D-PorCCA, a new tool to study the acoustic life of harbour porpoises

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In dedication to my younger self

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Last but not least, I would like to thank my family and friends for their love and support. Sonita, gracias por estar ahi. Por escucharme. Por apoyarme. Por todo.

Abstract

Despite decades of research, the social life of harbour porpoises in their natural environment is almost entirely unknown, although recent data suggest they are very social. Harbour porpoises produce only highly stereotyped clicks (narrow-band high-frequency -NBHF-) that are ideal for monitoring purposes. These are emitted in click trains: a series of clicks with regular or gradually changing inter-click intervals. The patterns in repetition rates are indicative of the behaviour of the clicking porpoise, which can be broadly divided into three main categories: orientation or travelling, feeding, and socialising. This means passive acoustic monitoring (PAM) methods can be used to study the behaviour of harbour porpoises. In this project, a series of algorithms to study the behaviour of NBHF species from acoustic recordings were developed and put together in a standalone application, D-PorCCA. The algorithms were developed and tested using data from Scotland and Denmark collected using static and mobile PAM devices. D-PorCCA and all algorithms were developed in MATLAB. The application includes a user-friendly interface, a simple transient-sound detector, a new porpoise click classifier (PorCC), and algorithms to identify behaviours. Additionally, the acoustic behaviour of harbour porpoises was studied while interacting with a solitary short-beaked common dolphin who inhabits the

Firth of Clyde (Scotland). The performance the algorithms in D-PorCCA was tested against manual labelling, varying from 69.2% to 98.5% of accuracy. These steps are automated and provide researchers with pre-selected data and summary data such as ’positive porpoise minute’ and day/night activities. D-PorCCA has many functionalities and the user can easily inspect and verify the data. The main results of this project are four. First, evidence was found of interspecies communication between a solitary short-beaked common dolphin and harbour porpoises in the Firth of Clyde (Scotland). Second, a series of patterns consistent with social calls reported in the literature as well as new ones were found for the first time using PAM in the wild. The most striking patterns were those known as ’phrases’, which are a series of similar calls produced in a short period of time. Third, the feeding and socialising patterns overlap, limiting our ability to distinguish between them. Lastly, the algorithms can be used in other species that produce NBHF clicks. These results suggest D-PorCCA can potentially be used for behavioural studies of wild harbour porpoises as well as other NBHF species, and to fill knowledge gaps in our understanding of the behaviour of these elusive species. Moreover, it has potential for application in large monitoring project, such as the Static Acoustic Monitoring of the Baltic Sea Harbour Porpoise, known as the SAMBAH Project.

Contents

Chapter 1

Introduction

1.1 Graphical abstract

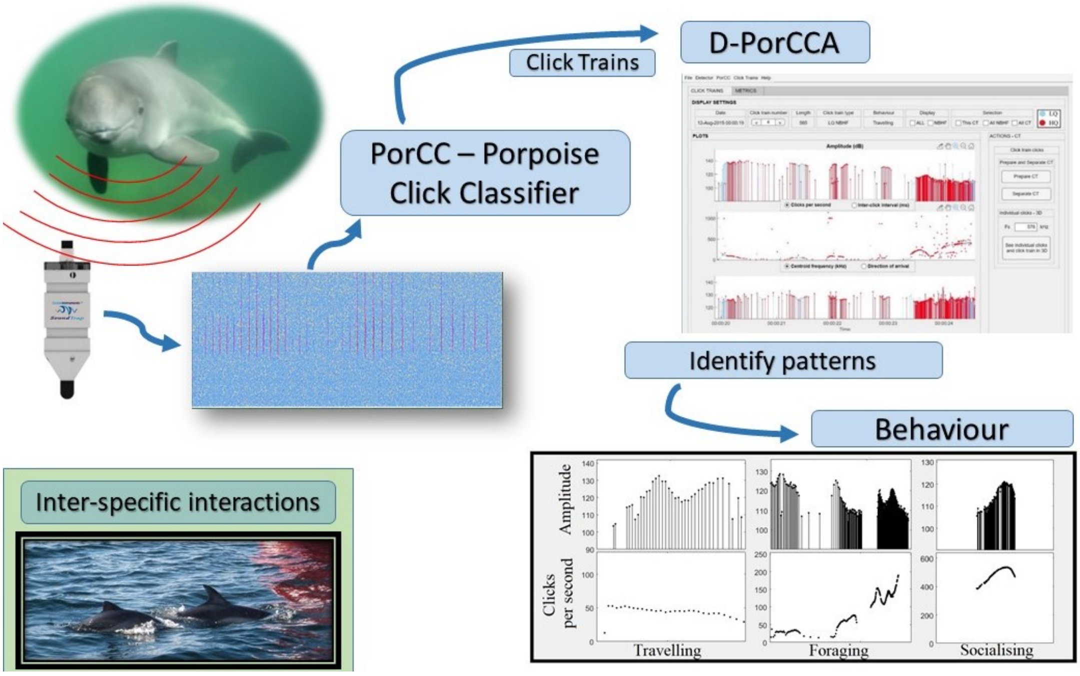


Figure 1.1: *Schematic of this project.*

1.2 Background

Harbour porpoises (*Phocoena phocoena*) are found in temperate and cold waters in the Northern Hemisphere, in both coastal and off-shore areas [1]. Despite decades of research in the wild and in captive settings, their social lives is still a mystery. They are small and are usually seen in groups of two or three individuals or alone, rarely gathered in large groups [2, 3]. This seemingly solitary life and the fact that they spend 95% of their time underwater [4] limit our ability to study harbour porpoises in the wild using typical visual methods.

Figure 1.2: **Harbour porpoises** (*Phocoena phocoena*) (©Solvin Zankl)

Luckily for researchers, harbour porpoises are very vocal and produce basically one type of sound: highly stereotyped narrow-band high-frequency (NBHF, *sensu* [5])) clicks, which are ideal for monitoring purposes. These NBHF clicks have peak and centroid frequency between 100 and 160 kHz, centred at 130 kHz, no spectral energy below 100 kHz, and duration between 50 and 175μs [6, 7]. These clicks are emitted in 'click trains', a series of clicks with regular inter-click interval or that changes gradually [8]. The repetition rate is indicative of the behaviour of the porpoise, which can be divided into three broad categories: orientation, foraging, and socialising. While the patterns for orientation (*i.e.*, repetition rates below 100 clicks per second) and foraging (*i.e.*, low repetition at first, ending in a high-repetition buzz) are known and understood [*e.g.*, 9], the vocalisation patterns during social interactions is almost entirely unknown.

A few studies conducted with animals in captivity and in the wild suggest harbour porpoises have specific calls (*i.e.*, click repetition rates patterns) for different social situations. Authors described several calls, including distress calls, mating calls, and contact call between a mother and her calf [10, 11, 12].

1.3 Motivation for this work

Recent data indicate that harbour porpoises are more social than visual surveys would suggest, spending almost all of their time within hearing distance of other porpoises [13]. Additionally, new technological advancements have made it possible to collect large amounts of acoustic data in a non-invasive and cost-effective manner. This opens the door for studies focused on the social lives of harbour porpoises, for which new analytical tools are necessary.

Harbour porpoises belong to a group of species commonly known as 'NBHF' cetaceans that includes at least 16 species of whales, dolphins, and porpoises that produce NBHF clicks. These species have in common their seemingly lack of social lives. Harbour porpoises are the best studied of these species and thus make an excellent model to understanding these less known species. In addition, parties of the 'Agreement on the Conservation of Small Cetaceans of the Baltic, North East Atlantic, Irish and North Seas' (ASCOBANS), including the UK, and are obliged to develop and adopt measures to protect harbour porpoises, as well as to acquire knowledge about their occurrence, abundance, and distribution. Moreover, the harbour porpoise is listed in the Annex II of the Habitats Directive (Council Directive 92/43/EC), which requires member states to set up Special Areas for Conservation (SACs) for them [14].

Effective conservation measures for harbour porpoises, require reliable data on distribution and abundance to minimise or eliminate the overlap with anthropogenic activities that threaten harbour porpoise survival. In other words, we need to know where they are and how many there are. Furthermore, knowledge of how porpoises use their environment is crucial to identifying key areas for them, such as breeding areas, that require special protection.

There is a large amount of acoustic recordings of harbour porpoises being collected throughout their distribution range that could be used to fill gaps in our understanding of their ecology and social behaviour in the wild. New analytical tools that are able to detect and classify harbour porpoise clicks accurately, as well as finding patterns in their repetition rate that can be used to identify underlying behaviours are warranted.

1.4 Aims and objectives of research

The necessary tools to study harbour porpoise behaviour from acoustic recordings must be able to automatically inspect hundreds of hours of recordings and provide researchers access to pre-selected acoustic events for further analysis. Such tools would highly reduce the time needed for data analysis and will allow to carry out behaviour studies. For this reason, the overall aim of this project is to develop a standalone application, D-PorCCA, with a user-friendly interface and the necessary functions and algorithms to study the behaviour of harbour porpoises in their natural environment from acoustic recordings.

To that end, the first objective was to develop a harbour porpoise click classifier (PorCC) based on machine learning techniques (*i.e.*, logistic regression). Identifying patterns in repetition rates require detecting as many clicks as possible. Therefore, the classifier works for clicks of both high and low quality (*e.g.*, clicks produce when the animal moves away from the recording device).

These clicks must be grouped and potential click trains produced by harbour porpoises identified. Therefore, the second objective was to develop a series of algorithms to identify these click trains, which are then cleaned from expected undesired sources of noise.

Within this topic, the third objective was to develop a series of algorithms to classify acoustic events into three main behavioural categories: 'Orientation' or inspection of the environment (or travelling), 'Foraging' or feeding, and 'Socialising'. Patterns that do not fit within known types would be classified as 'Unknown'.

Harbour porpoises interact with animals of the same species, but also with individual of other species. The fourth objective, therefore, was to study the acoustic behaviour of harbour porpoises during interactions with another species: a solitary female short-beaked common dolphin (*Delphinus delphins*) who has inhabited the Firth of Clyde (Scotland) since the early 2000s. Lastly, the fifth objective was to test D-PorCCA in recordings from another NBHF species: the Heaviside's dolphin (*Cephalorhynchus heavisidii*) from Namibia.

Due to time constrains, it was not within the objectives of this project to use D-PorCCA for behavioural studies, however, click train types and patterns found in the data are described in detail.

1.5 Contribution to knowledge

The major output of this project is a series of analytical tools that would allow for behavioural studies of harbour porpoises in their natural environment for the first time. In this context, the two most important contributions to knowledge are:

1.5.1 Harbour porpoise communication

Using the algorithms developed in this project a series of social calls were found in data from Danish and Scottish waters. Some of these calls had been described in the literature before, but others were not.

1.5.2 Interspecies communication

The interactions between a solitary short-beaked common dolphin (*Delphinus delphis*) and harbour porpoises in the Firth of Clyde was known by locals and the scientific community. Acoustic data available during three interactions showed the dolphin changes her sounds to produce signals similar to those of the porpoises. Moreover, the sounds of both animals were produced in patterns that suggested vocal communication, including turn taking behaviour.

1.6 Dissemination of results

A series of scientific publications were published as a result of this project. This includes 1 peer-reviewed publication with the results of the first objective (Cosentino et al., 2019 [15]) and four poster presentations at international conferences. Additionally, two manuscripts are in preparation, onw with the results of the fourth objective and another one with the results described in Chapter 6.

Conference presentations

Cosentino, M., Schwarzbach, P., Tougaard, J., Nairn, D., Guarato, F., Jackson, J.C., Windmill, J. F. C. (2019). D-PorCCA, a new tool to study the behaviour of harbour porpoises. Poster presentation. World Marine Mammal Conference. Barcelona, Spain.

Cosentino, M., Guarato, F., Tougaard, J., Nairn, D., Jackson, J.C., Windmill, J. F. C. (2019). PorCC: A new high-accuracy click classifier to study harbour porpoises in the wild. Poster presentation. Danish Marine Mammal Symposium. Odense, Denmark.

Schwarzbach1, P., Cosentino, M., Guarato, F., Nairn, D., Jackson, J.C., Dahne, M., Windmill, J. F. C. (2019). New detector / classifier to study harbour porpoise behaviour in the wild. Workshop paper. Presented at the annual SAMBAH meeting. Turku, Finland.

Cosentino, M., Nairn, D., Jackson, J., Windmill, J. (2018). I beg your pardon? Vocal communication between a wild solitary short-beaked common dolphin and a harbour porpoise. Poster presentation. European Cetacean Society annual meeting. La Spezia, Italy.

Peer-reviewed publications

Cosentino, M., Tougaard, J., Guarato, F., Nairn, D., Jackson, J.C., Windmill, J. F. C. (2019). PorCC: A new high-accuracy click classifier to study harbour porpoises in the wild. Journal of the American Society of Acoustics. See Appendix A - Derived data supporting the findings of this study and the classification algorithm are available at the Pure Data Repository of the University of Strathclyde here.

1.6.1 In preparation

Cosentino, F., Nairn, D., Jackson, J.C., Windmill, J. F. C. (2019). I beg you pardon? Vocal communication between a solitary common dolphin and harbour porpoises.

Cosentino, F., Nairn, D., Jackson, J.C., Windmill, J. F. C. (2019). The social lives of harbour porpoises.

Public outreach

2018

In early 2018, as a result of sharing highlights of this PhD project on Twitter, I was invited to participate in a science radio show from Australia to talk about the PhD as well as my previous experience as a marine biologist. The interview is now available at the RRR Australian Radio Station website and the TuneIn site (Einstein A Go Go).

In the summer of 2018, the *BBC The One Show* crew came to Scotland to film Kylie, a solitary dolphin in the Firth of Clyde who is occasionally seen with harbour porpoises, a topic of my project. The story was released in the One Show and the University of Strathclyde drafted a Press release concurrently, which attracted attention from all over the world. Kylie and preliminary results of this project made the front page of the BBC news (What did the dolphin say to the porpoise? and were featured in international popular sites such as "I fucking love science" (A Scottish Dolphin Has Learned How To "Speak" Porpoise) and "Forbes" (A Lonely Dolphin Has Learnt To Talk To Porpoises), as well as other sites in France and Germany.

2019

In 2019 I was featured in a documentary about the Hunterston building site, located close to where Kylie is usually seen (The Hunterston Proposal). Additionally, in April 2019 I was invited to participate in an event organised by the Royal Society for the Protection of Birds (RPBS). Although I was not able to attend I recorded the presentation, which was shown during the event at the University of Aberdeen (Scotland).

2020

Lastly, I gave a 15 minute presentation in the Argyll Community Centre in Saltcoats in January 2020 with some of the results of this thesis. The audience comprised elderly from the local community.

1.7 Thesis outline

This dissertation is divided into 9 chapters.

Chapter 1 presents a general introduction to the topic of this project and describes the goal and main objectives, as well as the main results and outreach efforts.

Chapter 2 presents a review of the current state of knowledge of several aspects of harbour porpoise ecology and natural behaviour, as well as the available tools to study them in their natural environment. The chapter also discusses aspects of animal communication within and between species, and the challenges of carrying out research of acoustic behaviour of cetaceans.

The datasets used in this thesis are described in Chapter 3, as well as the methodologies used for data collection in both study areas, Scotland and Denmark.

Chapter 4 presents a detailed description of the methods used to develop a new click classifier for harbour porpoises (PorCC). It also presents the results applied to the Scottish database in comparison to the performance of an existing classifier.

Chapter 5 presents the results of using a series of algorithms developed to group and classify click trains, clean them from undesired sources of noise, and extract existing patterns to identify the underlying behaviour of the harbour porpoise. Examples of each click train type and behaviour are presented, as well as general results such as the total number of click train types and behaviours found in the data. The algorithms are attached in Appendix C). The algorithms developed in the previous chapters were used in harbour porpoise data from Scotland and Denmark and the results are presented in Chapter 6. This chapter is focused on the behavioural patterns. The results showed that each of the three categories defined here (*i.e.*, orientation, foraging, and socialising) comprised more than one pattern. These are described and discussed.

Chapter 7 presents a description of the long-term interactions between harbour porpoises and a solitary short-beaked common dolphin who inhabits the Firth of Clyde. This include a general discussion of the types of interactions observed over the years, as well as the results of the acoustic interactions.

Chapter 8 introduces D-PorCCA, a stand-alone application that incorporates the algorithms I developed for this project, which allows researchers from anywhere in the world to analyse the data that has already been collected to learn more about their species, including all porpoise species and the additional seven species known to produce NBHF clicks. At the end of Chapter 8, the results of using D-PorCCA in acoustic recordings of Heaviside's dolphins, another species known to produce narrow-band high-frequency clicks, similar to those of the harbour porpoises.

Finally, Chapter 9 presents the general conclusions of this thesis and recommends future work.

Chapter 2

Literature Review

2.1 Introduction

This Chapter presents a review of the current state of knowledge of several aspects of harbour porpoise ecology and natural behaviour, as well as the available tools to study them.

2.2 Background

Humans have been fascinated by cetaceans for thousands of years, evidenced by the numerous paintings, sculptures, and myths that exist around them since prehistoric times. Despite this fascination, there are still many aspects of their biology, ecology, and natural behaviour that are poorly understood. Studying cetaceans at sea is a difficult task, they spend most of their time underwater and so our ability to see them depends on many factors, from weather conditions to observer experience

[16, 17]. In fact, even in good visibility conditions animals can remain visually undetected due to their behaviour. This is especially true for cryptic species, such as the harbour porpoise (*Phocoena phocoena*).

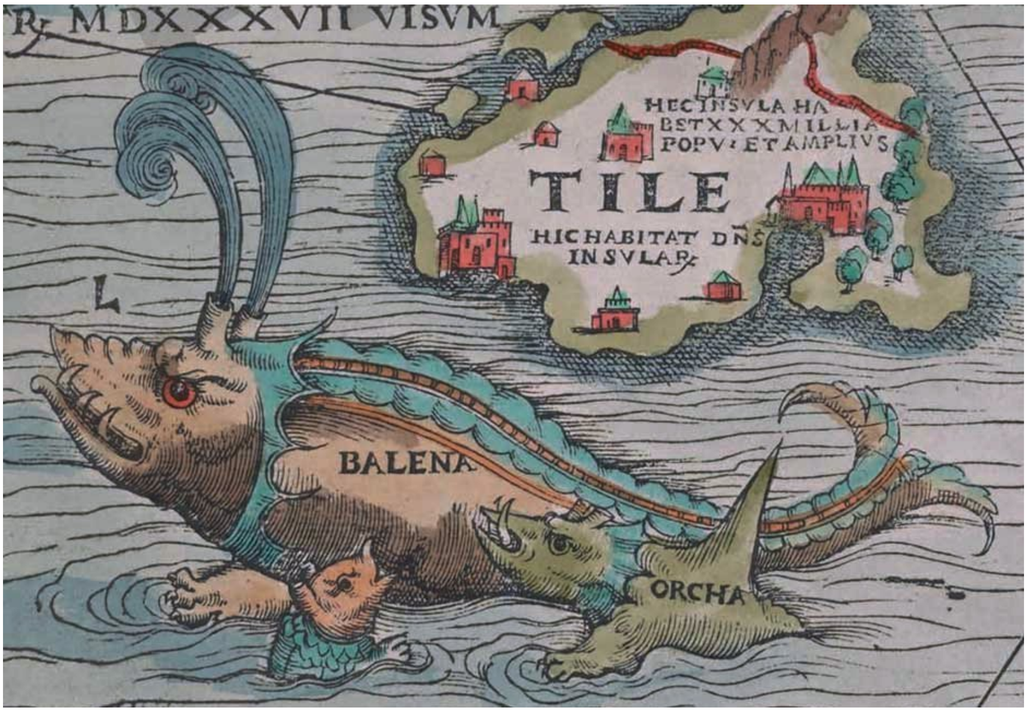


Figure 2.1: *Sixteenth Century interpretation of a 1st Century description by Pliny the Elder of killer whales (orcha) attacking whales (balena) and their calves near Cadiz (Spain). Illustration by Olaus Magnus in his "Carta Marina" (1539).*

Our knowledge of the lives of cetaceans in their natural environment has grown exponentially over the past few decades thanks to technological advances. It is now possible to collect large amounts of data in a cost-effective manner. At the same time, this requires long periods and many resources dedicated to data analysis, which often results in leaving data unanalysed. Therefore, tools that improve our ability to analyse data with minimum manual work will open doors for studies that were not possible before. When studying cetaceans, progress is inevitably linked to technological advancement.

2.2.1 Cetacean acoustics

Cetaceans evolved from land mammals that returned to the oceans, the hippopotamus being the closest relative alive today [18, 19, 20]. As they re-entered the water, cetaceans evolved a wide range of adaptations for the transition to a fully aquatic life. Their bodies became more hydrodynamic, losing the posterior limbs and evolving a smooth, hairless skin to reduce friction, and a thick blubber layer that allows them to maintain the body temperature around 36C, just like land mammals do. In addition, their nostrils displaced to an upwards position at the top of the head, facilitating breathing during travel, specially at high speeds [21, 22, 23].

Cetaceans are divided into two groups: odontocetes or toothed whales, with 73 recognised species, and mysticetes or baleen whales, with 14 recognised species. As a group, cetaceans produce a wide range of sounds, within and outside the human hearing range, from very low frequencies ($\sim$10 Hz), such as 'songs' produced by baleen whales, to impulsive sounds with high frequency content ($>$ 130 kHz) produced by toothed whales [6, 24, 25].

Odontocetes rely on sounds both via active production and passive hearing, to find preys and avoid predators, as well as for orientation, and to keep contact with other individuals and finding potential mates. The following are the three main types of sounds Odontocetes produce [26, 27]:

1) narrow-band tonal whistles: whistles are tonal sounds of long duration, usually few seconds long, with frequencies concentrated between 5 and 20 kHz [23]. Whistles are used for individual identification and communication purposes [*e.g.*, 28].

2) short-pulsed sounds: these are known as 'echolocation clicks'. Echolocation is 'the process in which an animal obtains an assessment of its environment by emit-

ting sounds and listening to echoes as the sound waves reflect off different objects in the environment' [29].

3) burst-pulsed calls: these are clicks produced at high repetitions rates, where the inter-click interval is too small to perceive them as separate clicks, and include sounds like 'cries' and 'barks', which are thought to be used for communication purposes[27, 30].

The term echolocation was coined in the 1950s by Griffin [31] to describe the ultrasonic impulsive sounds used by bats to forage and navigate their environment, and was later adapted for cetaceans [for a detailed review on echolocation in bats and dolphins see 32]. The temporal and spectral characteristics of echolocation clicks vary between species [33, 34, 35] and likely reflects the ecological adaptation to the habitat and local prey species [32]. Echolocation clicks can be divided into four groups:

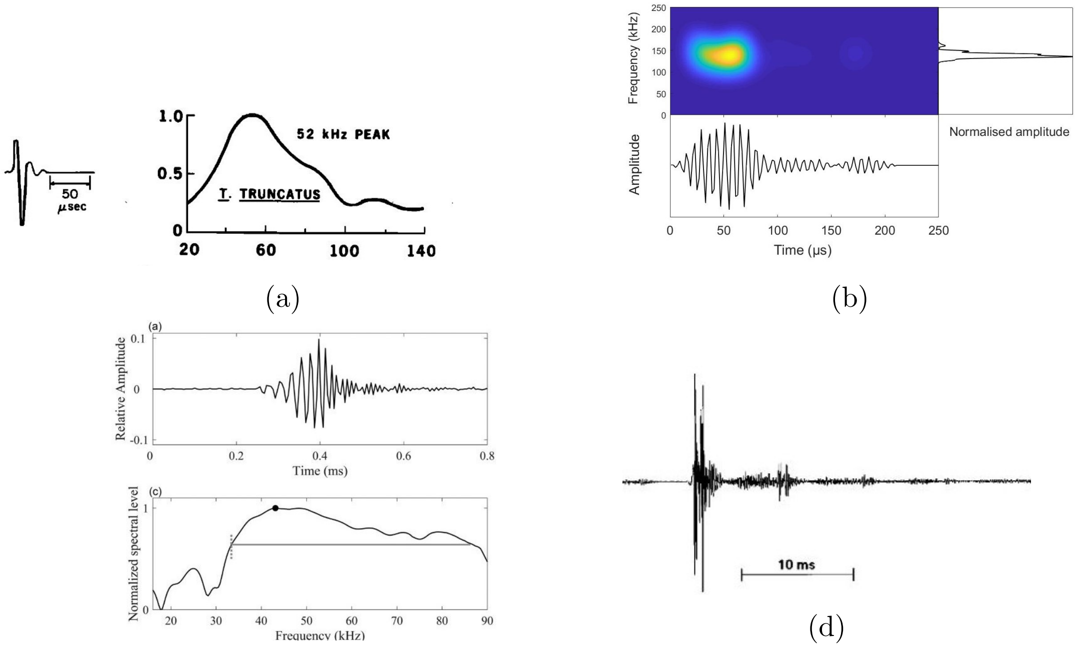
1) broadband, short-duration clicks, produced by most delphinids, such as the bottlenose dolphin (*Tursiops truncatus*) [36]

2) narrow-band, high-frequency (NBHF), long-duration clicks, produced by at least 16 species of whales, dolphins, and porpoises, including the harbour porpoise [6],

3) frequency-modulated up-sweep echolocation clicks produced by beaked whales, such as True's beaked whales (*Mesoplodon mirus*) [37], and

4) multipulsed, high powered low-frequency clicks produced by sperm whales (*Physeter macrocephalus*) [38].

Examples of these clicks are shown in Figure 2.2.



(a) (b) (c) (d)

Figure 2.2: *Echolocation signals of four odontocete species: (a) bottlenose dolphin (Tursiops truncatus) - from Evans (1973) [39] (b) harbour porpoise(Phocoena phocoena) - from this study (c) True's beaked whale (Mesoplodon mirus) - from DeAngelis et al. (2018) [40] (d) sperm whale (Physeter macrocephalus) - from Mohl et al. (2000) [38]*

2.2.1.1 Narrow-band high-frequency - NBHF - clicks

There are at least 16 species from five different taxonomic groups, usually referred to as narrow-band high-frequency (NBHF) species, who produce these clicks almost exclusively (Figure 2.3). These species are all seven *Phocoenids* [6, 41, 42], all four members of the genus *Cephalorhynchus* [*e.g.*, 43], two species of the genus *Lagenorhynchus* [44, 45, 46, 47], the pygmy (*Kogia breviceps*) [5] and dwarf sperm whales (*Kogia sima*) [48], and the franciscana (*Pontoporia blainvillei*) [49].

The temporal and spectral characteristics of these NBHF clicks are remarkably similar in all species where they have been described (Figure 2.4), even in species

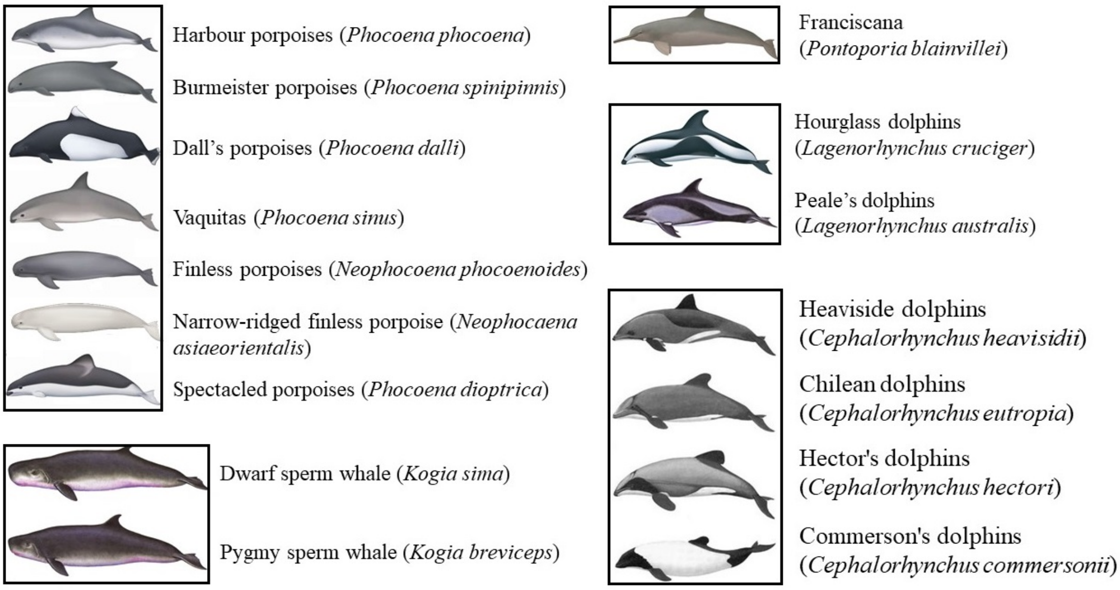
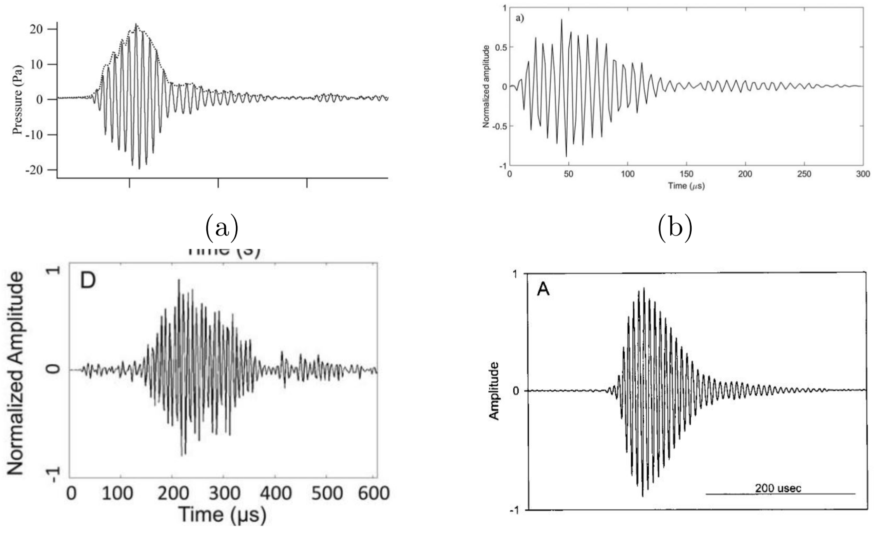


Figure 2.3: *NBHF species. Known species that produce narrow-band high-frequency (NBHF) clicks.*

with a wider acoustic repertoire, such as the Heaviside's and the Commerson's dolphins [47, 50]. NBHF clicks have peak and centroid frequencies between 100 and 160 kHz, little or no spectral energy below 100 kHz, duration between 57 and 212μs, and -3 dB bandwidths between 8 and 20 kHz [5, 6, 7, 41, 42, 43, 47, 50, 51, 52]. These NBHF clicks are emitted in trains in a narrow, forward-oriented beam [53, 54]. A click train can be loosely defined as a 'series of clicks separated by gradually or cyclically changing inter-click interval suggesting a unit during an echolocation event or a communication signal' [8].

The production of NBHF clicks evolved independently in these five groups [55], and thus comprises species with different distribution, habitat preferences, and diets. What all these species have in common, apart from the characteristics of their clicks, is their small size (compared to other odontocetes species) and their social



(a) (b)

(c) (d)

Figure 2.4: *Waveforms of narrow-band high-frequency (NBHF) clicks of four species (a) Heaviside's dolphin (Cephalorhynchus heavisidii) - from Morisaka et al. 2011 [51]). (b) Burmeister's porpoise (Phocoena spinipinnis) - from Reyes Reyes et al. 2018 [42] (c) Dwarf sperm whale (Kogia sima) - from Merkens et al. 2018 [48] (d) Pygmy sperm whale (Kogia breviceps) - from Madsen et al. 2005.*

lives, more specifically, the seemingly lack of it. In this context, it would seem that the characteristics of the NBHF clicks make them unsuitable for communication purposes, as these are stereotyped clicks, which individually likely carry little information, and because high frequencies attenuate fast, limiting communication to few hundred meters at most. However, a series of studies on harbour porpoises and Hector's (*Cephalorhynchus hectori*) and Heaviside's dolphins have found patterns in the repetition rates of NBHF clicks in relation to specific behaviours (*e.g.*, aggression), suggesting this is how information is transmitted to conspecifics [*e.g.*, 9, 11, 12, 13, 43, 50]. A summary of the NBHF clicks characteristics of all species where they have been described is shown in Table 2.2.

Table 2.1: *NBHF species and the clicks characteristics (mean ±SD)*

SPECIES	PF(kHz)	-3dB BW	Duration (μs)	Pattern	Other sounds	References
Harbour porpoise* (*Phocoena phocoena*)	137(±6)	17(±5)	54(±8)	Yes	No	[6, 7, 41]
Dall's porpoise (*Phocoenoides dalli*)	137(±4)	11(±5)	104(±37)	?	No	[41]
Burmeister's porpoise (*Phocoena spinipinnis*)	138(±11)	8(±2)	144(±64)	?	No	[42, 56]
Vaquita (*Phocoena sinus*)	128-139	10-28	79-193	?	No	[57]
Finless porpoise (*Neophocaena phocaenoides*)	121(±4)	17(±3)	80(±11)	?	No	[58]
Narrow-ridge finless porpoise (*Neophocaena asiaeorientalis*)	125(±7)	20(±4)	68(±14)	?	No	[59, 60]
Spectacled porpoise** (*Phocoena dioptrica*)	?	?	?	?	?	
Heaviside's dolphins*** (*Cephalorhynchus heavisidii*)	122 and 130			Yes	Yes	[50, 51, 61, 62]

*The authors analysed clicks from two populations and the values varied slightly between them [41]

**Nothing is known about the sounds of Spectacled porpoises, although it is thought they would be similar to those of other porpoises [63].

*** Heaviside's dolphins produce two different types of clicks, ones with peak around 122kHz another at 130kHz

Table 2.2: *NBHF species and the clicks characteristics (mean ±SD) (Cont.)*

SPECIES	PF(kHz)	-3dB BW	Duration (μs)	Pattern	Other sounds	References
Commerson's dolphins (*Cephalorhynchus commersonii*)	132(±6)	21(±3)	78(±1)	?	Yes	[64, 65]
Chilean dolphins (*Cephalorhynchus eutropia*)	126(±2)	18(±5)	82(±30)	?	No	[44]
Hector's dolphins (*Cephalorhynchus hectorii*)	129(±5)	20(±3)	57(±6)	Yes	No	[43, 46]
Hourglass dolphins (*Lagenorhynchus cruciger*)	126(±2)	8(±2)	115(±24)	Yes	No	[46]
Peale's dolphins (*Lagenorhynchus australis*)	123(±3)	15(±+4)	92(±2)	?	No	[65]
Dwarf sperm whale* (*Kogia sima*)	127(±1)	9(±1)	199(±54)	?	No	[48]
Pygmy sperm whale (*Kogia breviceps*)	130(±1)	8(±2)	119(±19)	?	No	[5, 66]
Franciscana (*Pontoporia blainvillei*)	139	19	212(±56)	?	Yes	[49, 67]

*The authors analysed clicks from two populations and the values varied slightly between them [48]

Two main hypotheses have been proposed about the evolutionary advantages of these clicks: reduced masking and acoustic crypsis [41, 50, 68]. Masking is the summation of ambient noise with the emitted signals, which reduces the probability of detection. In these species masking is reduced or avoided entirely because there are few natural sounds in that frequency range [27]. Acoustic crypsis is achieved as the effective hearing range of their main predator, the killer whale (*Orcinus orca*) [69, 70, 71], is below 100 kHz [72]. The latter might be partly incorrect, however. Galatius et al. (2019) showed that only *Lagenorhynchus* and *Cephalorhynchus* species evolved after the killer whales did, and therefore NBHF clicks in these species could have evolved in response to killer whale predation. For the other groups, NBHF could have evolved to avoid being heard by other predators that existed at the time, especially the 'killer sperm whale', an animal similar to modern sperm whales [55, 73].

Due to their cryptic behaviour, little is known about these species, some of which are rarely seen alive. An exception is the harbour porpoise, which has been studied thoroughly both in captive settings and in the wild, and even for them there is still many aspects of their natural behaviour that remain unknown.

2.3 The harbour porpoise

The harbour porpoise is one of the seven extant porpoise species and it is the most abundant and best-known species of all. They are dark grey on the dorsal area and lighter on the ventral side, and have a small, rounded head with no noticeable beak. The dorsal fin is small and triangular, positioned in the middle part of the body (Figure 2.5). Much is known about their life history, which was derived from data collected from stranded animals and individuals incidentally caught in fishing nets [*e.g.*, 74, 75]. Harbour porpoises are short-lived, compared to other Odontocetes, reaching usually between 10 and 12 years of age, with only about 7.5% of the population reach older ages, up to 20 years [74, 75]. The record is at 24 years for a male found stranded in the North Sea [74].

Figure 2.5: *Harbour porpoises off Cumbrae, in the inner Firth of Clyde (Scotland) in the summer of 2018. They were part of a larger group of 20-25 individuals. Photo: Melania Cosentino.*

Harbour porpoises are found exclusively in the northern hemisphere, in both sides of the Atlantic and Pacific Oceans, as well as in the Baltic and the Black Seas [76]. They are rarely seen in the Mediterranean Sea, although recent sightings suggest that a small population may be found off the coasts of Málaga, in southern Spain [77, 78]. There are four recognised subspecies, two in the North Pacific (*P. p. vomerina* and an unnamed one), one in the North Atlantic (*P. p. phocoena*), and one in the Black Sea (*P. p. relicta*) [76]. The Baltic Sea population is a genetically distinct population but does not qualify as a subspecies [76].

Although absolute abundance numbers throughout their entire distribution range are unknown, some harbour porpoise populations have been assessed. In the North Sea and adjacent waters abundance was estimated through large-scale surveys conducted in 1995, 2005, and 2016 [1, 79, 80, 81]. The most recent survey puts this population in over 424,000 animals (CV = 0.17; 95% CI = 313,151 – 596,827) [81]. However, not all populations are so abundant. The Baltic Sea population is critically endangered, with fewer than 500 individuals remaining [82].

Because of their small size and cryptic behaviour, harbour porpoises are specially difficult to observe at sea (Figure 2.6). They surface for a few seconds and spend only about 5% of their time at the surface, depending on geographic location, sex of the individual, time of day, and season [4]. They are shy and rarely approach vessels, diving for about 4 min [83], and are seen travelling in groups of two or three animals, or alone [17, 79]. Although they are occasionally seen in large groups, these observations are rare [*e.g.*, Nairn, unpublished data, 3], thus sightings are restricted to short distances and good weather conditions. Therefore, using typical visual monitoring methods, such as photo-identification and visual surveys from air, research vessels, or whale-watching platforms, to study the behaviour of harbour porpoises is limiting. In fact, few researchers have attempted to use photo-identification [*e.g.*, 84, 85], as the shape and colouration of their dorsal fin are similar between individuals, and have low levels of scaring compared to other species. These scars are the basis for individual identification in many species [*e.g.*, 86]. Maybe porpoises do not scar as easily as other species do or maybe they do not usually engage in playful or aggressive behaviour that leave scars, which are common behaviours in other species [87]. An additional reason for not so many scars in porpoises may be the very small blunt teeth of this species.

Several environmental factors influence harbour porpoise distribution and habitat use. The main are water depth (between 50 and 200 m) and slope [*e.g.*, 79, 88, 89, 90], which are in turn related to the distribution of their prey [91, 92]. Individual move-

Figure 2.6: *Harbour porpoise in the distance. Firth of Clyde, Scotland. Photo: Melania Cosentino*

ments vary greatly, however, as some porpoises travel dozens of km a day moving to far locations, while others stay in the same area for weeks [88, 91]. When looking at entire populations (*e.g.*, the North Sea), variations in sighting rates have been observed, within and between years [2, 17, 75, 79]. Evidence of coordinated migrations has been found in historic catch data of harbour porpoises in the Baltic Sea [*e.g.*, 93], and more recently in studies using passive acoustic monitoring [82]. Similarly, migration patterns have been identified in the population off West Greenland. Several individuals carrying satellite tags provided the first record of seasonal migration of harbour porpoises to offshore, deep waters. Some individuals moved hundreds of km to open waters, reaching deep areas in the middle of the North Atlantic Ocean, and performing dives of up to 410 m before returning to West Greenland [94]. These results were unexpected given what was known about porpoises. Another example of the importance of technological advances in our understanding of cryptic species.

2.3.1 Acoustics

The first recordings of harbour porpoises were made in the early 1960s using tape recorders. These recordings suggested harbour porpoises produce narrow band clicks with peak frequencies centred at 2 kHz and were emitted at different repetition rates, which seemed to be related to different behaviours, such as feeding and communication [10]. The high-frequency (HF) component described in subsubsection 2.2.1.1 were recorded and described a few years later [6]. A low-frequency (LF) component has been reported in other NBHF species, such as the Heaviside's dolphin [61] and the Yangtze finless porpoise (*Neophocoena phocoenoides asiaeorientalis*) [60]. There have been discussions within the scientific community about whether the LF component is real or just an artefact of the recording device, and if it is real, whether it has enough energy to be important for communication purposes [*e.g.*, 7], as low frequencies travel farther than high frequencies [95].

The discussion has settled now. The click production process delivers a click with both components [11, 96], but the LF component is between 50 and 60 dB weaker than the HF component [7] and thus unlikely to have any significant value for communication. Interestingly, however, the LF component is stronger than the HF one during the first 4 days after birth [96].

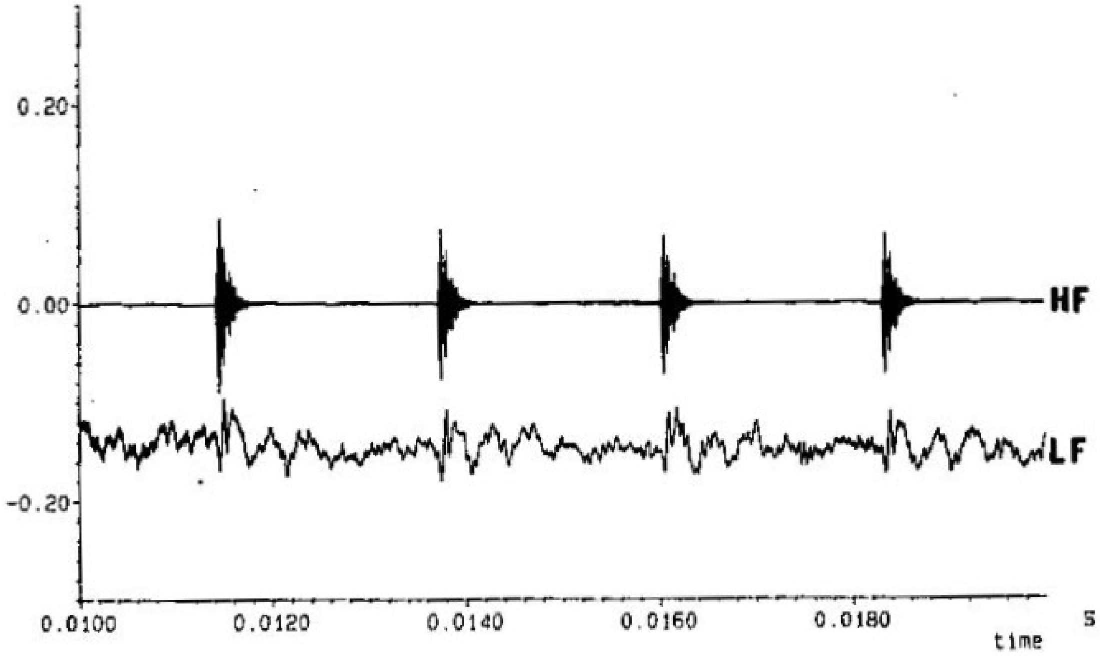


Figure 2.7: *A section of a click train from a 1 year-old male, showing the waveform of the low frequency (LF) and high frequency (HF) components. The two components were recorded with different hydrophones, on two separate tracks of the tape recorder. The LF component track has been low-pass filtered at 20 kHz, and the HF component has been high-pass filtered at 10 kHz. From Amundin 1991, p67 [11]*

2.3.1.1 Sound production

Unlike humans and other animals, toothed whales lack vocal cords in their larynx, and their respiratory system (in principle) is not connected to their digestive system (but see [97] and [98]), which means they have a different sound production mechanism. Toothed whales have one nasal opening located at the top of their heads, known as the 'blowhole'. A few centimetres below the blowhole, there is a series of structures, including two nasal passages each with a pair of 'phonic lips' in association with fat bodies. Sound is produced by air passing through the phonic lips, which are put in motion when the nasal passages are pressurised. The sound is then guided via the air sacs and the anterior side of the skull into the melon Figure 2.8.

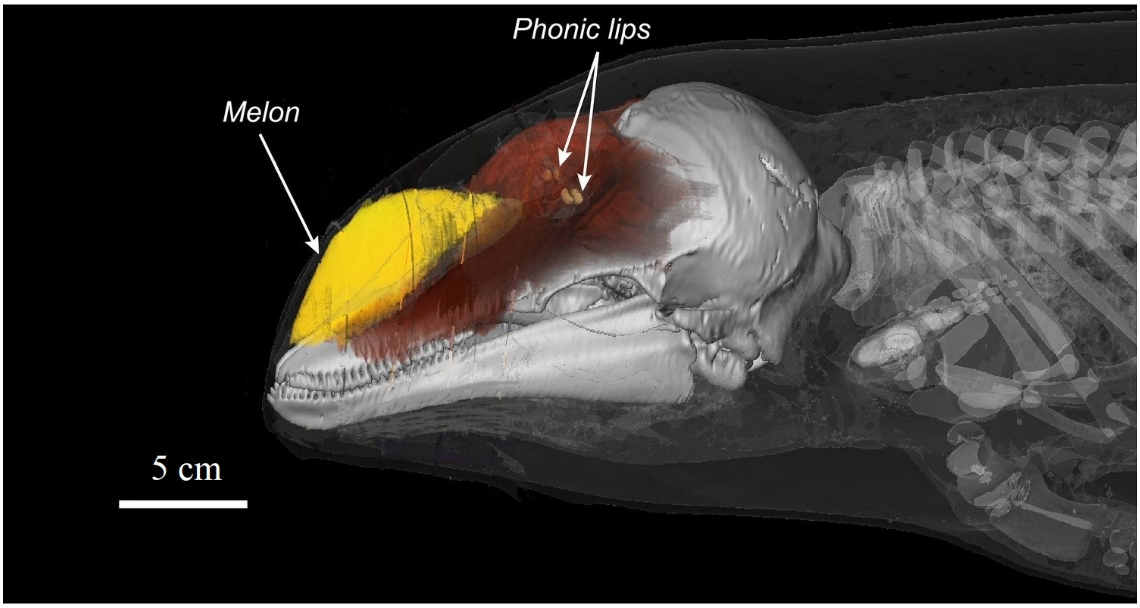


Figure 2.8: *Transverse MRI scans of a young harbour porpoise. The caudal part of the melon (yellow) abuts against layers of connective tissue, muscles, and tendons (red) forming a dense theca, which, along with the skull and a collection of nasal air sacs, reflect the vibrations that originate in the phonic lips (light brown) into the melon. The melon is under control of highly developed facial musculature. Adapted from Wisniewska et al. 2015 [99]*

The melon is a fatty tissue that acts as a lens and an impedance matcher, which creates a highly directional sound beam that is emitted into the water [11, 100]. The width and height of the sound beam is different between species but, in the case of click production, it is consistently narrow. In harbour porpoises, the -3dB beamwidth in both the horizontal and vertical planes is approximately 16 degrees [53]. The peak frequency is concentrated between 100 and 160 kHz (*i.e.*, wavelength approximately 1-1.5 cm), centred at 130 kHz [6]. Mean peak frequency values can vary between populations [*e.g.*, 41].

Because Odontocetes have two pairs of phonic lips (except for the three sperm whale species, which have one) it was proposed that sound is produced simultaneously by both phonic lips. However, a series of experiments with suction cups hydrophones and video cameras showed phonic lips and associated structures act independently during sound production. Moreover, each pair seems to be specialised in producing one type of sound, either tonal or pulsed sounds, which means that dolphins can whistle and click at the same time. Whistle production is associated with the movement of the left nasal passage (although the right passage may be able to produce whistles as well) while click production is associated with movement of the right nasal passage [52, 101, 102]. This sound production mechanism has been found in all species studied so far. In harbour porpoises (and likely other non-whistling species), clicks are produced exclusively by the right pair of phonic lips [52, 102].

2.3.2 Behaviour

Many aspects of the behaviour of harbour porpoises have been studied, although not all of them are well understood. Hall (2011) presented an exhaustive review of harbour porpoise behaviour on her PhD dissertation, which she divided into 12 categories, based on 9 categories proposed by Scott in his book Animal Behaviour (1958, cited by [3]). These categories are:

1) ingestive: foraging and feeding [*e.g.*, 9],

2) shelter-seeking: habitat selection, including side fidelity and migration [*e.g.*, 88, 94],

3) sexual: mating behaviour and as a form of play (*e.g.*, between males), and spatial segregation of the sexes [*e.g.*, 87, 103, 104],

4) agonistic: conflict or aggressive behaviour [*e.g.*, 11, 12],

5) epimeletic: caring for another individual that is injured or need helps in some way,

6) et-epimeletic: the calling or signalling for care and attention [*e.g.*, 8],

7) allelomimetic: behaviour leading other individuals to copy one's behaviour, such as synchronised surfacing during feeding or resting [*e.g.*, 3],

8) eliminative: excretion of waste,

9) investigative: examine their surroundings or specific objects in their environment [*e.g.*, 105],

10) avoidance: moving away from conspecifics, potential predators, or anthropogenic disturbances (*e.g.*, noise [106]),

11) social: engaging in social behaviour with conspecifics [*e.g.*, 10, 11], and

12) rest and sleep [*e.g.*, 107].

Social behaviour in Hall (2011) [3] refers specifically to socialising with individuals of the same species, including gathering in large groups and showing playful behaviour, such as surfing the waves. However, and although Hall mentions approaching vessels and discusses the existence of hybrids between harbour and Dall's porpoises, she does not mention social interactions with other species, which could be considered another type of behaviour (see subsection 2.3.5).

Our current understanding of harbour porpoise vocal behaviour suggests they have specific vocalisation pattern for some of the behaviours mentioned above. Because this project is focused on identifying behaviours based on patterns of click repetition rates, behaviours are re-organised into three broad categories: orientation or travelling (*i.e.*, 2 and 9), foraging or feeding (*i.e.*, 1), and social behaviour or communication (*i.e.*, 3, 4, 6, and 11). The behaviours not included in these categories (*i.e.*, 5, 7, 8, 10, and 12) either lack information about the corresponding acoustic emissions or the evidence is too scarce to be included (*e.g.*, sleep).

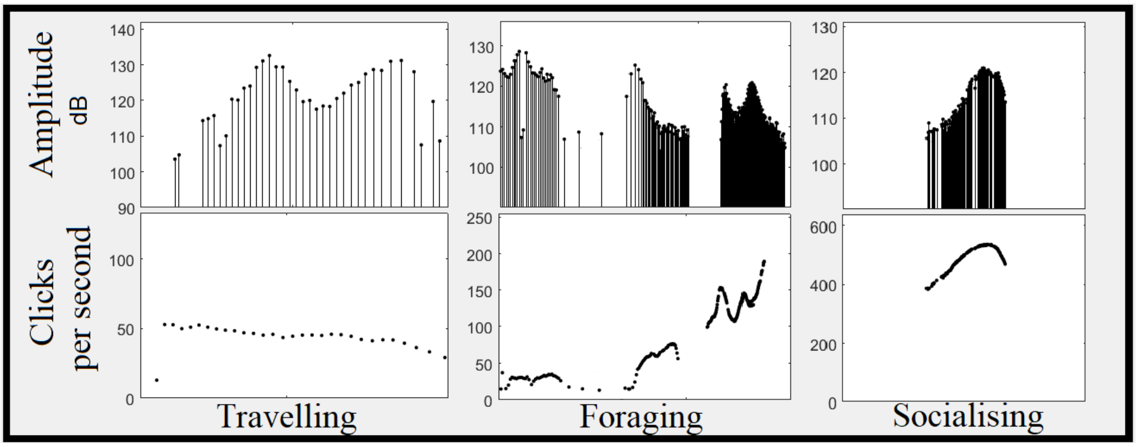


Figure 2.9: ***Behaviours***. *Examples of representative behaviours based on repetition rate patterns: orientation or travelling (left), foraging or feeding (middle), and socialising or communication (right)*

Technological advances had made it possible to study aspects of their lives that take place underwater that would not be possible with observations alone, from diving [94] and feeding abilities [108] to acoustic communication [13]. Although nearly 200 harbour porpoises have been tagged over the years in different areas of the North Atlantic [87], this represents a small number compared to population sizes. Although tags are relatively inexpensive and less invasive than they used to be, and can stay on the animals for long periods, it is not possible to tag every porpoise. On the other hand, tag data has provided information that can be used for behavioural studies using static acoustic monitoring (SAM) systems, which are cost-effective and non-invasive methods.

2.3.2.1 Orientation

Toothed whales use echolocation clicks to investigate or orient themselves in the environment they move through, and harbour porpoises are not an exception. Harbour porpoises vocalise almost continuously [13, 109], with 90% of silent intervals being no longer than 10 seconds [109], except during certain periods when they seem to be sleeping [107]. When they are travelling or navigating, the rate of click production is usually between 20 and 50 clicks per second, and not exceeding 100 clicks per second. During orientation or travelling, the relationship between the inter-click interval (ICI) is directly proportional to the distance to the target. In other words, the interval between clicks is long enough to allow for the echo to return and be processed before another click is produced, which is known as the two way travel time (TWTT). When the animal approaches a target object (*e.g.*, a rock), the ICI decreases because the signal and its echo travel smaller distances, thus arriving faster to the porpoise.

Verfuss et al. (2005) showed with a series of experiments with porpoises in captivity, that they use echolocation to orient themselves in their environment, even when they had been there for several years. The study found that porpoises echolocated continuously and that they used objects in their environment, which the authors called 'landmarks', to find their way to the target location. This behaviour is evident when looking at the variations of the ICI as the animal approaches the target (Figure 2.10). The ICI changed from ∼60 ms to ∼20 ms with decreasing distance. The ICI is always higher than the TWTT, which includes a 'lag time' necessary for processing the incoming information [110]. The lag time estimated in these experiments was between 26 and 36 ms when faced with difficult tasks and between 14 and 19 ms for simple ones [105].

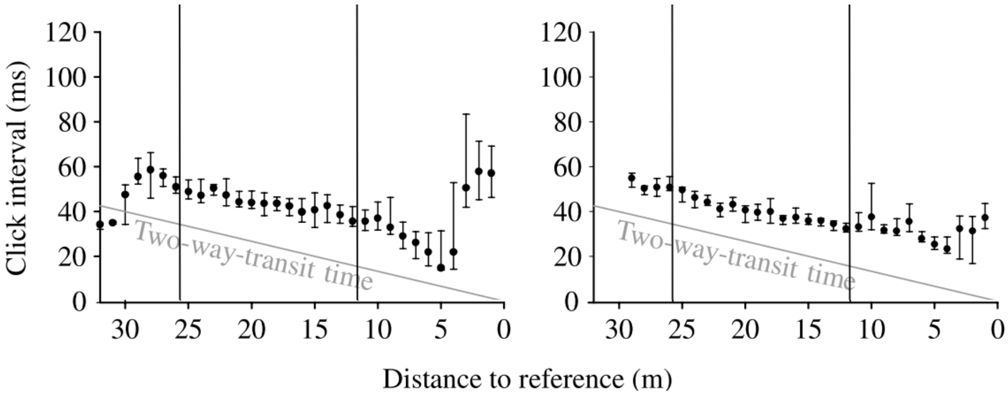


Figure 2.10: ***Landmark**. The median click interval (75% and 25% quartile) for each 1-metre bin distance to reference for each task. The two-way-transit time line of the click–echo pair is indicated (from Verfuss et al. (2005) [105]).*

Although the lag time appears to be a constant value, as if the animals 'lock' their clicking rate to maintain this lag time, they have control over the repetition rate and the intensity of the clicks, which they adjust depending on environmental conditions(*e.g.*, noisy background) [111].

This information can be used to estimate the active space of the animal, that is, the distance up to which porpoises can make up their environment. Although the actual distance will depend on the source level of the signals and the background noise level, we can make a rough estimate using this equation:

Distance = ((TWTT/2) + lag time) * speed of sound in water

So, for example, with an ICI of 40 ms, and assuming a lag time of 20 ms, porpoise are 'seeing' up to a distance of ∼45 m [109]. This is valid during orientation and exploration of the environment, but it cannot be applied to all cases, as porpoises are able to produce well over 1000 clicks per second (*i.e.*, ICI below 1 ms) [10, 11, 12, 13]. It is not yet understood how porpoises process information when clicking at high repetition rates.

2.3.2.2 Foraging

Data from stomach contents of stranded and bycaught animals suggest that harbour porpoises feed mainly on small demersal and pelagic fish, especially sand eel and cod, and whiting and herring, respectively. However, they can feed on many other fish, crustaceans, and cephalopods species. In addition, the importance of each prey type varies depending on season, area, and other factors [104, 112, 113]. Our understanding of what feeding looks like acoustically comes from experiments in captivity and data from wild animals carrying acoustic and behavioural tags. These data suggests porpoises use echolocation clicks to find and capture their prey in what can be thought of as a foraging event.

A successful foraging event can be separated into three phases: search, approach, and feeding buzz. These stages are common to all echolocating mammals, including toothed whales and bats [32]. During the search phase, the porpoise produces fewer than 100 clicks per second (*i.e.*, ICI $>$ 10 ms) in search of a potential prey. When the prey is located, the porpoise approaches it and the ICI becomes smaller and smaller, as the echo reaches the porpoise faster and faster. The final stage, the feeding buzz, is a period of high repetition rates (*i.e.*, the ICI can be $<$2 ms) [*e.g.*, 9, 83, 109]. During these buzzes, the amplitude of the clicks decreases, becoming 6 to 10 dB less intense than typical echolocation clicks [9].

2.3.2.3 Social behaviour and communication

The social lives of harbour porpoises in their natural environment is a mystery. When using visual methods, harbour porpoises are usually observed travelling alone or in small groups of two or three individuals [1, 17, 79, 114]. Large congregations do occur and have been reported in the literature [*e.g.*, 3, 87] and in social media, but remain rare. This seemingly solitary life might be just the result of how a cetacean 'group' is understood and defined during surveys. Most studies do not provide a definition of what a group is [*e.g.*, 115], and when they do, a group is usually defined as a sample of individuals that interact or showed coordinated behaviour or both [*e.g.*, 47]. Interaction refers to interactions seen by the observer, which hinders our understanding of social behaviour in cryptic species. Harbour porpoises spend 95% of their time underwater and although their phonations can travel a few hundred meters, animals can be interacting acoustically at large distances that the observer would not perceive. This is recognised by researchers, but it is rarely mentioned. Given group size numbers reported in most studies, 'group' is usually defined as it is understood for other species [*e.g.*, 76, 79, 81, 115]. There are exceptions, however [85, 116].

In fact, data from wild animals carrying acoustic tags have shown that harbour porpoises are more social than visual surveys tell us, spending much of their time at hearing distance of conspecifics [*e.g.*, 13]. The longest period recorded without sounds from other porpoises was $\sim$3 hours. Furthermore, the results were consistent with previous studies, showing that harbour porpoises produce two main types of click trains that are qualitatively different: foraging buzzes and social or communication calls. The distribution of the ICI of calls is bimodal, with peaks at $\sim$125 and ∼1000 clicks per second, with little overlap with feeding buzzes, which have the peak around 400 clicks per second [13]. The key difference between feeding buzzes and social calls, as a general rule, is that feeding buzzes show a gradual increase of repetition rates, while calls lack a preceding period of low repetition rates [13] [but see 12].

The use of the term 'communication' calls may prove problematic because, even though the field of animal communication has been active for many decades, there is not yet a definition of communication everyone agrees with. It is often defined as the process of conveying information from senders to receivers by means of signals, where signals are behaviours or structures that senders evolved in order to convey information [117]. This way of thinking about communication is not restricted to acoustic signals. Most animals, as well as plants, and cells, communicate using chemical, visual, and tactile signals, as well as acoustic ones [118, 119, 120, 121, 122]. For some authors, however, not all acoustic signals constitute a form of communication. For example, Au and Hastings (2009), in their book *Principles of Marine Bioacoustics* when talking about sounds produced by toothed whales, state that 'Social sounds are those that are used by odontocetes in a social context and could be, but not necessarily, used for communications' [123]. Given virtually nothing is known about the social lives of harbour porpoises in their natural environment, 'communication' calls here refer to burst pulses, which lack a preceding period at low clicking rates. Whether these calls carry information or if they are used for communication, is difficult to assert given the few existing studies on this topic [8, 10, 11, 12, 13].

Because the low-frequency (LF) component is produced at the same time as the high-frequency (HF) component, it is possible to use observations of early studies

based on the LF component to learn about harbour porpoises calls. Busnel and Dziedzic (1966) and Amundin (1991) described a series of calls that seemed to occur in specific contexts, including courtship, dominance, and distress. The repetition rates of these calls were different: while 'courtship' calls were long (∼1 s) and had high repetition rates (>500 clicks per second), 'dominance' calls looked like two or three consecutive short calls at an interval of 200 ms, with variable repetition rates of up to 1000 clicks per second [10]. 'Distress calls' were described in different studies, but the characteristics of the calls differed. Busnel and Dziedzic (1966) described these as calls with repetition rates between 130 and 250 clicks per second and duration between 0.4 and 1.55 s [10], while Amundin (1991) described them based on the HF component as calls with repetition rates between 100 and 500 clicks per second, but with repetition rates between 300 and 400 clicks per second based on the LF component [11].
Other calls include 'push threat call' (400-900 clicks per second), 'signals of pain' (500-800 clicks per second), 'contact call' between mother and calf (increasing from 10 to over 600 clicks per second - Figure 2.11), and 'aggression' (200-1000 clicks per second) [9, 10, 11, 12]. Additionally, Amundin found what he called 'phrases', comprising two or more (in general similar) calls repeated in a short period of time. He also found what he believed to be information that could be used for individual recognition, specifically variations in repetition rates at the end of the communication calls [11].

Clausen et al. (2010) found the duration of the click trains also varied markedly depending on the behaviour, for example contact calls are less than 1 s long, while

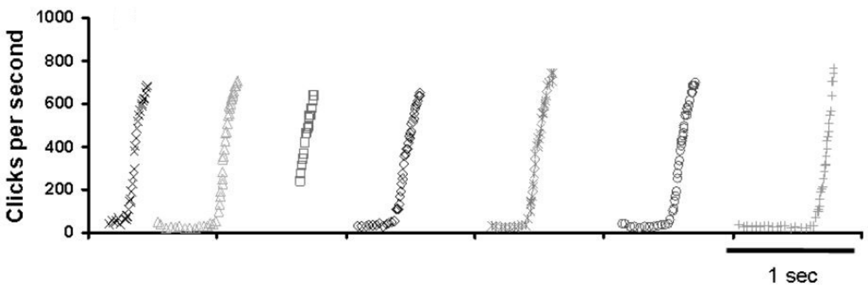


Figure 2.11: ***Contact call**. Click repetition rate pattern for contact calls produced during mother-calf interactions (extracted from Clausen et al. (2010) [12]).*

grooming can last up to 16 s. Moreover, the duration of the click itself varied slightly between behaviours [12].

Communication calls have been studied in wild porpoises for the first time in 2018, in a study based on six porpoises carrying acoustic tags [13]. Calls from studies using static acoustic monitoring devices, however, are rare. One example is Koschinski et al (2008). The authors witnessed a calf that was entangled in a gillnet in Clayoquot Sound (Canada) and were able to record it during this period. They found that 92% of the echolocation events had ICIs below 10 ms, suggesting these were communication calls. The patterns resembled those of 'distress calls' described by Amundin (1991), although the repetition rates were different [8, 11]. The authors also found calls with repetition rates at ∼160 clicks per second, which falls within the bimodal distribution found by Sorensen et al. [8, 13].

At the time of writing, no study using static or towed continuous recorder have reported communication calls in wild harbour porpoises.

2.3.3 Calves

Harbour porpoises are small, reaching a maximum of about 2 m in length and 72 kg in weight, and although there are variations between populations, females are larger and heavier than males. Sexual maturity is reached at about 5 years of age, depending on sex, and varies between populations. Pregnancy rates are high, with 60-75% of mature females being pregnant at any given time of the year. Females become pregnant every year or every second year and gestation lasts between 10 and 11 months. Newborns are less than 80 cm long and 7 kg at birth. In the North Sea and adjacent areas, birth occurs between May and August, and weaning between February and May, when the porpoises are between 8 and 11 months old [63, 74, 75, 124, 125].

Figure 2.12: *Harbour porpoise calf (and mother) - born in August 2007 in Fjord and Belt facilities in Kerterminde (Denmark).*

Little is known about the ontogeny of harbour porpoise clicks. The only study focused specifically on the vocal behaviour of harbour porpoise calves was carried out with data from three individuals born in the Fjord and Belt facilities in Kerteminde (Denmark) [96]. The calves were born on August 2007, July 2013, and July 2014 respectively, but only the first one survived long enough (*i.e.*, 9 months) to study how the temporal and spectral characteristics of the clicks changed over time [96]. Delgado found that calves can vocalise just seconds after being born, as the first clicks reliably coming from the calf were recorded 40 seconds after birth. For the first 3 or 4 days these clicks had a high (HF) and a low frequency (LF) component, with the latter being stronger. The HF component is similar to the clicks of adult harbour porpoises, with a peak between 100 and 150 kHz, while the LF component has its main peak centred at 2 kHz [96]. For the first 9 months, the clicks (Figure 2.15) have higher peak frequencies than those of adults, decreasing from nearly 150 kHz to 130 kHz over this period, having as well higher bandwidths [96].

The higher peak frequencies in young individuals was also reported by Goodson et al. [126], who described the spectral and temporal characteristics of two captive porpoises in Harderwijk Aquarium (The Netherlands), one of which was 8 months old at the time and the other 20 months old. The authors found that the younger individual had a higher -3dB bandwidth and peak frequency values (14 kHz and 148 kHz, respectively) than the older one (12.5 kHz and 144 kHz, respectively) [126]. Similarly, Clausen et al. reported centroid frequencies at 136 kHz and -3dB bandwidth at 16 kHz for a calf of age between 3 to 9 months [12].

Both the LF and HF components are part of the same click production process being produced simultaneously [11, 60, 96]. How the LF component is produced and whether it has a function during this crucial period (*e.g.*, for the calf to keep contact with the mother) is still unknown, but it seems to be present in other neonatal porpoise species as well, such as the Yangtze finless porpoises (*Neophocaena phocaenoides asiaeorientalis*) [60].

Because the LF component is long in duration, it cannot be detected by existing

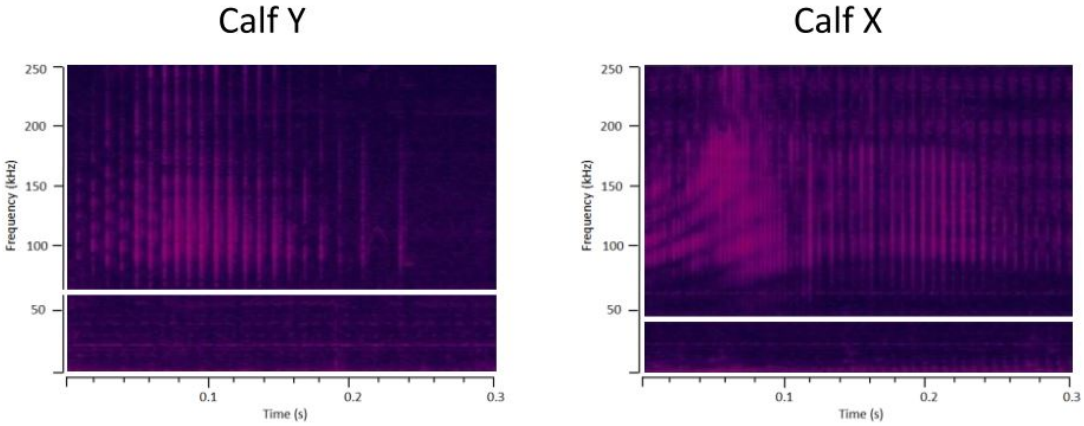


Figure 2.13: *Click train produced by a harbour porpoise calf - from Delgado 2016 [96]*

impulsive sounds detectors. Additionally, some researchers filter the data collected with broadband hydrophones before digitalisation, leaving out sounds with frequencies lower than 2 kHz. Moreover, much of the background noise is in low frequencies, thus a classifier for calves focused on the LF component would be ineffective. So far, no classifier exist to find calves based on acoustic information. Such classifier, would be crucial for conservation purposes as it would allow for identification of nursing areas that need protection.

2.3.4 Conservation status

The harbour porpoise, as a species, is listed as Least Concern by the International Union for Conservation of Nature (IUCN) [1], however, the European population is listed as 'Vulnerable' and the Baltic Sea population is 'Critically Endangered', with fewer than 500 individuals remaining [82]. In European waters, concerns for its conservation status due to, especially, lethal incidental catches in fishing nets, led to the Agreement on the Conservation of Small Cetaceans of the Baltic and North

Seas (ASCOBANS). The agreement was signed in 1992 and the area was extended in 2008. ASCOBANS parties are obliged to develop and adopt measures to protect harbour porpoises, as well as to acquire knowledge about their occurrence, abundance, and distribution. The harbour porpoise is also listed in the Annex II of the Habitats Directive (Council Directive 92/43/EC) [14], which requires member states to set up Special Areas for Conservation (SACs) for them.

The survival of harbour porpoises is threatened by human activities, especially fishing and underwater noise. Thousands of harbour porpoises get accidentally caught in fishing nets and die every year in the North Sea and adjacent waters, especially in gillnets [*e.g.*, 127, 128, 129]. Additionally, noise-producing activities, such as Navy operations, pile driving in windfarm constructions, and seismic surveys, can indirectly lead to death, for example by distracting the animals who swim towards fishing nets, but also by forcing them away from productive areas, resulting in starvation [106, 130, 131].

The designation of SACs requires identifying habitats that porpoises use for important life functions such as breeding (*i.e.*, identifying areas with mother-calf pairs) to minimise overlap with human activities. Given it is not possible to equip every animal with a tag, we can take advantage of recent technological developments and develop tools to use passive acoustic monitoring systems to fill gaps in our understanding of harbour porpoise behaviour and communication in the wild.

2.3.5 Interspecific interactions

Non-predatory interspecies interactions between cetaceans have been widely documented, of both aggressive and non-aggressive nature. Non-aggressive interactions usually consist of temporary feeding aggregations of two or more toothed (Odontocetes) or baleen whales (Mysticetes) species [132, 133, 134, 135], occasionally including other marine mammals and sea birds [136]. Social heterospecific interactions are infrequent compared to other non-predatory interactions, although they have been observed between groups of different species [137, 138, 139], between a group of one species and an individual of another species [140], and between two individuals of different species [141, 142]. These interactions are also usually temporary and involve either toothed or baleen whales or both [141, 142, 143].

Differences in body size do not seem to present a constraint for these interactions: in 2004 and again in 2006, a humpback whale (*Megaptera novaeangliae*) was seen what seemed like playing with a bottlenose dolphin off the coasts of Hawaii [141]. In both cases the dolphin was 'lifted' by the whale on top of its mouth and the interaction lasted just a few minutes. Interestingly, the observations were made two years apart (to the day) off different islands and neither the whale nor the dolphin were the same individual [141].

Interactions between a group of one species and an individual of another species are also usually temporary and have been reported for odontocetes as well as mysticetes. Species that in some areas are prey-predator or engage in interactions of aggressive nature can occasionally engage in social interactions [69, 143]. One of these unusual observations was made by myself in 2008, when a group of killer whales was seen socialising with a striped dolphin (*Stenella coeruleoalba*) in the Strait of Gibraltar, Spain.

The only known case of an individual of one species interacting having with a group of another species for a long period is Billie. She is an adult female bottlenose dolphin who lives in the Algeciras Bay, in the Strait of Gibraltar, with short-beaked common dolphins (*Delphinus delphis*) [144]. Despite bottlenose dolphins being resident in the area [145], she seems to spend of all her time with the common dolphins and was also seen caring for common dolphin calves and new-borns, which is a rarely observed type of interspecific interaction. Billie is thought to have recently give birth to a hybrid calf, although no genetic analysis have been done for confirmation yet [144].

2.3.5.1 Predatory interactions

The main natural predator of harbour porpoises is the killer whale [69, 70, 71], a cosmopolitan species and the most widely distributed marine mammal [146]. Although their distributions overlap, not all killer whale populations feed on marine mammals. In the North Pacific as well as in the North Atlantic, only one of the three populations feed on marine mammals [*e.g.*, 147, 148, 149]. Further, killer whales predating on harbour porpoises in the North Sea and adjacent waters are scarce [79, 81, 150, 151].

More recently, a new predator has been identified in the North Sea: the grey seal (*Halichoerus grypus*). Grey seals feeding on harbour porpoises have been reported for many European countries, including Belgium, France, the Netherlands, and the UK. These observations include reports of scavenging as well as active predation [152, 153, 154, 155]. Despite grey seals being present in West Scotland and Danish waters [156], no predation events have been reported in these areas so far. The impact of grey seals attacks on the population of harbour porpoises in the North Sea and surrounding areas is unknown.

2.3.5.2 Aggressive interactions

For reasons that are not well understood, harbour porpoises are killed by bottlenose dolphins in some areas around the UK [143] and in Californian waters [157]. In the UK, deaths due to bottlenose dolphin attacks are recorded along the entire Scottish coast and constitute the most common cause of death for the species, representing about a quarter of all cases [158]. The impact on the population is unknown.

Lethal interactions with other species have also been recorded. Baird et al. (1998) described an event that took place in the west coast of Canada, off British Columbia in 1994. A pair of Pacific white-sided dolphins (*Lagenorhynchus obliquedens*) were seen interacting with a neonate harbour porpoise for several hours. Although the dolphins were not visibly aggressive, they harassed the porpoise, which eventually died [159].

Another example of a harbour porpoise calf who died as a result of interacting with dolphins in Canadian waters is described in Larrat et al. (2012) [160]. In this case there were no observations of the event, as the report is based on rake marks found on the body of a young calf ($<$ 1 year old) found stranded off Quebec. The large number of markings on its body and their characteristics indicated the calf was a victim of aggressive behaviour from Atlantic white-side dolphins (*Lagenorhynchus acutus*) [160].

2.3.5.3 Affiliative interactions

Although rare, non-aggressive interactions between harbour porpoises and individuals or groups of other species have been reported throughout their distribution range. Recently, a juvenile harbour porpoise was seen travelling with a group of bottlenose dolphins in the Marmara Sea, spending much of its time in the echelon position [140]. This interaction is surprising as in other areas, as mentioned above, bottlenose dolphins are responsible for dozen of harbour porpoise deaths every year [143].

On the west coasts of the United States and Canada, harbour porpoises are sympatric with Dall's porpoises (*Phocoenoides dalli*), although there seems to be a temporal separation in their distribution. They have never been seen in mixed groups [3, 161], and yet hybrids of these two species have been confirmed in the area, which seem to occur at relatively high levels [162]. Willis et al. (2004) reported 20 cases of hybrid individuals within Dall's porpoise groups, of which nine were confirmed via genetic analyses. In all cases where tests were carried out (n = 5), the mother was a Dall's porpoise and the father a harbour porpoise, which explains why hybrids are observed in Dall's but not in harbour porpoise groups [162]. Unfortunately, no stranding of hybrids have been detected so far, which would provide opportunities to learn more about these individuals [3].

The only known case of 'ongoing' interspecific interaction between an individual of another species and a harbour porpoise is Kylie, a solitary female short-beaked common dolphin (*Delphinus delphis*) who lives in the Firth of Clyde [142]. Kylie inhabits the Firth of Clyde since at least the early 2000s and because she moves between different areas, she has received several names over the years, including Kylie, Donna, and Colin. Her sex was unknown until 2019, when was confirmed via underwater images taken by a local diver. She has lived a solitary life since she was first seen in the area, although she is known to be occasionally accompanied by a harbour porpoise [142]. Ryan et al. (2017) reported two observations of Kylie and a harbour porpoise, made in two different areas of the Firth of Clyde, four years apart. The authors were lucky enough to have access to underwater photographs of the porpoise, which showed that it was the same individual in both cases [142]. Opportunistic observations by many locals suggest Kylie spends time with a harbour porpoise regularly (Nairn, Unpublished data). To date, her vocal behaviour has not been studied, neither when she is alone nor when she is with a harbour porpoise. The interactions between Kylie and harbour porpoises provide a unique opportunity to study inter-specific vocal communication in wild cetaceans.

2.3.5.4 Short-beaked common dolphins

Short-beaked common dolphins are found in temperate and warm waters around the globe, except the Indian Ocean. Around the UK, common dolphins are mostly found off Wales in the Celtic Sea and off the Northwest coast of Scotland [79, 80, 81], rarely close to shore, but are also known to visit the Moray Firth [163] in the east and the Minch in Northwest Scotland where they are seen in coastal waters [164]. This area is over 400 km away from where Kylie now spends most of her days, and where common dolphins are rarely seen (Nairn, unpublished data). Common dolphins live and travel in large groups that regularly exceed 50 individuals and can reach thousands of animals [165].

Common dolphins produce a wide range of sounds, within and outside the human hearing range, that they use for foraging, orientation, and communication purposes. Communication calls include whistles, buzzes, barks, yelps, squeals, and burst pulsed calls. Studies on common dolphin sounds have been mainly focused on whistles and how these vary depending on behavioural context and time of day, as well as geographic location [165, 166].

So far, there are no studies focused specifically on common dolphin clicks. Gurevich

(1969) (cited in Evans 1973 [39, 167]) reported that common dolphin clicks have energy between 100 and 150 kHz but, unfortunately, the study was in Russian and details, such as peak frequency values, were not reported by Evans (1973) [39, 167]. Fish and Turl (1976) then reported that Evans said (in a personal communication) that the source level 'and most of the other data for *Delphinus* and *Globicephala* reported in Evans (1973) could have been an editorial error [168]. Although it is not clear which of the numbers they refer to, other non-NBHF delphinids species are known to produce short-duration clicks with energy in these frequencies. Unlike NBHF clicks, short-duration clicks are broadband and thus cover a wide range of frequencies, sometimes extending over 100 kHz [123]. With increased source levels and as the recording devices gets closer to the centre of the echolocation beam, the centroid frequency of these clicks increase [*e.g.*, 102, 169].

Since then, several studies have directly or indirectly investigated the temporal and spectral characteristics of common dolphin echolocation clicks. In these cases, the authors either used the studies discussed above as references or used methods inadequate for detecting high-frequency ($>$ 100 kHz) sounds, recording at sampling frequencies between 80 kHz and 200kHz, rendering a maximum detectable frequency of 40 kHz and 100 kHz, respectively [168, 170, 171]. Because of the reported high levels of energy in frequencies below 100 kHz, these clicks are fundamentally different from NBHF clicks. Further, common dolphin clicks have been described as oligocyclic (*i.e.*, waveform with few peaks) and of short duration, not exceeding 50μs.

The fact that information about the energy content is inconsistent between studies likely reflects the species ability to change the spectral characteristics of the clicks. Roch et al. showed that long-beaked common dolphin (*Delphinus capensis*) can produce clicks with a wide range of peak frequency, from about 20 kHz to 65 kHz [172], as shown in Figure 2.14. It is expected that short-beaked common dolphins have similar abilities, especially as new data suggests short-beaked and long-beaked common dolphins may be the same species [20].

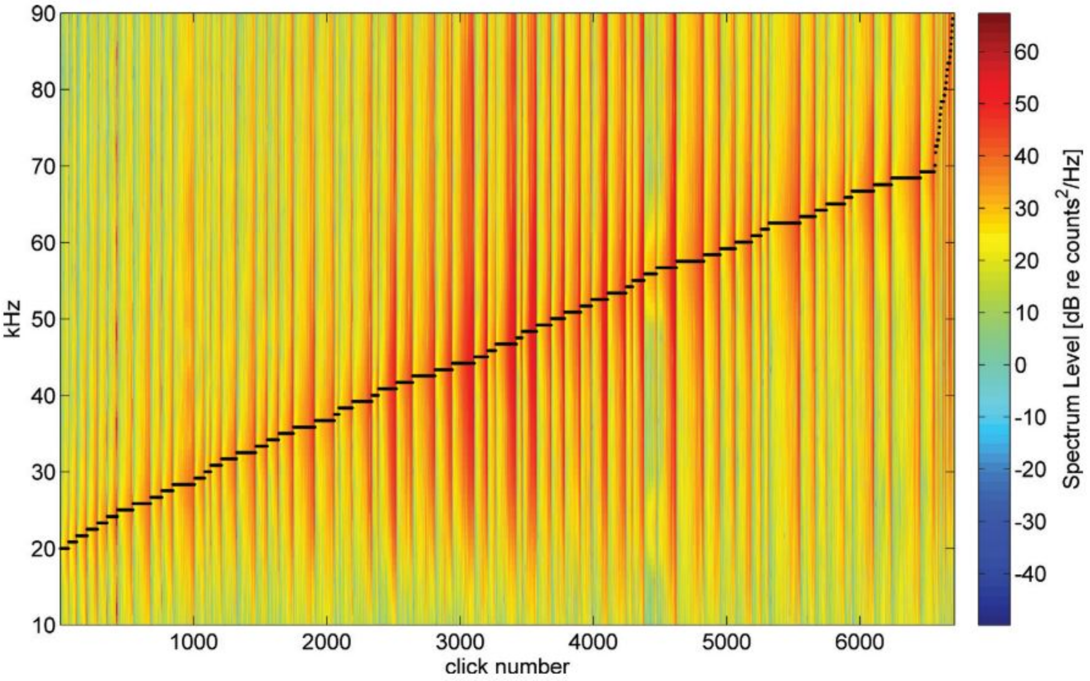


Figure 2.14: ***Long-beaked common dolphin***. *Concatenated spectrogram of long-beaked common dolphins (Delphinus capensis) clicks. Clicks were sorted by peak frequency which are highlighted by black points - Extracted from Roch et al. (2011) [172]*

The characteristics of Kylie's clicks are not known or whether the sounds she produces differ to those of conspecifics who live in groups. There are a few records of toothed whales leading a solitary (temporarily or permanently), most of which are bottlenose dolphins [173, 174]. Kylie is one of the seven cases of solitary common dolphins ever reported worldwide [173, 175]. In most cases it is unknown why or how these highly social animals become solitary [173, 176, 177, 178].

2.3.6 Vocal learning and interspecies communication

The ability to learn new behaviours as a result of interacting with other individuals is known as social learning, whether it occurs by interacting with individuals of the same or other species [179]. When it comes to vocal behaviour, learning can be divided between contextual and production learning. Contextual learning occurs when the use (or understanding) of a signal is associated with a novel context, and production learning when an individual modifies the acoustic characteristics of an existing signal producing a signal that was not previously part of its repertoire [180, 181].

Janik and Slater argue that these vocal modifications refer specifically to the frequencies of the signal and result from exposure to acoustic inputs, either artificial sounds or by interacting with individuals of the same or other species [181]. Thus, cases in which animals change the amplitude or duration of the signal in response to high levels of background noise (*i.e.*, the Lombard effect) would not constitute production learning.

In captive settings it is possible to design experiments to test the animal's ability for vocal learning, as Richards et al. [182] put it: 'To establish a capability for vocal mimicry [...] 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'. In that study, bottlenose dolphins were successfully trained to imitate artificial sounds and to use these sounds to label objects, such as 'person' and 'pipe' [182]. Killer whales have also been trained to imitate different sounds, including human speech in the form of simple words such as 'hello' and 'bye bye' [183]. Even more impressive results were recently seen in grey seals (*Halichoerus grypus*). A group of researchers were able to teach wild seals kept temporarily in captive setting to produce a wide range of sounds and imitate melodies of songs they could have never heard in the wild [184]. The ability to imitate human speech has been observed as well in marine mammals who did not receive any training. A trainer at the Vancouver Aquarium in Canada heard someone telling him to get out of the pool. To his surprise, it was a beluga (*Delphinapterus leucas*) in the pool who utter the words [185]. One of the most well-known cases is Hoover, a harbour seal (*Phoca vitulina*) who spontaneously started to produce sounds that resembled human speech, with a Boston accent [186].

Inter-specific interactions sometimes lead to changes in the acoustic behaviour of the animals involved. A study conducted with captive animals found that killer whales who spent time with bottlenose dolphins, had learned to produce sounds that were similar to bottlenose dolphins' sounds, in what is, presumably, an attempt to communicate with them [187]. Similarly, a beluga who spent time with bottlenose dolphins were recorded producing whistles similar to those of bottlenose dolphins sounds within months of being introduced in the same environment. Moreover, the beluga favoured those sounds over the ones she used before the interactions occurred [188].

Production learning as a result of interspecies interactions in the wild, however, have rarely been observed [189]. One of the few reported cases is a solitary killer whale who was recorded producing sounds similar to the 'barks' of California sea lions (*Zalophus californianus*) [190]. Tyack (2008) argues that the definition by Janik and Slater [180, 181] is limiting our understanding of vocal learning to cases where we can perform experiments in captive settings, which does not necessarily reflect what happens in their natural environment. Tyack argues that vocal convergence is a form of production learning, in which the animals match the sounds of conspecifics or individuals of another species [191]. However, developing new tools are necessary to study vocal learning (both contextual and production learning) and communication in wild cetaceans.

2.4 Available tools

Using non-invasive techniques to study the acoustic behaviour of harbour porpoises in their natural environment requires a series of tools, some of which already exist. These include an acoustic recorder that can stay underwater for long periods with minimum or no supervision, a detector of impulsive sounds (*i.e.* potential harbour porpoise clicks), a click classifier, and a series of algorithms to group acoustic events and extracts patterns to identify behaviours. The existing tools are described below.

2.4.1 Passive Acoustic Monitoring - PAM - devices

Visual surveys are the default method to study cetaceans. These range from land and boat-based surveys focused on individual animals using photo-identification [85, 192], to large-scale boat-based and aerial surveys carried out in pre-determined transects to estimate density and abundance [81, 89]. The use of acoustic devices, generally known as passive acoustic monitoring (PAM) systems, to study cetaceans began in the 1960s [193] and became widely used from the 1990s onwards, when many research groups started developing their own devices [see 194]. PAM systems have several advantages over visual surveys as they can be used during bad weather conditions (*e.g.*, high waves, fog) as well as at night, and data collection can be done with no supervision, which means their performance is not affected by the experience or levels of alertness of the observer. Moreover, because cetaceans spend up to 95% of their lives underwater, animals sometimes are only detected acoustically or are detected acoustically before they are detected visually [*e.g.*, 195].

There are now numerous PAM systems to choose from, and the choice depends on the research objectives, location, activity, and species to be monitored, as well as budget and time constrains. Acoustic recording devices can be mounted on vessel hulls [196], towed behind vessels [195, 197, 198, 199, 200], or moored to the seabed, which are also known as static acoustic monitoring (SAM) devices [201, 201, 202, 203]. Other systems include drifting buoys [204, 205] and small acoustic tags that can be attached to animals [*e.g.*, 206]. Furthermore, depending of the objective of the study, one can use a single hydrophone [207, 208] or an array, which in turn can be as simple as two hydrophones, or very complex with several hydrophones (or devices) arranged in a strategic configuration. For example, Thomson et al. [209] used an array of static devices (*i.e.*, C-PODs, Chelonia Ltd., UK) in the Moray Firth, Scotland, to investigate whether harbour porpoises changed their distribution as a result of seismic surveys in the area and Malinka et al. [204] studied the movement of harbour porpoises in tidal areas using PLA-Buoy (Porpoise Localising Array Buoy), a self-contained buoy-based system with a vertical hydrophone array comprising eight hydrophones [204]. The duration of the monitoring period also depends on the type of PAM used, ranging from a few hours (*e.g.*, towed systems [210]) to a couple of days or weeks (*e.g.*, D-tags [206]), to up to several weeks or months (*e.g.*, C-PODs [211]).

Existing SAM devices that can be used specifically to study harbour porpoises can be divided into two main types: devices that only log data about acoustic events and those that record continuously. The most used data logger is the C-POD and its predecessor the T-POD (Chelonia Ltd., Cornwall, UK). 'T' stands for timing and 'C' for cetacean. These are self-contained devices that can be deployed on the seabed for long periods without supervision. Additionally, they include a built-in classifier (*i.e.*, KERNO) for clicks and to separate click trains produced by harbour porpoises and other NBHF species, from those produced by dolphins, and those of non-animal origin (*e.g.*, sonar) [211]. This separation is based on a series of parameters estimated for each impulsive sound detected, including estimates of peak-to-peak amplitude and peak frequency, as well as inter-click intervals. Both C-PODs and T-PODs have been successfully used to monitor many NBHF species including the vaquita, the harbour and Burmeister's porpoises, and the Heaviside's and Hector's dolphins [56, 106, 212, 213, 214], as well as other odontocetes such as the bottlenose dolphin [*e.g.*, 201].

Figure 2.15: *CPOD (top) and DeepC-POD (bottom) - from https://www.chelonia.co.uk*

The PODs are used for a wide variety of studies, including seasonal and geographical changes in distribution [215] and response to anthropogenic noise [106, 203, 216], as well as porpoise acoustic behaviour, including diurnal variations in echolocation rates and click train patterns [202]. The embedded algorithms highly reduce the time needed for data analysis and provide researchers with pre-selected data. On the other hand, because the signals are not recorded and the algorithms are not publicly available, verification of the acoustic events is limited and subjective. Furthermore, although the false alarm levels seem to be rather small [*e.g.*, 82], the level of missed clicks is not well understood [217], especially in the context of high background noise levels [218].
Despite this, they showed potential for studying communication in harbour porpoises. Koschinski et al. (2008) used T-PODs to record and describe vocalisation patterns consistent with social calls of a harbour porpoise calf entangled in a fishing net off the coasts of Canada. It is worth noting, however, that the calls were searched for as the authors knew where to look in advance [8]. A new POD is being developed, the F-POD, which would potentially be able to detect social calls [219].
A new alternative to the PODs is the SoundTrap (Ocean Instruments, New Zealand). SoundTraps are self-contained acoustic devices and, unlike PODs, can record continuously, which means that not only verification is possible but also they can be used to study how noise types and levels affect the behaviour of harbour porpoises. Moreover, recordings made with SoundTraps could be used to study harbour porpoise social behaviour and communication. However, recording continuously at high sampling rates (> 300 kHz) required to record harbour porpoise clicks, generates enormous amount of data. Researchers are then faced with two challenges: limitations of storage capacity and available time necessary to analyse the data. Because

SoundTraps include a click (*i.e.*, impulsive sound) detector that saves them in small clips, these can be classified directly and the potential harbour porpoise clicks extracted for further analysis. To that end, an automated classification system that can accurately and reliably identify harbour porpoise clicks is required (especially for studies without concurrent visual information) as well as algorithms to group clicks, extract patterns, and identify behaviours.

2.4.2 Detectors and classifiers

In principle, the terms 'detector' and 'classifier' can be used interchangeably. In signal detection theory, the output of a detector is a yes/no answer as to whether the input is a known signal. In this sense, a detector is a classifier ([see 220]). However, when studying phonations of cetaceans, specifically echolocation clicks produced by toothed whales, using these terms interchangeable can be problematic. In much of the literature, the term 'click detector' is used to mean 'click classifier', when in practice, the detection and classification processes are consecutive steps that complement each other. What is usually referred to as 'click detectors' are energy detectors that detect transient sounds (*i.e.*, 'clicks') in the *.wav* files. These are sounds of short duration with abrupt onset and rapid decay and represent potential echolocation clicks, as the great majority are of non-animal origin and only a small proportion are produced by cetaceans.

One example is the PAMGuard's Click Detector Module. PAMGuard is a modular, open source software aiming to detect and classify marine mammal sounds. It was released in 2006 [221] and it is today one of the most used software for real time monitoring and off-line data analysis. PAMGuard has been shown to be crucial for real-time monitoring of harbour porpoises around underwater noise-producing activities, such as seismic surveys [*e.g.*, 222], as well as for others studies such as fine-scale distribution [90], and monitoring around risk areas for them [204, 223]. This click detector detects impulsive sounds with a signal-to-noise ratio (SNR) over a given threshold (*e.g.*, 6 dB) and extracts them as individual audio clips of very short duration, which includes the signal and a number of samples (*e.g.*, 40 samples) before and after the signal. These clips are then classified as porpoise/no porpoise. The standard settings of the classifier in PAMGuard include a pre-filter (4th order digital Butterworth IIR 10 kHz high-pass filter) and a trigger filter (4th order digital Chebyshev IIR 100-150 kHz band-pass filter, pass band ripple). Clicks are classified as produced by porpoises by comparing the test band (110-150 kHz) to control bands (40-90 kHz and 160-190 kHz), with a 6 dB threshold ('general configuration file – porpoise click detection', available at www.pamguard.com). As an open source software, PAMGuard is regularly improved, and although the user can manage the settings, there is no available information about the performance of the classifier. The precision (*i.e.*, percentage of individual clicks correctly classified as porpoise clicks) reported for an earlier version of this classifier was between 37% and 74%, depending on the settings and background noise, while the proportion of missed clicks was not reported [224]. The user can manually verify the potential porpoise clicks identified by the classifier, and then group them into echolocation events in order to be extracted for further analysis ([92, 116].

In simple terms, a classification system (*i.e.*, a discriminant function in statistics) assigns a given signal X to one of k pre-defined classes or categories according to a series of parameters or functions, where X is a multivariate random variable. For example, the multivariate random variable X (*i.e.*, person's appearance) comprises a series of variables such as x_1 = height, x_2 = weight, and x_3 = hair colour. When we talk about harbour porpoise clicks, these variables would be those that can be used for classification purposes, such as peak frequency and duration. It is clear, therefore, that the classification process takes place after the 'detection'. It is crucial to make the distinction between the detection and classification steps, as each is associated to performance errors which must be corrected for/taken into account using different approaches. Moreover, the settings of the detector impact the performance of the classifier, for example, if the detector uses a high SNR threshold, some clicks would not be detected and thus not classified, regardless of how accurate the classification system is.

Classifying cetacean signals have been a research topic of interest for some decades, as many sounds seem to be species specific. At first, detection and classification was restricted to certain species and conditions due to the limitations of the technology available at the time. One of the first systems was developed to study sperm whales, which produce loud, regular, broadband clicks that they emit approximately every second as they dive [38, 225]. The authors were not able to use any temporal information of the signal (*e.g.*, waveform) for classification purposes, but the rate at which sperm whales click is highly regular and this, together with the direction where the signal was coming from (*i.e.*, bearing), allowed them to separate sperm whale clicks from those signals that were likely noise [225]. This simple detector/-classifier was improved since then and it is still used to study sperm whales [226].

As technology improves, both in terms of PAM devices and computational capabilities, automatic classifiers for cetacean sounds are regularly developed [*e.g.*, 170, 172, 221, 224, 227]. Classification methods for toothed whales sounds have been developed for several species, for echolocation clicks as well as whistles and other tonal sounds. For example, Real-time Odontocete Call Classification Algorithm (ROCCA) is a MATLAB-based tool that extracts, measures, and classifies whistles. These are described using ten variables, including start and end frequencies, maximum and minimum frequencies, and duration. Subsequently, a multivariate discriminant function analysis (DFA) is used to classify whistles to known groups based on orthogonal linear functions derived from the ten selected variables, and regression tree analysis (CART) to create decision trees that separates data into groups through a series of binary splits [228]. ROCCA can achieve high correct classification rates (*i.e.*, precision) for individual clicks for several toothed whale species, with variations between species, ranging from 14.7% to 63.8%, with an overall correct classification of 33.5% [228].

Similarly, Oswald et al. (2003) [229] used DFA to classify whistles within and between nine different odontocete species. The authors used the spectrograms of the whistles and measured 12 variables that were then incorporated into the model. The classifier achieved between 29.9% to 91.2% accuracy within species, however, the performance between species was lower, between 6.7% and 66% [229]. And Romeu et al. (2017) [230] used DFA to classify whistles within the same species (*i.e.*, bottlenose dolphins - *Tursiops truncatus*) in different behavioural contexts. Dolphins from this population are known to forage cooperatively with fishermen in Laguna, in southern Brazil [231]. The authors used seven variables in this case and used DFA to successfully distinguish between whistles the dolphins produced when engaged in cooperative foraging with fishermen and those produced in other scenarios [230, 231].

Kyhn et al. 2013 [41] studied the spectral characteristics of harbour and the Dall's porpoises, which are sympatric NBHF species off west Canada, and harbour porpoises in Danish waters. The authors found enough differences in the spectral characteristics of their signals to distinguish between sympatric species (off the west coast of Canada) and animals of the same species but from different geographic areas (Canada and Denmark). To that end, they used a canonical discriminant analysis, using centroid frequency, root-mean-square bandwidth, and duration as explanatory variables [41].

Classification rates are generally higher than what is expected by chance, although there is high variability, which can be explained at least in part by the existing variability in whistles and clicks characteristics even within species, depending on geographic and behavioural contexts. The perfect classifier can hardly exist, however, as not only the temporal and spectral characteristics of the signal might be affected depending on the direction where the signals impinges on the hydrophone [232], but also the performance of the classifier also depends on how the data was collected and extracted.

2.4.3 Pattern identification algorithms

Unlike other sounds produced by cetaceans and other animals, harbour porpoise echolocation clicks are of very short duration ($< 100\ \mu$s) and it is thus possible to treat each click as a discrete point in time, much as footsteps. When we hear footsteps we have information about the inter-steps intervals and the amplitude (*i.e.*, loudness) of the sound. If the separation between steps is regular, then we assume these belong to just one person, but if the inter-step intervals are irregular, then it is likely that there are more than one person. Similarly, it is possible to use the relative amplitude of the steps to distinguish between the person closest to us, and whether they are approaching or moving away.

With this in mind, a simple method has been developed to separate overlapping click trains, in this case of bottlenose dolphin clicks [233]. Lepper et al. (2005) first estimated the mean and standard deviation of the distribution of the logarithm of the ICI and amplitude difference between consecutive clicks of their dataset. Then used the standard deviation values as a threshold to decide whether a click belonged to the same click train (*i.e.*, animal - Figure 2.16).

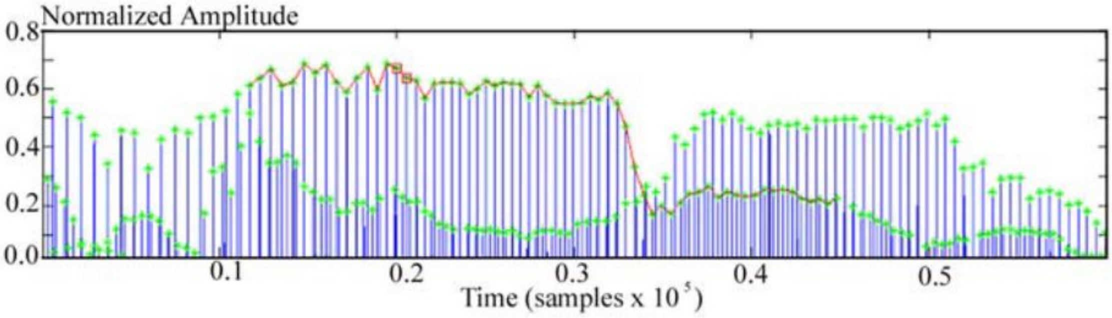


Figure 2.16: *Overlapping click trains. Figure extracted from Lepper et al. (2005) [233] showing two overlapping click trains produced by bottlenose dolphins (Tursiops truncatus) and the result of their algorithm (red line)*

Another similarly simple algorithm was developed by Starkhammar et al. (2011) [234], which uses the level of similarity between the power spectrum of consecutive clicks. Unlike the previous work, this algorithm begins at a random place of overlapping click trains and estimates the correlation of the power spectrum of consecutive clicks in an iterative process. Clicks with a correlation of 0.95 or more are assumed to belong to the same click train [234].

Both manuscripts reported success in the separation of overlapping click trains, although no specific numbers are provided, these algorithms have shown potential for other species [233, 234]. Both methods were developed using data collected by one hydrophone. Amplitude and inter-click intervals are always available to researchers, whether they are using data loggers or continuous recorders, and in the latter case also the power spectrum can be produced. Both methods can in principle, with minor modifications, work if the click trains are incomplete and if other impulsive sounds and multipath have not yet been removed, which is the case for most recordings made in the wild.

2.4.4 Challenges

There are many sources of noise in the ocean, some of which have energy within the frequency range of the porpoise clicks, therefore using acoustic events or click trains is more reliable than using individual porpoise clicks [219]. This is crucial as even though impulsive noise may be classified as a NBHF click, most noise sources are not patterned as NBHF click trains are. Additionally, background noise levels can degrade the porpoise click if the animal are at a limit of detectable distance from the recorder. The most important challenges are discussed below.

2.4.4.1 Directionality

Echolocation clicks are highly directional and as the main axis of the head of the porpoise moves away from the recording system, the signal is filtered and distorted. Although this is especially true for broadband echolocation clicks produced by delphinids, it does affect NBHF clicks [53, 235].

2.4.4.2 Masking

Certain noise types in the background can mask clicks with low signal-to-noise ratio, which can be missed by either the detector or the classifier. This is important because understanding the underlying behaviour of click train patterns, require access to most, if not all, clicks, which can have low amplitudes at the end (*e.g.*, feeding buzzes).

2.4.4.3 WUTS

WUTS refers to 'weak unknown train sources', and as the name indicates, the sources of these trains are unknown. Although they have been found only using T-PODs and C-PODs, WUTS have been reported in many places, including Australia mangroves, Gulf of Maine, Gulf of Alaska, Gulf of California, and the Baltic Sea. They have not been reported in studies using continuous recordings and everything we know about them comes from PODs [219]. These WUTS seem to have complex patterns of repetition rates, that can range from about 7,000 clicks per second to 100 clicks per second, although never below 40. The key feature is the variation in the peak frequency, which seems to be more random than expected in a NBHF click train. Because the POD does not record the sounds, it is not clear how the energy is concentrated, although they seem to have a minimum bandwidth [219].

2.4.4.4 Sonar

In many areas, fishermen use sonar to find fish. The frequencies are usually set at 50 kHz, 100 kHz, and/or 150 kHz. The last two can be a real problem for click train classification as the energy is within the porpoise range and because the inter-pulse intervals of sonars are highly regular. On the other hand, the regularity is relatively easy to identify and the frequency changes are small compared to variations in click trains.

2.4.4.5 Multipath

Multipath is the propagation phenomenon that results in the same signal to reach the hydrophone from different paths. In the case of harbour porpoise clicks, this can occur when the porpoise is facing the water surface (or the seabed) and the click reaches the hydrophone from the direct path as well as after being reflected in the water surface (or the seabed). Depending on the situation, this phenomenon can impact the performance of the classifier (*e.g.*, the multipath signal retains the same spectral characteristics), or the ability to group clicks belonging to the same echolocation event (*e.g.*, the multipath signal retains the amplitude levels or arrives at intervals that could overlap with the signal arriving through the direct path).

Chapter 3

Data description

This Chapter describes the study areas and how the acoustic data were collected and extracted. In Section 'Study areas and data Collection', both study areas in Scotland and Denmark are described as well as how the data were collected in each. In Section 'Data Extraction', the method used to extract the samples used to developed the algorithms throughout this project is explained. Lastly, in Section 'Derived Data' a description of the main variables used and how they were estimated is presented.

One additional dataset was used in this project. See Chapter 8 - D-PorCCA - from acoustics to behaviour for more information.

3.1 Study areas and data collection

3.1.1 Scotland

The Firth of Clyde (55.5254 N, 4.9333 W) in the West coast of Scotland is a large inlet with high freshwater input, characterized by deep channels and unique sediment types (Figure 3.1). It is an area with high biological diversity, and where at least 15 species of whales, dolphins, and porpoises have been observed in the area.

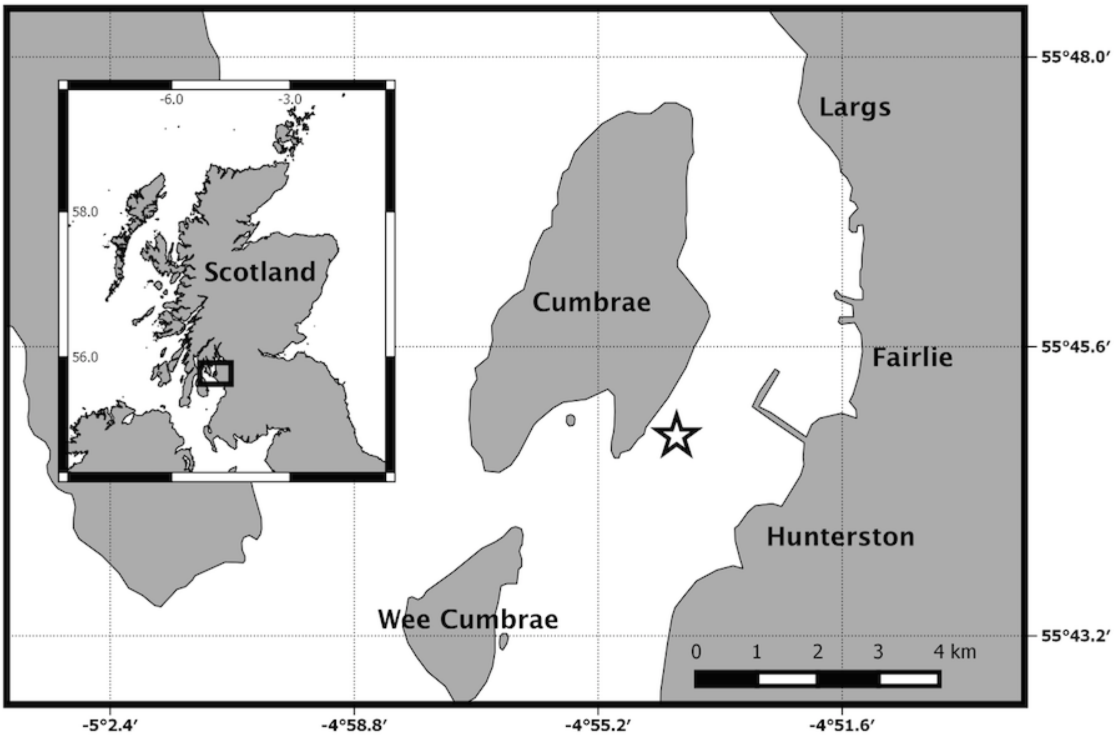


Figure 3.1: *Study area - Scotland. Firth of Clyde.*

Harbour porpoises are the most abundant and most widely distributed small cetacean species in the UK [2, 79, 80, 89, 236], and is a resident species in the Firth of Clyde [90], which is one of the areas with higher density of harbour porpoises in Europe, with a density of about 1 animal per square km [80, 81, 237]. The only abundance estimate for the Firth of Clyde was made over a decade ago from sightings made from July to September 2004, and resulted in 1,645 individuals (CV = 0.351) with a density of 0.823 animal per square km [237]. However, these numbers are likely an underestimation, as Brown (2018) found hot spots where porpoise density is up to 4 animals per square km [90].

3.1.1.1 Data Collection

The acoustic data from the Firth of Clyde used in this project were collected by the CIC Clyde Porpoise during systematic and opportunistic surveys. These were carried out under sail or engine from the 'Saorsa', a 40-foot sailing vessel. In the Firth of Clyde, data were collected in 25 days throughout all seasons, between 2016 (n = 20) and 2017 (n = 5), totalling over 210 hours of recordings. Additionally, data off the north-east coasts of Northern Ireland were collected on the 19th of September 2019 (16 hours). Systematic acoustic surveys were carried out in pre-determined transect lines aiming to provide equal coverage probability to the entire study area, which were designed using the software Distance 7. These transect lines were surveyed at a speed between 5 and 7 knots. Data collection was carried out in different weather and background noise conditions (*e.g.*, vessel traffic, sonar activity), during both day and night times. If the sea state reached $\geqslant 5$ in the Beaufort scale (Table 3.1), the survey was terminated. No concurrent visual efforts were made.

Data were collected using a towed hydrophone array connected to a computer running the software PAMGuard [221]. Different versions of PAMGuard were used, starting with version 1.15.10. The hydrophone array included four omnidirectional

Table 3.1: The Beaufort scale (0-6 only), developed by Sir Francis Beaufort in 1805.

WIND FORCE	WIND SPEED (kn)	DESCRIPTION
0	1	Calm, sea like a mirror.
1	1-3	Light air, ripples only.
2	4-6	Light breeze, small wavelets (0.2 m). Crests have a glassy appearance.
3	7-10	Gentle breeze, large wavelets (0.6 m). Crests begin to break.
4	11-16	Moderate breeze, small waves (1 m), some white horses.
5	17-21	Fresh breeze, moderate waves (1.8 m), many white horses.
6	22-27	Strong breeze, large waves (3 m), probably some spray.

hydrophones, comprising one low frequency hydrophone, one mid-frequency hydrophone, and two broadband hydrophones (Figure 3.2). These were two 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 1V/μPa at 150 kHz, and a flat response between 2 kHz and 150 kHz. The array was connected to a computer and towed behind the vessel using a Kevlar-strengthened 100 m long cable. The Magrec HP03 hydrophone units were 25 cm apart, enough to obtain direction of arrival of impulsive sounds [238]. Only recordings made with the broadband hydrophones were used in this project.

Recordings were digitised through a St Andrews Instrumentation Ltd. data acquisition card with 16-bit ADC resolution, at a sampling frequency of 500 kHz. Due to the large amounts of data collected at such high sampling frequencies using 4 channels, recordings were saved in 9-min long audio files (size of 2 GB) in *.wav* format. Additionally, the computer was connected to a GPS, and latitude and longitude were recorded every second.

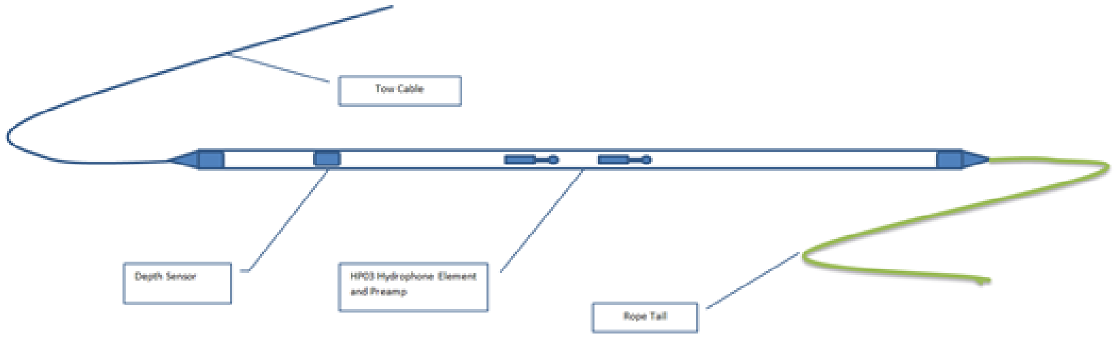


Figure 3.2: *Hydrophone array. Schematic of the hydrophone array system used to collect acoustic data in Scotland.*

3.1.2 Denmark

The Great Belt (55.3615 N, 10.9655 E) is the only deep water entrance to the Proper Baltic Sea and thus a high-traffic area, containing the shipping lane known as ”Route T”, with around 27,000 vessels passing by annually. The Little Belt (55.5295 N, 9.7535 E) is heavily trafficked, with maximum depth of 80 m. The seabed in the area is composed of mud and sand with no kelp. Both areas are known to have high harbour porpoise density in spring and summer months [239].

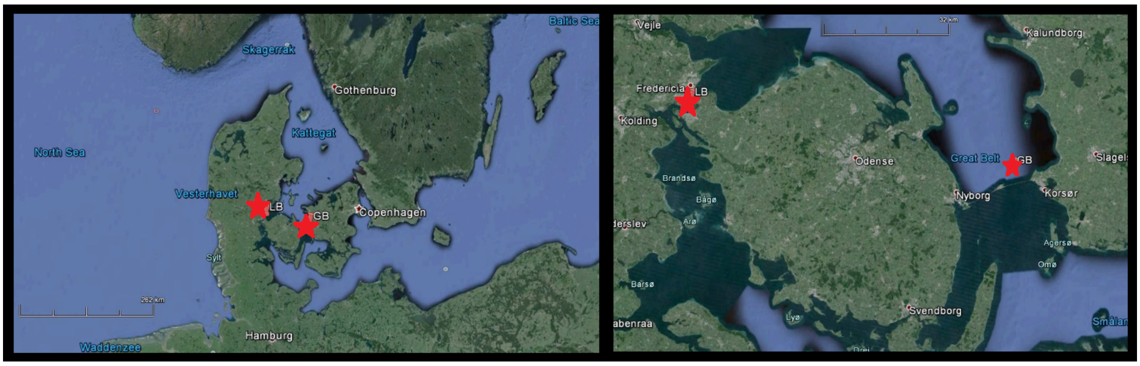


Figure 3.3: *Study area - Denmark. Left: Denmark. Right: Little Belt (LB) and Great Belt (GB). Image © 2015 Google and GeoBasis-DE/BKG (Data: SIO, NOAA, U.S. Navy, NGA, GEBCO).*

3.1.2.1 Data collection

Data were collected in Danish waters in 2015 using SoundTrap ST300 (Ocean Instruments, New Zealand), in two different locations (Figure 3.3). The data were obtained from a total of 7 deployments, 5 in the Great Belt area, in August, September, and November, and 2 in the Little Belt area in August. The deployments in the Great Belt were 1 km from the lane "Route T". SoundTraps are self-contained and recordings are made in *.wav* format, at a sampling rate of 576 kHz. The devices were set up in a structure with an anchor (*i.e.,* a cement block), an acoustic release unit (Sonardyne, UK) to recover the devices, and a submerged buoy to counteract the negative buoyancy of the SoundTrap [**?**].

According to SoundTrap User Guide, "in contrast to traditional hydrophone systems, with SoundTraps there is no need to be concerned with sensitivity in voltage terms. Because SoundTraps integrate the recorder and hydrophone in a single package, there is a fixed relationship between sound pressure and the resultant wav file data, thereby simplifying calibration and eliminating the need for voltage calculations". However, in order to estimate amplitude values in PAMGuard, it is necessary to provide these values. In this project the following were used: sensitivity of -182 1V/μPa, and peak to peak voltage range of 2.0 V as recommended by Ocean Instruments. For more details on how the data were collected see [217].

3.2 Data Extraction

For the completion of this project, two types of data were used: audio files (*.wav* files) which were recorded through PAMGuard, and small audio clips containing individual transient sounds, generated and saved by PAMGuard's 'Click Detector Plug-In' (see below). These are sounds of short duration with abrupt onset and rapid decay and represented potential harbour porpoise echolocation clicks (n = 37,760,282). The *.wav* files were inspected using different versions of Audacity, looking at both the amplitude variations in the time domain (*i.e.*, waveform) and the spectrogram using the default settings (*i.e.*, Hanning window, FFT: 512).
PAMGuard is a modular, open-source software developed to detect and classify marine mammal sounds [221]. The Click Detector Plug-In detects transient sounds above a given signal-to-noise ratio threshold, selected by the user (default = 6 dB). The detected sound is then saved as an individual audio clip, which also includes a very short recording period before and after the impulsive sound detected (default = 40 samples before and after the signal). By default, all impulsive sounds detected in a given hour of recording are individually saved in one *.pgdf* file. PGDF stands for PAMGuard Data File [240].

Individual audio clips from Scotland and Denmark were extracted using a MATLAB algorithm developed by J. Macaulay (available here) and adapted for this project. For each audio clip a series of parameters are provided such as date and

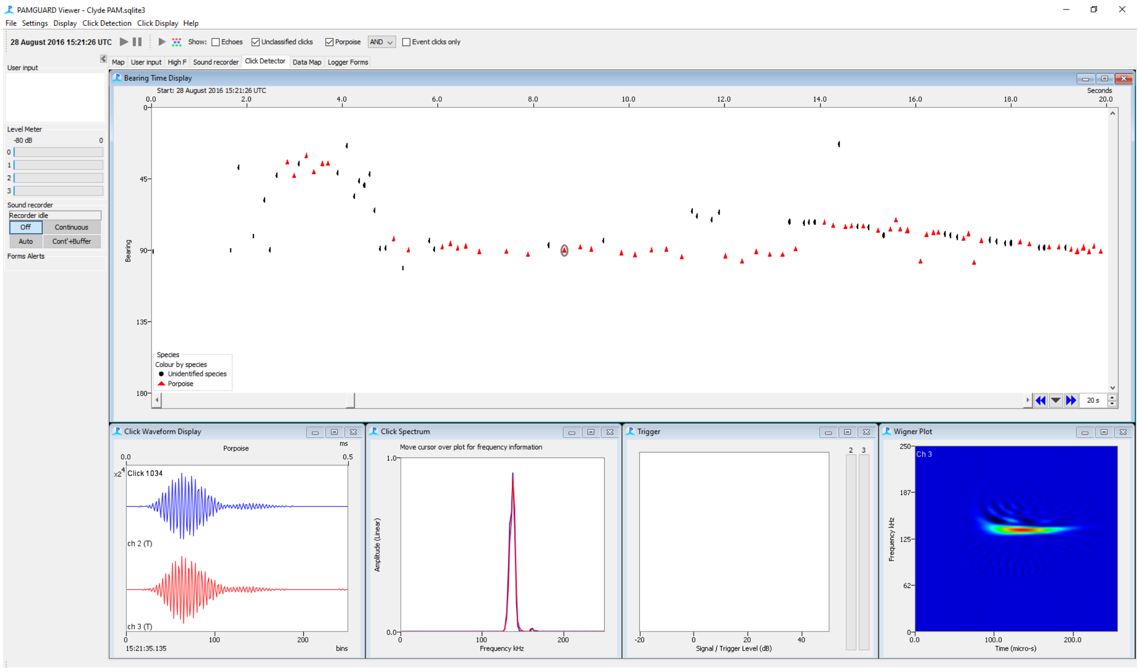


Figure 3.4: *Top: harbour porpoise clicks (in red) over a period of 20 s as seen in* PAMGuard*'s 'Click classifier' display (x = time, y = bearing). Bottom: temporal and spectral characteristics of a selected click (grey circle). Left: waveform in both channels. Centre: frequency domain (FFT - 256 samples). Right: Wigner plot.*

time and, when there are more than one hydrophone, time of arrival difference (*i.e.*, delay) with respect to the reference hydrophone, and direction of arrival, estimated using trigonometric methods based on said delay [224].

The audio clips extracted from Scottish and Danish data were used to test the different algorithms developed in this project. The entire Scottish and Irish dataset comprises over 3 million clips and the entire Danish dataset over 34 million clips.

3.3 Derived Data

A series of parameters were used throughout the project in audio clips extracted as mentioned in the previous Section. The following paragraphs describe these parameters and how they were estimated where applicable.

- **ID -** A unique identification number was assigned to each click in chronological order per day.
- **Date and time -** For clips extracted using PAMGuard, the programme provides date and time in numerical format, which was used like that or converted into text format (*e.g.,* 25 Jul 2017 15:28:34). In case of clips created from *.wav* files using a click detector developed for this project, date and time was obtained from the *.wav* file metadata and estimated for each clip using sampling frequency and number of samples.
- **Start sample -** Sample number where the click begins per day (in PAMGuard) or within the *.wav* file for the detector developed in this project. The sample number is used to estimate the inter-click interval.
- **Duration (μs) -** The duration of the signal was estimated as the 80% energy of the clip that contains the signal [238]. The samples PAMGuard saves contain the signal and samples before and after, which may sometimes include an echo. Moreover, the echo might arrive at the same time as the signal and thus the energy in the sample would be greater than that of the signal itself, therefore using 80% instead of 95 or 97% provided a more accurate approximation of the duration of the click of interest for modelling and comparison purposes.
- **Amplitude (dB re 1 μPa) -** Peak amplitude of the signal.
- **Peak frequency (PF, kHz) -** Frequency with the highest amplitude in the frequency domain (FFT = 256 points) [238].
- **Centroid frequency (CF, kHz) -** The point dividing the spectrum in halves

of equal energy, derived by the squared pressure over a 256-point (128 μs) window, symmetrical around the peak of the signal envelope [241].

- **-3dB Bandwidth (BW_{-3dB}, kHz) -** The -3 dB bandwidth is defined as the bandwidth around the peak frequency that contains half of the signal power [238].

- **RMS Bandwidth (BW_{RMS}, kHz) -** The root mean square bandwidth is defined as the spectral standard deviation around the centroid frequency on a linear scale. (Algorithm courtesy of J. Tougaard) [238].

- **Ambiguous bearing (degrees) -** Direction to the sound source estimated using time of arrival differences (*i.e.*, delays). This information is available in the output of PAMGuard's Click Detector [224]. It is ambiguous because there is no information on where in the water column the source is situated, nor which side of the hydrophone array the signal is coming from.

- **Cross Correlation (XC) -** Maximum cross-correlation (also known as 'matched filtering') coefficient between the clip and a typical harbour porpoise click. The click used as a 'template' is a click extracted from the snip samples, selected based on the waveform characteristics and peak-to-peak amplitude (~162dB re: 1μPa) [235, 238]. Additionally, the waveform was consistent in both hydrophones and the time of arrival difference between them was 0 (*i.e.*, the orientation of the animal was likely towards the array).

- Q_{RMS} **-** Relative width of the signal, and is estimated as the ratio between centroid frequency and BW_{RMS} [33]

- **Inter-click interval (ICI, ms) -** Time difference between the click and the previous one. The inter-click interval for the first click in a click train (click ID = 1) is 0.

- **Clicks per second (CPS) -** The number of clicks per seconds is estimated as 1000 divided the inter-click interval.

These variables and parameters are regularly used in studies on harbour porpoise acoustics characteristics and behaviour, and they are used throughout the thesis for different purposes. In Chapter 4, Q_{RMS}, duration, XC, CF, ratio, and BW_{-3dB} are used to develop a harbour porpoise click classifier for high and low-quality harbour porpoise clicks. In Chapter 5, the repetition rate (*i.e.*, clicks per second) and CF are used to identify click train types, subsequently the repetition rate and the amplitude are used to clean click trains from unwanted sources of sound, and lastly repetition rate is used to identify behaviours. Finally, these are used in different ways in D-PorCCA, the standalone application developed in this project, described in detail in Chapter 8. These parameters and variables are used for visualisation purposes as well as to generate summary data the user can download for further analysis.

Chapter 4

PorCC: the harbour porpoise click classifier

4.1 Introduction

The available acoustic continuous recordings made using passive acoustic monitoring (PAM) systems could be used to fill gaps in our understanding of harbour porpoise behaviour and communication in the wild. To that end, however, a classification system that can accurately and reliably identify as many harbour porpoise clicks as possible within an echolocation event is required. A classification system, in simple terms, assigns a given signal x to one of k pre-defined classes according to a series of parameters or functions. For continuous recordings, one of the most used harbour porpoise detector/classifier systems is PAMGuard's Click Detector and Classifier Module, which is used for real-time as well as offline detections and classifications [92, 116, 242]. PAMGuard is a modular, open-source software designed and developed specifically to detect and classify marine mammal sounds [221]. The standard settings of the porpoise classifier includes a pre-filter (4th order digital Butterworth IIR 10 kHz high-pass filter) and a trigger filter (4th order digital Chebyshev IIR 100-150 kHz band-pass filter, pass-band ripple). Clicks are classified by comparing the test band (110-150 kHz) to control bands (40-90 kHz and 160-190 kHz), with a 6 dB threshold ('general configuration file – porpoise click detection', available at PAMGuard's website.) As an open source software, PAMGuard is regularly improved, and although the user can manage many of the settings of the detector/classifier, there is no available information about its performance. The precision (*i.e.*, percentage of individual clicks correctly classified as porpoise clicks) reported for an earlier version of this classifier was between 37% and 74%, depending on the settings and background noise, although the proportion of missed clicks was not reported [224]. The performance of the current version remains unquantified (at the time of writing). The user can verify the classifications through the Click Detector Display (Figure 3.4) after the identified clicks have been highlighted and extract clicks for further analysis by either selecting everything or by selecting individual echolocation events [92, 116]. Alternatively, some researchers use custom-built classifiers, of which neither the algorithm, nor the performance are publicly available. As acoustic recordings continue to accumulate, assessing the performance of available classifiers for comparison purposes and automating these processes becomes essential.

Recently, different modelling and machines learning methods have been developed and applied to classify cetacean sounds [*e.g.*, 170, 172, 221, 224, 227]. One of such methods is the discriminant function analysis (DFA), which can predict a categorical response variable from a group of 4 or more numeric explanatory variables. Multivariate DFA has been used to classify cetacean sounds, both for odontocetes and mystecetes species, with varied results [*e.g.,* 228]. If the response variable is binary (*e.g.*, yes/no), there is an approach that makes fewer assumptions than DFA and it is more appropriate. This method is the generalised linear model (GLM), more specifically, the logistic regression model. GLMs are parametric because a probability distribution (binomial, in this case) is specified for the response variable. The logistic regression model can be used to estimate the probability that a given signal is a known signal, based on a series of predictor variables. For example, the multivariate random variable X (*i.e.*, harbour porpoise click) comprises a series of variables such as x_1 = peak frequency, x_2 = duration, and x_3 = -3dB bandwidth. The model to be fitted is

$$\mathrm{g(x)} = \beta_0 + \beta_1 * x_1 + \beta_2 * x_2 + \beta_3 * x_3 \ldots$$

Where β_i are the coefficients to be estimated; x_i are the values of the explanatory variables; g(x) is the logarithm base 10 (log) of the odds ratio of $y_i = 1$ *vs* $y_i = 0$ (*i.e.*, the log of the odds of a signal being a porpoise relative to not being one); and β_0 is the intercept or constant (*i.e.* the log of the odds of a signal being a porpoise relative to not being one when all explanatory variables are zero). Thus logistic regression models divide the data in two, on one side what we are looking for and on the other, everything else. Machine learning methods are based on consecutive logistic regression models.

Thus, logistic regression models make an excellent candidate to identify harbour porpoise clicks, which are highly stereotyped sounds [6, 7, 11].

4.2 Methods

4.2.1 Data collection and extraction

The data used for this Chapter were collected in the Firth of Clyde (55.5254 N, 4.9333 W), Scotland, by the Porpoise Clyde CIC. Surveys were conducted in 25 days throughout all seasons, between 2016 (n = 20) and 2017 (n = 5), totalling over 210 hours of recordings. No concurrent visual efforts were made. Surveys were carried out under sail or engine from the 'Saorsa', a 40-foot sailing vessel. See Chapter 3 - Data description for a detailed description of data collection and extraction.

4.2.2 Data exploration

To develop the classifier, a total of six potential explanatory variables were chosen, four of which are regularly used to describe harbour porpoise clicks. These are duration, centroid frequency (CF, kHz), -3dB bandwidth (BW_{-3dB}, kHz), and Q_{RMS}. Additionally, the ratio between the peak and centroid frequencies (Ratio) and the peak value of a cross correlation (XC) performed against a typical harbour porpoise click were used. This typical click was extracted from the original dataset, and was selected based on the characteristics of the waveform, the power spectrum, and the spectrogram, as well as the peak-to-peak amplitude (162dB re: 1μPa). Additionally, the waveform was consistent and overlapping in both hydrophones, as the time of arrival difference between them was 0, therefore the orientation of the animal was perpendicular to the array (See Chapter 3 - Data description for more details on the estimation of these variables).

Before developing the logistic regression models, the following assumptions were tested when required:

-*Linear relationship*: The logistic regression model does not require a linear relationship between the response and explanatory variables.

-*Normality*: The error terms (residuals) do not need to be normally distributed.

-*Homoscedasticity*: the variance of the explanatory variables are not required to be similar for the logistic regression model.

-*Independent observations*: the observations should not come from repeated measurements or matched data. To address this requirement, clicks were selected using a random number generator.

-*Multicollinearity*: Multicollinearity is when the explanatory variables are correlated with each other. The logistic regression model requires there to be little or no multicollinearity. Multicollinearity was tested using the Pearson $\tilde{\chi}^2$ coefficient. None of the variable pairs had a correlation coefficient higher than ± 0.36, except for Q_{RMS} and XC that had a correlation of 0.49 Figure 4.1. 'Multicollinearity was also tested using the generalised variance inflection factor (GVIF) and all pairs of variables had a GVIF value below 2, indicated they were not correlated.

-*Linearity*: The logistic regression assumes linearity of explanatory variables and log odds. Although this analysis does not require the response and explanatory variables to be related linearly, it does require that the explanatory variables are linearly related to the log odds.

-*Sample size*: This model requires a large sample size (n), which can be estimated as n = 100 + x * i, where x is 50 for logistic regression models, and i is the number of explanatory variables [243]. Thus, having a maximum of six explanatory variables, n must be at least 400. A total of 5,000 samples were used per model, 500 signals of interest against 4,500 unwanted signals.

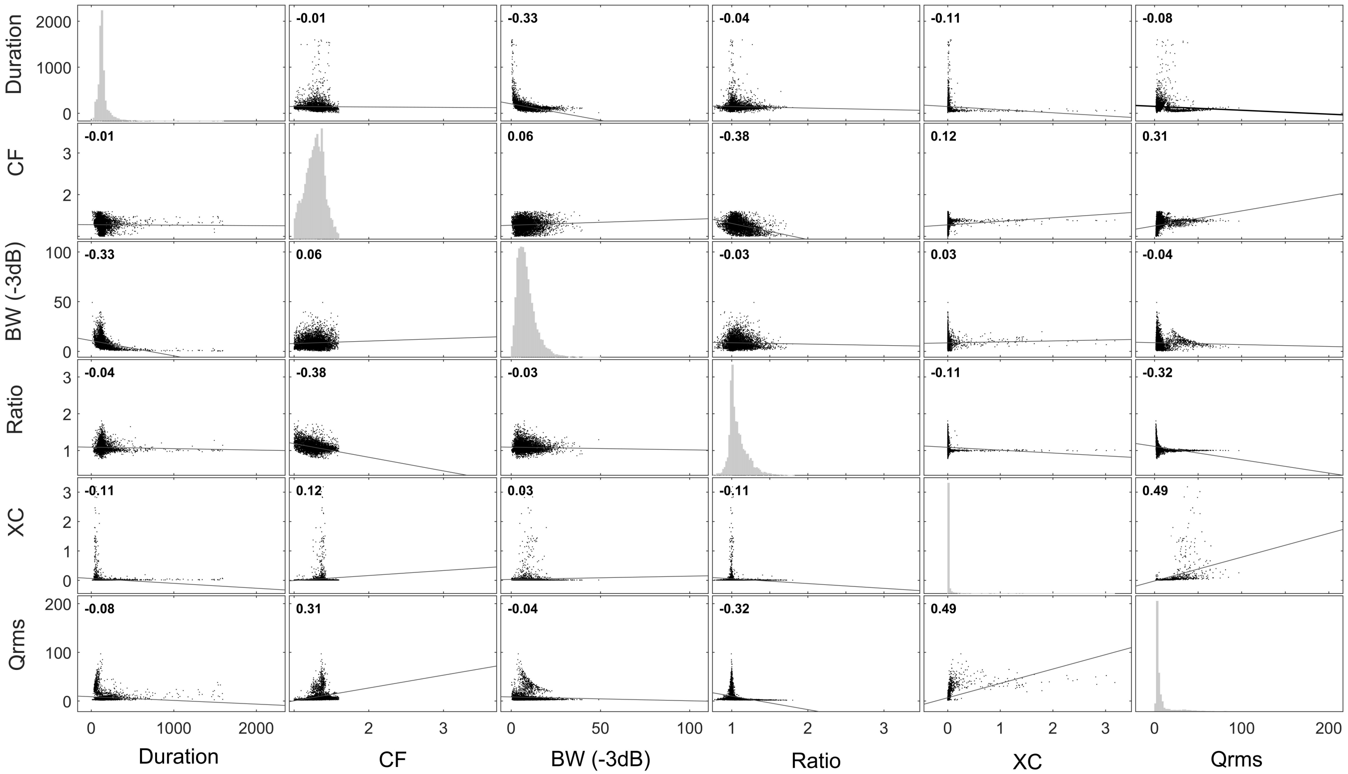
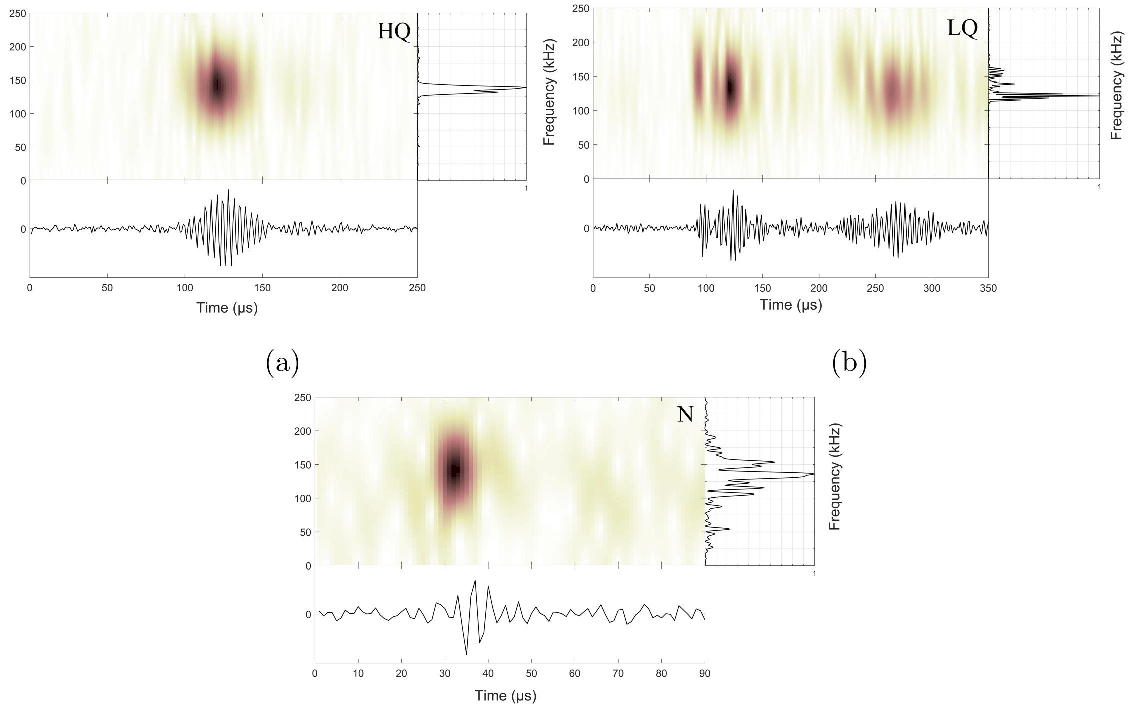


Figure 4.1: *Multicollinearity. Pair plots of predictor variables used in the logistic regression models for the harbour porpoise click classifier. The diagonal contains the histograms of each of the variables. The numbers represents the Pearson's* $\tilde{\chi}^2$ *correlation coefficient.*

4.2.3 Training data

Three categories of signals were defined for the development of the harbour porpoise click classifier (PorCC - for Porpoise Click Classifier): high quality porpoise clicks (HQ), low-quality porpoise clicks (LQ), and high-frequency noise (N), as shown in Figure 4.2. HQ are polycyclic signals with peak frequency between 100 and 160 kHz, no spectral energy below 100 kHz, and duration around 100 μs (Figure 4.2a), matching the description of on-axis harbour porpoise clicks [6, 7, 235]. LQ are signals slightly different to HQ (Figure 4.2b), for example presenting notches in the power spectrum, or no clear beginning or end of the signal when looking at the waveform. The need for this distinction is clear when investigating click trains, as these almost always contain a series of consecutive clicks with consistent the inter-click interval and amplitude variations, indicating that these are indeed clicks within the click train, but that are not of enough quality. Thus, LQ clicks comprise both off-axis and low amplitude clicks. In the decision-making path, clips with peak and centroid frequencies outside the range of interest (100-160 kHz) are discarded before the classification process takes place. Noise clips (N) are, therefore, signals with peak and centroid frequencies between 100 and 160 kHz but that do not share other characteristics with harbour porpoise clicks (*e.g.*, oligocyclic, do have energy below 100 kHz) (Figure 4.2c).

Over 2,500,000 impulsive sounds were detected and saved as small audio clips by PAMGuard's Click Detector Module from the entire survey period ($>$ 210 hours of recordings). The training data selected to develop the classifier consisted of a subsample of 125,416 (5% of the data) clips selected using a random number generator to ensure independence of the samples. Of these, 10,000 clips were further



(a)

(b)

(c)

Figure 4.2: *Categories. Examples of the categories defined to develop the harbour porpoise click classifier (PorCC). A) High-quality harbour porpoise click (HQ). B) low-quality harbour porpoise click (LQ). C) high-frequency noise (N).*

selected to develop a simple logistic regression model, which was used to aid in finding appropriate signals to develop the final logistic regression models for PorCC. This pre-step was necessary as it was not realistic to individually check all of the 125,416 clips to find samples that were representative of each of the defined categories. One volunteer (P. Martinez) and MC labelled these 10,000 clips individually, based on the characteristics described above (Figure 4.2). Because the samples were not consecutive, and because opening large (∼2 GB) audio files in search of a specific click in a spectrogram is a time-consuming task, the spectrogram of the original recordings were not used in this step. This could have led to mistakes when labelling clicks, however, it is expected that such mistakes were not significant for the overall training method, especially for the HQ category, as there are no other animal or human activity carried out in the area capable of producing sounds similar to porpoise clicks.

The logistic regression model estimates coefficients for each explanatory variable in the model and the error term, from which a probability of a given signal belonging to a specific category can be derived, in this case the probability that a given clip is a harbour porpoise (HQ or LQ) click. Thus, each of the 125,416 audio clips was assigned a probability of being a harbour porpoise click using the coefficients of the pre-classifier model. The probabilities ranged from 0 to 1. Those with high probability ($\geqslant 0.9$) were considered potential HQ, those with a probability between 0.5 and 0.9 were considered potential LQ, and those with a probability < 0.5 were considered potential N clips.

For the final step, a total of 5,500 signals were randomly selected using a random number generator. From these, 500 samples were selected from the potential HQ samples, 500 from the potential LQ samples, and 4,500 from the potential N samples. Before using these clips for training of the logistic regression models, all samples (n = 5,500) were verified individually to ensure each selected clip was a good representative of its respective category, removing unrepresentative clips and replacing them with clips randomly selected, again, from the original subsample for that particular category.

4.2.4 Logistic regression - PorCC Classification algorithm

All models and the final algorithm of the harbour porpoise click classifier (PorCC) were written in MATLAB 2017a (The Math Works TM, Inc., Natick, MA, USA).

The response variable for 'Model HQ' is binomial, with the possible outcomes being HQ and N, and it was built using 500 HQ and 4,500 N clips. The response variable for 'Model LQ' is also binomial with the possible outcomes being LQ and N, and it was built using 500 and 4,500 clips of each, respectively. The same N clips were used for both models to ensure that the training of the models was consistent. For each logistic regression model, a series of 63 reduced models were tested, which were built using all possible combinations of explanatory variables, without repetitions (*i.e.*, starting from all 6 variables combined, reducing until using just one variable at a time - see Appendix B). The best 'Model HQ' and 'Model LQ' were identified as the one with the lowest Akaike Information Criteria (AIC) value [244].
Although PorCC runs on clips previously saved by PAMGuard's Click Detector in *.pgdf* binary files, the coefficients and the decision making pathway can be applied to audio clips generated by any impulsive sound detector. The algorithms to extract the data from *.pgdf* using MATLAB, available online, were modified to function within PorCC. If the recordings were made using two or more hydrophones, the classification process takes place only in the sounds recorded by the first hydrophone on which they impinged, as these are expected to be of higher quality (*i.e.*, closer to the sound source). The decision-making pathway for each clip within PorCC is show in Figure 4.3.

The PorCC algorithm is included in D-PorCCA (see Chapter 8) where the user can choose threshold values for high- and low-quality clicks.

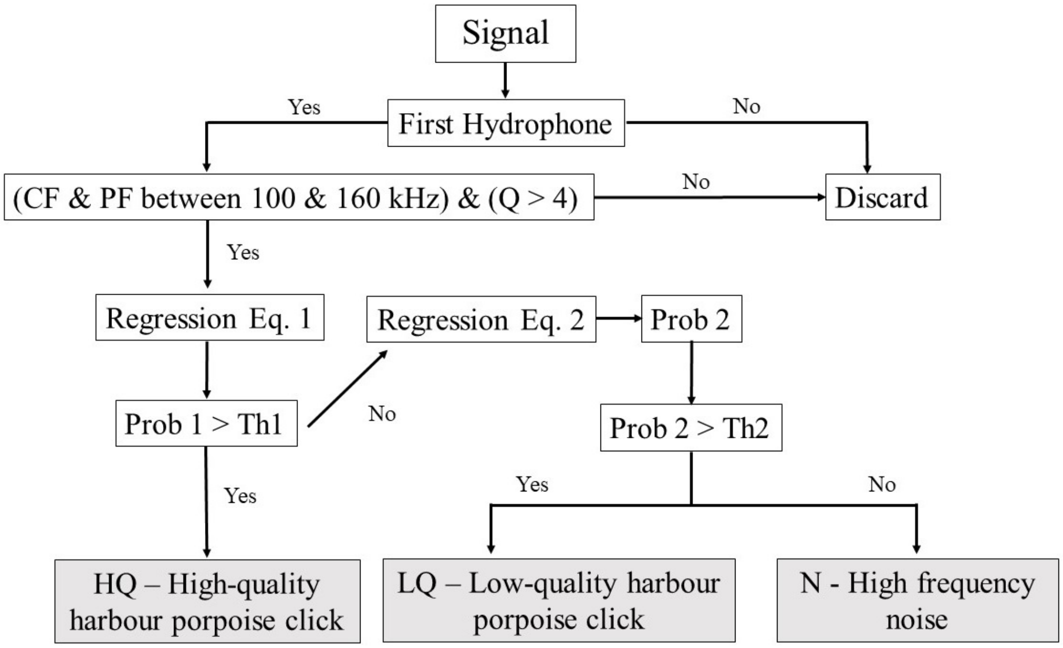


Figure 4.3: *Decision-making pathway. Flowchart illustrating the decision-making pathway of PorCC, the harbour porpoise click classifier. CF = centroid frequency. PF = peak frequency. Th = threshold. Prob = Probability.*

4.2.5 Testing data

To test the performance of PorCC against signals manually labelled, two datasets were created. The first dataset contained all clips (n = 265,918) extracted from 5% of the *.pgdf* files, which were selected using a random number generator. The second dataset contained all clips (n = 284,231) generated from all the recordings made on the 28th of August 2017, corresponding to 8 *.pgdf* files (*i.e.*, each *.pgdf* file stored all impulsive sounds detected in one hour of recording). Clips with peak and centroid frequencies between 100 kHz and 160 kHz and $Q_{RMS} \geqslant 4$ represented potential harbour porpoise clicks. These clips (n = 70,689) were extracted and manually labelled according to the three categories previously defined (Figure 4.2), based on the characteristics of the waveform, power spectrum, and spectrogram.

The overlap between the training (n = 5,500) and the testing (n = 70,689) datasets was of 442 clips only. The probability-threshold values used in PorCC were 0.9999 for HQ and 0.55 for LQ (Figure 4.3).

Confusion matrices and receiver operational characteristics (ROC) curves were used to assess the performance of PorCC against manual labelling. One harbour porpoise researcher labelled 500 clips of all three categories defined before and the level of agreement was 95%, therefore it was decided that using manual labelling as the reference was appropriate. Confusion matrices show how clips labelled manually are classified by PorCC. From the matrix it is possible to calculate hit rates, as well as the rate of misclassification (*i.e.*, false alarm and missed clicks) and precision levels. The hit rate in the strict criterion is the proportion of HQ (or LQ) clips classified as HQ (or LQ). The relaxed criterion is the proportion of HQ and LQ clips classified as either HQ or LQ. Three analyses were performed: one with only HQ clips, one with only LQ clips, and one with both HQ and LQ clips, all against the N clips. The false-alarm rate is the number of N clips classified as HQ (strict criterion), or HQ or LQ (relaxed criterion) divided by the total number of N clips. The missed-clicks rate is defined as 1 minus the hit rate. The precision is defined as the number of clips correctly classified divided by the total number of clips classified into that category. In total, this results in six different points of operation, from which the ROC plot is generated.

4.2.6 PorCC vs PAMGuard

A subset of the testing dataset for PorCC was also used to assess the performance of the porpoise click classifier built-in in PAMGuard and compared it to that of

PorCC. This dataset subset contained all clips from the 28th of August 2017 (n = 284,231) of which 30,897 clips had already been manually labelled. PAMGuard's classifier highlights potential harbour porpoise clicks as well as potential echoes (*i.e.*, multipath) that the user can verify and group into 'acoustic events' to later extract them for further analysis. For the purpose of this study, all highlighted clicks (including echoes) for the entire day were selected without verification, assigned to a unique acoustic event, and exported to an SQL database. Potential echoes were included because it was previously noted by Cosentino that PAMGuard's classifier sometimes misidentifies real harbour porpoise clicks as echoes (and vice versa) as well as for comparison purposes, as PorCC also identifies potential echoes (LQ). PAMGuard creates a table within the SQLite database, where information for each of the extracted potential harbour porpoise clicks is provided, including date, time, and an identification number within the *.pgdf* file where the waveform is saved. Using a custom-built script, and using the identification number, potential harbour porpoise clicks were extracted and saved in a MATLAB structure array for further analysis. Subsequently, clips that were highlighted by PAMGuard's classifier but were discarded by PorCC (*i.e.*, clips with peak and centroid frequencies outside the range of interest) were manually labelled.

Confusion matrices and receiver operational characteristics (ROC) curves were used to assess the performance of PAMGuard's classifier and to compare it against the performance of PorCC. False alarm, hit rates, and precision levels were also estimated, as well as the detectability index (d') [220, 245].

4.3 Results and Discussion

This section presents the result of this Chapter and discusses the relevance in context.

4.3.1 Logistic regression models

According to AIC values, the best 'Model HQ' was that with only Q_{RMS} and duration as explanatory variables. This was expected, as the histogram and distribution of each of the explanatory variables has shown that these were the only variables where there was little overlap for the three categories (see the upper left and bottom right panels in Figure 4.4).

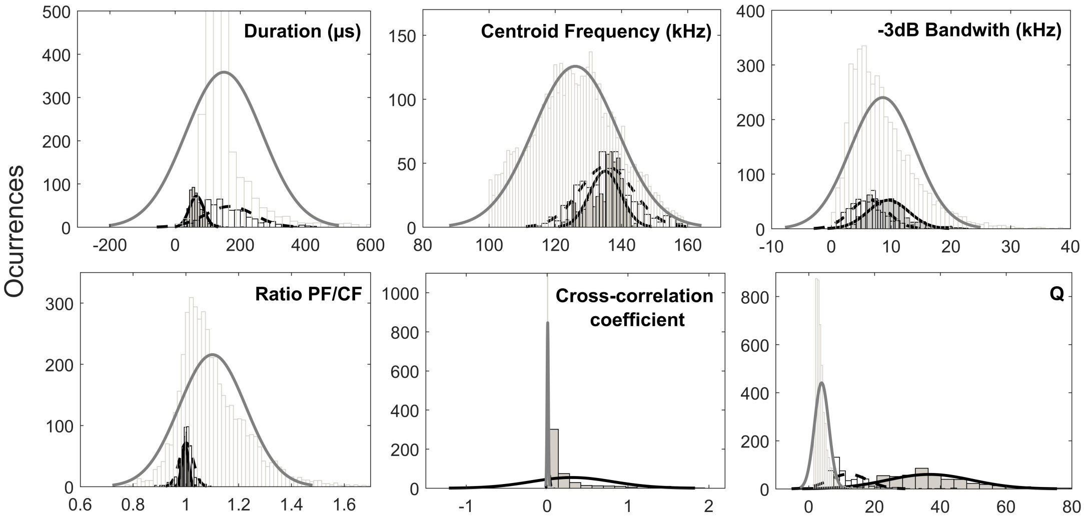


Figure 4.4: *Histogram and distribution of the variables used to develop PorCC. Black line: high quality clicks (HQ). Black dashed line: low quality clicks (LQ). Gray line: noise clips (N). The variables in the lower panel do not have a unit. Y axis truncated for the cross-correlation coefficient and duration*

The best 'Model LQ' included all six explanatory variables: Q_{RMS}, Duration, Ratio, XC, CF, and BW_{-3dB}. This was also expected and for similar reasons, as there was significant overlap for all variables in LQ and N categories (Figure 4.4). The best five models are show in Table 4.1. The table with all the results is in Appendix B. It is worth noting that in both cases, when looking at models with only one explanatory variable, the model with the cross-correlation coefficient (XC) as the only explanatory variable appears in the second position after Q_{RMS}. There is enough variation in the temporal and spectral characteristics of porpoise clicks, which are not blueprints of each other, and so a cross-correlation would not perform well. The cross-correlation coefficient value, in fact, ranged from 0.0038 to 4.5655, and thus using a simple threshold for a XC coefficient in a decision-making process would inevitably include HQ as well as LQ and N samples, thus rendering a low performance. In this case the samples were not scaled before the cross correlation was performed, which may also have affected the performance. The training and testing data were both obtained from wild individuals that were engaged in natural behaviour, and it included off and on-axis clicks and thus there is more variability than could be expected if the classifier had been developed using clicks recorded from captive individuals in controlled environments.

Table 4.1: ***Logistic regression models***. *Series of logistic regression models for 'Model HQ' and 'Model LQ'. Only the best five models are shown here. See text for description of the variables used. The outcomes of the response variable for 'Model HQ' are high-quality harbour porpoise clicks or high frequency noise, and for 'Model LQ' are low-quality harbour porpoise click or high-frequency noise. AIC = Akaike's Information Criterion.*

ID	Explanatory variables	Δ AIC
	Model HQ	
1	Q_{RMS} + Duration	-
2	Q_{RMS} + Duration + Ratio	1.64
3	Q_{RMS} + Duration + BW_{-3dB}	1.67
4	Q_{RMS} + Duration + CF	1.78
5	Q_{RMS} + Duration + XC	1.96
	Model LQ	
1	Q_{RMS} + Duration + Ratio + XC + CF + BW_{-3dB}	-
2	Q_{RMS} + Duration + Ratio + XC + BW_{-3dB}	1.19
3	Q_{RMS} + Duration + Ratio + CF + BW_{-3dB}	19.19
4	Q_{RMS} + Duration + XC + CF + BW_{-3dB}	20.07
5	Q_{RMS} + Duration + Ratio + BW_{-3dB}	20.87

4.3.2 PorCC performance

The perfect classifier cannot exist, as detection always will be limited by noise, either external from the environment, or internal. For electronic systems this internal noise is in amplifiers and hydrophones, and for biological systems, this noise will be in the form of spontaneous activity in the neurons. In real-world applications, noise also comes in the form of substantial variation in the temporal and spectral characteristics of acoustic signals. These are affected by many factors, including background noise and the direction from where the signals impinge on the hydrophone, as well as by how the data were collected (*e.g.*, hydrophone own noise, frequency characteristics of the hydrophones) [26].

PorCC classification process, including estimating all necessary parameters, takes approximately 1 ms per clip. Harbour porpoises produce between fewer than 10 and a few hundred clicks per second depending on their behaviour [12, 13, 107], PorCC shows, therefore, potential for real time application. The performance values for PorCC are shown in Table 4.2. As precision increases hit rate decreases, that is, fewer clicks of the total available to the classifier are going to be identified, demonstrating the well-known trade-off between errors: false alarms *vs.* misses in signal detection and Type I *vs.* Type II errors in conventional statistics.

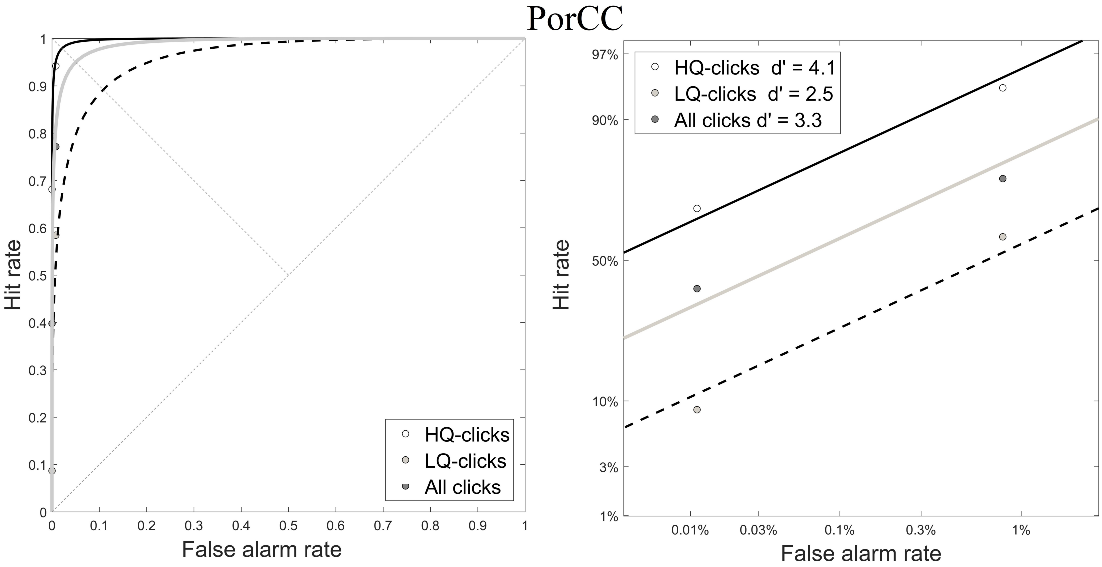


Figure 4.5: *Receiver operating characteristics (ROC) curves. Dots represent false alarm rates and hit rates associated with detection of HQ-clicks (solid black line), LQ-clicks (black dashed line) and both types combined (grey line), all against a background of N-clicks. Curves are best fitting ROC-curves, generated under the assumption of Gaussian underlying distributions with equal variance. Figures show performance by PorCC under two different criteria: strict (only clicks classified by PorCC as HQ) and relaxed (all clicks classified as either LQ or HQ). Figures to the left and right contain same data, but right figures are plotted on double probit (probability) axes*

PorCC is not exempt of errors, and attempts to increase the hit rate would lead to an increase in the false alarm rate (Figure 4.5), as seen in the change in performance going from a strict (using only HQ clicks) to a relaxed criterion (using both HQ and LQ). In other words, the smaller the probability threshold for the classifier, the larger the number of clicks that would be identified and greater the error too. However, the ultimate goal in acoustic event detection and classification is not to avoid errors, but to manage them. Thus, PorCC provides the user with a general assessment of its performance through the ROC curves, as these show the changes in hit rate with false alarm variations [220], which results from using different threshold values to classify harbour porpoise clicks.

Users can, *a priori*, manage the level of error according to the project needs using the ROC curves as reference to understand the expected level of error. Furthermore, because PorCC distinguishes between high and low-quality clicks, depending on the objectives of the study, users can focus on either or both HQ and LQ clicks as well as decide when LQ clicks should be ignored (*e.g.*, single LQ clicks) or taken into account (*e.g.*, studies of click train patterns - see Chapter 8).

It is expected that when using mobile and static recorders, many clicks within a click train would be off-axis and therefore any study aiming to understand the repetition pattern of harbour porpoise clicks in the context of their behaviour must include both HQ and LQ clicks. Available data suggest in fact that the variation pattern of inter-click intervals within a click train is indicative of specific behaviours [8, 11, 12, 13, 246]. The relatively-well understood pattern is that of foraging. The porpoise first investigates the surroundings emitting between 10 to 50 clicks per second. The interval between consecutive clicks is related to the distance to the target, thus the closer the porpoise gets to the prey, so the repetition rate increases, as the echoes also return faster too. It is usually agreed that when the ICI reaches less than 10 ms (*i.e.*, over 100 clicks per second), the porpoise is in the final stages close enough to the prey to make a catch, known as a feeding buzz.

The PorCC classification algorithm can be used with the output of any transient-sound detector for continuous recordings and, given the low misidentification levels, it is suitable for behavioural studies of wild harbour porpoises and other species that produce similar sounds, as the variations in inter-click intervals can only be detected if the majority of clicks within a click train are identified. Moreover, these studies can be carried out in data that has already been collected using either towed hydrophone arrays or static devices, such as SoundTraps (Ocean Instruments, New Zealand). The PorCC algorithm, including the functions to estimate the different variables and the resulting coefficients, are part of D-PorCCA, an application developed specifically to study harbour porpoises in the wild. Additionally, they are publicly available at the Pure Data Repository of Strathclyde University (here) and can be coded in other programming languages, such as Python. It could also be incorporated into PAMGuard.

4.3.3 PorCC vs PAMGUARD

A total of 30,897 clips from the 28th of August met the criteria for potential harbour porpoise clicks, that is, having peak and centroid frequency between 100 and 160 kHz and Q_{RMS} higher than 4. The results of the comparison of the performance of PorCC (using Th1 $\geqslant$ 0.9999 and Th2 $\geqslant$ 0.55) and PAMGuad's classifier for HQ are shown in Table 4.2. Based on the detectability indexes, PorCC outperforms PAMGuard's classifier in all cases, but especially for HQ clicks (Figure 4.5).

Table 4.2: *Confusion matrices. Comparison of correct and misidentification levels between PorCC and the Porpoise Click Detector/Classifier Module in PAMGuard, and overall performance of PorCC. HQ = high-quality harbour porpoise clicks. LQ - low-quality harbour porpoise clicks. Noise = high- and low-frequency noise (i.e., anything that is not a porpoise click).*

Labelled			PAMGuard			PorCC				PorCC	
	Total	HQ	LQ	Noise	HQ	LQ	Noise	Total	HQ	LQ	Noise
HQ	1,833	564^a	-	$1,269^b$	1,209	565	113^b	6,567	4,475	1,710	382
LQ	965	-	375	-	23	436	1,283	5,991	519	2,982	2,490
Noise	281,433	477 $+1601^{a,c}$	-	279,355	25^c	2,093	280,034	537,591	60	4,303	533,228

a) Of the total of 3,017 clips highlighted by PAMGuard as potential harbour porpoise clicks, 1601 had Q_{RMS}¡4 and peak and centroid frequencies outside of the 100 and 160 kHz range, therefore they were not captured by PorCC, as they were discarded at the first step.

b) Missed clicks (HQ clicks classified as N divided by the total number of HQ click).

c) False alarm (N clips classified as HQ clicks divided by the total number of N clips).

The overall precision for HQ for PorCC was 69.2% while it was 30.8% for PAMGuard's classifier, assuming that PAMGuard's classifier correctly classified HQ and LQ as such in 100% of the cases, as once clicks are extracted from PAMGuard, there is no information of whether a clip was originally classified as a harbour porpoise click or an echo, which can be considered as equivalent to the HQ and LQ categories (Figure 4.6).

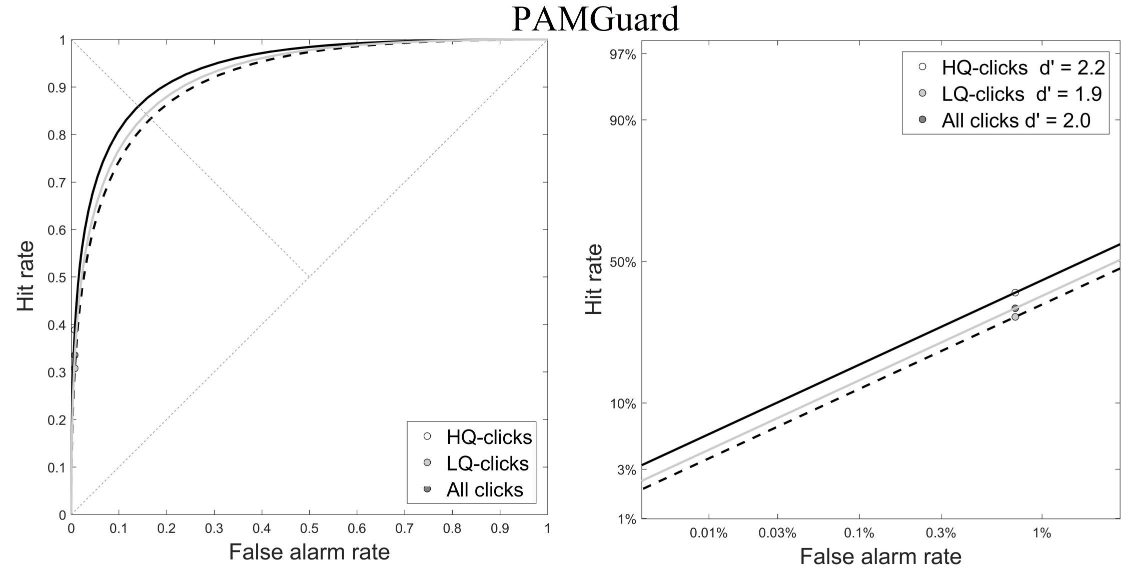


Figure 4.6: *Receiver operating characteristics (ROC) curves. Dots represent false alarm rates and hit rates associated with detection of HQ-clicks (solid black line), LQ-clicks (black dashed line) and both types combined (grey line), all against a background of N-clicks. Curves are best fitting ROC-curves, generated under the assumption of Gaussian underlying distributions with equal variance. Figures to the left and right contain same data, but right figures are plotted on double probit (probability) axes*

Although the data used to generate the ROC curves fall in the lower part of the curve (Figure 4.5 and Figure 4.6) and thus may be misleading, the false alarm rate, defined as N clips classified as HQ clicks, for PAMGuard's classifier was was between 19.08 (n = 477) and 83.1 (n = 2,078) times higher than PorCC's, when using the same dataset (Table 4.2). Moreover, PorCC algorithm correctly classified 65.9% of HQ clicks (n = 1,209), while PAMGuard's did so in 30.7% of HQ clicks (Table 4.2).

4.4 Applications

The PorCC algorithm is one of the algorithms within the application D-PorCCA, developed during this project (see Chapter 8 D-PorCCA - from acoustics to behaviour). Within D-PorCCA, once all HQ and LQ are classified and information about them stored, clicks are grouped into click trains. A click train is defined as a series of clicks (default = a minimum of 16 clicks and a maximum of 1,500 clicks) separated by less than a given time period (default = 1 s). See Chapter 5 Patterns of click trains and Chapter 6 Acoustic behaviour for a description of how click trains are analysed.

Although PorCC was trained and tested in data collected using a towed hydrophone array, given the nature of the harbour porpoise signals, it was expected that PorCC could be used to classify acoustic data collected using other devices, in this case SoundTrap (Ocean Instruments, New Zealand). SoundTraps are self-contained recorders with one hydrophone that can be deployed for long periods of time moored to the seabed or deployed temporarily, for example hanging over the side of a still vessel or the shore. Additionally, it was expected that PorCC would perform equally well for clicks produced by porpoises from a different population, in this case Denmark. Lastly, given narrow-band high-frequency (NBHF) clicks produced by harbour porpoises are similar to NBHF clicks produced by other species, such as Heaviside's dolphins (*Cephalorhynchus heavisidii*), it was expected that PorCC could be used for these species too. A series of tests were performed to investigate these hypotheses and the results are shown in Chapter 5 - Patterns of click trains, in Chapter 6 - Acoustic behaviour, and Chapter 8 - D-PorCCA - from acoustics to behaviour.

4.5 Summary

PorCC is an acoustic classifier developed using machine learning techniques that has been shown to be highly accurate in identifying NBHF clicks produced by harbour porpoises, with improved performance over the currently available classifier in PAMGuard. The algorithm is fast and thus shows potential for real time applications. Moreover, PorCC can be applied to data collected using both mobile and static PAM systems and in recording from different harbour porpoise populations. Furthermore, it can be used to study other species that produce NBHF clicks including other porpoise and dolphin species.

The inclusion of high and low quality clicks in the classification process means that most, if not all, clicks within a click train would be identified. The result of this study suggest that PorCC is an ideal tool for behavioural studies based on vocalisation patterns for harbour porpoises and other NBHF species.

Chapter 5

Patterns of click trains

5.1 Introduction

Acoustic data from animals in captive settings as well as in their natural environment have shown harbour porpoises emit clicks almost continuously and that these clicks are not produced randomly. Click production is patterned differently depending on the behaviour of the porpoise [*e.g.* 10, 11, 12]. Because clicks are very short in duration ($\sim 100\ \mu$s), they can be treated as discrete points in time, from where patterns of repetition rates can be identified. Data from acoustic tags are especially good for this purpose, as tags usually also collect data on animal movement as well as other environmental parameters such as water depths [13, 108].

Finding these patterns in data collected using passive acoustic monitoring, however, is not straightforward. First and foremost, click trains are not always complete because clicks are emitted in a narrow beam and porpoises are not always oriented towards the recorder. This is problematic because identifying patterns require access to most if not all clicks within a click train. A strict classifier that only identifies on-axis clicks would have high levels of false negatives, while a classifier with relaxed criteria will have high levels of false positives. The PorCC algorithm developed in this thesis (Chapter 4 - PorCC: the harbour porpoise click classifier [15]) includes two classifiers, a strict one for high-quality clicks (HQ), anda relaxed one for low-quality clicks (LQ). This means that click trains may include other sources of sounds, such as high-frequency noise or multipath signals, incorrectly classified as LQ. Therefore, to identify underlying patterns it is necessary to first remove undesired sounds.

A simple method developed to separate overlapping click trains of bottlenose dolphin (*Tursiops truncatus*) provides a good approach to this problem [233]. Lepper et al. (2005) used information about inter-click interval (ICI) and amplitude variations within click trains to group clicks from the same click train (*i.e.*, animal). The algorithm begins at the first click and identifies the following ones based on predefined threshold of inter-click interval and amplitude variations. These thresholds are defined as the standard deviation of the distribution of the logarithm of the ICI and amplitude differences of consecutive clicks [233]. Therefore, in this case it is assumed that the thresholds are fixed. Additionally, for these thresholds to work, the detector/classifier system used must have identified all clicks in the click train, and it also should be cleaned of noise incorrectly classified as echolocation clicks. Following the same logic, we can assume that there is a click train of interest and we can use the same approach to separate it from noise misclassified as clicks, using adaptable thresholds instead of pre-defined ones, as harbour porpoises can begin clicking with ICIs of over 50 ms and end at ICIs below 1 ms [*e.g.*, 8, 9, 10, 11, 12, 13, 108].

This Chapter presents a series of consecutive algorithms based on the ideas developed by Lepper et al. (2005) adapted to remove unwanted sound sources within click trains, exposing underlying patterns, and identifying behaviours.

5.2 Material and Methods

Two datasets were used to develop and test the algorithms in this Chapter. One dataset was constructed with acoustic data collected in two locations in Danish waters, between the Baltic Sea and the Kattegat Strait, and the other with acoustic data collected in the Firth of Clyde, Scotland, and off Northern Ireland.

5.2.1 Data collection and extraction

The acoustic data consisted of individual impulsive sounds (*i.e.*, potential harbour porpoise clicks) extracted from the *.pgdf* files generated by the Click Detector Module in PAMGuard, and classified using the Porpoise Click Classifier PorCC (Chapter 4 - PorCC: the harbour porpoise click classifier) with the default values. The default threshold value for high-quality (HQ) harbour porpoise clicks was 0.9999 and 0.55 for low-quality (LQ) ones. Data from Denmark were collected between August and November of 2015 using SoundTraps (Ocean Instruments, New Zealand), and the data from the Firth of Clyde and off Ireland were collected between 2016 and 2019 using a towed hydrophone array. The recordings (*i.e.*, *.wav* files) were used for verification purposes when available (*i.e.*, data from Scotland).

In this Chapter, the parameters used were peak-to-peak amplitude (dB re: 1μPa) and inter-click interval (ICI) in ms. See Chapter 3 - Data description for a detailed description of how the data were collected and extracted, and parameters estimated. Clicks were grouped in series of clicks separated from each other by no more than 1 second. This rendered a total of 139,338 potential click trains (n = 2,249,017 clicks). Only click trains with at least 16 clicks were selected for further work (n = 21,185). The algorithms in this Chapter were written in different versions of MATLAB (Mathworks, MA), from 2016b onwards. Three algorithms were developed for this Chapter, each with a different objective, which are meant to be used sequentially. The first aims to determine whether the clicks grouped in an acoustic event correspond to a click train produced by a harbour porpoise (or another NBHF species). The second aims to separate click trains from undesired sources of sounds. And the third aims to identify general behaviours from the click train pattern.

5.2.2 Click train type

In this first step, the aim is to identify click trains that were produced by harbour porpoises, both of high and low-quality, labelled narrow-band high-frequency (NBHF) and low-quality (LQ) NBHF, respectively. 'NBHF' click trains are those where patterns can be clearly recognised visually and thus have highly likely been produced by harbour porpoises or other NBHF species. In 'LQ-NBHF' click trains patterns sometimes can be seen but they are not always clear due to high levels of high-frequency background noise or multipath signals. Two more types of click trains were defined: 'Sonar' and 'Non-NBHF', the latter having no recognisable pattern for the human observer (Figure 5.1). Henceforth, this algorithm would be referred to as 'Type algorithm'.

The classification of click train types is based mainly on the percentage of variation in the repetition rate (*i.e.*, number of clicks per second - CPS) between consecutive clicks, specifically the median of the variation. This metric was selected as it

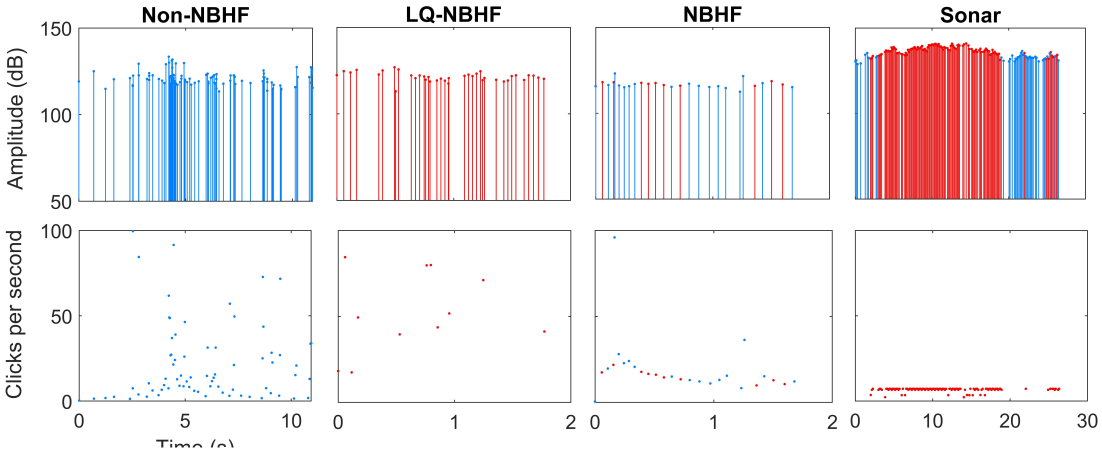


Figure 5.1: ***Click train types***. *Example of each click train type. NBHF = narrow-band high-frequency. LQ = low quality. The y axis is truncated. Red = high-quality clicks. Blue = low-quality clicks.*

was expected to predict best whether there is an underlying pattern. The threshold values were chosen based on data exploration. The algorithm includes several steps and iterations, which also uses information about the length of the click train and how many high-quality (HQ) clicks it has. A schematic of the decision tree is shown in (Figure 5.2).

In environments with high levels of high-frequency background noise silent periods longer than 1 second are rare, and thus a 'click train' would be thousands of clicks long. To avoid this problem, a maximum length of 1,500 clicks was set, in which case the train is divided into smaller click trains with a maximum of 1,500 clicks, and a series of steps are followed to classify them into either of the four categories described above. Click trains that are classified as LQ-NBHF are run again through the 'Type algorithm'. The reason for this step, is that the original click train could have been in fact more than one click train (*e.g.*, it was hidden behind noise) and thus the metrics used to classify click train into types may have changed.

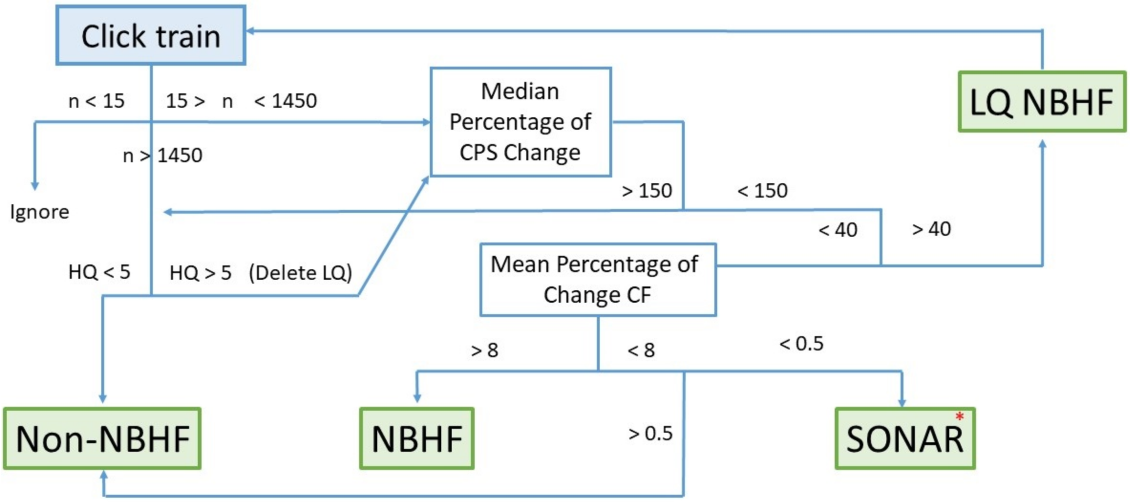


Figure 5.2: ***Click train types***. *Decision tree of the algorithm to identify different click train types. n = length of the click train. CPS = clicks per second. CF = centroid frequency. * A click train was labelled as 'Sonar' when the mean peak frequency exceeded 140 kHz, the median CPS was between 7 and 8.7, and the mean percentage of change of CF was below 0.5*

The 24th of November 2015 was selected for testing purposes as it contained the highest number of click trains (n = 5,140). Click trains were manually labelled first and subsequently using the algorithm developed in this Section. The results were used to assess the performance of the algorithm against manual labelling.

5.2.3 Extracting patterns

The algorithm to identify patterns (henceforth 'Pattern algorithm') consists of two steps described below:

5.2.3.1 Deleting unwanted sources of sounds

Click trains have different characteristics. Some have high signal-to-noise ratio and few outliers, while others are a mix of HQ and LQ porpoise clicks, and others have high levels of background noise. This means that different approaches are needed to maximise performance. The values used in this section are: clicks per second (CPS), obtained by dividing 1000 by the ICI (in ms); the maximum difference (*i.e.*, jump) in CPS, when sorted in ascending order. It indicates whether there are outliers (*e.g.*, multipath); median percentage of change of CPS; and mean percentage of change of centroid frequency.

At the end of this step there will be a new click train or the click train will go through an additional series of step (next section). The full algorithm is in Appendix C and includes comments in blue.

5.2.3.2 Identifying stable areas and extracting patterns

The second step is to identify areas with low variation in CPS, by estimating the moving average of CPS (n = 5 consecutive clicks). Positions where the variation is under 5% are used as starting points. From these starting points, the algorithm moves backwards and forwards in an iterative process in search of clicks that are consistent in both CPS and amplitude variations. The reference and threshold values are updated in each iteration, as these depend on the click selected in the last iteration.

The full algorithm is in Appendix C and includes comments in blue.

5.2.4 Identifying behaviours

Three main behaviours were defined for the purpose of this study: 'Orientation', 'Foraging', and 'Socialising'. Patterns that did not fit in either of these categories were labelled 'Unknown'. Henceforth, this algorithm would be referred to as 'Behaviour algorithm'.

5.2.4.1 Orientation

Orientation is characterised by having a relatively regular inter-click interval greater than 10 ms. In other words, the porpoise produces under 100 clicks per second, typically between 20 and 60 (Figure 5.3), while it inspects the environment it moves through [*e.g.*, 109, 208].

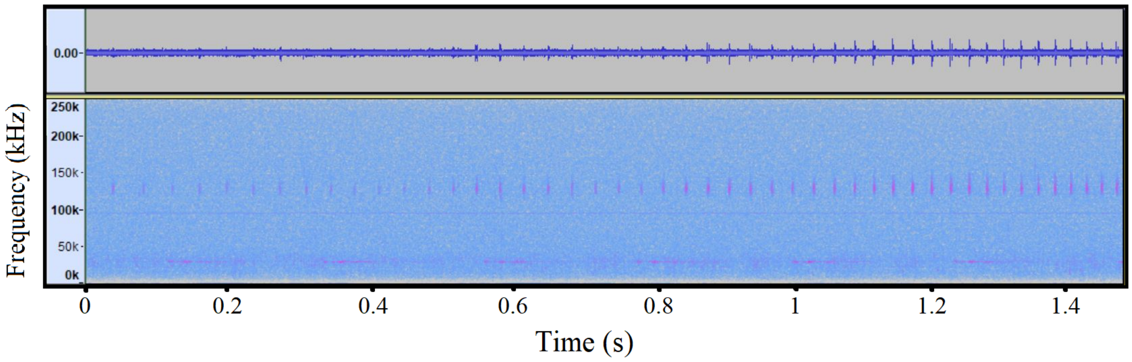


Figure 5.3: ***Orientation***. *Spectrogram (Hann window, FFT size = 512) of a typical click train produced by a harbour porpoise while orienting itself or inspecting its environment. Upper panel: amplitude variation in arbitrary units.*

Click trains are labelled as 'Orientation', if at least 90% of all clicks have repetition rates below 100 CPS.

5.2.4.2 Foraging

Foraging or feeding events are characterised by a change in clicking rate that follows a specific pattern: a search phase where the porpoise produces fewer than 100 clicks per second, indicating that the animal is not focused on an specific object yet, an approach phase that occurs when a prey is found during which the CPS increases rapidly, and a final stage of high-production rate that can reach up to 640 clicks per second [*e.g.* 9]). The final stage is known as a feeding buzz [123].

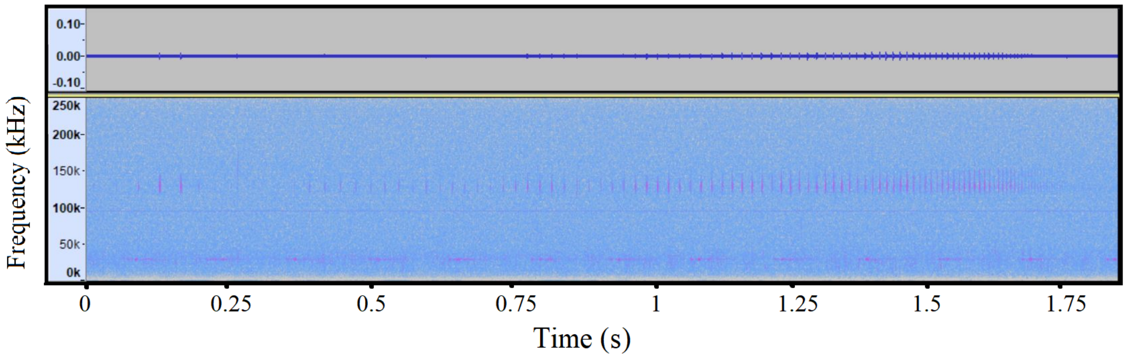


Figure 5.4: ***Foraging***. *Spectrogram (Hann window, FFT size = 512) of a click train produced by a harbour porpoise during a foraging/feeding event. The final phase is known as a feeding buzz, reaching in this case up to 200 clicks per second. Upper panel: amplitude variation in arbitrary units.*

The algorithm labels a click train as 'Foraging' when it finds an increase in consecutive clicks from below 100 to over 100 CPS. In other words, the algorithm finds the first click with a repetition rate of over 100 CPS, and estimates the mean CPS for the previous and following 5 clicks.

5.2.4.3 Socialising

Communication or social calls are patterned in many ways, which are different from feeding buzzes and click trains used for orientation purposes. However, there might be overlap between them, for example, the contact call described in Clausen et al. (2010) [12] is similar to the foraging event described in Deruiter et al. (2009) [9]. Social calls lack the low-repetition period that characterise feeding buzzes. An example of a spectrogram of social call is shown in Figure 5.5

The patterns of communication or social calls include V-shaped (Figure 7.15), decreasing CPS, and short and long calls with stable CPS values throughout (see Chapter 6 - Acoustic behaviour). The algorithm labels a click train as 'Socialising'

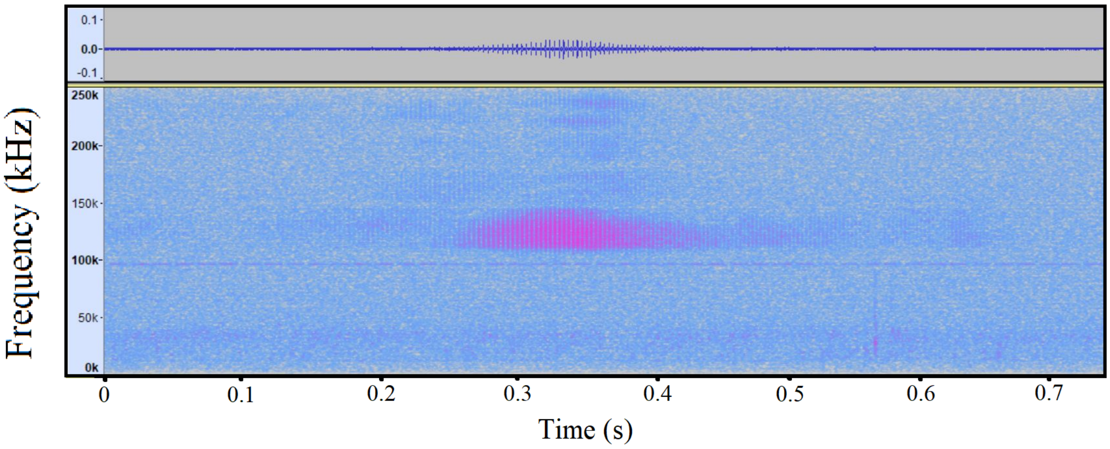


Figure 5.5: ***Burst pulse***. *Spectrogram (Hann window, FFT size = 1,024) of a social call produced by a harbour porpoise. The repetition rate ranges between 550 and 650 clicks per second. Upper panel: amplitude variation in arbitrary units.*

when all clicks have CPS over 100, or when CPS decreases regularly from over 100. It is expected that this algorithm is not able to identify all communication calls, as knowledge of the different patterns is lacking and there is overlap with foraging buzzes. Additionally, the arbitrary selection of 1 second as a separation time between click trains also means some click trains identified might include more than one echolocation event, hindering the performance of the algorithm.

5.2.4.4 Unknown

Click trains that did not have a pattern found by the previous algorithms are labelled as 'Unknown' (Figure 5.6).

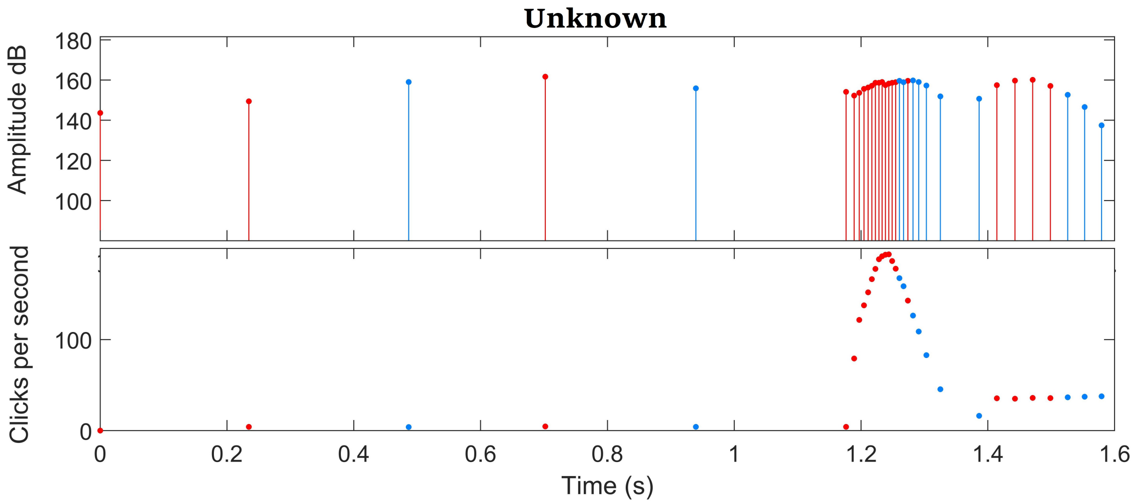


Figure 5.6: ***Unknown***. *Example of a click train produced by harbour porpoises where the underlying behaviour is not clear. Red = high-quality clicks. Blue = low-quality clicks.*

5.3 Results and discussion

A total of 20,516 click trains were found on the 24th of November 2015 (n = 390,528 clicks), of which 5,140 had at least 16 clicks. Of these 1,048 were NBHF, 1,607 were LQ-NBHF, and 3,025 were Non-NBHF. No 'Sonar' click trains were found. The algorithm correctly labelled 93.8% of click trains (n = 4,819). The algorithm was used to label all click trains in both datasets.

5.3.1 Click train type

A total of 139,338 click trains (n = 2,249,017 clicks) were found in both datasets, of which 2,436 were NBHF (see Table 5.2 - NBHF click trains include 8 click trains classified as 'Sonar'. Recordings of sonar were only found in Scottish data (Figure 5.7). It is likely, however, that sonar in Danish waters have different acoustic characteristics (*e.g.*, peak frequency) or repetition rates and therefore the algorithms would need to be area specific.

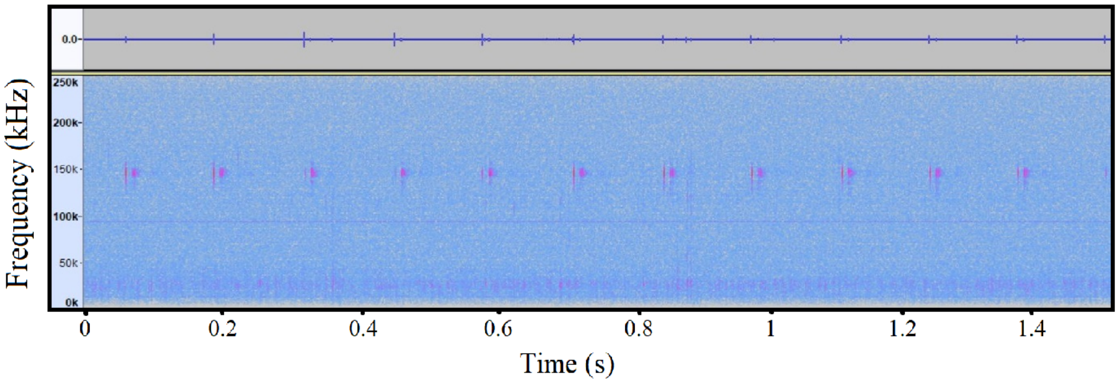


Figure 5.7: ***Sonar***. *Example of a spectrogram (Hann window, FFT size = 1024) of a sonar in Scottish waters, recorded on the 13th of October 2016. Upper panel: amplitude variation in arbitrary units.*

The chosen minimum separation time (*i.e.*, 1 second) between consecutive echolocation events, as well as the minimum and maximum click train lengths are arbitrary and thus results should not be interpreted as having biological importance.

Additionally, this means that the number of click trains found here is likely an underestimation. Moreover, an extra 118,153 potential click trains with fewer than 16 clicks were found (Table 5.2). The decision to not consider click trains with under 16 clicks may also impact the ability to identify behaviours (*e.g.*, resting or sleeping), which needs to be taken into account in future work.

Table 5.1: *Click trains (CT) per day in data collected in Danish waters using static devices.*

Denmark						
Date	CT	Clicks	NBHF	LQNBHF	NonNBHF	$n < 16$
12 Aug 2015	7,694	92,763	222	442	530	6,500
13 Aug 2015	6,994	132,046	113	125	1,778	4,978
24 Aug 2015	6,406	306,929	171	1,520	236	4,479
25 Aug 2015	4,152	579,197	186	1,577	156	2,233
27 Aug 2015	11,484	259,598	291	1,917	670	8,606
26 Sep 2015	12,779	146,856	44	835	1,563	10,337
27 Sep 2015	572	5,695	1	11	84	476
08 Nov 2015	5,772	17,298	27	30	90	5,625
09 Nov 2015	15,528	62,472	56	54	523	14,895
10 Nov 2015	14,053	50,860	195	45	226	13,589
11 Nov 2015	4,951	13,488	48	9	32	4,862
24 Nov 2015	20,516	390,528	1,048	1,607	3,025	15,376
25 Nov 2015	5,183	95,999	150	312	954	3,767
Total	**116,684**	**2,153,729**	**2,552**	**7,942**	**9,867**	**95,723**

Table 5.2: *Click trains (CT) per day in data collected in Scottish waters using towed devices. *NBHF include 8 'Sonar'*

			Scotland			
Date	CT	Clicks	NBHF	LQNBHF	NonNBHF	n < 16
28 Aug 2016	167	926	6	2	3	156
29 Aug 2016	389	945	4	1	2	382
30 Aug 2016	800	1,637	3	0	1	796
31 Aug 2016	101	145	0	0	0	101
18 Sep 2016	1,072	4,172	36	4	4	1,028
19 Sep 2016	435	2,019	18*	0	4	413
20 Sep 2016	1,153	4,364	25*	5	1	1,122
01 Oct 2016	455	1,825	15*	3	1	436
02 Oct 2016	944	2,016	8	0	1	935
04 Oct 2016	1,657	7,423	47	6	11	1,593
05 Oct 2016	1,679	4,349	21	3	5	1,650
06 Oct 2016	1,553	3,649	16	0	5	1,532
12 Oct 2016	1,433	3,151	10	1	2	1,420
13 Oct 2016	1,607	4,371	25	0	5	1,577
23 Oct 2016	1,023	5,504	33	5	11	974
24 Oct 2016	879	3,567	19	3	7	850
02 Nov 2016	719	3,227	34	1	6	678
03 Nov 2016	1,622	4,708	24	4	11	1,583
07 Nov 2016	726	3,875	22	11	8	685
04 Sep 2017	447	2,228	16	0	2	429
29 Oct 2017	293	1,342	8	2	2	281
01 Nov 2017	596	1,503	4	1	3	588
19 Aug 2019	3,541	15,797	68	36	84	3,353
Total	**23,291**	**82,793**	**462**	**88**	**179**	**22,562**

5.3.2 Patterns

Only click trains previously identified as NBHF were used in this section (n = 3,010), of which 2,548 were from Denmark and 462 from Scotland. A large number of clicks were removed from click trains exposing the existing patterns (Figure 5.8).

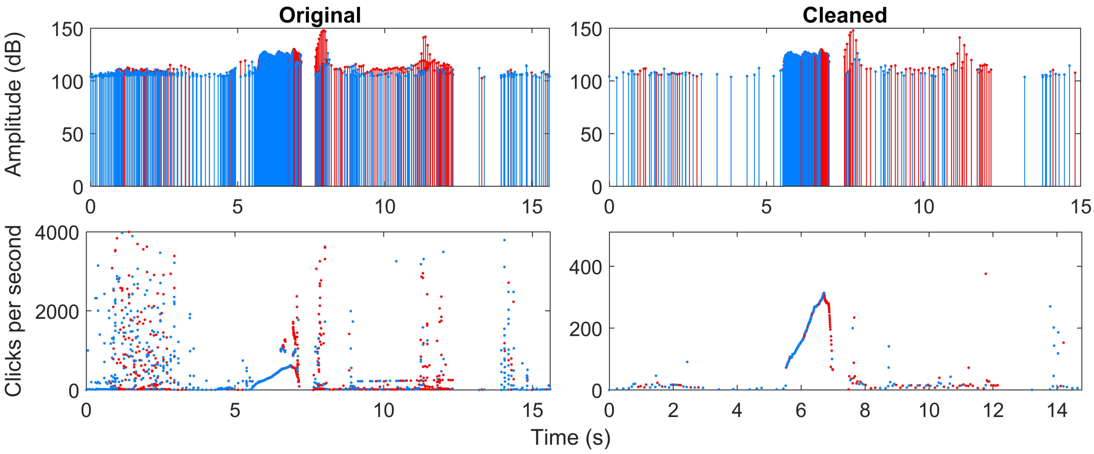


Figure 5.8: ***Patterns***. *Original and cleaned versions of a NBHF click train, recorded in Danish waters on the 27th of August 2015. Red = high-quality clicks. Blue = low-quality clicks.*

After this step, the number of clicks trains with at least 16 clicks was reduced to 2,656, of which 2,240 were from Denmark and 416 from Scotland. The algorithm failed in some cases, removing clicks that were part of the click train and keeping clicks that were supposed to be removed. The performance of the algorithm was tested by applying the 'Behaviour algorithm' (from next section), before and after the 'Pattern algorithm'. The results are presented in the next section.

5.3.3 Behaviour

A total of 2,656 click trains were used in this Section, of which 416 were from Scotland and 2,240 from Denmark. These had at least 16 clicks after applying the

'Pattern algorithm'. The three main behavioural states defined above were identified in the data when manually and automatically labelled (Figure 5.9).

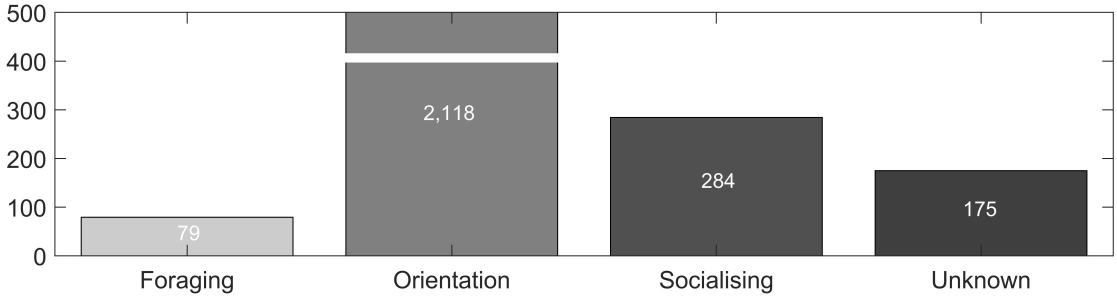


Figure 5.9: ***Behaviours***. *Number of click trains of each behaviour found in this study. See text for a description of each. Note: the Orientation bar is truncated.*

The algorithm correctly labelled 66.3% (n = 1,759) and 92.3% (n = 2,452) of click trains before and after the 'Pattern algorithm' was applied, respectively.

Table 5.3: *Confusion matrix of classification of behaviours in data collected in Danish and Scottish waters using static and towed devices, respectively.*

Behaviour	Orientation	Foraging	Socialising	Unknown	Total
Orientation	2,113	3	0	2	2,118
Foraging	0	66	6	7	79
Socialising	1	71	199	13	284
Unknown	3	66	32	74	175

This means that applying the algorithm to extract patterns improved the ability to classify behaviours by 39.6%.

5.3.3.1 Orientation

A total of 2,118 click trains were labelled as 'Orientation', with repetition rates below 100 clicks per second throughout the click train. This represents 79.7% of all click trains. These had a mean length of 41.5 (SD = ±42.8) clicks, ranging from 16 to 637. The algorithm correctly classified 99.9% of click trains (n = 2,113)

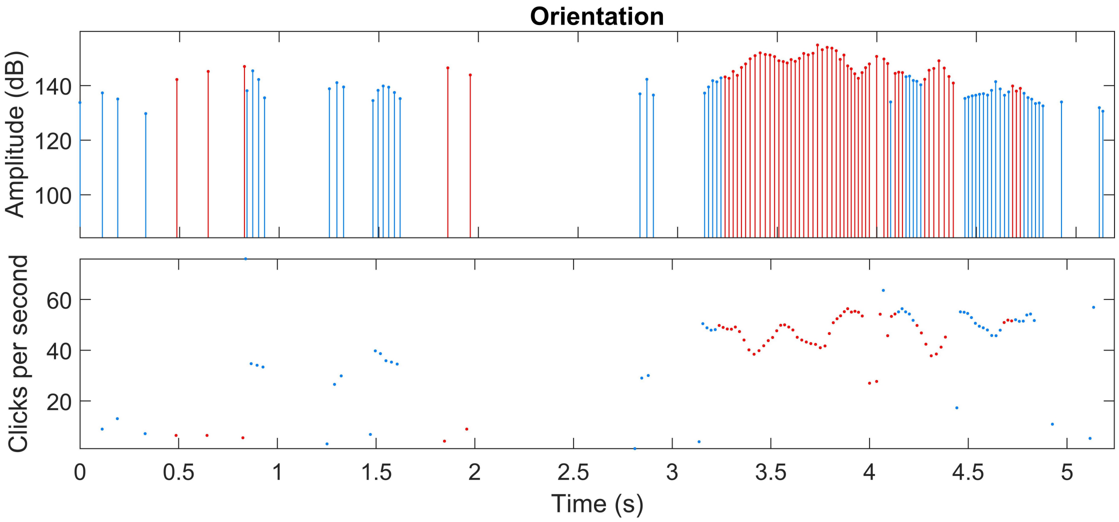


Figure 5.10: ***Orientation***. *Typical click train produced by a harbour porpoise while moving through its environment. Red = high-quality clicks. Blue = low-quality clicks*

Within these click trains, two patterns were found: landmarks and potentially resting behaviour. Landmarks are characterised by increasing repetition rates from 20 to 60 CPS, which indicates that the porpoise is using fixed objects in the environment to orient themselves [105]. Porpoise acoustic behaviour during rest or sleeping is not well understood, but evidence suggest they remain silent or click at low repetition rates [107]. See Chapter 6 - Acoustic behaviour.

5.3.3.2 Foraging

A total of 79 (3%) click trains were clear 'Foraging' events, showing a gradual increase of repetition rates, reaching up to ∼600 CPS. These values are consistent with what has been found in porpoises in captivity and in the wild, using both static recorders as well as acoustic tags [*e.g.*, 8, 9, 13]. Foraging events had a mean of 137.7 clicks (SD = ±149.6), ranging from 18 to 970. The algorithm correctly classified 83.5% (n = 66) of click trains.

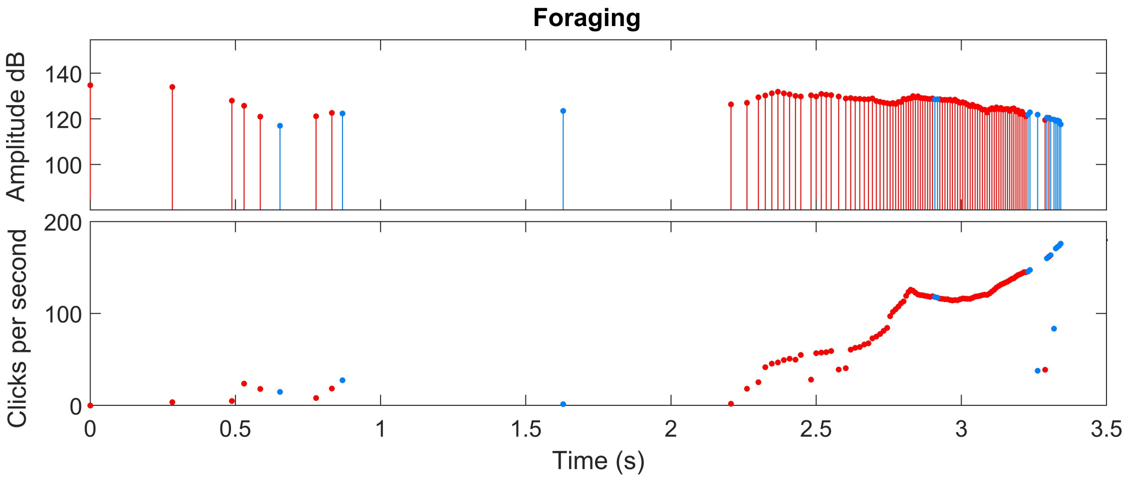


Figure 5.11: ***Feeding***. *Example of a click train produced by a harbour porpoise during a foraging/feeding event. Red = high-quality clicks. Blue = low-quality clicks*

An example of a typical foraging event is shown in Figure 5.11. Note that the amplitude of individual clicks decreases as the repetition rate increases. Although in some cases this may indicate that the animal is moving away from the acoustic recorder, it is consistent with what have been observed in tag data [*e.g.*, 108].

5.3.3.3 Socialising

A total of 284 click trains (10.7%) contained patterns that were consistent with communication calls. Different patters were found, some of which have been described in the literature before and some that have not. Social calls are described in detail in Chapter 6 - Acoustic behaviour. Some of these click trains may represent the end of foraging events, which were not detected in their entirety, either because the animal was vocalising in a direction away from the hydrophone or because the classifier did not identify the other clicks. This would explain why there are no preceding periods with high inter-click intervals, however, for many of these, there is a clear leap from low repetition rates to high, without the intermediate values as seen in Figure 5.11.

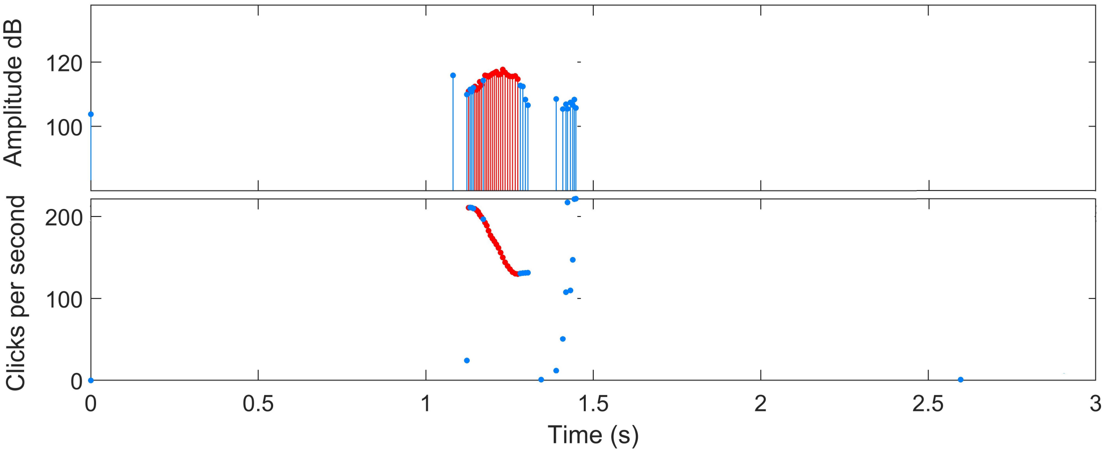


Figure 5.12: ***Socialising***. *Example of a social call produced by a click train produced by a harbour porpoise. Red = high-quality clicks. Blue = low-quality clicks*

Additionally, regular clicks are usually of higher amplitude and so if the final buzz is detected, it is expected that the previous clicks would be detected too, especially due to the short duration of these click trains. In the literature, a threshold of 10 ms is used to classify a given click train as a foraging event [*e.g.* 9, 247, 248]. These results suggest that using this threshold in all cases might over estimate foraging events, as most of the social calls found here and in other studies have repetition rates over 100 CPS [10, 11, 13].

The overall performance of the algorithm was 70.1% (n = 199). The algorithm performed poorly distinguishing between foraging and social calls with 25% (n = 71) of social calls classified as 'Foraging' and 4.6% (n = 13) as 'Unknown'. Similarly, 7.6% of 'Foraging' were classified as 'Socialising' and 8.9% (n = 7) as 'Unknown'. This result was expected due to the overlap in repetition rates between these behaviours.

5.3.3.4 Unknown

Click trains that did not fit in any of the patterns were labelled as 'Unknown', which comprised 6.6% (n = 175) of all click trains. Some of these may represent partial click trains, due to the porpoise moving away from the recorder or due to mistakes made by the 'Pattern algorithm'. In other cases, the click train may be complete but the pattern has not been reported before in the literature (see Chapter 6 - Acoustic behaviour).

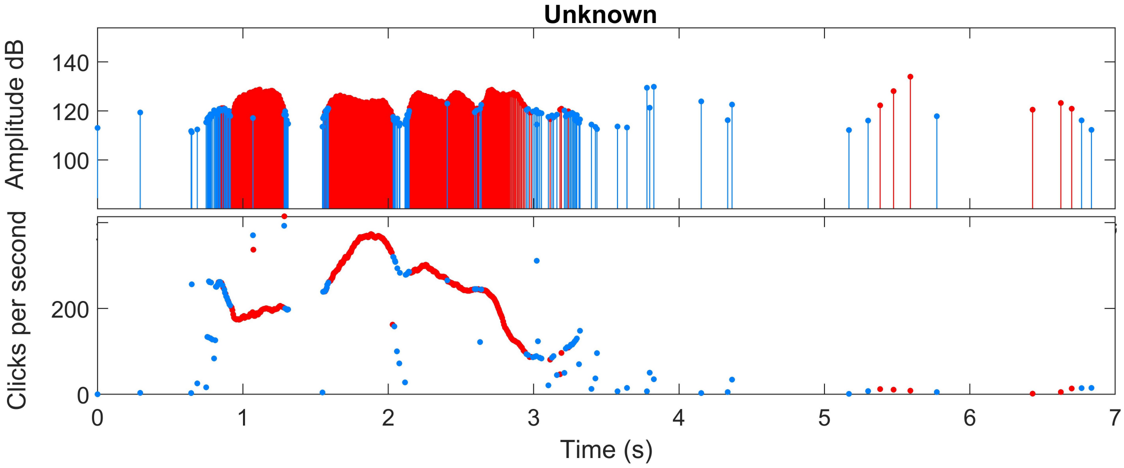


Figure 5.13: ***Unknown***. *Example of a click train produced by harbour porpoises where the underlying behaviour is not clear. Red = high-quality clicks. Blue = low-quality clicks.*

Moreover, some patterns may be the result of an unsuccessful foraging event. The pattern in Figure 5.13, for example, could be formed by a porpoise who missed its prey in the first attempt and continued to chase it in the water column using echolocation.

5.4 Limitations

The algorithms developed and tested in this Chapter showed high levels of accuracy. However, because the values chosen here for minimum separation time and maximum length were arbitrary, it means that some click trains would be missed. For example, the 'Type algorithm' assumes that when a click train is longer than 1,500 clicks, this is due to high background noise levels and thus LQ clicks are discarded. This decision could result in removing NBHF click trains (Figure 5.14).

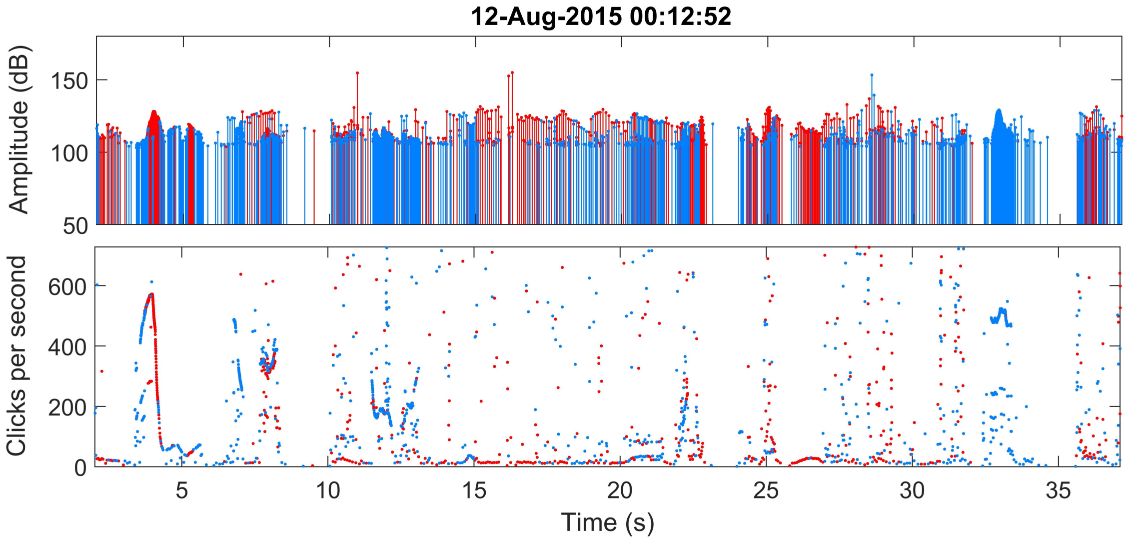


Figure 5.14: ***Limitations**. Example of a long 'click train' (n = 6,341) before the 'Pattern algorithm' is applied. Red = high-quality clicks. Blue = low-quality clicks.*

This outcome is a direct consequence of the decision-making pathway of the algorithms and means it can be improved. It also means that for monitoring purposes, click trains can be lost and potentially the absence of porpoises is a false negative. To explore this matter, 'positive porpoise minutes' (PPM) were estimated before and after the 'Pattern algorithm' was applied in all days in the Danish data, which was collected with static recording devices (Figure 5.15 and Figure 5.16).

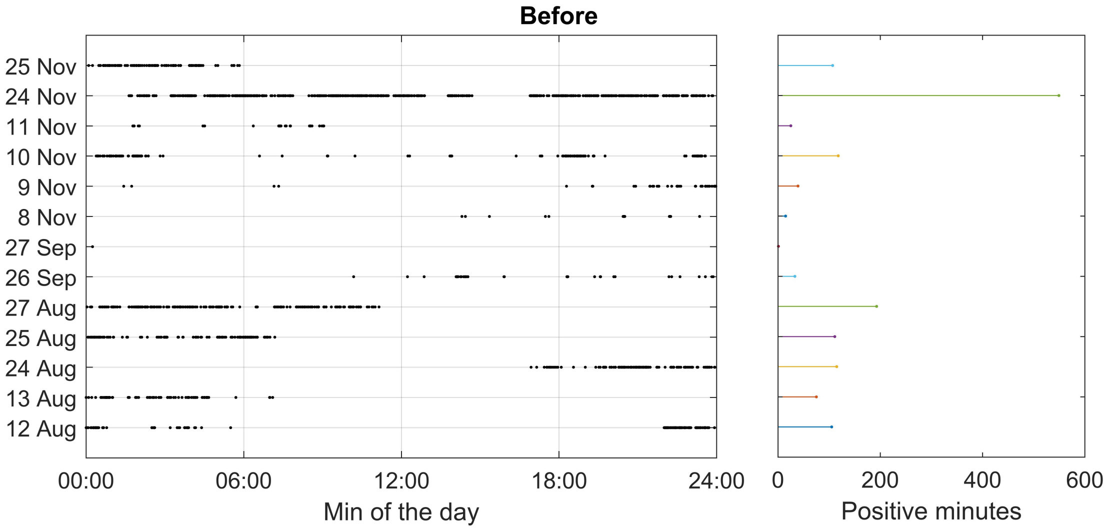


Figure 5.15: ***Positive porpoise minutes***. *Values obtained before the 'Pattern algorithm' was applied.*

The results show that the time periods with PPM remain similar before and after the 'Pattern algorithm' was applied and that it although removes ∼12.1% of click trains (n = 308), representing ∼9.9% of PPM, the overall pattern does not change (Figure 5.15 and Figure 5.16).

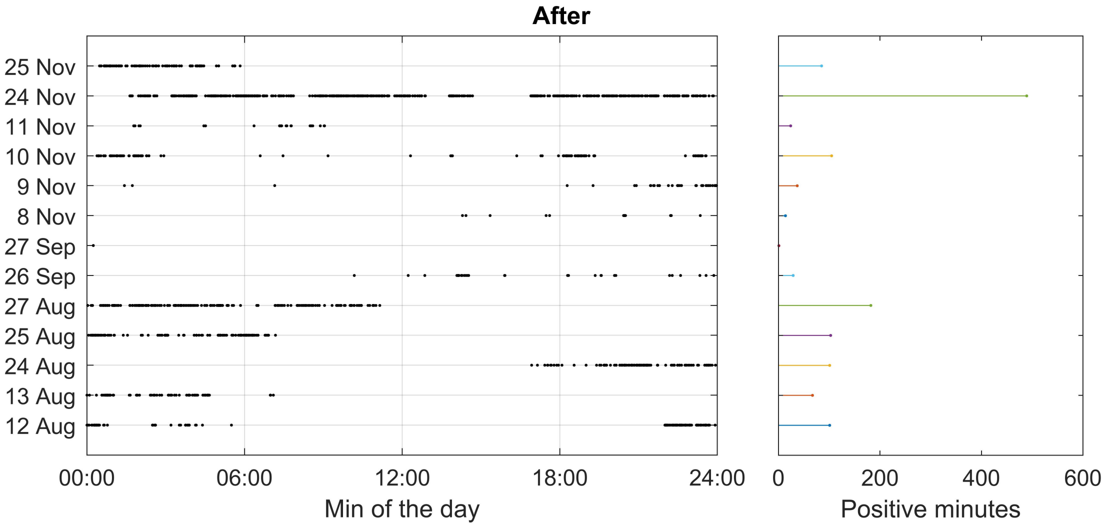


Figure 5.16: ***Positive porpoise minutes***. *Values obtained after the 'Pattern algorithm' was applied.*

5.5 Summary

In order to use passive acoustic monitoring devices (*e.g.*, SoundTraps - Ocean Instruments, New Zealand) to study the behaviour of harbour porpoises in the wild, a series of analytical tools are necessary. Several algorithms were developed and tested in this Chapter, which are meant to use sequentially, to identify click trains produced by harbour porpoises, extract patterns, and identify underlying behaviours. The performance ranged from 69.2% to 92.7% accuracy.

The method developed here to extract underlying patterns (*i.e.*, the 'Pattern algorithm') was based on a algorithm developed by Lepper et al. (2005) who used pre-defined thresholds of inter-click interval and amplitude variations to separate overlapping click trains [233]. The method was not directly applicable for harbour porpoises and instead an adaptable threshold was implemented. Although the 'Pattern algorithm' did not provide fully cleaned click trains, it improved the performance of the 'Behaviour algorithm' by 39.6%.

The 'Behaviour algorithm' performed relatively well, and several patterns were found both in click trains classified as 'Orientation' as well as in 'Socialising'. These were consistent with social calls, found here for the first time in data collected using static acoustic devices that record continuously.

The number of clicks per click trains was varied, but because harbour porpoises click almost continuously, the length likely provides little information about their natural behaviour. Moreover, length depends on how a click train is defined, as well as the spatial orientation of the animal, which may move its head away from the recording device or be too far to be detected.

The results from this Chapter show these algorithms can potentially be used for monitoring programmes, such as the Static Acoustic Monitoring of the Baltic Sea Harbour Porpoise, known as the SAMBAH Project.

Chapter 6

Acoustic behaviour

6.1 Introduction

Even though large groups of a few dozens to hundreds of harbour porpoises have been observed, porpoises are usually seen alone or in groups of two or three individuals [*e.g.*, Nairn, unpublished data and 2, 3, 17, 79, 114]. Our understanding of their social behaviour and communication is limited to visual observations in captivity and data obtained from wild animals carrying acoustic tags [9, 10, 11, 12, 13]. The few existing descriptive studies were conducted in captive settings due to the unique opportunities it provides for behavioural observations [9, 10, 11, 12].

These studies showed harbour porpoises emit clicks at different repetition rates, and that at least some of the patterns in repetition rates can be linked to specific behaviours. However, the name and characteristics of the calls is not always consistent between studies. For example, 'distress calls' were reported in several studies, but the characteristics of the calls differed between them. Busnel and Dziedzic (1966) described these as calls with repetition rates of between 130 and 250 clicks per second (CPS) and duration between 0.4 and 1.55 s [10], while Amundin (1991) described distress calls based on the HF component as calls with repetition rates of between 100 and 500 CPS, but with repetition rates between 300 and 400 CPS based on the LF component only [11]. Other social calls include 'contact call' between mother and calf, 'aggression', 'courtship', and 'dominance' calls.

Social calls have rarely been reported in the wild. Koschinski et al (2008) found a series of calls emitted by a calf that was accidentally caught in a fishing net in Canadian waters, which were recorded with a T-POD. In this case, the authors knew in advance where to look for those calls [8]. The only study to date which specifically looked at repetition rates of wild harbour porpoises clicks is Sorensen et al. (2018). A total of six porpoises, accidentally caught in pound nets in Danish waters, were mounted with acoustic and behavioural tags and released into the wild [13]. This study confirmed what other studies found: harbour porpoises emit calls which are qualitatively different from feeding buzzes. The distribution of repetition rates of social calls found by Sorensen et al. was bimodal with peak around 125 CPS and 1,200 CPS [13].

Sorensen et al. (2018) also provided unique insights into the social lives of harbour porpoises. The authors found they spend much of their time (between 9.9% and 58.8% of all one-minute intervals) at hearing distance from other porpoises, as the longer period without calls from other porpoises was 180 minutes. The production rate of social calls for all individuals was between 0.2 and 1 call per minute [13], remarkable evidence that porpoises are social animals.

The aim of this Chapter is to describe vocalisation patterns found in data from wild harbour porpoises collected using passive acoustic monitoring systems. The data used in this Chapter were the click trains identified as 'Orientation' (n = 2,118) and 'Socialising' (n = 284") from Chapter 5 - Patterns of click trains. High-quality and low-quality harbour porpoise clicks are shown in red and blue, respectively, throughout this Chapter.

6.2 Orientation

Click trains labelled 'Orientation' are characterised by having repetition rates below 100 CPS. These indicate porpoises are inspecting the environment they move through. Within these click trains, additional patterns were identified, which are described below.

6.2.1 Landmarks

In a series of experiments conducted in captivity, Verfuss et al. (2005) found that harbour porpoises use objects in their environment to orient themselves, even during day time and despite having been in the enclosure for several years. During these experiments, porpoises produce click trains with repetition rate that increased from ∼20 to ∼60 CPS, at which point it dropped. The authors called this pattern 'landmarks' [105].

This pattern was found in 0.9% of click trains (n = 103) labelled as 'Orientation'. In most cases the repetition rate increased from ∼20 to ∼60 CPS, although in some cases it reached 100 CPS before it dropped.

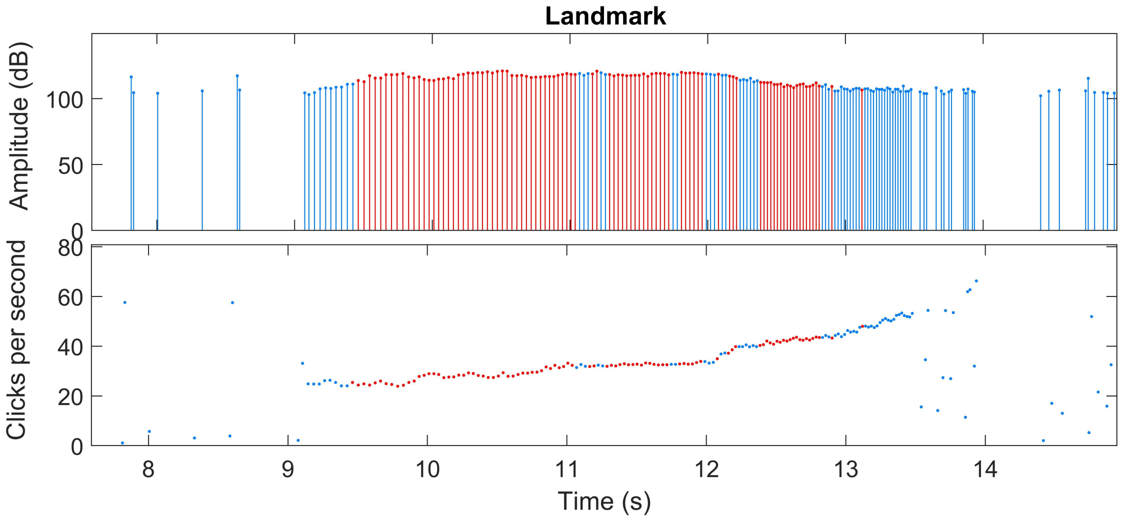


Figure 6.1: ***Landmark***. *Example of a 'landmark' recorded in Danish waters using a static passive acoustic device.*

6.2.2 Sleeping or resting?

Little is known about the sleeping habits of harbour porpoises in their natural environment. Wright et al. (2017) analysed acoustic and behavioural data from six tagged porpoises in Danish waters and found what seems like sleeping behaviour. These periods were characterised by shallow, parabolic-shaped dives of short duration (under 1 min). Further, 43% of parabolic dives were silent (*i.e.*, fewer than 10 clicks per dive) and during these dives porpoises were less likely to roll than during other dive types. Additionally, when clicking, they produced a maximum of $\sim$ 23 CPS [107].

At least 16 click trains (0.07%) classified as 'Orientation' had very low clicking rates (∼5 CPS), which could indicate resting or sleeping periods (Figure 6.2). It is possible that the low clicking rate observed in some of the data is the result of erroneous click classification by the PorCC algorithm or removal of clicks by

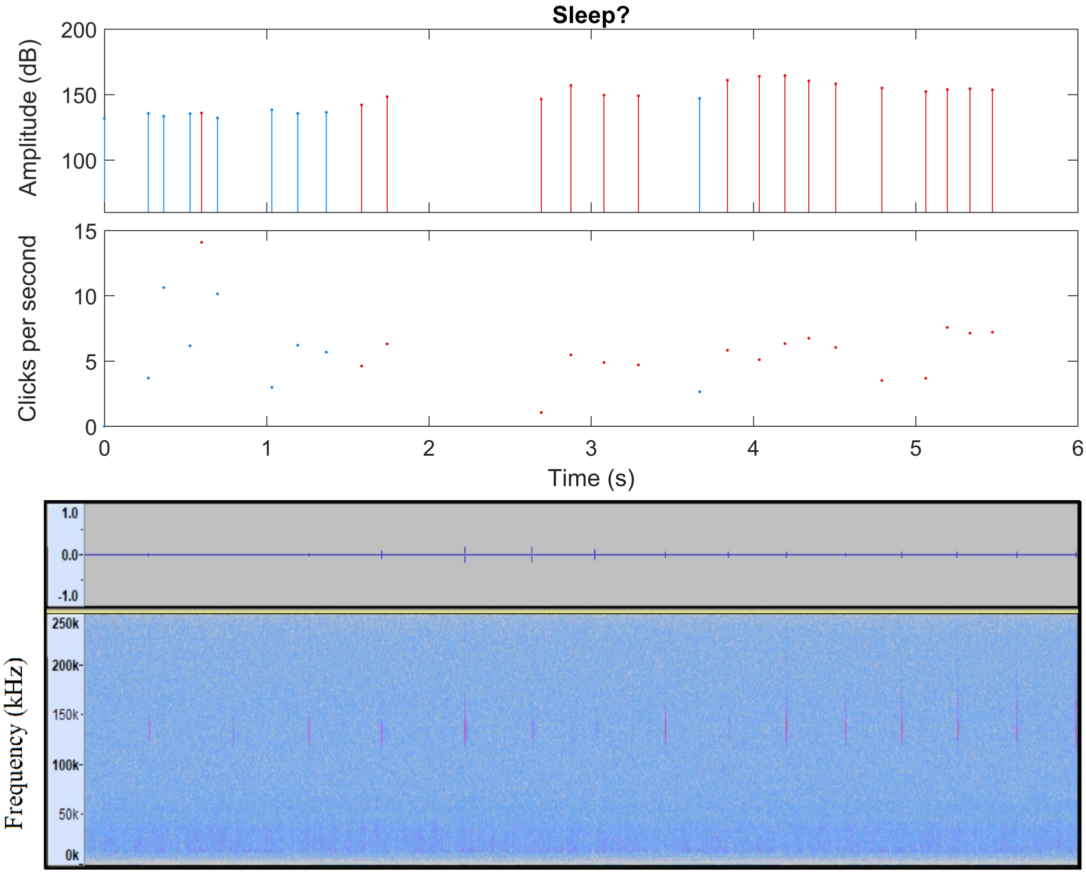


Figure 6.2: ***Sleep?***. *Click train produced by a harbour porpoise potentially representing resting or sleeping behaviour.*

any of the algorithms used in this study. Low repetition rates can also be sonar misidentified as NBHF click trains (see Figure 5.7). However, at least in cases when verification was possible, these were real harbour porpoise clicks and the only ones detected in the recordings (Figure 6.2).

6.2.3 Other

Unlike the two patterns described above, some patterns with repetition rates below 100 CPS were not described before in the literature. Two examples are shown in

Figure 6.3 and Figure 6.4

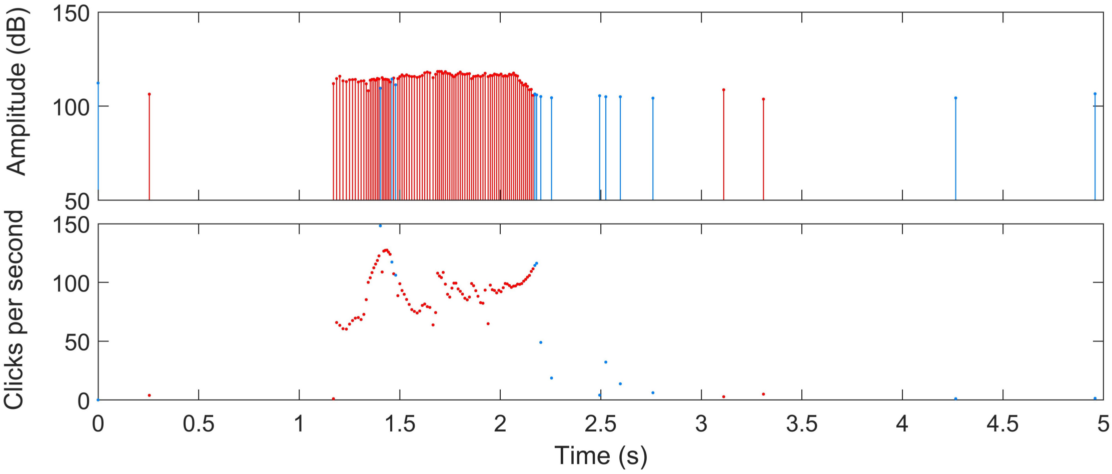


Figure 6.3: ***Unknown***. *Click train produced by a harbour porpoise.*

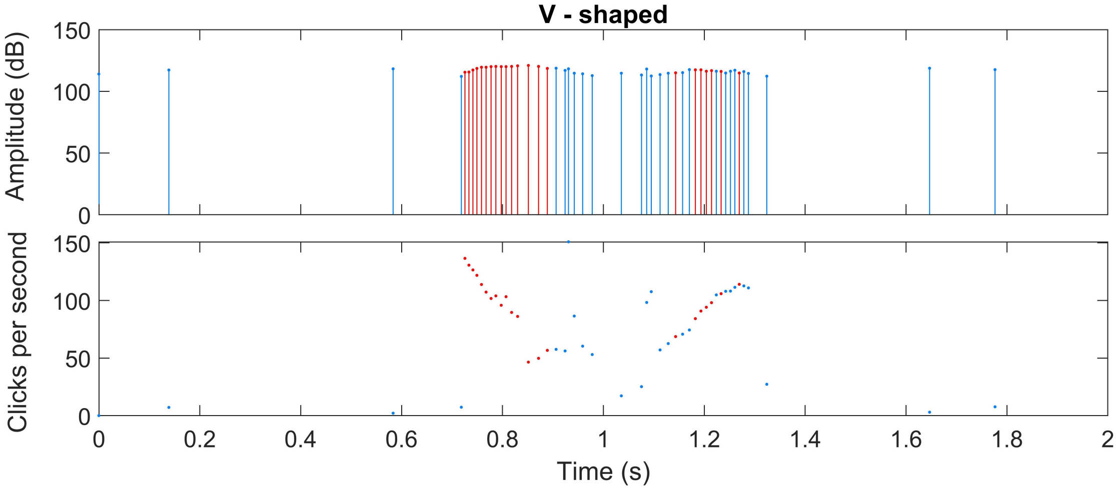


Figure 6.4: ***V-shaped?***. *Click train produced by a harbour porpoise.*

It is difficult to hypothesise what these patterns may represent. The pattern in Figure 6.3, for example, may be simple inspection of objects at sea, something floating the animal echolocates to. The pattern in Figure 6.4, on the other hand, is similar to a series of calls detected both in Scottish and Danish waters (see subsection 6.3.1).

6.3 Social calls

This Section presents a description of the types of potential social calls found in this study. Some of these were similar to calls described in the literature, both from the repetition rate of the low and the high-frequency components of the porpoise clicks [10, 11, 12].

6.3.1 V-shaped

V-shaped calls are, as the name indicates, calls that look like a V. They begin at about 300 CPS, go down to fewer than 150 CPS and back to 300. These call types were detected in Scottish and Danish waters. In Scotland, it was detected during an interaction with a solitary short-beaked common dolphin (see Chapter 7 - Interspecies communication), and it was detected three times in a short period of time (two are shown in Figure 6.5).

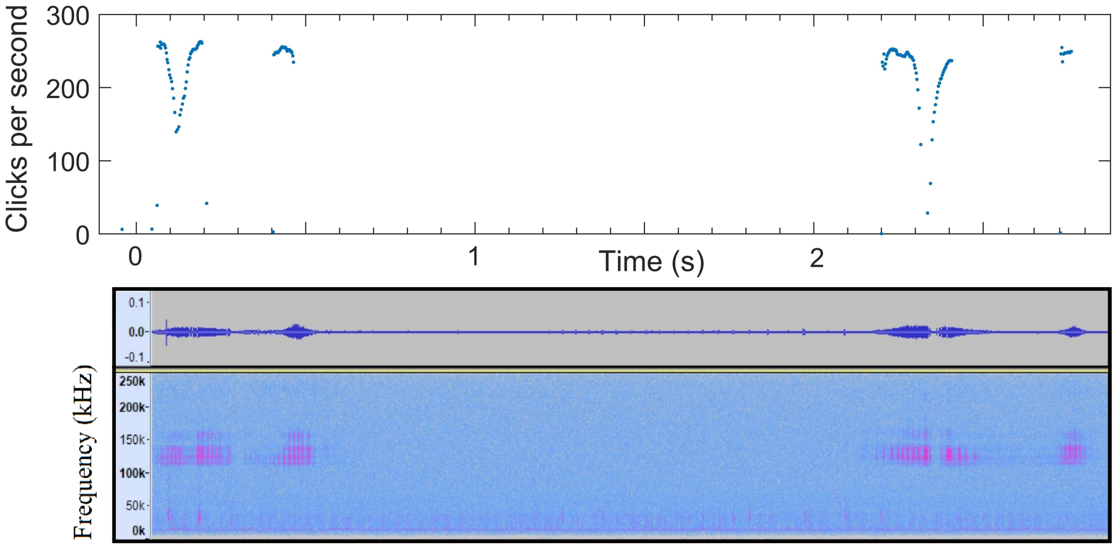


Figure 6.5: *V-shape. Example of a potential social call produced by harbour porpoises in Scottish waters.*

In Danish waters, the V-shaped call was detected at the end of a five-second period that included what are potentially also social calls (Figure 6.6).

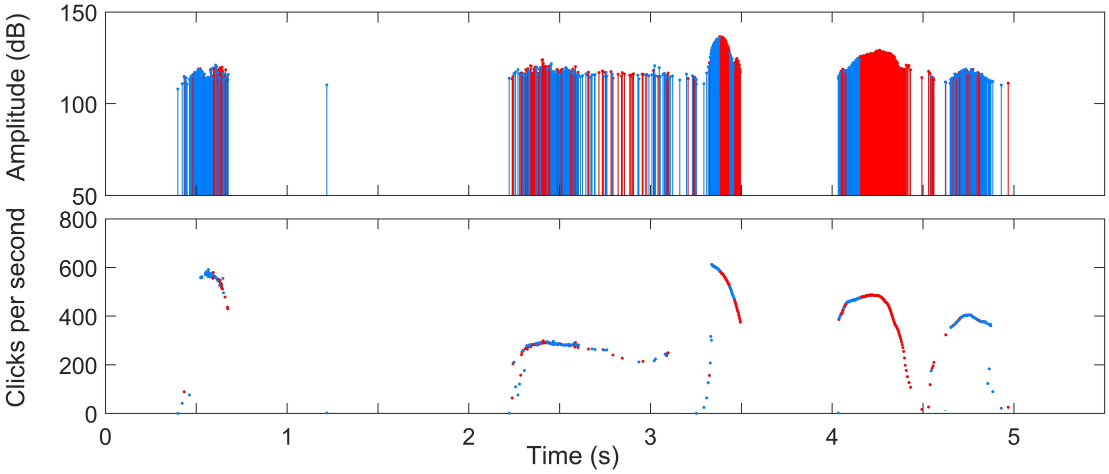


Figure 6.6: *V-shape. Example of a potential social call produced by harbour porpoises in Danish waters.*

It is encouraging that the patterns in Figure 6.5 and Figure 6.6 are so similar, as they have been recorded in two populations hundreds of km apart. This pattern has not been described in the literature before.

6.3.2 Downsweep

There are at least three types of click trains that have a downsweep pattern. A first type begins at repetition rates around 600-700 CPS and decreases to 400 CPS. A second type begins at repetition rates around 300-400 CPS and decrease to 100 CPS. Lastly, a third type begins at 200-250 CPS and decrease steadily to 50 CPS or less (Figure 6.7).

It is possible these are the same type of call and that the last two types are simply incomplete click trains. However, are least in some of them, the repetition

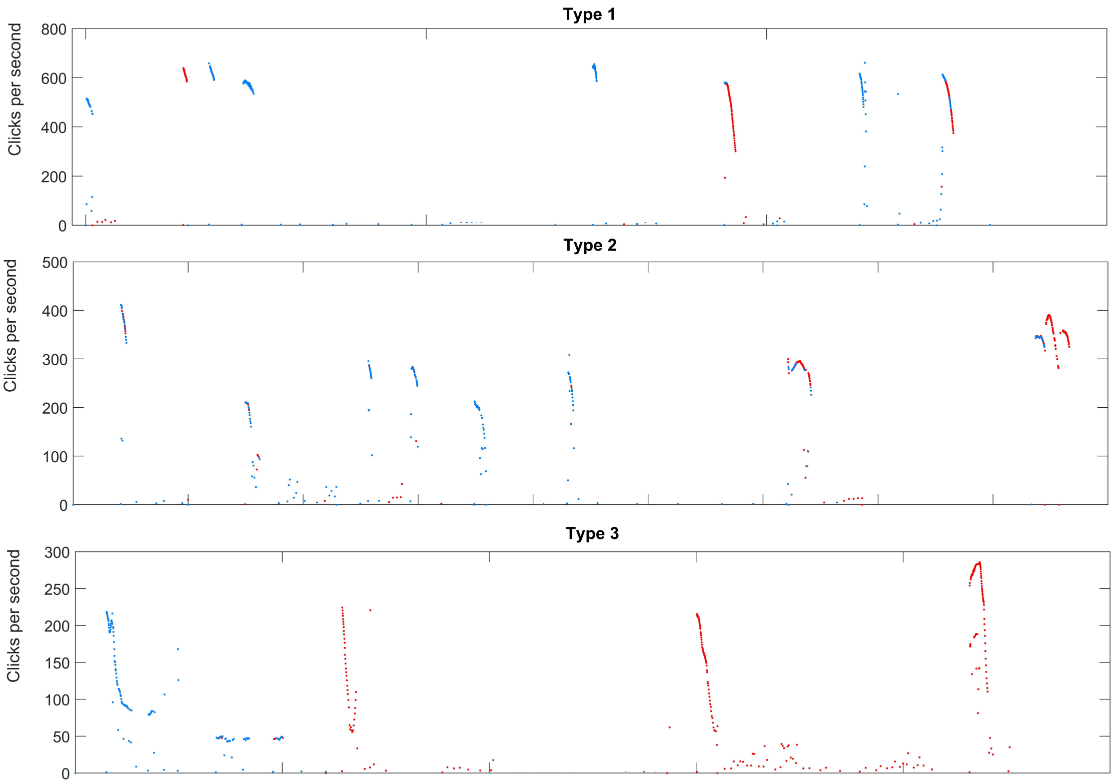


Figure 6.7: ***Downsweep**. Examples of types of communication call produced by harbour porpoises with a downward pattern, with different repetition rates.*

rate increases slightly at the beginning, which means they either begin at 600-700 CPS or at 200-250 CPS.

6.3.3 Upsweep

These calls are characterised by an increasing repetition rate (Figure 6.8). The patterns in Type 1 resemble 'aggressive' calls described by Clausen et al. 2010 [12], while the patterns in Type 2 resemble 'distress' calls of short duration reported by Amundin (1991) [11].

Repetition rates during feeding events overlap with the click trains represented

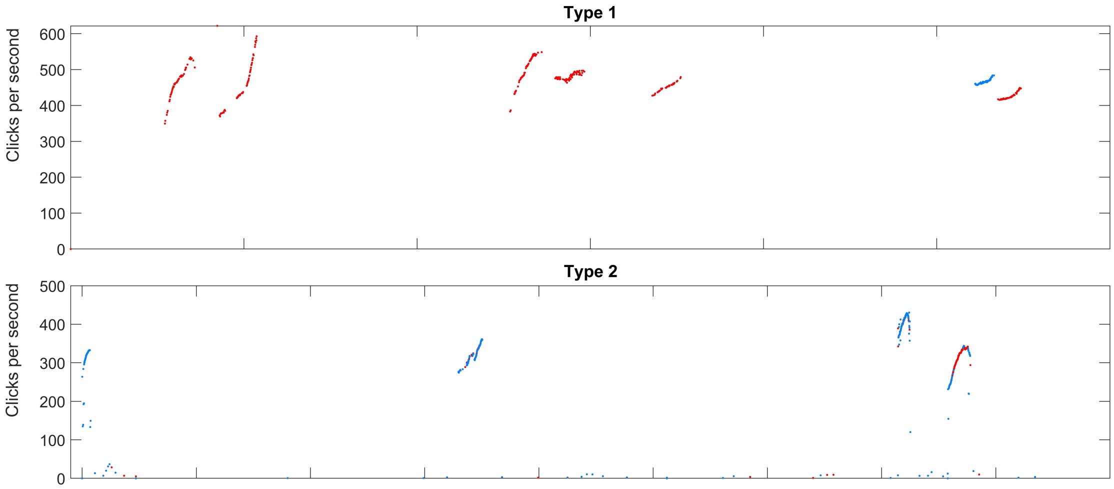


Figure 6.8: ***Upsweep***. *Examples of types of communication call produced by harbour porpoises with a upward pattern in repetition rates.*

here, limiting the ability to distinguish between them. Moreover, Clausen et al. (2010) described 'contact' and 'grooming' calls which are very similar to feeding events [12].

6.3.4 Short

This was the most common type of call in the datasets. They are characterised by a stable repetition rate between 100 and 300 CPS. These resemble calls described by Amundin (1991) and Busnel (1966) as 'distress calls' [10, 11].

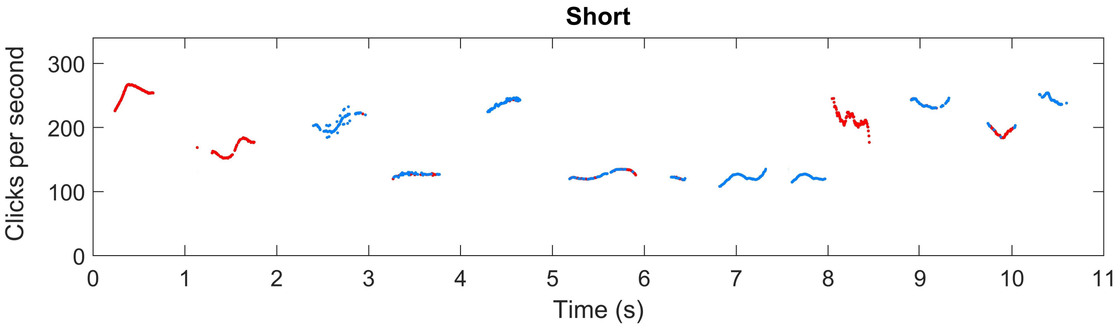


Figure 6.9: ***Short calls***. *Examples of short calls produced by harbour porpoises.*

6.3.5 Long calls

These calls had low, relatively constant repetition rates, between 100 and 250 CPS, and duration around 1 second (Figure 6.10). Amundin described these as long distress calls

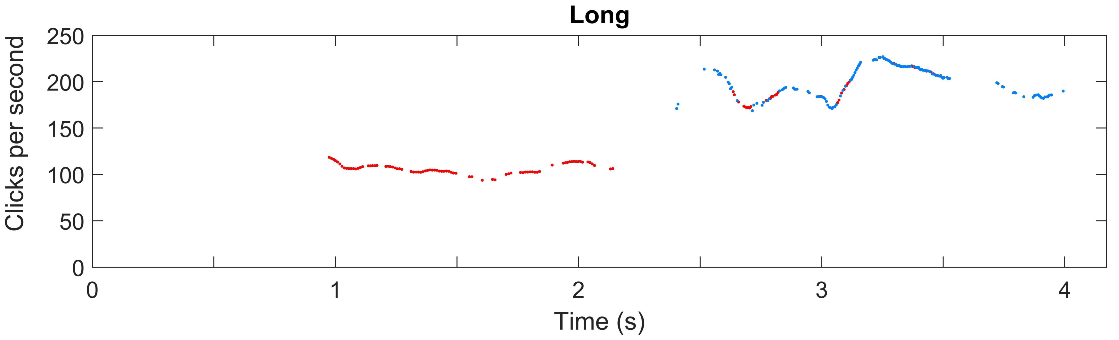


Figure 6.10: ***Long calls***. *Examples of long calls produced by harbour porpoises.*

Busnel and Dziedzic (1966) described 'courtship calls' as long calls with repetition rates around 500 CPS, from the low-frequency component of the porpoise click. One call that resemble this description is shown in Figure 6.11. This call was deleted by the 'Pattern algorithm' as it was comprised exclusively by low-quality clicks (see Chapter 5 - Patterns of click trains).

Identifying these calls would provide crucial information about the natural be-

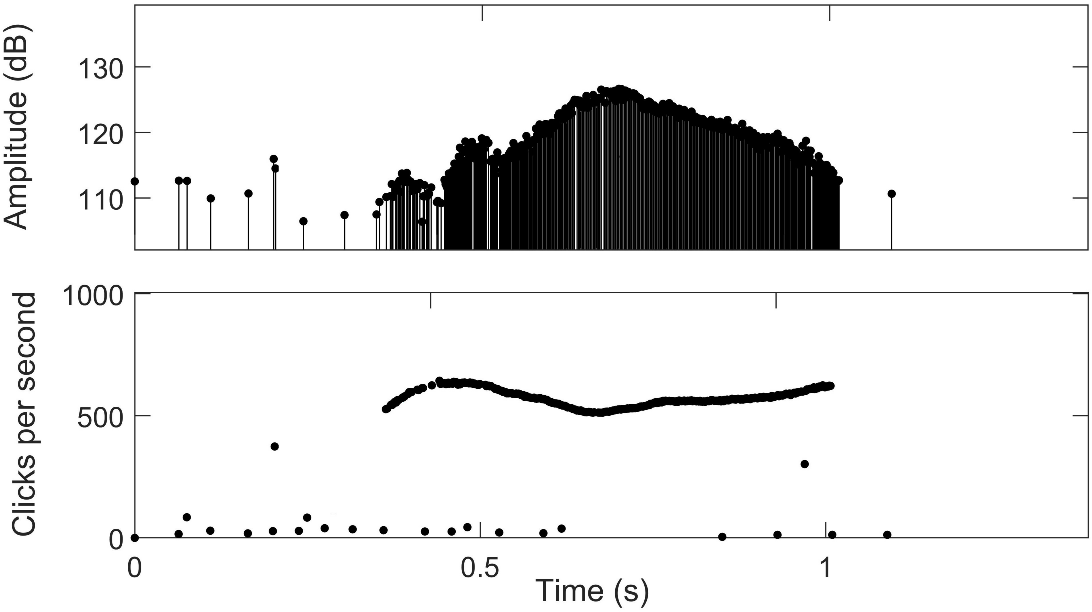


Figure 6.11: ***Courtship?***. *Social call produced by harbour porpoises.*

haviour of harbour porpoises and would help identify important areas for them that require protection.

6.3.6 Phrases

Amundin (1991) used the word 'phrase' to describe calls that comprised at least three calls produced in a short period of time. These include the same or different call types [11]. At least three phrases were found in this study. The first type was described in the 'V-shaped' section, found in data collected in Scotland. The second type is shown in (Figure 6.12), which comprised six nearly identical calls repeated in just below 8 seconds, also found in Scottish data.

The third comprised short calls with repetition rates around 120 CPS (Figure 6.13).

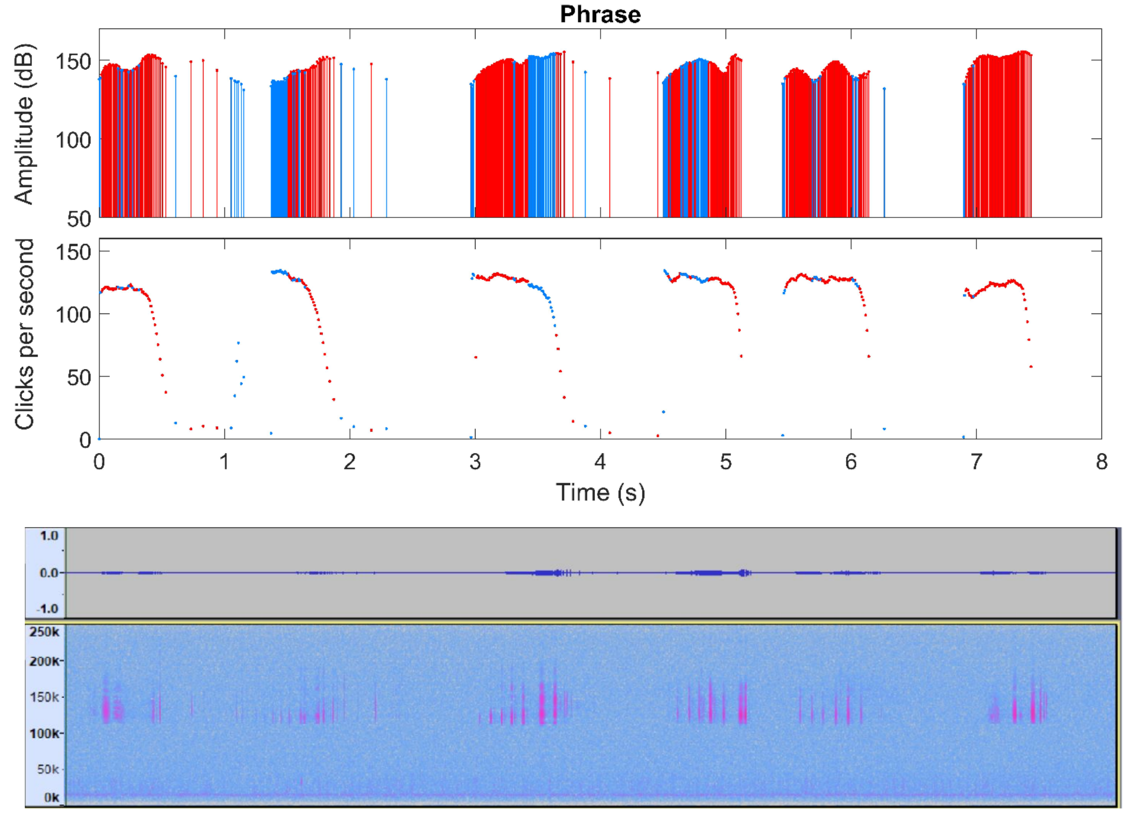


Figure 6.12: ***Phrase***. *Example of a 'phrase', a series social calls produced by harbour porpoises [11]. Top: amplitude. Middle: Clicks per second. Bottom: time domain and spectrogram. Recordings made on the 13th of October 2016 in the Firth of Clyde (Scotland).*

Other potential phrases were found in the data, comprising different call types. Detecting phrases in data from passive acoustic devices would depend on many factors, including selecting a suitable minimum time separation between consecutive click trains. If the separation is too short, then click trains that are not related may be pushed together, while if the separation is too long, calls that make up a phrase may be separated.

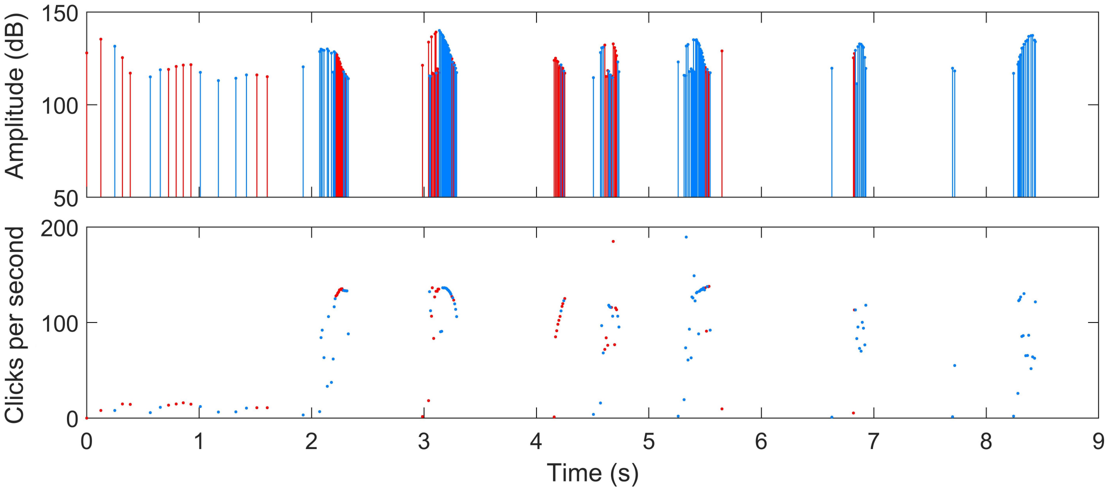


Figure 6.13: ***Phrase***. *Example of a 'phrase', a series social calls produced by harbour porpoises [11].*

6.3.7 Phrase?

There were other calls that did not belong to any of the types described before. It is likely that these click trains were incomplete due to the animal moving away from the hydrophone or because they represent another type that is not common or were not recorded often enough.

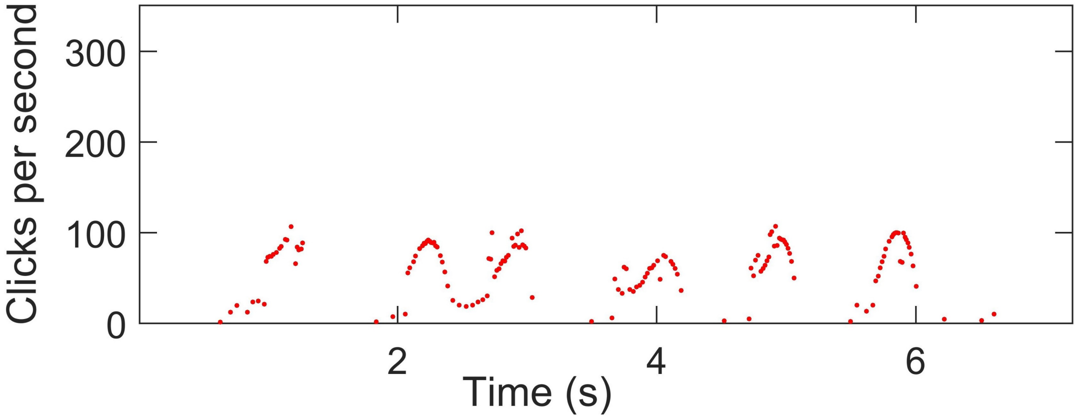


Figure 6.14: ***Phrase?***. *Example of a click train produced by harbour porpoises.*

Others, however, showed clear patterns but at very low repetition rates, below 100 CPS, such as the one shown in Figure 6.14. Note this pattern was recorded over a period of six seconds. A similar pattern was found where repetition rates reached 400 CPS in data from Denmark.

6.4 Overlaps

Although rare in the datasets, there were several click trains in which it was possible to see there were more than one harbour porpoise vocalising at the same time. One of the clearest cases is shown in Figure 6.15, where at least two (and possibly three) animals are emitting sounds simultaneously.

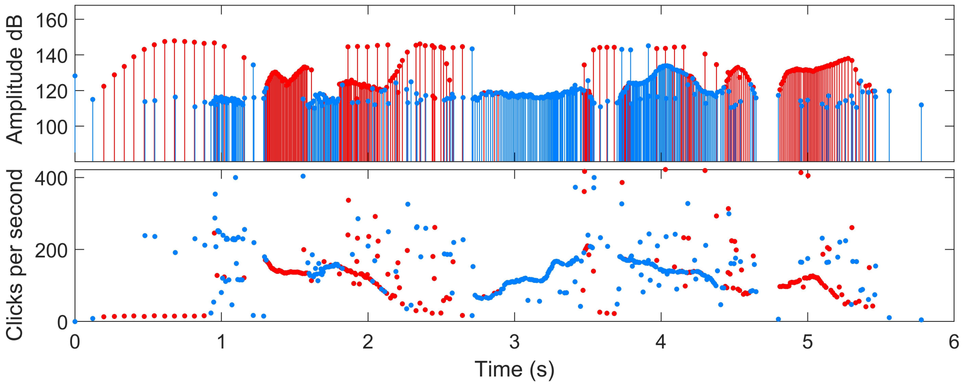


Figure 6.15: ***Overlap****. Example of multiple harbour porpoises vocalising simultaneously.*

These were rare, but the algorithms developed here would have a difficult time dealing with cases like these, despite being correctly classified as NBHF click trains.

6.5 Summary and implications

This chapter presented a detailed description of different patterns of repetition rates of harbour porpoise clicks. Many of these are consistent with patterns described in the existing literature, which seem to correspond to specific behaviours. For example, patterns consistent with using fixed objects in the environment to orient themselves (*i.e.*, landmarks) [105] and social calls consistent with 'distress' calls [11].

Unfortunately, the database from Denmark did not include the recordings and therefore it was not possible to verify click trains, especially incomplete ones and those with patterns that did not fit in any of the known categories. This Chapter shows the algorithms developed in this thesis can be used to study the behaviour of harbour porpoises in their natural environment using acoustic recorders, including static as well as towed ones. Although visual observations are necessary to verify the patterns described here correspond to social calls, at least some of the patterns have been described in the literature before. This is the first time social calls are found in data collected in the wild using continuous recordings. Although it is likely that some foraging events were misidentified as social calls (and vice versa) there were more social calls than foraging events detected in both datasets (34 *vs* 29 in Scotland and 251 *vs* 50 in Denmark). The data is not directly comparable to the tag data from Sorensen et al. (2018) as they were collected and analysed using different methodologies. However, no social calls were found with repetition rates over 800 CPS. This may be due to how impulsive detectors work, which could result in over or under estimation of inter-click interval values (and therefore CPS), as well as misidentification of clicks as noise. Algorithms exist to identify buzzes which could be adapted for behavioural studies.

This study constitutes a proof of concept and it shows that simple algorithms could be used for behavioural studies. Moreover, new analytical tools, such as machine or deep learning, could be easily implemented to identify patterns in a most effective manner once patterns have been described and verified.

Chapter 7

Interspecies communication

7.1 Introduction

Kylie (Figure 7.1) is a solitary female short-beaked common dolphin (*Delphinus delphis*) who has inhabited the Firth of Clyde, in the west of Scotland, since the early 2000s. In 2017, Ryan reported that Kylie was seen with a harbour porpoise in two different locations within the Firth of Clyde, four years apart [142]. While observations of both species engaging in interspecific interactions are commonly observed in areas where they overlap with other species [140, 174, 249], Kylie's association with harbour porpoises is unique and rare on several levels. Firstly, there are only 7 reported cases of common dolphins leading a solitary life on a permanent basis [175, 237]. Secondly, common dolphins in the Firth of Clyde are rarely seen (Nairn, unpublished data), while the harbour porpoise is a resident species to the inner Firth of Clyde, where several hotspots have been identified [90].

Thirdly, their social behaviour is also unalike. Common dolphins live and travel

Figure 7.1: *Kylie. Solitary short-beaked common dolphin in the Firth of Clyde, West Scotland.*

in large groups that regularly exceed 50 individuals but can reach thousands of animals [165], while harbour porpoises are usually seen in groups of two or three animals, or as solitary individuals [79], rarely congregating in large groups [*e.g.*, Nairn, unpublished data 1, 3, 114]. Lastly, these two species are also acoustically quite different. Unlike harbour porpoises, common dolphins produce a wide range of sonic and ultrasonic sounds that they use for foraging and communication purposes (Figure 7.2). These include whistles (*i.e.*, frequency modulated, long duration, tonal calls), buzzes, barks, yelps, squeals, and other burst-pulsed calls (*i.e.*, a series of rapidly produced clicks that occur both in echolocation and communication) [165, 166].

This Chapter presents the results of observations of Kylie accompanied by a harbour porpoise since 2009 to date, as well as the acoustic behaviour of Kylie and a harbour porpoise when travelling together, from recordings made in three different

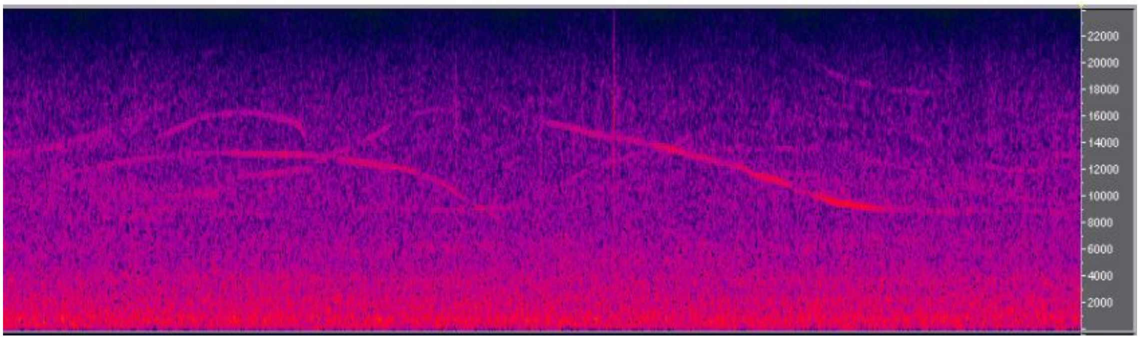


Figure 7.2: *Whistles and clicks. Example of whistles (horizontal lines) and clicks (vertical lines) produced by short-beaked common dolphins in the Celtic Deep - extracted from Scullion (2004) [250].*

days in 2016 and 2017. These recordings provided an exceptional and unprecedented opportunity to study their acoustic behaviour as a case study of interspecific vocal communication in wild cetaceans.

7.2 Methods

7.2.1 Data collection

Acoustic data were collected during systematic and opportunistic boat-based surveys in the Firth of Clyde (Figure 3.1), from June 2016 to July 2018. These surveys were conducted from the 'Saorsa', a 40-foot-long sailing vessel, and recordings were made using a towed hydrophone array (See chapter 3 for more details). Additionally, and using a SoundTrap ST300 (Ocean Instruments, New Zealand), Nairn (unpublished data) was able to record Kylie's sounds for a period of 7 days in the summer of 2019. The recorder (sampling frequency = 576 kHz) was positioned under one of the navigational buoys in the Hunterston/Fairlie channel where she spends much of her time. Nairn discovered that Kylie produces a wide range of sounds, including whistles and burst pulsed of low frequency range (< 20 kHz) much of the time. These data was not used for this project, but the recordings were key to interpreting the implications of the results of this study.

7.2.2 Data extraction and analysis

Recordings were run through the Click Detector Module built-in in PAMGuard [221], which detects impulsive sounds and saves them as individual clips. All potential dolphin and porpoise clicks were selected based on direction of arrival, observed inter-click intervals (ICI), the characteristic of the waveform, power spectrum, and Wigner plot, all of which are also available in PAMGuard's Click Detector display. They were selected manually and extracted using custom-built algorithms written in MATLAB 2017a (Mathworks, MA), together with date and time, and direction of arrival estimated using trigonometric methods within PAMGuard's algorithms [224]. For all extracted clicks additional variables were estimated, including amplitude, duration (estimated as the 80% of the energy of the clip), centroid frequency (kHz), root mean square bandwidth (BW_{RMS}, kHz) [238], and ICI, estimated as the time difference between the beginning (*i.e.*, sample number in the recording) of the click and the previous one (ms) (See Chapter 3 for a detailed description of each of the variables).

Once extracted, all clicks were individually checked and assigned to either the porpoises or Kylie (*i.e.*, non-harbour porpoise clicks). The discrimination was based on the unique characteristics of narrow-band high-frequency (NBHF) clicks produced by harbour porpoises (Figure 7.3). The direction of arrival of the click, amplitude, the inter-click interval, and the spectrogram of the original recording were used to avoid assigning echoes or other sounds to Kylie. The decision to focus on individual clicks instead of click trains, was made because there were cases where click trains slightly overlapped (*e.g.*, Figure 7.20). Moreover, although there are available classifiers for porpoises and dolphins, the discrimination was made manually as the performance of existing dolphin click classifiers is either low or unknown [170]. Moreover, using a classifier would overlook changes in Kylie's clicks, as classifiers are trained to identify specific temporal and spectral characteristics of the clicks [172].

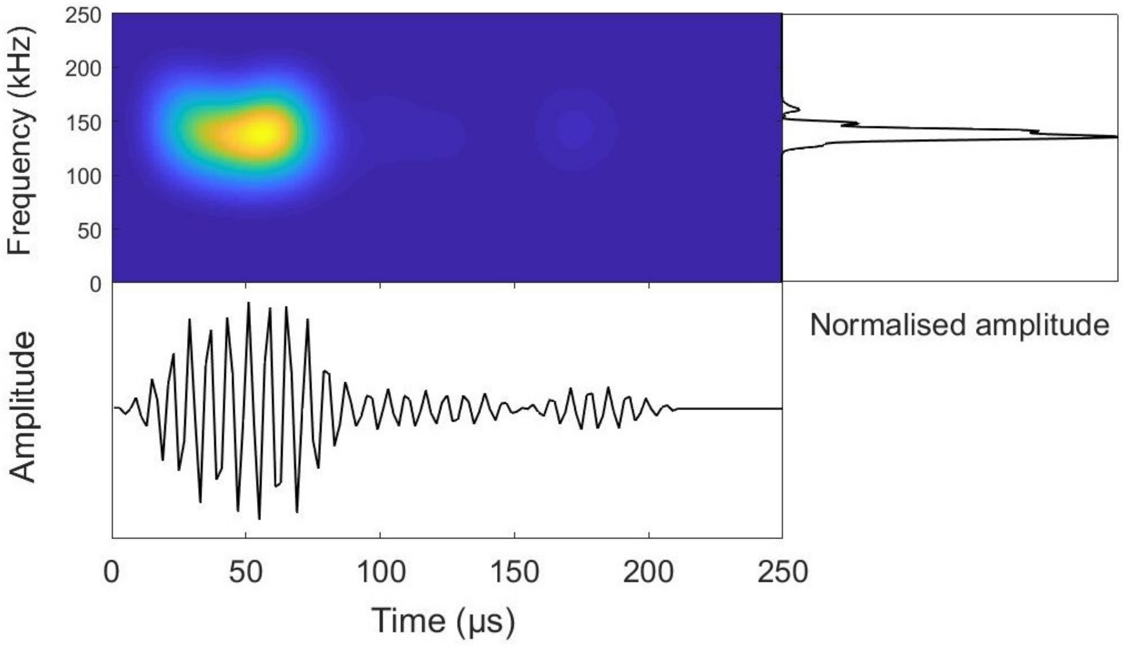


Figure 7.3: *Porpoise click. Typical harbour porpoise click from a sample saved by PAMGuard Click Detector Module (bottom), and its power spectrum (right) and Wigner plot (top).*

In order to validate the click discrimination method described above, a total of eight volunteers were trained to identify NBHF clicks. The volunteers were given written instructions (in English or Spanish) for training and testing purposes. In order to avoid bias, volunteers were not given information about what the study was about. For training purposes, the volunteers were provided with 50 high-quality harbour porpoise clicks. These were selected from data collected in Danish waters during the summer of 2015 using a SoundTrap 300 (Ocean Instruments, New Zealand), and 250 clicks (20%) from the three days of recordings of Kylie and a porpoise, which were selected randomly using a random number generator. The signals were provided as black and white images consisting of the waveform, frequency spectrum, and Wigner plot, without axes. The reliability of agreement between Cosentino's and the volunteers' discrimination was estimated using Fleiss' Kappa [251] with a MATLAB function developed by Cardillo [252]. Spectrograms of the recordings were inspected using Audacity version 2.3.0, for verification purposes and in search of whistles and other tonal and pulsed calls Kylie may have produced.

Once echoes and other unwanted sounds were removed from the database, clicks were plotted in time against their direction of arrival (*i.e.*, bearing), colour coded by species, in order to identify periods during which the dolphin and the porpoise were travelling next to each other (Figure 7.16). This was indicated by the simultaneous changes in bearing of consecutive clicks, regardless of which animal produced them [238]. In other words, if clicks were coming from the same direction at almost the same time it was assumed that the animals were travelling close to each other. If, on the other hand, the direction was different, it was assumed that the animals were not travelling in close proximity, although remained in the same area. Clicks produced when the animals were close together (n = 1,248) were separated for further analysis.

7.2.3 High frequency clicks

High-frequency clicks were defined, for the purpose of this study, as clicks with peak and centroid frequencies above 100 kHz, as this is the lower limit of energy content in harbour porpoise clicks [7]. The density distributions of high-frequency clicks produced by the dolphin were estimated using a bootstrap method, with 5,000 iterations for four scenarios:

1) when Kylie was seen alone (n = 419) - these are periods where no porpoise was seen around Kylie. It was not possible, however, to confirm that no porpoises were within hearing distance from Kylie.

2) periods when she was seen with a porpoise (n = 2,023) - these periods include both when travelling next to a porpoise (3) as well as when the porpoise was visible in the vicinity (4)

3) when seen with a porpoise but not travelling next to it - these are periods when the porpoise and Kylie are interacting, yet not next to each other (n = 775), and

4) when travelling in close proximity to the porpoise (n = 1,248) - this include only periods where the animals were assumed to be close enough so received signals did not vary in direction of arrival.

Subsequently, a Tukey's honestly significant difference (HSD) test was performed to test whether the proportion of high frequency clicks was significantly different between scenarios.

7.2.4 Click trains

A click train can be loosely defined as a 'series of clicks separated by gradually or cyclically changing inter-click intervals suggesting a unit during an echolocation event or a communication signal' [8]. Two types of click trains were defined to study the vocalisation patterns of Kylie and the porpoise when travelling together. The first type, was defined based on the ICI only, where an ICI of one second or more separated two consecutive click trains, regardless of whether it contained clicks produced by both or one animal. The second type was defined by species and ICI, in other words, whenever a click was produced by the other species, or if there was a gap of one second or more, a new click train would begin, even if it contained only 1 click. Subsequently, and in order to investigate whether the order in which Kylie and the porpoise vocalised when travelling next to each other (n = 1,248) was random, the non-parametric Wald–Wolfowitz Runs Test was performed on both types of click trains. The runs test reveals whether the observed pattern is the result of random vocalisation or not.

Additionally, in order to estimate the transition probabilities between porpoise and Kylie clicks, and because Kylie produced two types of clicks (low- and high-frequency clicks), three states were defined: low-frequency clicks (LF), high-frequency clicks (HF), and harbour porpoise clicks (P). These states were used to estimate the transition probabilities in two scenarios: travelling close to each other and together in the same area but not travelling next to each other. The transition probabilities between states, including self-transitions, were compared using the Markov chain method [253].

7.3 Results and discussion

Harbour porpoises were detected throughout the Firth of Clyde on all survey days. A detailed analysis of the distribution and density of harbour porpoises in the Firth of Clyde using these data is presented in Brown (2018) [90]. No common dolphins were observed, except for Kylie, who, in all cases, was seen swimming around the same navigational buoy located off Cumbrae in the Fairlie/Hunterston Channel Figure 3.1. Kylie was seen alone on the 4th of October, and 7th and 23rd of November 2016 as well as the 1st of November 2017 and the 19th of July 2018, when she was also acoustically detected. She was seen with a harbour porpoise on the 2nd and 3rd of November 2016 (day 1 and 2), and the 4th of 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, as the vessel discontinued a systematic survey and abandoned its transect line so as to better observe the animals. 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) [142] and with photographs from 2004, 2009, and 2015 (Figure 7.4).

How or why Kylie became a solitary individual is, and will remain, a mystery. Female short-beaked common dolphins live up to 30 years of age and become sexually mature at 6-8 years of age [23]. Eye witnesses reported that Kylie had a calf when she was first seen in the area, which means she was already an adult when she became solitary. However, she may have been with a porpoise, which are much smaller than common dolphins [23] and could have been misidentified as a calf. Regardless, she is now an adult and has spent almost 20 years in the area on her own. It is likely she has not interacted with conspecifics during this time while she has been exposed to harbour porpoise clicks regularly, as the inner Firth of Clyde is an area of high harbour porpoise density year round [90].

Kylie spends much of her time around navigational buoys, especially three buoys located in the Fairlie/Hunterston channel (Figure 3.1), where locals see her regularly and year-round. She has never been seen interacting with other common dolphins. In 2017, Ryan [142] reported that Kylie was seen with the same individual porpoise in two different locations within the Firth of Clyde, 4 years apart. One of the sightings (June 2011) took place around a navigational buoy in the Fairlie/Hunterston channel and the other one (August 2015) in Loch Fyne. The authors were lucky to obtain good quality images from both encounters and thus were able to individually identify the harbour porpoise [142]. In this study, and using opportunistic data collected since 2004 by several parties, including the Clyde Porpoise CIC and their volunteers, as well as by third parties, it was possible to compare photographs with those reported by Ryan [142]. The data showed that not only Kylie interacts with harbour porpoise more often than previously thought, but also that she interacts with different individual porpoises, although with one at a time (Figure 7.4).

When Kylie is alone, her behaviour is almost stereotyped. She surfaces for a few seconds (to breathe) approximately once per minute, heading in the direction away from the buoy, at a distance of two to three metres from it (Figure 7.5). This behaviour repeats for hours on end until she moves to other areas (*e.g.*, to another buoy or to feed) or to approach passing vessels.

Kylie is regularly visited by locals and tourists in recreational vessels, especially during the summer season. Many visitors try to tease her to follow them or engage in some aerial display (*e.g.*, breaching), by passing close to her at a high speed. Vessels types include sailing boats, zodiacs, and jet skis (Figure 7.6). She occasionally engages and follows the vessels for a few hundred metres, but then quickly returns to the buoy. She has also been seen approaching passing vessels on her own, including

Figure 7.4: *Travelling together. Solitary short-beaked common dolphin, 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.*

recreational boats as well as the research vessel used in this study (Figure 7.6).

Figure 7.5: *Kylie. Solitary short-beaked common dolphin next to navigational buoy off Cumbrae, in the Fairlie/Hunterston Channel, in the Firth of Clyde, West Scotland.*

Figure 7.6: *Recreational vessels. Kylie is regularly visited by recreational vessels*

7.3.1 Kylie's sounds

Three of the volunteers who participated in this project to validate the methodology to assign clicks to either the porpoise or the dolphin (see Methods above) either over or under-assigned signals to the NBHF class. Of the 250 signals used for testing purposes, a total of 31 signals were assigned as harbour porpoise clicks (12.5% of the dataset) by MC, while these volunteers found 114, 117, and 8 respectively. The null hypothesis of the Fleiss' Kappa test (*i.e.*, the level of agreement is accidental) was rejected both when including (p = 0, k = 0.28, level of agreement 'Fair') and excluding (p = 0, k = 0.6, level of agreement 'Substantial') the results of the above-mentioned volunteers. It was therefore assumed that the method used to assign clicks to either the porpoise or the dolphin was adequate.

A total of 2,023 clicks were recorded during the encounters with the dolphin-porpoise pair. Of these, 1,499 were produced by Kylie and 524 by the porpoise, and were either single clicks or part of click trains. Additionally, 419 clicks were recorded when the dolphin was seen alone in November 2017 (n = 72) and July 2018 (n = 347). These clicks were mostly of two types: low-frequency ($<$ 50 kHz) and high-frequency clicks ($>$ 100 kHz), and although clicks with intermediate centroid frequency were detected, these were the minority of clicks, and were produced as a transition state between low and high-frequency clicks (Figure 7.7). The centroid frequency ranged from 23.4 kHz to 187 kHz, with low and high-frequency clicks being narrow-band and clicks with intermediate centroid frequency being broadband (Figure 7.8).

Despite the fact that Kylie is known to produce a wide range of sounds (Nairn, unpublished data), she was recorded producing only two types: a burst pulsed call (n = 1) and echolocation clicks (n = 1,786). No other tonal sounds that are typically produced by common dolphins while socialising, such as whistles, were recorded. Given Kylie is capable of producing typical common dolphin sounds, it is possible that whistles and other tonal sounds were not recorded due to the short duration of the encounters. However, this apparent preference for producing clicks must be interpreted in the context in which they were recorded.

The proportion of high-frequency clicks produced by Kylie was a significantly

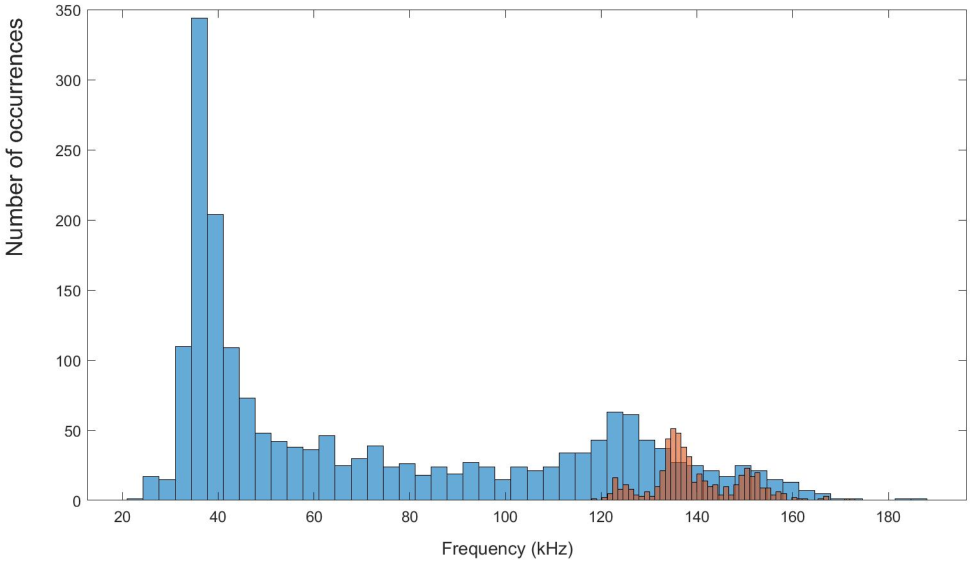


Figure 7.7: *Centroid Frequency. Histogram of the centroid frequency of clicks produced by the porpoise (orange) and by Kylie (light blue) when travelling together.*

higher when she was accompanied by a porpoise than when she was seen alone. When she was on her own, the proportion was 0.21 (SD = ± 0.02), which increased to 0.32 (SD = ± 0.01) when seen around a porpoise. When, on the other hand, the porpoise was around but not next to Kylie, she produced a proportion of high-frequency clicks of only 0.03 (SD = ± 0.01), which significantly increased to 0.44 (SD = ± 0.02) when travelling next to it. This is shown graphically in Figure 7.9 and numerically in Table 7.1.

The null hypothesis (H_0) of the Tukey's honestly significant difference (HSD) test was that these proportions were the same in all scenarios. The null hypothesis was rejected and all comparisons between proportions of high frequency clicks were significantly different ($\alpha = 0.05$).

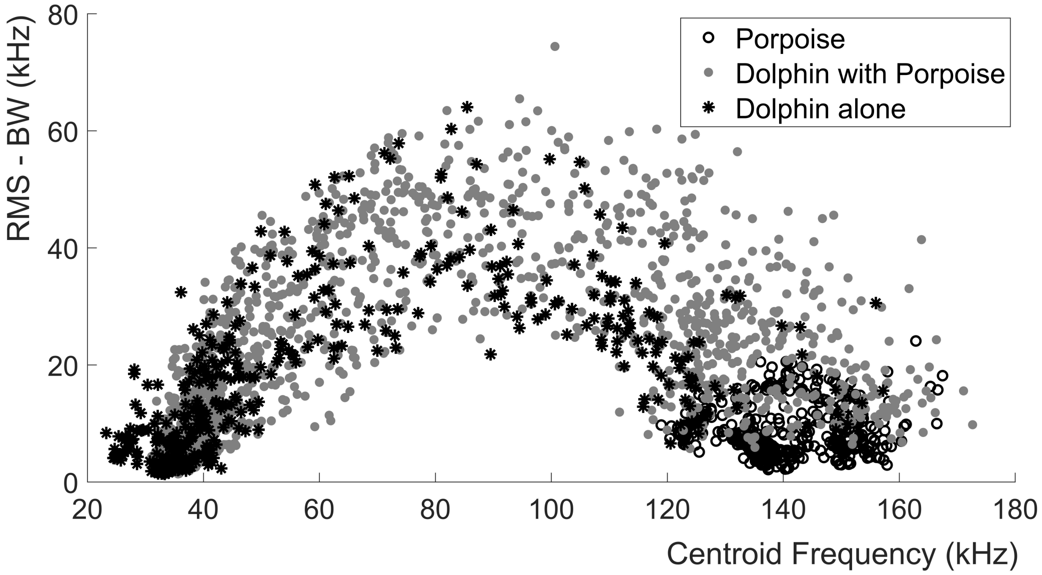


Figure 7.8: *Bandwidths. Variation of the bandwidth of clicks produced by Kylie and the porpoise in different scenarios. The bandwidth was plotted against the centroid frequency. Note that low and high frequency clicks are narrow-band (low y values), while mid-frequency clicks are broadband (high y values).*

The fact that Kylie produces only clicks and a higher proportion of high-frequency ones when travelling with porpoises, especially when in close proximity to them, suggests that she is actively using clicks instead of other communication sounds. The maximum hearing sensitivity for harbour porpoises is around 125 kHz, however, their hearing abilities extend to both higher (>150 kHz) and lower frequencies (<10 kHz), with a decreased sensitivity at 63 kHz [254]. Curiously, common dolphins' highest sensitivity is around 64 kHz, decreasing sharply in frequencies beyond 100 kHz [255]. It is expected, therefore, that at short distances they are capable of hearing each other, even without the dolphin having to produce high-frequency clicks, suggesting there is another reason why she prefers them.

The variability of clicks produced by Kylie was high, both in the temporal and

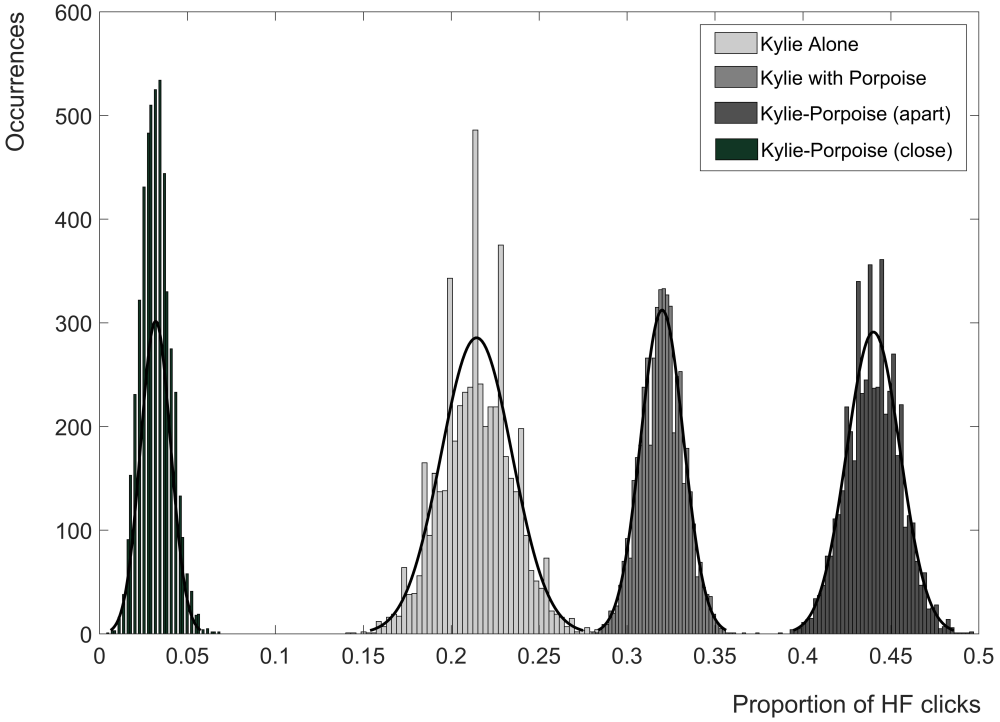


Figure 7.9: *High frequency clicks. Histograms and density distribution of the proportion of high frequency clicks produced by a short-beaked common dolphin in four scenarios. 1) Dolphin alone (n = 419). 2) Dolphin nearby a harbour porpoise (n = 2,024). 3) Dolphin and porpoise in the same area, but not travelling next to each other (n = 775). 4) Dolphin and porpoise travelling next to each other (n = 1,248).*

spectral domains. The typical low-frequency click had a centroid frequency at 37 kHz, with most of the energy concentrated around it (Figure 7.11). Some of the high-frequency clicks were oligocyclic, similar to low-frequency clicks and high-frequency clicks reported for other dolphin species, such as the Dusky dolphin (*Lagenorhynchus albirostris*) [33]. However, some of Kylie's high-frequency clicks seem to have most of the energy between 100 and 150 kHz than the broadband clicks produced by other dolphin species (Figure 7.10).

Moreover, some of Kylie's high-frequency clicks were polycyclic and similar, in

Table 7.1: *Tukey's HSD test. Result table of a Tukey's HSD multiple comparisons test among proportions (n = 4) performed in the proportion of high frequency clicks emitted by a short-beaked common dolphin while travelling alone or with a harbour porpoise in the Firth of Clyde, Scotland. SE = Standard error. q = value obtained in the test, which is compared to a critical q value (qc) from the studentised range distribution. If q is larger than qc from the distribution, the two means are significantly different. S = Significant (α = 0.05). Scenarios: 1 = Travelling alone, 2 = Accompanied by a porpoise but not travelling next to it, 3 = Travelling very close to a porpoise, 4 = Overall when travelling near a porpoise.*

Comparison	Difference	SE	q	qc	Decision
4 - 3	7.11	0.814	8.74	3.633	S
4 - 2	23.94	1.098	21.80	3.633	S
4 - 1	6.73	1.119	6.01	3.633	S
3 - 2	31.05	1.149	27.03	3.633	S
3 - 1	13.84	1.169	11.84	3.633	S
2 - 1	17.21	1.382	12.45	3.633	S

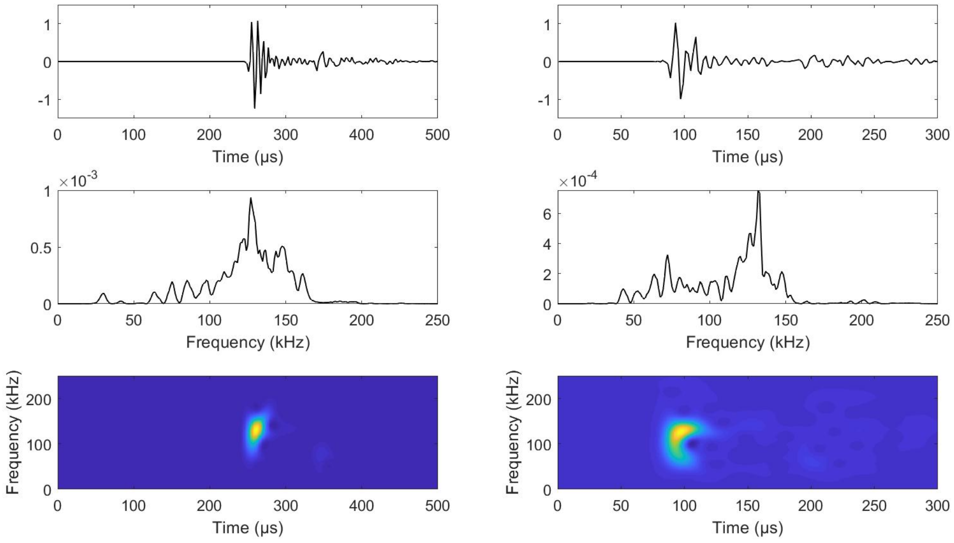


Figure 7.10: *High frequency. High-frequency click produced by Kylie when travelling together with a harbour porpoise. Note that the waveform is olygocyclic, with few peaks, compared to the waveform of harbour porpoise clicks*

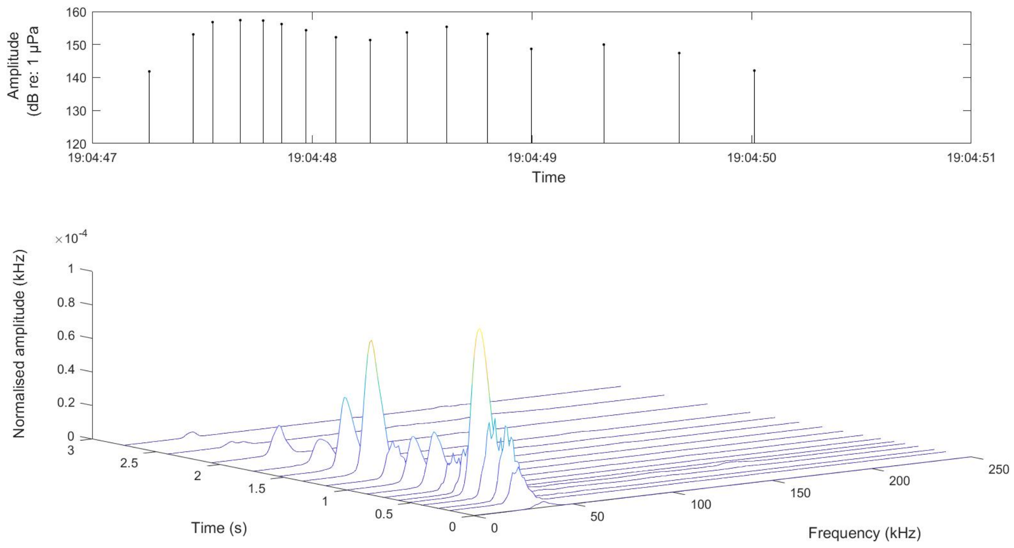


Figure 7.11: *Low frequency. Typical click train of low-frequency clicks produced by Kylie when travelling together with a harbour porpoise. Top: variation of amplitude levels (dB re: 1μPa) in time. Bottom: power spectrum of consecutive clicks.*

both time and frequency domains, to those produced by harbour porpoises (Figure 7.12). Note, however, that while the spectral characteristics are very similar, it is still possible to distinguish between Kylie's and the porpoise clicks, as Kylie's clicks have energy below 100 kHz (visible in the power spectrum and the Wigner plot) and the envelope of the signal in the time domain is different to the Gaussian shape of the porpoise click.

Some clicks with high-frequency peaks are an intermediate between low and high-frequencies (Figure 7.13), with mixed characteristics in the power spectrum, but different enough to distinguish from porpoise clicks. Two examples are shown in Figure 7.14, both of which are broadband but with most of the energy between 100 and 150 kHz. Figure 7.13 shows a spectrogram of all clicks produced by Kylie in this study, sorted by centroid frequency. It is clear that Kylie shows great ability to

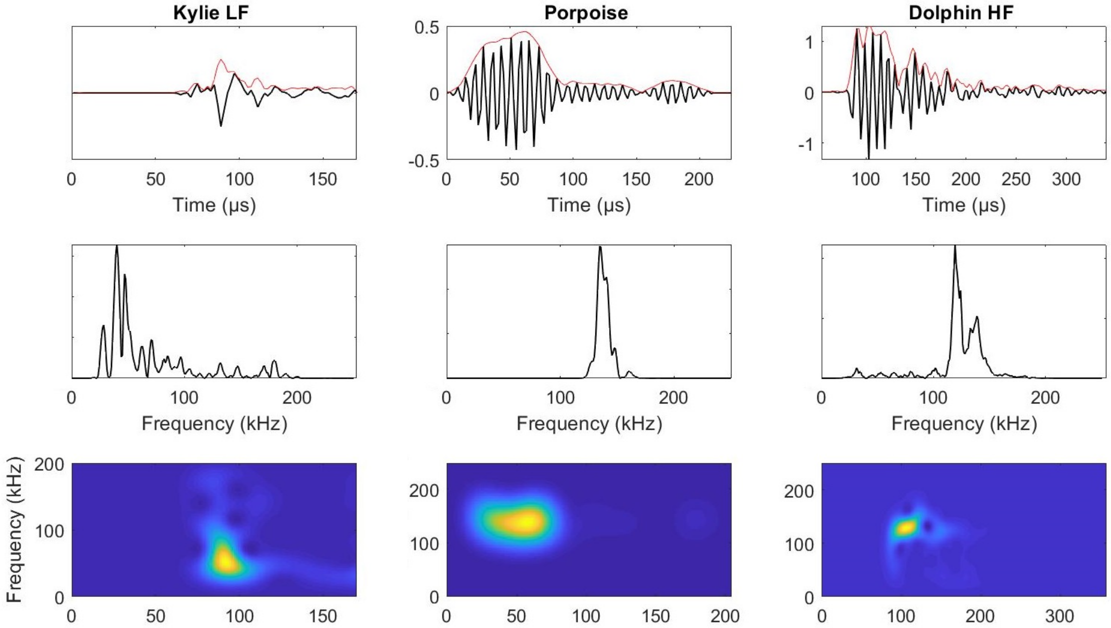


Figure 7.12: *Matching. Left: Typical low-frequency click produced by Kylie when alone. Middle: typical click produced by harbour porpoises. Note the lack of energy below 100 kHz. Right: High-frequency click produced by Kylie when travelling close to a porpoise. Note that while most of the energy is concentrated between 100 and 150 kHz, there is significant energy below 100 kHz. Additionally, the waveform is unlike a porpoise click as it begins with an abrupt onset.*

change the spectral characteristic of the clicks. This ability was previously observed in long-beaked common dolphins [172].

Production learning as a result of interactions with another species is not uncommon for cetaceans kept in closed enclosures [*e.g.*, 185, 188, 256]; however, they are rare in the wild [190]. This is the first study to present evidence for vocal production learning in short-beaked common dolphins. The results of this study show Kylie alters the spectral characteristics of her echolocation clicks by increasing its centroid frequency to match those of the porpoise. She was able to do this within a few seconds (Figure 7.17). Moreover, she produced a higher proportion of high fre-

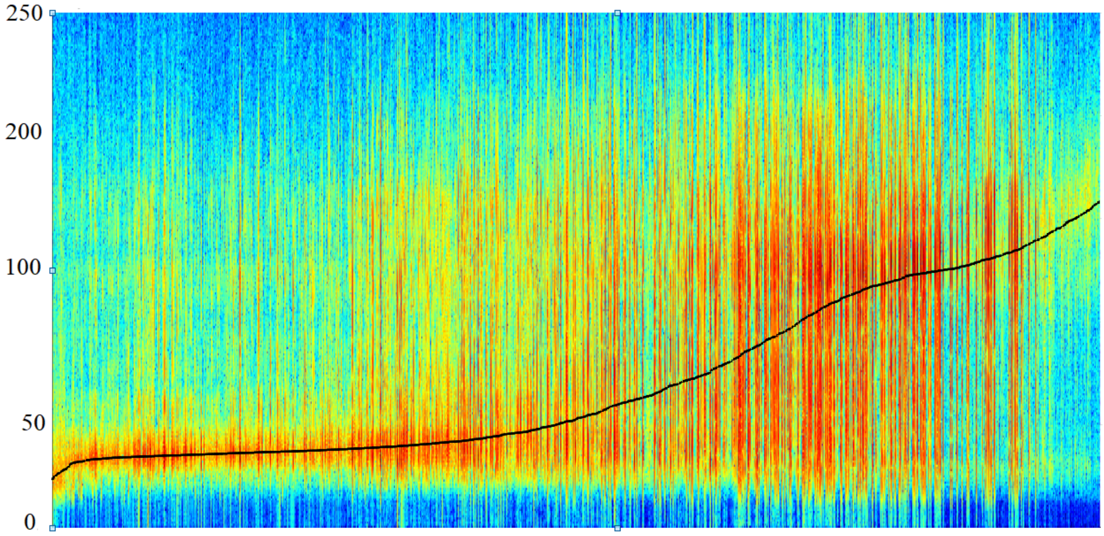


Figure 7.13: *Concatenated spectrogram of Kylie's clicks. Clicks were sorted by centroid frequency which are highlighted by the black line - as per [172].*

quency clicks when travelling close to a harbour porpoise than in any other scenario. Furthermore, these results support the hypothesis of interspecific vocal communication, and constitutes the first report of this kind for cetaceans in their natural environment.

Janik and Slater [180, 181] state that production learning requires modifications of the frequencies of the signal to produce a signal that was not previously in the animal's or species' repertoire. Such modifications should result from exposure to acoustic inputs, either artificial sounds or by interacting with individuals of the same or another species [181]. It is known that long-beaked common dolphins have the ability to produce clicks with a wide range of centroid frequencies [172], and this study supports those findings. Nonetheless, the data indicates that this is not a case of contextual learning (*i.e.*, producing an existing signal in another context), but a case of production learning in the form of vocal convergence, following Tyack

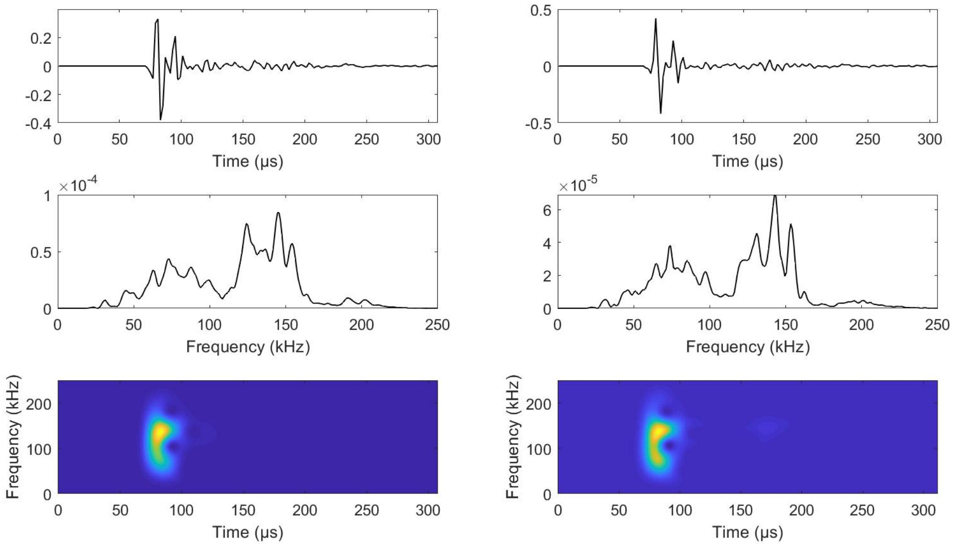


Figure 7.14: *High frequency. Broadband high-frequency clicks produced by Kylie when travelling together with a harbour porpoise.*

(2008) [191]. Tyack suggests that vocal convergence in adult individuals are, in fact, the result of production learning [191]. All echolocation clicks with energy over 100 kHz described for dolphins are oligocyclic, of short-duration, and broadband [33, 170, 241], while at least some of the high-frequency clicks produced by Kylie were polycyclic, resembling NBHF clicks (Figure 7.12).

These findings suggest Kylie is actively modifying the characteristics of her clicks to match those of the harbour porpoise. The transition probabilities showed that Kylie was significantly more likely to keep producing high-frequency clicks when travelling next to the porpoise, while the porpoise was more likely to vocalise when not close to Kylie. Moreover, these results support the results of the runs test, indicating that the animals did not interrupt each other.

7.3.2 The porpoises

The spectral characteristics of the harbour porpoise clicks were consistent with what is known for this species, with centroid frequencies centred at 139.7 kHz (SD = ±9.4 kHz) [6, 7, 114]. These values are also within the values found for the porpoises in the Firth of Clyde recorded throughout 2016 and 2017, which had a mean centroid frequency of 136.4 kHz (SD = ±0.6 kHz), ranging from 107 kHz to 159.9 kHz (Table 7.2). The centroid frequency values for the porpoises that interacted with Kylie are slightly higher than the overall population in the Firth of Clyde, but still within range. A recent unpublished work (PhD Thesis - [96]) found that young porpoises produce clicks with a higher peak and centroid frequencies than adults during the first 9 months. While the results come from one calf only, born in captivity, if this is representative, it is possible that Kylie is in fact visited by young individuals. Photographs of Kylie with porpoises also support this hypothesis (Figure 7.4).

The porpoise that accompanied Kylie on the first day emitted a total of 3 buzzes or calls and all of them were recorded while it was moving in a different direction than Kylie. These calls were between 100 and 180 ms long and consisted of several dozen clicks each (mean = 70). All calls followed the same pattern resembling a

Table 7.2: *Porpoise clicks. Centroid frequency values for porpoise clicks per day and the overall, and the population*

	Mean (±SD)	Min	Max
Day 1 (n = 379)	136.5 (±8.1)	118.9	172.7
Day 2 (n = 119)	147.1 (±7.2)	120.5	161.2
Day 3 (n = 29)	151.9 (±5.8)	136.7	162.9
All 3 days (n = 527)	139.7 (±9.4)	118.97	172.7
All porpoises (n = 25764)	136.4 (±8.1)	107.0	159.96

V: the calls begin with a repetition rate of between 250 and 270 clicks per second (CPS), going below 150 CPS and back to 150-170 CPS again Figure 7.15.

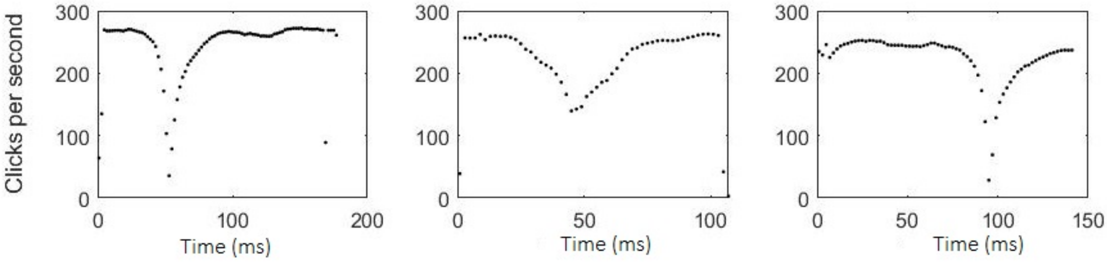


Figure 7.15: *Communication calls? clicks per second produced by the porpoise while spending time with Kylie, recorded on the 2nd of November 2016.*

Potential communication calls in harbour porpoises have been recorded in at least three studies carried out on captive and free-ranging animals [10, 11, 12, 13]. The first study to describe potential communication calls was conducted in the 1960s. Not much attention was given to these, as only 3 studies focused on communication in harbour porpoises since then (see Chapter 6 for more information). The stereotyped pattern of these buzzes suggest these may be communication calls, which may function to maintain cohesion or contact with other individuals [189].

7.3.3 Consecutive clicks

Visual inspection of all clicks organised in chronological order against direction of arrival (estimated using the time of arrival differences [224]) revealed Kylie and the porpoise travelled close to each other, at least part of the time, which is evident by the consistency in the direction of where the clicks are coming from during a long period (Figure 7.16). Additionally, Kylie can rapidly change the spectral characteristics of the clicks, moving from low to high frequencies within a few ms (Figure 7.16). This variation of the spectral characteristics of Kylie's clicks was previously reported for long-beaked common dolphins [172]. This, and the fact that low- and high-frequency clicks were narrowband, while mid-frequency clicks are broadband, could explain the inconsistent descriptions in the literature [39, 171, 257].

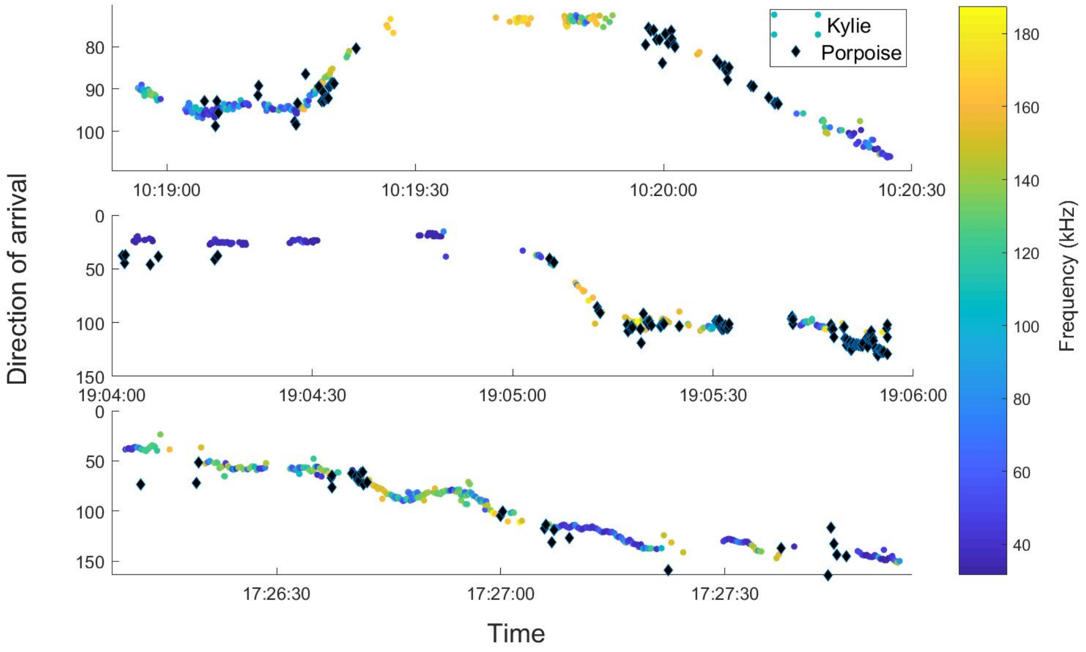


Figure 7.16: *Consecutive clicks. Clicks produced by Kylie and a harbour porpoise while travelling in close proximity (evidenced by the consistency of the direction where these clicks come from (i.e., y axis)) plotted in chronological order (n = 1,248). The position of the vessel is at* 0°. *Porpoise clicks are represented as a black rhombus and dolphin clicks are dots colour coded by centroid frequency (in kHz). Recordings were made on 2nd (top figure) and 3rd (middle figure) November 2016, and 4th September 2017 (bottom figure) in the Firth of Clyde, Scotland.*

Echolocation signals are highly directional and so the waveform and spectral content suffer from distortion at the edges of the beam. This spectral filtering due to orientation is not significant for harbour porpoises [53], but it is for delphinids. It is therefore possible that the variability observed could, at least in part, be the result of changes in the orientation of Kylie with respect to the hydrophones. However, off-axis clicks are biased towards low frequencies [232] and the changes observed in this study are the opposite, with the increased proportion of high-frequency clicks. Figure 7.17 shows an example of a click train produced by Kylie when she changes from low-frequency to high-frequency clicks within seconds, moving through broadband or bimodal clicks.

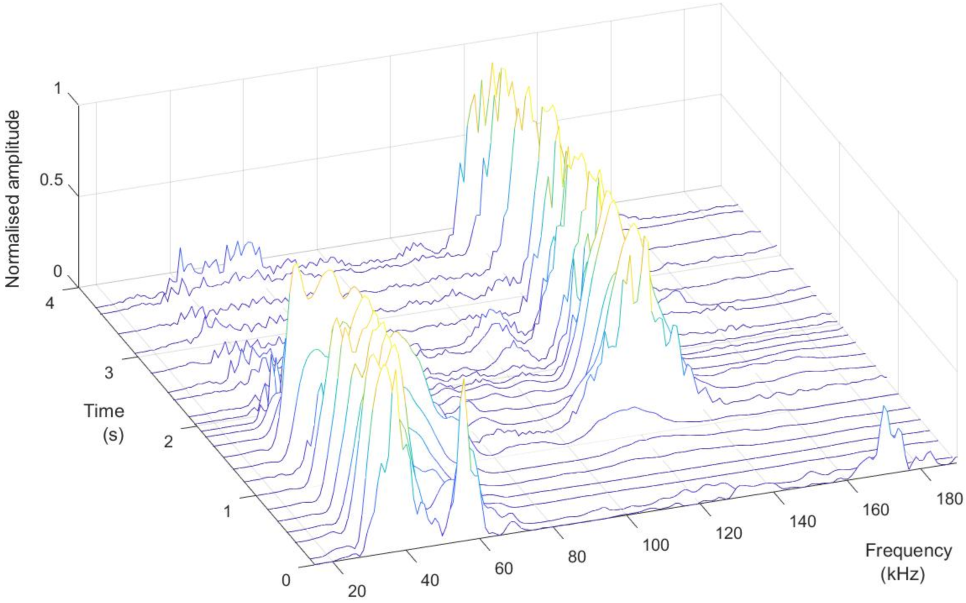


Figure 7.17: *Waterfall. Click train produced by Kylie over a period of 4 s (above). Recordings were made on the 2nd of November 2016 while seen travelling with a harbour porpoise.*

The transition probabilities showed that Kylie was significantly more likely to produce consecutive high-frequency clicks when travelling with the porpoise than when the porpoise was far from her. Self-transitions for Kylie were higher than transitions into other states, which means that once she started vocalising she was more likely to continue to vocalise (Figure 7.18). On the other hand, the porpoise was less likely to continue vocalising when it was close to Kylie than when far from her, suggesting the porpoise tried to keep in contact with Kylie when far, and that it did not interrupt Kylie when next to her. These results are consistent with the results of the Wald–Wolfowitz runs test for individual clicks and click trains (see below).

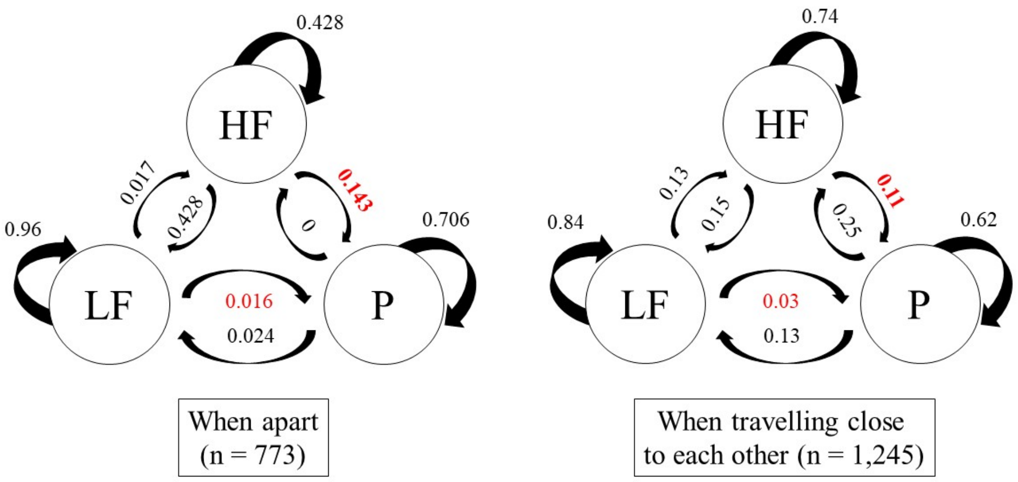


Figure 7.18: *Markov Chains. Transition probabilities between low-frequency, high-frequency, and porpoise clicks in two different scenarios: while travelling close to each other (left) and while being in the same area but not close to each other (right).*

7.3.4 Overlap

During periods when Kylie and a porpoise were travelling next to each other, a total of 166 click trains were recorded, based on ICI and species, 135 of which were produced by Kylie. Based on ICI only, 49 click trains were detected (Table 7.3). Of these, 27 were produced by Kylie, 5 by the porpoise, and 17 had clicks produced by both individuals. In most cases when there was overlap, it was the porpoise producing few clicks as Kylie vocalised. The null hypothesis for the Wald–Wolfowitz runs test performed on consecutive clicks when the dolphin and the porpoise were travelling next to each other (n = 1,248) was rejected ($p = < 1^{-50}$, $\alpha = 0.05$), indicating that clicks were not produced at random. This means that once the porpoise (or Kylie) started vocalising, they were more likely to continue vocalising and, therefore, there was no significant overlap in their clicks (*i.e.*, they do not interrupt each other). These results are consistent with the results of the Markov Chains.

The potential turn-taking behaviour indicated by these results is apparent in Figure 7.19, especially for day 1 (top figure) and day 3 (bottom figure).

Turn taking has not been studied thoroughly in non-human animals except, maybe, in non-human primates, although it seems to be present in many species of birds and mammals, including cetaceans [258]. The phenomenon is not always described as turn-taking, however, and the terminology is not consistent between studies, making it difficult to identify [259]. A recent study based on a 34-sec recording of two captive bottlenose dolphins reported a clear case of turn-taking. The author also claimed that the dolphins form sentences, much as humans do [260]. Similarly, Schulz reported that different sperm whale (*Physeter macrocephalus*) groups show a similar pattern when it comes to coda production. Codas are a series of clicks emit-

Table 7.3: *Click trains. Mean and median lengths of click trains based on inter-click intervals (>1 s) and/or species*

		Median	Mean (±SD)	Min	Max
ICI	Both (n = 17)	36.5	54.3 (±52.6)	3	189
	Kylie (n = 27)	6	11.1 (±11.1)	1	37
	Porpoise (n = 5)	4	5.7 (±3.9)	2	13
ICI and Species	Kylie (n = 135)	1	8.1 (±20.7)	1	163
	Porpoise (n = 27)	3	5.4 (±5.7)	2	22

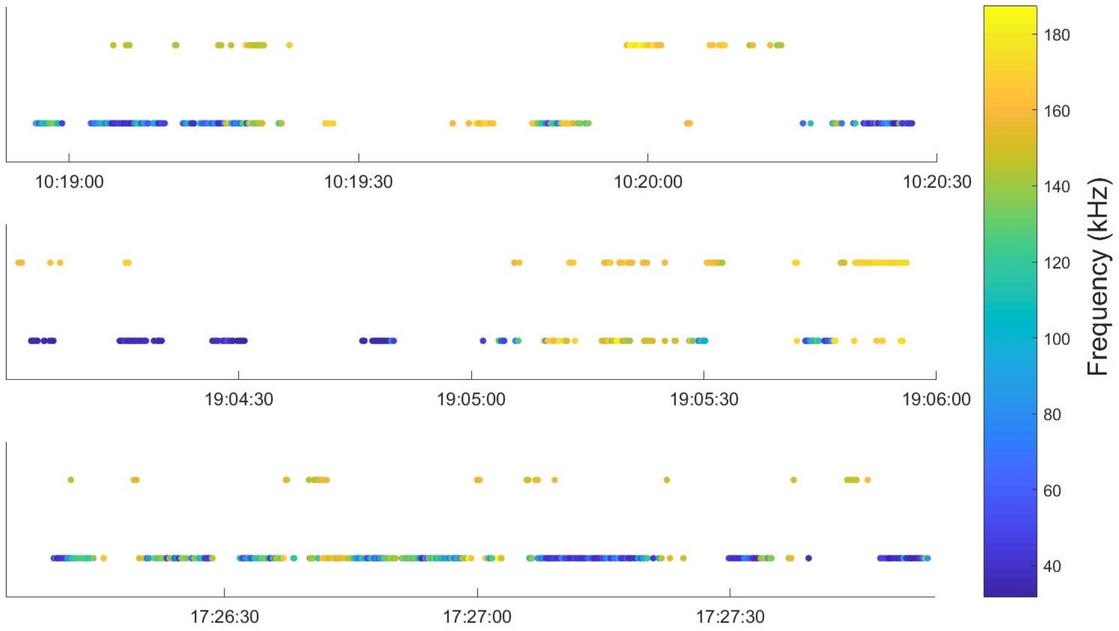


Figure 7.19: *Turn taking. Click trains of both the harbour porpoise (top lines) and Kylie (bottom lines) for 2nd of November 2016 (top figure), 3rd of November 2016 (middle figure), and 4th of September 2017 (bottom figure), colour-coded by centroid frequency (kHz).*

ted with a particular pattern and are thought to be used for communication. Schulz found that most of the time codas from different animals did not overlap (only in 15-16% of cases) and that in 22% of cases they were followed by codas produced by another individual. In addition, the authors found evidence of matching of the coda types by either the responder (*i.e.*, the whale that produces the codas later) and the initiator (*i.e.*, the first whale to produce a coda) [258]. More studies focused on this behaviour are needed before any conclusions can be drawn, but the available data suggest it might be more common in the animal kingdom than previously thought [259].

Turn taking in spontaneous conversations in humans follows a series of rules described by Sacks et al. (1974) [261]. For two speakers these rules are (1) Speaker-change recurs, or at least occurs (2) Overwhelmingly, one party talks at a time (*i.e.*, when one speaker starts vocalising, it is more likely to continue vocalising) (3) Occurrences of more than one speaker at a time are common, but brief (*i.e.*, they usually do not interrupt each other) (4) Transitions (from one turn to a next) with no gap and no overlap are common. (5) Turn order is not fixed (6) Turn size is not fixed (7) Length of conversation is not specified in advance (8) What parties say is not specified in advance (9) Relative distribution of turns is not specified in advance (10) Number of parties can vary (11) Talk can be continuous or discontinuous (12) Repair mechanisms exist for dealing with turn-taking errors and violations; *e.g.*, if two parties find themselves talking at the same time, one of them will stop prematurely, thus repairing the trouble [261]. The vocalisation pattern observed during the periods where Kylie and a porpoise were travelling next to each other follows these rules almost in its entirety.

Whether communication signals carry information is still a matter of debate. Some authors argue that the senders emit signals to manipulate or elicit a behaviour change in the receiver [262], while others argue that the purpose of signalling is to transmit information regardless of what the receiver does with it (see [117]). It is possible that some of Kylie's high-frequency clicks were misidentified as porpoise clicks and vice versa, however, given the stereotypical characteristic of NBHF clicks, it is expected that the error rate is low. The overall results, therefore, indicate Kylie is actively producing more high-frequency clicks when in close proximity to the harbour porpoise and that there is little overlap in their sounds. Moreover, this is consistent with the hypothesis of vocal communication between Kylie and the porpoises. Furthermore, the evidence suggests vocal production learning abilities,

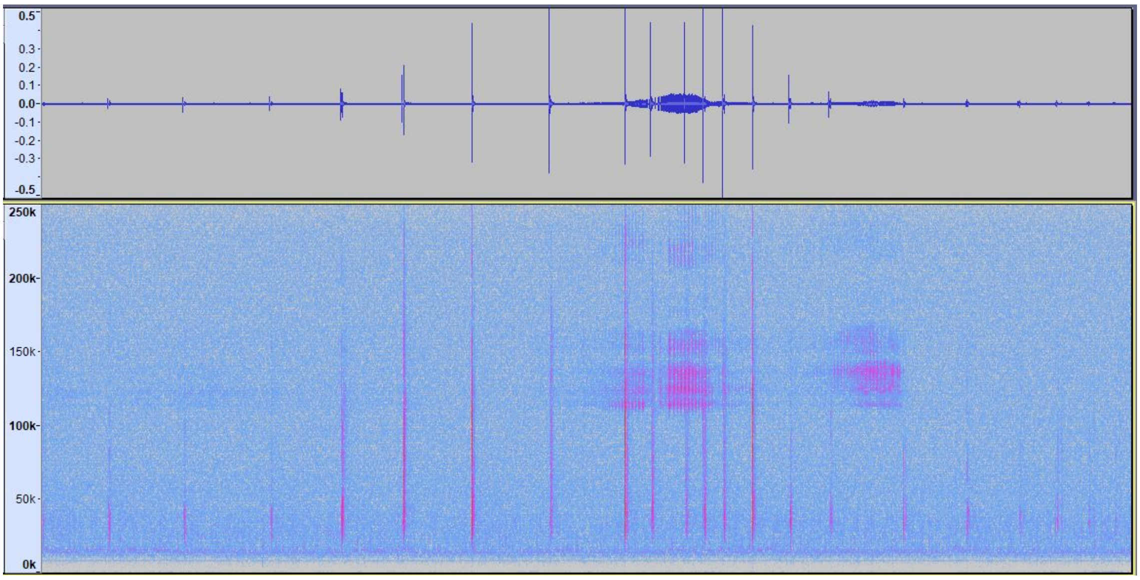


Figure 7.20: *Turn taking. Example of overlapping clicks produced by a harbour porpoise (vertical lines restricted to frequencies over 100 kHz) and Kylie, the solitary short-beaked common dolphin (remaining vertical lines). Top = waveform. Bottom = spectrogram. Recording made on the 2 of November 2016 at 1021 in the inner Firth of Clyde.*

not previously reported for short-beaked common dolphins.

7.4 Summary

The results of this study provide evidence of vocal communication between Kylie and harbour porpoises. Kylie only produced clicks despite being able to produce other sounds, and emitted a higher proportion of high-frequency clicks while in close proximity to a porpoise. The results also indicate neither the porpoise or Kylie's clicks were produced at random and that there was little overlap in their sounds, suggesting turn-taking behaviour. Moreover, because the majority of clicks were clearly produced by either (*e.g.*, Figure 7.14 and Figure 7.10), even if mistakes were made in assigning clicks to either of the animals, the overall results suggest Kylie is capable of production learning in the form of vocal convergence.

These interactions may be similar to when humans and their dogs bark at each other. However, the results must be interpreted in the context in which they took place. Whistles are one of the commonest sounds detected during common dolphin aggregations [165]. With frequencies below 20 kHz, whistles are in the lower limit of the harbour porpoise hearing range [254], but Kylie produced exclusively clicks with peak frequencies of at least 23 kHz, some of which had similar temporal and spectral characteristics similar to harbour porpoise clicks (Figure 7.12).

In summary, these results support the hypothesis of vocal convergence and interspecies vocal communication, and constitute the first report of this kind for cetaceans in their natural environment.

Chapter 8

D-PorCCA - from acoustics to behaviour

In this Chapter the algorithms developed in the previous chapters are brought together into a standalone application, D-PorCCA (available here). D stands for 'detector', PorCC for 'porpoise click classifier' and A for 'application'.

8.1 Introduction

Recent technological advancement, in both storage and processing power capabilities, have made it possible to use passive acoustic monitoring (PAM) devices that record continuously to monitor different cetacean species for long periods of time. This, however, leaves bioacousticians with the challenge of having the time and resources to analyse the large amounts of data they collected. Data analysis is time-consuming and this usually results in leaving data unanalysed. But, it is now possible to develop analytical tools that are capable of providing researchers with pre-selected acoustic events with minimal input to overcome this problem.

This Chapter describes the main functionalities of D-PorCCA. The application includes the algorithms developed in the previous Chapters, which together aim to study the behaviour of harbour porpoises in their natural environment from the repetition patterns of their acoustic signals.

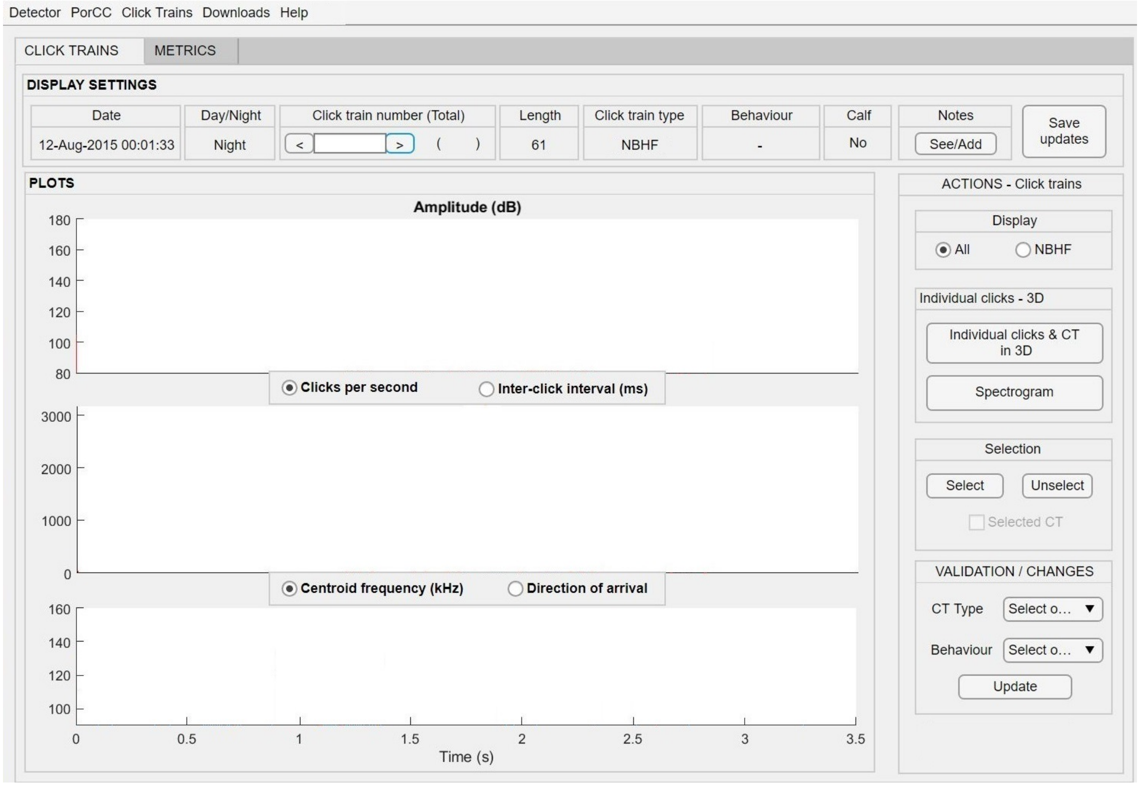
8.2 Description

D-PorCCA is a standalone application with a user-friendly interface. It was developed using App Designer, a MATLAB (Mathworks, MA) development environment that allows to create desktop or web apps that can be used without having a MATLAB account. The executable file automatically downloads 'MATLAB Compiler' for installation, after which the user can open the application like any other desktop application. App Designer was introduced with the 2016a version of MATLAB. The environment is easy to use and has most functionalities that exist in the older 'GUIDE' environment. With App Designer adding components and functions is straightforward, facilitating improvements and updates work.

D-PorCCA has two main tabs: the Main Display where individual click trains can be explored and the Metrics Display, to visualise summary data.

8.2.1 Main display

The application opens on the main page (Figure 8.1). Here, the user can see simultaneously three aspects of the click trains: variations in amplitude, repetition rates or inter-click intervals, and centroid frequency or direction of arrival of each click, if available.



Date: 12-Aug-2015 00:01:33

Day/Night: Night

Length: 61

Click train type: NBHF

Behaviour: -

Calf: No

Display: ● All ○ NBHF

● Clicks per second ○ Inter-click interval (ms)

● Centroid frequency (kHz) ○ Direction of arrival

Figure 8.1: ***Main page***. *D-PorCCA main page.*

Additionally, a series of parameters are available, including date and time, length and type of click train, as well as behaviour. The user can also make changes and add notes. These functions are described in detail below:

- **Date and time**: date and time of the beginning of the click train.
- **Day/Night**: available if the user provides latitude and longitude (in decimal degrees) of the devices, whether they are moored to the seabed or of the central area, in the case of surveys conducted using towed hydrophones. If the survey area is relatively small, it is expected to have minimal or no impact

on the results. The coordinates are used to estimate sunrise and sunset times of each day using the function 'sunrise' developed by Beauducel (2019) [263]. Subsequently, this information is used to determine whether the click train was recorded at day or night time.

- **Length**: total number of clicks in the click train.
- **Click train type**: there are four categories of click train types: 'NBHF', 'LQ-NBHF', 'Sonar', or 'Non-NBHF'. More information on the decision-making pathway for these categories is provided in Chapter 5 - Patterns of click trains.
- **Behaviour**: there are four behavioural categories: 'Orientation', 'Foraging', 'Socialising', and 'Unknown', and are available for click trains classified as 'NBHF'. More information on how click trains are assigned to either of these categories is provided in Chapter 5 - Patterns of click trains. Further information and examples of each category are also available in Chapter 6 - Acoustic behaviour.
- **Calf**: D-PorCCA does not currently include a classifier for young harbour porpoises, however, there is potential to develop such classifier in future work and add it to the application.
- **Notes**: add (or see existing) notes for the click train.
- **Save updates**: save changes.
- **Display**: select to display only 'NBHF' click trains or all types.
- **Individual click trains - 3D**: prompt a 3D display (Figure 8.2). The user can

inspect each click individually for verification purposes as well as to visualise specific aspects of it that cannot be appreciated in other ways (*e.g.*, energy content). In this display it is also possible to delete clicks individually.

- **Spectrogram**: prompt spectrogram of the click train if the recordings (*.wav* files) are available.
- **Selection**: select individual click trains to extract for further analysis.
- **Validation**: change the type and behaviour of the click train manually.

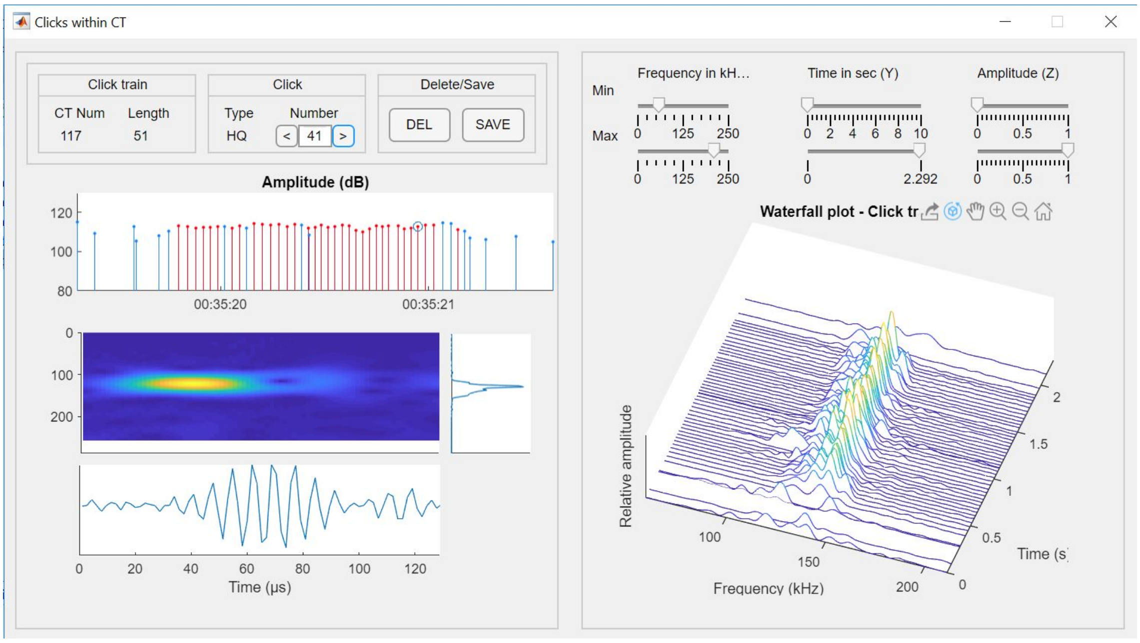

Click train: CT Num 117, Length 51
Click: Type HQ, Number 41

Figure 8.2: ***Individual click trains***. *Pop up window showing a waterfall image of a click train.*

Visualising click trains in 3D is useful for verification purposes as the energy content is evident in the power spectrum. Additionally, each click can be inspected, including the waveform, power spectrum, and spectrogram. The user can delete clicks manually from this window if so desires.

8.2.1.1 Click trains

In D-PorCCA, a click train is defined as a series of consecutive clicks separated by less than a given time period (in ms), which the user can select (default = 1,000 ms). The user can also select the minimum (default = 16 clicks) and maximum (default = 1,500 clicks) number of clicks. Clicks displayed were classified by the PorCC algorithm [15] as either high-quality (HQ) or low-quality (LQ) clicks, which are seen in red and blue, respectively. Clips classified as 'Noise' are not displayed.

8.2.1.2 Behaviour

Four behavioural categories are used in D-PorCCA, which are described below:

- **'Orientation'**: characterised by repetition rates below 100 clicks per second (CPS). This indicates the porpoise is inspecting the environment it moves through.
- **'Foraging'**: Foraging events are characterised by three phases: search, approach, and feeding buzz [123]. In the search phase the porpoise produces fewer than 100 CPS; in the approach phase the repetition rate increases rapidly, and a final stage of high-production rate that can reach up to 640 CPS [*e.g.* 9]).
- **'Socialising'**: social calls are characterised by not having a period with slow repetition rates as feeding events do.
- **'Unknown'**: Click trains without a recognisable pattern.

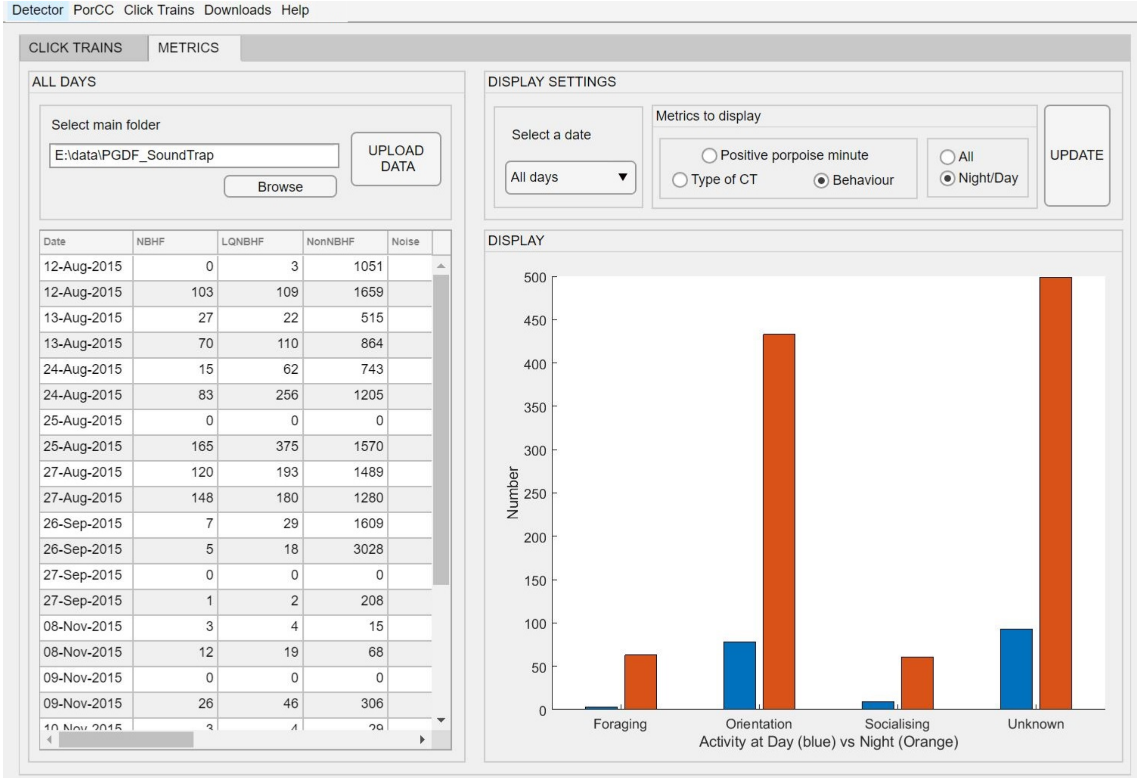
A description of the algorithms developed to identify behavioural states from click trains is given in Chapter 5 - Patterns of click trains.

8.2.2 Metrics display

Within the Metrics display, there are two sections. On the left side, the user can see a summary table with information about click trains detected in the study period. On the right side, the user can choose between a series of metrics to be displayed (Figure 8.3). The metrics estimated are described below.

8.2.2.1 Metrics

A series of metrics are available as a summary data the user can inspect and download. These metrics were selected because they are already used in the literature or because they provide an easy way to visualise the data.



Select main folder: E:\data\PGDF_SoundTrap

Select a date: All days ▼

Metrics to display: ○ Positive porpoise minute ○ Type of CT ● Behaviour ○ All ● Night/Day

Date	NBHF	LQNBHF	NonNBHF	Noise
12-Aug-2015	0	3	1051	
12-Aug-2015	103	109	1659	
13-Aug-2015	27	22	515	
13-Aug-2015	70	110	864	
24-Aug-2015	15	62	743	
24-Aug-2015	83	256	1205	
25-Aug-2015	0	0	0	
25-Aug-2015	165	375	1570	
27-Aug-2015	120	193	1489	
27-Aug-2015	148	180	1280	
26-Sep-2015	7	29	1609	
26-Sep-2015	5	18	3028	
27-Sep-2015	0	0	0	
27-Sep-2015	1	2	208	
08-Nov-2015	3	4	15	
08-Nov-2015	12	19	68	
09-Nov-2015	0	0	0	
09-Nov-2015	26	46	306	

Figure 8.3: ***Metrics***. *Metrics tab in D-PorCCA.*

1. **Positive Porpoise Minute**: for each minute of the day, a positive porpoise minute is one where at least a NBHF click train is detected. This metric is available only if the data was collected using a static device. The plot is divided into two parts, one with the total number of positive minutes per day, and the other one plotting each positive minute in the 24 hours of the day (see Figure 5.16).
2. **Types of click trains**: four categories of click trains are shown: 'NBHF', 'LQ-NBHF', 'Non-NBHF', and 'Sonar'.
3. **Behaviour**: four categories of behaviour are shown: 'Orientation', 'Foraging', 'Socialising', and 'Unknown'.

For each of these metrics, the user can visualise either the total, or the numbers divided into day *vs* night if available (Figure 8.3). Additionally, the user can select to plot data from the entire survey period or from a specific date. These plots are made from the summary table shown on the left side of the Metrics panel. Lastly, the user can save the plots as *.jpeg* or other format directly from the figure.

8.2.3 Menus

D-PorCCA includes a series of Menus to make the user's experience easier.

8.2.3.1 Detector

The built-in detector extracts potential clicks from the *.wav* file. The signal is filtered with a 6th order Butterworth band-pass, with the low cut-off frequency set at 2 kHz and the high cut-off frequency at 95% of half of the sampling frequency. These filters are applied to reduce the background noise at low frequencies. In the next step, and to find potential clicks, an adaptive threshold is set based on the first 10,000 samples (*i.e.*, maximum value under 0.1). All peaks over that threshold, separated by at least 200 samples (*i.e.*, 400 μs for a 500 kHz sampling frequency) are considered potential clicks, and are extracted by adding 120 sample to each side of the peak of the signal. Subsequently, all necessary variables and parameters are estimated, and files constructed to function within D-PorCCA.

8.2.3.2 PorCC

The user can run the ProCC classifier [15] by accessing individual clicks directly from the *.pgdf* files generated by PAMGuard's Click Detector Module.

Input values

The user must input a series of parameters for PorCC to function, which are also requested in the Detector menu. These are:

- **Number of hydrophones** or channels used in the recording process.
- **Sampling frequency (kHz) - Fs**: The sampling frequency is the number of samples per second in a sound recording.
- **Hydrophone sensitivity (dB re 1V/1μPa)**: is the amplitude (dB re 1μPa) of the sound necessary to generate 1 Volt. This value is provided by the manufacturer and is used to estimate the amplitude of the signals.
- **Gain (dB)**: total gain of the recording system. This value is used to estimate the amplitude of the signals.
- **Peak to Peak (Volts)**: refers to the clipping value of the recording system. This information is provided by the manufacturer and is use to estimate the

amplitude of the given signals.

- **Probability thresholds**: PorCC estimates the probability of a given signal to be a high-quality (HQ) or low-quality (LQ) harbour porpoise (or narrow-band high-frequency -NBHF- click). The probability threshold value in the PorCC Menu is the threshold of selected by the user. The default (and recommended) values for HQ is 0.999999 and for LQ is 0.6.

8.2.3.3 Click trains

In this menu, the user can run the algorithms to organise the data (*e.g.*, tables created by the Detector or the PorCC algorithm) into click trains, applying the 'Pattern algorithm' and 'Behaviour algorithm' developed in Chapter 5 - Patterns of click trains.

Once these algorithms are applied, the user can open existing projects.

8.2.3.4 Download

The user is provided with a list of summary data they can download in *.csv* format:

- **Click trains**: Information about each click train is stored in a table, which contains the following parameters: Identification number, date and time, where it is stored (*i.e.*, *.pgdf* or *.wav* file), length (number of clicks), day or night time, type, behaviour, selected (0/1), and notes.
- **Summary table**: Summary of parameters for each day (*e.g.*, total number of NBHF click trains).

8.2.3.5 Help

In this section, the user can find information about D-PorCCA, and they can search for specific topics, including input values, how to set up the application, and what each of the behaviours represent.

8.3 Other applications

There are at least 16 species of whales, dolphins, and porpoises that produce narrowband high-frequency (NBHF) clicks. Due to the similarities in the characteristics of these clicks, tools developed to study porpoises were successfully used to study other NBHF species [*e.g.*, 212]. This suggests that D-PorCCA can potentially be used to study other NBHF species. This Chapter presents the results of using D-PorCCA on data from Heaviside's dolphin (*Cephalorhynchus heavisidii*).

8.3.1 Heaviside's dolphins

Heaviside's dolphins are small, coastal dolphins (Figure 8.4) endemic to the west coast of southern Africa. They mainly occur within the Benguela ecosystem, which comprises the shelf waters of the west coast of South Africa, Namibia, and southern Angola. Heaviside's dolphins have small home ranges and at least some individuals show site fidelity [264]. Moreover, there is evidence of a temporal and spacial segregation of behaviours, resting and socialising close to the coast during the day, and foraging far from shore at night [265].

The first study which focused on the sounds of Heaviside's dolphins was carried out in the 1970s [61]. The authors used equipment that was not able to record high-frequency sounds and therefore only low-frequency sounds were reported. Watkins et al did not record whistles or other tonal sounds typical of other delphinids [*e.g.*, 266], only pulsed sounds (*i.e.*, clicks) with energy below 5 kHz. Depending on repetition rates, three sound types were described: 'clicks at slow rates, short bursts of pulses, and series of pulses at a rapid enough rate to produce a tonal "cry" sound' [61].

Figure 8.4: *Heaviside's dolphins. Picture by Stephani Flynn from the Namibian Dolphin Project*

In 2011, Morisaka et al. used technologies able to record and describe the high-frequency components of the Heaviside's dolphin clicks for the first time. These are narrow-band high-frequency (NBHF) clicks with temporal and spectral characteristics similar to those produced by other non-whistling species, like the harbour porpoise [6]. They are polycyclic, with several peaks in the time domain, and have their energy concentrated between 100 and 150 kHz. Unlike other NBHF clicks, the distribution of the centroid frequency is bimodal, with peaks at 122 kHz and at 130 kHz. Individual clicks have one or two peaks at 122 kHz and 130 kHz, respectively, in the power spectrum. The reason for the double peak in the power spectrum is unknown [51].

More recently, Martin et al. (2018, 2019) found that Heaviside's dolphins also produce clicks with broader frequency bandwidths that have energy well below 100 kHz, which they produced both as click trains at slow rates and as burst pulses, which are thought to be used for communication purposes [50]. As shown in Figure 8.5, the repetition rates of these buzzes is variable and might be indicative of their behaviour, which has been observed for other NBHF species, such as the harbour porpoise and the Hector's dolphin (*Cephalorhynchus hectorii*) [11, 13, 43].

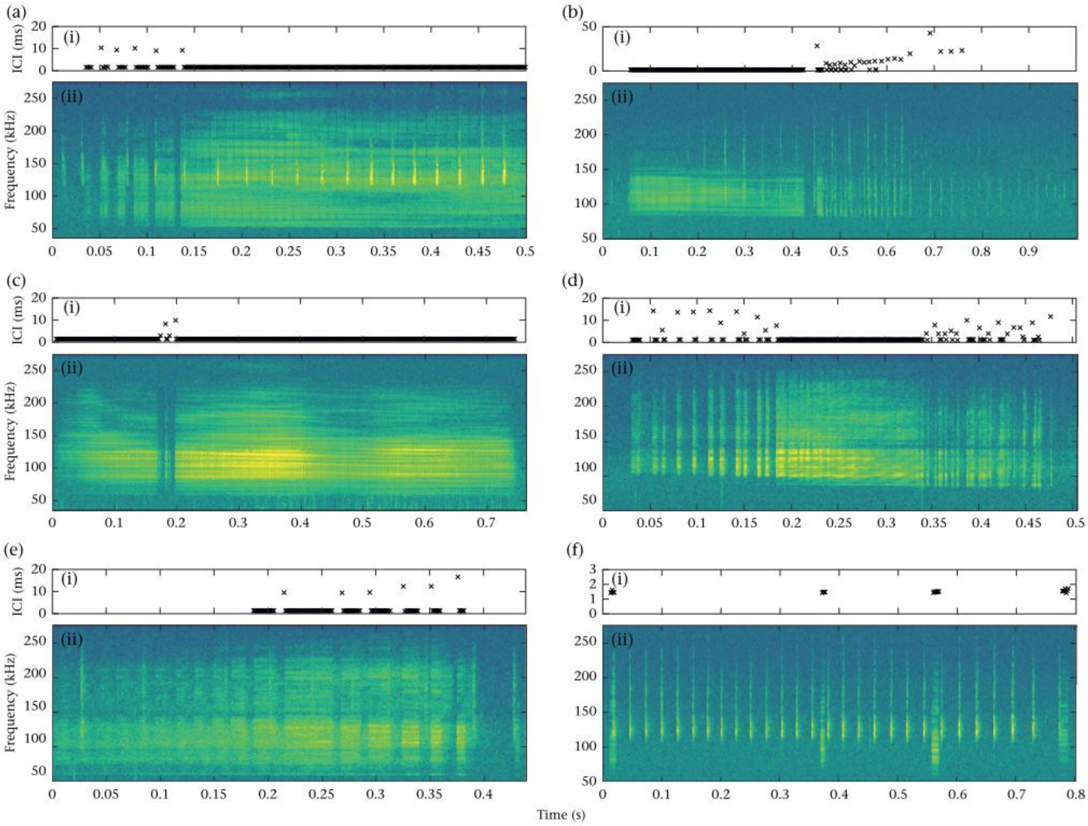


Figure 8.5: *Examples of Heaviside's dolphin burst-pulse signals. (a) Patterned at the beginning, (b) patterned at the end, (c) patterned in the middle, (d) patterned at both the beginning and the end, (e) continuous segmented pattern and (f) series of four short burst-pulses. For each signal, (i) the interclick intervals (ICIs) throughout the signal and (ii) the spectrogram of the signal (512-pt, FFT, Hamming window, 50% overlap; MATLAB version 2017b) are shown. NBHF click trains from other individuals can be seen overlapping in all spectrograms except in (c) and (d). Note only the latter half of the continuously segmented patterned signal shown was suitable for click detection. From Martin et al. 2019 [62]*

The aim of this Section was to test the algorithms in D-PorCCA for acoustic data from Heaviside's dolphins.

8.3.2 Methods

The acoustic data used in this Section were collected using a SoundTrap ST300 HF off Walvis Bay (Namibia) during June 2019. The data were collected by The Namibian Dolphin Project as part of an ongoing project aiming to compare the performance of two existing static passive acoustic monitoring devices. The SoundTrap was deployed 3 m below the water surface from a drifting boat in the vicinity of Heaviside's dolphins. No other cetacean species were seen in the area. A total of seven *.wav* files were used, corresponding to approximately 37 min of recordings. Three files were from the 10th, three from the 11th, and one from the 26th of June 2019.

A custom-built impulsive-sound detector (see Section 8.2.3.1) was used to detect potential dolphin clicks within the *.wav* files. Each of these potential clicks were classified by PorCC ([15] - also see Chapter 4 - PorCC: the harbour porpoise click classifier) into one of three categories: high-quality clicks (HQ), low-quality clicks (LQ), and noise. The probability thresholds were the default values, that is for HQ clicks was set at 0.999999 and for LQ at 0.6. For LQ and HQ clicks, a series of parameters were estimated (see Section 3.3) and saved for further analysis in D-PorCCA (see Chapter 8 D-PorCCA - from acoustics to behaviour).

8.3.3 Results and discussion

A total of 1,936 Heaviside's dolphin clicks were found. Of these, PorCC classified 1,272 as LQ and 664 as HQ. Using 500 ms as the maximum separation time between two consecutive clicks, these clicks were found in click trains (n = 24) of between 11 and 333 clicks, including 2 buzzes (n = 493 clicks). Some of the clicks were likely noise or echoes, but because the data were collected in a quiet environment, it was not necessary to do any further cleaning of the click trains. Most clicks were typical NBHF clicks, with centroid frequencies around 130 and 132 kHz, but some had peaks below 110 kHz, as those reported by Martin et al [50, 62]. The data used here did show a bimodal distribution of peak frequencies but not the one reported before [51], as the peak at 122 kHz is not visible (8.6). This discrepancy could be due to the small sample size used here.

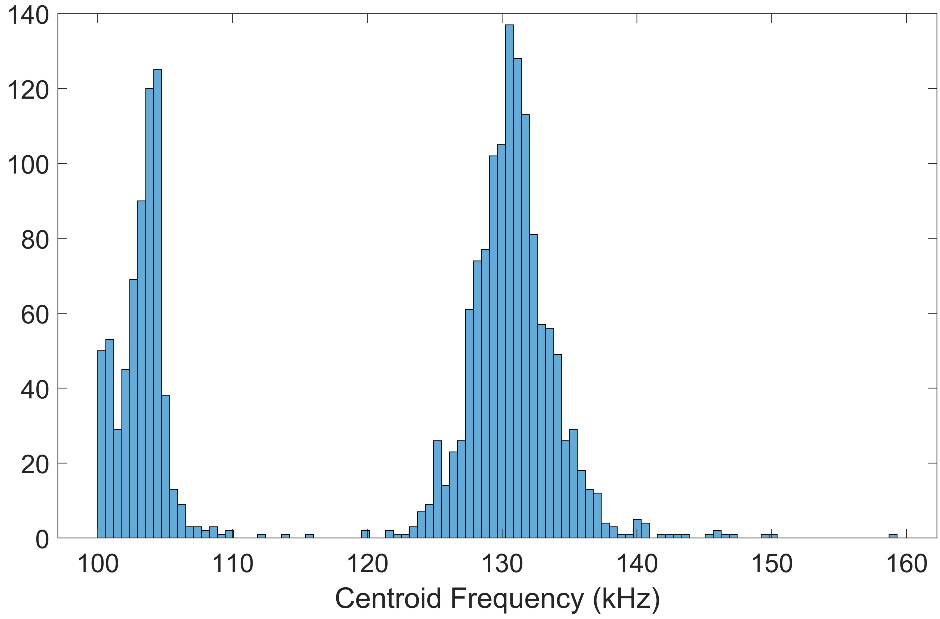


Figure 8.6: ***Centroid frequency***. *Histogram of the centroid frequencies of all the Heaviside's clicks found in this study (n = 1,940).*

Almost a third of the clicks had peak frequencies between 100 and 110 kHz, which is clearly visible in Figure 8.6. Because PorCC ignores clicks with peak or centroid frequency below 100 kHz, some clicks may have been missed, given the abrupt cut at frequencies close to 100 kHz seen in Figure 8.6. These clicks made up the buzzes and are the broadband clicks previously described by Martin et al [50, 62], which they hypothesised were used for communication purposes. No attempts were made to match the pattern of the buzzes with the visual observations made concurrently with the recordings.

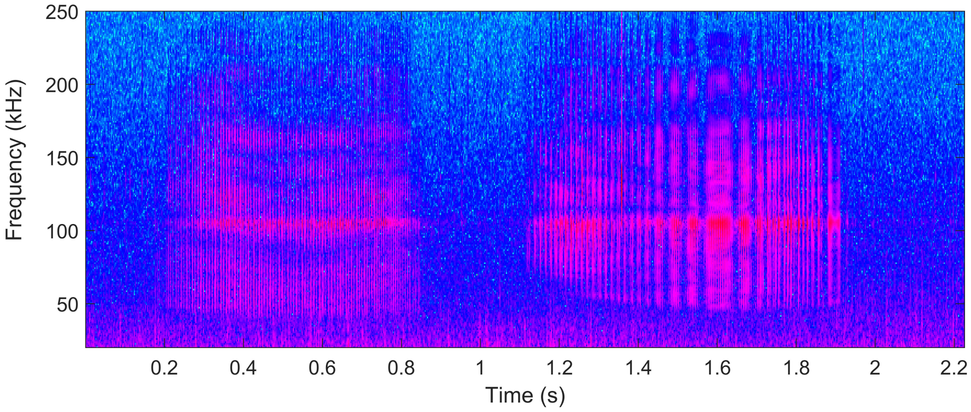


Figure 8.7: *Heaviside's dolphins. Broadband buzz produced by a Heaviside's dolphins off Namibia - spectrogram of the buzz from the original recording.*

The broadband nature of these clicks is visible in Figure 8.7, showing they do have energy below 100 kHz, unlike harbour porpoise clicks [7], yet PorCC classified them as NBHF clicks using the default threshold values. This is counter-intuitive, however PorCC classification does not use -10 dB bandwidth, which is the parameter that better describes the broadband feature of these clicks. This is evident in the power spectrum of the buzz (Figure 8.8).

The repetition rate of the buzz was over 500 clicks per second, which can be ap-

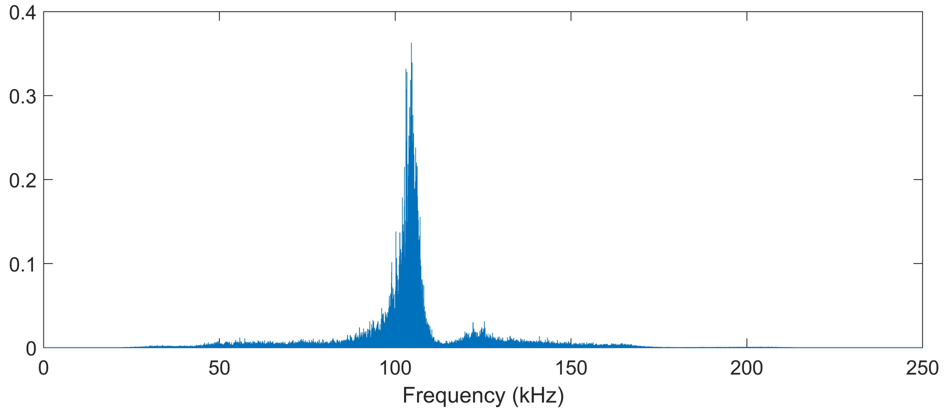
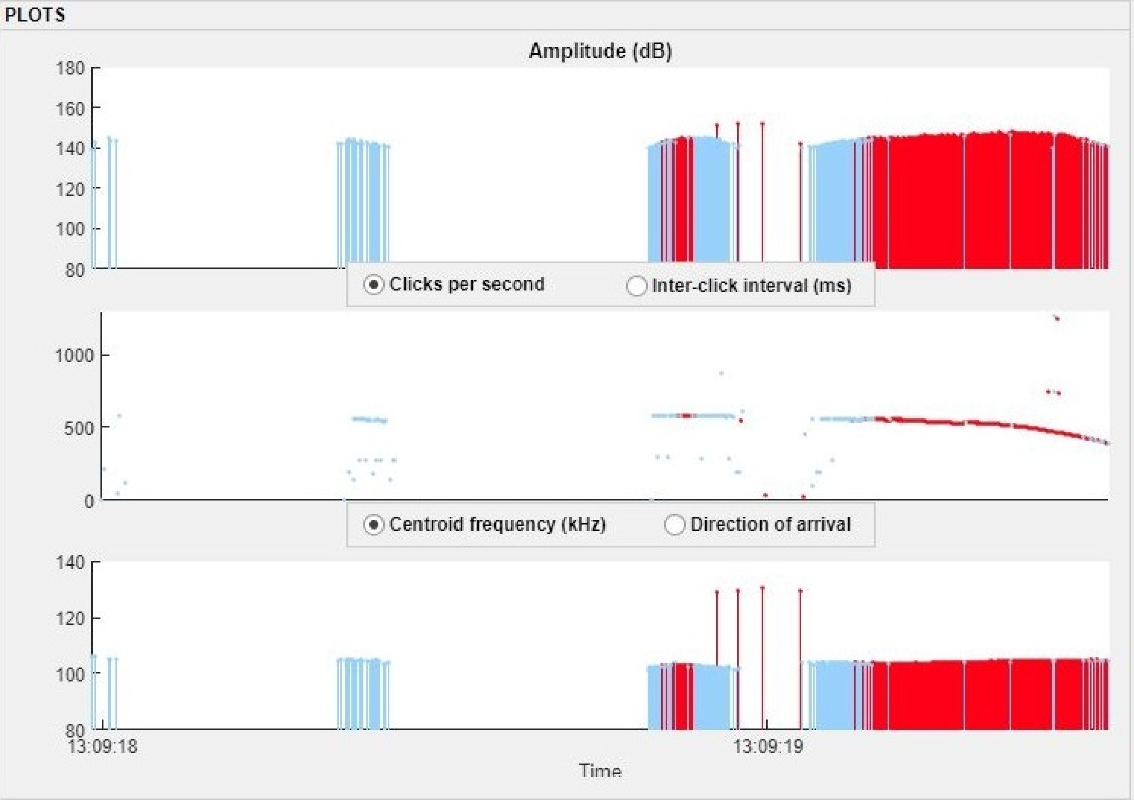


Figure 8.8: *Heaviside's dolphins. Broadband buzz produced by a Heaviside's dolphins off Namibia - spectrogram of the buzz from the original recording.*

preciated in the main display of D-PorCCA (Figure 8.9), where also two overlapping click trains are visible: the broadband buzz, and few clicks with higher amplitude and higher centroid frequency. The latter are not visible in the spectrogram (Figure 8.7).

Typical NBHF click trains had higher peak and centroid frequency and were produced at low repetition rates, ranging between 10 and 60 clicks per second. Low repetition rates indicate these clicks are typical echolocation clicks used by dolphins to orient themselves in the environment.

These are promising results. Although the recordings were made in a quiet environment, the potential application for other NBHF is clear. More research is needed to test whether PorCC and other algorithms in D-PorCCA can identify the broadband clicks in an area with different levels and types of background noise.



● Clicks per second ○ Inter-click interval (ms)

● Centroid frequency (kHz) ○ Direction of arrival

Figure 8.9: *Heaviside's dolphins. Broadband buzz produced by a Heaviside's dolphins off Namibia - buzz as seen in D-PorCCA.*

8.3.4 Conclusions

A small sample of recordings of Heaviside's dolphins was used to test the potential of using D-PorCCA to study other NBHF species. The results suggest it is indeed possible, even using the default values. Moreover, PorCC, the harbour porpoise click classifier developed in this thesis [15], was able to identify both the typical NBHF and the broadband clicks produced by Heaviside's dolphins [50, 62]. Modifications may be needed to detect the whole range of Heaviside's dolphins clicks.

Overall, the results indicate all algorithms within D-PorCCA, including those to detect behavioural patterns (*i.e.*, travelling/orientation, foraging/feeding, and socialising/communication) can also be used for Heaviside's dolphins.

Chapter 9

Conclusions

This Chapter presents an overview of the thesis, highlighting the main results and discussing the implications in context. Lastly, future lines of research are recommended.

9.1 Overview of the Thesis

The main goal of this thesis was to develop a standalone application, D-PorCCA, to study the behaviour of harbour porpoises in their natural environment. Harbour porpoises vocalise almost continuously producing only stereotyped clicks, and available data prior to this thesis indicated that the behaviour could be inferred from the patterns in repetition rates. The behaviours could be divided into three main categories: travelling or orientation, foraging and feeding, and socialising and communication.

Data on social calls came almost exclusively from experiments conducted in captive settings. These studies found several call types, including 'distress', 'aggression', 'contact', and 'courtship' [10, 11, 12]. In the wild, one study found a series of sounds that resemble social calls previously described in the literature [8, 11]. The authors recorded opportunistically a young harbour porpoise trapped in a fishing net using a static acoustic device that logs data about acoustic events (*i.e.*, T-POD - Chelonia Ltd., UK). In this case the authors knew where to look in the data, which is almost never possible when using passive acoustic monitoring (PAM) devices.

The most recent study focused on repetition rates in wild harbour porpoise is Sorensen et al. (2018). In this case, the data came from six porpoises that were accidentally caught in fishing nets in Denmark. The animals were mounted with behavioural and acoustic tags, and released into the wild. Data confirmed porpoises produce social calls that are qualitatively different from other sounds.

This means that PAM could be used for behavioural studies. However, the required analytical tools for such studies were not yet available. This is the first study focused on vocalisation patterns of harbour porpoise in the wild using PAM devices that record continuously.

A series of tools have been developed in this thesis, which can identify clicks produced by harbour porpoises and other species with similar sounds, and use the underlying patterns of repetition rates to identify behaviours. These algorithms were tested in two datasets from different study areas (Denmark and Scotland) and collected with different devices (SoundTrap - Ocean Instruments, New Zealand, and towed hydrophone arrays). All algorithms showed high levels of accuracy, between 69.2% and 98.5%. These results suggest D-PorCCA and the algorithms within it have potential for behavioural studies as well as for monitoring purposes using non-invasive methods.

Additionally, in this thesis, the interspecific interactions of wild harbour porpoises with a solitary short-beaked common dolphin was studied, as a study case of potential interspecific communication. Using two hydrophones it was possible to use the direction of arrival of individual clicks, as well as the temporal and spectral characteristics to study the acoustic behaviour of the dolphin and the porpoises.

9.2 Summary of Findings

The main results of this thesis are highlighted below.

9.2.1 Behaviours

Using the algorithms developed in this thesis, the three main behavioural categories were observed, based on the patterns of repetition rates. Moreover, subpatterns within those categories were also found, suggesting there is potential for more detailed studies.

9.2.1.1 Orientation

Within 'Orientation', two subpatterns were found. First, patterns called 'landmarks', which indicate that the porpoises are using fixed objects in their environment to orient themselves. The second were a series of click trains with very low repetition rates, from 3 to 10 clicks per second. These may represent sleeping or resting behaviour.

9.2.1.2 Feeding in water column?

Harbour porpoises feed on pelagic (*e.g.*, herring) and demersal species (*e.g.*, sand eel). It is expected that the foraging technique used to catch free-swimming herrings is different than the one used to catch sand eels. Such differences are also likely reflected in the acoustic behaviour of the porpoise. In both cases a search phase and a final feeding buzz are expected, however, the approach phase could take different forms.

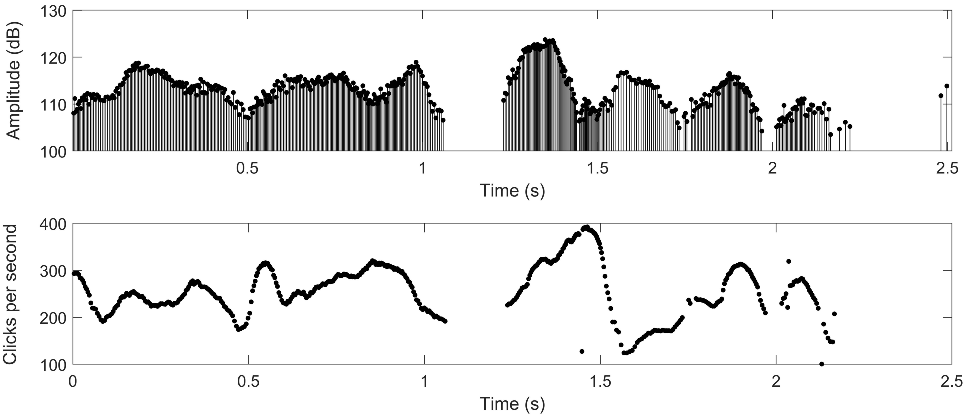


Figure 9.1: ***Foraging?***. *Example of a click train produced by harbour porpoises.*

Some repetition rates did not have a clear pattern nor were similar to any of the patterns from the rest of the data. Although no visual data was available, some of these patterns could potentially represent unsuccessful foraging events where the porpoise chased a fish in the water column. One possible example of this, is shown in Figure 9.1.

9.2.1.3 Social calls

For the first time, social calls of wild harbour porpoises were detected and described using passive acoustic monitoring devices that record continuously. These include calls previously reported (*e.g.*, consistent with distress calls [*e.g.*, 11]) as well as new ones (*e.g.*, calls with V-shape pattern). The most striking discovery is the identification of 'phrases', which are comprised by a series of calls (the same type or not) produced in a short period of time. Phrases were first described by Amundin in 1991 [11] and were never reported again.

9.2.2 Vocal imitation

The acoustic data collected during interactions between harbour porpoises and a solitary short-beaked common dolphin in the west of Scotland yielded noteworthy results. First, the data suggest the dolphin changes the characteristics of her echolocation clicks to match, or imitate those of the porpoise. Second, at least one of the porpoises emitted a 'phrase' comprising three V-shaped calls during these interactions. Lastly, the data suggest turn-taking behaviour, as the animals vocalised with little or no overlap.

9.3 Implications of the Research

The implications of this research are two-fold. First and foremost, this thesis provide new analytical tools that would make behavioural studies possible in a non-invasive way. Secondly, using D-PorCCA to analyse existing and new data can reveal important areas for harbour porpoises that need protection.

9.3.0.1 Behavioural studies

The results of this study confirmed harbour porpoises produce sounds with different patterns in repetition rates, many of which are consistent with social calls. Moreover, it suggest the patterns may be similar between populations as similar calls were found in both Scottish and Danish data. Most of these calls had repetition rates over 100 clicks per second (*e.g.* , with inter-click intervals below 10 ms). Further, some calls overlapped with patterns of feeding buzzes.

Our understanding of harbour porpoise feeding behaviour may need to be reconsidered due to the results of this study. First, many studies use the 10 ms inter-click interval as a threshold to detect a feeding event, which may lead to overestimation of feeding activity, given the characteristics of social calls. Second, foraging events have been described using the same characteristics in repetition rates, namely a search phase, an approach phase, and a final feeding buzz. Although this pattern has been reported widely and been used to detect feeding events from passive acoustic monitoring data, some of the patterns found in this study may challenge that idea.

Lastly, harbour porpoises belong to a group commonly known as 'non-whistling' cetaceans. At least 16 species from this group, including whales, porpoises, and dolphins, produce very similar sounds. These species also have in common their seemingly lack of social life. The tools developed here can potentially be used to study the acoustic behaviour of those species.

9.3.1 Conservation

Knowledge about how porpoises use their environment is crucial to identifying key areas for them and to develop effective conservation measures, such as Special Areas of Conservation required under the EU Habitats Directive [14]. For example, identifying patterns related to courtship or mating can be used to identify breeding areas and thus avoid overlap with human activities.

In addition, harbour porpoises are highly sensitive to noise and these tools can help us understand how noise-producing human activities affect their behaviour and if it interferes with life functions (*e.g.*, feeding), and thus provide countries with tools to collect robust data to fulfil their legal obligations.

9.4 Recommendations for Future Research

Throughout this Thesis, a number of practical or theoretical limitations were encountered. These are discussed here to provide insight into how these limitations could be overcome. In doing so, the potential for future research is elucidated.

9.4.1 Compare with existing tools

The T-PODs and C-PODs (Chelonia Ltd., UK) are the most used passive acoustic monitoring devices to study harbour porpoises in the wild. Given these devices do not record the waveform of the signals and that the algorithms are not publicly available, validation is subjective and not always possible, especially with regard to missed events. D-PorCCA has similar functionalities and thus the performance should be tested against each other. This is specially important in areas with high background noise.

9.4.2 Visual data

Many of the patterns found in this study are consistent with communication or social calls reported in the literature. However, many patterns had not been described before, and therefore visual surveys carried out concurrently with acoustic recordings are necessary to understand these patterns. Although data could be obtained from experiments in captivity, behavioural data is best from the wild.

9.4.3 Separation of click trains

If data is collected with at least two hydrophones it is possible to estimate the direction of arrival of each signal, facilitating separation of click trains. However, data is usually collected using one hydrophone and thus algorithms able to separate overlapping click trains based on one sensor would be needed. The algorithms developed in this thesis were not able to deal with this problem.

9.4.4 Calves

Calves and young harbour porpoises produce clicks with different temporal and spectral characteristics than those of adults. The existing data suggest that this information could be used to identify the presence of young individuals during acoustic events. An algorithm able to distinguish between adults and young individuals could be easily incorporated into D-PorCCA and supplemented with visual data.

9.4.5 Other species

There are at least 16 species of whales, dolphins, and porpoises that produce narrow-band high-frequency clicks similar to those of the harbour porpoises. It was shown in this thesis that D-PorCCA can potentially be used to study those species, such as the pygmy and dwarf sperm whales, of which we know next to nothing.

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Appendix A

Porpoise click classifier (PorCC): A high-accuracy classifier to study harbour porpoises (*Phocoena phocoena*) in the wild

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Harbour porpoises are well-suited for passive acoustic monitoring (PAM) as they produce highly stereotyped narrow-band high-frequency (NBHF) echolocation clicks. PAM systems must be coupled with a classification algorithm to identify the signals of interest. Here, the authors present a harbour porpoise click classifier (PorCC) developed in MATLAB, which uses the coefficients of two logistic regression models in a decision-making pathway to assign candidate signals to one of three categories: high-quality clicks (HQ), low-quality clicks (LQ), or high-frequency noise. The receiver operating characteristics of PorCC was compared to that of PAMGuard's Porpoise Click Detector/Classifier Module. PorCC outperformed PAMGuard's classifier achieving higher hit rates (correctly classified clicks) and lower false alarm levels (noise classified as HQ or LQ clicks). Additionally, the detectability index (d') for HQ clicks for PAMGuard was 2.2 (overall $d' = 2.0$) versus 4.1 for PorCC (overall $d' = 3.4$). PorCC classification algorithm is a rapid and highly accurate method to classify NBHF clicks, which could be applied for real time monitoring, as well as to study harbour porpoises, and potentially other NBHF species, throughout their distribution range from data collected using towed hydrophones or static recorders. Moreover, PorCC is suitable for studies of acoustic communication of porpoises. © *2019 Acoustical Society of America*.

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I. INTRODUCTION

Studying harbour porpoises *Phocoena phocoena* in their natural environment is a difficult task. They are small and surface for only a few seconds at a time, travelling in groups of three or fewer animals, or as solitary individuals (Hammond *et al.*, 2002). However, they are highly vocal (Linnenschmidt *et al.*, 2013) and are therefore well suited for passive acoustic monitoring (PAM). Harbour porpoises produce highly stereotyped narrow-band high-frequency (NBHF) clicks for echolocation and communication. These clicks have peak and centroid frequencies between 100 and 160 kHz, centred around 130 kHz (Møhl and Andersen, 1973), with no spectral energy below 100 kHz (Hansen *et al.*, 2008). The duration of individual clicks ranges from 50 μs to 175 μs and the half-power (-3 dB) bandwidth is around 15 kHz (Kyhn *et al.*, 2010). Clicks are emitted in series, often referred to as "trains." A click train is loosely defined as "any series of clicks separated by gradually or cyclically changing inter-click interval suggesting a unit during an echolocation event or a communication signal" (Koschinski *et al.*, 2008). Other odontocetes that produce NBHF clicks are all the porpoises (Phocoenidae), some dolphins of the Lissodelphininae subfamilily, pygmy, and dwarf sperm whales (Kogiidae), and the river dolphin *Pontoporia blainvillei* (Galatius *et al.*, 2019).

Different PAM devices are used to study harbour porpoises, including animal-borne devices (Akamatsu *et al.*, 2007), towed hydrophone arrays (e.g., Gillespie *et al.*, 2005; Sveegaard *et al.*, 2011), and static devices (e.g., Carlström, 2005; Carstensen *et al.*, 2006). Static PAM devices can be roughly divided between those that record continuously (e.g., SoundTrap-Ocean Instruments, New Zealand) and click detectors or data loggers that only store information about the transient sounds detected, such as date and time, peak frequency, and amplitude (e.g., C-PODs; Chelonia Ltd., Cornwall, UK). C-PODs, and the earlier version T-POD, are used for a wide variety of studies, including seasonal and geographical changes in distribution (Verfuß *et al.*, 2007) and response to anthropogenic noise (Carstensen *et al.*, 2006; Pirotta *et al.*, 2014). Moreover, they have been used to study porpoise acoustic behaviour (Koschinski *et al.*, 2008), including diurnal variations in echolocation rates and click train patterns (Carlström, 2005). Continuous recordings at high sampling rates, required to record harbour porpoise clicks, generate an enormous amount of data and so the storage capacity limits the length of the data collection period. Moreover, data analysis is time consuming and so often part of the data remains unanalysed. On the other hand, click data loggers do not require high storage capacity and thus are more suitable for long-term studies and, since they are coupled with an automatic real-time classifier,

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[a)] Electronic mail: melania.cosentino@strath.ac.uk, ORCID: 0000-0001-7837-8669 the time invested in post-deployment data analysis is reduced significantly. However, it is not possible to carry out *post hoc* verification as the C-POD does not record the sound itself, and the detection and classification algorithms are not publicly available.

On the other hand, there are vast amounts of acoustic continuous recordings made using PAM systems that could be used to fill gaps in our understanding of harbour porpoise behaviour and communication in the wild. To that end, however, a classification system that can accurately and reliably identify harbour porpoise clicks is required. A classification system, in simple terms, assigns a given signal x to one of k pre-defined classes according to a series of parameters or functions. For continuous recordings, one of the most used harbour porpoise detector/classifier systems is PAMGuard's Click Detector and Classifier modules. PAMGuard is a modular, open source software designed to detect and classify marine mammal sounds (Gillespie *et al.*, 2009), and it is used worldwide for a wide range of studies (Cucknell *et al.*, 2016; Lawrence *et al.*, 2016; Pinn *et al.*, 2010). The standard settings of the classifier include a pre-filter (4th order digital Butterworth IIR 10 kHz high pass filter) and a trigger filter (4th order digital Chebyshev IIR 100–150 kHz band pass filter, pass band ripple 2.0). Clicks are classified as produced by porpoises by comparing the test band (110–150 kHz) to control bands (40–90 kHz and 160–190 kHz), with a 6 dB threshold ("general configuration file—porpoise click detection," available at www.pamguard.com). As an open source the software is regularly improved, and although the user can manage the settings, there is no available information about its performance. The precision (i.e., percentage of individual clicks correctly classified as porpoise clicks) reported for an earlier version of this classifier was between 37% and 74%, depending on the settings and background noise, while the proportion of missed clicks was not reported (Gillespie and Chappell, 2002). However, the performance of the current version remains unquantified. Additionally, the classifier requires manual verification after the identified clicks have been highlighted and clicks have to be manually selected in echolocation events in order to be extracted for further analysis (Cucknell *et al.*, 2016; Lawrence *et al.*, 2016). Alternatively, many researchers use custom-built classifiers (such as the KERNO classifier of the C-POD), of which neither the algorithm, nor the performance is available. As acoustic recordings continue to accumulate, assessing the performance of available classifiers for comparison purposes and automating these processes becomes essential.

The objective of this study was to develop a harbour porpoise click classifier (PorCC) that improves the performance of existing classifiers, reducing the occurrence of both false alarms and missed clicks, and that provides the user with a simple assessment of the quality of the classified click. PorCC was developed using the output of PAMGuard's Click Detector Module, and uses the coefficients of two logistic regression models to estimate a probability that a given signal was produced by a harbour porpoise. The predictor variables used to build the two logistic regression models were selected because these are the variables most commonly used to describe the temporal and spectral characteristics of harbour porpoise vocalisations (e.g., Kyhn *et al.*, 2013). Once the probabilities are estimated, each signal is assigned to one of three categories: high-quality clicks (HQ), low-quality clicks (LQ), and high-frequency noise (N). These categories were defined based on the characteristics of the waveform, power spectrum, and spectrogram (Fig. 1). The performance of PorCC was tested against manually labelled samples from 18 h of data collected in two different seasons and in different background noise conditions. Additionally, the performance was tested against PAMGuard's Classifier in a subset of the dataset, consisting of 8 h of data from one summer day.

II. MATERIAL AND METHODS

A. Data collection

Acoustic data were collected during systematic surveys conducted in the West coast of Scotland, in the Firth of Clyde (55.5254° N, 4.9333° W) during 25 survey days throughout all seasons, between 2016 (n = 20) and 2017 (n = 5), totalling over 210 h of recordings. Surveys were carried out under sail or engine from the "Saorsa," a 40-ft sailing vessel. Transect lines were determined in advance and surveyed at a speed between 5 and 7 knots, in different weather conditions, during both day and night times. Surveys were terminated if the sea state reached $\geq$5. No concurrent visual observations were made. Recordings were made using a towed omnidirectional 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 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 response between 2 and 150 kHz. The array was towed using a Kevlar-strengthened 100 m long cable and the units were 25 cm apart.

PAMGuard's Click Detector Plug-In detects impulsive sounds (i.e., sounds of short duration with abrupt onset and rapid decay) over a given SNR threshold selected by the user (e.g., 6 dB). The detected sound is then saved as an individual audio clip, which also includes a very short recording period before and after the impulsive sound detected. All impulsive sounds detected in a given hour of recording are individually saved in one *.pgdf* file (for PAMGuard Data File) (Gillespie and Oswald 2017). For each audio clip, additional information is attached, such as date and time, time of arrival difference (i.e., delay) with respect to the reference hydrophone, and direction of arrival, estimated using trigonometric methods based on time of arrival differences (Gillespie and Chappell, 2002). By extracting individual clips from these files, two datasets were created, one to train PorCC and one to test its performance against manually labelled clips. Additionally, a subset of the testing data was used to compare the performance against PAMGuard's Classifier.

B. Training data

Three categories of signals were defined for the development of PorCC: high quality porpoise clicks (HQ), low-quality

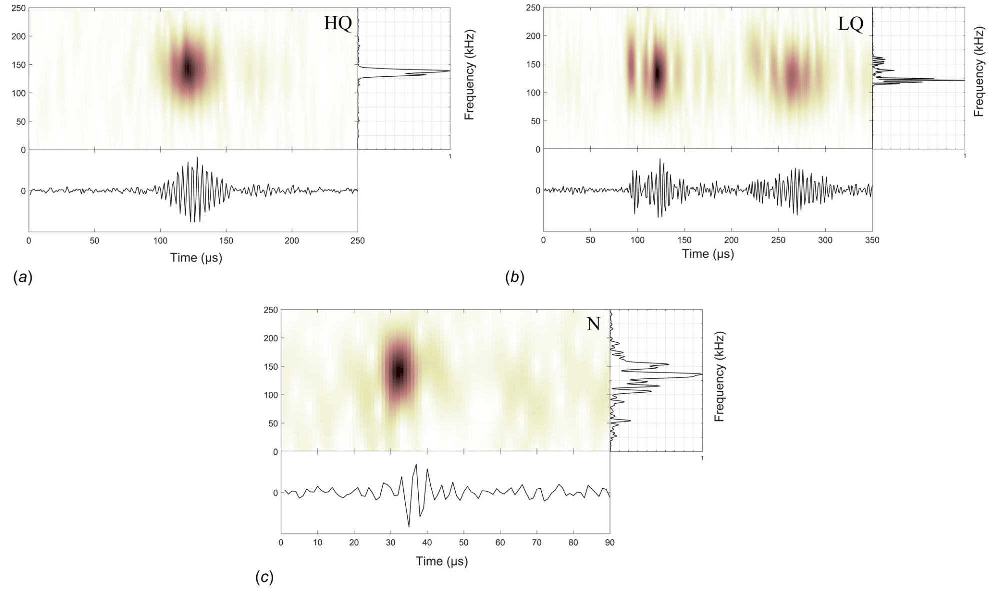

FIG. 1. (Color online) Examples of the categories defined to develop the harbour porpoise click classifier (PorCC). (a) High-quality harbour porpoise click (HQ), (b) low-quality harbour porpoise click (LQ), (c) high-frequency noise (N). Wigner plot (centre plot), waveform (lower plot), and power spectrum (right plot).

porpoise clicks (LQ), and high-frequency noise (N) (Fig. 1). HQ are polycyclic signals with peak frequency between 100 and 160 kHz, no spectral energy below 100 kHz, and duration around 100 μs, matching the description of on-axis harbour porpoise clicks (Au *et al.*, 2006; Hansen *et al.,* 2008). LQ consist of signals slightly different to HQ, for example presenting notches in the power spectrum, or no clear beginning or end of the signal (low signal-to-noise ratio). Noise clips (N) are signals with peak and centroid frequencies between 100 and 160 kHz that do not share other characteristics with harbour porpoise clicks (e.g., oligocyclic, do have energy below 100 kHz).

Of the over 2 500 000 audio clips detected and saved by PAMGuard's Click Detector during the survey period, a subsample of 125 416 (representing 5% of the total) was extracted using a random number generator to ensure they were independent from each other. In order to find good signals to develop the logistic regression models for the classifier (PorCC), an early version was used to assign to each clip a probability of being a harbour porpoise click. Those with high probability ($\geq$0.9) were considered to be potential HQ, those with a probability between 0.5 and 0.9 were considered to be potential LQ, and those with a probability $<$0.5 were considered to be potential N clips. Subsequently, from these, 5500 were randomly selected from their respective category to build two logistic regression models, thus 500 were potential HQ, 500 were potential LQ, and 4500 were potential N. In order to ensure each clip was a good representative of its respective category, all 5500 clips were then manually verified. Unrepresentative clips were discarded and replaced with clips randomly selected from the original subsample for that particular category.

1. Logistic regression models

In simple terms, the logistic regression model estimates coefficients for each predictor variable in the model and the error term, from which a probability is derived. The predictor variables used were the duration of the signal (estimated as the 80% energy of the clip, μs), peak frequency (PF, kHz) and centroid frequency (CF, kHz), -3 dB (BW_{-3dB}, kHz) and root mean square bandwidths (Madsen and Wahlberg, 2007), and Q_{RMS} (ratio between CF and BW_{RMS}). Additionally, the ratio between peak and centroid frequencies (Ratio) and the peak value of a cross correlation (XC) performed against a typical harbour porpoise click were used. The click used for the cross correlation was extracted from the original dataset,[1] and was selected based on the waveform, power spectrum and spectrogram characteristics and peak-to-peak amplitude (162 dB re: 1μPa). Additionally, the waveform was consistent in both hydrophones, and the time of arrival difference between them was 0 (i.e., the orientation of the animal was perpendicular to the array). All predictor variables were explored for normality.[1] Multicollinearity, that is, when the predictor variables are correlated with each other, was tested using the Pearson χ^2 coefficient and none of the variable pairs had a correlation coefficient higher than ± 0.36, except Q_{RMS} and XC that had a correlation of 0.49.[1]

The response variable for model 1 is binomial with the outcomes HQ/N and was built using 500 and 4500 clips of each, respectively. The response variable for model 2 is also binomial with the outcomes LQ/ N and was built using 500 and 4500 clips of each, respectively. The same N clips were used for both models. For each logistic regression model, a total of 63 models were tested as a series of reduced models using all possible predictor variable combinations, and the best of each model was identified as the one with the lowest Akaike Information Criteria (AIC) value (Table I).[1]

C. PorCC—Classification algorithm

The algorithm of the PorCC was written in MATLAB 2017a (The Math Works TM, Inc., Natick, MA) and runs on clips previously saved by PAMGuard's Click Detector Plug-In, analysing only those recorded by the first hydrophone on which they impinged. For each clip, the predictor variables identified in the model selection procedure are estimated and two probabilities are calculated using the coefficients obtained from the logistic regression models. Subsequently, a series of if/then statements is applied to assign the clip to one of the three categories previously defined (Fig. 2).

D. Testing data

To test the performance of PorCC, a dataset was created with all clips (n = 265 918) extracted from 5% of *.pgdf* files (i.e., 11 h of recordings, from ten survey days), which were selected randomly, and all clips (n = 284 231) from the 28th of August 2017 (i.e., 8 h of recordings). Clips with peak and centroid frequencies between 100 and 160 kHz and $Q_{RMS} > 4$ represented potential harbour porpoise clicks, and so these (n = 70 689) clips were extracted and manually labelled according to the three categories previously defined (Fig. 1), based on the characteristics of the waveform, power spectrum, and spectrogram. The overlap between the training and the testing data was of 442 clips. Subsequently, PorCC was used to classify the clips automatically by estimating the predictor variables and the probability-threshold values of 0.9999 and 0.55 (Fig. 2).

Confusion matrices and receiver operational characteristics (ROC) curves were used to assess the performance of PorCC. The hit rate was calculated for all categories as well as the rate of misclassification (i.e., false alarm and missed clicks) and the precision level. The hit rate is the number of HQ and LQ clips classified as HQ (strict criterion), or as either HQ or LQ (relaxed criterion), divided by the total number of non-N clips. Three analyses were performed: one with only HQ clips, one with only LQ clips, and one with both HQ and LQ clips, all against the N clips. The false-alarm rate is the number of N clips classified as HQ (strict criterion), or HQ or LQ (relaxed criterion) divided by the total number of N clips. In total, this results in six different points of operation in the ROC plot (strict or relaxed criterion combined with HQ, LQ, or both). The missed-clicks rate is defined as 1 minus the hit rate. The precision is defined as the number of clips correctly classified divided by the total number of clips classified into that category.

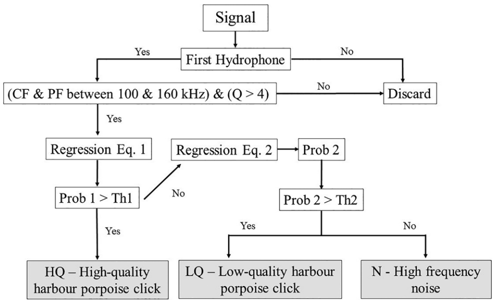

FIG. 2. Flowchart illustrating the decision-making pathway of the harbour porpoise click classifier (PorCC). CF = centroid frequency. PF = peak frequency. Th = probability thresholds. Prob = Probability.

TABLE I. Series of logistic regression models for model 1 and model 2. Only the best five are shown here. See text for description of the variables used (footnote 1). The outcomes of the response variable for model 1 are high-quality harbour porpoise clicks or high frequency noise, and for model 2 are low-quality harbour (LQ) porpoise click or high-frequency noise (N). AIC = Akaike's Information Criterion.

ID	Predictor variables—Model 1	ΔAIC
1	Q_{RMS} + Duration	0
2	Q_{RMS} + Duration + Ratio	1.64
3	Q_{RMS} + Duration + BW	1.67
4	Q_{RMS} + Duration + CF	1.78
5	Q_{RMS} + Duration + XC	1.96
ID	Predictor variables—Model 2	ΔAIC
1	Q_{RMS} + Duration + Ratio + XC + CF + BW	0
2	Q_{RMS} + Duration + Ratio + XC + BW	1.19
3	Q_{RMS} + Duration + Ratio + CF + BW	19.19
4	Q_{RMS} + Duration + XC + CF + BW	20.07
5	Q_{RMS} + Duration + Ratio + BW	20.87

E. PorCC vs PAMGuard

A subset of the testing dataset for PorCC was used to assess the performance of the porpoise click classifier built-in in PAMGuard and compared it to that of PorCC. This dataset subset contained all clips from the 28th of August 2017 (n = 284 231) of which 30 897 clips had already been manually labelled, having peak and centroid frequencies within the 100–160 kHz range, and Q > 4. PAMGuard's classifier highlights potential harbour porpoise clicks and echoes that the user can manually verify and group into "acoustic events" to later extract them for further analysis. For the purpose of this study, all highlighted clicks were selected without manual verification, assigned to a unique acoustic event, and exported to an SQL database. Putative echoes were included because it was previously noted that this classifier sometimes misidentifies real harbour porpoise clicks as echoes (and vice versa) as well as for comparison purposes, as PorCC also identifies potential echoes (LQ). PAMGuard creates a table within the SQLite database, where information for each of the extracted potential harbour porpoise click is provided, including date, time, and an identification number within the *.pgdf* file where the waveform is saved. Using a custom-built script, and using the identification number, all clips identified by PAMGuard's classifier as potential harbour porpoise clicks were extracted from the *.pgdf* files and saved in a MATLAB structure array for further analysis. Subsequently, clips that were highlighted by

PAMGuard's classifier but were discarded by PorCC were manually labelled.

Confusion matrices and receiver operational characteristics (ROC) curves were used to assess the performance of PAMGuard and compare it against PorCC. False alarm, hit rates, and precision levels were also estimated, as well as the detectability index (d') (see, e.g., Egan, 1975; Tougaard, 2002).

III. RESULTS

A. Logistic regression models

According to AIC values, the best model 1 (for HQ signals) was that with only Q_{RMS} and duration as explanatory variables, while the best model 2 (for LQ signals) had five explanatory variables, Q_{RMS}, duration, ratio between peak and centroid frequency, cross-correlation coefficient, centroid frequency, and −3 dB bandwidth.[1]

B. PorCC performance

PorCC classification process, including estimating all necessary parameters, takes approximately 1 ms per clip. Harbour porpoises produce between fewer than 10 and few hundred clicks per second depending on their behaviour (Clausen *et al.*, 2010; Sørensen *et al.*, 2018; Wright *et al.*, 2017), PorCC shows, therefore, potential for real time application. For HQ, precision was 88.5% (4475 out of 5054, 519 of which were LQ and 60 N), false alarm (i.e., N classified as HQ) was 0.0001% (60 out of 537 591 N clips were classified as HQ), and 31.8% of clicks were missed (1710 were classified as LQ and 382 as N) (Table II). As precision increases hit rate decreases, that is fewer clicks, of the total available to the classifier, are going to be identified, demonstrating the well-known trade-off between errors: false alarms vs misses in signal detection and type I vs type II errors in conventional statistics (Fig. 3).

C. PorCC vs PAMGUARD

A total of 30 897 clips from the 28th of August met the criteria for potential harbour porpoise clicks, that is, having peak and centroid frequency between 100 and 160 kHz and Q_{RMS} higher than 4. The results of the comparison of the performance of PorCC (using $Th1 \geq 0.9999$ and $Th2 \geq 0.55$) and PAMGuad's classifier for HQ are shown in Table II. Based on the detectability indexes (Fig. 3), PorCC outperforms PAMGuard's classifier in all cases, but especially for HQ clicks. The overall precision for HQ for PorCC was 30.8% for PAMGuard's classifier, assuming that PAMGuard's classifier correctly classified HQ and LQ as such in 100% of the cases, as once clicks are extracted from PAMGuard, there is no information of whether a clip was originally classified as a harbour porpoise click or an echo, which can be considered as equivalent to the HQ and LQ categories.[1]

TABLE II. Confusion matrices. Comparison of correct and misidentification levels between PorCC and the Porpoise Click Detector/Classifier Module in PAMGuard, and overall performance of PorCC. HQ = high-quality harbour porpoise clicks. LQ = low-quality harbour porpoise clicks. Noise = high- and low-frequency noise (i.e., anything that is not a porpoise click).

Labelled		PorCC		PAMGuard			PorCC	
	Total	HQ	Noise	HQ	N	Total	HQ	Noise
HQ	1833	564[a]	1269[b]	1209	113[b]	6567	4475	382
Noise	965	477 + 1601[a,c]	279,355	25[c]	280 034	537 591	60	533 228

[a] Of the total of 3017 clips highlighted by PAMGuard as potential harbour porpoise clicks, 1601 had $Q_{RMS} < 4$ and peak and centroid frequencies outside of the 100 and 160 kHz range, therefore they were not captured by PorCC, as they were discarded at the first step.

[b] Missed clicks (HQ clicks classified as N divided by the total number of HQ click).

[c] False alarm (N clips classified as HQ clicks divided by the total number of N clips).

IV. DISCUSSION

The perfect classifier cannot exist, as detection always will be limited by noise, either external from the environment, or internal. For electronic systems this internal noise is in amplifiers and hydrophones, and for biological systems, this noise will be in the form of spontaneous activity in the neurons. In real-world applications, noise also comes in the form of substantial variation in the temporal and spectral characteristics of acoustic signals. These are affected by many factors, including background noise and the direction from where the signals impinges on the hydrophone, as well as by how the data were collected (e.g., hydrophone own noise, frequency characteristics of the hydrophones) (Richardson *et al.*, 1995). Moreover, in this study, the performance of the classifier is intrinsically linked to the performance of the Click Detector Plug-In in PAMGuard, which in turn depends on the settings selected by the user (e.g., number of samples before and after the signal, SNR thresholds). Despite this, the results of this study show that a classification system based on logistic regression models to identify NBHF vocalisations produced by harbour porpoises outperforms existing classifiers. PorCC can achieve hit rates of over 90% while keeping the false alarm rate below 1% and maintaining high precision levels. The performance of PorCC is expected to be similar, or higher, in data collected using static devices, or in areas with low background noise. Moreover, it has potential for real time application, as it can analyse the equivalent of 1 h of data in under 1 min.

For both logistic regression models, one model was better than the others. It is worth noting that in both cases, the model with the cross-correlation coefficient (XC) as the only explanatory variable appears in the second position after Q, when looking at models with only one explanatory variable.[1] To classify HQ clicks, cross-correlation analysis, which can be a time costly process, is not necessary and introduces a lot of variation as porpoise clicks are not blueprints of each other. In fact, the cross-correlation coefficient value ranged from 0.0038 to 4.5655, and thus using a threshold in a decision-making process would inevitably include HQ as well as N. The first model containing XC for click detection is fifth on the list. For LQ, on the other hand, XC explains more of the variance in the model, being necessary in the best model, and therefore helps in the classification process. There is likely to be both intra- and inter-animal variation in

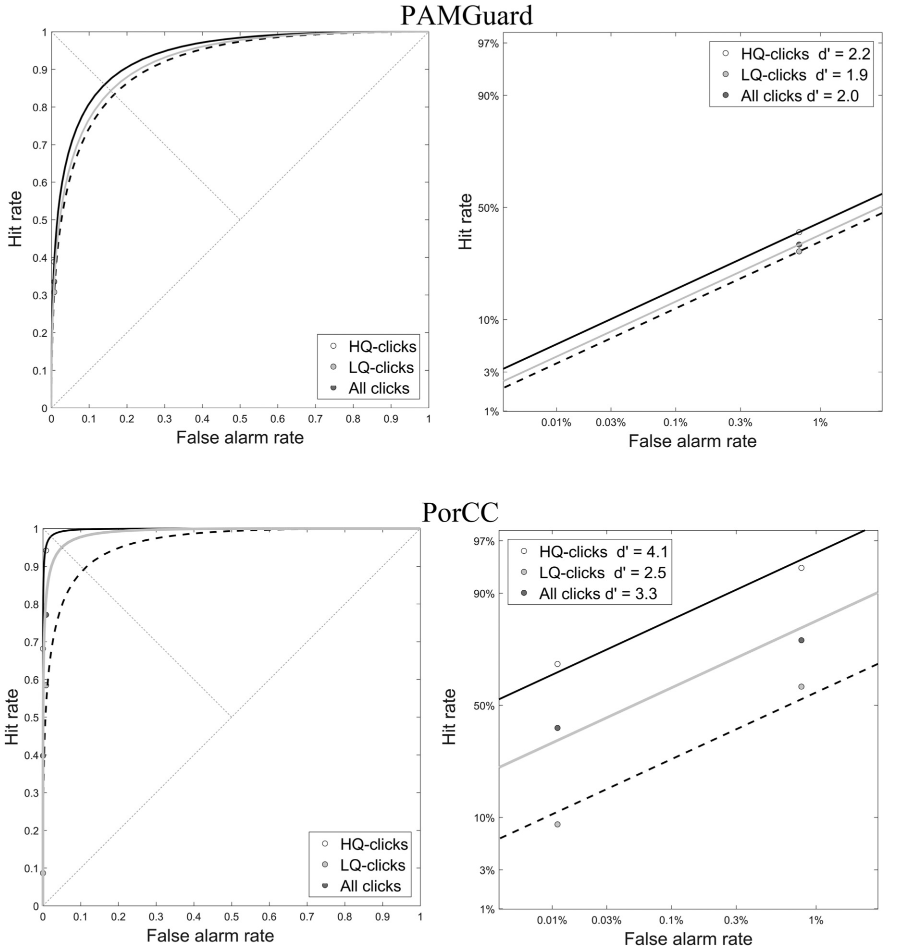

FIG. 3. Receiver operating characteristics (ROC) curves. Dots represent false alarm rates and hit rates associated with detection of HQ-clicks (solid black line), LQ-clicks (black dashed line) and both types combined (grey line), all against a background of N-clicks. Top figures show performance of PAMGuard. Curves are best fitting ROC-curves, generated under the assumption of Gaussian underlying distributions with equal variance. Bottom figures show performance by PorCC under two different criteria: strict (only clicks classified by PorCC as HQ) and relaxed (all clicks classified as either LQ or HQ). Figures to the left and right contain same data, but right figures are plotted on double probit (probability) axes.

signals, as well as substantial effects on the frequency spectrum caused by the directionality of the beam and the frequency dependent absorption in the water. This variation is illustrated by the differences in the recorded signals shown in Fig. 1, most evident by the lack of overlap in frequency spectra of the HQ and the LQ signals. For signals where the parameters are very variable, but where means may be more stable, other types of detectors can be predicted to outperform a cross-correlation receiver. One such receiver is a simple energy detector, which integrates energy within a specified frequency band and a specified duration (Green and Swets, 1966), and this is essentially what the HQ-classifier of PorCC is.

Available data suggest that the variation pattern of inter-click intervals within a click train is indicative of specific behaviours (Clausen *et al.*, 2010; Koschinski *et al.*, 2008; Wisniewska *et al.*, 2018; Sørensen *et al.*, 2018). This is especially true for foraging and feeding behaviour, characterised by inter-click intervals below 10 ms after a phase with much larger inter-click intervals (e.g., Koschinski *et al.*, 2008). PorCC's classification algorithm can be implemented in the output of any transient-sound detector for continuous recordings and, given the low misidentification levels, it is suitable to study the behaviour of wild harbour porpoises, as the variations in inter-click intervals can only be detected if the majority of clicks within a click train are identified.

Moreover, these studies can be carried out in data that has already been collected using continuous recordings at an adequate sampling rate, both using towed hydrophone arrays or static devices, such as SoundTrap. The PorCC classification algorithm, including the functions to estimate the different variables and the resulting coefficients, is publicly available and can be coded in other programming languages, such as Python. It could also be incorporated into PAMGuard.

PorCC, like other classifiers, is not exempt of errors, and trying to increase the hit rate would in turn lead to an increase in the false alarm rate, as seen in the change in performance going from a strict to a relaxed criterion. However, the ultimate goal in classification is not to avoid errors, but to manage them. Thus, PorCC provides the user with a general assessment of its performance through the ROC curves, as these show the changes in hit rate with false alarm variations (Tougaard, 2002), which results from using different threshold values to classify harbour porpoise clicks. Therefore, users can, *a priori*, manage the level of error according to their needs. Furthermore, depending on the objectives, the user can extract either or both HQ and LQ clicks as well as decide when LQ clicks should be ignored (e.g., single LQ clicks) or taken into account (e.g., studies of click train patterns).

The performance of PorCC for HQ clicks is very high, yet much lower for LQ clicks. This could be the result of some high-frequency noise clips having similar characteristics to LQ clicks, which means the coefficients derived from the second logistic regression model are inefficient to distinguish between LQ clicks and high frequency noise. However, this low performance can also be the result of a level of subjectivity when assigning signals to these categories. This happens to be a fundamental limitation for almost all studies of this kind, where performance of detectors is evaluated on real world data. One must have some means of determining the "true state of the world," i.e., separating signals into those truly originating from porpoises and those that are just random noise. In this study, as in most others, we relied on the superior ability of the human brain to perform pattern recognition in noise and thus measure the performance of the detectors essentially against the performance of a skilled human observer. There is no objective way of determining whether a signal in the array recordings really originated from a porpoise or not. Only under extremely well controlled circumstances, such as when one has a single animal isolated in a pool and a recorder attached to the animal to monitor each and every vocalisation from the animal is it possible to evaluate the absolute detection performance of the detection system and even in such cases, one would suffer difficulties in transferring the experimental settings (limited depth and distance to receiver, training or habituation of the animal etc.) to the situation in real world monitoring.

V. CONCLUSIONS AND FUTURE WORK

The performance of PorCC greatly exceeds that of the currently available classifier in PAMGuard and has potential for real time application as well as to study the acoustic behaviour of harbour porpoises and other NBHF species in the wild, in data collected using both towed hydrophone arrays or static recorders.[2] Future work includes testing PorCC in data obtained using a different recording device (e.g., SoundTrap-Ocean Instruments, New Zealand) and under different survey conditions, and in recordings of harbour porpoises from another population. Additionally, the performance of PorCC will be tested against the performance of C-PODs in data collected simultaneously by a C-POD and a SoundTrap (Sarnocinska *et al.*, 2016).

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[1] See supplementary material at https://doi.org/10.1121/1.5110908 for a figure (Fig. S1.1) of the click used as a model against which a cross-correlation is performed in the PorCC classification algorithm; for the histogram and distributions of all variables used to develop the logistic regression models (Fig. S2.1); for a correlation plot (Fig. S2.2) of all variable pairs; for a complete list of all logistic regression models performed to develop the PorCC classification algorithm (Tables S1 and S2); for examples of signals misclassified by both PorCC (Fig. S3.1 to S3.6) and by PAMGuard's Click Classifier Module (FIG. 3.7).

[2] Preliminary results suggest that PorCC algorithm can be successfully applied to harbour porpoise data recorded with different devices and in different areas, as well as other NBHF species, such as Heaviside's dolphins (*Cephalorhynchus heavisidii*).

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Appendix B

Table A1. Series of logistic regression models for Model 1. See text for description of the variables used. The outcomes of the response variable for Model 1 are high-quality harbour (HQ) porpoise click or high-frequency noise (N). AIC = Akaike's Information Criterion.

ID	**Predictor Variables**	**ΔAIC**
1	Q_{RMS} + Duration	0
2	Q_{RMS} + Duration + Ratio	1.64
3	Q_{RMS} + Duration + BW	1.67
4	Q_{RMS} + Duration + CF	1.78
5	Q_{RMS} + Duration + XC	1.96
6	Q_{RMS} + Duration + Ratio + BW	3.34
7	Q_{RMS} + Duration + CF + BW	3.46
8	Q_{RMS} + Duration + Ratio + CF	3.51
9	Q_{RMS} + Duration + Ratio + XC	3.64
10	Q_{RMS} + Duration + XC + BW	3.64
11	Q_{RMS} + Duration + XC + CF	3.73
12	Q_{RMS} + Duration + Ratio + CF + BW	5.21
13	Q_{RMS} + Duration + Ratio + XC + BW	5.33
14	Q_{RMS} + Duration + XC + CF + BW	5.41
15	Q_{RMS} + Duration + Ratio + XC + CF	5.50
16	Q_{RMS} + Duration + Ratio + XC + CF + BW	7.20
17	Q_{RMS} + Ratio + XC + CF + BW	108.96
18	Q_{RMS} + Ratio + XC + BW	109.15

19	Q_{RMS} + XC + CF + BW	110.57
20	Q_{RMS} + XC + BW	111.85
21	Q_{RMS} + Ratio + BW	116.14
22	Q_{RMS} + Ratio + CF + BW	116.52
23	Q_{RMS} + CF + BW	118.26
24	Q_{RMS} + BW	119.09
25	Q_{RMS} + Ratio + XC + CF	141.89
26	Q_{RMS} + Ratio + XC	143.13
27	Q_{RMS} + XC + CF	144.38
28	Q_{RMS} + XC	145.08
29	Q_{RMS} + Ratio + CF	153.37
30	Q_{RMS} + Ratio	153.86
31	Q_{RMS} + CF	155.41
32	Q_{RMS}	155.76
33	Duration + Ratio + XC + BW	374.23
34	Duration + Ratio + XC + CF + BW	376.23
35	Duration + Ratio + XC	384.45
36	Duration + Ratio + XC + CF	386.38
37	Duration + XC + BW	455.57
38	Duration + XC + CF + BW	456.22
39	Duration + XC	472.27
40	Duration + XC + CF	473.66
41	Ratio + XC + CF + BW	632.67

42	Ratio + XC + BW	633.62
43	Ratio + XC + CF	649.11
44	Ratio + XC	649.47
45	XC + CF + BW	731.51
46	XC + BW	741.19
47	XC + CF	742.95
48	XC	754.22
49	Duration + Ratio + BW	1022.92
50	Duration + Ratio + CF + BW	1024.33
51	Duration + Ratio	1166.78
52	Duration + Ratio + CF	1168.77
53	Duration + CF + BW	1266.04
54	Duration + BW	1272.47
55	Duration + CF	1449.11
56	Duration	1449.55
57	Ratio + CF + BW	2608.89
58	Ratio + CF	2618.05
59	Ratio + BW	2756.10
60	Ratio	2768.74
61	CF + BW	2978.54
62	CF	2981.04
63	BW	3213.82

Table A2. Series of logistic regression models for Model 2. See text for description of the variables used. The outcomes of the response variable for Model 2 are low-quality harbour (LQ) porpoise click or high-frequency noise (N). AIC = Akaike's Information Criterion.

ID	Predictor Variables	ΔAIC
1	Q_{RMS} + Duration + Ratio + XC + CF + BW	0
2	Q_{RMS} + Duration + Ratio + XC + BW	1.19
3	Q_{RMS} + Duration + Ratio + CF + BW	19.19
4	Q_{RMS} + Duration + XC + CF + BW	20.07
5	Q_{RMS} + Duration + Ratio + BW	20.87
6	Q_{RMS} + Duration + XC + BW	22.21
7	Q_{RMS} + Duration + CF + BW	38.05
8	Q_{RMS} + Duration + BW	41.05
9	Q_{RMS} + Duration + Ratio + XC + CF	41.33
10	Q_{RMS} + Duration + Ratio + XC	43.84
11	Q_{RMS} + Duration + XC + CF	63.10
12	Q_{RMS} + Duration + Ratio + CF	63.57
13	Q_{RMS} + Duration + Ratio	66.89
14	Q_{RMS} + Duration + XC	67.66
15	Q_{RMS} + Duration + CF	83.99
16	Q_{RMS} + Duration	89.98
17	Q_{RMS} + Ratio + XC + CF	366.58
18	Q_{RMS} + Ratio + XC + CF + BW	368.58
19	Q_{RMS} + Ratio + XC	368.88

20	Q_{RMS} + Ratio + XC + BW	370.82
21	Q_{RMS} + Ratio + CF	374.82
22	Q_{RMS} + Ratio + CF + BW	376.78
23	Q_{RMS} + Ratio	376.86
24	Q_{RMS} + Ratio + BW	378.86
25	Q_{RMS} + XC + CF	410.75
26	Q_{RMS} + XC + CF + BW	412.74
27	Q_{RMS} + XC	413.15
28	Q_{RMS} + XC + BW	415.10
29	Q_{RMS} + CF	418.06
30	Q_{RMS} + CF + BW	419.98
31	Q_{RMS}	419.99
32	Q_{RMS} + BW	421.99
33	Duration + Ratio + XC + CF + BW	1042.02
34	Ratio + XC + CF + BW	1103.10
35	Duration + Ratio + XC + CF	1124.00
36	Duration + Ratio + XC + BW	1129.92
37	Ratio + XC + CF	1143.50
38	Ratio + XC + BW	1199.11
39	Duration + Ratio + XC	1206.99
40	Ratio + XC	1233.64
41	Duration + XC + CF + BW	1296.13
42	XC + CF + BW	1350.30

43	Duration + Ratio + CF + BW	1387.39
44	Duration + XC + CF	1394.01
45	Ratio + CF + BW	1394.34
46	XC + CF	1407.15
47	Duration + XC + BW	1472.01
48	Duration + Ratio + CF	1500.27
49	Ratio + CF	1500.61
50	XC + BW	1531.41
51	Duration + XC	1553.00
52	Duration + Ratio + BW	1556.81
53	Ratio + BW	1560.40
54	XC	1573.10
55	Duration + Ratio	1657.53
56	Ratio	1658.48
57	Duration + CF + BW	1679.28
58	CF + BW	1680.73
59	Duration + CF	1809.32
60	CF	1815.33
61	BW	1960.22
62	Duration + BW	1961.49
63	Duration	2061.31

Appendix C

The algorithm below extracts underlying patterns by removing unwanted sources of sounds in click trains in order to later identify behaviours.

Abbreviations:

- **Amp**: Amplitude (dB re: 1μPa).
- **CF**: Centroid frequency (kHz).
- **CPS**: Clicks per second.
- **CTTemp**: Temporary click train. This is the click train being treated.
- **Fs**: Sampling frequency (Hz).
- **ICI**: inter-click interval (ms).
- **MaxDiffSorted**: The maximum difference (*i.e.*, jump) in CPS, when sorted in ascending order. It indicates whether there are outliers (*e.g.*, multipath signals).
- **NewCT**: New click train. This is the resulting click train.

ALGORITHM

```
% Add row numbers for a later step
CTTemp.RowN(1,1) = 1; CTTemp.RowN(1:end,1) = 1:size(CTTemp,1);
% Save in another variable for a later step
CTTemp1 = CTTemp;
% A large maximum difference indicates the presence of outliers
SortedCPS = sort(CTTemp.CPS); DiffSorted = diff(SortedCPS);
[MaxDiffSorted, ~] = max(DiffSorted);
% A small maximum difference indicates a good click train
if MaxDiffSorted < 28
    % Do nothing
else
    Outlier = isoutlier(CTTemp.CPS);
    HighCPS = CTTemp.CPS > 50;
    Both = Outlier + HighCPS;
    CTTemp(Both == 2,:) = [];
    % The function 'NewICI' estimates the ICI and CPS of all
        clicks in the click train
    CTTemp = NewICI(CTTemp,Fs);
    SortedCPS = sort(CTTemp.CPS);
    DiffSorted = diff(SortedCPS);
    % Recalculate the maximum difference
    [MaxDiffSorted, ~] = max(DiffSorted);
end
% If after removing outliers the maximum difference is small
if MaxDiffSorted > 10 && MaxDiffSorted < 28 && size(CTTemp,1) <
    100
```

```
    NewCT = CTTemp; % This step ends here
    NewCT = NewICI(NewCT,Fs);
else
     % Remove local minimum - these are clicks with amplitude
         smaller that the previous and following clicks, with at
         least 5 dB difference with the previous click
     S1 = size(CTTemp,1); S2 = 1;
     while S1 ~= S2
          S1 = size(CTTemp,1);
          DiffAmps(1,1) = 0;
          DiffAmps(2:S1,1) = diff(CTTemp.Amp);
          LocMin = islocalmin(CTTemp.Amp);
          LargeDiff = DiffAmps < -5;
          DeleteRows = LocMin + LargeDiff;
          CTTemp(DeleteRows == 2,:) = [];
          CTTemp = NewICI(CTTemp,Fs);
          S2 = size(CTTemp,1);
     end
end
SortedCPS = sort(CTTemp.CPS);
DiffSorted = diff(SortedCPS);
[MaxDiffSorted, ~] = max(DiffSorted);
if MaxDiffSorted > 35 && size(CTTemp,1) > 100
      % Finding the stable areas with low CPS variation
      CPSDiff = diff(CTTemp.CPS);
      PercChangeS = (CPSDiff./CTTemp.CPS(1:end-1))*100;
```

```
PercChangeS = abs(PercChangeS(2:end));
PercCPSDiff = movmean(PercChangeS,4); % Moving average
StartRow = find(PercCPSDiff < 5);
StartRow = StartRow + 2;
DiffStartRow = diff(StartRow);
Here = find(DiffStartRow == 1);
% Go into the CT
Keep = 1;
if size(StartRow,1) == 0
  RowN = 1;
else
  RowN = StartRow(Here(1));  % Low variability in CPS (for
      the next 4)
end
RowsToKeep(1,1) = RowN;
FirstRowN = RowN;
% Look backwards
while RowN > 10
ClickCPS = CTTemp.CPS(RowN,1);
ClickAmp = CTTemp.Amp(RowN,1);
ClickStartSample = CTTemp.startSample(RowN,1);
ICIs = abs(ClickStartSample - CTTemp.startSample(RowN-9:
   RowN-1,1))/(Fs/1000);
CPSs = 1000./ICIs;
Amps = CTTemp.Amp(RowN-9:RowN-1,1);
Amps = abs(ClickAmp - Amps);
```

```
DiffCPSs = abs(ClickCPS - CPSs);
[~, ixCPS] = min(DiffCPSs); % Position of the next click
    if Amps(ixCPS) < 5
      DiffCPSs(ixCPS) = 1000;
      [~, ixCPS] = min(DiffCPSs); % Position of the next
          click
      RowN = RowN - ixCPS;
    else
      RowN = RowN - ixCPS;
    end
Keep = Keep + 1;
RowsToKeep(Keep,1) = RowN;
end
% Look forwards
RowN = FirstRowN;
while CTTemp.ICI(RowN,1) < 1000 && RowN < size(CTTemp,1)-10
ClickCPS = CTTemp.CPS(RowN,1);
ClickAmp = CTTemp.Amp(RowN,1);
ClickStartSample = CTTemp.startSample(RowN,1);
ICIs = abs(CTTemp.startSample(RowN+1:RowN+9,1) -
   ClickStartSample)/(Fs/1000);
CPSs = 1000./ICIs;
Amps = CTTemp.Amp(RowN+1:RowN+9,1);
Amps = abs(Amps - ClickAmp);
DiffCPSs = abs(CPSs - ClickCPS);
[~, ixCPS] = min(DiffCPSs); % Position of the next click
```

```
          if Amps(ixCPS) < 5
            DiffCPSs(ixCPS) = 1000;
            [~, ixCPS] = min(DiffCPSs);  % Position of the next click
            RowN = RowN + ixCPS;
          else
            RowN = RowN + ixCPS;
          end
     Keep = Keep + 1;
     RowsToKeep(Keep,1) = RowN;
     end
 % Delete loose clicks
        L1 = size(CTTemp,1);
        L2 = 1;
    while L2 ~= L1
       L1 = size(CTTemp,1);
       CTTemp = NewICI(app, CTTemp, Fs);
       LooseClicks = find(CTTemp.ICI > 250);
       Positions = find(diff(LooseClicks) == 1);
       RowsToDelete = LooseClicks(Positions);
       CTTemp(RowsToDelete, :) = [];
       L2 = size(CTTemp,1);
    end
RowsToKeep = sort(unique(RowsToKeep));
NewCT = CTTemp(RowsToKeep,:);
NewCT = NewICI(NewCT, Fs);
```

```
else
 NewCT = CTTemp;
 NewCT = NewICI(NewCT, Fs);
end
RowsLeft = NewCT.RowN(:,1);
CTTemp2 = CTTemp1;
CTTemp2(RowsLeft,:) = [];
end
```