation signals. The electronic noise floor prohibits lower thresholds (Akamatsu *et al.* 2005a). However, the animal's own signal recorded at the dorsal fin is attenuated by 30–40 dB relative to the source level recorded 1 m in front of the animal. Villadsgaard *et al.* (2007) reported source levels of wild harbor porpoises in Danish waters ranging between 178 and 205 dB re 1  $\mu$ Pa peak-to-peak, and our A-tag recordings confirm these values (see Fig. 7). This means that the minimum source level at the dorsal fin of a tagged wild harbor porpoise would be about 148–175 dB re 1  $\mu$ Pa, which is greater than the threshold level of the A-tag (142 dB re 1  $\mu$ Pa). We therefore believe that most echolocation signals from our tagged porpoises were recorded. However, during the buzz the source levels are low and the repetition rate is very high, about 500 clicks per second (Beedholm and Miller 2007, Atém *et al.* 2009, DeRuiter *et al.* 2009). Thus buzz clicks most likely did not trigger our system.

The settings of the software temporal filters were chosen in order to avoid detections caused by splash noise to a depth of 0.3 m and surface reflections with click intervals shorter than 2.5 ms. Surface reflections with longer click intervals were rarely recorded, probably due to the distance related transmission loss and the rather high threshold of the A-tag. High rate detections not produced by a porpoise were sporadic and did not limit our analyses. Thus, we believe that the differences in biosonar activity among animals are real and not influenced by our instrumentation.

Inevitably, all forms of tags may influence an animal's behavior. However, harbor porpoises can carry functional satellite tags for a year while moving over long distances thus indicating that satellite tags alone are tolerated (Edrén *et al.* 2010, Sveegaard *et al.* 2010). Also, two harbor porpoises carrying satellite tags were bycaught in gillnets by fishermen. Both animals were in good nutritional status and had full stomachs (Sonne *et al.* 2012), suggesting natural behavior of satellite tagged harbor porpoises. A captive harbor porpoise showed minor changes in behavior immediately after tagging. The altered behaviors, which were likely due to valium sedation, continued for the next 7–24 h after which the behaviors returned to normal (Geertsen *et al.* 2004). Although no valium sedation was used in the present study, the behavior of our animals could have been influenced by the tags and the tagging procedure.

### *Biosonar Activity*

Although three tagged harbor porpoises is a small sample size, we found some interesting differences in acoustic and dive behavior among the animals. All animals showed higher click activity during the night (Table 1), which was expected considering the advantage of biosonar for orientation and foraging during darkness. If light availability should influence biosonar activity, then we would expect captive harbor porpoises with blinding eyecups to alter their biosonar signals. However, there is no significant difference between click source



levels used by a captive harbor porpoise with and without blinding eyecups (*t*-test,  $P > 0.05$ ; LAM, unpublished data). Also DeRuiter *et al.* (2009) found no differences in click phases, intervals and levels during prey capture for porpoises with or without eyecups. Therefore we assume that the day-night differences we report here are influenced by something other than just illumination.

Porpoises will change biosonar levels depending on circumstances. Porpoise #2 stayed entirely in shallow sandy-bottom waters near the coast (Fig. 1). Harbor porpoises, and other odontocetes, decrease the source level of their biosonar with decreasing distance to a target (Rasmussen *et al.* 2002, Au and Benoit-Bird 2003, Beedholm and Miller 2007, Atém *et al.* 2009, DeRuiter *et al.* 2009). Hence, the shallow water depth does not demand intense, long-range echolocation unless the animal was detecting fish while swimming horizontally. Also proximity to the bottom will increase clutter echoes that might cause the porpoise to further reduce the level of its clicks. Porpoise #2 had the longest period with no triggers on the A-tag (Table 1) indicating it used less intense clicks while in shallow waters. Porpoises #1 and #3 spent some time in deeper water. Villadsgaard *et al.* (2007) recorded the highest source levels from animals in the deepest waters. From the results presented here and from our experience with animals in captivity, we conclude that harbor porpoises echolocate almost continuously, although diurnal variations and infrequent silent periods of several minutes may occur. We thus conclude that the diurnal behavior in both echolocation and diving and the variability between animals is real and not an artifact of the technical limitations of the equipment. However it is important to note that not all clicks the tagged porpoises emit are necessarily recorded because of the A-tag threshold.

Porpoise #2, which stayed in the shallow sandy-bottom waters near the coast, used more biosonar at night (Fig. 3) and had most feeding bouts at night (Fig. 5). We assume this individual was feeding on fish like juvenile flat fish (*Pleuronectiformes*) that are commonly found in the area according to fishermen. These fish show nocturnal activity and movements (Verheijen and De Groot 1967) that could explain the diel biosonar activity by porpoise #2. Furthermore, this animal had higher diving activity at night (Table 1, Fig. 4) that correlated with higher biosonar activity (Fig. 3, 4, 6), both of which support our suggestion that porpoise #2 was taking nocturnal fish. Porpoises #1 and #3 foraged both in daylight and darkness (Fig. 5). Thus, these two porpoises were probably foraging on fish like sandeels (*Ammodytes sp.*) during the day (Winslade 1974) and at night on fish like herring, sprat (*Sprattus sprattus*), and flatfish that are night active (Verheijen and De Groot 1967, Cardinale *et al.* 2003).

The high biosonar activity of porpoise #3 is difficult to explain by foraging activity alone in that porpoise #1 also foraged in offshore waters, but showed lower biosonar activity (Fig. 3). Perhaps porpoise #3, a larger female that used more intense signals, had higher energetic requirements and thus more biosonar activity to find prey, or there were significant differences in prey type and availability in the two areas. A combination of the above factors probably accounts for the greater number of registered clicks from porpoise #3 compared to the other two porpoises.

### *Diving Activity*

The hourly mean dive frequencies of about 45 dives per hour (range 4–185) were similar for the three porpoises (Table 1). We define a dive as exceeding 6 s

at a depth below 2 m. In comparison 14 porpoises tagged in the same general area as our study had 29 dives per hour on average (range 1–53) during April to August with little variation between months (Teilmann *et al.* 2007). The differences between earlier studies in the same general geographical area and this one may reflect individual or habitat dependent variations. It might also be due to the slightly different definition of a dive. Teilmann *et al.* (2007) defined a dive as lasting longer than 10 s at a depth below 2 m. The number of dives per hour recorded for porpoises in the western Atlantic (Westgate *et al.* 1995) ranged from 12 to 109, which is similar to our study. Westgate *et al.* (1995) defined a dive as lasting longer than 3 s at a depth below 2 m. The differences in minimum dive duration certainly affect the number of dives counted, especially in shallow waters where dive rates, according to the present study, tend to increase drastically. Comparing the present study with the one by Teilmann *et al.* (2007), the greater minimum dive duration in their study probably excluded many dives and therefore revealed fewer high dive rates. The study by Westgate *et al.* (1995) was conducted in the Bay of Fundy, Canada, which has deeper waters than our study area. However, Westgate *et al.* (1995) did not correlate the dive rates to water depth and, therefore, we cannot say if their highest recorded dive rate (109 dives per hour), which occurred in shallow waters, was due to the affect of tagging or simply due to the variability of natural behavior among animals.

Dive activity was equally distributed throughout the day, but one porpoise (#2) showed a diel diving pattern with fewer and sometimes deeper dives during the day. The increased diving frequency at night could indicate a higher effort in finding night active juvenile flat fish as discussed above. Porpoises #1 and #3 did not show such correlations or diel diving patterns, but rather they had constant dive frequencies throughout most of the recording time. However, porpoise #3 showed extremely high dive rhythms (up to 180 dives per hour) for six hours after tagging (Fig. 4). That its behavior was affected by the tagging procedure can therefore not be excluded. But according to observations at the facility in Kerteminde, Denmark, dive frequencies of captive harbor porpoises in shallow waters of the enclosure can easily reach similar high values under normal non-stressed conditions.<sup>3</sup> All three porpoises were tagged in pound nets that are set in shallow waters. Two of the three animals showed high diving frequencies after tagging, but the third (#2) did not, so we cannot conclude that the tagging procedure alone was responsible for initial high diving frequencies.

#### *Possible prey capture*

Trained harbor porpoises in simulated prey capture experiments (Atém *et al.* 2009, DeRuiter *et al.* 2009, Verfuß *et al.* 2009, Miller 2010) show the same three phases in their echolocation behavior during prey capture as do bats (Griffin 1958); search, approach and buzz. A similar pattern has been described earlier for bottlenose dolphins (Evans and Powell 1967, Johnson 1967, Morozov *et al.* 1972). During the terminal part of the approach the click interval and click intensity continually decreases and ends in a “buzz.” At this time the prey is 2–4 m from the porpoise or it would take the porpoise about 1 s to reach the

<sup>3</sup>Personal communication from Janni Damsgaard-Hansen, Fjærd&Bælt, Margrethes Plads 1, 5300 Kerteminde, Denmark, 20 January 2011.

prey based on results from experiments with captive harbor porpoises (Verfuß *et al.* 2009). We record similar acoustic behaviors from our tagged wild harbor porpoises where a reduction in click interval to less than 10 ms can happen in about 0.5 s (Fig. 7). Prey detection occurs earlier as indicated from captive harbor porpoises (Verfuß *et al.* 2009). The terminal buzz could not be recorded from our tagged wild harbor porpoises since the source level of the individual clicks presumably fell below the trigger level of the A-tag. Porpoise #3 showed the most intense foraging activity (Table 2), based on sequences with sudden decreasing click intervals (see Fig. 7B). We assume these sequences ended in prey capture or attempted capture. Porpoises #2 and #3 probably did some of the foraging at the sea bottom (Fig. 5, Table 2), a behavior others have also reported (see Santos and Pierce 2003). However, there was variation in the presumed foraging activity among animals with most activity within the surface layer (0–2 m) and the bottom of the dive (Table 2). Obviously we do not know the species of fish our tagged porpoises were taking, but two species that harbor porpoises feed on in Danish inner waters are herring (*Clupea harengus*) and whiting (*Merlangius merlangus*), both of which spend time near the surface, especially at night.<sup>4</sup> Flat fish (*Pleuronectiformes*) and sandeels (*Ammodytes sp.*) are common on the bottom at night.

The number of foraging events resulting in prey capture cannot be stated since some may have been unsuccessful or the characteristic click pattern may have been used in a different context. The low rate of possible foraging for porpoise #2 is probably due to the 142 dB threshold of the A-tag since the porpoise could have been using low intensity signals in the shallow coastal waters where it spent all of the time it was tagged.

Harbor porpoises feed on a large variety of fish species (Santos *et al.* 2004) that live within the water column as well as near and on the seafloor. Therefore it is not surprising that we found possible foraging events in all dive phases for the three animals. This supports the conclusion that harbor porpoises are highly adaptive and opportunistic in their foraging ecology.

Click intervals in captive animals during the search phase are between 50 and 60 ms (Verfuß *et al.* 2009). One might expect wild harbor porpoises to use longer and more variable click intervals when scanning an unknown, open environment. However, our results show that click intervals in the search phase of tagged animals were from 30 to 150 ms (see Fig. 7 as an example). Captive porpoises use landmarks as orientation points (Verfuß *et al.* 2005). The distance to a landmark can be calculated from the time interval between searching clicks and the estimated “lag time” (Thomas and Turl 1990, Au 1993). According to Verfuß *et al.* (2005) lag time ranges between 14 and 36 ms in captive harbor porpoises depending on the difficulty of the task. Thus, the click interval minus the minimum lag time divided by two and multiplied with the speed of sound in water (1.5 m/ms) gives the scanning distance. The maximum scanning distances are between 12 m and 102 m for click intervals of the two possible feeding events shown in Figure 7, or about the same distances as for captive porpoises in Kerteminde. If these values hold in general then harbor porpoises are not long distance hunters.

<sup>4</sup>Personal communication from Finn Larsen, DTU Aqua, Danmarks Tekniske Universitet Charlottenlund Slot, Jægersborg Allé 1, 2920 Charlottenlund, Denmark, 12 December 2011.

### Conclusions

This study demonstrates that recording bioacoustics and dive activity combined with satellite-transmitted positions is possible over several days while providing considerable insight into the behavior of free ranging harbor porpoises. Large variability was observed among the three porpoises with echolocation activity varying from <100 to >50,000 clicks per hour and the dive frequency from 6 to 179 dives per hour down to a maximum of 34 m for up to 213 s. This variation can be attributed to individual behavior, depth, type of habitat and the prey species available. For the porpoise (#2) that stayed in the same habitat throughout the deployment, the behavior was linked to the environment as shown by a consistent diurnal variation in echolocation and diving. Such behavior can be expected in a uniform habitat where porpoises specialize on certain prey species. On the other hand, the ever changing physical and biological environment in the waters connecting the Baltic Sea and North Sea requires a high level of behavioral adaptability to be able to survive, which is probably the main explanation for the behavioral variations we found for porpoises moving to other habitat types. However, to be able to differentiate between individual behavior and behavior determined by the characteristics of a particular habitat, data from several animals exploiting the same habitat are required.

In future studies it is recommended to take advantage of the rapid technological advances in miniaturizing devices like video for monitoring hunting behavior and prey species, on-board GPS for more frequent and accurate positioning, accelerometers, swim speed and compasses to monitor movements in three dimensions. When these advances are combined with acoustic tags we will be able to give a context related description of the bioacoustics and behavior of free-ranging porpoises as has been done, to some extent, for larger cetaceans in recent years.

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