Diel echolocation activity of harbour porpoises (*Phocoena phocoena*) around North Sea offshore gas installations

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Echolocation clicks of harbour porpoises (*Phocoena phocoena*) were detected with T-PODs, autonomous, passive, acoustic-monitoring devices, deployed from an offshore-exploration-drilling-rig and gas-production-platform complex in the Dogger Bank region of the North Sea from 2005 to 2006. Echolocation-click trains were categorized into four phases of the diel cycle: morning, day, evening, and night. Porpoises were present near ($<$200 m) the platform, and there was a pronounced diel pattern in echolocation activity; the number of porpoise encounters (visits) was greater by night than by day. The number of click trains with a minimum inter-click interval of $<$10 ms also increased at night. This was confirmed by a comparison of the ratios of feeding buzzes to search-phase clicks (feeding buzz ratios) and an analysis of the changes in pulse-repetition frequencies within each train. A reasonable interpretation of this pattern was that porpoises were feeding below or around the platform at night. The evidence for changes in activity during the morning and evening was less clear, so these may be transitional phases. The pattern of porpoise-echolocation behaviour around this platform is related most probably to the diel activity of their prey. If porpoises cluster regularly around such installations within 500-m shipping exclusion zones, they may be omitted from population surveys. We conclude that offshore installations may play an important role as nocturnal porpoise-feeding stations in an overfished environment, but that further replicated and controlled studies are required. These findings should be taken into consideration during offshore-installation-decommissioning decisions in the North Sea.

Keywords: acoustic monitoring, North Sea, platform, porpoise echolocation, rigs-to-reef, T-POD.

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Introduction

The harbour porpoise (*Phocoena p. phocoena*) is the most widely distributed cetacean in European waters (Reid *et al*., 2003). They forage frequently around inshore and continental-shelf areas, including reefs, straits, and gullies, where waters are cool, tidal flows are often strong, and aggregations of prey are concentrated (Watts and Gaskin, 1985; Johnston *et al*., 2005; Goodwin, 2008). Acoustic research on the echolocation behaviour of porpoises has therefore focused on inshore populations (e.g. Carlström, 2005), usually in summer when the weather is more clement, or on weather-independent, captive animals (see Nachtigall *et al*., 1995, and references therein). Our understanding of the echolocation behaviour of free-ranging harbour porpoises remains limited, however, and there are currently no published data on their offshore echolocation patterns.

Harbour porpoises are not seen generally in anything more than a Beaufort Sea State 2 (Teilmann, 2003), and they spend a limited amount of time at the surface (Westgate *et al*., 1995). These factors, coupled with their small size, barely visible blow, and undemonstrative surface behaviour, make them among the most difficult cetacean species to detect visually. Porpoises are highly vocal animals, however, and wild individuals in Danish waters have been shown to produce sonar-click trains on average every 12.30 s (Akamatsu *et al*., 2007a). They can, therefore, be surveyed acoustically, which has the advantages of gathering automated 24 h data in weather or sea-state conditions that limit the effectiveness of visual observations, and independently of individual observer skills.

Porpoise-echolocation clicks are relatively short and tonal (Schevill *et al*., 1969), emitted in a narrow beam width (16° in the vertical and horizontal plane; Au, 1999) with dominant narrow-band, high-frequency click components within 110–150 kHz (Møhl and Andersen, 1973; Verboom and Kastelein, 1995, 1997; Au, 1999; Teilmann *et al*., 2002; Villadsgaard *et al*., 2007). Porpoise-click durations range from 61 to 300 ms (Verboom and Kastelein, 1997; Teilmann *et al*., 2002). Clicks can be emitted singularly or in groups known as trains.

The echolocation signal-repetition rate reflects the time-scale at which an animal gathers information about its environment

(Kastelein *et al.*, 1995). In some captive odontocete species, including harbour porpoises, there is a linear correlation between echolocation pulse intervals and target range (Thomas and Turl, 1990; Au, 1993, Verfuß *et al.*, 2005). Porpoise click-repetition rates during an echolocation series reach a peak in *accelerando* or "burst pulsing" as the animal arrives close to the target (Schevill *et al.*, 1969), akin to the "terminal buzzes" regularly observed in echolocating bats (Griffin, 1958). The term "buzz", however, was not introduced to odontocete biosonar until recently (Miller *et al.*, 1995). Determination of a successful prey-capture event in echolocating bats has been successfully achieved using a combination of infrared filming techniques, to observe any deviation from normal flight associated with a feeding buzz, and simultaneous recording by a bat detector (Todd and Waters, 2007). For free-ranging odontocetes, however, underwater filming of diurnal prey-capture attempts is, at best, extremely difficult and at night practically impossible. In the wild, therefore, without the aid of visual observations, correlation between buzz activity and feeding success should not be assumed *a priori* without experimental evidence, because a high buzz rate could just, in theory, mean that more effort is put into capturing the same amount of prey. Nonetheless, it is plausible that using acoustics alone, a proxy of potential feeding activity could be inferred by examining the relative incidence of rising click rates, emitted during range-locking echolocation behaviour, and the associated decreasing interval between clicks, known as "inter-click intervals (ICIs)" (Carlström, 2005). Although this assumption is based on little experimental evidence to date, a link between feeding and ICI has been demonstrated for foraging Blainville's beaked whales (*Mesoplodon densirostris*), which produce distinct click types matched to different phases of echolocation (Johnson *et al.*, 2006). Similar results have been reported for trained porpoises during orientation and prey capture in controlled, semi-natural conditions using synchronized video and high-frequency sound recordings (Verfuß *et al.*, 2002).

There are huge gaps in our knowledge of the offshore distributions of harbour porpoises, particularly in remote regions of the North Sea. Although oil and gas installations could facilitate cetacean studies as platforms of opportunity in such areas, the politically sensitive nature of their operations and associated publicity has meant that scientists are rarely permitted access. Many offshore North Sea oil and gas activities are located within the Dogger Bank candidate Special Area of Conservation (cSAC) and potential Marine Protected Area. The Dogger Bank is an extensive, isolated shoal of submerged glacial moraine in the central North Sea situated within the 200-nautical mile zones or Exclusive Economic Zones of Germany (eastern end), UK, the Netherlands, and Denmark, or in some cases, both of these areas (see Gubbay *et al.*, 2002, for more information).

Offshore installations can act as artificial reefs, and their three-dimensional structure, which can extend vertically down the entire water column, is effective in aggregating benthic, demersal, and pelagic fish (Stanley and Wilson, 1991), along with a great diversity of other marine life (Carlisle *et al.*, 1964; Shinn, 1974; Wolfson *et al.*, 1979; Guerin *et al.*, 2007). Moreover, in the North Sea, fishing is not permitted within the 500-m exclusion zone around each installation, further enhancing the properties of these "reefs" as refuges for marine life.

In 1986, the National Marine Fisheries Service (NMFS) developed a rigs-to-reef policy in the Gulf of Mexico based on the creation of artificial reefs from decommissioned offshore installations left *in situ*. Although the rigs-to-reefs concept has not yet been adopted in the North Sea, there have been a few isolated studies there (e.g. Soldal *et al.*, 2002; Guerin *et al.*, 2007). Worldwide rigs-to-reef studies have focused mostly on quantifying aggregations of marine life such as fish and invertebrates, but none to date has considered the potential of offshore installations as foraging habitats for marine mammals. We hypothesized that areas in the near vicinity and between the legs of such structures might serve as reefs for potential prey of harbour porpoises in otherwise significantly overfished or disturbed parts of the North Sea.

Within the offshore oil-and-gas industry, personnel access to installations is costly and restricted to helicopter or boat access. There is, therefore, an increasing tendency for operators to create unmanned, shore-controlled platforms, and the use of autonomous monitoring techniques is encouraged. Harbour porpoise-echolocation behaviour has been studied successfully using underwater, autonomous, click-timing detectors called T-PODs (Tougaard *et al.*, 2003, Carlström, 2005, Madsen *et al.*, 2006). T-PODs are deployed manually, but they can be set to record for extended periods without the need to download data. Both visual and acoustic observations have shown porpoises to be present all year-round near exploration-drilling-rig and gas platforms in remote areas of the open North Sea (Todd *et al.*, 2007). This work has also shown that the short-term activity of porpoises is unaffected by routine oil-and-gas operations such as drilling, tender-boat operations, and cementing and casing.

Between 2004 and 2006, as part of a larger environmental impact survey, we gained a rare opportunity to access an exploration drilling rig towed between two sites and one gas-production platform in the Dogger Bank region, to establish, using T-PODs, whether porpoises were present around the installations. The work was undertaken under restricted permissions, time, logistical, and financial conditions. We were not permitted access to other installations or moorings in the area, nor were we allowed to access the area before the exploration drilling. We were not able to undertake replicated work, although this was not a comparative study, and we made no assumptions on whether porpoises were attracted to installations. The objectives of the T-POD study described here were to (i) determine whether porpoises were present around offshore installations, (ii) examine any patterns in the diel echolocation activity, and (iii) attempt to classify echolocation activity into foraging activity using various click-train properties as proxy feeding indicators. Data of this nature are restricted usually to internal reports and are bound by strict client confidentiality, so this is a rare opportunity to present these data to the wider scientific community. As far as we can ascertain, this is the first acoustic study of porpoises around offshore installations to be published.

Material and methods
Study locations and timing

Two pilot studies and a field trial were performed from North Sea offshore installations operating under the jurisdiction of the oil-and-gas branch of BASF (Wintershall AG) in the Northeast "Entenschnabel" German Sector of the Dogger Bank (Figure 1). Pilot study 1 was undertaken over 12 d (15–26 December 2004) from the "jackup" drilling rig *Noble Kolskaya* in sector B4-05 located at 55°40′94.203′′N 004°05′23.810′′E. All B4-05 T-POD observations took place during a "waiting on weather" period when the operators were waiting for the wind and wave heights to subside before the rig
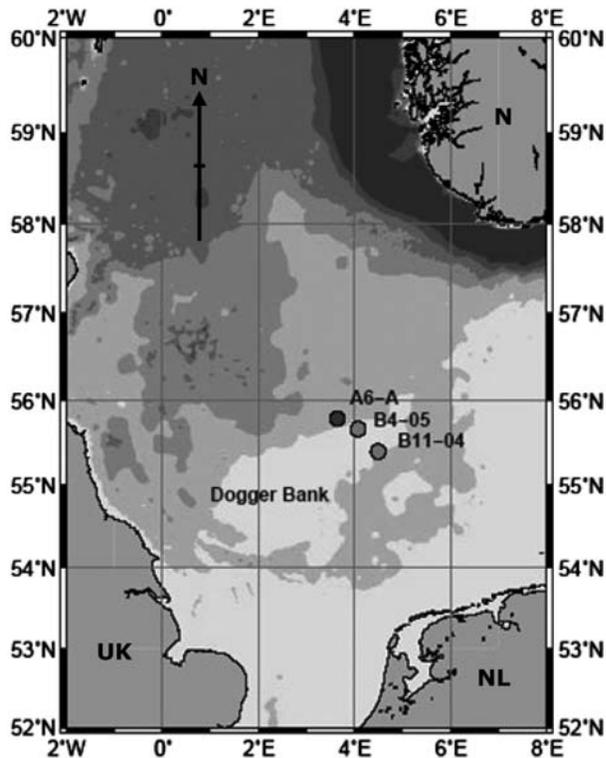
Figure 1. Location of sectors A6–B4 (A6–A platform), B4–05, and B11–04 in the German sector of the North Sea. The lightest grey bathymetry region delineates the 30-m contour.

Figure 2. A schematic depicting the *Noble Kolskaya* fixed onto the southern end of the A6–A gas production platform and the T-POD deployment locations and depths.

was moved to its next location. The *Noble Kolskaya* was then jacked down and towed with tugs to sector B11-04 (55°24′57.000″N 004°32′03.000″E), where a 24-d pilot study was undertaken from 6 to 29 January 2006. B11-04 was located 41.56 km from B4-05 at a bearing of 137.60°. The longer term trial was undertaken from the A6-A gas-production platform, which has been in position (55°47′28.895″N 003°59′39.584″E) in natural-gas field sector A6-B4 since July 1999. A6-A was located 12.48 km from B4-05 at a bearing of 321.10°, and 53.75 km from B11-04 at a bearing of 331.40°. During the monitoring period, the *Noble Kolskaya* was positioned and fixed alongside A6-A at its southern end to drill a new well. Monitoring at A6-A took place over a six-month period from 30 July 2005 to 27 January 2006. In chronological order, the two pilot studies and the trial are referred to as B4-05, B11-04, and A6-A. Detailed analysis of the pilot studies' data is omitted from this manuscript, because of their short deployment duration and poor weather conditions; however, we present comprehensive analysis on the A6-A dataset.

It is important to note that all these observations were based on an area where porpoises have a long history of exposure to activity and noise from other installations and shipping. Prior observations from B4-05, undertaken over six days in December 2004, counted 53 vessels, including traffic from passenger ferries, ocean liners, cargo carriers, coastguard, naval and fishing vessels, and offshore-installation support vessels, the last of which often remained alongside for several hours.

Installation and site description

The *Noble Kolskaya* has a typical triangular-shaped barge hull, with a deck area of 1765 m^2 and three legs at 53.95 m spacing. The
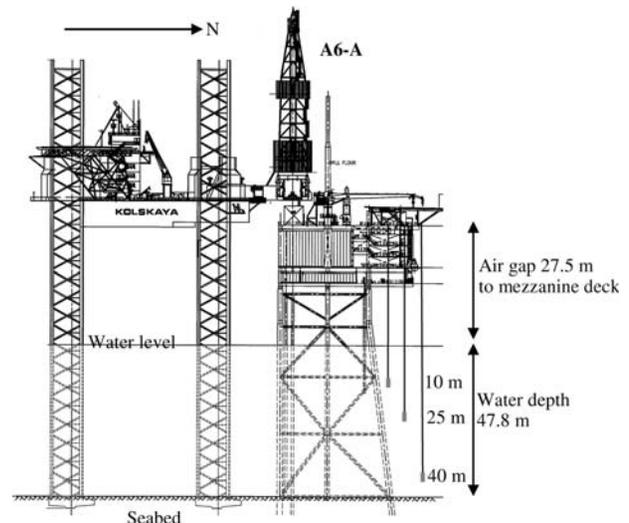
overall length of the hull was 69.25 m, with a maximum centre-depth of 8.55 m. When in sector B4-05, the rig was located in a water depth of 40 m on a seabed of very soft clay and a heading of 135°. The seabed and depth (42 m) of the *Noble Kolskaya*'s second location (B11-04) were similar to B4-05 on an identical heading. The sites cannot be viewed as identical replicates, although various features (e.g. rig specifications, rig activities, depth, heading, and bottom type) were exactly alike or similar. A6-A was situated in a water depth of 47.80 m on a seabed also composed of very soft clay and sand on a heading of 180.30°. The platform had a typical six-legged steel construction with a base area of 1015 m^2. The platform was 52 m long and 33 m wide. The A6-A *Kolskaya* complex is illustrated in Figure 2.

The semi-diurnal tidal heights around all three locations were predicted using POLTIPS-3 for Windows® (Proudman Oceanographic Laboratory Tidal Information and Prediction Software). We received hindcast-modelled weather and hydrographic data (e.g. significant wave height) generated by the European Centre for Medium Weather Forecast (ECMWF) that were ground-truthed to local-buoy empirical data (also provided by ECMWF). Empirical *in situ* installation observations were logged by the crew every 3 h.

Logging harbour-porpoise activity

A detailed description of the T-PODs and associated software, including a manual for data acquisition and analysis, can be found at http://www.chelonia.co.uk. T-POD functionality and settings are reviewed comprehensively in Thomsen *et al.* (2005), Tougaard *et al.* (2005), Philpott *et al.* (2007), and Kyhn *et al.* (2008).

The T-POD comprises a hydrophone, an analogue processor, a digital timing/logging system, and analysis software (TPOD.exe) that filters the data for porpoise clicks automatically, after they have been transferred to a PC. T-PODs log the times and duration, to 10 μs resolution, of clicks resembling the echolocation of porpoises. TPOD.exe then identifies and classifies trains of clicks within the logged data. Trains are also produced by boat sonars

and can arise by chance from random sources of clicks. This process of click-train recognition filters out non-porpoise clicks and gives reliable data on the presence of the animals and of their echolocation behaviour.

Train recognition and classification

Click trains are identified by reference to a probability model of a train, in which a *p*-value is ascribed to each element based on the prevailing rate of occurrence of elements and the offset from an estimated time for each element that is derived from a localized autocorrelation function. This algorithm favours trains that are regular and occur against a quiet background. A set of numerical descriptors of the train is compared with a set derived from extensive real-world T-POD field data collected by the manufacturer, in which the presence or absence of different noise or train sources is known for the deployment context, e.g. deployments in zones of intense surface or sediment noise that are known to contain no cetaceans and which provide large samples of "chance" trains that arise in the absence of any actual train source. Datasets from unobserved deployments are used in this process by examining the clustering of trains, because actual cetacean encounters typically produce more than one train detection.

Trains are classified into CetHi (high-probability cetacean trains), CetLo (low-probability cetacean trains), doubtful trains, very doubtful trains, and boat (fixed rate) sonar trains (see Thomsen *et al.*, 2005, for a full definition of the various categories). The click train and classification-recognition process introduces some predictable biases that have been verified in actual data. The largest biases are that shorter and slower trains are less likely to be classified as having a high probability of arising from a cetacean encounter. This is because they are less improbable as chance events, or because they entail a greater risk of misclassification, because their information content is too low to allow reliable classification at higher levels. This means that the T-POD system does not have a completely uniform, ICI sensitivity. Overlapping trains are sometimes identified by this process and are either attributable to multipath propagation or, less often, arise from different animals. They are not identified automatically by the software as overlapping trains, and because visual examination of the data does not show them to be either common or unevenly distributed, we have not analysed them separately.

Train identification does not recognize trains crossing the end of a scan unless the part wholly within one or each scan meets the criteria. This results in train durations being shortened, but the effect is not large, because logged trains are on average much shorter than scans. Logged trains are also much shorter than trains emitted by the animal, because they represent only those fragments of a train that are detectable as the narrow beam of the porpoise's sonar sweeps across the hydrophone.

The detection software T-POD.exe v8.17 was used to classify recorded click times, to assess monitoring performance in field conditions, and to optimize settings before long-term deployment. For porpoise detection, we used the default, normal sensitivity settings. This enabled us to maintain identical settings throughout a wide range of environmental conditions, such as a moving substratum or a high-frequency surface noise (e.g. rain, entrained air in waves during storms, or cooling-water outlets), which could have created excessive numbers of false detections. This further avoided the masking of train detection by non-cetacean clicks and the possibility of filling up the memory during long periods of deployment.

Table 1. T-PODs function base on the output of the two bandpass filters.

Version 3 T-PODs (identification numbers 406, 407, 408, and 409)						
Scan	1	2	3	4	5	6
Target A filter frequency (kHz)	130	130	130	130	130	130
Ref. B filter frequency (kHz)	90	90	90	90	90	90
Selectivity ratio (A/B)	5	5	5	5	5	5
A integration period	Short	Short	Short	Short	Short	Short
B integration period	Long	Long	Long	Long	Long	Long
Minimum intensity	6	6	6	6	6	6
Scan limit no. clicks logged	160	160	160	160	160	160
Version 4 T-POD (identification number 516)						
Scan	1	2	3	4	5	6
Target A filter frequency (kHz)	130	130	130	130	130	130
Ref. B filter frequency (kHz)	92	92	92	92	92	92
Click bandwidth	4	4	4	4	4	4
Noise adaptation	++	++	++	++	++	++
Sensitivity	6	6	6	6	6	6
Scan limit no. clicks logged	240	240	240	240	240	240

T-PODs function by comparing the output of the two bandpass filters A and B (Table 1). The target filter (A) was set to the frequency of the porpoise clicks, and the reference filter (B) to another frequency known to contain the least energy within a click. T-PODs scanned six times per minute targeting 130 kHz for porpoise clicks. High bandwidth values (e.g. 5) admit sounds of broad bandwidth, that are spread across a wide spectrum of frequencies. Low values (e.g. 4) only admit sounds that have a lot of energy at the target frequency compared with the reference frequency. Values of 3 are extremely restrictive, and admit only highly tonal clicks, and values of 6 are weak and admit a lot of noise. Bandwidth 4 was therefore chosen because it preferentially admits porpoise clicks over dolphin clicks. This key parameter significantly affects detection performance, so the bandwidth was not altered throughout all T-POD trials, to maintain uniformity. On the V4 T-POD, the noise-adaptation level was set to "++", which is the normal operational setting. This meant that the energy passing through the reference filter lowers the effective value of the bandwidth setting. The V3 T-PODs operate with a fixed bandwidth setting, the "ratio" setting. The term "minimum intensity" on V3 T-PODs is essentially the same as the term "sensitivity" on the V4 T-POD. Intensity/sensitivity operates on a 15-point scale, where 10 is the normal operational setting. After a review of trial data, we set the intensity/sensitivity to 6, and maintained it constant on all T-PODs. All T-PODs were set to exclude logging click durations of <10 ms to avoid filling up the memory with short tonal pulses of non-cetacean origin.

T-POD deployment

For pilot studies 1 and 2 (in sectors B4−05 and B11−04, respectively), three V3 T-PODs—alternations of T-PODs 406, 407, 408, and 409—were suspended within the water column from the *Noble Kolskaya* barge, above each of the three legs. The T-PODs were deployed at depths of 10, 25, and 35 m, respectively. Prior

trials had found that shallower deployments had a tendency for wind-induced currents to carry them into the legs, and deeper T-POD deployments tended to interact with the rig's "spud cans" (the feet), which had not fully penetrated the seabed. This mooring configuration therefore had the added advantage of sampling the whole water column, because no assumptions were made about porpoise utilization of the three-dimensional space around offshore installations. All T-PODs were assumed to be able to monitor the entire region around the installation, because Tougaard *et al.* (2006) showed, through comparison of simultaneously sampled T-POD and visual observation data, that in some cases T-POD detection of porpoises was possible out to a range of >300 m, with an effective detection range of ∼70 m. For the Tougaard *et al.* (2006) case, for an average water depth of 6 m, the 16° vertical beam width of the animal would effectively fill the water column for ranges more than 22 m. In our study, however, with an average water depth of ca. 48 m, the same animal's vertical beam width would provide a footprint just 20 m high at a range of 70 m, the effective detection range noted by Tougaard *et al.* (2006), i.e. ∼42% of the total water column. This would mean that, depending on T-POD position in the water column, the animal could swim either above or below it and remain undetected. Therefore, for the deeper environment in this study, the effective detective range within a specific detection probability is lower than that noted by Tougaard *et al.* (2006). The feasibility of detection of an on-axis animal out to 300 m, however, is likely to be similar.

For the A6-A platform trial, three T-PODs were also deployed. These were alternations of V3 T-PODs 406, 407, and 408, along with a new V4 T-POD 516. The choices of deployment location were relatively limited on the A6-A, because of various health-and-safety requirements and the presence of two cooling-water outlets between the legs at the northern and southern ends of the platform, which generated high-frequency noise that had previously interfered with the T-PODs' click-train detection ability.

Each T-POD was equipped with 128 MB RAM and 12 × 3.4 V D-cell alkaline batteries, which, depending on echolocation activity and background noise, generally ensured autonomous monitoring operation for ∼2 months. Every 4–5 weeks, the T-PODs were retrieved and the logged data downloaded onto a laptop PC (Sony Vaio VGN-S1XP, PGC-6C1M, Tokyo, Japan). D-cells were subsequently replaced and T-PODs re-deployed. At no point were all T-PODs recovered simultaneously, ensuring a continuous monitoring dataset.

Indicators of porpoise activity

Only CetHi trains were analysed, which is the designation TPOD.exe uses for trains most likely to have been produced by the target species. The data for each porpoise train were exported from T-POD.exe into Microsoft Excel™ for analysis. We used four indicators of porpoise echolocation behaviour that each measured different aspects of activity and, as a consequence, there was no statistical bias in investigating correlations between the indicators.

Encounter rate

The encounter rate is the number of echolocation encounters measured per hour, where an encounter is defined as a group of trains that are separated by periods of silence with a minimum duration of 10 min, after Carlström (2005). The encounter rate (encounters per h) was calculated as the number of porpoise encounters divided by the mean duration of each diel phase multiplied by the number of recording days:

$$\text{Encounter rate (encounters/hour)} = \frac{\text{total number of encounters in diel phase}}{\text{mean length of diel phase (hours)} \times \text{recording days}}.$$

Minimum ICI

A description of the minimum ICI (MICI) per train is given in Carlström (2005) and Philpott *et al.* (2007). An MICI of <10 ms was used as a proxy indication of porpoise-feeding activity, as per the Carlström (2005) study.

Feeding-buzz ratio

Feeding-buzz ratio (FBR) is a term borrowed from bat literature (e.g. Vaughan *et al.*, 1996; Turner, 2002). These were generated by dividing the number of trains with MICIs of <10 ms by those with MICIs of >10 ms for each diel phase. A value >1 would indicate that a greater proportion of porpoise trains have ICIs <10 ms, indicative of potential feeding, and vice versa.

Pulse-repetition frequency

Although the pulse-repetition frequency (PRF) and the ICI are each other's reciprocal, we use the term PRF here as a measure of the rate at which echolocation clicks were being emitted within each train, and as such this measure is distinct from the MICI. We studied the proportion of a click train that contained decreasing ICI values, i.e. a greater proportion of trains containing increasing PRF values, because a greater proportion of trains with increasing PRFs would indicate a decreasing distance between the porpoise and its target (prey), signifying a possible feeding attempt. PRFs were analysed to verify whether the use of the MICI was a reliable estimate of feeding attempts in porpoises.

Diel classification

Porpoise trains were categorized by a custom-written computer algorithm into four diel phases (morning, day, evening, and night), by comparison with civil twilight and sun-state tables from the US Naval Observatory (http://www.usno.navy.mil/) – see Figure 3. Technical definitions for precise rise, set, and twilight are explained on the USNO site at http://www.usno.navy.mil/USNO/astronomical-applications/astronomical-information-center/rise-set-twi-defs. The effects of the lunar cycle were not considered. The algorithm revealed the diel phase in which a train was detected and sorted the trains by whether they had an MICI of <10 ms, a proxy indicator of feeding behaviour.
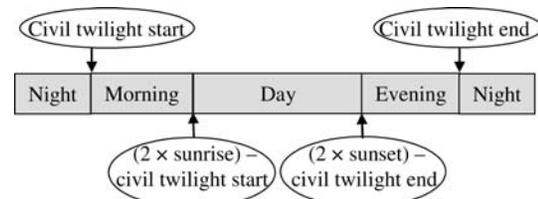
Figure 3. A graphical representation of the assignment of the diel phase. The start and end of each phase was calculated using the formulae shown inside each oval, with values, and civil twilight definitions, taken from the US Naval Observatory.

Statistical analysis

Statistical tests were performed using SigmaStat v.3.1 (Systat software Inc., CA, USA). Data from each T-POD were analysed separately for all MICI calculations. All train datasets were non-normally distributed (Kolmogorov–Smirnov tests, $p < 0.05$), and logarithmic and arcsine transformations failed to normalize the data. Non-parametric Kruskal–Wallis, one-way ANOVAs, with the appropriate *post hoc* tests, were therefore employed to assess significant differences for the indicators of porpoise activity. For the PRF analysis, morning and evening diel-phase data were excluded, because preliminary analysis had found these periods to be transitional (see Results section below). Spearman's rank-order correlations between MICI and the percentage of the train in which the MICI was decreasing and Kruskal–Wallis, one-way ANOVAs of diel phase vs. the percentage of decreasing ICIs per train (with *post hoc* Dunn's tests) were performed. For the A6-A data, however, each T-POD deployment was treated as a replicate, and Kruskal–Wallis ANOVAs of the encounter rates in each diel phase were employed.

Results

Tidal heights and currents at all three locations were minimal (0.5 m and 0.51–1.03 m s^{-1}, respectively), because of the installations' proximity to an amphidromic point, i.e. a position within a tidal system where the tidal range is almost zero, in the German Bight. The tidal currents in all three areas ran with the directions largely constrained to 080° flood and 240–290° ebb. At all three locations, local surge, wind, wave, and installation-induced currents between the legs were also observed.

Pilot studies B4-05 and B11-04

The monitoring periods at both locations were plagued by bad weather. At B4-05, data from T-PODs 406, 407, and 409 were too few to be analysed statistically ($n = 20$ click trains in total). The remaining T-POD 408 logged 31 porpoise encounters during a total of 23 570 monitoring minutes (16.37 d). At B11-04, T-POD 407 developed a hardware fault during deployment and ceased logging after 11 d. T-POD 409 was lost when its mooring line was severed by a supply-vessel's propeller. Nonetheless, T-PODs 407 and 408 logged 128 porpoise encounters during a total of 62 142 monitoring minutes (43.15 d).

Trial 1: A6-A

All T-PODs logged 2479 porpoise encounters during a total of 756 369 monitoring minutes (525.26 d). Figure 4 shows a solar plot of the monitoring period at A6-A, with the four curves representing the transitional changes between each phase.

Encounter rate

Significantly more porpoise encounters were recorded at night (Kruskal–Wallis, one-way ANOVA on ranks, d.f.=3, $H = 8.638$, $p = 0.035$). All *post hoc*, pairwise, multiple-comparison procedures (Tukey method) revealed this difference to exist between night and day ($p < 0.05$).

Minimum ICI

From Figure 5, it is clear that the median MICI was shorter at night. This result was significant throughout all T-POD deployments (Kruskal–Wallis, one-way ANOVA, $p < 0.001$; all *post hoc*, pairwise, multiple-comparison procedures, Holm–Sidak method, are illustrated in Figure 5). The shortest ICI in the entire dataset was 0.74 ms.

### Feeding-buzz ratios

Figure 6 shows that a large proportion of nocturnal click trains had MICI values of < 10 ms and hence an FBR of > 1 (Kruskal–Wallis ANOVA, $H = 13.194$, $p < 0.005$, all *post hoc*, pairwise, multiple-comparison procedures, Tukey method).

Pulse-repetition frequency

Figure 7 shows the change in PRFs over the diel cycle. Patterns in PRF decrease when approaching sunrise, and increase after sunset. PRFs followed the same pattern as MICI, in that there was a significant negative correlation between MICI and percentage of the train in which ICI was decreasing (increasing PRF) for all T-POD deployments (Spearman's rank order
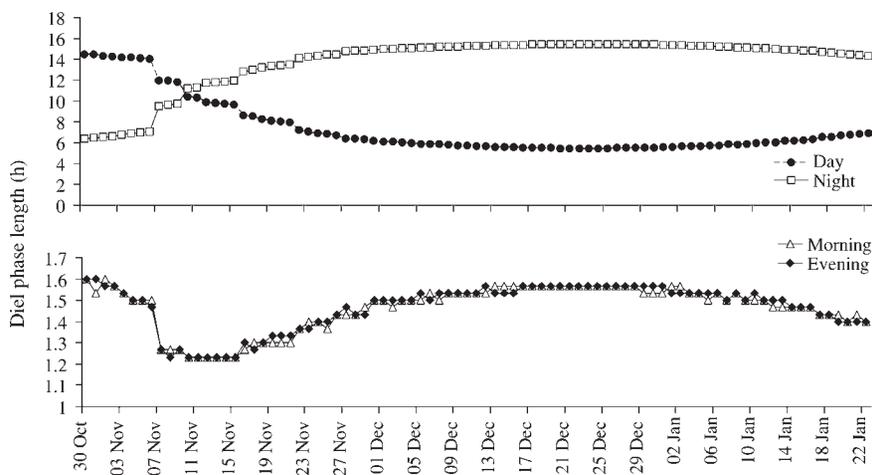
Figure 4. Solar plot of diel-phase lengths for the monitoring period at A6–A. Note that the scale of the lower figure has been expanded to distinguish between the two phases.
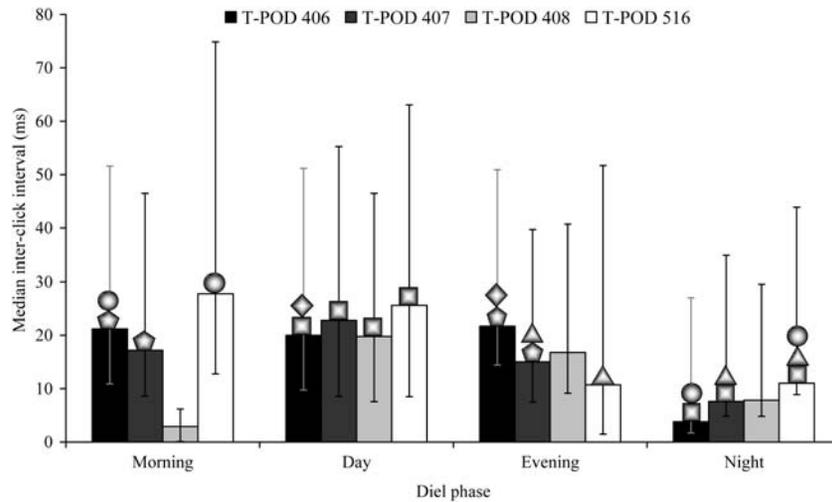
Figure 5. Trial 3 (A6 – A) MICIs and interquartile ranges. The shapes refer to *post hoc* Dunn's tests that gave significant results at the level $p < 0.05$: squares, day vs. night; circles, morning vs. night; triangles, evening vs. night; diamonds, day vs. evening; rhomboids, morning vs. evening.
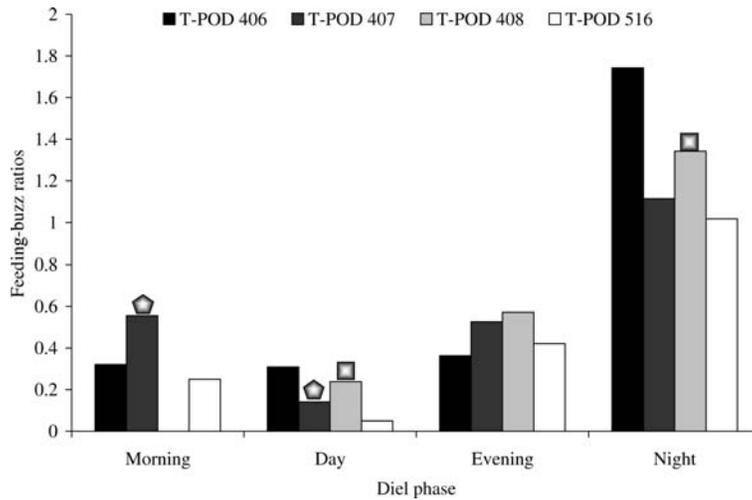
Figure 6. Trial 3 (A6 – A) FBRs calculated as the number of trains with MICIs of < 10 ms divided by the number of trains with intervals of > 10 ms, in each diel phase. The symbols refer to *post hoc* Tukey tests that gave significant results at the $p < 0.05$ level: squares, day vs. night; rhomboids, morning vs. day. Note that during the morning phase, T-POD 408 revealed only feeding buzzes, so a ratio could not be calculated.

correlations: T-POD 406: $r = -0.52$, $p < 0.0001$, $n = 5644$; T-POD 407: $r = -0.554$, $p < 0.0001$, $n = 4445$; T-POD 408: $r = -0.392$, $p < 0.0001$, $n = 795$; T-POD 516: $r = -0.534$, $p < 0.0001$, $n = 2301$).

There was a significant increase in porpoise PRFs during the night compared with the day (*t*-test, $t = 7.257$, d.f. $= 16$, $p > 0.001$). There were also significantly more trains containing an increase in FBR at night than by day (Mann–Whitney rank sum test, $T = 197$, $p = 0.007$).

Discussion

There was a significant variation in all the investigated echolocation variables within the diel cycle. The overall results support the views that (i) porpoises are present at the offshore installations or, at least, within a few hundred metres of them, (ii) there is a pronounced diel pattern in echolocation activity, and (iii) a

reasonable interpretation of this pattern is that porpoises are feeding at night below or around the platform. They may, in fact, be in both areas.

Each of the independent measures of the echolocation activity was correlated, indicating a coherent fingerprint to echolocation behaviour that is consistent with the possibility that this represents increased feeding activity. Although a correlation between low ICIs on T-POD recordings and feeding behaviour has not been verified experimentally, if we assume this relationship is plausible, then the MICI, FBR, and PRF data suggest that around these installations, porpoises may allocate a greater proportion of their echolocation to target-locking and inferred feeding attempts by night than by day. PRF analysis would then support the use of MICI as a potentially reliable indicator of target-locking behaviour. This research cannot prove *per se* that the MICI is a reliable indicator of feeding behaviour in porpoises; however, we can conclude at the very least that it is a
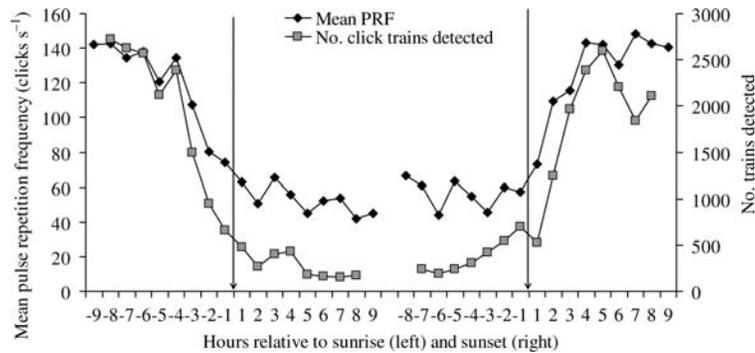
Figure 7. Trial 3 (A6 – A) mean PRF on the left *y*-axis, and total number of porpoise-echolocation click trains detected throughout the diel cycle on the right *y*-axis. Time is given as relative to sunrise and sunset (e.g. 1 denotes the first hour after sunrise or sunset), and the vertical arrows indicate the time of sunrise (left) and sunset (right). The total number of trains detected and not the encounter rate are plotted to avoid double-counting of encounters that cross diel categories, so the graph is split because sunset does not come as an integer number of hours after sunrise.

useful indicator of the presence of a certain type of train, though further evidence involving independent information about the behaviour of the porpoises, from cameras, time-depth recorders or similar instruments, is needed to establish the link to feeding.

There were clear diel echolocation patterns observed during the A6-A trial, and day-to-night distinctions were clearer when morning and evening phases were excluded from proxy feeding analyses, as also found by Carlström (2005). The morning and evening could be inferred as transitional or changeover phases, when porpoises may have left and arrived at the installations, respectively. Alternatively, porpoises may have taken a significant quantity of prey by night, through to the morning, gradually becoming sated by daylight, or perhaps prey availability diminishes, although there may be some supplementary feeding during these periods (Amano *et al.*, 1998).

A review of diurnal rhythms in Cetacea (Klinowska, 1986) indicates some diel patterns in feeding behaviour for most species, but it is still not clear whether these patterns are related to circadian rhythms, external cues (e.g. light/lunar cycles), diel activity in their prey species, or to some combinations of these factors. Moreover, much of the literature confuses the term "diurnal" with "diel", when in fact the former term should be taken to mean "daily" and the latter to the 24 h, night-time, daytime cycle. Although there are no *a priori* reasons to expect diel patterns to be the same for all porpoises around the world and at all times of the year, the overall diel patterns observed here agree essentially with those of Carlström (2005), who reported that the rate of harbour porpoise echolocation encounters, MICI per train, and proportion of trains with MICI < 10 ms all peaked at night and were at their minima by day. Carlström's (2005) data were gathered from a single POD (v.1) moored at 40 m in the Sound of Mull (Scotland). Similar diel patterns have also been reported for wild porpoises in the Bay of Fundy, Canada, by Cox *et al.* (2001) from a POD, version not specified but, according to Carlström (2005), an earlier model than the v.1 moored 10 m deep during a pinger-playback-and-control experiment. Those authors reported higher porpoise echolocation-detection rates at night than by day, for both playback and control conditions. Conversely, Cox and Read (2004) later report that four PODs (version not specified), also stationed in the Bay of Fundy, recorded a higher echolocation rate, number of clicks recorded per h, and echolocation occurrence, proportion of 10 s intervals

during which clicks were detected per hour, by day than by night. The last study, however, was carried out around chemically enhanced and control gillnets in a mitigation experiment, and may not be indicative of wild porpoise echolocation behaviour in general. Moreover, the influence of tide on porpoise activity has been demonstrated in the Bay of Fundy (Johnston *et al.*, 2005), and indeed elsewhere (e.g. Pierpoint, 2008), and may explain the lack of or deviating diel patterns in that region.

We observed significantly shorter median MICIs at night than by day, which contradict the findings of Carlström (2005), who reported a higher mean (not median) MICI at night in terms of distance from porpoises to their targets affecting the two-way travel time of echolocation clicks. She concluded that, at night, the porpoises in her study used echolocation to explore the environment at greater distances than they did by day. Applying the same logic, the results of this study would indicate that at night, porpoises use their echolocation to explore the environment at shorter distances than by day, although we caution that our study was not designed to investigate the underwater, acoustic-sensing behaviour of individual porpoises. Additionally, T-PODs cannot identify specific individuals. Overall, when moving through an environment where vision is limited, prior acoustic inspection of the area ahead is essential to porpoises (Akamatsu *et al.*, 2007b), especially around the metal legs of installations. Finless porpoises (*Neophocaena phocaenoides*), for instance, inspect distances of up to 77 m ahead before swimming into an area (Akamatsu *et al.*, 2005, 2007b). If porpoises in this study were using installations as hunting grounds, it is likely that they were foraging close to the structures' legs, because this is where species assemblages are likely to be concentrated. This would bring the animals closer to targets for longer durations than in Carlström's (2005) open-water study, perhaps explaining the discrepancy between the two sets of results.

Porpoises may produce more click trains and click bursts (inferred feeding attempts) at night than by day for several reasons. First, as Carlström (2005) suggested, porpoises may increase their rate of echolocation during darkness to compensate for the loss of visual information and, second, there may be more food available to porpoises at night, which is why more target-locking pulses are recorded. There is evidence both for and against these hypotheses from studies on wild and captive animals.

Echolocation studies of captive porpoises in light and darkness have so far been inconclusive or based on small sample sizes, or both these factors have been in play (Kastelein *et al.*, 1995). For example, Akamatsu *et al.* (1992) conducted experiments to investigate the rate at which a harbour porpoise uses echolocation at night. The animal in that study was caught in Japanese coastal waters and kept in a net-mesh sea pen, where it was subjected to two nights of observations, and for one night in a pool, in both dark and artificially lit conditions. In the sea pen, the average rate of echolocation (ARE) was high in the evening and low in the morning. Switching on a 100 W light decreased the ARE by one-third; conversely, it increased tenfold when the light was switched off. A repeat of the experiment confirmed the observation. In the pool, the ARE was relatively lower in the morning than at midnight. Akamatsu *et al.* (1992) showed clearly that the rate of porpoise echolocation was affected by light conditions, yet this study is often misquoted in the literature.

The porpoises in Akamatsu's *et al.* (1992) study were probably familiar with and became acclimatized to their milieu. Echolocation rates may be infrequent in familiar surroundings (W. A. Watkins, pers. comm.), which may explain partly why less echolocation activity was detected during the morning and evening around A6−A. This platform had been in position for more than five years, so it is likely that it was a well-known foraging site for local animals.

In the ocean, light attenuates quickly with increasing depth, especially in temperate waters (Jerlov, 1976). Wild harbour porpoises are known to dive as deep as the local topography permits, often deeper than 200 m, by both day and night (Westgate *et al.*, 1995; Otani *et al.*, 1998). The Dogger Bank is unusual in that it exhibits year-round phytoplankton production (Berry, 2004) and, at 48 m, light levels in this turbid region may be expected to be low all year-round. Poor levels of ambient light would logically necessitate an increase in echolocation rate at night, in association with investigating objects at close range and, more specifically, as we suggest here, attempted prey-capture.

Porpoises use click bursts to investigate specific objects at close range, but also during the pursuit of live fish (Kastelein *et al.*, 1995). The nocturnal increase in the proportion of click trains that contain a terminal buzz may have been related to the concurrent nocturnal increase in the availability of their prey. In general, there is good evidence that feeding behaviour in porpoise species is related principally to prevalence and activity of prey. For example, it was originally hypothesized that Dall's porpoises (*Phocaenoides dalli*) foraged mostly at night or at dawn, because animals captured in the morning tended to have more food remains in their stomachs (Stroud *et al.*, 1981, cited in Amano *et al.*, 1998). Subsequent research, however, revealed that feeding times were region-specific and related to availability and diel activity of dominant prey (Amano *et al.*, 1998; Ohizumi *et al.*, 2000), as opposed to time of day. Harbour porpoises are thought to be opportunistic feeders (Recchia and Read, 1989), and their behaviour is probably related to prey location, because porpoises are small, have limited ability to store energy (Koopman *et al.*, 2002), and have a demanding reproductive schedule.

Worldwide studies have shown porpoise diet to vary seasonally, geographically, species-specifically, and three-dimensionally (benthic, mesopelagic, and pelagic), with long-term shifts in prey preference (Aarefjord *et al.*, 1995; Benke and Siebert, 1996; Jepson, 2001; DTI, 2002; Szefer *et al.*, 2002; Das *et al.*, 2003; Santos and Pierce, 2003; Víkingsson *et al.*, 2003; Santos *et al.*,

2004; Fontaine *et al.*, 2007; Pierce *et al.*, 2007). In our study we have no empirical evidence on fish species diversity, distribution and behaviour, or the prey-preferences of porpoises around installations; however, North Sea porpoises are known to feed on sandeels (Ammodytidae) and herring (*Clupea harengus*; Santos, 1998; Vergeer, 2006). More specifically, in German waters west of Denmark, including the Dogger Bank region, sandeels account for ~40% of harbour-porpoise diet (Benke and Siebert, 1996). There are sandeel spawning grounds, and a fishery, in the Dogger Bank region, and they are present year-round (ICES, 2007). Raitt's small or lesser sandeel (*Ammodytes marinus*) constitutes >95% of the sandeels in the North Sea and is dominant offshore (Hawkins *et al.*, 1998). It is a reasonable assumption, therefore, that these and other species could form part of the diet of the porpoises near the installations, particularly as fish within the 500 m exclusion zone are excluded from commercial fishing. The diel activity of porpoises, therefore, may be related to that of their prey, and we explore that possibility further here.

Sandeels also exhibit diel patterns in behaviour. By day they feed in open water, and by night they rest or avoid predators by burrowing into the sediment (Winslade, 1971, cited in Freeman *et al.*, 2004). If porpoises feed on sandeels around the installations, the absence of a sandeel swimbladder (Reay, 1970, cited in Freeman *et al.*, 2004) may result in only faint porpoise-echolocation target strengths in the water column by day, which renders this prey species an easy, concentrated, food source to locate in the sediment at night. Moreover, Raitt's sandeels rarely emerge from the seabed between September and March, except in December and January, to spawn (Bergstad *et al.*, 2001), coinciding with most of the A6−A study period, further supporting the possibility that porpoises could target that species by night at depth. The probability of sandeel distribution around installations is enhanced by the fact that sandeels need to maintain a proximity to zooplankton prey by day (Freeman *et al.*, 2004), and it is an accepted tenet that zooplankton concentrations are higher around installations than in surrounding areas, because platforms act as large plankton accumulators through hydrodynamic and illumination effects (Keenan *et al.*, 2003).

The consensus is that pelagic fish are highly dispersed at night and aggregated by day (Blaxter and Holliday, 1969; Fréon *et al.*, 1996). Herring are also abundant on the Dogger Bank (Zijlstra, 1969), exhibit diel, vertical-migration behaviour (Blaxter and Holliday, 1969), and come to the surface at night where they disperse and swim more slowly (Blaxter and Batty, 1987; Cardinale *et al.*, 2003). Read (2001) suggested that porpoises may find it easier to hunt for herring that cease or reduce shoaling and disperse, further supporting the rationale for porpoises to feed at night, should herring feature among their prey around installations. The attenuated trends in porpoise echolocation behaviour at dawn and dusk may, in part, be attributable to the differences in schooling dynamics between dawn (fast aggregation) and dusk (slower dispersion) for some of the potential prey species of porpoise, such as herring and sprat (*Sprattus sprattus*; Fréon *et al.*, 1996).

Finally, diel patterns in fish behaviour and concentrations have also been shown around installations. Soldal *et al.* (2002) found that, by day, mackerel (*Scomber scombrus*) schooled around a platform in the Norwegian sector of the North Sea and, concurrently, demersal fish tended to be located beneath the platform, near the legs and close to the bottom, where they could not be measured acoustically. At night, demersal fish spread throughout the water

column in such a manner that their distribution was suitable for acoustic biomass estimation. The greatest fish densities were close to and within 10 m of the seabed, which is where porpoises are presumed to feed (Santos and Pierce, 2003). Significantly higher acoustic values of fish density were recorded at night (Soldal *et al.*, 2002), further supporting our hypothesis that porpoises feed more frequently at night around installations. Clearly, detailed discussions on the prey preferences of porpoises around installations are beyond the scope of this work, but we propose that the possibilities suggested here be explored further by studies that employ the long-term use of underwater cameras in concert with fish density and abundance estimation and diversity techniques.

In conclusion, the harbour porpoises we recorded frequented offshore installations, possibly to feed, with surprising regularity, particularly at night. Offshore installations may be important foraging areas for harbour porpoises, so replicated and controlled experiments should be carried out to explore this possibility further. Given the historical effects of overfishing in the North Sea (Lotze, 2007), this research should be considered whenever decisions regarding the costly nature of decommissioning offshore installations are made. If installations are left *in situ*, they may serve to benefit porpoise populations that are already subjected to unsustainable rates of bycatch in fisheries (Vinther and Larsen, 2004). Moreover, if harbour porpoises regularly cluster around installations within the 500-m exclusion zones, then they may historically have been unintentionally omitted from population surveys, resulting in potentially significant underestimations of their true population status, e.g. by Small Cetacean Abundance in the North Sea or SCANS I (Hammond *et al.*, 1995, 2002), SCANS II (see http://biology.st-andrews.ac.uk/scans2/index.html), and Cetacean Offshore Distribution and Abundance (CODA).

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