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I beg your pardon? Acoustic behaviour of a wild solitary common dolphin who interacts with harbour porpoises

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ABSTRACT

Kylie is a solitary common dolphin who inhabits a restricted area within the Firth of Clyde (Scotland). She spends most of her time around navigational buoys in the Hunterston/Fairlie channel, where she has been seen interacting with harbour porpoises. Recordings from 2016 and 2017 were used to study her acoustic behaviour when seen alone and with a porpoise. Clicks were classified as potential porpoise or dolphin clicks based on the waveform, power spectrum, and spectrogram, as well as direction of arrival, inter-click interval, amplitude, and centroid frequency variations. Kylie emitted clicks exclusively, which were of variable nature, including low, mid, and high-frequency (HF, centroid frequency >100 kHz) as well as broad or narrowband. Some of Kylie's HF clicks were similar to porpoise clicks both in the time (e.g. polycyclic) and frequency (e.g. narrowband with most energy between 100 and 150 kHz) domains, which cannot be explained by physical phenomenon alone.

Introduction

Studying wild cetaceans is a challenging task. Setting up experiments is difficult because researchers cannot predict when and where the animals will be seen, and much less which behaviour they are going to engage in. This is especially true for rare behaviours, such as interspecific interactions, and thus our knowledge and understanding of them depend on being in the right place at the right time. One example of rare scenarios is the long-lived interaction between Kylie, a solitary female common dolphin (*Delphinus delphis*), and harbour porpoises (*Phocoena phocoena*) that take place in the Firth of Clyde, west Scotland (Ryan et al. 2017; Nairn, unpublished data). Kylie is regularly seen by locals in different areas of the Firth of Clyde, especially the Fairlie-Hunterston channel, and occasionally reported to be with a porpoise (Nairn, unpublished data, Ryan et al. 2017). No report exists of Kylie with other common dolphins, which rarely enter the Firth of Clyde.

Common dolphins can be found off the coasts of northwest Scotland (Hammond et al. 2002) and regularly visit the coastal waters of the Minch (Weir et al. 2009), both areas located over 400 km from the Fairlie-Hunterston channel.

This study is the result of exceptional and unprecedented opportunities to carry out acoustic recordings when Kylie was accompanied by a porpoise during three encounters in 2016 and 2017. While harbour porpoises basically produce one type of sound: highly stereotyped high-frequency clicks, common dolphins have a wide repertoire, emitting clicks as well as whistles. Harbour porpoise clicks are polycyclic (i.e. waveform with 8 to 15 peaks), with a bell-shaped envelop, and a duration between 50 and 175 µs. They are narrow-band, with the energy concentrated between 100 and 150 kHz (peak centred at 130 kHz) and distinctly, contain no energy below 100 kHz (Møhl and Andersen 1973; Hansen et al. 2008) (Figure 1(a)). These characteristics remain similar when the animal is not oriented directly towards the recorder (Au et al. 1999, 2006).

While common dolphin whistles have been widely studied, the temporal and spectral characteristics of their clicks had received much less attention. They have been described as oligocyclic (i.e. waveform with fewer than 5 peaks), of short duration (not exceeding 50 µs, Figure 2(b)), with peak frequency between 23 and 67 kHz but also having energy between 100 and 150 kHz (Gurevich 1969 – in Evans 1973; Fish and Turl 1976; Soldevilla et al. 2008; Palmer et al. 2017). These descriptions are incomplete, however, because most studies used equipment that cannot detect high frequencies (Fish and Turl 1976; Soldevilla et al. 2008; Palmer et al. 2017). Common dolphins also emit few-seconds long, low-frequency whistles and broadband burst pulses (i.e. clicks produced at high repetition rates), which they use for communication purposes (Ansmann et al. 2007; Perrin et al. 2009; Henderson et al. 2012).

Porpoise clicks are referred to as narrow-band high-frequency (NBHF) clicks and have been recorded in all porpoise species studied to date, as well as in other nine cetacean species including both *Kogia* species, and six species of the genera *Cephalorhynchus* and *Lagenorhynchus*. NBHF clicks are remarkably similar in all species where there have been described (Møhl and Andersen 1973; Dawson 1991; Silber 1991; Madsen et al. 2005; Kyhn et al. 2009, 2010; Melcón et al. 2012; Reyes Reyes et al. 2016, 2018; Merkens et al.
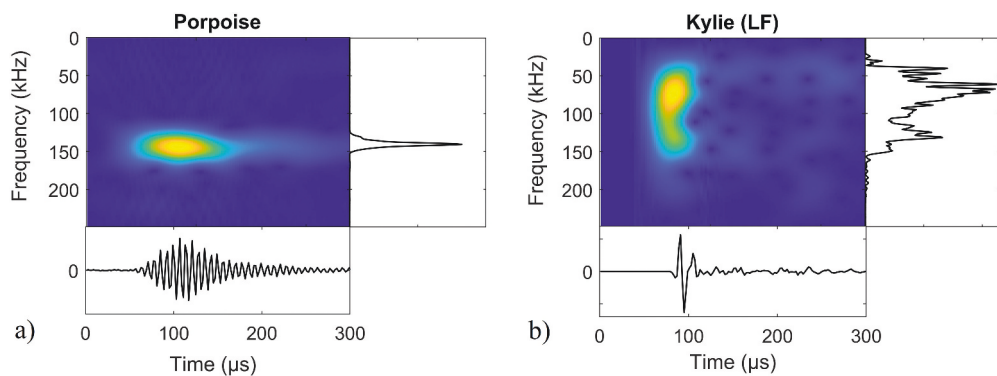

Figure 1. Temporal (bottom) and spectral (top, right) characteristics a) of a typical harbour porpoise (*Phocoena phocoena*) click (note lack of energy below 100 kHz – centre) and b) of a typical broadband click produced by Kylie, the solitary common dolphin (*Delphinus delphis*).
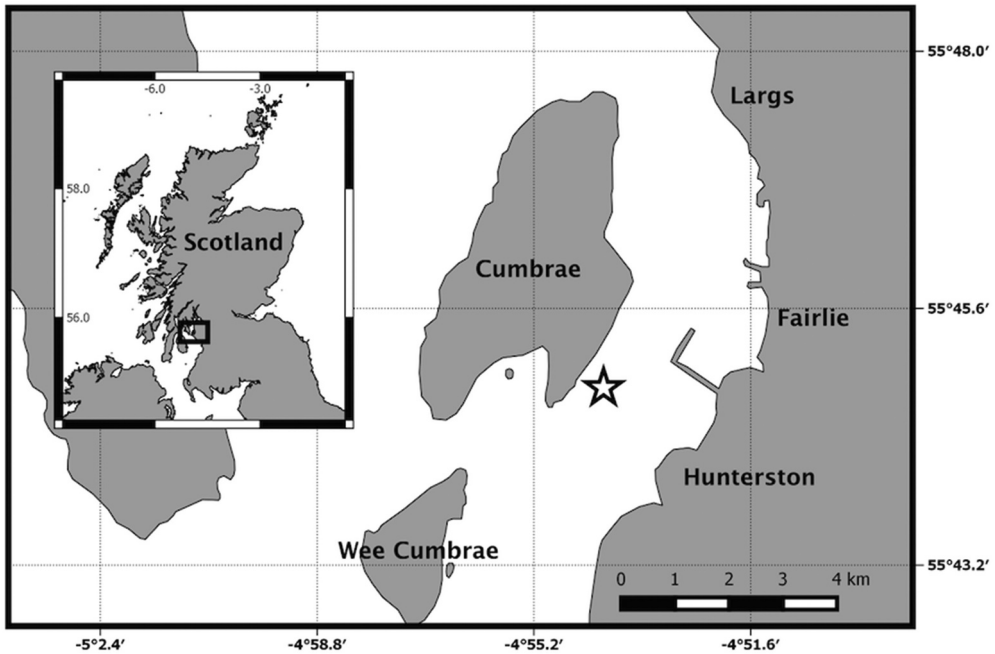
Figure 2. Inner firth of clyde (West Scotland). The star marks the position of a navigational buoy around which all observations of the solitary common dolphin with a harbour porpoise were made during this study.

2018), and only recently some of these NBHF species have been recorded emitting low-frequency whistles and broadband clicks (Reyes Reyes et al. 2016; Martin et al. 2018). Although non-NBHF *delphinids*, such as bottlenose dolphins (*Tursiops truncatus*), are known to produce clicks that contain energy in the 100–150 kHz frequency band, these clicks are oligocyclic and have significant energy below 100 kHz (e.g. Soldevilla et al. 2008; Madsen et al. 2013; Au and Wei 2016). The energy content in these high frequencies seems to be dependent on the amplitude of the click and the orientation towards the recorder. Louder and on-axis clicks have more energy in higher frequencies, although remain oligocyclic (Au 1997; Wahlberg et al. 2011; Madsen et al. 2013; Au and Wei 2016), clearly distinguishable from NBHF clicks.

To the best of our knowledge, there are no reports of non-NBHF species producing NBHF clicks as part of their normal repertoires or as a result of vocal learning.

Vocal learning is divided between production and contextual learning. Production learning is when an individual produces a new signal or modifies an existing one to resemble a model, while contextual learning is using or understanding an existing signal in a new context (Janik and Slater 1997, 2000). Imitation is a form of production learning, where '. . . the following two conditions are necessary and sufficient: (a) The vocalization produced by the animal in response to a presented "model" sound must resemble that model, and (b) the model must not resemble sounds present in the established baseline pretraining repertoire of the animal' (Richards et al. 1984). Imitation has been reported in several taxa, especially birds and marine mammals (Tyack 2008). For example, bottlenose dolphins were trained to imitate artificial sounds and to use them to label objects

(Richards et al. 1984), killer whales (*Orcinus orca*) learned to imitate different sounds, including human speech (Abramson et al. 2013), and grey seals (*Halichoerus grypus*) were taught to produce a wide range of sounds and to imitate melodies of songs (Stansbury and Janik 2019).

Spontaneous imitation as a result of interspecific interactions has also been observed in animals kept in captivity. For example, killer whales and belugas (*Delphinapterus leucas*) who spent time with bottlenose dolphins learned to produce sounds that were similar to bottlenose dolphins' sounds (Musser et al. 2014; Panova and Agafonov 2017). Production learning as a result of interspecies interactions in the wild, on the other hand, have rarely been reported (Janik 2014). One of the few cases is a solitary killer whale who was recorded producing sounds similar to the 'barks' of California sea lions (*Zalophus californianus*) (Foote et al. 2006).

In this study, we used recordings made with two wideband hydrophones to investigate the acoustic behaviour of Kylie, the solitary common dolphin in the Firth of Clyde. Recordings were made when she was seen alone as well as during interactions with harbour porpoises. The results suggest Kylie can produce clicks with temporal and spectral characteristics that resemble NBHF porpoise clicks, an ability not previously reported for common dolphins.

Material and methods

Data collection

Data were collected during systematic and opportunistic surveys in the Firth of Clyde (Figure 2), conducted between June 2016 and September 2017 from the 'Saorsa', a 40-foot -long sailing vessel. Recordings were made using a towed hydrophone array connected to the software PAMGuard (Gillespie et al. 2009), version 1.15.10, and digitised through a St Andrews Instrumentation Ltd. data acquisition card with 16-bit resolution, at a sampling frequency of 500 kHz. The array included two omnidirectional Magrec HP03 hydrophone units, each comprising a spherical ceramic and a HP02 preamp, with a preamp high pass filter set at 2 kHz. The hydrophones had a sensitivity of −201 dB re 1 V/μPa at 150 kHz, and a flat frequency response between 2 kHz and 150 kHz. The array was towed using a Kevlar-strengthened 100 m long cable and the hydrophones were 25 cm apart. The computer was connected to a GPS, and latitude and longitude were recorded every second.

Data preparation

Potential cetacean clicks were extracted using PAMGuard's Click Detector Plug-In, using the default values (Table A1). Transient sounds are saved as individual small audio clips that include the signal as well as a short recording period (40 samples) before and after. Attached metadata used in this study were date, time, and direction of arrival, estimated using trigonometric methods based on time of arrival differences (Gillespie and Chappell 2002). Using custom-built algorithms written in MATLAB 2018a (Mathworks, MA), potential dolphin and porpoise clicks were selected from the time periods when observations were made. The following parameters were estimated per clip: maximum amplitude

(dB re: 1μPa), centroid frequency (kHz, frequency where the energy content is divided into two equal parts (Madsen and Wahlberg 2007), and inter-click interval (ICI), estimated as the time difference between the beginning of the click and the beginning of the previous one (ms).

Data analysis

A desktop application was built using the AppDesigner environment in MATLAB 2018a (Mathworks, MA) to manually classify the selected clicks, as well as to delete echoes and other sources of sounds. The application simultaneously displays the waveform, power spectrum, and spectrogram of the click being audited, as well as the amplitude, centroid frequency, and direction of arrival of the click and the previous and following 10 clicks, plotted with a timestamp to also visualise the inter-click intervals (Figure 3). Classification was based on the unique characteristics of harbour porpoise clicks (e.g. lack of energy below 100 kHz, polycyclic waveform), aided by the variations of the parameters of consecutive clicks mentioned above.

Manual classification was used because the performance of existing dolphin click classifiers is either low or unknown (Soldevilla 2008; Roch et al. 2011), and because it would also allow to study the full range of variations in the spectral or temporal characteristics of Kylie's clicks. For validation purposes, eight volunteers were trained to identify NBHF clicks produced by harbour porpoises. Volunteers were given written instructions for training and testing purposes and to prevent bias, they were not given information about what the study was about. The training samples consisted of 50 high-quality harbour porpoise clicks from Danish waters (recorded using a SoundTrap, Ocean Instruments, which was attached to the seabed and recorded at a sampling rate of 576 kHz). The testing samples were 250 clicks (20%) from the three days of recordings
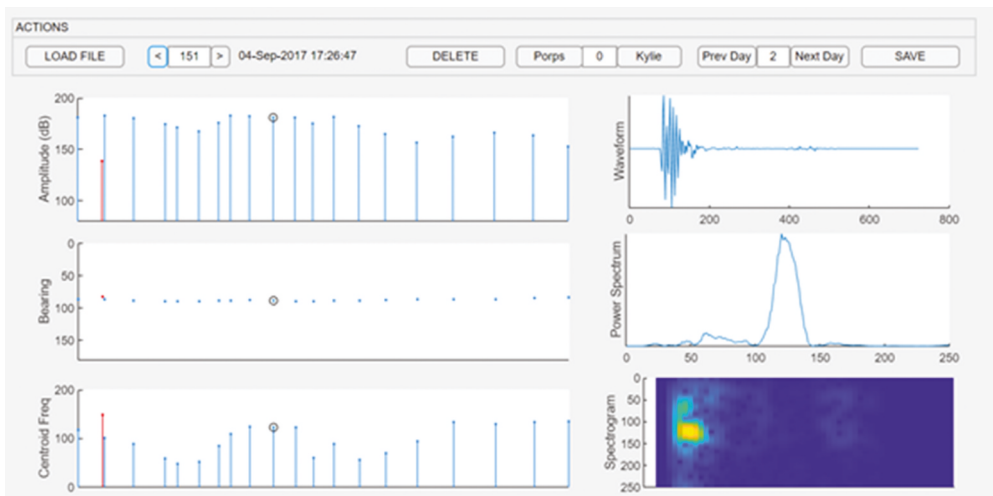

Figure 3. Main display of an application created in the MATLAB (Mathworks, MA) environment AppDesigner (version 2017a). Common dolphin clicks are shown in blue and harbour porpoise clicks in red. Smoothed Pseudo Wigner-Ville Distribution (FFT = 512, window size = 64, overlap 50%).

of Kylie and a porpoise, which were selected randomly using a random number generator. The signals were provided as black and white images that consisted of the waveform, frequency spectrum, and Wigner plot without axes (Figure A1). The reliability of agreement between ours and the volunteers' discrimination was estimated using Fleiss' Kappa (Fleiss 1971) function developed for MATLAB by Cardillo (2007).

Click selection

Clicks were plotted in time against direction of arrival, colour coded by species, to facilitate the identification of periods during which the dolphin and the porpoise were travelling close to each other (Figure A2). These periods were indicated by the simultaneous changes in direction of arrival of consecutive clicks. In other words, if consecutive porpoise and dolphin clicks were coming from the same or similar direction, the animals were assumed to be travelling close to each other. If, on the other hand, the direction was different, either the sounds suffered from reflexion and did not arrive at the same time, or the animals were not travelling close to each other. The latter were excluded from further analysis to minimise errors.

Spectrograms of the recordings were visually inspected in search of whistles and other tonal and pulsed calls using Audacity version 2.3.0.

High-frequency clicks

In this study, high-frequency clicks are defined as those with centroid frequency over 100 kHz, as this is the lower limit of energy content in harbour porpoise clicks (Hansen et al. 2008). The ratio of the energy content between two frequency bands (below and over 100 kHz), was estimated by filtering the clicks using 6th order Butterworth low and a high-pass filters. An unbalanced (i.e. unequal sample size) ANOVA was carried out to compare the ratios in Kylie low-frequency clicks, Kylie high-frequency (HF) clicks, and porpoise clicks.

Results

Kylie was seen alone on 4 October, and 7 and 23 November 2016 as well as 1 November 2017 and 19 July 2018, when she was also acoustically detected. She was seen with a harbour porpoise on 2 and 3 November 2016 (day 1 and 2), and 4 September 2017 (day 3). These encounters lasted less than 5 min on day 1, just over 6 min on day 2, and 12 min on day 3. A fourth encounter with Kylie and a porpoise took place on 7 June 2018, although no acoustic recordings were made. Photographs of the porpoise from the observations in 2017 and 2018 were compared to those in Ryan et al. (2017) and with photographs from 2004, 2009, and 2015, which provided by third parties, showing Kylie interacts with multiple porpoises, although with one at a time (Figure 4). A short video was recorded on 4 September 2017 (Figure 4, bottom left). The video and photographs showed they can interact at very close distance, as previously reported (Ryan et al. 2017).

Fleiss' Kappa

The null hypothesis (i.e. the level of agreement is accidental) was rejected (p = 0, k = 0.28, level of agreement 'Fair'). It was therefore assumed that the method used to assign clicks to either the porpoise or the dolphin was adequate for the purpose of this study.

Figure 4. Travelling together. Solitary common dolphin, locally known as Kylie, travelling together with a harbour porpoise (Top: photo by D. Nairn, 2018. Bottom left: photo by P. Nichols, 2017. Bottom right: photo by G. Patterson, 2009). All pictures were taken off Cumbrae, in the Fairlie/Hunterston Channel, in the Firth of Clyde, West Scotland.

Clicks

A total of 2 575 clicks were classified as potential dolphin or porpoise clicks. Of these, 2 099 were assigned to Kylie and 476 to the porpoises. One of the porpoises was recorded emitting 6 burst pulses which seemed to have been produced while moving in a different direction than Kylie. The patterns in the production rates of these burst pulses suggest these were social calls (Figure A3). Additionally, potential 419 clicks were identified when Kylie was seen alone in November 2017 (n = 72) and July 2018 (n = 347). She was recorded producing only two types of sounds: clicks and 2 burst pulsed calls. No other sounds that are typically produced by common dolphins while socialising, such as whistles, were recorded during this study.

High-frequency clicks

Only the loudest 10% of clicks assigned to each animal were selected for further analysis, under the assumption that these were more likely to be on-axis, and therefore correctly assigned to each animal. The centroid frequency of porpoise clicks ranged from 119.4 kHz to 175.7 kHz, with RMS bandwidth between 2.1 kHz to 13.7 kHz. The energy ratio ranged between 33.89 and 203 871.3 times, with a mean of 22 936.6. Kylie's clicks were of variable nature, with centroid frequencies ranging from 31.25 kHz to 159.18 kHz and were either narrow or broadband, with the RMS bandwidth between 5.7 kHz and 48.6 kHz. A total of 125 out of the loudest 210 Kylie's clicks had centroid frequency over
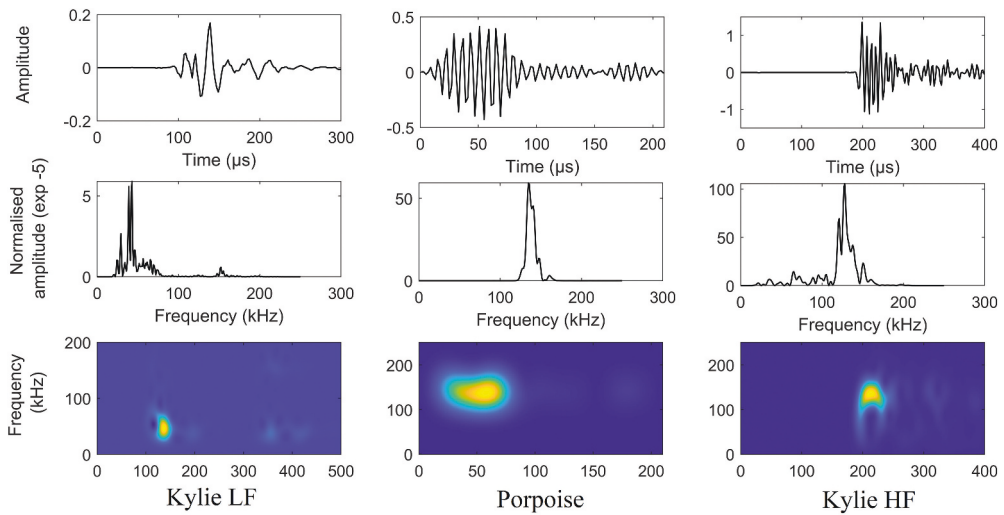
Figure 5. Comparison. Left: Typical low-frequency click produced by Kylie. Middle: typical click produced by harbour porpoises. Right: High-frequency click produced by Kylie (recorded when seen alone). Top panels: waveform (amplitude is normalised using the clipping level of the hydrophone as the maximum value). Central panels: normalised power spectral density. Bottom panels: Smoothed Pseudo Wigner-Ville Distribution (FFT = 512, window size = 64, overlap 50%).

100 kHz, 56% of which (n = 70) were recorded when she was alone. The energy ratio ranged from 0.003 to 288.7. Only clicks with energy ratio greater than 25 (n = 30) were similar to porpoise clicks, with polycyclic waveforms and most energy concentrated between 100 and 150 kHz (Figure 5), while others were not (Figure A4). Although these clicks had amplitudes over 180 dB (re: 1μPa), not all clicks with such high amplitudes were similar to porpoise clicks, as they had a few peaks in the waveform and energy in a much wider frequency band, extending well below 100 kHz. Only 3 of the 30 clicks were the loudest of the click train they were part of. An example of the evolution of Kylie's clicks within a click train is shown in Figure 6 and Figure A5.

The null hypothesis of the unbalanced ANOVA (the energy ratio of Kylie's and porpoise clicks were the same) was rejected. The energy ratio of Kylie's clicks, both low and high frequency, was significantly different to porpoise clicks (Tables A2 and A3).

Discussion

Kylie has interacted with harbour porpoises in the Fairlie-Hunterston channel in the Firth of Clyde during a period spanning at least 14 years. The data presented here suggests these events take place more often than previously thought, and confirm the affiliative nature of the interactions (Ryan et al. 2017). During this period, she has not been seen with other common dolphins, and it is likely she had little or no contact with conspecifics while being resident in the Firth of Clyde. In the meantime, she has been regularly exposed to harbour porpoise vocalisations during these interactions, but also because the inner Firth of Clyde is a high-density area for harbour porpoises year round (Goodwin and Speedie 2008; Brown 2018). Some of Kylie's clicks resemble narrow-band
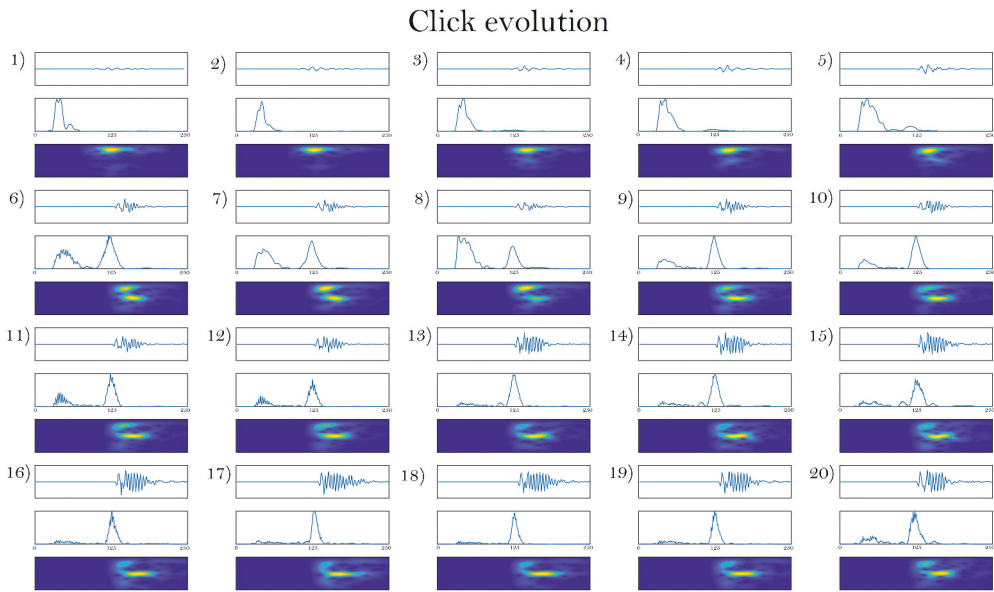
Click evolution

Figure 6. Click evolution. Click train emitted by Kylie where the evolution from low-frequency, oligocyclic click to narrow-band, high-frequency, polycyclic click. The click train was recorded when Kylie was seen with a porpoise.

high-frequency (NBHF) clicks like those emitted by porpoises. On-axis, high-amplitude dolphin clicks have centroid frequencies over 100 kHz, even those recorded from the back of the skull (Au et al. 2012). So far, however, there are no reports of whistling dolphins emitting NBHF clicks. The data presented here show Kylie can emit clicks that resemble harbour porpoise clicks, which are similar not just in the frequency band where most energy is concentrated, but also in the polycyclic waveform, unlike high-frequency clicks reported elsewhere (Au et al. 2012). The generation of these clicks seem to be a gradual process, shifting the energy content and changing the number of peaks in the waveform. Although at least some of these changes could be the result of changes in the orientation of Kylie with respect to the hydrophones, however, such phenomenon would not result in the observed waveform.

Tyack (2008) argues that limiting the evidence of imitation to exposure to arbitrary sounds in controlled experiments, ignoring vocal convergence, restricts our understanding of production learning. He further argues that the increasing evidence of vocal convergence in adults of several species of birds and mammals, can help fill gaps in our understanding of the evolution and prevalence of vocal production learning (see Tyack 2008 for a review). Given the lack of dedicated studies, it is unknown whether common dolphins can emit NBHF clicks as part of their normal repertoire, or if the observations in this study represent evidence of production learning, in the form of vocal convergence as a result of exposure to harbour porpoise vocalisations for over a decade.

Production learning in wild cetaceans has rarely been reported (e.g. Foote et al. 2006) but are more commonly reported from animals kept in captive settings, as it is easier to observe unusual behaviours as well as to set up experiments. For example, a captive beluga whale (*Delphinapterus leucas*) showed spontaneous imitation abilities producing

vocalisations similar to those of bottlenose dolphins just 2 months after it was first introduced in the dolphin enclosure. The beluga produced whistles with similar frequency modulation patterns but it also stopped producing biphonic pulsed-tonal contact calls typical of the species (Panova and Agafonov 2017). These results are similar to those found in this study, as Kylie produced clicks (and burst pulses) exclusively, not producing whistles or other tonal sounds, which she is known to produce (Nairn, unpublished data).

Common dolphins seem to be vocally flexible (Roch et al. 2011), being able to shift the energy content of their clicks in a wide band, reaching frequencies well over 100 kHz (as reported by Gurevich (1969) cited by (Evans 1973). Moreover, the change of the waveform and energy content in Kylie's clicks showed an increase in centroid frequency with increasing amplitude, as it has been reported for other odontocetes (Wahlberg et al. 2011). Yet, clicks with energy over 100 kHz are not necessarily narrow-band high-frequency (NBHF) clicks, as those reported for porpoises, *Kogia*, and several dolphin species (Li et al. 2005; Madsen et al. 2005; Martin et al. 2019). Au et al. (2012) recorded bottlenose dolphin clicks using a hydrophone array configuration designed to investigate the waveform and energy content of clicks detected at different angles, including the rear. Clicks recorded from the back of the head had the energy concentrated between 100 and 150 kHz, resembling some of the clicks detected in this study, although the waveform remained oligocyclic (Au et al. 2012). Although this phenomenon has not been studied in common dolphins, some of Kylie's clicks may have been recorded from the back of her head. More research is needed to understand the temporal and spectral characteristics and how far away they can be detected.

The sound production mechanism is not understood, but recent studies have shown that NBHF species can also emit low-frequency whistles and broadband clicks (Reyes Reyes et al. 2016; Martin et al. 2018), while the opposite was not been reported before this study.

Although one of the porpoises emitted a series of social calls while close to Kylie, whether her acoustic behaviour represents a communication attempt is unknown

Conclusions

Kylie's affiliative interactions with harbour porpoises have taken place for at least 14 years, time during which she has been exposed to their vocalisations. Some of Kylie's clicks recorded in this study had temporal and spectral characteristics that resemble harbour porpoise clicks. The polycyclic waveform and observed shift in energy content cannot be explained by physical phenomenon alone, such as off-axis orientation, and may represent evidence of production learning.

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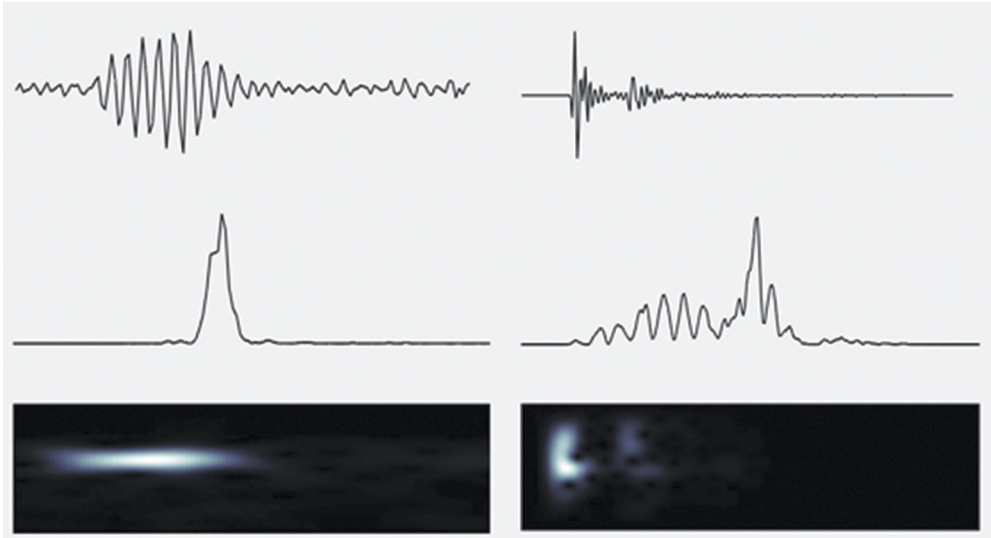
Appendix

Figure A1. Examples of training (left – harbour porpoise click) and testing (right – Kylie's high-frequency click) of the data volunteers used to validate (or not) the visual method used to assign each click to a harbour porpoise or Kylie. Top: waveform. Centre: power spectrum (frequencies ranging from 0 to 250 kHz). Bottom: Smoothed Pseudo Wigner-Ville Distribution (FFT = 512, window size = 64, overlap 50%).
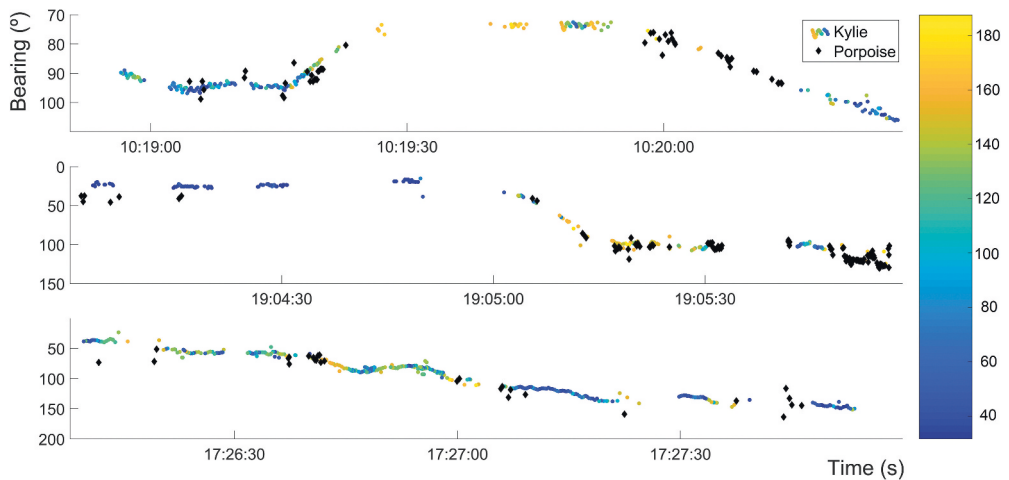

Figure A2. Consecutive clicks. Clicks produced by a solitary common dolphin and a harbour porpoise while travelling together (evidenced by the consistency of the direction where these clicks come from (i.e. y axis)) plotted in chronological order (n = 1 717). The position of the vessel is at 0°. Porpoise clicks are represented as a black rhombus and dolphin clicks are colour coded (online version) by centroid frequency (in kHz). Recordings were made on 2nd and 3 November 2016 (day 1 and 2), and 4 September 2017 (day 3) in the Firth of Clyde, Scotland.
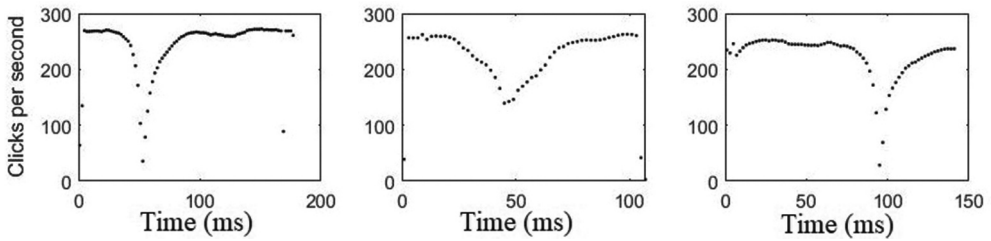
Figure A3. Burst pulses produced by a harbour porpoise on 2nd of November 2016 while travelling with Kylie.
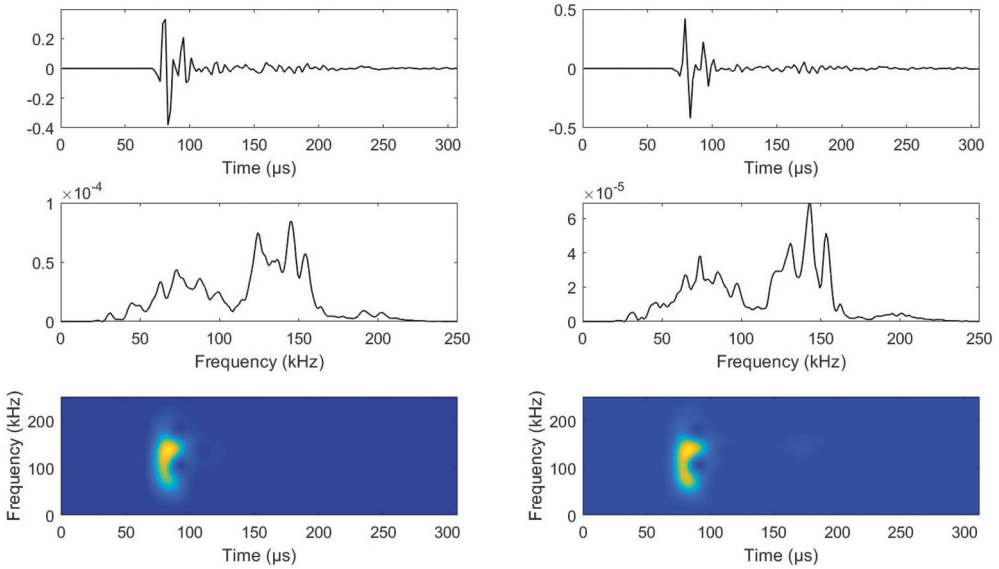

Figure A4. High-frequency and broadband clicks. Clicks produced by Kylie while together with a harbour porpoise. Unlike harbour porpoise clicks, the waveform (top) is oligocyclic and the power spectrum of signal (centre) shows there is significant energy below 100 kHz. Smoothed Pseudo Wigner-Ville Distribution (bottom) (FFT = 512, window size = 64, overlap 50%).
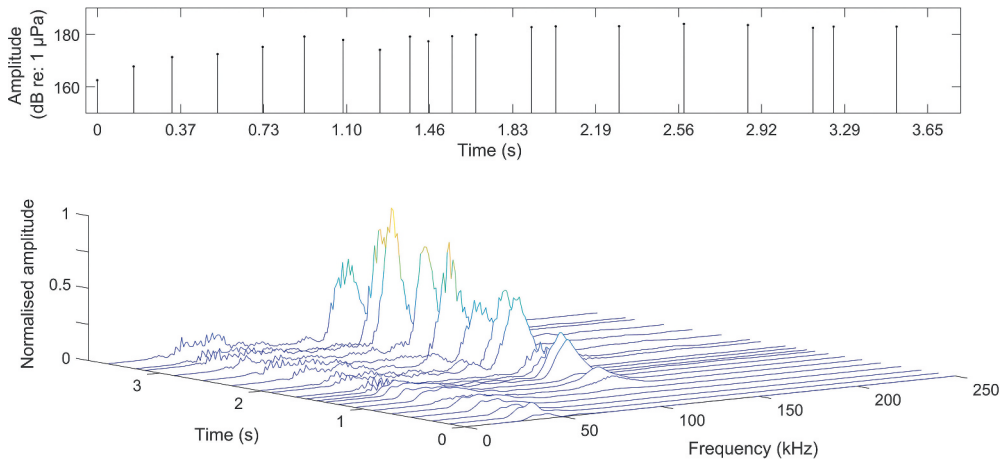

Figure A5. Waterfall of click train. Amplitude variation and waterfall plot of the evolution of a click within a click train, from low-frequency to high-frequency (see also Figure 6 in main text).

Table A1. Settings of PAMGuard's Click Detector Module.

Detector parameters	Value
Detector	
Short filter	0.1
Long filter 1	0.00001
Long filter 2	0.000001
Pre-filter (Butterworth) – number of poles	4
Pre-filter – high-pass frequency (kHz)	20
Trigger filter – Minimum frequency (kHz)	100
Trigger filter – Maximum frequency (kHz)	150
Detector threshold (dB)	6
Clicks	
Pre-samples	40
Post-samples	40
Maximum length (samples)	1024
Minimum length (samples)	90
Minimum separation between clicks (samples)	100

Table A2. Unbalanced ANOVA. Comparison of the energy ratio between two frequency bands: over and below 100 kHz Group 1: Kylie's low-frequency clicks. Group 2: Kylie's high-frequency clicks. Group 3: Porpoise clicks. * = Significant.

Source	SS	df	MS	F	Prob >F
Groups	2.1 e + 10	2	1.02 e + 10	26.89	2.55 e-11*
Error	9.7 e + 10	254	3.8 e + 08		
Total	1.2 e + 11	256			

Table A3. Unbalanced ANOVA. Comparison of the energy ratio between two frequency bands: over and below 100 kHz Group 1: Kylie's low-frequency clicks. Group 2: Kylie's high-frequency clicks. Group 3: Porpoise clicks. S = Significant. NS = No significant.

Comparison	p-value	Decision
1–2	0.99	NS
1–3	1.18e-09	S
2–3	9.71e-10	S