

Categorizing click trains to increase taxonomic precision in echolocation click loggers.

K.J. Palmer^{1*}, Kate Brookes², Luke Rendell¹

¹ School of Biology, University of St. Andrews, Sir Harold Mitchell Building, St. Andrews, Fife KY16 9TH, UK

² Marine Scotland Science, Marine Laboratory, PO Box 101, 375 Victoria Road, Aberdeen AB11 9DB, UK

*Corresponding Author (kp37@st-andrews.ac.uk)

Running Title: Categorizing clicks from echolocation click loggers

Key Words: passive acoustic monitoring; odontocete; echolocation click logger

PACS code: 43.80.Ev

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19

A. ABSTRACT

Passive acoustic monitoring is an efficient way to study acoustically active animals but species identification remains a major challenge. C-PODs are popular logging devices that automatically detect odontocete echolocation clicks. However, the accompanying analysis software does not distinguish between delphinid species. Click train features logged by C-PODs were compared to frequency spectra from adjacently deployed continuous recorders. A generalized additive model was then used to categorize C-POD click trains into three groups: broadband click trains, produced by bottlenose dolphin (*Tursiops truncatus*) or common dolphin (*Delphinus delphis*), frequency-banded click trains, produced by Risso’s (*Grampus griseus*) or white beaked dolphins (*Lagenorhynchus albirostris*), and unknown click trains. Incorrect categorization rates for broadband and frequency banded clicks were 0.02 (SD 0.01), but only 30% of the click trains met the categorization threshold. To increase the proportion of categorized click trains, model predictions were pooled within acoustic encounters and a likelihood ratio threshold was used to categorize encounters. This increased the proportion of the click trains meeting either the broadband or frequency banded categorization threshold to 98%. Predicted species distribution at the 30 study sites matched well to visual sighting records from the region.

20 II. INTRODUCTION

21 Passive acoustic monitoring is an established method of studying the movement, distribution and
22 behavior of acoustically active species (Fenton, 1982; Van Parijs *et al.*, 2009; Brookes *et al.*,
23 2013; Kalan *et al.*, 2015; Kloepper *et al.*, 2016). The field of cetacean ecology has especially
24 benefited from advances in acoustic monitoring as these animals are largely visually inaccessible
25 to researchers for the majority of their lives. Moreover, most cetaceans produce acoustic signals
26 that can be detected by acoustic recorders and data loggers over large distances. Accordingly,
27 passive acoustic monitoring has provided invaluable insights into the habitat use (Mellinger *et*
28 *al.*, 2007; Van Parijs *et al.*, 2009), communication (Parks *et al.*, 2009), population size
29 (Jaramillo-Legorreta and Rojas-Bracho, 2011; Harris *et al.*, 2013), and behavior (Buckstaff,
30 2004; Koschinski *et al.*, 2008; Nuutila *et al.*, 2013; Pirotta *et al.*, 2014b) of multiple genera.
31 Moreover, passive acoustic monitoring is directly involved in both long-term and real-time
32 conservation efforts for protected cetacean species (Clark *et al.*, 2005; Van Parijs *et al.*, 2009;
33 Jaramillo-Legorreta and Rojas-Bracho, 2011; Klinck *et al.*, 2012).

34 Taxonomic classification of the echolocation clicks of odontocetes is an ongoing problem
35 in passive acoustic surveys. The received characteristics of any given click depend on the
36 animal's behavior as well as the filtering effects of the cranial anatomy, the propagation
37 environment and the parameters of the recording system (Au *et al.*, 1985; Au *et al.*, 1995;
38 Carlström, 2005; Johnson *et al.*, 2006; DeRuiter *et al.*, 2009; Au *et al.*, 2012a; Roch *et al.*, 2015).
39 Since echolocation signals are highly directional, the received amplitude and spectral
40 characteristics of echolocation clicks further depends on the orientation of the vocalizing animal
41 with respect to the receiver (Rasmussen *et al.*, 2004; Wahlberg *et al.*, 2011; Au *et al.*, 2012b).

42 Together, these filtering effects render it virtually impossible to classify individual echolocation
43 clicks to species.

44 Researchers have addressed the classification task by averaging echolocation click
45 characteristics across multiple clicks, click trains, and/or acoustic encounters. In doing so, group
46 and species-specific features in echolocation clicks have been discovered. For example,
47 Baumann-Pickering *et al.* (2013) compared the location of satellite tagged animals to passive
48 acoustic recordings and was able to describe species-specific characteristics of false killer whale
49 (*Pseudorca crassidens*) and short finned pilot whale (*Globicephala macrorhynchus*)
50 echolocation clicks. Similarly, distributions of peak frequency, center frequency, click duration,
51 inter-click interval (ICI) and bandwidth have been useful in discriminating between the
52 echolocation clicks of melon-headed whales (*Peponocephala electra*), Gray's spinner dolphins
53 (*Stenella longirostris longirostris*) and to a lesser extent, bottlenose dolphins (*Tursiops*
54 *truncatus*) (Baumann-Pickering *et al.*, 2010).

55 In other studies, the structure of the frequency spectrum has proven useful in classifying
56 click trains. In the Pacific, the echolocation clicks of white-sided dolphins (*Lagenorhynchus*
57 *obliquidens*) and Risso's dolphins (*Grampus griseus*) have been shown to display consistent
58 peaks and notches in spectral energy below 48 kHz (Roch *et al.*, 2007). Risso's dolphins click
59 trains contained peaks in energy at 22.4, 25.5, 30.5 and 38.7 kHz and at 22.2, 26.6, 33.7 and 37.3
60 kHz for white-sided dolphins. The spectral location was sufficient to discriminate between the
61 two species but site and instrument-specific anomalies reduced the confidence of the
62 classifications (Roch *et al.*, 2007). In the same habitat, bottlenose dolphin and common dolphin
63 (*Delphinus delphis*) echolocation clicks were found to have a more uniform energy distribution
64 between 40 and 80 kHz (Soldevilla *et al.*, 2008). Echolocation clicks from these species were

65 nearly indistinguishable but easily discriminated from the peak and notch structure of Risso's
66 and white-sided dolphins, especially when site and instrument specific parameters were
67 accounted for (Roch *et al.*, 2011; Roch *et al.*, 2015). Uniform energy between 40-120 kHz was
68 recorded for on-axis clicks of bottlenose dolphins in the Indian Ocean, and held for off axis
69 angles up to $\sim 13^\circ$, beyond which peaks and notches in energy were observed but were dependent
70 on the angle between the animal and the recording system (Wahlberg *et al.* 2011). Similarly, in
71 the North Atlantic Calderan *et al.* (2013) investigated whether the peaks and notches in spectral
72 energy observed in Pacific animals were also present in clicks produced by Risso's and white-
73 beaked dolphin (*Lagenorhynchus albirostris*), the latter having morphologically similar cranial
74 structure to Pacific white-sided dolphins. Towed arrays in western Scottish waters suggested that
75 a similar peak-and-notch structure was present in both species. Taken together, these studies
76 suggest that the presence of stable peak-and-notches in spectral energy may be useful for
77 increasing taxonomic resolution from acoustic recordings.

78 While significant progress has been made in classifying echolocation clicks in continuous
79 recordings, little effort has been directed toward classifying echolocation clicks in click logging
80 devices. C-PODs (Chelonia, Ltd.) are commercially available click logging devices popular in
81 marine studies. The C-POD system returns a series of summary parameters related to detected
82 clicks but does not save the waveform of the clicks themselves. Consequently, the volume of
83 data collected by these systems is drastically less, while some of the click frequency/time
84 information is preserved. Such systems are efficient, have low false positive detection rates, and
85 produce generally consistent output between units (Dähne *et al.*, 2013; Roberts and Read, 2014).
86 For these reasons, C-PODs are a popular tool used to study odontocete behavior and ecology
87 worldwide (Carstensen *et al.*, 2006; Koschinski *et al.*, 2008; Bailey *et al.*, 2010; Pirota *et al.*,

88 2014a; Jaramillo-Legorreta *et al.*, 2016). For species with mid- to high-frequency echolocation
89 clicks, long-term and full spectrum ($f_s > 200$ kHz) continuous recordings are often impractical
90 due to the high up-front cost of continuous recorders, high data volumes, time-consuming post-
91 processing to extract echolocation clicks, and limited recording duration compared to click
92 loggers.

93 Data collected by the C-POD data are generally processed to detect the presence of
94 odontocete echolocation click trains with the accompanying KERNO classifier. The KERNO
95 software is capable of discerning between dolphin and porpoise clicks based on the frequency
96 and bandwidth of the detections. However, C-PODs currently lack the ability to discriminate
97 between most dolphin species. Thus, where users can be relatively confident that only the target
98 dolphin species is present, the use of C-PODs has proven to be both cost and time effective
99 (Simon *et al.*, 2010; Pirodda *et al.*, 2015). However, where the scientific and/or regulatory
100 concern focuses on a single species within a large habitat, the ability to discriminate between
101 target and non-target species becomes a critical aspect of the research methodology.

102 The motivation for this study is the need to efficiently monitor the population of
103 bottlenose dolphins resident along the eastern coast of Scotland. This population is protected by
104 a variety of UK and EU regulations including the designation of special areas of conservation
105 (SAC) in the Moray Firth and the Firth of Tay. However, in recent years the population appears
106 to have undergone significant range expansion; while animals are consistently observed within
107 the SAC's, a large proportion of the population partially or fully resides outside of the protected
108 areas (Cheney *et al.*, 2014). Additionally, the construction of large offshore wind farms is
109 planned off Eastern Scotland for the coming years. Determining what effect, if any, the
110 construction, operation, and decommissioning of these structures will have on these animals is

111 important for long term conservation goals. Thus, a better understanding of how the population
112 uses the entire Eastern Scottish coast habitat is needed. One of the primary challenges to meet
113 this objective using passive acoustic monitoring techniques lies in discriminating between target
114 (bottlenose dolphin) and non-target species known to occur in the area. These include common
115 dolphin, Risso's dolphin and white beaked dolphin (*Lagenorhynchus albirostris*) (Weir *et al.*,
116 2007; Quick *et al.*, 2014). Thompson *et al.* (2013) addressed the multi-species concern by
117 integrating visual observations of various dolphin species and echolocation click detections from
118 C-PODs. In their study, effort controlled visual survey data from 1980 through 2010 were
119 combined with up to three seasons worth of C-POD detections from the Moray Firth. Results
120 from their study strongly suggested that bottlenose dolphins primarily occupy the nearshore areas
121 (<10 km from the coast) within the inner Moray Firth while a greater diversity of dolphin species
122 were found in the offshore waters.

123 Discriminating between any dolphin species in C-POD data would represent a major step
124 forward in the application of such systems in multi-species contexts. This challenge of species
125 discrimination has been recognized and approached by researchers working with a similar group
126 of species in Irish waters (Robbins *et al.*, 2015). In that study the authors used multi-dimensional
127 scaling techniques to try and discriminate between visually-confirmed Risso's, common and
128 bottlenose dolphin detections in C-POD data. The authors found that the limited metrics
129 produced by the C-POD system in combination with their own post-processing metrics were
130 insufficient to classify detections to species. This result is unsurprising given the difficulty in
131 discriminating between common and bottlenose dolphin clicks even with continuous, full-
132 spectrum recordings (Soldevilla *et al.*, 2008; Roch *et al.*, 2011).

133 In the present study we investigated the potential for discriminating between echolocation
134 clicks with distinct peaks and notches, hereafter termed “frequency banded” and those that, when
135 averaged across encounters, lack distinct peaks and troughs in spectral energy below 48 kHz,
136 referred to hereafter as “broadband”. We denote this task as “categorization” rather than
137 classification as we are not seeking to identify the exact species producing the click-types. We
138 used data from acoustic recorders deployed alongside C-PODs to build a model that
139 discriminated between broadband and frequency-banded clicks in C-POD data, and then used
140 this model to classify data from a larger set of C-PODs for which there was no co-deployed
141 recorder.

142

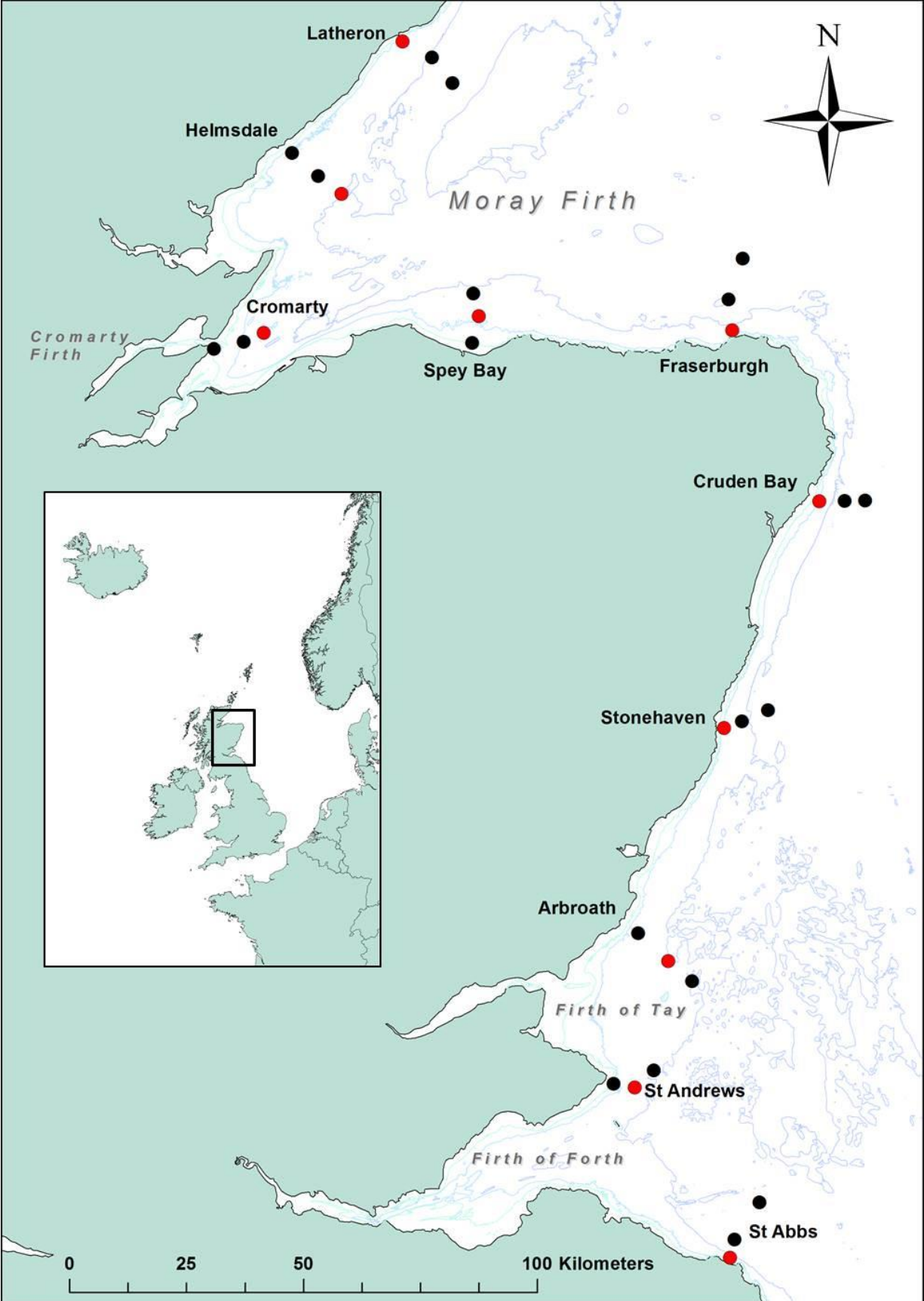
143 III. METHODS

144 A. *Data Collection*

145 In the spring of 2013, 30 C-PODs and 10 SM2M (Wildlife Acoustics) recorders were
146 deployed along the eastern Scottish coast (Figure 1). Deployment locations were chosen to
147 maximize acoustic coverage and minimize the likelihood of being displaced by storms or fishing
148 activity. All units were moored to the seafloor using 100kg chain weights. Some were furnished
149 with surface markers, while others had acoustic releases to facilitate recovery. The choice of
150 mooring type was based upon vessel traffic in the deployment location. C-PODs were deployed
151 in ten groups of three, with moorings within the group deployed approximately 5, 10 and 15 km
152 from the coast. Mooring locations are hereafter referred to as 5, 10, and 15 to indicate that
153 distances from shore were approximate values only. One SM2M was co-deployed with one of
154 the C-PODs at each group. The SM2M was attached to the same mooring line as the C-POD and
155 the units were separated by more than one meter. This configuration allowed us to compare the

156 continuous recordings from the SM2Ms, from which we could identify broadband and frequency
157 banded echolocation click trains, to the C-POD detection logs. The C-PODs logged continuously
158 from the deployment date, while SM2Ms were programmed to commence recording on Aug 13th
159 2013 with a 10 minute on/off duty cycle and sampling rate of 96 kHz and 12 dB gain. All units
160 recorded until their battery capacity was exhausted and were recovered between October and
161 November of the same year, as weather allowed (Table 1). For units displaced during the
162 deployment, the C-POD outputs related to temperature, angle of the device and sonar detection
163 were examined to determine the date on which the device was moved out of position. All data
164 from midnight of that day onwards were removed from the analysis.

165



167 **FIGURE 1** Survey locations for the ECOMMAS project C-POD and joint C-POD/SM2M
 168 deployment sites on the Eastern Scottish Coast. Deployment sites indicated by nearest large
 169 town: Latheron (Lat), Helmsdale (Hel), Cromarty (Cro), Spey Bay (Spe), Fraserburgh (Fra),
 170 Cruden Bay (Cru), Stonehaven (Sto), Arbroath (Abr), St Andrews (StA), St Abbs (Stb). All units
 171 were placed at approximately 5, 10, or 15km from the coast (color online).

172

173 **TABLE I**

174 Locations, dates and number of days for which usable data were obtained for all deployed
 175 devices (SM suffix indicates SM2M units, all others are C-PODs). For C-PODs, the number of
 176 click trains logged, the number of acoustic encounters, and the number of broadband or
 177 frequency banded click trains contributed to the training dataset, along with – in parentheses –
 178 the number of unique days represented by that contribution, are also given All dates are dd/mm
 179 in 2013. Five C-POD deployments that returned no usable data are omitted – Spey Bay 15,
 180 Fraserburgh 10 and 15, Cruden Bay 10, and Stonehaven 10.

181

Location name (SM=SM2M unit)	Data From	Data To	# Days	# Click Trains	# Encounters	Training Data	
						Broadband	Frequency- banded
Latheron 5	31/07	23/10	84	480	26		337 (9)
Latheron 5 SM	10/08	14/10	65				
Latheron 10	20/06	09/10	111	71	3		
Latheron 15	20/06	07/10	109	36	4		
Helmsdale 10	20/06	10/10	112	144	6		
Helmsdale 5	01/08	22/10	82	0	0		
Helmsdale 15	20/06	06/10	108	5	1		
Helmsdale 15 SM	10/08	25/09	46				
Cromarty 5	01/08	21/10	81	3680	199		
Cromarty 10	01/08	25/08	24	105	9		
Cromarty 15	01/08	23/10	83	23	4	22 (2)	

Cromarty 15 SM	10/08	15/10	66				
Spey Bay 5	24/07	22/10	90	330	24		
Spey Bay 10	20/06	06/10	108	0	0		
Spey Bay 10 SM	10/08	12/10	63				
Spey Bay 15	-	-	-				
Fraserburgh 5	25/07	24/10	91	859	21		303 (8)
Fraserburgh 5 SM	10/08	07/10	58				
Fraserburgh 10	-	-	-				
Fraserburgh 15	-	-	-				
Cruden Bay 5	26/07	26/11	123	910	29		
Cruden Bay 5 SM	10/08	12/10	63				
Cruden Bay 10	-	-	-				
Cruden Bay 15	19/06	26/11	160	541	31		
Stonehaven 5	26/07	26/11	123	955	34	226 (7)	32 (2)
Stonehaven 5 SM	10/08	03/10	54				
Stonehaven 10	-	-	-				
Stonehaven 15	19/06	26/11	160	1047	77		
Arbroath 5	27/07	26/10	91	224	16		
Arbroath 10	27/07	25/10	90	20	2		
Arbroath 10 SM	10/08	11/10	62				
Arbroath 15	21/06	27/11	159	887	44		
St Andrews 5	27/07	28/10	93	183	22		
St Andrews 10	27/07	28/10	93	0	0		
St Andrews 10 SM	10/08	18/10	69				
St Andrews 15	21/06	10/10	111	55	3		
St Abbs 5	27/07	27/11	123	55	6	5 (1)	
St Abbs 5 SM	10/08	03/10	54				
St Abbs 10	27/07	25/10	90	71	4		
St Abbs 15	20/06	27/11	160	72	8		

182

183

184

185

186 ***B. C-POD Click Detection and Feature Extraction***

187 C-POD data were downloaded and processed for echolocation click detections using the

188 manufacturer's software and accompanying KERNO classifier (v2.042). The KERNO software

189 classifies impulsive detections into one of the following four groups: "Sonar", "NBHF"

190 (narrowband high-frequency click trains often indicative of porpoise species), “Other Cet”
191 (wideband clicks indicative of most dolphin species) and “Unk” (representing
192 unclassified/unknown clicks). The C-POD software and KERNO classifier group “NBHF” and
193 “Other Cet” signals into short “click trains” based on temporal proximity and assign a “click
194 train ID” to each such group. The manufacturer states that this detection and classification
195 system allows multiple clicking animals to be differentiated from each other. The KERNO
196 classifier also assigns a quality class to each detection (high, moderate, or low) indicating the
197 probability that the click train was correctly discriminated from other “non-train” sources such as
198 snapping shrimp or rain (Tregenza, 2016).

199 The click features (referred to as “details” in the accompanying software) logged by C-PODs
200 are non-standard in the acoustics field and so require careful interpretation. Specifics of the click
201 features are proprietary and defined by the manufacturer as the time of the click, measured with
202 5 μ s resolution, dominant zero-crossing frequency (fZC, which should not be confused with peak
203 frequency), end zero-crossing frequency (derived from the last zero-crossing interval),
204 bandwidth measured on an “arbitrary scale” (manufacturers description), and click duration
205 measured as the number of cycles at the dominant frequency (NCycles). C-PODs also document
206 a metric of amplitude which, though reported as sound pressure level, is not corrected for
207 hydrophone frequency response (Dähne *et al.*, 2013). For this analysis, all “high” or “moderate”
208 quality “Other Cet” detections were selected and the accompanying click features, referred to as
209 “click details” by the manufacturer, were exported to a text file. For each click train (i.e. all
210 clicks with the same “click train ID”), we also calculated the median inter-click-interval, mean
211 dominant zero-crossing frequency, mean bandwidth and mean click duration (NCycles).

212 **C. C-POD Data Quality**

213 Initial data exploration was undertaken to identify collinearity between click train features
214 documented by the C-POD. The distributions of all train features were visually inspected and we
215 excluded all click trains for which there were insufficient data to produce reliable models (i.e. the
216 tails of the distributions). Thus, all click trains with median inter-click-intervals greater than or
217 equal to 0.4 seconds, mean click durations greater than or equal to 11 cycles (NCycles), mean
218 bandwidths greater than or equal to 7 (manufacturers arbitrary units), or dominant frequencies
219 less than 30 kHz were excluded from the categorization portion of the analysis (resulting in the
220 removal of ~1% of all logged click trains).

221 We then grouped C-POD click trains into “acoustic encounters,” consisting of all click trains
222 on the same C-POD occurring within 30 minutes of another click train (Thompson *et al.*, 2011).
223 In this process we assume that each encounter was produced by the same animal or group of
224 animals and that groups of acoustically dissimilar species (e.g., Risso’s and bottlenose dolphins)
225 were not represented in the data. This is consistent with visual observations indicating that mixed
226 odontocete groups, especially any containing bottlenose dolphins, are extremely rare in Scottish
227 coastal waters (Ross and Wilson, 1996; Hammond *et al.*, 2002).

228

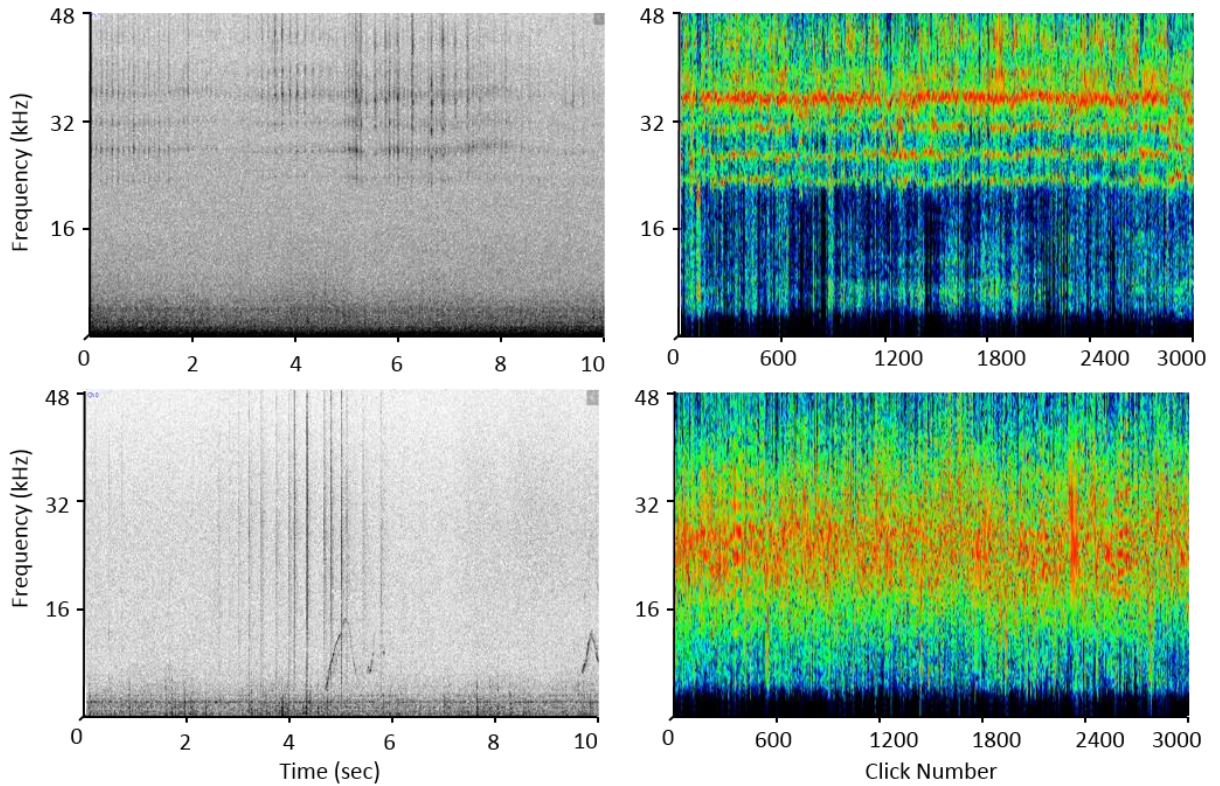
229 **D. Identifying Broadband and Frequency Banded Click Trains in the C-**
230 **POD Detections**

231 The few click features documented by the C-POD system are not sufficient to allow users
232 to visually discriminate between click trains matching the broadband and frequency banded
233 categories described above. Thus, we used continuous recordings to identify time periods with
234 clearly identifiable bouts of broadband or frequency banded click trains. These periods were
235 compared to the click log produced by the C-POD at to the same mooring. Where echolocation

236 click trains were present on both instruments at the same time, we assumed that the echolocation
237 click trains had originated from the same animal or group of animals.

238 Data from the SM devices were downloaded, converted to spectrograms (1024 point fast-
239 Fourier transform , 10.67 ms window, and 50% overlap) and processed for echolocation clicks
240 using PAMGuard click detecting software (Gillespie *et al.*, 2009). Click detection trigger was set
241 to 10 dB and click detections were manually scanned for the presence of high signal-to-noise
242 echolocation click encounters and annotated as such. Echolocation clicks from high SNR
243 encounters containing at least 500 clicks were extracted and the average spectrum was inspected
244 for the presence of either distinct peaks or notches in energy indicative of white-beaked or
245 Risso’s dolphins or unimodal energy between 20 and 40 kHz suggestive of bottlenose and/or
246 common dolphins. While visually inspecting the continuous recordings for high SNR frequency
247 banded click trains, we did not seek an exact match the location of the spectral energies as
248 reported by reported by Calderan *et al.* (2013) or Soldevilla *et al.* (2008). Both environment and
249 recording equipment impart site and equipment-specific filter effects on the received signals
250 (Roch *et al.*, 2015). We expect some variation in the received characteristics of echolocation
251 clicks. Neither did we attempt to differentiate between species within the two click encounter
252 types (e.g. common vs bottlenose dolphin). Instead encounters where the average spectrum
253 contained at least two peaks in energy between 35 and 43 kHz and with >3 dB peak-to-peak
254 difference between successive peaks and notches were annotated as “frequency banded”. Click
255 encounters for which there was a unimodal peak in energy between 20 and 30 kHz were
256 annotated as broadband (Figure 2).

257



258

259

260 **FIGURE 2** Spectrograms (left) (*fs* 96 kHz, 10.67 ms Hann window, 50% overlap) and
 261 concatenated click spectrums (right) of echolocation clicks within from frequency banded (top)
 262 and broadband (bottom) acoustic encounters. Top row: 10 seconds of recordings from a frequency
 263 banded encounter consistent with white beaked and/or Risso's dolphins and 3000 concatenated
 264 echolocation clicks from the frequency banded encounter. Bottom row: 10 seconds of recordings
 265 from a broadband encounter containing whistles and echolocation clicks consistent with bottlenose
 266 and/or common dolphins (color online).

267

268 The timing of acoustic encounters documented by the C-PODs were compared with the
 269 times of broadband and frequency banded click trains observed in the continuous SM2M

270 recordings. The train features from “high” or “moderate” quality “other cetacean” trains
271 coinciding with visually confirmed broadband and frequency banded encounters in the
272 continuous recordings were used to build and train categorization models.

273 To increase the volume of C-POD click trains from broadband encounters, click train
274 features from the Cromarty 5 C-POD, for which there was no adjacent SM2M recorder, were
275 randomly selected for inclusion in the broadband training dataset. Despite the lack of concurrent
276 acoustic recordings, we are confident that the vast majority of the click trains logged by the C-
277 POD at this location were produced by bottlenose dolphins and as such represented our
278 broadband category. The area in and around the Cromarty and inner Moray Firths has been
279 continuously surveyed for the last 25 years and is a well-known bottlenose dolphin habitat that
280 (Hammond and Thompson, 1991; Wilson *et al.*, 2004; Cheney *et al.*, 2013; Thompson *et al.*,
281 2014; Pirodda *et al.*, 2015). These studies strongly suggest that no dolphin species besides
282 bottlenose regularly occupy the area. To further reduce the probability of including frequency
283 banded click trains in the broadband training data, only click trains from the month of August,
284 coinciding with the majority of visual surveys, were added to the training dataset.

285 Obtaining a representative sample of echolocation click behaviors is important in order to
286 produce an accurate categorization system. Of the 1195 C-POD click trains that could be linked
287 to trains in the adjacent SM recordings only 270 (22%) were broadband. We added only as many
288 click trains from the Cromarty 5 site as needed to provide an equal number of broadband and
289 frequency banded click trains for the categorization task. We could have reasonably included all
290 of the data from the Cromarty 5 C-POD based on the overwhelming evidence showing that the
291 area is primarily occupied by bottlenose dolphins. However, we chose to limit the number of
292 auxiliary click trains included from this C-POD for two reasons. First, the Cromarty 5 unit

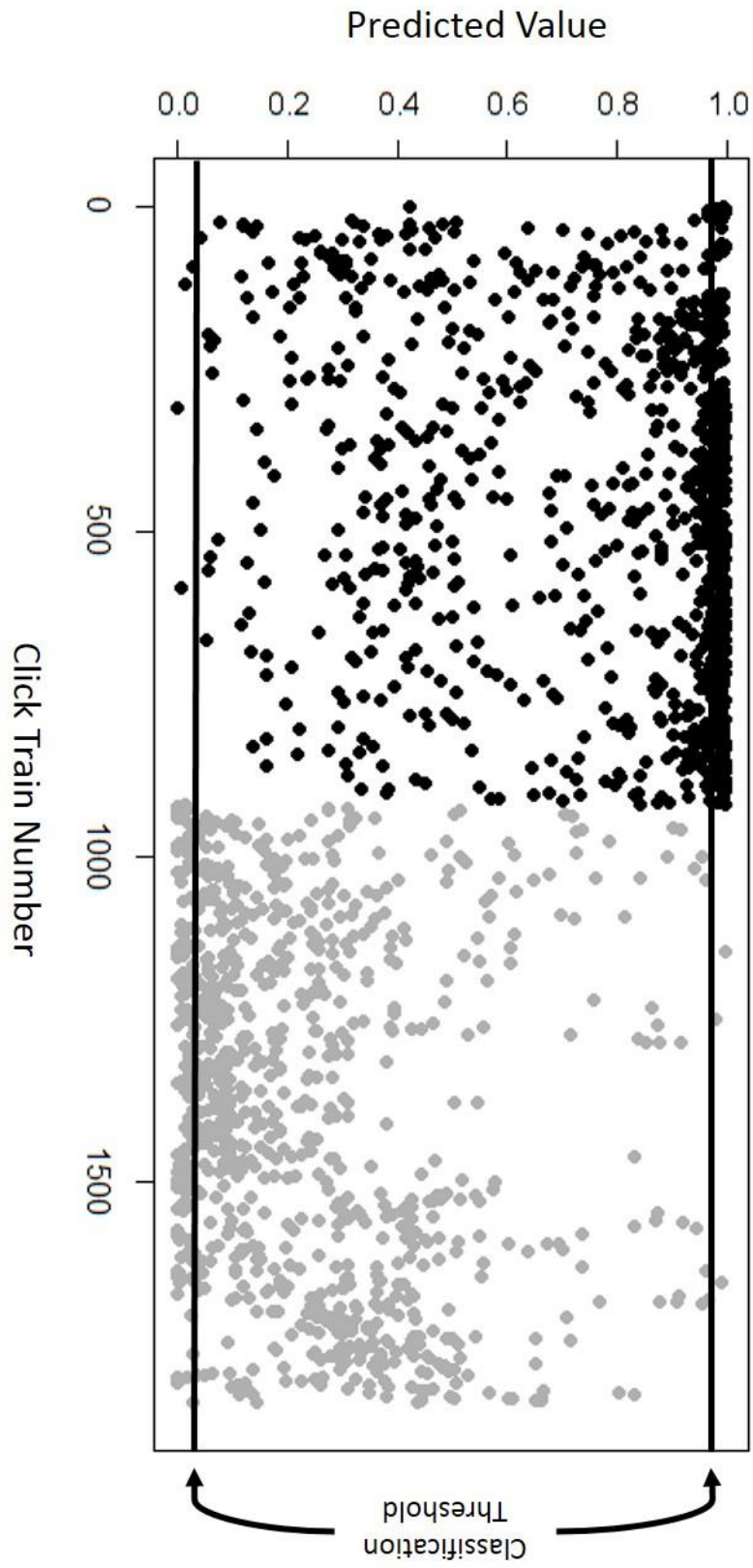
293 contained almost as many “OtherCet” click trains as the other 25 recovered C-PODs combined.
294 Therefore, we sought to reduce potential bias introduced by site-specific behavior present in the
295 data from that unit. Second, the Cromarty Firth is a known “hot-spot” for bottlenose dolphin
296 foraging activity (Hastie *et al.*, 2004; Hastie *et al.*, 2006; Pirotta *et al.*, 2014b). Thus, we would
297 expect to document more clicks with shorter inter-click-interval (reflecting the production
298 terminal buzzes characteristic of prey capture attempts) near that location (Pirotta *et al.*, 2014b).
299 Including an excessive number of buzzes in the training data would introduce bias towards low
300 ICI’s within the broadband category.

301 ***E. Model-based Prediction and Categorization***

302 The above procedures generated a set of C-POD click trains, with measured features, for
303 which we were reasonably confident of the species group producing the clicks. We used these
304 acoustically verified click trains to build and characterize a binomial family generalized additive
305 model (GAM) that output the predicted probability that each click train consisted of broadband
306 clicks. The covariates for this model included: median inter-click-interval, mean zero-crossing
307 frequency, mean click bandwidth and mean click duration. The GAM categorization model was
308 created in R version 3.2.4 revised (R Core Team, 2016) with the MGCV package version 1.8-12
309 (Wood, 2006).

310 Here, our goal was to build and select the GAM model best able to discriminate between the
311 two echolocation click types commonly documented on the eastern Scottish coast. Thus, a *k*-fold
312 cross validation approach was used to characterize candidate GAM models and provide
313 parameters for final model selection.

314



315

316 **FIGURE 3** Predicted probability of a C-POD echolocation click train being associated with
 317 broadband encounter from the adjacent recordings (P , Equation 1). Points represent C-POD click
 318 trains associated with broadband (black) and frequency banded (grey) click encounters in the
 319 adjacent SM2M recordings. Horizontal lines represent the minimum classification threshold (T_t ,
 320 Equation 2) above and below which click trains were classified as broadband and frequency
 321 banded, respectively. Click trains failing to meet the threshold (i.e. between the lines) were
 322 deemed too ambiguous to classify and left uncategorized.

323

324

325 For model comparison, all candidate GAMs were assessed using 200 iterations of a 5-fold
 326 cross-validation procedure and train categorization threshold of 0.425 (T_t ; Equation 1). Thus, all
 327 click trains with predicted P exceeding 0.925 were categorized as broadband and those less than
 328 0.075 were categorized as frequency banded (Equation 1, Figure 3). Click trains with predicted
 329 probabilities between 0.075 and 0.925 were considered too ambiguous to categorize and were
 330 therefore denoted as “unknown”.

331

332

$$333 \text{ Train Classification}(P) = \begin{cases} P \geq 0.5 + T_t \rightarrow \text{Broadband} \\ P \leq 0.5 - T_t \rightarrow \text{Frequency banded} \\ 0.5 - T_t < P < 0.5 + T_t \rightarrow \text{Unclassified} \end{cases} \quad (\text{Equation 1})$$

334

335

336 For each model iteration 1/5th of the verified C-POD click trains were randomly selected and
 337 used as the validation set. The remaining 4/5ths of the verified C-POD click trains were used to

338 build the GAM models. In this portion of the analysis acoustic encounters were not considered
339 and all verified click trains were treated as independent. For each iteration, we calculated the
340 following metrics: proportion of broadband and frequency banded click trains that met either
341 categorization threshold (proportion classified), the proportion of correctly categorized click
342 trains (correct categorization rate), and the proportion of incorrectly categorized click trains
343 (incorrect categorization rate). Performance values for each GAM were calculated using the
344 same train threshold for all models (T_r , Equation 1). We then calculated the mean and standard
345 deviation of all performance metrics across the 200 iterations and used these values to select the
346 model meeting our selection criteria.

347 Model selection focused on reducing the proportion of frequency banded click trains
348 incorrectly categorized as broadband, and thereby minimize the chances of artificially inflating
349 the bottlenose dolphin occupancy rates throughout the survey area. We also sought to categorize
350 the highest proportion of click trains possible, regardless of type. Thus, our model selection
351 criterion (SC) was defined as:

352

$$353 \quad SC = 3FP_f + U \quad \text{(Equation 2)}$$

354

355 Where FP_f was the false positive rate for frequency banded click trains and U was the
356 proportion of uncategorized click trains. We introduce a scalar value of three representing our
357 qualitative decision to penalize frequency banded click trains incorrectly categorized as
358 broadband over click trains left uncategorized. The selection criterion was calculated for all
359 candidate models and the GAM with the lowest criterion score was used to predict the
360 probability that each click train was comprised of broadband clicks.

361 ***F. Encounter Likelihood***

362 By itself, the GAM model could not account for the fact that click trains recorded in close
 363 succession were most likely produced by the same individual or group of animals (Quick *et al.*,
 364 2014). To incorporate this information and increase the proportion of categorized click trains, we
 365 calculated the joint likelihood of each acoustic encounter by taking the product of all GAM
 366 predictions within the acoustic encounter. We then calculated the joint likelihood that all click
 367 trains comprising each encounter were either broadband or frequency banded. The two
 368 likelihoods were then combined into a likelihood ratio (*LR*; Equation 3) calculated as;

369

$$370 \quad LR = \frac{\prod_{i=1}^n P_i}{\prod_{i=1}^n (1 - P_i)} \quad \text{(Equation 3)}$$

371

372 where P_i is the predicted probability from the GAM categorization model that the i^{th} of n click
 373 trains in the acoustic encounter was broadband. Since the model was binary, the likelihood that
 374 an encounter was comprised of frequency banded click trains was calculated by simply replacing
 375 P_i with $(1 - P_i)$ to give the denominator of Equation 3. As with the click train analysis, a
 376 minimum likelihood encounter threshold (T_e ; Equation 4) was chosen above and below which all
 377 trains within acoustic encounters were categorized as broadband or frequency banded:

378

$$379 \quad \text{Encounter Classification} = \begin{cases} \text{Broadband, } LR \geq T_e \\ \text{Frequency Banded, } LR \leq 1/T_e \\ \text{Unclassified, } 1/T_e < LR < T_e \end{cases} \quad \text{(Equation 4)}$$

380

381 In this portion of the analysis we therefore needed to choose a minimum likelihood threshold
 382 (T_e) that balanced the risk of incorrectly classifying encounters against the risk of failing to

383 classify most encounters. We compared the encounter categorization produced by the likelihood
384 ratios to the validated training data to determine the correct and incorrect encounter classification
385 rates. Through a process of trial and error we found that $T_e=5$, so that the evidence had to be five
386 times as strong for one option than the other for a positive classification to be made, produced
387 the optimal balance of maximizing classification rates while minimizing classification errors.
388 Thus all encounters with likelihood ratios above 5 were classified as broadband and encounters
389 with likelihood ratios below 1/5 were classified as frequency banded. All click trains from
390 encounters with likelihood ratios (LR) between 1/5 and 5 were deemed too ambiguous for
391 categorization and were left uncategorized. Finally, the GAM and the encounter analysis were
392 applied to the full C-POD data set for which simultaneous acoustic recordings were not
393 available.

394

395 IV. RESULTS

396 A. *Echolocation Click Encounters in C-PODs and Continuous* 397 *Recordings*

398 All SM2M units were successfully recovered in late 2013, but four C-PODs were not
399 recovered, while four others were on moorings that had been displaced, or had stopped recording
400 early, and subsequently excluded from the analysis (Table 1, Figure 6). The number of usable
401 recording days varied considerably between units based on battery life and/or displacement
402 during the survey period. The median number of usable days for the C-PODs was 108 (range 24-
403 160). Due to the increased power and storage requirements, the SM2M units recorded for fewer
404 days than the C-PODs, with a median number of recording days of 62.5 (range 46 -69; Table 1).

405 Together the C-PODs identified 10,753 high or moderate quality “Other Cet” click trains,
406 representing undetermined delphinid species (Table 1). The number of “Other Cet” click trains

407 logged by each C-POD varied from zero (recorded by the Helmsdale 10, Spey Bay 10 and St
408 Andrews 10 units; Figure 1) to a maximum of 3662 (recorded by the Cromarty 5 unit).
409 Of these, 1% represented click trains from the tails of the click feature distributions where there
410 therefore excluded from the analysis. Data exploration indicated that dominant frequency and
411 end frequency were collinear and so the latter was excluded from the categorization analysis.

412 **B. C-POD Echolocation Click Features**

413 Five of the 10 C-PODs deployed with adjacent SM2Ms registered click trains that were also
414 identifiable in the full spectrum SM2M recordings (Table 1). The lack of concurrent detections
415 in the other five C-POD/SM2M pairs could partly be attributed to the very few echolocation
416 click detections by either the SM2M or the C-POD those locations (e.g., Spey Bay and St
417 Andrews 10). In other cases, such as Cruden Bay 5, the failure to detect clicks on the adjacent
418 SM2M likely arose from the duty cycle of the SM2M units which precluded visual
419 categorization of the echolocation clicks. Last, differences in detection probability between the
420 C-PODs and SM2M units may result in fewer click trains overall being recorded by the C-PODs.

421 In total, 925 click trains detected by the KERNO classifier occurred concurrently with
422 visually confirmed broadband (n=253) or frequency banded (n=672) click train encounters in the
423 continuous recordings. The vast majority of verifiable broadband click trains (89%) were
424 extracted from the Stonehaven 5 deployment. This distribution was therefore not representative
425 of either the spatial or temporal scale of the survey. To obtain a more representative sample of
426 broadband click features, 419 click trains were randomly selected from the Cromarty 5 C-POD,
427 where long term sighting records confirm the overwhelming presence of bottlenose dolphins, and
428 added to the broadband training. Four hundred and nineteen were used so as to include an equal
429 number of frequency banded and broadband click trains with which we built the GAM for
430 categorization (see Methods).

431

432 **C. Categorization Model Performance**

433 The model with the best categorization score was a tensor product smooth with mean zero-
434 crossing frequency, mean bandwidth and median inter-click interval (Table 2). Tensor smooths
435 are multi-variate functions that allow for interactions between inputs with different units (e.g.
436 frequency in kHz, and Number of Cycles). Five-fold cross validation resulted in a mean false
437 categorization rate of 1.4% for verified frequency banded click trains and, on average,
438 categorized 40% of the training data (Figure 4, Table 3).

439 **TABLE II**

440 Mean and standard deviation for the true classification rate (TCR), false classification rate (FCR),
441 and proportion of unclassified click trains for each model as estimated by the k-fold cross
442 validation. Mean and standard deviation of the GAM classification model performance metrics
443 for the top 15 models using a classification threshold (T_t , Equation 2) of ± 0.425 . Grey highlight
444 indicates model selected for this analysis and (*) indicates the initial ‘best guess’ model used to
445 establish a classification threshold (T_t) for all analysis. (Equation 1)

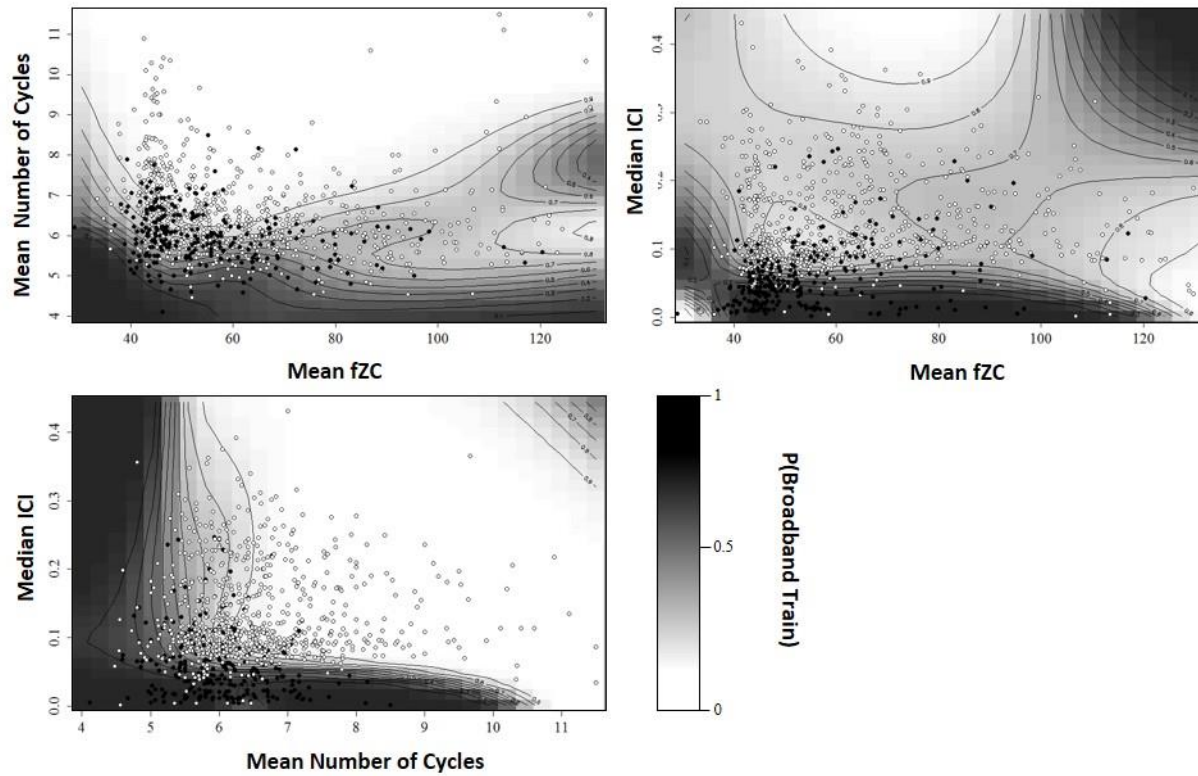
Formula	Broadband Click Trains		Frequency Banded Click Trains		Unclassified	Selection Criterion
	TCR	FCR	TCR	FCR		
Speciesid~te(MedICI, MeanNCycles, Meanzfc)	0.49 ± 0.02	0.02 ± 0.01	0.29 ± 0.02	0.01 ± 0.01	0.60 ± 0.01	0.638
Speciesid~te(MedICI, MeanNCycles, Meanzfc)+s(MeanBW)	0.49 ± 0.02	0.02 ± 0.01	0.29 ± 0.02	0.02 ± 0.01	0.59 ± 0.01	0.640
Speciesid~te(MedICI, MeanNCycles, MeanBW)+s(Meanzfc)	0.48 ± 0.03	0.03 ± 0.01	0.28 ± 0.04	0.02 ± 0.01	0.60 ± 0.03	0.644
Speciesid~te(MedICI, MeanNCycles, MeanBW, Meanzfc)	0.47 ± 0.03	0.03 ± 0.01	0.27 ± 0.03	0.02 ± 0.01	0.61 ± 0.02	0.658
Speciesid~te(MedICI, MeanNCycles, MeanBW)	0.47 ± 0.03	0.03 ± 0.01	0.27 ± 0.03	0.02 ± 0.01	0.61 ± 0.02	0.659
Speciesid~te(MedICI, MeanBW, Meanzfc)+s(MeanNCycles)	0.52 ± 0.03	0.02 ± 0.02	0.20 ± 0.05	0.02 ± 0.01	0.62 ± 0.05	0.681
Speciesid~te(MedICI, MeanNCycles)+s(MeanBW)+s(Meanzfc)	0.48 ± 0.03	0.02 ± 0.01	0.19 ± 0.03	0.02 ± 0.01	0.65 ± 0.02	0.693
Speciesid~s(MedICI)+te(MeanNCycles, MeanBW, Meanzfc)	0.48 ± 0.03	0.01 ± 0.01	0.21 ± 0.03	0.02 ± 0.01	0.64 ± 0.03	0.693
Speciesid~te(MedICI, MeanNCycles)+s(Meanzfc)	0.49 ± 0.03	0.02 ± 0.01	0.19 ± 0.03	0.02 ± 0.01	0.65 ± 0.02	0.698
Speciesid~te(MedICI, MeanNCycles)+s(MeanBW)	0.48 ± 0.03	0.02 ± 0.01	0.18 ± 0.02	0.02 ± 0.01	0.65 ± 0.02	0.704
Speciesid~s(MedICI)+te(MeanNCycles, Meanzfc)+s(MeanBW)	0.48 ± 0.03	0.01 ± 0.01	0.18 ± 0.02	0.02 ± 0.01	0.66 ± 0.02	0.717
Speciesid~te(MeanNCycles, Meanzfc)+s(MedICI)	0.47 ± 0.03	0.01 ± 0	0.16 ± 0.02	0.02 ± 0.01	0.67 ± 0.02	0.728
Speciesid~te(MedICI, Meanzfc)+s(MeanNCycles)+s(MeanBW)	0.47 ± 0.02	0.01 ± 0.01	0.14 ± 0.02	0.02 ± 0.01	0.68 ± 0.02	0.729
Speciesid~s(MedICI)+te(MeanNCycles, MeanBW)+s(Meanzfc)	0.47 ± 0.03	0.01 ± 0.01	0.14 ± 0.03	0.02 ± 0.01	0.68 ± 0.02	0.734
Speciesid~s(MedICI)+s(MeanNCycles)+te(Meanzfc, MeanBW)	0.46 ± 0.03	0.01 ± 0.01	0.15 ± 0.03	0.02 ± 0.01	0.68 ± 0.02	0.735

448 **TABLE III**

449 Results of the binomial GAM used to analyze click type (ClickTrain) using a tensor smooth of median inter-click interval (MedICI),
 450 mean number of cycles in clicks (MeanNCycles) and mean zero crossing frequency (meanzfc).

Parametric Coefficients				
Formula: ClickTrain~te(<i>MedICI</i> , <i>MeanNCycles</i> , <i>Meanzfc</i> , family= <i>Binomial</i> ,link= <i>logit</i>)				
Intercept Estimate	Standard Error	z-value	Pr(> z)	
-0.3500	0.1254	-2.791	0.00525	
Approximate Significance of Smooth Terms				
Est. df	Reference df	Chi squared	P-value	
69.28	79.31	612	<.001	

451



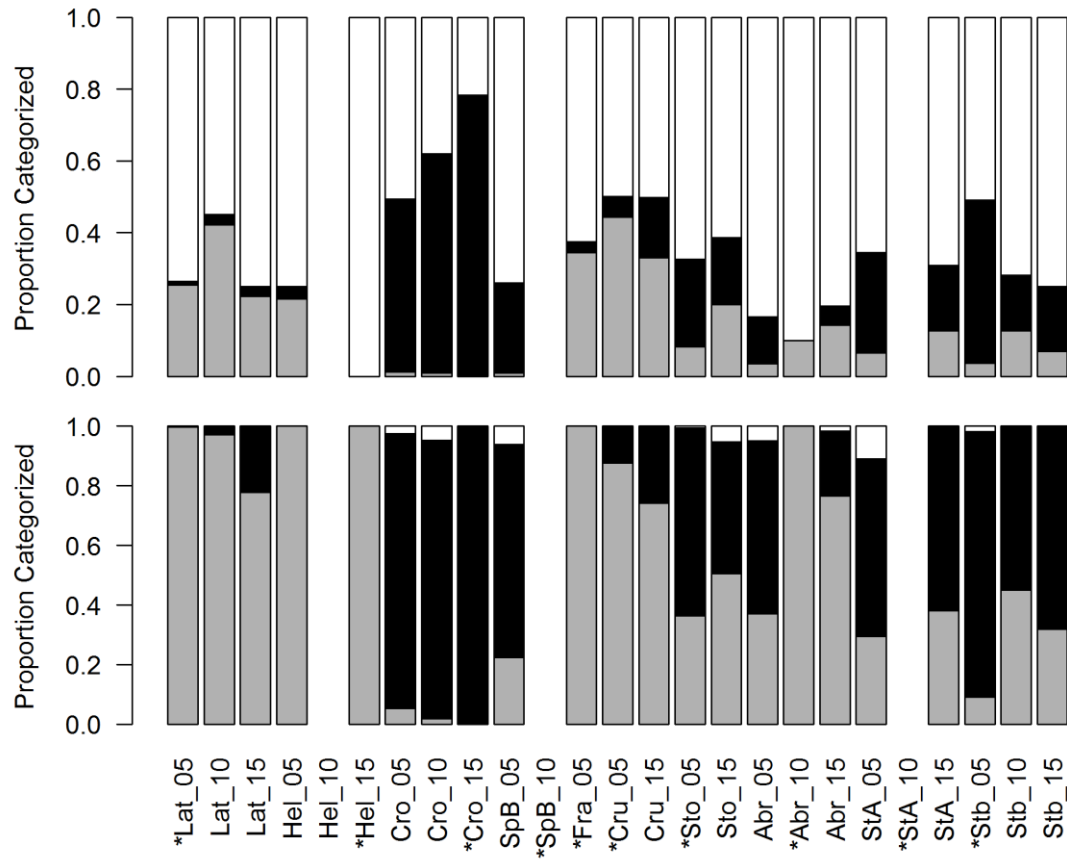
452

453 **FIGURE 4** Two dimensional representations of the for-dimensional tensor-smooth binomial classification GAM. Shade indicates the
 454 probability that a given click train was broadband (black) or frequency banded (white) based on the mean inter-click-interval (Median
 455 ICI), mean number of cycles (e.g. duration) of the clicks, and mean zero-crossing frequency (Mean fZC) of the click trains. Points
 456 represent training data for broadband (black) and frequency banded (light gray) click trains.

457

458

459 When applied to the full C-POD dataset (minus the training data), the model categorized a total of 3968 (37%) of the click
460 trains, of which 2737 were identified as broadband and 1231 frequency banded. The remaining 63% of the click trains failed to meet
461 either categorization threshold (T_i). As expected, the proportion of click train types varied across the deployment sites. C-PODs near
462 the inner Moray Firth (Cromarty and Spey Bay) contained primarily broadband click trains and units to the north and south
463 (Helmsdale and Fraserburgh) contained primarily frequency banded click trains. Uncategorized click trains were present on all units
464 and, with the exception of the Cromarty locations, generally represented the majority of the click trains detected at each deployment
465 site (Figure 5).



466

467

468 **FIGURE 5** Upper Panel: The proportion of click trains classified as broadband (black), frequency banded (gray) or unknown (white)
 469 by the GAM classification model with a minimum classification threshold of ± 0.425 (Tt Equation 1). Lower Panel: The proportion of
 470 click trains classified as broadband, frequency banded or unknown by the combination of the GAM click-train classification and the

471 encounter likelihood ratio. Asterisks indicate joint C-POD/SM2M deployment locations from which training data were derived.
472 Displaced units (SpB 05, Fra 10, Fra 15, Cru 10, Sto 10) not shown.

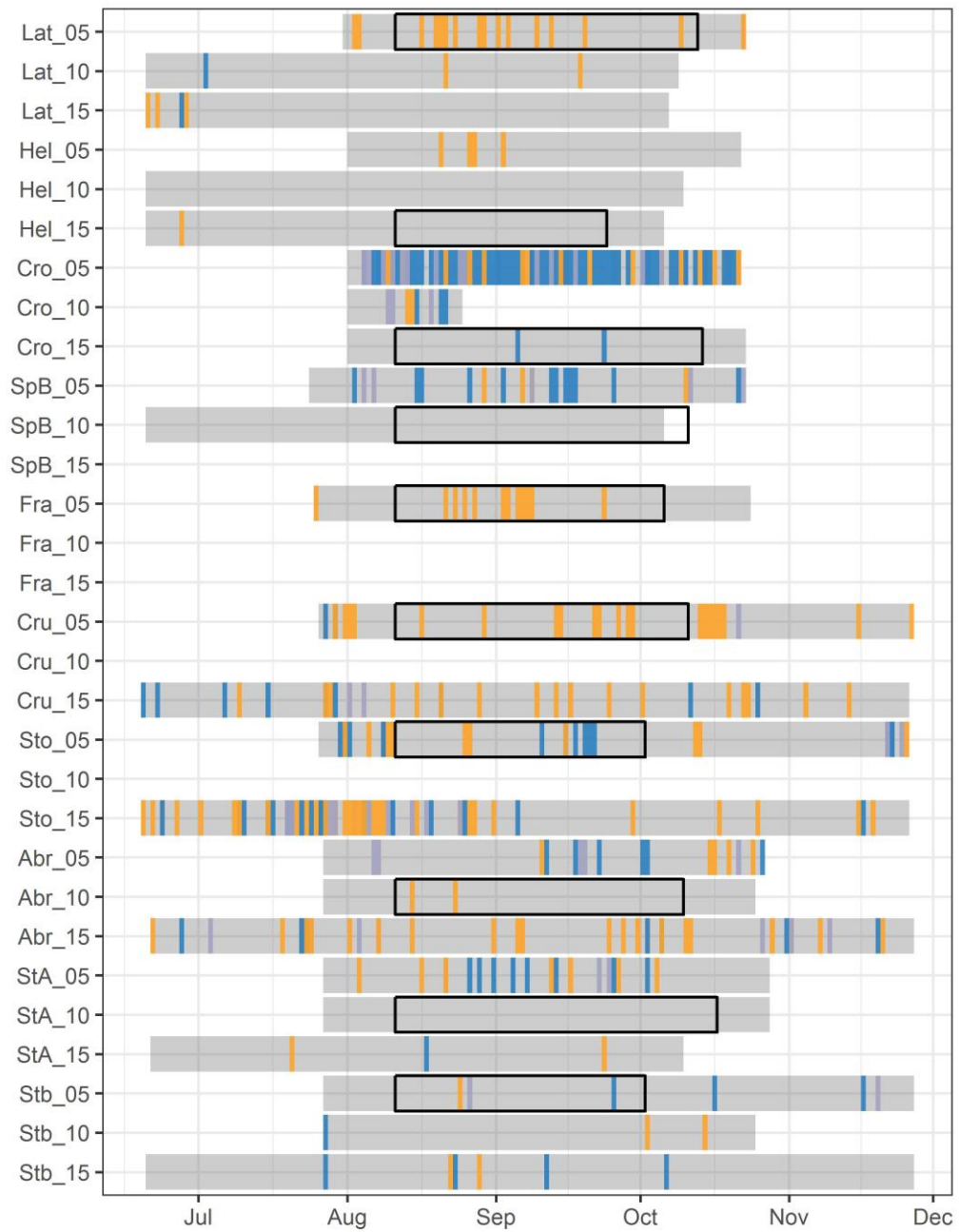
473

474 D. Encounter Likelihood

475 The 10,753 click trains documented by the 26 recovered C-PODs represented 573 encounters. Twelve encounters coincided with
476 visually verified broadband trains recorded by the adjacent SM2M recordings and 27 encounters coincided with visually verified
477 frequency-banded click trains in the SM2M recordings (Table 1). Using a minimum likelihood ratio of five ($T_e = 5$ in Equation 4), 10
478 of the verified broadband click-train encounters were correctly categorized, two were incorrectly categorized as frequency banded
479 encounters and none were left unclassified, while 24 of the 27 verified frequency banded encounters were correctly categorized, none
480 were incorrectly categorized and three were left unclassified. When the likelihood model was applied to the remaining data, 264
481 (43%) total encounters were categorized as broadband, 273 (45%) as frequency banded and the remaining 75 (12%) were left
482 unclassified (Figure 5). The Helmsdale 15 unit contained a single acoustic encounter for which no click trains met the GAM
483 categorization threshold, but the likelihood ratio of the encounter was less than 1/5 allowing classification, therefore the proportion of
484 click trains classified on the Helmsdale unit was 0 in the GAM only model, but 100% when the encounter likelihood ratio was applied.

485 The highest daily occupancy rates were observed at the Cromarty 5 deployment location, with other peaks around the Latheron,
486 Fraserburgh, Arbroath and St Andrews sites (Figure 6). No encounters of either type were documented by the Helmsdale 10, Spey Bay
487 10 and St Andrews 10 units. The daily occupancy rates of broadband and frequency banded click encounters differed between

488 locations. Deployments near the inner Moray Firth showed higher broadband daily occupancy rates while the converse was true for
489 the Latheron, Fraserburgh and Cruden Bay sites. These results are consistent with long-term studies in the area that have shown
490 regular bottlenose dolphin presence in and around the SAC (Hammond and Thompson, 1991; Wilson *et al.*, 1997; Quick *et al.*, 2014).
491 Interestingly, encounters in Stonehaven, Arbroath, and to a lesser degree St Andrews and St Abbs, showed similar rates of detection
492 positive days for both broadband and frequency-banded click types, indicating the presence of multiple species.
493



495 **FIGURE 6** Daily occupancy of broadband echolocation click encounters (blue), frequency banded echolocation click encounters
496 (yellow) and uncategorized echolocation click train encounters (dark gray). Gray blocks indicate times when the C-PODs were recording
497 (see also table 1) and
498 black rectangles indicate periods for which there were simultaneous SM2M recordings (color online).

499

500 V. DISCUSSION

501 The categorization results reported here for C-POD detections are consistent with the few visual surveys available for areas
502 outside of the Moray Firth. This study identified primarily broadband encounters in the data from all three Cromarty C-PODs. This
503 finding is unsurprising given that a portion of the broadband training detections were derived from the Cromarty 5 unit. However, the
504 prevalence of broadband click trains at the other two Cromarty deployment sites is consistent with previous studies in the area.
505 Similarly, broadband encounters were more prevalent than frequency banded click trains in the C-POD detections at the St Andrews
506 and St Abbs sites, where bottlenose dolphins are the most frequently sighted species (Cheney *et al.*, 2013). Approximately equal
507 numbers of broadband and frequency banded detections occurred through the Grampian region (Cruden Bay, Stonehaven and
508 Arbroath), which agrees well with reported sighting rates for bottlenose and white-beaked dolphins between Cruden Bay and
509 Stonehaven (Anderwald and Evans (2010). Similarly, Weir *et al.* (2007) report multiple sightings of white-beaked dolphins in and
510 around the Aberdeen area (between Cruden Bay and Stonehaven).

511 Daily occupancy rates from the C-POD data suggest a degree of spatial partitioning between species producing broadband and
512 frequency-banded clicks. Broadband click encounters comprised the vast majority of the detection positive days logged by the C-
513 PODs deployed in the inner Moray Firth (Cromarty). Contrary to our expectations, the acoustic encounters on the Helmsdale C-PODs,
514 which were located within the Moray Firth SAC, were dominated by frequency banded click trains. This suggests that, over the 2013
515 deployment period, bottlenose dolphins were not the most common species using this portion of the SAC.

516 Outside of the SAC, both broadband and frequency banded click encounters were frequently observed. However, for each
517 deployment group (e.g., St Andrews, Arbroath etc.) broadband click trains were more common in the nearshore (~5 km) than the
518 offshore deployment sites (~10 and 15 km). This is consistent with previous studies that suggest bottlenose dolphins preferentially use
519 nearshore areas (Arso Civil, 2014; Quick *et al.*, 2014). The Stonehaven C-PODs contained a mix of broadband and frequency banded
520 encounters, matching visual surveys indicating that both bottlenose and white beaked dolphins are commonly sighted in that area
521 (Weir *et al.*, 2007; Anderwald and Evans, 2010). These results hint at the possibility of areas along the eastern Scottish coast having
522 different ecological importance for the two groups. This has been confirmed for bottlenose dolphins in the inner Moray Firth where
523 foraging buzzes are more frequently documented near known “hot-spots” (Hastie *et al.*, 2004; Pirotta *et al.*, 2014b). However, fewer
524 data are available for the other species present in the area and/or outside of the Moray Firth.

525 The similarity between our results and previously published sightings data indicates that the C-POD encounter categorization
526 system presented here works well for eastern Scottish waters. However, it would be inappropriate to directly apply this categorization
527 tool to C-POD detections collected from other regions. Recent classification studies on similar species groups using full spectrum

528 recording ($f_s = 200$ kHz) have shown that deployment location and instrument type can adversely affect the performance of click train
529 classifiers (Roch *et al.*, 2015). It is unclear whether this might be the case with C-POD data for which fewer click features are
530 collected. While it is possible that the zero-crossing method combined with the limited click parameters are more robust to site and/or
531 instrument specific variations, it could just as easily be the case that the limited click features recorded by the C-PODs are *more*
532 susceptible to such variations. Thus, future studies seeking to use this classifier or these methods must not omit a validation process.
533 Ideally this would involve comparing C-POD detections with concurrent visual sightings (e.g., Roberts and Read 2014, Robbins *et al.*
534 2015, Nuutilia *et al.* 2013). However, where visual observations are not possible or practical, pairing C-PODs with continuous
535 recorders is an alternative method.

536 The use of C-POD data processed only with the KERNO classifier is justified in surveys where the researchers can be confident
537 that the majority of detections represent single dolphin and/or porpoise species. This is the case for the dolphin detections within the
538 inner Moray Firth where bottlenose dolphins represent the principle dolphin species. Similarly, throughout the North Sea, harbor
539 porpoise (*Phocoena phocoena*) represent the only resident cetacean capable of producing “NBHF” clicks and are, therefore, unlikely
540 to be confused with other species. In such contexts, C-PODs and similar devices can directly inform studies of cetacean abundance
541 and behavior (Jaramillo-Legorreta and Rojas-Bracho, 2011; Kyhn *et al.*, 2012; Brookes *et al.*, 2013; Wilson *et al.*, 2013; Pirota *et al.*,
542 2014b; Williamson *et al.*, 2016). However, where multiple odontocete species with similar click features are present, additional
543 methods are needed to increase taxonomic resolution. This study highlights the benefits of developing methods to increase taxonomic
544 precision in detections from low-cost click loggers when full acoustic audits are impossible or impractical. This is especially pertinent

545 given that C-PODs and their predecessor T-PODs are widely used for monitoring and mitigation associated with offshore industrial
546 activities (Carstensen *et al.*, 2006; Scheidat *et al.*, 2011).

547 In this work we relied on several assumptions, but a key one was that all click trains detected by the C-PODs were produced by
548 one of the four most common species seen in the area. C-PODs are capable of recording echolocation clicks from all odontocetes with
549 the exception of sperm whales (*Physeter macrocephalus*) for which the energy is below the sensitivity of the instruments (Dähne *et*
550 *al.*, 2013). This includes clicks from species that, while infrequent, are known to visit the eastern Scottish coast including killer whales
551 (*Orcinus orca*), long-finned pilot whales (*Globicephala melas*), and Atlantic white sided dolphins (*Lagenorhynchus acutus*). Based on
552 published click characteristics (Deecke *et al.*, 2005; Eskesen *et al.*, 2011), click trains from these species would likely be classified as
553 broadband click encounters by this categorization system. Thus, it is possible that some of the “Other Cet” click trains detected by the
554 C-PODs represented one or more of these species. However, previous visual surveys indicate that such species are infrequent visitors
555 to the eastern Scottish coast and could therefore contribute only a trivial amount of noise to the encounter rates presented here.
556 Regardless, the ambiguity in dolphin detections reiterates the need to inform acoustic-only methods with other sources of information
557 about the study system.

558 The interpretation of these results assumed that stable frequency banding, or the lack thereof, in echolocation clicks was diagnostic
559 of the species-group producing them. This assumption is debated in the literature, with several authors providing evidence of species
560 discrimination based on the spectral location of peaks and notches (Houser *et al.*, 1999; Soldevilla *et al.*, 2008; Calderan *et al.*, 2013),
561 while others have postulated that spectral banding cannot be diagnostic of species (Wahlberg *et al.*, 2011). While an in-depth analysis

562 of this debate is outside of the scope of this study, careful consideration is prudent to understand the validity of the categorization
563 analysis presented here. Currently two hypotheses exist regarding how frequency banding might be produced. Wahlberg et al. (2011)
564 and Rasmussen et al. (2004) measured on-axis clicks from free-ranging bottlenose and white sided dolphins, respectively. Both studies
565 fitted a baffled piston model to the received clicks, and Wahlberg et al. (2011) suggested that the banding found in other species was
566 attributed to the off-axis banding effects dictated by the piston aperture size. However, these studies primarily analyzed clicks from
567 on-axis angles and may therefore have missed the filter effects caused by the cranial anatomy. If this is the case then it does not
568 preclude the independent documentation of stable spectral peaks and notches in the spectra of clicks recorded off-axis from a number
569 of species with similar cranial morphology (Soldevilla *et al.*, 2008; Au *et al.*, 2012b).

570 The off-axis spectral characteristics of echolocation clicks have been measured for bottlenose dolphins. Au *et al.* (2012b)
571 measured the entire biosonar field around captive bottlenose dolphins and found that, off-axis, echolocation clicks degraded into
572 discrete pulses most likely produced by the phonic lips and internal reflections from within the animal's head (Au et al., 2012b).
573 Multiple pulses, when processed with an FFT or DFT algorithm, result in "ripples" in the spectrum consistent with the peaks and
574 notches described by Soldevilla *et al.* (2008). However, as with sperm whales, the inter-pulse-interval in bottlenose dolphin
575 echolocation clicks is highly sensitive to the off-axis angle (Goold, 1996). Therefore, when energy is averaged across multiple clicks
576 collected from a variety of angles relative to the animal, the peaks and notches in spectral energy from this species become less
577 distinct.

578 Unfortunately, detailed studies of off-axis clicks from “frequency banded” species including Risso’s, white-beaked and white-
579 sided dolphins are lacking. However, it is possible that differences in cranial morphology between the species groups could account
580 for differences in the stability of spectral peaks and notches. For example, assuming the multi-pulse model of echolocation click
581 propagation, more uniform path lengths between the phonic lips and melon for frequency banded species would result in consistent
582 inter-pulse-intervals. This would subsequently lead to less variation in the spectral location in peak and notch energy for off-axis
583 clicks in these species. Additional studies are needed to determine whether or not this is the case.

584 Assuming the presence of stable spectral peaks and notches is diagnostic of species group, on-axis clicks will necessarily confound
585 our ability to discriminate between broadband and frequency banded click trains in both the SM2M recordings and the C-POD
586 encounter categorization model (Au *et al.*, 1974; Au *et al.*, 1999; Rasmussen and Miller, 2002; Rasmussen *et al.*, 2004; Wahlberg *et*
587 *al.*, 2011; Au *et al.*, 2012a). Moreover, if a disproportionately large selection of on-axis click trains were included in the training data,
588 this would add considerable noise to the final categorization task. We limited this outcome by restricting the selection of C-POD click
589 trains used to build the GAM to periods during which more than 500 high SNR click trains could be identified in the adjacent SM2M
590 recordings. This conservative selection criterion reduced the probability of creating a biased sample of clicks from any particular beam
591 angle and thereby increased our confidence in the accuracy of the categorization task.

592 Our categorization model included ICI as a predictor, yet it is known that odontocetes modify their inter-click-interval depending
593 on their behavioral state (Janik, 2000; Johnson *et al.*, 2006; Pirotta *et al.*, 2014b). This has the potential to introduce two confounding

594 factors into the analysis presented here. First, there is question of whether ICI can be used to discriminate between different species
595 (or groups) of dolphins. Additionally, there is the potential that the categorization task is describing behavior (e.g. foraging vs. travel)
596 rather than species group.

597 In addressing whether ICI can be used for species discrimination we note that the GAM model selected here used a tensor smooth
598 across all three click train features recorded by the C-POD. Thus, ICI itself did not predict the click-train category. Instead, prediction
599 was based on the relationship between median ICI, mean zero-crossing frequency and mean bandwidth. Accordingly, while ICI itself
600 has not been widely used to discriminate between species, Johnson *et al.* (2006) note that in Blainsville's beaked whales (*Mesoplodon*
601 *densirostris*) there is a species-specific relationship between ICI, peak frequency and bandwidth of the individual clicks. For this
602 species, as the animal approaches a prey target decreasing ICI's are linked with decreasing click durations and increasing click
603 bandwidths and peak frequencies. Thus, while inter click interval, bandwidth or peak frequency alone would be inadequate to
604 categorize echolocation clicks, the relationship between these variables may be sufficiently different in some species to allow for
605 categorization and/or classification.

606 Concerning whether our sample of echolocation clicks represented a biased distribution of clicking behaviors (e.g. primarily click
607 trains associated with foraging or travelling), we note that the training data were obtained from multiple times and locations
608 throughout the survey. Therefore, click trains associated with foraging, travelling and socializing activities should all be represented in
609 the training data for both echolocation click types (Pirota *et al.*, 2014b). *K*-fold cross validation involved subsetting trains from
610 multiple acoustic encounters. This methodology was necessary as very few acoustic encounters could be correlated with the adjacent

611 SM2M recordings (10 broadband and 17 frequency banded encounters; Table 1). This also meant we were forced to train and test our
612 model on the same data - with more verified acoustic encounters we could have better characterized in vs. out of sample model
613 performance, and this should still be the aim for future studies.

614 As with any acoustic classifier, ours is not immune to miscategorization. There are a number of ways in which future studies may
615 account for this misclassification error. First, the performance of this categorization system should be tailored to the research
616 objectives by modifying encounter thresholds based on cost functions derived from study objectives. For example, in this study a
617 single encounter threshold was set above and below which encounters were categorized as broadband or frequency banded. However,
618 studies for which there is a high cost to false negative detections may wish to take a more conservative approach. In such cases, the
619 likelihood categorization threshold (T_e) could be either decreased or excluded altogether; opting instead to include all click trains with
620 a GAM prediction score above a given threshold (T_p) in the final analysis. Alternatively, future studies may seek to incorporate
621 misclassification error directly into the analysis. Bayesian occupancy models, in particular, offer sufficient flexibility to allow for the
622 incorporation of correct and incorrect classification rates across all categories (Miller *et al.*, 2011).

623 Provided the above considerations are kept in mind, it would be worthwhile to investigate whether this categorization system
624 might perform comparably to C-POD detections collected from other habitats. Similar dolphin species compositions have been
625 observed in western Scotland (MacLeod *et al.*, 2005), Ireland (Robbins *et al.*, 2015), California (Soldevilla *et al.*, 2008), and in the
626 Mediterranean sea (Frantzis and Herzing, 2002). If the C-POD categorization system derived here performs comparably in other
627 habitats, it suggests a wider application of these GAM/likelihood methods may be possible.

628

629 VI. CONCLUSIONS

630 Our study indicates that it is possible to increase the taxonomic resolution of low-cost click loggers by using statistical methods to
631 discriminate between acoustically similar species groups. By comparing continuous recordings to logged C-POD detections we were
632 able to identify and discriminate between the broadband and frequency banded click trains produced by the two pairs of dolphin
633 species most commonly encountered in Eastern Scottish coastal waters.

634

635 VII. ACKNOWLEDGEMENTS

636 We are especially grateful to the deployment and recovery crews from Marine Scotland Science, Moray First Marine, and the crew of
637 the Northern Lighthouse Board vessel Polestar. Doug Gillespie provided extensive support throughout the analysis portion for which
638 we are much indebted. We are also grateful to Debbie Russell for her assistance in building and validating the GAM classification
639 model as well as Mick Wu, Ellen Garland and Ian Davies and two anonymous reviewers for their comments on the manuscript. LR
640 and KP were supported by Marine Scotland Science and the Marine Alliance for Science and Technology for Scotland (MASTS)
641 pooling initiative and their support is gratefully acknowledged. MASTS is funded by the Scottish Funding Council (grant reference
642 HR09011) and contributing institutions.

643 VIII. REFERENCES

- 644 Anderwald, P., and Evans, P. G. (2010). "Cetaceans of the East Grampian Region," <http://www.abdn.ac.uk/marfish/SeaWatch/CetEG2010.pdf>.
645 Accessed: June, 12, 2017
- 646 Arso Civil, M. (2014). "PhD Thesis: Population ecology of bottlenose dolphins (*Tursiops truncatus*) of the East Coast of Scotland,"
647 <http://hdl.handle.net/10023/6543>. Accessed: June, 12, 2017
- 648 Au, W. W., Branstetter, B., Moore, P. W., and Finneran, J. J. (2012a). "The biosonar field around an Atlantic bottlenose dolphin (*Tursiops*
649 *truncatus*)," *The Journal of the Acoustical Society of America* **131**, 569-576.
- 650 Au, W. W., Branstetter, B., Moore, P. W., and Finneran, J. J. (2012b). "Dolphin biosonar signals measured at extreme off-axis angles: Insights to
651 sound propagation in the head," *The Journal of the Acoustical Society of America* **132**, 1199-1206.
- 652 Au, W. W., Carder, D. A., Penner, R. H., and Scronce, B. L. (1985). "Demonstration of adaptation in beluga whale echolocation signals," *The*
653 *Journal of the Acoustical Society of America* **77**, 726-730.
- 654 Au, W. W., Floyd, R. W., Penner, R. H., and Murchison, A. E. (1974). "Measurement of echolocation signals of the Atlantic bottlenose dolphin,
655 *Tursiops truncatus* Montagu, in open waters," *The Journal of the Acoustical Society of America* **56**, 1280-1290.
- 656 Au, W. W., Kastelein, R. A., Rippe, T., and Schooneman, N. M. (1999). "Transmission beam pattern and echolocation signals of a harbor porpoise
657 (*Phocoena phocoena*)," *The Journal of the Acoustical Society of America* **106**, 3699-3705.
- 658 Au, W. W., Pawloski, J. L., Nachtigall, P. E., Blonz, M., and Gisner, R. C. (1995). "Echolocation signals and transmission beam pattern of a false
659 killer whale (*Pseudorca crassidens*)," *The Journal of the Acoustical Society of America* **98**, 51-59.
- 660 Bailey, H., Clay, G., Coates, E. A., Lusseau, D., Senior, B., and Thompson, P. M. (2010). "Using T-PODs to assess variations in the occurrence of
661 coastal bottlenose dolphins and harbour porpoises," *Aquatic Conservation: Marine and Freshwater Ecosystems* **20**, 150-158.
- 662 Baumann-Pickering, S., McDonald, M. A., Simonis, A. E., Berga, A. S., Merckens, K. P., Oleson, E. M., Roch, M. A., Wiggins, S. M., Rankin, S., and
663 Yack, T. M. (2013). "Species-specific beaked whale echolocation signals," *The Journal of the Acoustical Society of America* **134**, 2293-
664 2301.
- 665 Baumann-Pickering, S., Wiggins, S. M., Hildebrand, J. A., Roch, M. A., and Schnitzler, H.-U. (2010). "Discriminating features of echolocation clicks
666 of melon-headed whales (*Peponocephala electra*), bottlenose dolphins (*Tursiops truncatus*), and Gray's spinner dolphins (*Stenella*
667 *longirostris longirostris*)," *The Journal of the Acoustical Society of America* **128**, 2212-2224.
- 668 Brookes, K. L., Bailey, H., and Thompson, P. M. (2013). "Predictions from harbor porpoise habitat association models are confirmed by long-term
669 passive acoustic monitoring," *The Journal of the Acoustical Society of America* **134**, 2523-2533.
- 670 Buckstaff, K. C. (2004). "Effects of watercraft noise on the acoustic behavior of bottlenose dolphins, *Tursiops truncatus*, in Sarasota Bay, Florida,"
671 *Marine Mammal science* **20**, 709-725.
- 672 Calderan, S., Wittich, A., Harries, O., Gordon, J., and Leaper, R. (2013). "White-beaked dolphin and Risso's dolphin click characteristics and the
673 potential for classification and species identification," *Scottish Natural Heritage Commissioned Report*
674 http://www.snh.org.uk/pdfs/publications/commissioned_reports/624.pdf Accessed: June, 12, 2017
- 675 Carlström, J. (2005). "Diel variation in echolocation behavior of wild harbor porpoises," *Marine Mammal Science* **21**, 1-12.

- 676 Carstensen, J., Henriksen, O., and Teilmann, J. (2006). "Impacts of offshore wind farm construction on harbour porpoises: acoustic monitoring of
677 echolocation activity using porpoise detectors (T-PODs)," *Marine Ecology Progress Series* **321**, 295-308.
- 678 Cheney, B., Corkrey, R., Durban, J. W., Grellier, K., Hammond, P. S., Islas-Villanueva, V., Janik, V. M., Lusseau, S. M., Parsons, K. M., and Quick, N.
679 J. (2014). "Long-term trends in the use of a protected area by small cetaceans in relation to changes in population status," *Global Ecology*
680 *and Conservation* **2**, 118-128.
- 681 Cheney, B., Thompson, P. M., Ingram, S. N., Hammond, P. S., Stevick, P. T., Durban, J. W., Culloch, R. M., Elwen, S. H., Mandleberg, L., and Janik,
682 V. M. (2013). "Integrating multiple data sources to assess the distribution and abundance of bottlenose dolphins *Tursiops truncatus* in
683 Scottish waters," *Mammal Review* **43**, 71-88.
- 684 Clark, C. W., Calupca, T., Gillespie, D., Von der Heydt, K., and Kemp, J. (2005). "A near-real-time acoustic detection and reporting system for
685 endangered species in critical habitats," *The Journal of the Acoustical Society of America* **117**, 2525-2525.
- 686 Dähne, M., Verfuß, U. K., Brandecker, A., Siebert, U., and Benke, H. (2013). "Methodology and results of calibration of tonal click detectors for
687 small odontocetes (C-PODs)" *The Journal of the Acoustical Society of America* **134**, 2514-2522.
- 688 Deecke, V. B., Ford, J. K., and Slater, P. J. (2005). "The vocal behaviour of mammal-eating killer whales: communicating with costly calls," *Animal*
689 *Behaviour* **69**, 395-405.
- 690 DeRuiter, S. L., Bahr, A., Blanchet, M.-A., Hansen, S. F., Kristensen, J. H., Madsen, P. T., Tyack, P. L., and Wahlberg, M. (2009). "Acoustic behaviour
691 of echolocating porpoises during prey capture," *Journal of Experimental Biology* **212**, 3100-3107.
- 692 Eskesen, I. G., Wahlberg, M., Simon, M., and Larsen, O. N. (2011). "Comparison of echolocation clicks from geographically sympatric killer whales
693 and long-finned pilot whales (L)," *The Journal of the Acoustical Society of America* **130**, 9-12.
- 694 Fenton, M. (1982). "Echolocation Calls and Patterns of Hunting and Habitat Use of Bats (Microchiroptera) from Chillagoe, North Queensland,"
695 *Australian Journal of Zoology* **30**, 417-425.
- 696 Frantzis, A., and Herzing, D. L. (2002). "Mixed-species associations of striped dolphins (*Stenella coeruleoalba*), short-beaked common dolphins
697 (*Delphinus delphis*), and Risso's dolphins (*Grampus griseus*) in the Gulf of Corinth (Greece, Mediterranean Sea)," *Aquatic Mammals* **28**,
698 188-197.
- 699 Gillespie, D., Mellinger, D. K., Gordon, J., McLaren, D., Redmond, P., McHugh, R., Trinder, P., Deng, X. Y., and Thode, A. (2009). "PAMGUARD:
700 Semiautomated, open source software for real-time acoustic detection and localization of cetaceans," *The Journal of the Acoustical*
701 *Society of America* **125**, 2547-2547.
- 702 Goold, J. C. (1996). "Signal processing techniques for acoustic measurement of sperm whale body lengths," *The Journal of the Acoustical Society*
703 *of America* **100**, 3431-3441.
- 704 Hammond, P., Berggren, P., Benke, H., Borchers, D., Collet, A., Heide-Jørgensen, M., Heimlich, S., Hiby, A., Leopold, M. F., and Øien, N. (2002).
705 "Abundance of harbour porpoise and other cetaceans in the North Sea and adjacent waters," *Journal of Applied Ecology* **39**, 361-376.
- 706 Hammond, P., and Thompson, P. (1991). "Minimum estimate of the number of bottlenose dolphins *Tursiops truncatus* in the Moray Firth, NE
707 Scotland," *Biological Conservation* **56**, 79-87.
- 708 Harris, D., Matias, L., Thomas, L., Harwood, J., and Geissler, W. H. (2013). "Applying distance sampling to fin whale calls recorded by single
709 seismic instruments in the northeast Atlantic," *The Journal of the Acoustical Society of America* **134**, 3522-3535.

710 Hastie, G., Wilson, B., and Thompson, P. (2006). "Diving deep in a foraging hotspot: acoustic insights into bottlenose dolphin dive depths and
711 feeding behaviour," *Marine Biology* **148**, 1181-1188.

712 Hastie, G. D., Wilson, B., Wilson, L., Parsons, K., and Thompson, P. (2004). "Functional mechanisms underlying cetacean distribution patterns:
713 hotspots for bottlenose dolphins are linked to foraging," *Marine Biology* **144**, 397-403.

714 Houser, D., Helweg, D., and Moore, P. (1999). "Classification of dolphin echolocation clicks by energy and frequency distributions," *The Journal of*
715 *the Acoustical Society of America* **106**, 1579-1585.

716 Janik, V. (2000). "Food-related bray calls in wild bottlenose dolphins (*Tursiops truncatus*)," *Proceedings of the Royal Society of London. Series B:*
717 *Biological Sciences* **267**, 923-927.

718 Jaramillo-Legorreta, A., and Rojas-Bracho, L. (2011). "Monitoring a small marine cetacean population using passive acoustic techniques: Vaquita,
719 a critically endangered species," *The Journal of the Acoustical Society of America* **130**, 2419-2419.

720 Jaramillo-Legorreta, A., Cardenas-Hinojosa, G., Nieto-Garcia, E., Rojas-Bracho, L., Ver Hoef, J., Moore, J., Tregenza, N., Barlow, J., Gerrodette, T.,
721 and Thomas, L. (2016). "Passive acoustic monitoring of the decline of Mexico's critically endangered vaquita," *Conservation Biology*.

722 Johnson, M., Madsen, P. T., Zimmer, W., De Soto, N. A., and Tyack, P. (2006). "Foraging Blainville's beaked whales (*Mesoplodon densirostris*)
723 produce distinct click types matched to different phases of echolocation," *Journal of Experimental Biology* **209**, 5038-5050.

724 Kalan, A. K., Mundry, R., Wagner, O. J., Heinicke, S., Boesch, C., and Kühl, H. S. (2015). "Towards the automated detection and occupancy
725 estimation of primates using passive acoustic monitoring," *Ecological Indicators* **54**, 217-226.

726 Klinck, H., Mellinger, D. K., Klinck, K., Bogue, N. M., Luby, J. C., Jump, W. A., Shilling, G. B., Litchendorf, T., Wood, A. S., and Schorr, G. S. (2012).
727 "Near-real-time acoustic monitoring of beaked whales and other cetaceans using a Seaglider™," *PloS one* **7**, e36128.

728 Kloepper, L. N., Linnenschmidt, M., Blowers, Z., Branstetter, B., Ralston, J., and Simmons, J. A. (2016). "Estimating colony sizes of emerging bats
729 using acoustic recordings," *Royal Society open science* **3**, 160022.

730 Koschinski, S., Diederichs, A., and Amundin, M. (2008). "Click train patterns of free-ranging harbour porpoises acquired using T-PODs may be
731 useful as indicators of their behaviour," *Journal of Cetacean Research and Management* **10**, 147-155.

732 Kyhn, L. A., Tougaard, J., Thomas, L., Duve, L. R., Stenback, J., Amundin, M., Desportes, G., and Teilmann, J. (2012). "From echolocation clicks to
733 animal density—Acoustic sampling of harbor porpoises with static dataloggers," *The Journal of the Acoustical Society of America* **131**,
734 550-560.

735 MacLeod, C. D., Bannon, S. M., Pierce, G. J., Schweder, C., Learmonth, J. A., Herman, J. S., and Reid, R. J. (2005). "Climate change and the
736 cetacean community of north-west Scotland," *Biological Conservation* **124**, 477-483.

737 Mellinger, D. K., Nieukirk, S. L., Matsumoto, H., Heimlich, S. L., Dziak, R. P., Haxel, J., Fowler, M., Meinig, C., and Miller, H. V. (2007). "Seasonal
738 occurrence of North Atlantic right whale (*Eubalaena glacialis*) vocalizations at two sites on the Scotian Shelf," *Marine Mammal Science*
739 **23**, 856-867.

740 Miller, D. A., Nichols, J. D., McClintock, B. T., Grant, E. H. C., Bailey, L. L., and Weir, L. A. (2011). "Improving occupancy estimation when two types
741 of observational error occur: non-detection and species misidentification," *Ecology* **92**, 1422-1428.

742 Nuuttila, H. K., Thomas, L., Hiddink, J. G., Meier, R., Turner, J. R., Bennell, J. D., Tregenza, N. J., and Evans, P. G. (2013). "Acoustic detection
743 probability of bottlenose dolphins, *Tursiops truncatus*, with static acoustic dataloggers in Cardigan Bay, Wales," *The Journal of the*
744 *Acoustical Society of America* **134**, 2596-2609.

745 Parks, S. E., Urazghildiiev, I., and Clark, C. W. (2009). "Variability in ambient noise levels and call parameters of North Atlantic right whales in
746 three habitat areas," *The Journal of the Acoustical Society of America* **125**, 1230-1239.

747 Pirotta, E., Brookes, K. L., Graham, I. M., and Thompson, P. M. (2014a). "Variation in harbour porpoise activity in response to seismic survey
748 noise," *Biology Letters* **10**, 20131090.

749 Pirotta, E., Harwood, J., Thompson, P. M., New, L., Cheney, B., Arso, M., Hammond, P. S., Donovan, C., and Lusseau, D. (2015). "Predicting the
750 effects of human developments on individual dolphins to understand potential long-term population consequences," *Proceedings of the*
751 *Royal Society of London. Series B: Biological Sciences* **282**, 2109-2115.

752 Pirotta, E., Thompson, P. M., Miller, P. I., Brookes, K. L., Cheney, B., Barton, T. R., Graham, I. M., and Lusseau, D. (2014b). "Scale-dependent
753 foraging ecology of a marine top predator modelled using passive acoustic data," *Functional ecology* **28**, 206-217.

754 Quick, N. J., Arso, M., Cheney, B., Valentina, I., Janik, V., Thompson, P., and Hammond, P. S. (2014). "The east coast of Scotland bottlenose
755 dolphin population: Improving understanding of ecology outside the Moray Firth SAC. ," in *UK Department of Energy and Climate*
756 *Change*.

757 R Core Team (2016). "R Foundation for Statistical Computing, Vienna, Austria," (R Foundation for Statistical Computing, Vienna, Austria).

758 Rasmussen, M. H., and Miller, L. A. (2002). "Whistles and clicks from white-beaked dolphins, *Lagenorhynchus albirostris*, recorded in Faxaflói
759 Bay, Iceland," *Aquatic Mammals* **28**, 78-89.

760 Rasmussen, M. H., Wahlberg, M., and Miller, L. A. (2004). "Estimated transmission beam pattern of clicks recorded from free-ranging white-
761 beaked dolphins (*Lagenorhynchus albirostris*)," *The Journal of the Acoustical Society of America* **116**, 1826-1831.

762 Robbins, J. R., Brandecker, A., Cronin, M., Jessopp, M., McAllen, R., and Culloch, R. (2015). "Handling dolphin detections from C-PODs, with the
763 development of acoustic parameters for verification and the exploration of species identification possibilities," *Bioacoustics*, 1-12.

764 Roberts, B. L., and Read, A. J. (2014). "Field assessment of C-POD performance in detecting echolocation click trains of bottlenose dolphins
765 (*Tursiops truncatus*)," *Marine Mammal Science* **31**, 169–190.

766 Roch, M. A., Klinck, H., Baumann-Pickering, S., Mellinger, D. K., Qui, S., Soldevilla, M. S., and Hildebrand, J. A. (2011). "Classification of
767 echolocation clicks from odontocetes in the Southern California Bight," *The Journal of the Acoustical Society of America* **129**, 467-475.

768 Roch, M. A., Soldevilla, M. S., Burtenshaw, J. C., Henderson, E. E., and Hildebrand, J. A. (2007). "Gaussian mixture model classification of
769 odontocetes in the Southern California Bight and the Gulf of California," *The Journal of the Acoustical Society of America* **121**, 1737-
770 1748.

771 Roch, M. A., Stinner-Sloan, J., Baumann-Pickering, S., and Wiggins, S. M. (2015). "Compensating for the effects of site and equipment variation
772 on delphinid species identification from their echolocation clicks," *The Journal of the Acoustical Society of America* **137**, 22-29.

773 Ross, H. M., and Wilson, B. (1996). "Violent interactions between bottlenose dolphins and harbour porpoises," *Proceedings of the Royal Society*
774 *of London B: Biological Sciences* **263**, 283-286.

775 Scheidat, M., Tougaard, J., Brasseur, S., Carstensen, J., van Polanen Petel, T., Teilmann, J., and Reijnders, P. (2011). "Harbour porpoises
776 (*Phocoena phocoena*) and wind farms: a case study in the Dutch North Sea," *Environmental Research Letters* **6**, 025102.

777 Simon, M., Nuuttila, H., Reyes-Zamudio, M. M., Ugarte, F., Verfub, U., and Evans, P. G. (2010). "Passive acoustic monitoring of bottlenose dolphin
778 and harbour porpoise, in Cardigan Bay, Wales, with implications for habitat use and partitioning," *Journal of the Marine Biological*
779 *Association of the United Kingdom* **90**, 1539-1545.

780 Soldevilla, M. S., Henderson, E. E., Campbell, G. S., Wiggins, S. M., Hildebrand, J. A., and Roch, M. A. (2008). "Classification of Risso's and Pacific
781 white-sided dolphins using spectral properties of echolocation clicks," *The Journal of the Acoustical Society of America* **124**, 609-624.

782 Thompson, P., Brookes, K. L., Cordes, L. S., Barton, T., Cheney, B., and Graham, I. M. (2013). "Assessing the Potential Impact of Oil and Gas
783 Exploration Operations on Cetaceans in the Moray Firth," Final Report for DECC, Scottish Government, COWRIE, and Oil & Gas UK
784 https://www.gov.uk/government/uploads/system/uploads/attachment_data/file/50021/mf-results2.pdf Accessed: Sep. 8, 2016

785 Thompson, P., Cheney, B., Ingram, S. N., Stevick, P. T., Wilson, B., and Hammond, P. S. (2011). "Distribution, abundance and population structure
786 of bottlenose dolphins in Scottish waters," in *Scottish Natural Heritage Commissioned Report No. 354*.
787 http://www.snh.org.uk/pdfs/publications/commissioned_reports/354.pdf Accessed: June 12, 2017.

788 Thompson, P. M., Brookes, K. L., and Cordes, L. S. (2014). "Integrating passive acoustic and visual data to model spatial patterns of occurrence in
789 coastal dolphins," *ASSESSING THE POTENTIAL IMPACT OF OIL AND GAS EXPLORATION OPERATIONS ON CETACEANS IN THE MORAY*
790 *FIRTH*, 11.

791 Tregenza, N. (2016). "Chelonia Limited Cetacean Monitoring Systems," http://www.chelonia.co.uk/cpod_downloads.htm Accessed: June 12,
792 2017

793 Van Parijs, S. M., Clark, C. W., Sousa-Lima, R. S., Parks, S. E., Rankin, S., Risch, D., and van Opzeeland, I. (2009). "Management and research
794 applications of real-time and archival passive acoustic sensors over varying temporal and spatial scales," *Marine Ecology Progress Series*
795 **395**, 21-36.

796 Wahlberg, M., Jensen, F. H., Soto, N. A., Beedholm, K., Bejder, L., Oliveira, C., Rasmussen, M., Simon, M., Villadsgaard, A., and Madsen, P. T.
797 (2011). "Source parameters of echolocation clicks from wild bottlenose dolphins (*Tursiops aduncus* and *Tursiops truncatus*)," *The Journal*
798 *of the Acoustical Society of America* **130**, 2263-2274.

799 Weir, C. R., Stockin, K. A., and Pierce, G. J. (2007). "Spatial and temporal trends in the distribution of harbour porpoises, white-beaked dolphins
800 and minke whales off Aberdeenshire (UK), north-western North Sea," *Journal of the Marine Biological Association of the United Kingdom*
801 **87**, 327-338.

802 Williamson, L. D., Brookes, K. L., Scott, B. E., Graham, I. M., Bradbury, G., Hammond, P. S., and Thompson, P. M. (2016). "Echolocation detections
803 and digital video surveys provide reliable estimates of the relative density of harbour porpoises," *Methods in Ecology and Evolution*.

804 Wilson, B., Benjamins, S., and Elliott, J. (2013). "Using drifting passive echolocation loggers to study harbour porpoises in tidal-stream habitats,"
805 *Endangered Species Research* **22**, 125-143.

806 Wilson, B., Reid, R. J., Grellier, K., Thompson, P. M., and Hammond, P. S. (2004). "Considering the temporal when managing the spatial: a
807 population range expansion impacts protected areas-based management for bottlenose dolphins," *Animal Conservation* **7**, 331-338.

- 808 Wilson, B., Thompson, P., and Hammond, P. (1997). "Habitat use by bottlenose dolphins: seasonal distribution and stratified movement patterns
809 in the Moray Firth, Scotland," *Journal of Applied Ecology*, 1365-1374.
- 810 Wood, S. (2006). *Generalized additive models: an introduction with R* (Chapman & Hall/CRC Taylor & Francis Group, Boca Raton, FL).162-167

811