

Click train patterns of free-ranging harbour porpoises acquired using T-PODs may be useful as indicators of their behaviour

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ABSTRACT

Harbour porpoise signals consist of directional, high frequency stereotypic clicks which can be logged using T-PODs. Variation in interclick intervals (ICIs) can be used to distinguish different acoustic behaviours. So far, studies on ICI variation are mostly descriptive and the behavioural context in which certain click train patterns are emitted is poorly understood.

In this study, the behaviour of free-ranging porpoises was quantified by using typical ICI patterns known from the literature. These were recorded using two T-PODs deployed at a wind farm site (Nysted, Denmark) between 14 June and 12 July 2005 and during the entanglement of a porpoise calf in a gillnet (Clayoquot Sound Canada). It was possible to distinguish between feeding, approach behaviour and communication and known ICI patterns associated with these behaviours were used to categorise acoustic data.

During feeding typical click trains start with long ICIs (30–70ms) and end with ICIs down to about 2ms. In a transition phase ICIs rapidly decrease. Click trains attributed to feeding were found in the wind farm data at a rate of $6.3d^{-1}$ ($n=174$) with a patchy distribution. We found 20 to 74s long click train sequences with ICIs gradually decreasing from a median of 72ms (range 34 to 143ms) down to 5ms at a rate of $1.6day^{-1}$ ($n=45$). This was interpreted as approach behaviour, in which the animal was acoustically 'locked on' to a reflective structure. Communication signals are built up of click trains with very short ICIs (<7.7ms). During the entanglement of a porpoise calf, three different call types were determined at a rate of $8.9min^{-1}$ ($n=89$). One call with variable duration (100 to 890ms) and relatively stable ICIs as low as 3.6ms resembled 'distress calls' described by Amundin (1991b). Another call type with durations from 780 to 830ms and ICIs ranging from 3.0 to 10 ms and thus different with respect to ICI curve progression was found only three times. These had a U-shaped ICI curve, similar to an 'alarm' or 'fright' call described by Busnel and Dziedzic (1966). A third and previously unreported call is characterised by a long call duration (up to 1,270ms) and sometimes oscillating ICIs with an initial decrease from about 9ms to around 7ms and an increase towards the end.

The data presented suggest that the T-POD is a promising tool for behavioural studies. It is possible to recognise certain acoustic behavioural categories described in the literature, but it is important to look at the temporal context with other vocalisations in T-POD data, such as ICIs of preceding click trains.

KEYWORDS: COMMUNICATION; ECHOLOCAION; FEEDING, FOOD/PREY; BIOSONAR; HARBOUR PORPOISE; ACOUSTICS; NORTHERN HEMISPHERE

DEFINITIONS

To describe the nature of click series, some authors use the term 'pulse repetition frequency' (PRF, given in Hz or clicks per second) while others relate to 'interclick intervals' (ICIs) or 'click intervals' (in ms), meaning the time elapsed between the peaks of the envelopes of two consecutive clicks (Madsen *et al.*, 2005). Interclick intervals are the reciprocal of pulse repetition frequency. The term ICI is used throughout this paper. When necessary, pulse repetition frequency is converted into ICI.

Some authors use the term 'click train' only for click series with certain ICIs (e.g. Verboom and Kastelein, 1995), while most others use it for any series of clicks regardless of their ICI (*cf.* Au, 1993). In this study, the term click train is used for any series of clicks separated by gradually or cyclically changing ICIs suggesting a unit during an echolocation event or a communication signal. Click trains may be separated from others by distinctly longer intervals. If these are emitted in a certain behavioural context such as approach behaviour a number of click trains form a 'click train sequence'.

INTRODUCTION

Harbour porpoises emit stereotypic acoustic click signals to navigate and communicate under water (Amundin, 1991b; Au, 1993). The acoustic patterns vary with behaviour

(Amundin, 1991b), but determining the behaviour associated with specific acoustic patterns is difficult as visual observations are logistically challenging and can rarely be conducted simultaneously with the recording of acoustic data. High-frequency click train data can be acquired via T-PODs, and this static acoustic monitoring instrument is commonly used to record the presence or absence of harbour porpoises (Carstensen *et al.*, 2006; Tougaard *et al.*, 2006). This paper proposes that the data recorded with T-PODs may also be used to examine specific click trains or click train sequences to illuminate porpoise behaviour. It is hypothesised that typical sequence patterns can be found regularly within T-POD data and can be used as indicators for certain types of behaviour. This study reviews existing information and uses data recorded by T-PODs to identify typical patterns in click train data.

Harbour porpoises emit narrowband pulses with distinct peaks at frequencies between 110 and 160kHz, mainly around 130kHz, and a typical duration of 75 to 150 μ s (e.g. Amundin, 1991b; Kamminga and Wiersma, 1981; Verboom and Kastelein, 1997; Villadsgaard *et al.*, 2007). For a 3yr old individual, the average 3dB bandwidth of the peak was 16.4kHz (Au *et al.*, 1999). For juveniles, the peak frequency is higher and the bandwidth narrower than for adults (Au *et al.*, 1999; Goodson and Datta, 1995; Goodson *et al.*, 1995; Goodson and Sturtivant, 1995). The -3 dB beam width (a measure for the directionality of the echolocation beam) in the horizontal and the vertical plane was 16.5° (Au *et al.*,

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1999). Peak to peak source levels (SL) ranged from 133–172 dB re $1\mu\text{Pa}$ @ 1m for captive harbour porpoises (Au *et al.*, 1999; Goodson *et al.*, 1995) and 175–205 dB re $1\mu\text{Pa}$ @ 1m for free-ranging harbour porpoises (Villadsgaard *et al.*, 2007). The latter translates into a maximum energy level for an echolocating harbour porpoise of 150 dB re $1\mu\text{Pa}^2 \text{ s}$ @ 1m (Villadsgaard *et al.*, 2007).

The ultrasonic echolocation signal was first described independently by Dubrovskii *et al.* (1971) and Møhl and Andersen (1973). In some early studies (e.g. Amundin, 1991b; Busnel and Dziedzic, 1967; Schevill *et al.*, 1969), a narrowband low-frequency component of harbour porpoise vocalisations was used for the analysis of click train patterns. Since the latter seems to be part of the same sound production event (Amundin, 1991a) and may be a byproduct of tissue generated ultrasonic clicks data from these studies were applied to our findings.

High-frequency narrow-band click trains of harbour porpoises can be logged with T-PODs which are self-contained, anchored click detectors that record the time and duration of each ultrasound click to $10\mu\text{s}$ resolution. Harbour porpoise clicks are identified by the comparison of the outputs of two bandpass filters with different centre frequencies. When the set ratio between the target filter and the reference filter output is exceeded, the T-POD logs the start and end times of a sound. This ratio makes it possible to exclude noise clicks as well as clicks from other odontocetes. Custom made software analyses the T-POD data to identify characteristic harbour porpoise click trains using an algorithm which defines the regularity of ICIs within the train.

Signal-to-noise ratio (SNR), transducer sensitivity, sound radiation and directional properties of the sonar beam limit the detection range of a T-POD. A directivity related effect of click intensity is often obvious in T-POD data, even though received intensity of the clicks is only recorded indirectly through click duration (Fig. 1). In biosonar recordings of free-ranging porpoises, Goodson and Sturtivant (1995) described a similar sharp fading and strong reappearing of the signal intensity in an almost regular pattern, producing the effect of a series of very short click trains as fragments of longer trains. They suggested that porpoises were scanning a small sector ahead of their path by body or head movements. Such scanning movements during echolocation are known from captive animals (Akamatsu *et al.*, 1992).

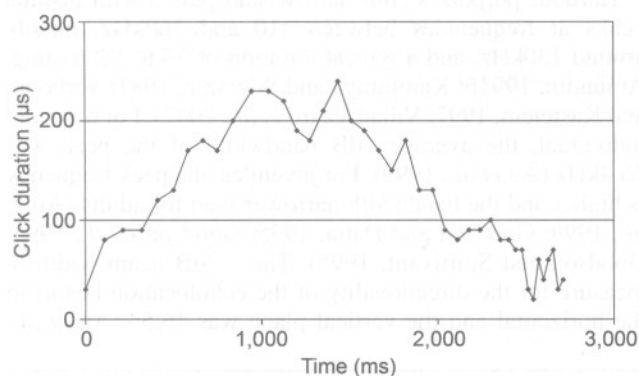


Fig. 1. Artefact related to the directivity of the echolocation beam of harbour porpoises as recorded by a T-POD. The changes in signal intensity at the receiver are expressed indirectly by a corresponding variation in click duration.

Given the SL mentioned above, under ideal conditions harbour porpoise vocalisations can be recorded by a T-POD over 300 to 400m away (Tougaard *et al.*, 2006; Villadsgaard *et al.*, 2007). Matching theodolite and T-POD data resulted in an effective detection distance of T-PODs between 86 and 107m (Culik and Koschinski, 2004; Tougaard *et al.*, 2006); (T-POD v. 1 and 3) with detection probability decreasing rapidly at greater distance. T-PODs are often employed in habitat use studies where factors describing porpoise activity are limited to porpoise presence or absence (Tougaard *et al.*, 2006).

Since harbour porpoise clicks are remarkably stereotypic (Au *et al.*, 1999; Villadsgaard *et al.*, 2007), a key factor in different acoustic behaviour seems to be the high variation in ICI. Studies on harbour porpoise vocalisations with respect to ICI variation are mostly descriptive (e.g. Verboom and Kastelein, 1995; 1997). The behavioural context in which certain click train patterns are emitted has so far only been addressed in captive studies (e.g. Amundin, 1991b; Busnel and Dziedzic, 1967; Nakamura *et al.*, 1998; Verfuss *et al.*, 2005). Knowledge on how harbour porpoises utilise their biosonar in the wild is thus limited.

Generally, harbour porpoises send out the next click within an echolocation click train after reception of the echo of the previous click, thus ensuring that the echo is not disturbed by subsequent clicks. ICIs are thus greater than the two-way transit time (TWT) of the sound between animal and target. The difference between TWT and ICI, called 'lag time', varied between 14 and 36ms in different studies (Au *et al.*, 1999; Verfuss *et al.*, 2005). As a consequence, animals would delimit the distance they inspect acoustically at a certain range behind expected targets when locked on a target. The use of different ICIs of animals observing floating objects in a pool and navigating around ropes may simply express such differences in focal distance above which porpoises adjust their ICIs (Kastelein *et al.*, 1995).

If the animal is locked on a clearly identified target, the ICI is generally rather stable in the decrease during an approach (Akamatsu *et al.*, 2007; Akamatsu *et al.*, 2005; Verfuss *et al.*, 2005). Sometimes porpoises increased ICIs suddenly after gradually decreasing intervals, indicating a switch from a close target to another target further away. The use of prominent features on the seabed or in the water column as navigation aid by free-ranging porpoises and the approach to prey are possible explanations. An acceleration indicated by a steeper slope of decreasing ICIs sometimes followed by a sudden decrease in swim speed at the end may indicate approach to prey (Akamatsu *et al.*, 2005 for *Neophocaena phocaenoides*). If not locked on the target, the ICI most often varies, possibly indicating that the animal is exploring the existence of anticipated targets at different distances. Then a lag time cannot be specified.

Short ICIs around 2ms with no or a very short lag time (cf. Au, 1993) are commonly found for harbour porpoises when observing an object at close range (Verboom and Kastelein, 1995), closely inspecting a hydrophone (Amundin, pers. obs.), when inspecting the sea floor at close range during a foraging activity called 'bottom grubbing' (Lockyer *et al.*, 2001) or during hand-feeding of dead fish in an enclosure (Busnel and Dziedzic, 1967; Schevill *et al.*, 1969). A typical echolocation pattern found by Busnel and Dziedzic (1967) and Schevill *et al.* (1969) which can be used to describe foraging behaviour is presented in Fig. 2. It is characterised by click trains beginning with relatively long ICIs and ending with very short ones (still being longer than the TWT to the fish).

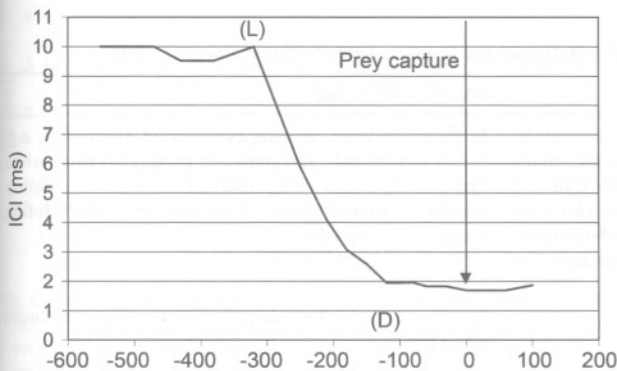


Fig. 2. Harbour porpoise interclick intervals immediately before and during prey capture when hand-fed in a pool (redrawn from Busnel and Dziedzic, 1967). (L) indicates the 'localisation point', about 20 to 40cm from prey, (D) indicates the 'decision point', about 5cm from the prey.

In the initial phase, harbour porpoises used ICIs between 5.2 and 15.6ms (mean 8.6ms, $n=27$). At a 'localisation point' (L), 11-37cm (mean 28.4cm) from the prey, ICIs decreased rapidly. The end of this transition phase was marked by the 'decision point' (D) (0-11cm mean 5.8cm from the fish, $n=26$). In the terminal phase animals used relatively stable ICIs with mean values of 2.1ms during which the prey was captured. Such 'buzzes' are also known from free-ranging porpoises during foraging (Chappell and Gordon, 1993). Very short ICIs may be necessary in the terminal phase to avoid losing moving prey as the time it takes a prey to leave the acoustic beam is proportional to the distance from the porpoise.

Like echolocation, harbour porpoise communication signals are exclusively built up of click trains (Amundin, 1991b). The message conveyed may be dependent on the social and ecological context in which they are emitted. During social communication harbour porpoises seem to use click trains with very short intervals consistently below 7.7ms (Amundin, 1991b; Busnel and Dziedzic, 1966; Nakamura *et al.*, 1998). Amundin (1991b) recorded a variety of social signals, mostly 'threat' and 'distress' calls. His sonagrams and click repetition rate graphs were based either on the low or the high-frequency component of porpoise clicks. The much stronger high-frequency component seems to carry the information because the range within which a porpoise is able to detect the signal will always be larger than that of the low-frequency component (Hansen *et al.*, 2008). In some cases, porpoises turned their rostrum towards the addressee (Amundin, 1991b; Nakamura *et al.*, 1998), indicating that the high frequency directional sound is purposefully used. In these cases high-intensity signals with very short ICIs may cause a painful hearing sensation providing 'discomfort' in the addressee ('acoustic box on the ear'; (Amundin, 1991b)) especially in the light of recent findings of source levels up to 205dB re 1 μ Pa@1m (Villadsgaard *et al.*, 2007).

The communication calls described by Amundin (1991b) are presented in some detail in Table 1 and Figs. 3-6. Data were acquired via high-frequency¹ (251 calls) and low-frequency (15 calls) recording equipment². The ICIs of the low-frequency calls were derived from the harmonic

¹ B&K 8103 hydrophone fastened to the study animals' melon via suction cup, or hand held to the surface of the melon, custom made preamplifier, B&K 2607 measuring amplifier, Krohn Hite 3322 filter, Lyrec TR-47 instrumentation recorder at 60 ips

² LC32 hydrophone suspended in the centre of a 41m², 1m-deep pool, custom made preamplifier, B&K 2607 measuring amplifier, Krohn Hite 3322 filter, Nagra IV-D tape recorder at 15 ips.

interval in the sonagrams (cf. Watkins, 1967). Table 1 further shows the characteristics of communication calls recorded by Busnel and Dziedzic (1966) and Nakamura *et al.* (1998).

This study presents examples of certain vocalisation patterns expressed in two T-POD data sets from Nysted, Denmark and Clayoquot Sound, Canada, and compares these with patterns described above in order to explore whether behaviour of wild porpoises can be inferred from acoustic patterns recorded via T-POD.

METHODS

Data files were acquired by T-PODs (Chelonia Ltd, UK) versions 1 and 4. T-POD1 (version 4, nr. 458) was chosen at random from 20 T-PODs which logged harbour porpoise clicks within the Danish Baltic Sea wind farm 'Nysted' (54°34.2'N, 11°40.02'E) between 14 June and 12 July 2005. The distance to the nearest wind power generator was 148m. T-POD1 was positioned 1.5m above the bottom at a water depth of 6m. Since this data set represents a long time period it was assumed that a number of different behaviours may have occurred in the vicinity and typical signals been picked up by the T-POD. Due to the large size of the data set from T-POD1 only obvious click train patterns, such as feeding and approach behaviour were searched for. Click trains were classified as feeding behaviour if they showed a rapid decline of intervals to less than 10ms, preceded by an initial phase with much longer intervals (e.g. Busnel and Dziedzic, 1967). Click trains were classified as approach behaviour if they showed a gradual decrease in ICIs over a period of many seconds (Verfuss *et al.*, 2005).

T-POD2 (version 1, nr. 68) recorded data associated with a single incident of a porpoise calf becoming entangled in a gillnet panel positioned in up to 30m deep water in Clayoquot Sound/Canada (49°11'N, 125°46.5'W) (Koschinski *et al.*, 2006). Data from T-POD2 were searched for communication sounds because they could be matched with visual observations of behaviour during this incident. A period of 10min was searched from the collision and entanglement of the calf in the net panel. The calf's mother collided with the net just before the calf, but did not become entangled. She swam around the net until the calf was released. Entanglement took place about 20m from the T-POD and 1m below the surface. The T-POD was suspended at the net panel 4.5m below the surface. Click trains were classified as communications if they showed relatively regular intervals below 10ms, and did not show a marked decline in the beginning.

Data were processed and displayed using the custom made *TPOD.exe* software v. 7.41. This program uses an algorithm determined empirically to identify click trains based on the regularity of the train. The algorithm takes variation between consecutive ICIs into account and can identify click trains in which ICIs increase or decrease by 38%. Based on the ICI variation *TPOD.exe* assigns each identified click train one of four levels of confidence, ranging from high probability trains ('CET HI') to very doubtful trains ('..??..'). The software can also display the raw data using the display setting 'cluster', also containing clicks which are not classified in trains, e. g. clicks very close together such as echoes or multi-path duplicates. During train classification usually only the first of these duplicates is processed. However, sometimes multi-path duplicates have to be removed manually even from classified click trains. In a quiet environment, it is often useful to have a look at doubtful and very doubtful click

Table 1
Communicative call types noted by different authors (A: Amundin 1991b, B: Busnel and Dziedzic 1966, N: Nakamura *et al.* 1998).

Call type	Duration	ICIs	Observed behaviour
'Distress calls' (A)	Varying duration (100ms to >1s long)	Rather evenly spaced clicks with intervals of between 2 and 3ms. Some click trains showed a slight increase of intervals followed by a prominent decrease before reaching the steady level (Figs. 3a and b). Sometimes grouped into click train sequences or 'phrases' of several calls	In situations when animals experienced discomfort, e.g. 1-2 yr old animals, just retrieved from pond nets, in the first few days after being installed in captivity, possibly thereby separated from their mothers, also during transport in a stretcher
'Fear from removal from familiar surroundings'/'alarm or fright calls' (B)	400ms to 1.55s	4 to 7.7ms	Signals emitted when animals were newly introduced into a pool
'Signal of pain' (A)	200ms followed by another 300ms long call	First call: decreasing click intervals of 1.7 to 1.2ms, second call: modulating intervals between 1.4 and 1.7ms (Fig. 4)	Only one signal recorded when an animal accidentally was inflicted pain
'Sideward turn threat call' (A)	200ms	Starting at 2.5ms decreasing steeply to 1.4 – 1ms (Fig. 5a)	Agonistic behaviour between subadult males during which the aggressive porpoise quickly turns its head and hence its sonar beam towards the head of the other
'Push threat call' (A)	Over 1 to 1.5s	1.3ms with a (sometimes sharp) decrease in the beginning and an increase at the end, sometimes grouped into click train sequences or 'phrases' of several calls (Fig. 5b)	Agonistic behaviour between subadult males during which an aggressive male chased after another at full speed
Trains during 'snouting behaviour' (N)	Cannot be extracted from paper written in Japanese	Mean=3.7ms, SD=1.7ms	'Snouting' - assumingly agonistic behaviour found in males and females
'Signal of dominance' (A)	Sequence of calls with a duration of 50 to 100ms	0.8ms (Fig. 6)	During food competition situations
'S-display sound' (A)	Total duration of sometimes >10s	A click train with very long intervals (>100ms) interrupted by bursts of somewhat shorter intervals (about 40ms)	Subadult males during sexual display

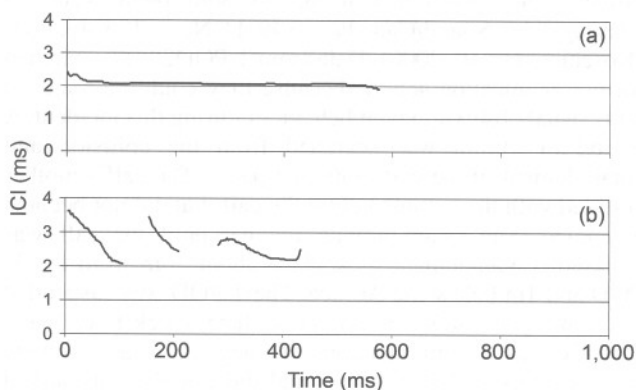


Fig. 3 Examples of long (a) and short (b) 'distress calls' as recorded by Amundin (1991b) using high-frequency equipment during situations in which animals experienced discomfort (e.g. when juveniles were separated from their mothers).

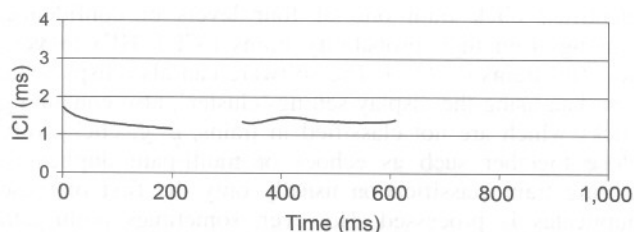


Fig. 4 'Signal of pain' as recorded as low-frequency pulsed call by Soren Andersen (in Amundin, 1991b) when an animal experienced pain.

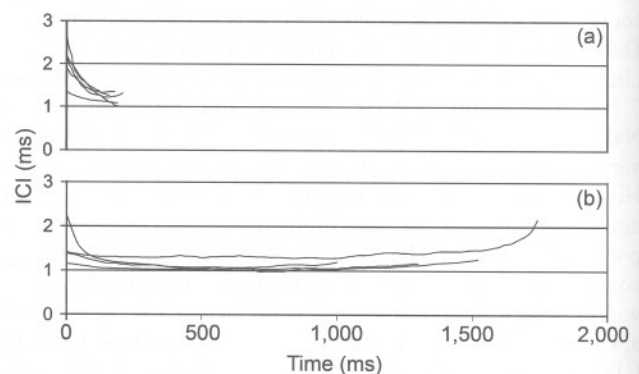


Fig. 5 Calls produced during agonistic behaviour recorded as low-frequency pulsed calls by Amundin (1991b). Several 'Sideward turn threat calls' plotted on top of each other (a). These calls were recorded when an aggressive porpoise turned its rostrum and thus the high frequency sound beam towards the head of another individual by quickly turning sideward with the anterior part of the body; the other animal reacted by avoidance. Several 'push threat calls' plotted on top of each other (b). These calls were heard when an aggressive animal chased after another at full speed, often making contact by nodding with its rostrum against the other's back.

trains. Thomsen *et al.* (2005) were able to show in an experiment with captive harbour porpoises that 41% of porpoise click trains were classified as doubtful trains. In order not to lose valuable information these should be carefully investigated. The category chosen depends on field conditions such as noise.

A manual search for click train patterns described in the literature in T-POD data was undertaken. By switching between the settings '...' and 'cluster', all four levels of

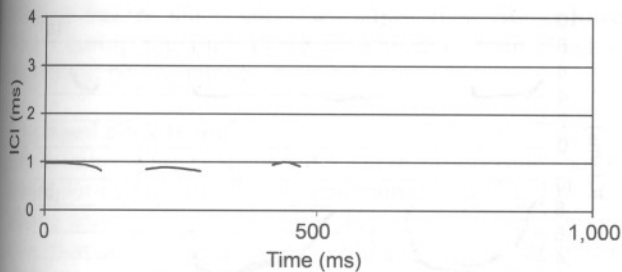


Fig. 6 'Signal of dominance', recorded as low-frequency pulsed call by Soren Andersen (in Amundin, 1991b). This type of signal was recorded in a food competition situation where an adult female intimidated younger males and thereby got access to hand-fed fish.

confidence and neighbouring clicks unclassified by the algorithm were searched in order to avoid clicks within click trains being lost due to processing by the algorithm.

To account for multi-path clicks in the ICI distribution clicks with ICIs below 1ms were omitted and ICIs recalculated. Multi-path propagation of sound waves may result in double clicks due to different delays arriving at the T-POD along different paths, e.g. by reflections from structures such as nearby deployment gear or water surface.

RESULTS

Inter-click interval distribution

ICIs within very doubtful click trains from T-POD1 showed a wide distribution, with 79% of ICIs between 2 and 50ms (Fig. 7). ICIs from T-POD2 were mostly below 10ms (92%, Fig. 7). Although clicks with intervals below 1ms were removed, the data used to produce Fig. 7 may still have contained some multi-path intervals between 1 and 2ms.

Feeding

A total of 174 click trains were found associated with feeding at a rate of 6.3day⁻¹ in the T-POD1 data. However, the distribution of feeding-like click trains was very patchy (Fig. 8). For example, 53 of the 174 observed trains occurred within 81min, and another 19 within 113min (0.5% of the recorded time). In all cases where initial, transition and terminal phases were present, these were classified as different trains by the *TPOD.exe* software, most often as

different levels of confidence. Some parts of the click trains were not detected by the algorithm of the software and hence only found by manually searching the raw data.

The mean interval from which the transition phase started was 26.7ms (SD=12.7, n=174). Fig. 9 shows an example with an initial phase with ICIs oscillating between 30 and 70ms and rapidly decreasing ICIs from about 40 to 2ms marking the transition to the terminal phase which is characterised by the buzz with ICIs of 2-3ms (cf. Busnel and Dziedzic, 1967). At the end, in some click trains an increase to longer ICIs could be found.

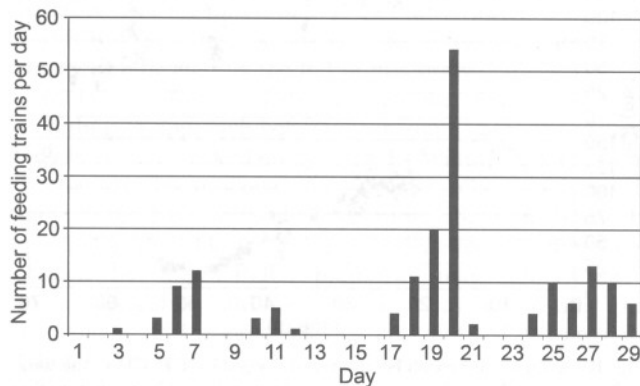


Fig. 8. Number of observed feeding-like click trains per day in T-POD1 data.

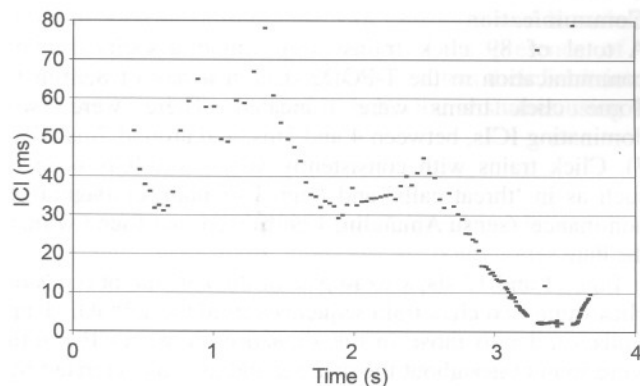


Fig. 9. Click train of presumably echolocating porpoise during prey capture as recorded by T-POD1 in the wind farm area of Nysted (display setting: 'cluster').

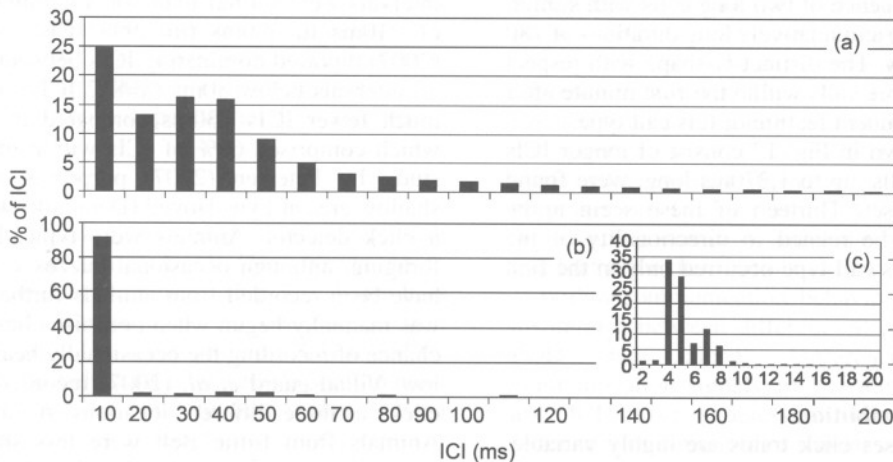


Fig. 7. Distribution of interclick intervals classified as '...?' (in 10ms classes, inset c in 1ms classes) within a 27.52d period in a Danish wind farm, (a: T-POD1 data; n=138,558 ICIs) and within a 10 minute period after entangling of porpoise calf in a gillnet (b and c: T-POD2 data, n=4,200 ICIs). Intervals counted from 2 to 200ms, multi-path clicks with intervals below 1ms were removed.

Approach behaviour

A total of 45 click train sequences were found associated with approaches to a target at a rate of 1.6 day⁻¹ in the T-POD1 data. In a randomly chosen subset of the data, click train sequences were 20–74s long (median=32s, $n=19$) and two examples of this are shown in Fig. 10. The difference between them is the ICI at the end of the sequence which decreases to 30ms in Fig. 10a, whereas the example shown in Fig. 10b ends with ICIs at around 5ms.

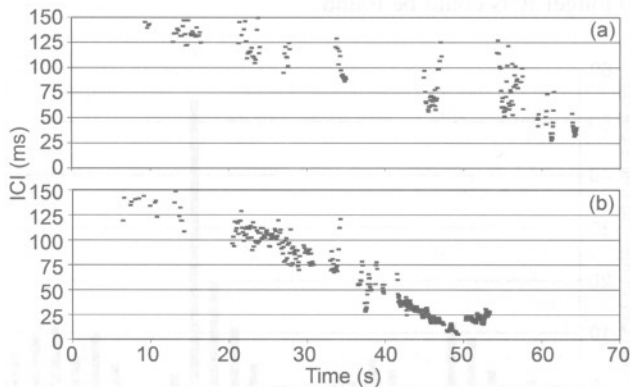


Fig. 10. Acoustic approach behaviour as logged by T-POD1 in the wind farm area of Nysted starting with highest ICIs of 120ms and ending with ICIs of down to 30ms (a) and 5ms (b) (click train category: '...??..').

Communication

A total of 89 click trains were found associated with communication in the T-POD2 data at a rate of 8.9min⁻¹. Some click trains were truncated. There were two dominating ICIs, between 4 and 5ms, and around 7ms (Fig. 7). Click trains with consistently very short ICIs (<2ms) such as in 'threat calls' and 'signal of pain' or 'signal of dominance' (sensu Amundin, 1991b) were not found within the data set.

Figs 11 and 12 show examples of three different types of click trains and click train sequences from the T-POD2 data. Calls similar to those in the sequence shown in Fig. 11a were found throughout the data set and are characterised by ICIs as low as 3.6ms and a flat ICI curve progression and thus are similar to 'distress calls' described by Amundin (1991b); (Fig. 3b). The call duration is variable in the data set (range <100 to 890ms). Twelve out of 66 of these calls appeared to be truncated.

Fig. 11b shows a sequence of two long calls with similar ICIs (ranging 3.0–10ms) and relatively long durations of 780 and 830ms, respectively. The distinct U-shape with respect to ICIs, seen only in three calls within the first minute after entanglement, is a prominent feature of this call type.

The click trains shown in Fig. 12 consist of longer ICIs (5.7–11.2ms). These calls, up to 1,270ms long, were found 17 times in the data set. Thirteen of these seem to be truncated, which may be related to directionality of the echolocation beam. This call type occurred only in the first 2.5min of the data set.

DISCUSSION

Interclick interval distribution

ICIs in harbour porpoise click trains are highly variable. The distribution of ICIs can indicate the occurrence of certain acoustic behaviours associated with communication or feeding which contain short ICIs. T-POD2 data contains 92% of ICIs <10ms because T-POD2 almost exclusively

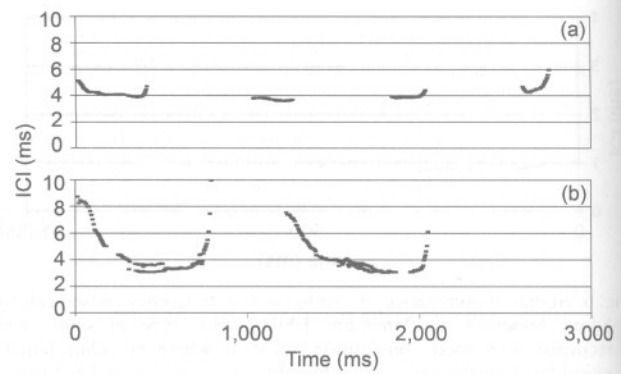


Fig. 11. Sequences recorded by a T-POD in Clayoquot Sound, Canada, as part of T-POD2 data; display setting: 'cluster'. (a) Sequence of four short calls with a duration of 195 to 395ms and minimum intervals of 3.6ms resembling 'distress calls' (cf. Amundin, 1991b) (Fig. 3); (b) sequence of two long calls with a duration of 780 and 830ms and minimum intervals of 3.0ms. In contrast to (a), these show a distinct u-shape. The double traces around 400ms and 1.6s on the time axis are probably caused by multi-path propagation from the sea bed, or the surface (N. Tregenza, pers. comm.).

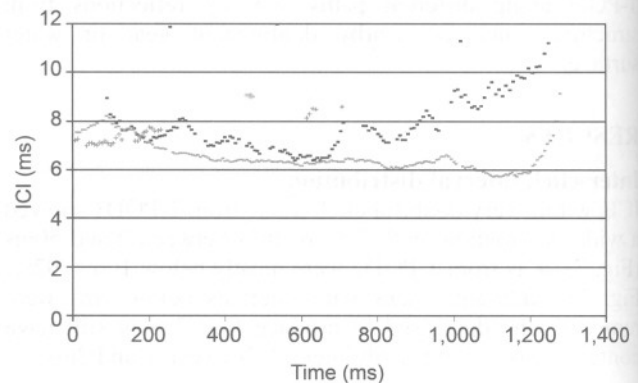


Fig. 12. Previously unreported possible communication sounds found within the first 2.5min of T-POD2 data. Calls plotted on top of each other. ICIs are longer than in the calls shown in Figs 11a and b. Calls plotted in black show a distinct oscillation whereas the call plotted in grey is characterised by a flat curve progression. '+' symbols mark a truncated call. All sequences were recorded by a T-POD in Clayoquot Sound, Canada, as part of T-POD2 data; display setting: 'cluster'.

recorded communication behaviour. In free-ranging, travelling harbour porpoises, Petersen (2007) found ICIs between 61 and 70ms to be most common, and only <2% of intervals were shorter than 30ms within the analysed range of <10ms to 300ms ($n=2,993$ ICIs). Villadsgaard *et al.* (2007) reported dominating ICIs between 41 and 50ms and no intervals below 30ms ($n=822$ ICIs). Both studies found much fewer ICIs <30ms compared to our T-POD1 data which comprised 60% of ICIs within these classes. In the study by Petersen (2007) porpoises passing through a shallow area at Fyns Hoved (Denmark) were recorded using a click detector. Animals were typically not engaged in foraging, although occasional buzzes were heard and may have been recorded from animals further away. Recording was manually begun when porpoise clicks were heard. The chance of recording the occasionally heard buzzes was thus low. Villadsgaard *et al.* (2007) recorded harbour porpoise clicks at three different locations in inner Danish waters. Animals from Little Belt were less shy and were more intense in foraging compared to the other areas Aarhus Bay and Bogense where presumably more animals were involved in travelling behaviour. However, the recording equipment in their study was not set to detect the weaker

feeding buzzes since porpoises adjust their SL to lower range during the final phase of a feeding train (Magnus Wahlberg, pers. comm.).

U-shaped click trains

Click trains with U-shaped ICI curve progression can be found during feeding (Fig. 9), communication (Fig. 11b) and during approach behaviour (Fig. 10) when choosing another time domain (the time axis would have to be stretched). Verboom and Kastelein (1995) describe a tendency in a captive animal to start with a certain ICI, decrease intervals and increase them again. There may be different explanations for U-shapes in separate behavioural categories. U-shaped click trains may reflect a pre-adjustment to an unknown or expected range in the initial phase during foraging or during travelling. In communication, it is more likely that this interval pattern belongs to the signal and may carry part of the information since the ICIs in such signals do not refer to a certain range and morphological reasons can be ruled out. As shown in Figs 4, 5 and 6 porpoises are able to produce very short ICIs at once without 'tuning' in.

Echolocation during feeding

ICI patterns attributed to feeding were found 174 times in the T-POD1 data (e.g. Fig. 9). The long ICIs during the initial phase, the short transition and the terminal phase with short ICIs are similar to those observed by Busnel and Dziedzic (1967); Fig. 2. However, ICIs during the initial phase were markedly longer in T-POD1 data (transition starting from a mean of 26.7ms) compared to mean intervals of 8.6ms reported by Busnel and Dziedzic for captive harbour porpoises. The high variability of ICIs in the initial phase may reflect a more variable search range in free-ranging animals compared to hand-feeding in a pool. The lower value in the captive animals is probably due to the limited search range of only 7m and the fact that dead fish is easier to catch than moving live prey. ICI oscillations shown in Fig. 9 indicate that animals explore a range of distances ahead of them before locking on a target in the beginning of the transition phase. In contrast to the data presented here, the possible foraging related data of a free-ranging harbour porpoise equipped with an acoustic tag only show gradually decreasing ICIs and lack typical terminal buzzes (Akamatsu *et al.*, 2007). This may be explained by the low sensitivity of the laterally attached hydrophone and buzzes adjusted to a lower SL for short detection ranges in the terminal phase of feeding trains. While the acoustic pattern recorded for harbour porpoises is similar to presumably foraging free-ranging spinner dolphins, *Stenella longirostris*, (Lammers *et al.*, 2004; Lammers *et al.*, 2003), it remains unknown how free-ranging harbour porpoises operate their biosonar during prey capture.

Approach behaviour

Sequences built up of click trains with gradually decreasing lowest ICIs starting at a median of 72ms (range 34 to 143ms) indicate approaches to a target (Fig. 10). These ICIs translate into an acoustically inspected distance of 54m (range 25.5 to 107.3m). The most common ICIs found by Petersen (2007) and Villadsgaard *et al.* (2007) point to most often inspected distances of 45.8 to 52.5m and 30.8 to 37.5m, respectively. Thus, these data fall within the range of inspection distances reported in other studies.

The performance of biosonar with respect to range is more dependent on the target strength (TS) than only the TWT. The TS of a T-POD in side aspect can be calculated as

$TS = -1.3dB^3$ (Urlick, 1983). The resulting prominent echo is much stronger than from a prey sized fish ($TS = -35$ to $-38dB$ in Klinowska *et al.*, 1992; Urlick, 1983). Since the auditory system typically processes acoustic information by detecting acoustic energy, the energy flux density in the echo is the appropriate parameter to determine (Kastelein *et al.*, 1999; Villadsgaard *et al.*, 2007). Assuming a maximum source energy level of an echolocating harbour porpoise of 150 dB re $1\mu Pa^2 s @ 1m$ (Villadsgaard *et al.*, 2007), the T-POD housing may be detected at a range of 310 to 350m under the most favourable conditions (assuming 20logR spreading loss, detection threshold 22.4 to 27.4 dB re $1\mu Pa^2 s$ (Kastelein *et al.*, 1999), absorption coefficient $0.035dBm^{-1}$). This is above the maximum inspected distances indicated by the ICI in this study.

It is therefore realistic to assume that during the recording of approach behaviour in some cases the animals may have been locked on the T-POD. Within the wind farm, the foundations produce even stronger echoes and may in some cases have attracted even more attention. It can be speculated that due to the (aspect dependent) strong echo created by the T-POD, porpoises may either use it as a navigation aid or regard it as interesting and investigate it. If porpoises are not directed towards the T-POD, the approach phase will be cut off at higher ICIs when the T-POD becomes off-axis (Fig. 10a). In Fig. 10b, with much shorter ICIs at the end, porpoises may have been locked on the T-POD and investigated the T-POD closely using decreasing ICIs as short as 5ms – similar to investigation of objects in a pool (Verboom and Kastelein, 1995). It is therefore possible that the presence of a T-POD distracts harbour porpoises or alters their behaviour. This needs to be considered in behavioural studies using T-PODs.

Communication

Click trains used during social communication show consistently very short intervals. In bottlenose dolphins, these communicative click trains appear to have a more prominent <20kHz frequency component than echolocation trains (Blomqvist, 2004). Such differences are not seen in harbour porpoises (Hansen *et al.*, 2008). For this species, communicative signals cannot be defined by the duration of intervals alone, as porpoises use similarly short ICIs during prey capture and close investigation of objects. We propose that communication sounds can be distinguished by the absence of immediately preceding ICIs distinctly longer than 10ms and a transition with rapidly decreasing intervals (such as in click trains used during foraging, Figs 2 and 9) and a gradual decrease in ICI over many seconds (typical for approach behaviour, Fig. 10). However, in some cases isolated fish catching buzzes may occur when porpoises are not orientated towards the T-POD during their search and then suddenly turn towards it, e.g. bottom grubbing porpoises (cf. Lockyer *et al.*, 2001) searching for benthic fish standing vertically above the bottom and chasing after fish that leave their bottom shelter to escape.

Within communication behaviour, it is also difficult to distinguish between different categories (Table 1) from T-POD data alone. Differences between certain communication signals are the duration of sequences, ICI and ICI curve progression. Further, the formation of sequences of a number of similar calls may be meaningful. However, there is substantial variability within communication signals. For example, Nakamura *et al.*

³ $TS_{cylinder} = 10\log(\text{radius} \times \text{length}^2 / 2 \times \text{wavelength})$.

(1998) described threat calls during agonistic 'snouting' behaviour with ICIs much longer than in threat calls described by Amundin (1991b); (*cf.* Table 1, Figs 5 and 6).

Vocalisation patterns with similar and consistently short ICIs are found throughout T-POD2 data. It is thought that these are not fragments of other sequences during other behaviours such as 'feeding' or 'observation of objects', because such behaviours did not occur in this short and clearly defined incident. As sequences were obtained during entanglement of a porpoise calf in a gillnet, 'signals of pain' and 'distress calls' were expected, however no click train sequences similar to the 'signal of pain' were found. As the 'signal of pain' has been recorded only once (Amundin, 1991b) before it is proposed that porpoises may have different vocalisations to express pain.

Patterns found in T-POD2 data do not unequivocally match with categories from earlier studies. While the click train duration is similar to that described by Amundin (1991b) for distress calls, the ICIs are generally longer and seem to be more variable. It was not possible to determine which of the calls were produced by the mother vs. the calf. It is possible that the two dominating ICIs reflect calls from the mother and the calf, respectively, and represent individual variability in ICI patterns.

It is hypothesised that the calls in T-POD2 data represent three different call types with specific meanings. The first call type (Fig. 11a) with short ICIs down to 3.6ms, a varying duration between 100 and 890ms and flat curve progression probably represents 'distress calls' similar to those recorded by Amundin (1991b). Amundin (1991b) found variable (duration 100 to 1,000ms) 'distress calls' in juveniles and sub-adults up to two years of age that had been separated from their mothers during entrapment in pond nets. Thus these calls have been interpreted as having been produced by the entangled calf when it was separated from its mother.

Another call (Fig. 11b) was different with respect to ICI and curve progression. This call with a distinctly U-shaped curve and with ICIs as low as 3.0ms and a duration of 780 to 830ms is very similar to the 'fear from removal from familiar surroundings (alarm) or fright' call (Table 1) with respect to duration, ICI and interval pattern (see fig. 48 in Busnel and Dziedzic, 1966). In their study, ICIs within an approximately 800ms long call decrease at the beginning and increase at the end of the call and therefore also show a characteristic U-shape. We speculate that this call may have been produced by the adult female since there are hints in Busnel and Dziedzic's study that the three females which produced this call were adults. Thus, this rarely seen call may represent an adult signal.

The third and previously undescribed call type seen in T-POD2 data is shown in Fig. 12. Typical features are the much longer ICIs (around 7ms) decreasing from 8-9ms in the beginning and increasing towards the end of the call (sometimes with oscillations) and a long duration of up to 1,270ms. It is hypothesised that this call was produced by the adult female indicated by the higher rate of truncated calls in T-POD data compared to the 'distress calls'. Truncation may have been caused by the directivity of echolocation of the moving female in connection with the static deployment of the T-POD.

T-PODs as a tool for comparative behavioural studies

This study shows that certain click sequences from T-POD data have a potential link to the behavioural categories described above. Hence, the T-POD is a promising tool for comparative behavioural studies using passive acoustic monitoring. The ICI alone is not enough to differentiate

between categories. Moreover, when trying to recognise certain acoustic behavioural categories in T-POD data sets, it is important to look at the temporal context with other vocalisations such as preceding intervals or click trains. For example, the end of an approach (Fig. 10b) sometimes looks very similar to the terminal phase during presumed feeding (Fig. 9), but both are preceded by typical sequences which allow their categorisation. The buzz in echolocation during feeding may also be similar to communication calls such as 'distress' or 'alarm or fright' calls. Again, echolocation during prey capture can be distinguished from social or communication signals by their two phases with distinct ICIs and transitions.

A problem with T-POD data is that frequently only fragments of click trains are logged due to the static deployment of the T-POD and the narrow echolocation beam of harbour porpoise biosonar. These fragments can be erroneously assigned to different categories even though they belong to the same click train. Further, click trains of different individuals may overlap, rendering classification of an individual's click train difficult. During feeding, the initial phase, the transition and the terminal phase are often classified as different click trains by the T-POD software because the relative change in ICIs differs between the phases. This makes it difficult to search for certain behaviours using automatic data processing. Given the large amount of data recorded by static acoustic monitoring devices, an automatic search routine for potentially meaningful sequences is desirable. In order to deduct useful information on porpoise behaviour from T-POD data it is crucial to understand the classification algorithm of automatic pattern detection software. Therefore developers of classification software should be encouraged to communicate the details of algorithms used and to implement settings that can be defined by users to enable a more flexible classification scheme. Further work should concentrate on developing algorithms that identify behavioural categories from raw data automatically.

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