The diel pattern in harbour porpoise clicking behaviour is not a response to prey activity

Anna N. Osiecka1,2*, Owen Jones2,3 & Magnus Wahlberg1,2

Wild harbour porpoises (Phocoena phocoena) mainly forage during the night and, because they rely on echolocation to detect their prey, this is also when they are most acoustically active. It has been hypothesised that this activity pattern is a response to the diel behaviour of their major prey species. To test this hypothesis, we monitored the acoustic activity of two captive harbour porpoises held in a net pen continuously during a full year and fed by their human keepers during daylight hours, thus removing the influence of prey activity. The porpoises were exposed to similar temperature and ambient light conditions as free-ranging animals living in the same region. Throughout the year, there was a pronounced diel pattern in acoustic activity of the porpoises, with significantly greater activity at night, and a clear peak around sunrise and sunset throughout the year. Clicking activity was not dependent on lunar illumination or water level. Because the porpoises in the pen are fed and trained during daylight hours, the results indicate that factors other than fish behaviour are strongly influencing the diel clicking behaviour pattern of the species.

Acoustic communication and echolocation are of extreme importance for harbour porpoises (Phocoena phocoena) and are used as means of finding food, navigation, and communication1–4. Porpoises only produce one type of acoustic signal, a very high frequency (130 kHz) and short duration (50 µs) click5. By varying the repetition rate of clicks they can either use them for echolocation6 or communication3. Clicks are produced throughout the day and night, and year round7,8. Harbour porpoises have acute hearing abilities already fully developed in neonate animals9 and one of the lowest hearing thresholds found in any animal10, indicating the importance of acoustic cues for this species.

The porpoise stereotypical and easily recognisable signal makes this species extremely suitable for passive acoustic monitoring (PAM) to provide information on their presence in time and space, as well as on their bioacoustic behaviour11–13. Porpoises emit signals in a very narrow beam14,15, which decreases the likelihood of detecting the signals. However, the fact that clicks are produced almost continuously and that animals are constantly moving around has made PAM a very important tool for studying this species in the field. It is also widely used to successfully assess the impact on porpoises from many man-made activities, such as noise from coastal wind farms1,16–19 and deterrent signals intended to keep them away from gill nets20–24.

From PAM studies, distinct diel rhythms in harbour porpoise acoustic activity have been described in the inner Danish and Swedish west coast waters8,25,26, and the North Sea27,28, with a strong peak in echolocation activity around midnight and considerably lower activity during the day. An even more pronounced nocturnal peak was observed in the proximity of industrial in-water structures, such as bridge pillars29. The increased night-time clicking activity might be attributed to the loss of visual information at night, diel movement patterns of prey, or intrinsic physiological diurnal phases and/or lunar cycles31. Lunar (and thus, in some waters, tidal) cycles, as well as light (both solar and lunar), are of great importance triggering behaviours such as vertical migrations and schooling patterns in many species of fish that are preyed upon by porpoises30–34.

Here, the acoustic activity patterns of captive harbour porpoises are investigated over a full year to understand which extrinsic cues are triggering their daily clicking behaviour. The porpoises are kept in a net pen under ambient water conditions and fed regularly at specific times during daylight. Therefore, when compared to wild porpoises, cues generated by prey behaviour can be ruled out, but a strong additional cue, feeding events in the

1Marine Biological Research Centre, Department of Biology, University of Southern Denmark, Hindsholmvej 11, 5300 Kerteminde, Denmark. 2Department of Biology, University of Southern Denmark, Campusvej 55, 5230 Odense, Denmark. 3Interdisciplinary Centre on Population Dynamics (CPOP), University of Southern Denmark, Campusvej 55, 5230 Odense, Denmark. *email: ann.osiecka@gmail.com
The daytime, has been introduced. The acoustic activity analysis investigates whether the porpoises have a steady diel clicking pattern also in the net pen, and whether factors other than fish behaviour are influencing the acoustic activity patterns of this species.

Methods
Location and study subjects. Recordings were made 15 m from the porpoise pen of Fjord&Bælt facility in Kerteminde, Denmark. At the time of the study, this facility kept two adult female harbour porpoises in captivity for research and educational purposes. Both animals were wild-born and brought to the facility after getting accidentally caught in demersal nets in 1997 (porpoise named Freja) and 2004 (porpoise named Sif). The porpoises are kept in a 30 × 20 m pen with large-meshed nets keeping the animals in ambient water conditions year round. The animals receive food during several daily training sessions using positive reinforcement. Specialised caretakers regularly monitor their health, behaviour, and general well-being. The animals are held at the Fjord&Bælt under permit J.nr. SVANA-610-00084, Ministry of Environment and Food, Denmark. All methods were carried out in accordance with relevant guidelines and regulations. This study did not directly involve the animals and used passive monitoring instead, thus no additional permits were required.

Data collection. A C-POD data logger (Chelonia, Inc.) was anchored in Kerteminde harbour, 15 m from one end of Fjord&Bælt’s porpoise pool (Fig. 1). The C-POD was calibrated both before and after the deployments using standard methods to confirm that the equipment functioned properly and to establish its detection threshold for porpoise clicks (115 dB re 1 µPa rms).

The logger was anchored at 3 m depth, 1 m above the bottom, and more than 1 m away from the harbour wall. It was located 15 m from the closest part of the harbour porpoise enclosure. The C-POD monitored porpoise acoustic activity in the period from the 6th of June 2016 to the 7th of June 2017. The equipment was retrieved eight times to download the collected data, change batteries, and ensure the gear was still running correctly, remaining on land for 20–60 min each time before being deployed again.

Data collected from 12:00 on the 6th of June 2016 to 11:59 on the 6th of June 2017 were selected for analysis. During the entire 365 days of recordings, there were in all 7 days with no collected data due to technical issues with the data logger and data retrieval. Only the periods with no missing data were included in the analysis, further limiting the sample size to 345 for daylight and 354 for night-time.

Porpoise data analysis. The acoustic data were analysed using CPOD.exe software V2.044 (Chelonia Ltd., Mousehole, UK). Porpoise click trains were identified using the KERNO classifier with “Hi” quality (the highest level of probability) and “NBHF” (narrow band high frequency) filters. Data were exported as the number of clicks detected per minute. Data from 5 min after each deployment and from 2 min before each retrieval of...
the equipment were removed to exclude data before the logger had stabilised itself in the water as well as any immediate curious biosonar inspection by the animals to the logger’s presence.

Data on abiotic factors. R package lunar was used to obtain the lunar phase and illumination data and R package suncalc to obtain sunrise and sunset times. Data on sea surface height during the recording period were obtained from the Danish Coastal Authority’s measurement station in Kerteminde harbour less than 50 m from the porpoise facility at Fjord&Bælt.

Statistical analysis. First, median clicks emitted per minute was calculated for each period of darkness (i.e. between sunset and sunrise) and each period of light (i.e. between sunrise and sunset). This resulted in a total of 699 measures (345 for daylight and 354 for night-time—the difference between these sample sizes is caused by short periods of incomplete data collection mentioned above).

Randomisation tests were used to determine whether the recorded number of clicks per minute differed between daytime and night-time, and between the crepuscular hours (defined here as 2 h before sunrise and after sunset) and other times. The same approach was used to determine whether there is an association between night-time click activity and (a) lunar phase and (b) water level. To conduct the tests, each night was assigned to one of the lunar phases: new, waxing, full, and waning. Lunar illumination was discretised into equally spaced groups of 0.00–0.25, 0.25–0.5, 0.5–0.75 and 0.75–1.00. Sea surface height was discretised into groups of low tide (− 59–28 cm) and high tide (28–115 cm).

Randomisation tests are a class of distribution-free method that ask where an observed test statistic (in this case the difference in average (median) number of clicks emitted per minute between two groups) falls in relation to a null distribution that is generated by randomising the explanatory variable in the data at hand many times. If the variable has little explanatory power, then randomising it would have very little effect on the test statistic. A p-value can thus be calculated as the proportion of replicates where the randomised test statistic is greater than or equal to the absolute value of the observed test statistic. A major advantage of using randomisation tests is that they do not violate the assumptions of ordinary linear models such as normality, homogeneity of variances, and independence of errors. 5,000 replicates were used for all randomisation tests.

The time of the highest concentration of clicks and its 95% confidence interval were obtained from the maximum likelihood estimate of the parameters of a circular normal (von Mises) distribution using the mle.vonmises function from package circular. In addition to the randomisation test described above, a Rayleigh test was used to test the significance of departure from a uniform (non-directional) distribution of click intensity. All analyses were performed using R 3.5.2.

Results

The influence of abiotic factors on porpoise clicking activity. The average clicking activity was considerably higher during the night than during daylight hours throughout the year (Figs. 2A and 3). This difference was highly significant (two-tailed randomisation test: n = 5,000, p < 0.01). Clicking activity was found to be significantly higher in the crepuscular hours than at other times (two-tailed randomisation test: n = 5,000, p < 0.01). The Rayleigh test also indicated a highly significant departure from a uniform circular distribution of click intensity (test statistic = 0.262, p-value < 0.01). The overall peak-click time was estimated to be at 23:59 UTC + 2 (95% CI 23:50–00:09; Fig. 4). This midnight peak appeared to be present only during the summer months (April–September; Fig. 4), but this pattern is caused by the merging of the pre-dawn and post-sunset peaks that occur throughout the year.
Water level ranged from extremes of −59 cm to 115 cm relative to the local average sea level, but the variation was normally much more modest (1st and 3rd quartiles were −12 and 15 cm, respectively). There was no significant difference in average clicking activity between the high and low water level groups (Fig. 2B; two-tailed randomisation test: n = 5,000, p = 0.130). Lunar phase also had no significant effect on clicking activity (Fig. 2C; two-tailed randomisation tests: n = 5,000, p-values for the pairwise comparisons ranged between 0.210 and 0.490).

The highest clicking activity was observed in June and July (Fig. 3). Other than this, porpoise clicking activity gradually rose as light availability decreased over the autumn and winter months.

Discussion

A strong diel clicking pattern with higher night-time activity and a strong midnight peak has often been reported for wild harbour porpoises in many different areas.25–28.44 However, field-collected data cannot determine whether the porpoises increased their general clicking activity, whether the animals were simply more likely to visit the vicinity of the data logger, or whether they clicked with a higher intensity over certain periods. In this study, two of these factors could be ruled out, as both porpoises were kept in the vicinity of the data logger throughout the study year, and as the data logger was sufficiently sensitive to detect porpoise clicks over their range of produced sound levels. This study clearly indicates that captive harbour porpoises fed during daylight hours have a similar diurnal clicking pattern to wild porpoises, with most activity occurring during night-time hours.

The overall increase in night-time acoustic activity and a summertime midnight peak confirmed in this study makes it very likely that wild porpoises exhibit their night-time peak due to increased clicking activity. As this pattern is found in both wild and captive animals, it further suggests another factor determining this behaviour.
than their foraging behaviour, such as porpoises having an intrinsic circadian rhythm or supplementing visual information in poor light conditions by echolocating.

Interestingly, a clear peak in clicking activity can be seen around sunset and sunrise throughout the year, with a “rest period” of a lowered night-time activity during the winter months. The activity peak is particularly strong during the summer months, so that, when all year’s data are pooled together, the overall activity pattern can be obscured by the summertime peak. Therefore, this study indicates that the midnight peak in clicking activity observed from studies in the wild is either a result of shorter monitoring times performed during the more accessible summertime months, or reflects an annual pattern obscured by the especially high summertime activity. The details of the clicking activity pattern of wild porpoises call for further investigation.

The highest average clicking activity in this study was observed in some of the months with the longest days (June and July). This was the case also outside of the opening hours at the facility and is therefore not the result of the tourist high season at the facility. Even though the acoustic activity gradually rose with the decreasing light availability from the beginning of autumn until January, it did not reach the activity levels observed in June and July. The high clicking levels in the summertime coincide with the harbour porpoise mating season\textsuperscript{45}. It has been shown previously that harbour porpoises produce frequent social calls\textsuperscript{9} and can convey precise behavioural information by modifying repetition rate patterns of their clicks\textsuperscript{9}. Their mating vocalisations, if such exist, have never been described. While it is not whether the peak activity times observed here are related to the mating season, it is possible that they might be a result of the hormonal status of the two captive females. Since the individuals studied here live in partial seclusion far away from any observed wild animals, and taking into account the high directionality and rather small active space\textsuperscript{1} of the sounds produced by these animals, it can be ruled out that vocalisations of wild porpoises, e.g. males attempting to mate, contributed to the observed peak. In any case, these observations open a door to further studies of harbour porpoise social behaviour. Furthermore, the higher clicking activity in the summertime cannot be explained by porpoises only regulating the sonic output to supplement the lack of visual information.

Stedt et al.\textsuperscript{25} had shown a significant effect of lunar phase on the acoustic activity of wild porpoises, with higher activity recorded at full moon than at new and quarter moon. In the same study, they detected no effect of water level on porpoise activity. In our study, there was neither an effect of lunar phase nor of water level. A strong lunar and tidal effect on clicking activity was previously reported for spinner, dusky and common dolphins\textsuperscript{14,46} and short-finned pilot whales\textsuperscript{47}. It is likely that the correlation between sound production and lunar phases is due to prey activity patterns, as many species of fish and squid adjust their behaviour according to both tide and moon cycles. In some areas, there is a strong relationship between lunar phases and tides, and it is therefore difficult to separate how they affect both predators and prey. In Danish waters, however, water levels are only to a small extent determined by lunar phases and to a much larger degree by prevailing wind conditions. The fact that wild porpoises in inner Danish waters are affected by lunar cycles but not by water level strongly indicates that their prey is also more affected by moon phases rather than water height, which is not surprising due to the erratic pattern of water level changes in these waters. Moon cycles are also connected to varying lunar illumination, which can explain the higher or lower acoustic activity of an echolocating animal during different lunar phases. The fact that the activity pattern of captive porpoises seems unaffected by lunar phase may therefore be explained in two ways. Firstly, the patterns of wild porpoises could indicate that they do indeed respond to the behaviour of the prey species that depend on moon cycles but that are absent in captive conditions. However, as there seems to be no effect of lunar phases on the amount of produced feeding buzzes of wild porpoises\textsuperscript{32}, it is possible that lunar illumination simply improves the ability of porpoises to use visual cues as a complement to echolocation. This could explain that the lunar phases are less obvious in the porpoise pen than in the open coastal waters, due to artificial street and building lights adjacent to the pen, providing night-time light sources dominating over moon light.

Caution needs to be taken interpreting behavioural data from captive animals. Perhaps the largest issue that needs to be taken into account in this study is the presence of training sessions several times a day. Even though porpoises in the pen of Fjord&Bælt do catch and search for wild fish entering their enclosure, they obtain a major part of their diet from the trainers during 3–5 daily feeding sessions spaced between 9.00 and 15:30. The fact that the Fjord&Bælt porpoises have a similar diel pattern as wild porpoises could indicate that their diel activity rhythm is not dictated by the behaviour of their prey, but rather a response to the changing light availability. The presence of a night-time “rest period” during the winter and a pronounced crepuscular peak in acoustic activity of both wild and captive porpoises may indicate an intrinsic physiological rhythm or an undescribed behavioural pattern maintained in captive animals that is not caused by external stimulation and that calls for further investigation.

Data availability
The datasets generated during the current study are available from the corresponding author on reasonable request.

Received: 16 February 2020; Accepted: 20 August 2020
Published online: 10 September 2020

References
1. Verfuss, U. K., Sparling, C. E., Arnot, C., Judd, A. & Coyle, M. Review of offshore wind farm impact monitoring and mitigation with regard to marine mammals. In The Effects of Noise on Aquatic Life II (eds Popper, A. N. & Hawkins, A.) 1175–1182 (Springer, New York, 2016).
2. Villadsgaard, A., Wahlberg, M. & Tougaard, J. Echolocation signals of wild harbour porpoises, *Phocoena phocoena*. *J. Exp. Biol.* 210(1), 56–64 (2007).
3. Clausen, K. T., Wulffberg, M., Beedholm, K., Derüter, S. & Madsen, P. T. Click communication in harbour porpoises (Phocoena phocoena). Bioacoustics 20(1), 1–28 (2011).
4. Sørensen, P. M. et al. Click communication in wild harbour porpoises (Phocoena phocoena). Sci. Rep. 8(1), 9702 (2018).
5. Møhl, B. & Andersen, S. Echolocation: high-frequency component in the click of the harbour porpoise (Phocoena Ph. L.). J. Acoust. Soc. Am. 54(5), 1368–1372 (1973).
6. Wisniewska, D. M., Johnson, M., Beedholm, K. & Madsen, P. T. Adaptive prey tracking by echolocating porpoises studied with acoustic tags. J. Acoust. Soc. Am. 131(4), 3523–3623 (2012).
7. Linnenschmidt, M., Teilmann, J., Akamatsu, T., Dietz, R. & Miller, L. A. Biosoan, dive, and foraging activity of satellite tracked harbor porpoises (Phocoena phocoena). Mar. Mamm. Sci. 29(2), E77–E97 (2013).
8. Wisniewska, D. M. et al. Ultra-high foraging rates of harbour porpoises make them vulnerable to anthropogenic disturbance. Curr. Biol. 26(11), 1441–1446 (2016).
9. Wålberg, M., Delgado-Garcia, L. & Kristensen, J. H. Precocious hearing in harbour porpoise neonates. J. Comp. Physiol. 203(2), 121–132 (2017).
10. Kastelein, R. A., Hoek, L., de Jong, C. A. F. & Wensveen, P. J. The effect of signal duration on the underwater detection thresholds of a harbor porpoise (Phocoena phocoena) for single frequency-modulated tonal signals between 0.25 and 160 Khz. J. Acoust. Soc. Am. 128(5), 3211–3222 (2010).
11. Vertx, U. K. et al. Geographical and seasonal variation of harbour porpoise (Phocoena phocoena) presence in the German Baltic Sea revealed by passive acoustic monitoring. J. Mar. Biol. Assoc. UK 87(1), 165–176 (2007).
12. Kyhn, L. A. et al. Harbour porpoise (Phocoena phocoena) static acoustic monitoring: laboratory detection thresholds of T-Pods are reflected in field sensitivity. J. Mar. Biol. Assoc. UK 88(6), 1085–1091 (2008).
13. Brandt, M. J., Diederichs, A., Betke, K. & Nehls, G. Responses of harbour porpoises to pile driving at the Horns Rev II offshore wind farm in the Danish North Sea. Mar. Ecol. Prog. Ser. 421, 205–216 (2011).
14. Koblitz, J. C. et al. Asymmetry and dynamics of a narrow sonar beam in an echolocating harbor porpoise. J. Acoust. Soc. Am. 131(3), 2315–2324 (2012).
15. Wisniewska, D. M. et al. Fast dynamic control over acoustic field of view by echolocating porpoises. Elife (2015).
16. Carstensen, J., Henriksen, O. D. & Teilmann, J. Impacts of offshore wind farm construction on harbour porpoises: acoustic monitoring of echolocation activity using porpoise detectors (T-Pods). Mar. Ecol. Prog. Ser. 321, 295–308 (2006).
17. Tougaard, I., Damsgaard Henriksen, O. & Miller, L. A. Underwater noise from three types of offshore wind turbines: estimation of impact zones for harbor porpoises and harbor seals. J. Acoust. Soc. Am. 125(6), 3766–3773 (2009).
18. Brandt, M. J. et al. Disturbance of harbour porpoises during construction of the first seven offshore wind farms in Germany. Mar. Ecol. Prog. Ser. 596, 213–232 (2018).
19. Graham Isla, M. et al. Harbour porpoise responses to pile-driving diminish over time. R. Soc. Open Sci. 6, 190335 (2019).
20. Cox, T. M., Read, A. J., Solow, A. & Tregenza, N. Will harbour porpoises (Phocoena phocoena) habituate to pingers? J. Cetacean Res. Manage. 3(1), 81–86 (2001).
21. Larsen, F., Krogh, C. & Eigaard, O. R. Determining optimal pinger spacing for harbour porpoise bycatch mitigation. Endang. Species Res. 20(2), 147–152 (2013).
22. Larsen, F. & Eigaard, O. R. Acoustic alarms reduce bycatch of harbour porpoises in Danish North Sea gillnet fisheries. Fish. Res. 153, 108–112 (2014).
23. Kyhn, L. A. et al. Pingers cause temporary habitat displacement in the harbour porpoise Phocoena phocoena. Mar. Ecol. Prog. Ser. 526, 253–265 (2015).
24. Kindt-Larsen, L., Berg, C. W., Northridge, S. & Larsen, F. Harbor porpoise (Phocoena phocoena) reactions to pingers. Mar. Mamm. Sci. 35(2), 552–573 (2019).
25. Stedel, J. et al. Diurnal and lunar effects on acoustic detections of harbour porpoises (Phocoena phocoena) around Kullaberg, Sweden. In: Proceedings of the 29th annual conference of the European Cetacean Society, 2015 March 23–25, St Julian’s Bay, Malta. Abstract number ACO-16 (2015).
26. Schaffeld, T. et al. Diet and seasonal patterns in acoustic presence and foraging for free-ranging harbour porpoises. Mar. Ecol. Prog. Ser. 547, 257–272 (2016).
27. Carlström, J. Diel variation in echolocation behavior of wild harbor porpoises. Mar. Mamm. Sci. 21(1), 1–12 (2005).
28. Benjamins, S., van Geel, N., Hastie, G., Elliott, J. & Wilson, B. Harbour porpoise distribution can vary at small spatiotemporal scales in energetic habitats. Deep Sea Res. Part II 141, 191–202 (2017).
29. Brandt, M. J., Hansen, S., Diederichs, A. & Nehls, G. Do man-made structures and water depth affect the diel rhythms in click recordings of harbor porpoises (Phocoena phocoena)? Mar. Mamm. Sci. 30(3), 1109–1121 (2014).
30. Cardinale, M., Cressini, M., Artheenius, F. & Skaklaness, N. Diel spatial distribution and fecundity of herring (Clupea harengus) and sprat (Sprattus sprattus) in the Baltic Sea. Aquat. Living Resour. 16(3), 283–292 (2003).
31. Nilsson, F. L. A. et al. Vertical migration and dispersal of sprat (Sprattus sprattus) and herring (Clupea harengus) schools at dusk in the Baltic Sea. Aquat. Living Resour. 16(3), 317–324 (2003).
32. Neat, F. C. et al. Residency and depth movements of a coastal group of Atlantic cod (Gadus morhua L.). Mar. Biol. 148(3), 643–654 (2006).
33. Benoit-Bird, K. J., Dahood, A. D. & Würsig, B. Using active acoustics to compare lunar effects on predator–prey behavior in two marine mammal species. Mar. Ecol. Prog. Ser. 395, 119–135 (2009).
34. Grabowski, T. B., McAdam, B. J., Thorsteinsson, V. & Marteinsdottir, G. Evidence from data storage tags for the presence of lunar and semi-lunar behavioral cycles in spawning Atlantic cod. Environ. Biol. Fishes 98(7), 1767–1777 (2015).
35. Dáhle, M., Verfuß, U. K., Brandecker, A., Siehert, U. & Beinke, H. Methodology and results of calibration of tonal click detectors for small Odontocetes (C-Pods). J. Acoust. Soc. Am. 134(3), 2514–2522 (2013).
36. Culk, B., von Dorrien, C., Müller, V. & Conrad, M. Synthetic communication signals influence wild harbour porpoise (Phocoena phocoena) behaviour. Bioacoustics 24(3), 201–221 (2015).
37. Scheidat, M. et al. Harbour porpoises (Phocoena phocoena) and wind farms: a case study in the Dutch North Sea. Environ. Res. Lett. 6(2), 025102 (2011).
38. Lazaridis, E. Lunar phase: distance, seasons and other environmental factors. R package version 0.1–04 (2019).
39. Thiermel, B. & Elmarhraoui, A. Suncalc: compute sun position, sunlight phases, moon position and lunar phase. R Package version 50 (2019).
40. Peres-Neto, P. R. & Olden, J. D. Assessing the robustness of randomization tests: examples from behavioural studies. Anim. Behav. 61(1), 79–86 (2001).
41. Agostinelli, C. & Lund, U. R package Circular: circular statistics (version 0.4–93). CA: Department of Environmental Sciences, Informatics and Statistics, Ca’foscari University, Venice, Italy. UL: Department of Statistics, California Polytechnic State University, San Luis Obispo, California, USA (2017).
42. Ruxton, G. D. Testing for departure from uniformity and estimating mean direction for circular data. Biol. Lett. 13(1), 20160756 (2017).
43. R Core Team. R: A Language and Environment for Statistical Computing (R Foundation for Statistical Computing, Vienna, 2018).
44. Akamatsu, T., Hatakeyama, Y., Kojima, T. & Soeda, H. The rate with which a harbor porpoise uses echolocation at night. In Marine Mammal Sensory Systems (eds Kastelein, R. A. et al.) 299–315 (Springer, New York, 1992).
45. Sørensen, T. B. & Kinze, C. C. Reproduction and reproductive seasonality in Danish harbour porpoises, Phocoena phocoena. *Ophelia* **39**(3), 159–176 (1994).

46. Simonis, A. E. *et al.* Lunar cycles affect common dolphin *Delphinus delphis* foraging in the Southern California Bight. *Mar. Ecol. Prog. Ser.* **577**, 221–235 (2017).

47. Owen, K., Andrews, R. D., Baird, R. W., Schorr, G. S. & Webster, D. L. Lunar cycles influence the diving behavior and habitat use of short-finned pilot whales around the main Hawaiian Islands. *Mar. Ecol. Prog. Ser.* **629**, 193–206 (2019).

**Author contributions**

A.N.O. and M.W. designed the study. A.N.O. and M.W. acquired and processed the data. O.R.J. and M.W. performed the statistical analysis. All authors interpreted the data, discussed the results and contributed to the final manuscript.

**Competing interests**

The authors declare no competing interests.

**Additional information**

**Correspondence** and requests for materials should be addressed to A.N.O.

**Reprints and permissions information** is available at www.nature.com/reprints.

**Publisher’s note** Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.

© The Author(s) 2020