

1 MARK RECAPTURE DISTANCE SAMPLING: USING ACOUSTICS TO ESTIMATE THE FRACTION OF
2 DOLPHINS MISSED BY OBSERVERS DURING SHIPBOARD LINE-TRANSECT SURVEYS

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20 recapture distance sampling, trackline detection probability, double observer methods,
21 abundance estimation, dolphins

22 ABSTRACT

23 Cetacean abundance estimation often relies on distance sampling methods using shipboard
24 visual line-transect surveys, which assumes that all animals on the trackline are detected and
25 that the detection of animals decreases with increasing distance from the trackline. Mark-
26 Recapture Distance Sampling (MRDS) typically employs a secondary visual observation team
27 and may be used to identify the fraction of animals detected on the trackline when it is
28 suspected that animals may have been missed. For species that are difficult to detect using
29 visual observation methods, such as deep-diving species or those with cryptic surfacing
30 behavior, this secondary team may be prone to the same limitations in detection as the primary
31 observation team and alternative modes of detection may improve estimates. Here we
32 examine the potential use of passive acoustic detection as a secondary platform for MRDS of
33 rough-toothed dolphins (*Steno bredanensis*) during a combined visual and acoustic shipboard
34 line-transect survey. The average trackline detection probability for rough-toothed dolphins
35 was less than one for both the trial configuration (average $p(0) = 0.45$ for the visual team) and
36 independent observer configuration (average $p(0) = 0.37$ for the visual, $p(0) = 0.77$ for the
37 acoustic and $p(0) = 0.84$ for both teams combined). This study, while limited in scope, strongly
38 suggests that passive acoustic methods may be an effective alternative for estimating $p(0)$ for
39 cetaceans.

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43 1. INTRODUCTION

44 Cetacean abundance estimation typically relies on shipboard line-transect surveys using visual
45 detections. Here, a ship travels along predefined tracklines and the visual observers record the
46 species identification, number of animals in the group, and the distances at which the group
47 was detected. For line-transect sampling, it is frequently assumed that *all* animals on the
48 trackline are detected and the probability of detecting a group of animals, $g(x)$, decreases with
49 distance x from the transect line. Detection of animals on the trackline is often referred to
50 as $g(0)$, however, to avoid confusion we follow the convention suggested by Laake and
51 Borchers (2004) and refer to it as $p(0)$. Mark-Recapture Distance Sampling (MRDS - Borchers
52 et al. 1998) is an alternative to traditional line-transect methods that allows estimation of
53 trackline detection probability, $p(0)$, and thus, does not rely on perfect detection on the
54 trackline. MRDS generally requires two independent or conditionally independent observation
55 platforms, where all covariates that affect detectability are included in the model. This
56 independence requires that, at a minimum, platforms do not cue each other (see below for
57 further criteria). For shipboard surveys, these are typically two visual platforms on the same
58 survey vessel (Borchers et al. 2006; Laake and Borchers 2004).

59 Visual detection of cetaceans may be adversely affected by variables such as weather or diving
60 behavior (Barlow et al. 2001). If this results in a failure to detect animals on the trackline, then
61 the assumption that $p(0) = 1$ will be violated, resulting in negatively biased abundance
62 estimates. There are two main biases that may lead to violation of this assumption: availability
63 bias and perception bias. Availability bias occurs when animals are missed because they are not
64 available for detection, a common problem with long-diving species. Perception bias occurs

65 when animals are available for detection but are missed for other reasons, such as cryptic
66 surfacing behavior, poor weather conditions, or observer fatigue.

67 Using independent observation platforms allows us to quantify these biases. However, it is
68 crucial that detections made from the two platforms are truly independent (Burt et al. 2014). If
69 both platforms are subject to the same limitations (as is often the case when using two visual
70 platforms on the same vessel), MRDS can only address some aspects of perception bias, such as
71 observer experience or fatigue. Perception bias due to behavior, weather conditions and
72 availability biases remain. Consideration of a second independent platform using an alternative
73 method of detection that does not have the same limitations as the primary platform may allow
74 for consideration of both perception and availability bias.

75 The use of passive acoustic monitoring (PAM) methods during shipboard cetacean surveys has
76 increased dramatically in recent years (vanParijs et al. 2009; Marques et al. 2013); however,
77 one role that has received little attention is its use as an independent platform to evaluate the
78 fraction of cetaceans missed during shipboard line-transect surveys. Passive acoustic detection
79 of cetaceans is not limited to calm sea states (Rankin et al. 2008b) and has proven a valuable
80 tool for detecting species with cryptic surface behavior (Rankin and Barlow 2005; Gerrodette et
81 al. 2011). Many long-diving species are acoustically active during their dives (Barlow and Taylor
82 2005; Barlow et al. 2013; Pérez et al. 2017), when they are not available for visual observation.
83 In these cases, passive acoustic methods may provide a more suitable independent detection
84 method for MRDS than a second team of visual observers because acoustic methods can also
85 detect submerged animals.

86 Here we present an example of how passive acoustic detections may be used to estimate the
87 fraction of dolphins missed by the visual observer team during line-transect surveys. To this
88 end, we used acoustic detections of rough-toothed dolphins (*Steno bredanensis*) to ‘mark’
89 detections and set up ‘trials’ for the visual observation team during a combined visual and
90 acoustic line-transect survey conducted in the eastern tropical Pacific (ETP). This species was
91 chosen for study because of their distinctive vocalizations that could be easily identified by an
92 experienced acoustician in real-time during the survey (Rankin et al. 2015). We analyzed these
93 detections using MRDS methods to estimate the number of groups missed by the visual team
94 within the strip width. The emphasis of this paper is on future research needs and method
95 development, rather than providing reliable results of $p(0)$ that can be used for population
96 estimates of rough-toothed dolphins.

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98 2. MATERIALS AND METHODS

99 2.1. Visual line transect data

100 The data were collected during the *Stenella* Abundance Research Line Transect and Ecosystem
101 cruise (STARLITE) conducted by the Southwest Fisheries Science Center (SWFSC) in 2007 on
102 board the NOAA Ship *McArthur II* (Archer et al. 2008). Visual observation followed standard
103 SWFSC protocol (Kinzey et al. 2000), using two visual observers on 25×150 ‘big eye’ binoculars
104 scanning forward of the vessel and one visual observer recording data and scanning the near
105 field with naked eye. When cetaceans were detected, observers obtained species identification
106 (to the lowest taxonomic level possible) and group size estimates. Standard SWFSC surveys are
107 conducted in “closing” mode, where the visual team usually suspends survey effort upon

108 sighting a cetacean group and the ship approaches the group for accurate group size estimates
109 and species identification. During STARLITE, the survey alternated between a day of closing
110 mode, followed by a day of “passing” mode along the same segment covered in the previous
111 day. In passing mode, search effort remained uninterrupted and sighting information (species
112 identification and group size estimates) was obtained from a distance. Sighting information was
113 relayed to the acoustics team, but the visual team was not aware of acoustic detections.

114 2.2. Acoustic line transect data

115 We towed a hydrophone array 300 m behind the ship during daylight hours on passing mode
116 days, which allowed for a direct comparison of visual and acoustic detection of cetaceans.
117 Hydrophones had internal pre-amplification and sensitivity from 1 kHz to 40 kHz (± 5 dB re 1
118 μ Pa at 1 m); a minimum of two hydrophones with 4 m separation provided localization
119 capabilities using time difference of arrival between the hydrophones. High-frequency
120 recordings were made on a computer hard disk (96 kS/sec) using a MOTU Traveler digital audio
121 interface with Raven software (Center for Conservation Bioacoustics 2011) on a desktop
122 computer.

123 The acoustician on watch monitored sounds in real-time aurally via headphones and visually
124 using a spectrographic display. ISHMAEL software (Mellinger 2001) was used for real-time
125 spectrographic monitoring and estimation of bearing angles to the sound source. Bearing
126 angles were plotted with a custom mapping program (Whaltrak) and the location of the sound
127 source was estimated by the convergence of successive bearing angles (Rankin et al. 2008a).
128 The vessel traveled in an imperfect straight line, and this, combined with the slight delay
129 between detecting and plotting a bearing angle would lead to variations in convergence on

130 either side of the vessel. Therefore, we calculated beam distance (distance at which the sound
131 source passed 90°) as the average perpendicular distance from the trackline to the left and
132 right localizations at the time the group passed the hydrophone array. For species that spend
133 limited time at depth, such as rough-toothed dolphins, this perpendicular distance is assumed
134 to equal the beam distance (slant angle = 0).

135 We identified visual and acoustic detections as matches (duplicate ID for MRDS) when visual
136 and acoustic detections of the same (or similar) species occurred in close proximity to each
137 other. Specifically, acoustic bearing angles and approximate distances as estimated from
138 acoustic detections must match those recorded by the visual team, ideally for multiple sighting
139 updates as well as when the animals passed the beam of the ship. In the case of potential
140 ambiguity, the acoustician would specifically request an updated location for a group to confirm
141 a match. For MRDS analyses, it is necessary to assign a single perpendicular distance to a group
142 of animals, regardless of which observer detected it. Due to potential animal movement and a
143 time delay between detections made by the visual and acoustic teams, perpendicular distances
144 for a given group differed between these two observer platforms. It is generally recommended
145 to use the perpendicular distance from the observer who first detected the group as it is
146 assumed that the animals will have had less of a chance to move in response to the observers
147 (in this case, the ship; Burt et al. 2014). For the same reason, we used the perpendicular
148 distances from the visual team when possible as these were obtained at the time of first
149 detection (perpendicular distances for acoustic detections were obtained when animals passed
150 the beam). Perpendicular distances were truncated at $w = 5$ km following recommendations by
151 Buckland et al. (2001).

152 An experienced acoustician (S. Rankin) made acoustic identification of rough-toothed dolphins
153 in the field. This species frequently produces stepped whistles, which feature several distinct
154 frequency jumps with no time gap (Rankin et al. 2015). The stepped whistles produced by
155 rough-toothed dolphins are unique in that the entire whistle and/or the individual components
156 are often downswept. The echolocation clicks and burst pulses of rough-toothed dolphins have
157 low-frequency energy (extending below 15 kHz) and are often produced in short repeated
158 ‘packets’. These characteristics are both common to rough-toothed dolphins and rare to other
159 species encountered in the study area. Detection of calls with these distinct features has been
160 found to be indicative of the presence of rough-toothed dolphins (Rankin et al. 2015).

161 2.3. Mark-recapture distance sampling

162 In the following we speak of ‘observers’, instead of ‘teams of observers’ or ‘observation
163 platforms’ for brevity. Laake and Borchers (2004) identified three observation configurations
164 for MRDS which each have two observers: independent, trial, and removal configuration. Each
165 configuration differs according to which observer sets up the trials for the other and which
166 observer may be cued by the other. For the independent observer configuration, two
167 observers, say observer 1 and observer 2, search independently of each other and their
168 detections serve as trials for the other. Here it is essential that neither observer cues the other.
169 For the trial configuration, only one of the observers (observer 2), who is usually looking further
170 ahead, sets up trials for observer 1. In this trial configuration, observer 2 may be cued by
171 observer 1, however, it is essential that observer 1 is not cued by observer 2. For the removal
172 configuration, observer 2 is aware of what observer 1 detects and detects objects missed by
173 observer 1 (here again, observer 1 must not be cued by observer 2).

174 Another concern for MRDS studies is the level of independence between the two observers
175 (Borchers et al. 2006; Buckland et al. 2009; Burt et al. 2014). Even if observers are not directly
176 cued by one another, there may be preferential detection of the 'most observable', which
177 effectively violates the assumption of independence. This unmodelled heterogeneity may
178 include body size (larger animals are easier to detect visually) or group size (larger group sizes
179 may be easier to detect by both visual and acoustic methods). Ideally, all variables that affect
180 the probability of detection would be included as covariates in the model; in reality, it may be
181 difficult to observe or record all sources of heterogeneity. A test to identify unmodelled
182 heterogeneity can be made by comparing the detection functions of the mark-recapture (MR)
183 model and the distance-sampling (DS) model; the shape of the detection function for these
184 models should be the same if the observers are independent (Burt et al. 2014). If the shape of
185 the models is similar, full independence may be considered. The more limiting point
186 independence can be used when there is potential dependence in detections (unmodelled
187 heterogeneity). For point independence we only assume that observers make independent
188 observations at distance zero. Here, we exploit the fact that the distribution of distances can
189 generally be assumed known for DS data, e.g. uniform for line transects, as long as the survey
190 followed a random design (Buckland et al. 2001). We can estimate the shape of the detection
191 function with only the DS model fitted to the observed distances, i.e. without using the MR data
192 (i.e. the trials) (Burt et al. 2014). However, the MR model is needed to estimate the detection
193 probabilities at distance zero (which the DS model assumes to be 1). See below for further
194 details.

195 For our study, we considered both the simpler trial configuration and the more complete
196 independent configuration. For each configuration, we tested for both full and point
197 independence between the visual and acoustic detections. The removal configuration assumes
198 equal detection probability for each observer and is inappropriate for most applications
199 considering acoustics as the secondary observer (Laake and Borchers 2004).

200 In the trial configuration, a trial consisted of a distinct group of rough-toothed dolphins
201 detected by the acoustics team (observer 2). If the visual observers (observer 1) also detected
202 the same group, the trial was a success, otherwise a failure. For the independent observer
203 configuration, detections by each team (visual and acoustic) set up trials for the other. In this
204 case, if detections were made by both teams they were considered successes (if not, they were
205 considered failures). Visual observations were independent of acoustic detections and acoustic
206 cues were unlikely to be biased by visual detection even though the acoustics team were
207 informed of sightings.

208 MRDS analyses were done in R (vs 3.4.4, R core team 2018) using the mrds package (vs 2.1.18,
209 Laake et al. 2018). Here, we must specify an MR model and, for point independence, a DS
210 model, describing the conditional and relative detection functions, respectively, as a function of
211 perpendicular distance y from the trackline. The MR model, $p(y)$, is a binomial generalized
212 linear model fitted to the trial data which specifies the form of the conditional detection
213 functions, i.e. the probability the group is seen by observer 1 given it was seen by observer 2, or
214 vice versa. The DS model is the relative detection function, $g(y)$, which is fitted to the distances
215 of all detected groups combined (the unique observations detected by either observer). The DS

216 model assumes $g(0) = 1$ and that groups are uniformly distributed with respect to the transect
217 line.

218 The detection function, $d(y)$, is equal to the MR model for full independence, such that $d(y) =$
219 $p(y)$, while for point independence it is a combination of the DS and MR models, $d(y) =$
220 $p(0)g(y)$. The average detection probability, P_a , within the search strip a , is estimated using
221 $P_a = \int_0^w d(y) dy/w$, where w is the truncation distance (i.e., the largest y included in the
222 analyses).

223 For the DS model, we tested the fit of hazard-rate and half-normal key functions with or
224 without covariates (Buckland et al. 2001). For either key function the scale parameter can be
225 expressed as a function of covariates to model heterogeneity in detection probabilities (e.g.
226 Marques et al. 2007).

227 We also tested Beaufort sea state both as a linear covariate and as a factor covariate in the DS
228 and MR models. As a linear covariate, we assumed a linear relationship on the link scale
229 between the response and the covariate and estimated one extra coefficient for the respective
230 model. To test as a factor covariate, we fitted the a separate coefficient for each Beaufort sea
231 state (where the coefficient for the lowest observed Beaufort sea state, 1, is absorbed in the
232 intercept) and estimated four extra parameters for the respective model (one each for Beaufort
233 sea states 2-5), allowing more flexibility in the relationship compared to the linear term.

234 Differences between observation platforms were tested under the independent observer
235 configuration by including *observer* as a covariate in the MR model (note that *observer* cannot

236 be included as a covariate in the DS model as each detected group is only included once in the
237 analyses, regardless of which observer detected it).

238 Model selection for a given configuration was done using minimum AIC (Akaike 1973), including
239 the level of independence (full or point), choice of key function and covariates for the MR and
240 DS models. The Δ AIC values were calculated as the AIC value of the respective model minus the
241 minimum AIC of all contending models; AIC weights were calculated using methods described in
242 Wagenmakers and Farrell (2004). AIC cannot be used for choosing the configuration (i.e.
243 independent observer, trial or removal) as the data included in the analyses differs between
244 them.

245

246 3. RESULTS

247 A total of 19 days of combined visual and acoustic effort were conducted in passing mode
248 during the 2007 STARLITE survey (Fig. 1). There were 46 detections of rough-toothed dolphins
249 using visual and acoustic detection methods. Visual observation included 18 groups, of which
250 four groups were detected exclusively using visual methods (these groups were not detected
251 using passive acoustics). Acoustic methods detected 42 groups, of which 28 were detected
252 exclusively using acoustic methods.

253 The frequency of detection decreased with increasing distance from the trackline for all
254 detections (Fig. 2a) and for the visual and acoustic observers (Fig. 2 b, c). For any given distance,
255 a higher proportion of groups were acoustic detections (Fig. 2b vs 2c) and the acoustics team
256 did not miss any of the visual detections at distances greater than 2 km (Fig. 2c).

257

258 3.1. Trial configuration

259 In the trial configuration, where acoustic detections set up trials for visual detections, the best
260 fitting model with the minimum AIC score considered point independence with a hazard-rate
261 detection function without covariates for the DS model and Beaufort fitted as a linear covariate
262 for the MR model (Table 1). An additional five models scored Δ AIC values < 2 . The three models
263 with full independence scored the highest AIC values out of the 15 models tested. According to
264 the best model, average trackline detection probability $p(0)$ across all Beaufort sea states was
265 0.45 (SE=0.16) for the visual team (Table 1).

266

267

268 Table 1. MRDS models under the trial configuration including Δ AIC values (calculated as the AIC – minimum AIC) and AIC weights
 269 (Wagenmakers and Farrell 2004), estimates and standard errors (SE) of the trackline detection probability ($p(0)$) and average
 270 detection probability (P_a) of the visual team within the covered area. Only models with Δ AIC < 2 are shown; results for all models
 271 provided in supplementary table S1. Note that $p(0)$ values are averaged across all Beaufort sea states and that models which did not
 272 converge are not listed here. Key to abbreviations: DS = distance sampling, MR = mark recapture, AIC = Akaike information criterion,
 273 SE = standard error, HR = hazard-rate, HN = half-normal, Bft = linear *Beaufort*, fac(Bft) = *Beaufort* fitted as factor.

Model	Level of independence	DS model		MR model	Δ AIC	AIC weight	$p(0)$ visual	SE	P_a	SE
		Key function	Covariates: distance+	Covariates: distance+						
PI.DS(HR).MR(Bft)	Point	HR	--	Bft	0.00	0.178	0.45	0.16	0.18	0.08
PI.DS(HN,Bft).MR(Bft)	Point	HN	Bft	Bft	0.34	0.150	0.49	0.16	0.19	0.07
PI.DS(HR,Bft).MR(Bft)	Point	HR	Bft	Bft	0.41	0.145	0.50	0.16	0.21	0.08
PI.DS(HN).MR(Bft)	Point	HN	--	Bft	0.85	0.116	0.45	0.16	0.19	0.07
PI.DS(HR).MR(fac(Bft))	Point	HR	--	fac(Bft)	1.28	0.094	0.52	0.17	0.21	0.09
PI.DS(HN,fac(Bft)).MR fac(Bft))	Point	HN	fac(Bft)	fac(Bft)	1.37	0.090	0.52	0.17	0.18	0.08

274

275 A comparison of the detection functions $d(y)$ and $p(y)$ revealed different shapes, suggesting
 276 there was additional unmodelled heterogeneity in the data (compare shape of solid black lines
 277 in Figure 3). This provided further evidence – besides the lower AIC values – that point
 278 independence was the appropriate level of independence.

279 The estimated trackline probability $p(0)$ for the detection of rough-toothed dolphins by the
 280 visual team was estimated for Beaufort sea states 1-5 (Table 2). The estimates of $p(0)$ ranged
 281 from 0.71 for Beaufort sea state 1 to 0.09 for Beaufort sea state 5. This study did not include
 282 detections during Beaufort sea state 0; hence, we note that the estimated trackline probability
 283 of 0.84 for Beaufort sea state 0 was predicted outside the observed range of values.

284

285 Table 2. Estimated trackline detection probability $p(0)$ under the trial configuration for the
 286 visual team of detecting groups of rough-toothed dolphins shown for individual Beaufort sea
 287 states. We note that estimates of $p(0)$ for Beaufort sea state 0 are predicted outside the range
 288 of observed values.

Beaufort	0	1	2	3	4	5
$p(0)$ visual	0.84	0.71	0.53	0.34	0.18	0.09

289

290 3.2. Independent observer configuration

291 The best model under the independent observer configuration included the hazard-rate key
 292 function without covariates for the DS model (assuming point independence) and linear
 293 *Beaufort* and *observer* as covariates for the MR model (Table 3). Two additional models scored
 294 Δ AIC values < 2 in comparison to the best model; these included fitting *observer* as a covariate
 295 for the MR model or linear *Beaufort* as a covariate in the DS model. We found that the hazard-

296 rate key function typically provided a better fit for any given covariate combination in the DS
297 model, and that fitting *Beaufort* as a linear term was preferred over the corresponding factor
298 term. Including *observer* in the MR model was always preferred over not including it, regardless
299 of other covariates in the MR model. According to the best model, average $p(0)$ estimates
300 across all Beaufort sea states for rough-toothed dolphins were 0.37 (SE=0.14) for visual teams,
301 0.77 (SE=0.15) for acoustic teams, and 0.84 (SE=0.14) for both teams combined. The average
302 detection probability \hat{P}_a within the covered area was 0.40 (SE=0.10) for both teams combined.

303 Table 3. MRDS models under the independent observer configuration, including Δ AIC values (calculated as the AIC – minimum AIC)
 304 and AIC weights (Wagenmakers and Farrell 2004), estimates and standard errors (SE) of the trackline detection probability ($p(0)$) for
 305 visual, acoustic and combined visual/acoustic, as well as average detection probability (P_a) within the covered area. Only models
 306 with Δ AIC < 2 are shown; results for all models provided in supplementary table S3. Note that $p(0)$ values are averaged across all
 307 Beaufort sea states and that models which did not converge are not listed here. Key to abbreviations: DS = distance sampling, MR =
 308 mark recapture, AIC = Akaike information criterion, SE = standard error, key = key function, HR = hazard-rate, HN = half-normal, Bft =
 309 linear *Beaufort*, obs = *observer*, fac(Bft) = *Beaufort* fitted as factor.

Model	Level of independence	DS model		MR model	Δ AIC	AIC weight	$p(0)$ visual	SE	$p(0)$ acoustic	SE	$p(0)$ combined	SE	P_a combined	SE
		Key	Covariates: distance +	Covariates: distance +										
PI.DS(HR).MR(Bft,obs)	Point	HR	--	Bft+obs	0.00	0.303	0.37	0.14	0.77	0.15	0.84	0.14	0.40	0.10
PI.DS(HR).MR(obs)	Point	HR	--	obs	1.26	0.162	0.41	0.13	0.83	0.10	0.90	0.08	0.43	0.08
PI.DS(HR,Bft).MR(Bft,obs)	Point	HR	Bft	Bft+obs	1.43	0.148	0.38	0.14	0.78	0.14	0.85	0.12	0.41	0.09

310

311 The best model for the independent observer configuration showed different shapes in the
 312 detection functions $d(y)$, which combines the DS and MR models, and $p(y)$, the MR model
 313 only (Fig. 4), again supporting the choice of a model with point independence.

314 As the best model in the independent observer configuration included both *Beaufort* and
 315 *observer* as covariates in the MR model, we were able to predict $p(0)$ values for each observer
 316 and Beaufort sea scale (Table 4). The best model predicted that $p(0)$ values were generally
 317 lower for the visual team compared to the acoustic team and declined with increasing sea
 318 state. Neither team had perfect detection on the trackline; however, combining both teams
 319 improved detection to 0.97 for Beaufort sea state 1 to 0.56 in Beaufort sea state 5. We note
 320 that this study did not include detections during Beaufort sea state 0; hence, the estimated
 321 trackline detection probability of 0.99 for both teams combined for Beaufort sea state 0 was
 322 predicted outside the observed range of values.

323

324 Table 4. Estimated trackline detection probability $p(0)$ under the independent observer
 325 configuration for visual, acoustic, and combined detection of groups of rough-toothed dolphins
 326 shown for individual Beaufort sea states. We note that estimates of $p(0)$ for Beaufort sea state
 327 0 are predicted outside the range of observed values.

Beaufort	0	1	2	3	4	5
visual	0.73	0.60	0.46	0.32	0.21	0.13
acoustic	0.95	0.91	0.85	0.77	0.64	0.50
combined	0.99	0.97	0.92	0.84	0.72	0.56

328

329

330 4. DISCUSSION

331 In our analyses, the best fitting model for both the independent observer and trial
332 configuration assumed point independence and used the hazard-rate detection function
333 (without covariates) for the DS model. For the trial configuration, the best model included
334 Beaufort as a linear covariate for the MR Model (Table 1); the best model for the independent
335 observer configuration included linear Beaufort and observer as covariates for the MR model
336 (Table 3). The average trackline detection probability for rough-toothed dolphins was less than
337 one for both the trial configuration (average $p(0) = 0.45$) and independent observer
338 configuration (average $p(0) = 0.37$ for the visual, $p(0) = 0.77$ for the acoustic and $p(0) = 0.84$ for
339 both teams combined). Furthermore, the trackline detection probability was found to decrease
340 with an increase in Beaufort sea state (Table 2, 4). This study is limited in scope and sample size,
341 and our intention was to explore the potential of these methods. While we do not represent
342 the final values as true, these are reasonable (see Barlow 2015) and add validation to the
343 methods considered.

344 For shipboard line transect cetacean surveys, estimating the fraction of animals missed by the
345 primary observation team ($1 - p(0)$), is critical to the accuracy of the overall abundance
346 estimate. This study suggests that passive acoustic methods may offer a strong alternative for
347 estimating $p(0)$ for cetaceans. We expect this to be especially true for species with small group
348 sizes and cryptic surfacing behavior, such as rough-toothed dolphins, or in regions where
349 inclement weather may affect sighting conditions. In order to apply these methods to
350 combined visual and acoustic shipboard surveys, a number of considerations must be made.

351 The first consideration is the type of MRDS configuration: independent observer, trial, or
352 removal configuration. The less desirable removal configuration is generally not appropriate as
353 the different detection probabilities of the visual and acoustic methods violate a fundamental
354 assumption (Laake and Borchers 2004). The preferred independent observer configuration
355 requires that the two observation platforms, in this case the visual and acoustic teams, work
356 independently of each other. In our study, the visual team was independent of the acoustic
357 team; however, the acoustic team was informed of visual observations. Given this one-way
358 independence in our protocol, the trial configuration was the most conservative approach, with
359 the fewest assumptions. Nonetheless, it could be argued that visual and acoustic methods have
360 fundamentally different cues that are not expected to be causally dependent on one another
361 and therefore acoustic detection of animals should not be improved when their presence is
362 identified using visual methods. Application of independent observer configuration allows
363 estimating $p(0)$ for visual and acoustic platforms as well as both platforms combined. Future
364 surveys may consider a protocol that ensures full independence of the platforms.

365 Next, we must identify the level of independence. Even when the platforms seem independent
366 on first inspection, the detection probabilities for the visual and acoustic platforms may be
367 correlated, which may lead to induced dependence. These correlated variables must be
368 considered in the detection probability model, otherwise they may lead to unmodelled
369 heterogeneity in detection probability and biased abundance estimates (Laake et al. 2011). If
370 unmodelled heterogeneity remains, then the assumption of full independence is not
371 appropriate and must be replaced with the weaker point independence assumption. We can
372 identify potential unmodelled heterogeneity by comparing the shapes of the MR and DS

373 models; the shapes of these models should be the same when no unmodelled heterogeneity
374 remains. In our study, the differences in the shapes of the MR and DS models suggest that
375 additional unmodelled heterogeneity remains and therefore the point independence model is
376 appropriate unless we can identify and include measures for all correlated variables into the
377 MR model.

378 While variables affecting the detection probability of visual observation platforms are well
379 studied, less is known about the variables affecting acoustic detection of cetaceans. One
380 variable that may explain our apparent unmodelled heterogeneity is group size. There is strong
381 evidence that the probability of visual detection increases with large group sizes (Barlow 1995).
382 Likewise, there is some evidence that small dolphin schools may be less vocal, effectively
383 decreasing the probability of detecting them using acoustic methods (Rankin et al. 2008c). If
384 the detection probability for both observer platforms (here, visual and acoustic detection
385 methods) are affected by group size, then this variable should be included in the MR model.
386 Unfortunately, acoustic estimation of group size is a notoriously difficult endeavor and may be
387 impractical for groups detected using only acoustic methods. In fact, it may be unrealistic to
388 assume that all covariates will be identified and adequately addressed in the model. If
389 unmodelled heterogeneity is identified through the different shapes of the MR and DS models,
390 as is the case in our study, then the study should consider apply point independence.

391 Abundance estimation of dolphin species during cetacean surveys commonly assumes that all
392 animals on the trackline are observed, or that $g(0)= 1$ (see Barlow 2015). While this
393 assumption may hold for species found in large, conspicuous groups, it may be problematic
394 with species found in smaller group sizes, or those with cryptic surfacing behavior. Rough-

395 toothed dolphins exhibit both of these characteristics, and it has been suggested that the
396 abundance of rough-toothed dolphins may be underestimated using visual observation
397 methods (Rankin et al. 2008b; Barlow 2015). Gerrodette et al. (2008) found that the probability
398 of detection of rough-toothed dolphins should consider group size as a covariate. Likewise,
399 sightability is known to decrease with an increase in Beaufort sea state, especially for animals
400 with these same behavioral characteristics. Barlow (2015) developed models for estimating
401 trackline detection probabilities from distance sampling data without the mark-recapture
402 component and estimated that the fraction of rough-toothed dolphins sighted on the trackline
403 ranged from 0.5 in Beaufort 1 (excellent conditions) to 0.04 in Beaufort 5 (marginal conditions).
404 In his study, Barlow assumed perfect detection on the trackline in Beaufort sea state 0
405 conditions. While our results were similar for Beaufort sea states 1-5; we estimated $p(0)$ for
406 the visual team in Beaufort 0 to be 0.84 and 0.73 for trial and independent configurations,
407 respectively. Our results suggest imperfect trackline detection in Beaufort 0 conditions. If this is
408 indeed the case, then the trackline detection probabilities estimated by Barlow (2015), which
409 are already lower than our estimates, may in fact be overestimated for rough-toothed dolphins.
410 While these methods show great potential, there are complications related to passive acoustics
411 (in general) and towed array methods, in particular, that require consideration. Here we discuss
412 cross-platform availability bias, range estimation prior to vessel response, understanding
413 covariates related to acoustic detection, differences between passing and closing mode, and
414 complications related to acoustic species classification.

415 Availability bias is of particular concern when using a visual and acoustic observer for MRDS
416 methods. For many deep-diving species, they may be 'available' for acoustic detection while

417 submerged and unavailable for visual detection. Conversely, many of these species are silent
418 during their relatively short surface intervals, when they are available for visual detection. For
419 these situations, the trial configuration, where the acoustics team sets up trials for the visual
420 team, may be more appropriate than the independent observer configuration if acoustic
421 detection distance is sufficiently large to detect most animals at distance. An increased range of
422 availability by the acoustics team may help reduce correlation due to availability by separating
423 the time animals are first available for the acoustics and visual observation team (see Burt et al.
424 2014). While availability bias between visual and acoustic platforms is well documented for
425 beaked whales and sperm whales (Barlow and Taylor 2005, Marques et al. 2013), we do not
426 expect a cross-platform availability bias for most dolphin species (Rankin et al. 2008b).

427 A fundamental assumption of distance sampling is that animals are detected prior to any
428 responsive movement to the vessel; this typically requires detection of the group ahead of the
429 vessel. Towed hydrophone arrays are at a disadvantage for detecting and localizing cetaceans
430 directly ahead of the ship due to masking by propeller cavitation, physical interference caused
431 by the ships' hull, and problems inherent with towing hydrophones behind a vessel (Rankin et
432 al. 2008a). Limitations in localization within 30 degrees of the bow are related to the
433 localization methods; these could be mitigated through improved hardware design (e.g.,
434 volumetric arrays) and more sophisticated localization methods.

435 Due to the intrinsic differences in localizing detections using visual and acoustic methods, it is
436 important to identify potential responsive movement of the animals. Responsive movement
437 has potential to affect both the DS and MR models, muddying the effects of unmodelled
438 heterogeneity (Burt et al. 2014). The limited sample size of this study is insufficient for

439 identifying possible responsive movement; however, data pooled from additional SWFSC
440 surveys (Rankin et al. 2008b) suggest rough-toothed dolphins do not exhibit responsive
441 movement to these vessels in these geographic regions (Fig. 5). As visual distances were
442 measured on first detection (ahead of the ship) and acoustic distances were measured as the
443 group passed the beam, acoustic distances larger than visual distances would give an indication
444 of ship avoidance while acoustic distances smaller than visual would give an indication of ship
445 attraction. Consideration of acoustic data for MRDS should include a simple linear regression
446 where acoustic perpendicular distances are regressed against visual perpendicular distances to
447 identify potential responsive movement of animals (see Fig. 5 for details).

448 To prevent introducing biases in MRDS methods, it is important to include variables that affect
449 acoustic detection probability. The influence of covariates will likely vary by species, and to
450 date only piecemeal descriptions of the limitations to acoustic detection of cetaceans has been
451 examined (e. g., Rankin et al. 2008b). Future work should include examination of these
452 covariates for shipboard surveys using towed hydrophone arrays.

453 This study examined survey data collected in passing mode, which is atypical for surveys
454 conducted by SWFSC. For closing mode surveys (where visually detected cetacean schools are
455 approached for species identification and group size estimation), it may be possible for acoustic
456 detections of non-sighted groups to be used following the less desirable removal configuration
457 of MRDS if the detection probabilities of the visual and acoustic methods are equivalent (a
458 fundamental assumption for removal configuration). In this scenario, the 'first observer makes
459 detections of which the second observer is fully aware and the second observer detects
460 observations that are missed by the first observer' (Laake and Borchers 2004). Considering that

461 equal detection probability by these two methods is unlikely, there may be a need for
462 development of novel statistical methods to apply in these cases.

463 Consideration of acoustic methods in the MRDS framework requires reasonable acoustic
464 species classification. In this exercise, we assume that all acoustic detections were accurate.
465 While this may be a simple task for some species, especially sperm whales, it is imperfect for
466 most species. While ongoing research is continually improving acoustic classification methods
467 (e.g, Rankin et al. 2017), analytical methods should include addressing errors in acoustic species
468 classification of detections.

469 Despite the limitations of this study, our results suggest that passive acoustic detection may
470 serve as an independent observer in MRDS studies to estimate $p(0)$ for shipboard cetacean
471 line-transect surveys. In fact, for some species it may be a preferred method to estimate $p(0)$.
472 Studies that intend to apply these methods should take measures to insure full independence
473 of acoustic and visual teams, as the combined results may greatly improve the precision of
474 abundance estimates, especially for cryptic species such as rough-toothed dolphins. Realizing
475 this potential requires further examination of the covariates relevant to model acoustic
476 detections, improvement of acoustic localization and acoustic species identification, and
477 possibly implementing double-blind methods for mark-recapture where the acoustics team is
478 unaware of the visual detections and vice versa.

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599

600 FIGURE HEADINGS

601 **Figure 1** Map of STARLITE study area and tracklines, with detections of rough-toothed dolphins
602 by visual (red), acoustic (black), or both methods (green)

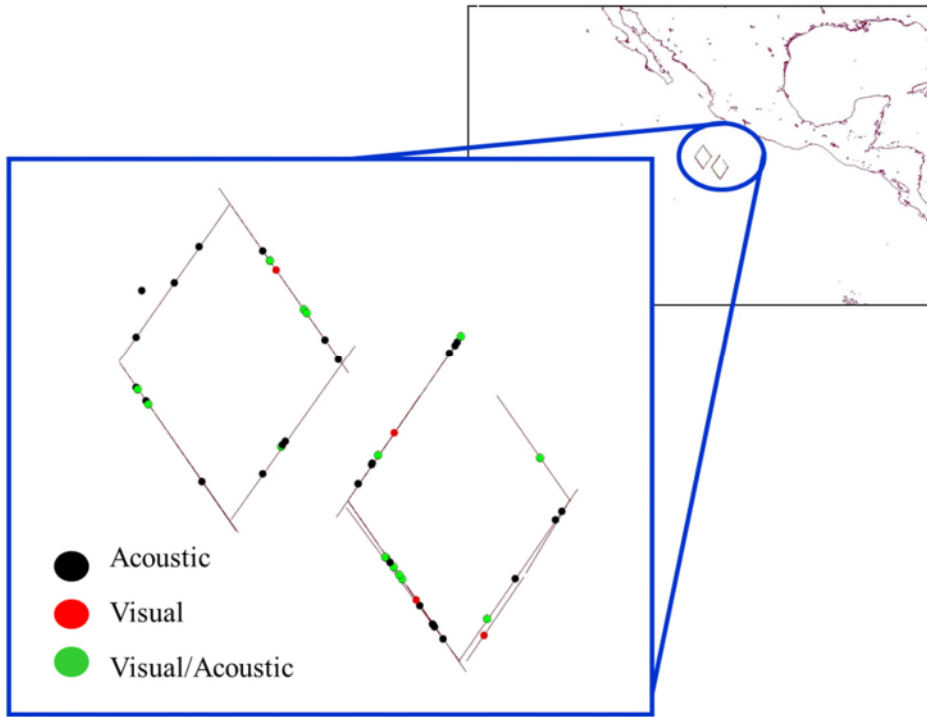
603 **Figure 2** Detection frequencies made by a) either platform (visual and/or acoustics), b) visual
604 (observer 1) conditional on detection by acoustics (observer 2), and c) acoustics conditional on
605 detection by visual

606 **Figure 3** Detection functions for best fitting model for the trial configuration (point
607 independence with the hazard-rate key function and no covariates besides distance for the DS
608 model and linear Beaufort as a covariate for the MR model). Left: solid line shows the average
609 detection function $d(y)$ across all Beaufort sea states and circles represent the detection
610 probabilities $d(y)$ for the individual detections. Right: solid line shows the average conditional
611 detection function $p(y)$ across all Beaufort sea states and circles represent the $p(y)$ for the
612 individual detections

613 **Figure 4** Detection functions for best fitting independent observer model (point independence
614 with a hazard-rate key function/no covariates for the DS model and linear Beaufort and
615 observer as covariates for the MR model). Top two rows: black lines are the detection function
616 $d_j(y) = p_j(0)g(y)$ averaged over all sea states scaled by the different $p_j(0)$ for the different
617 observers, i.e. (a) for visual only, (b) acoustic only, (c) both teams pooled and (d) duplicates
618 between teams; circles indicate the detection probabilities $d(y)$ for each observation,
619 histogram bars represent the relative frequencies of detections. Bottom row: black lines are the
620 conditional detection function $p(y)$ averaged over all sea states and circles indicate the
621 detection probabilities $p(y)$ for each observation, histogram bars represent the proportion of
622 all groups detected by observer 2 that were also detected by observer 1 (e) and vice versa (f)

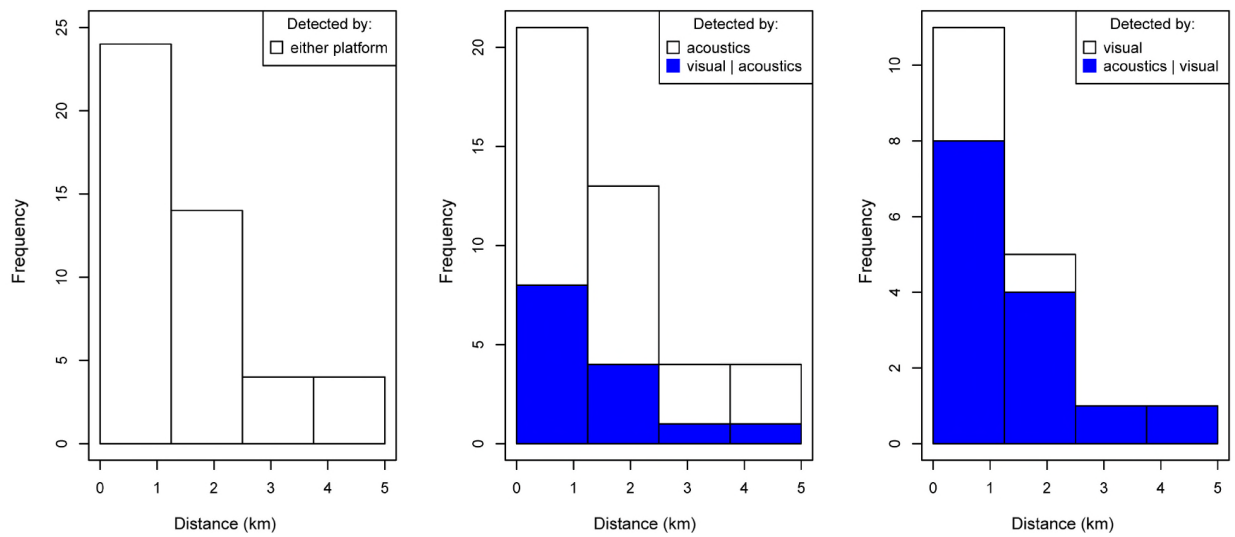
623 **Figure 5** Scatterplot of perpendicular trackline distance estimated using acoustic methods (x-
624 axis) and visual methods (y-axis) for combined visual/acoustic sightings of rough-toothed
625 dolphins during passing mode on SWFSC (truncated within 3 km of the vessel). The green line is
626 represents the best fit of a linear model to the data where acoustic perpendicular distances
627 were regressed against visual perpendicular distances; the black line identifies a potential 1:1
628 relationship. Points that fall below the black line represent potential vessel avoidance; points
629 that fall above the line represent potential vessel attraction

630



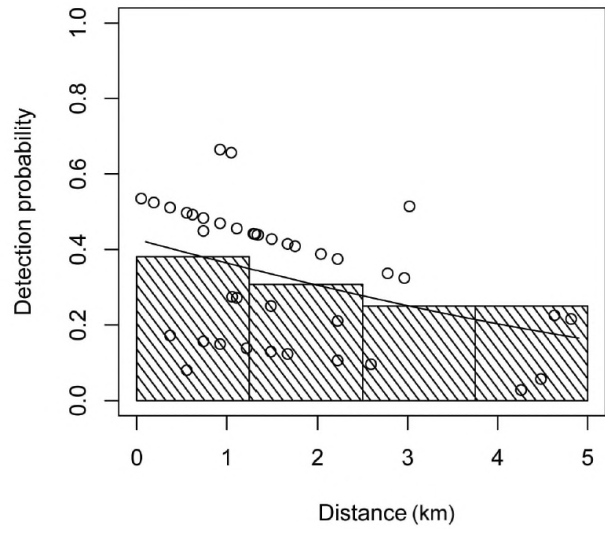
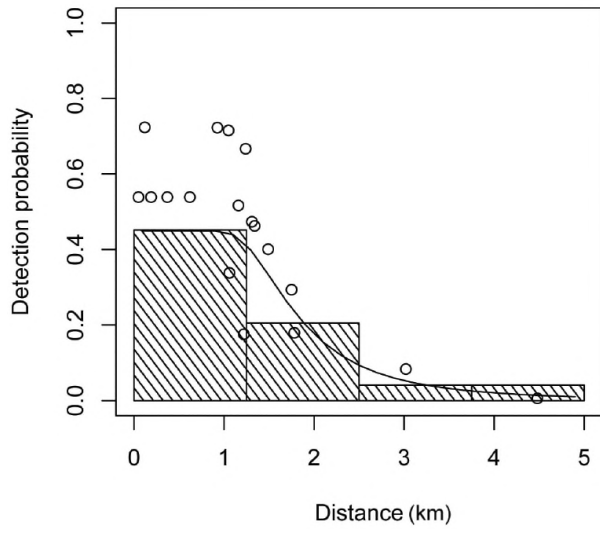
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633 **Figure 1**



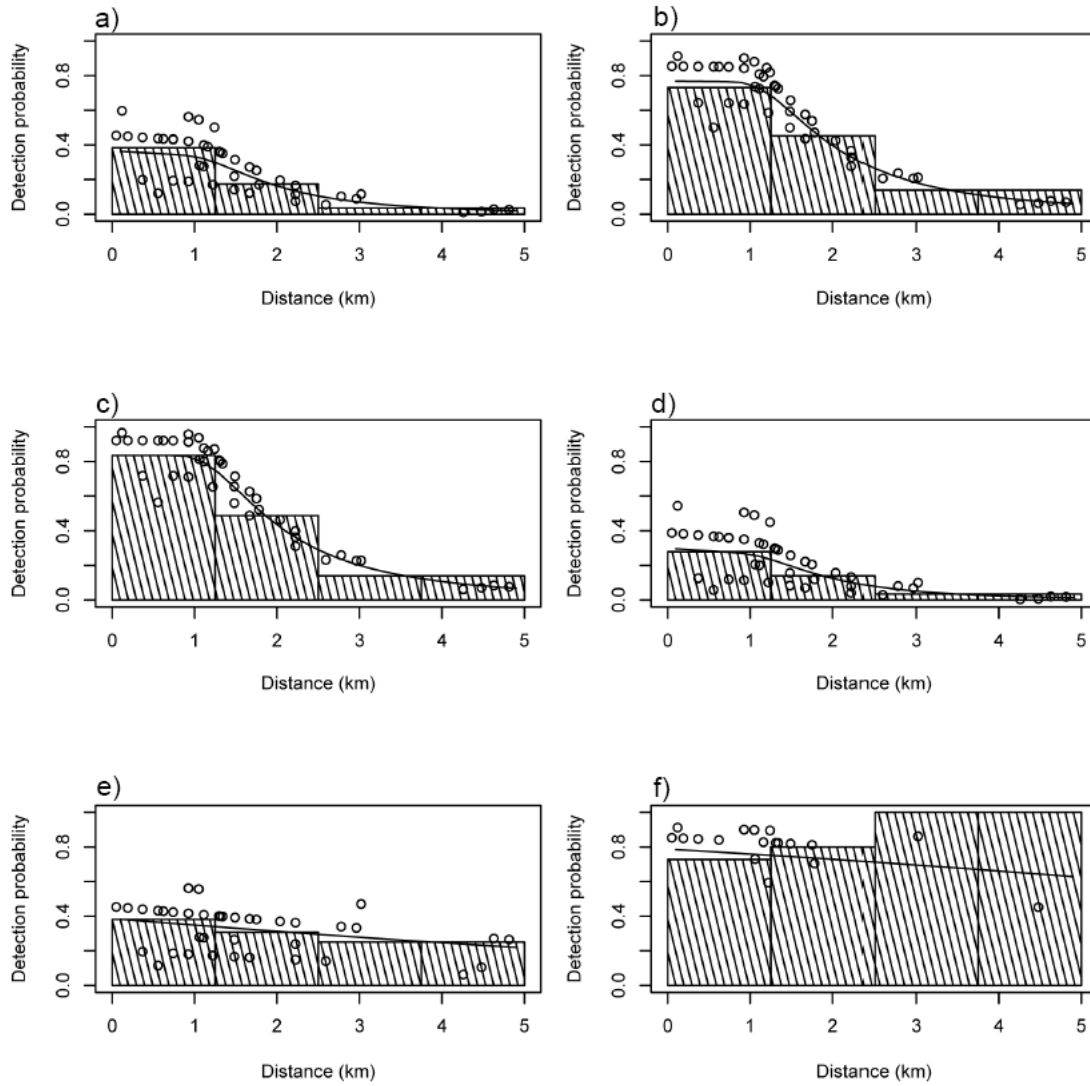
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635 **Figure 2**



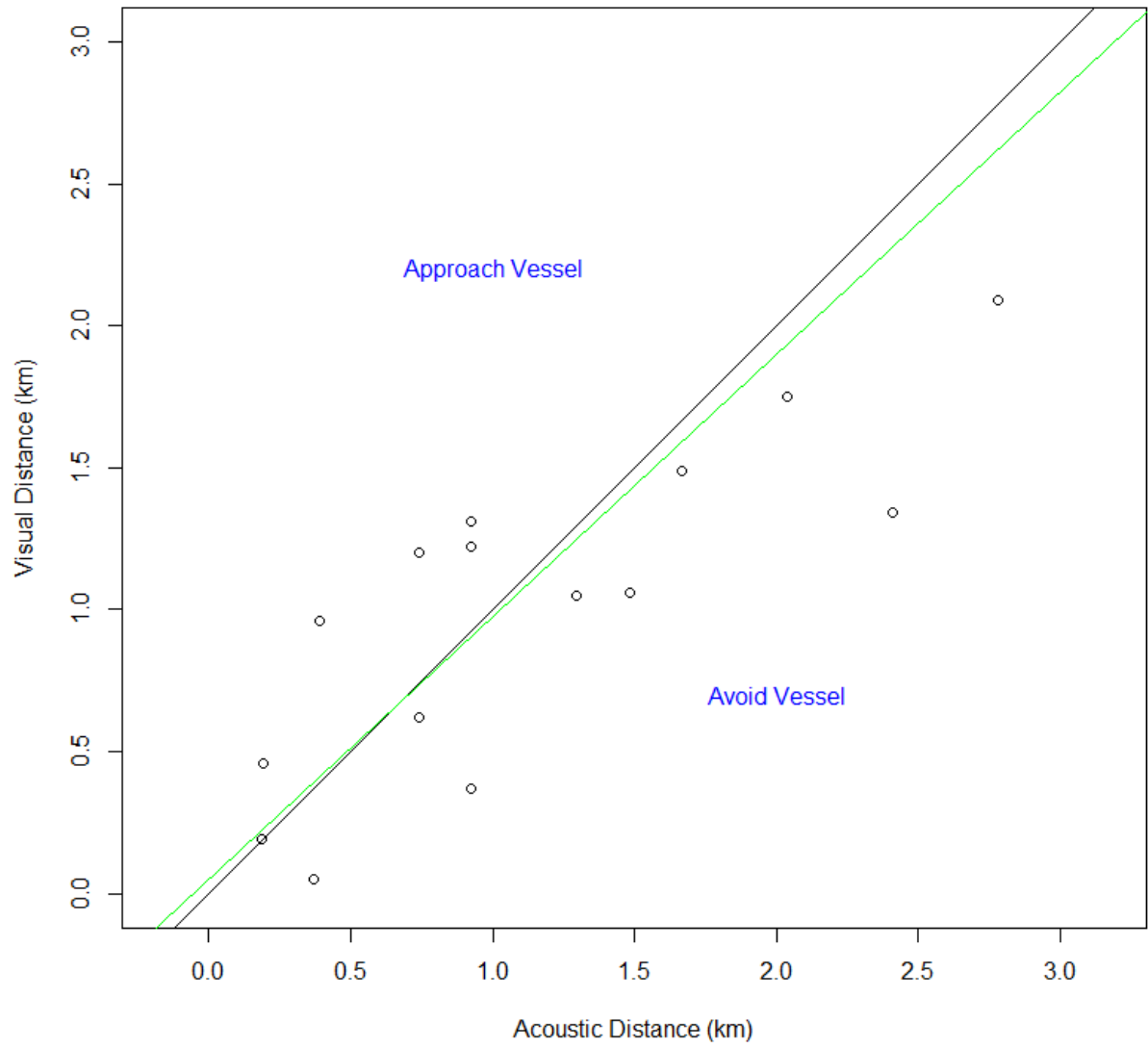
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637 **Figure 3**



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639 **Figure 4**



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641 **Figure 5**