

Seabird bycatch loss rate variability in pelagic longline fisheries

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1 Abstract:

2 The incidental mortality of seabirds from fisheries ranks as the greatest threat impacting
3 seabirds globally. However, its impact on seabird populations may have been
4 substantially underestimated due to lost, undetected bycatch. To estimate the full extent
5 of the bycatch problem, knowledge about the magnitude and variability of lost bycatch is
6 necessary. Based on a long-term dataset, this study aims to facilitate the loss-corrected
7 bycatch estimates for pelagic longline fisheries that do not have a concurrent bycatch loss
8 observation component. We analyze information from all types of fishery interactions of
9 seabirds to improve the estimate of bycatch loss rate and also reveal its variability.
10 Specifically, we analyze how environmental and ecological factors affect seabird bycatch
11 loss rate using Bayesian state-space models. Results show strong species effects in the
12 bycatch loss rate. Inclement weather and strong competition among seabird species also
13 affect bycatch loss rate. Estimates of the species-specific bycatch loss rate indicate that,
14 for some species, the loss can well exceed the average loss rate, suggesting that seabird
15 bycatch loss cannot be further ignored in assessing the fishery impact on seabird
16 populations. To gauge the full scale of seabird bycatch, it is critical to account for this
17 lost bycatch in bycatch assessments, at minimum, using an average loss rate with the
18 ultimate goal of species-specific loss-corrected assessments.

19 Keywords: Bayesian statistics; state-space models; bycatch assessment; cryptic bycatch

20

21 1 Introduction

22 The seabird bycatch problem in pelagic longline fisheries has been exposed for
23 only about three decades (Brothers 1991), and yet bycatch in fisheries ranks as the top
24 threat by impact to populations of albatrosses, large petrels/shearwaters and penguins
25 (Anderson et al. 2011; Croxall et al. 2012; Dias et al. 2019). The incidental mortality
26 from fisheries is currently recognized as a serious global concern (ACAP 2019a). It
27 threatens 17 of the 22 albatross species with extinction and puts an additional 7 petrel
28 species under elevated risk (ACAP 2019b; Anderson et al. 2011; IUCN 2019; Robertson
29 and Gales 1998).

30 Seabirds foraging near a longline fishing vessel are vulnerable to being
31 incidentally caught primarily during two windows of opportunity/risk, when the baited
32 hook is accessible to seabirds either in the line-setting stage or in the line-hauling stage
33 (Brothers et al. 2010). Many seabirds are surface-scavengers that take baits from hooks,
34 and this behavior makes them vulnerable to longline fishing operations (Camphuysen et
35 al. 1995). Those hooked or entangled at the setting stage are subject to loss during set,
36 soak and haul (Brothers et al. 2010). Almost all fishery observer protocols to date only
37 record bycatch at the haul, and consequently those caught at the setting stage that drop off
38 the gear before they can be observed, i.e., cryptic bycatch (Gilman et al. 2013), are not
39 included in the records. Due to this, the actual seabird bycatch in pelagic longline
40 fisheries could well exceed what is reported (Anderson et al. 2011; Brothers et al. 2010).
41 Cryptic seabird bycatch has also been documented in trawl fisheries, such as mortalities
42 from warp strikes (Maree et al. 2014; Sullivan et al. 2006; Watkins et al. 2008).

43 In order to recover the cryptic seabird bycatch in pelagic longline fisheries, it is
44 necessary to consider a much broader class of seabird-fishery interactions, which
45 themselves are observable and cover both the apparent and cryptic bycatch events (Figure
46 1). Seabird-fishery interactions can be classified into different types based on whether the
47 sequence of interactions leads to a bycatch event and the associated observation
48 uncertainty (Figure 2A) (Brothers et al. 2010). Based on the seabird interactions with the
49 highest certainty of getting caught or entangled by the fishing gear (observed caught type;
50 also type O in Figure 2A), more than 50% of the observed caught seabirds were not
51 retrieved at the haul (Brothers et al. 2010). Similar estimates of loss rate were also
52 reported in Brothers (1991); Gilman et al. (2007) and Gilman et al. (2003). For this type
53 of interaction (observed caught type), observation uncertainty, i.e., mistakenly classifying
54 an interaction of an uncaught seabird into a caught category, is relatively low and can be
55 ignored to a first approximation. However, only a small fraction of all recorded
56 interactions qualifies as this type, e.g., less than 2.9% of all interactions were classified as
57 observed caught (Brothers et al. 2010), with the majority of interactions unutilized in the
58 estimation of loss rate, thus substantially limiting the inferential power of the analysis.

59 Pooling information from all recorded interactions has the potential to improve
60 the estimate of bycatch loss rate and also reveal its variability. A recent study based on
61 the same set of observation records as in Brothers et al. (2010) but making use of all
62 interaction types estimates the average bycatch loss rate at 29.8% with a 95% credible
63 interval of [0.24%, 51.88%] (Zhou et al. 2019a). The estimate is consistent with two
64 regional bycatch loss rate estimates: 27% for the Japanese longline tuna vessels operating
65 in the region of Tasmania, Australia (Brothers 1991) and 28% for the Hawaii longline

66 tuna and swordfish fisheries (Gilman et al. 2003; Gilman et al. 2007). Regional
67 differences in the percentages of observed seabirds caught during setting and
68 subsequently retrieved at the haul were noted in Brothers et al. (2010); however, it is
69 unclear whether regional differences contribute significantly to the variability of loss rate.

70 Since revelation of the bycatch loss problem at the global scale (Brothers et al.
71 2010), little has been done to try to estimate the lost portion of seabird bycatch in bycatch
72 assessments, with a few notable exceptions. In the assessment of seabird bycatch risk
73 from New Zealand commercial fisheries, a multiplier of 2.08 was used for all the
74 observed bycatches on pelagic longlines (Richard et al. 2017), taking into account the
75 sampling effect but still ignoring observation uncertainty. Such an approach is useful in
76 gauging the approximate scale of the total bycatch. The multiplier approach has also been
77 developed for trawl and demersal longline fisheries (Richard et al. 2017; Watkins et al.
78 2008). To avoid the problem of over-estimation, an integrated bycatch assessment model
79 built for the US Western North Atlantic pelagic longline fishery incorporates both
80 observation uncertainty in the bycatch loss process and bycatch origin (Zhou et al. 2019a).
81 By comparison with results from this integrated model, the corresponding loss-free
82 assessment model substantially under-estimated both total bycatch and the associated
83 uncertainty in that fishery. A loss-free assessment model is thus harmful both in
84 discounting the actual impact of bycatch and in making that false statement
85 overconfidently.

86 The aim of this study is to facilitate loss-corrected bycatch estimation based on
87 existing data for pelagic longline fisheries that do not have a concurrent bycatch loss
88 observation component (most qualify as such). The strategy is to extend models to test

89 variability of the bycatch loss rate among alternative factors and conditions to improve
90 our understanding of loss rate and the seabird bycatch process in longline fisheries. Using
91 Bayesian state-space models we analyze how environmental factors at the time of the
92 bait-taking interaction and ecological traits of seabirds affect bycatch loss rate.

93 2 Material and methods

94 2.1 Bait-taking attempts and outcome confirmation

95 The seabird bait-taking attempt and confirmation observations data in pelagic
96 longline fisheries was collected by XX from 11 fishing vessels. over a 15-year period,
97 from 1988 to 2003, in four geographical regions: Indian Ocean, Coral Sea, Southern
98 Ocean and Central Pacific. This data set contains a total of 5,969 observed seabird
99 interactions on a total of 726,626 baited hooks. The same data were previously presented
100 in Brothers et al. (2010).

101 The focal point of Brothers et al. (2010) was interacting seabirds, whereas, in this
102 study, the focus is instead on the baited hooks. A baited hook may be pursued by a single
103 individual or multiple individuals. When multiple individuals compete over the same
104 baited hook, the bait-taking attempt of each individual registers as a separate count of
105 interaction. While multiple bycatch incidences on the same hook are theoretically
106 possible, they have not been observed in the field, and in this study, we assume that a
107 baited hook may catch at most one individual. Due to this change of focus, the count of
108 different types of bait-taking attempts (Table 1) differs from that of Brothers et al. (2010).

109 The seabird interaction methodology was developed in 1988 by Brothers (1991).
110 Here, we present the methodology on a conceptual level and refer the reader to Gilman et

111 al. (2003) for a detailed description. The seabird interaction methodology involves two
112 linked observation components (Figure 2), one at the line setting stage and one at the
113 hauling stage. Time and other positional aids, such as the interaction location relative to
114 line surface floats distances, which provide time intervals, are used to link an observed
115 seabird interaction at the line setting stage to a retrieved carcass during the haul. In
116 contrast, a traditional observer protocol only involves observations at the hauling stage.

117 Multiple hooks are observed simultaneously and independently of each other; for
118 simplicity, the following description only pertains to the observations of a single baited
119 hook. At the line setting stage, a bait-taking attempt is classified into one of five types
120 based on whether the sequence of interactions that lead to a bycatch event and also the
121 classification uncertainty (Figure 2A). Indeterminate (I) will be assigned if an individual
122 is seen to successfully take the bait but circumstances do not allow further confirmations;
123 a possibly caught (P) individual is seen to successfully take the bait, display one of the
124 typical capture responses momentarily but circumstances do not allow the final
125 confirmation of the capture; an observed caught (O) individual displays clear evidence of
126 struggle and its inability to escape the line. I, P and O bait-taking attempts, in decreasing
127 uncertainty, eventually lead to a bycatch event. On the other hand, the attempt is
128 successful (S) if an individual was seen to successfully remove the bait from the hook
129 and not be caught in the process; it is unsuccessful (U) if the individual made no contact
130 with the fishing gear during the attempt. Multiple individuals may attempt to interact with
131 the same hook, and all attempts were recorded, but in this study, we are only concerned
132 with the last observed attempt. At the line hauling stage, a carcass is either retrieved from

133 the observed hook or not, and this result is recorded as the final confirmation of the
134 interaction (Figure 2B).

135 Note that all observations are based on behavioral responds of seabirds towards
136 baited hooks above the surface of the water, and underwater attacks cannot be observed
137 *directly*. However, each underwater attack attempt, i.e., the underwater dive pursuit, and
138 its outcome, e.g., successful or unsuccessful bait take when the bird that dived returns to
139 the surface, can be observed and accounted for in the model.

140 2.2 Probability model of the seabird bycatch and observation processes

141 To remove observation uncertainty from the estimation of bycatch loss rate and
142 also to pool information from different stages of bait-taking attempts (I, P and O) leading
143 to a bycatch event, a state-space probability model was developed. In this model, other
144 attempts and bycatch events are two hidden states, upon which two sets of observations
145 are made (Figure 2). The probability of classifying a bait-taking attempt (A) that does not
146 lead to a bycatch event as one of five types is

$$147 \text{Prob}(A=i) = \beta_i,$$

148 where $i \in \{O, P, I, S \text{ and } U\}$ with the constraint $\sum_i \beta_i = 1$, and similarly for an attempt

149 leading to a bycatch event, the classification probability is

$$150 \text{Prob}(A=i) = \gamma_i,$$

151 with the constraint $\sum_i \gamma_i = 1$. For a no-bycatch event, no carcass will be retrieved, and for

152 a bycatch event, a carcass will be retrieved with a probability of $1 - p_{loss}$. Non-

153 informative Dirichlet priors, i.e., Dirichlet (1,1,1,1,1), were used for both the vectors of
154 β_i s and γ_i s for $i \in \{O, P, I, S \text{ and } U\}$. It is assumed that the observations for different
155 hooks are independent and identically distributed.

156 2.3 Predictors of the loss rate

157 Two sets of predictors were tested for their performance to predict bycatch loss
158 rate in this study: 1) environmental factors and 2) ecological traits. Environmental factors
159 include physical conditions and also biological competition, and these factors were
160 recorded concurrently with the bait-taking observations; ecological traits of seabirds were
161 extracted from published literature.

162 For the environmental factors, three variables were analyzed, i.e., *reg*: the four
163 fishing regions where the interaction is taking place, *phy*: the physical oceanic condition
164 at the time of the bait-taking attempt and *cmp*: the risk score at the nearest bird abundance
165 count interval. Variable *phy* is the sum of the wind score and sea score at the time of the
166 bait-taking attempt. It measures the roughness of the oceanic condition. The wind score is
167 a combination of wind speed and wind direction with respect to the vessel to determine
168 the score with a range from 1 (calm) to 8 (rough), and the sea score is based on the
169 Douglas sea scale with a score of 2 denoting slight waves and 8 denoting very rough
170 conditions. Three levels of *phy* representing calm, intermediate and rough conditions
171 were used, i.e., $phy \leq 4$, $4 < phy \leq 8$, and $8 < phy$. Most of the observed interactions
172 occurred when the condition was calm, and the least interactions occurred when the
173 condition was rough. Variable *cmp* is the sum of the counts of seabirds by species around
174 the vessel weighted by their respective bycatch risk score. Spot counts of seabird

175 abundance around the vessel were recorded mostly at either 15- or 30-min intervals
176 throughout the duration of line sets. The weight for each observed seabird species ranges
177 from 0 to 10 based on their tendency to engage in bait-taking interactions, with 0
178 denoting species that do not interact with fishing operations and 10 denoting species most
179 adept at bait locating and recovery. Four levels of competition severity were used, i.e.,
180 $cmp \leq 200$, $200 < cmp \leq 400$, $400 < cmp \leq 600$, and $600 < cmp$. See supplementary
181 material for a detailed description of the bycatch risk score for each species.

182 For the ecological traits, three variables were analyzed, i.e., *spp*: the species
183 identity of the seabird making the final bait-taking attempt, *diver* and *scavenger*: the
184 primary feeding strategies of the species. While all seabirds are capable of taking baits
185 close to the surface, some species regularly dive to snatch items at some distance below
186 the surface and some species are regular scavengers. These different feeding strategies
187 may have incurred different forms of hooking and/or entanglement, which consequently
188 led to different loss rates.

189 2.4 Hypotheses

190 Eight hypotheses on the variability of the bycatch loss rate were tested (Table 2).
191 The null hypothesis (H0) assumes a constant loss rate ($p_{loss} = p_0$). Here, the domain of p_0
192 is on the interval $[0, 1]$, and we used the probit link function to transform the domain
193 from $[0, 1]$ into the entire real line, i.e., $probit(p_{loss}) = c$. The use of probit link simplifies
194 the choice of the non-informative prior for c , which is the standard normal because of the
195 probability integral transformation between variables c and p_{loss} . All the following
196 hypotheses were constructed by adding covariates (predictors) to $probit(p_{loss})$.

197 The first three hypotheses test for the effect of environmental factors on loss rate.
198 Hypothesis H1 tests for the effect of the fishing region on loss rate. In H1, the loss rate of
199 an interaction occurred in region i with a probit link of $probit(p_{loss}[i]) = reg_i$, where the
200 prior of region effect is the standard normal for each region i =Central Pacific, Coral Sea,
201 Indian Ocean and Southern Ocean. In addition, the physical oceanic condition and
202 competitive species circumstances at the time of the interaction may affect the form of
203 hooking and/or entanglement and subsequently affect the bycatch loss rate. H2 tests for
204 the effect of oceanic condition on the loss rate. In H2, the loss rate of an interaction with
205 physical condition phy_j at the time of the interaction and a probit link is modeled as
206 $probit(p_{loss}[j]) = phy_j$, where the prior of the effect of physical condition is the
207 standard normal for each condition j =calm, intermediate and rough. H3 tests for the effect
208 of the severity of competition on loss rate. In H3, the loss rate of an interaction with risk
209 level cmp_k at the time of interaction and a probit link is $probit(p_{loss}[k]) = cmp_k$, where
210 the prior of the risk level effect is the standard normal for each bycatch risk level.

211 The other four hypotheses test for the effects of ecological traits of seabirds on
212 loss rate. The species-specific hypothesis (H4) assumes that each species has a species-
213 specific loss rate. In H4, the loss rate of species l with a probit link is
214 $probit(p_{loss}[l]) = spp_l$, where the prior of the species effect spp_l is the standard normal
215 for each species. Next, the hierarchical species hypothesis (H5) postulates an average
216 bycatch loss rate among all species, from which the loss rate for each species deviates. In
217 H5, the loss rate of species m with a probit link is $probit(p_{loss}[m]) = c + spp_m$, where the
218 prior for the average effect is $c \sim Normal(0, v[1])$, the prior for the species effect is

219 $spp_m \sim Normal(0, v[2])$, and the prior for the variance components is $v \sim Dirichlet(1,1)$
 220 to ensure non-informativity on p_{loss} . H5 estimates both an average loss rate based on the
 221 entire data set and the species effect for each species without partitioning the data set. H5
 222 is a compromise between H0 and H4 in the sense that H0 assumes a constant loss rate
 223 across all bait-taking attempts and estimates the loss rate based on the entire data set,
 224 while H4 assumes a separate loss rate for each species and partitions the data according
 225 to species identity.

226 In the next two hypotheses, we try to decompose the species effect into
 227 components based on seabird ecological traits. Differences in primary feeding strategies
 228 among different species may affect loss rate. Specifically, we test whether regular divers
 229 and scavengers have a different loss rate than primarily surface feeding species. In H4e1,
 230 the loss rate of species n with a probit link is $probit(p_{loss}[n]) = diver(n)$, where $diver(n)$ is
 231 an indicator function of species n ,

$$232 \quad diver(n) = \begin{cases} 1, & \text{if species } n \text{ regularly dives for food} \\ 2, & \text{otherwise} \end{cases},$$

233 and in H4e2, the loss rate of species n with a probit link is

$$234 \quad probit(p_{loss}[n]) = scavenger(n), \text{ where } scavenger(n) \text{ is an indicator function of species } n,$$

$$235 \quad scavenger(n) = \begin{cases} 1, & \text{if species } n \text{ regularly scavenges for food} \\ 2, & \text{otherwise} \end{cases},$$

236 and the prior for each factor level is the standard normal for both hypotheses. Results
 237 show that none of the environmental factors improved model performance, and therefore,
 238 environmental factors were not included in H4e1 and H4e2.

239 2.5 Model fitting and selection

240 A Bayesian approach was used for parameter estimation. We used exclusively
241 non-informative priors for model coefficients. To simulate MCMC (Markov Chain
242 Monte Carlo) samples from the posterior distribution, we used JAGS 4.3 (Plummer 2003)
243 in the statistical program R 3.6.1 (R Development Core Team 2016).

244 Model performance was measured based on deviance information criterion (DIC,
245 (Plummer 2002)),

$$246 \quad DIC = \bar{D} + pD,$$

247 where deviance D is twice the negative log-likelihood, \bar{D} is the posterior mean of the
248 deviance, and pD is an estimate of the effective number of parameters in the model
249 based on the algorithm proposed by (Plummer 2002). The model with the minimum DIC
250 is the recommended model, and as a rule of thumb, a less than 2 difference in DIC
251 relative to the recommended model suggests substantial evidence for the model,
252 differences between 3 and 7 indicate that the model has considerably less support,
253 whereas a larger than 10 difference indicates that the model is very unlikely (Burnham
254 and Anderson 2003; Burnham et al. 2011).

255 3 Results

256 Species identity has a significant effect on the bycatch loss rate. Based on DIC,
257 the species-specific model H4 has the best performance in modeling bycatch loss rate
258 (Table 2). The selected model incorporates species identity as a fixed effect with a
259 reduction of 8.6 points with respect to the null model. Efforts to decompose the species

260 effect into ecological components were not successful. The species effect cannot be
261 explained by either the dive feeding behavior or the scavenging behavior, the
262 incorporation of which did not improve model fit against the null model. The inclusion of
263 the fishing region and physical oceanic conditions did not improve model fit against the
264 null model (Table 2). In addition, we did not find any effect of environmental factors on
265 bycatch loss rate.

266 Based on the null model H0, the posterior estimate of the average bycatch loss
267 rate peaks around 42.82% (Figure 3). The posterior estimate has a mean of 31.02% and a
268 95% credible interval [2.17%, 54.19%]. Compared to an earlier estimate of the average
269 bycatch loss rate on the same data set but based on the counts of bait-taking attempts in
270 three aggregate types (Zhou et al. 2019a), the posterior estimate in this study is more
271 concentrated around the region with the highest posterior density (Figure 3), suggesting
272 more information on the loss rate in the unaggregated form of the data. Both the mean
273 and interval estimates of the loss rate were slightly higher than the earlier estimate.

274 Based on the selected model (H4), species-specific bycatch loss rates were
275 estimated for 22 albatross, petrel and shearwater species (groups) encountered as bycatch
276 during the entire period of the experiment. The estimates of median and interquartile
277 range varied considerably among species (Figure 4). Among all 22 seabird species
278 (groups), grey petrel, great-winged petrel and white-chinned petrel were the top three
279 species (groups) with the highest median bycatch loss rate ($p_{loss} > 70\%$). Flesh-footed
280 shearwater, grey-headed albatross and northern royal albatross were among the bottom
281 three with the lowest median bycatch loss rate ($p_{loss} < 20\%$). Posterior estimates for

282 black petrel, Buller's petrel, Salvin's albatross, sooty albatross, soft-plumaged petrel and
283 wandering albatross did not differ much from the prior distribution due to the limited
284 number of observations available for these species. The species-specific bycatch loss rate
285 of these species is therefore inconclusive based on the available observations.

286 The median loss rate for a given fishing operation can well exceed 50% or more.
287 Although the posterior density of the average loss rate drops significantly in the range of
288 values larger than 50% (Figure 3), e.g., the posterior probability of $\bar{p}_{loss} > 60\%$ is less
289 than 0.001, the median loss rate for the top three species (groups) with the highest loss
290 rate exceeds 60%. The reason for this apparent contradiction is that the entire sample is
291 dominated by two species (groups), i.e., black-browed albatross and Laysan albatross,
292 which constitute 39% of all the recorded bait-taking attempts, and both species (groups)
293 have a similar median loss rate between 30% and 40% (Figure 4).

294 Stressful environmental conditions at the time of bait-taking interaction generally
295 result in a lower bycatch loss rate. Based on model H2, median estimates of the loss rate
296 under different physical conditions reveal that the loss rate is relatively stable at calm and
297 intermediate physical conditions but is actually lower when physical conditions are rough
298 (Figure 5). More competitive species situations also lead to slightly lower loss rates
299 according to the median estimate of loss rate at different levels of competition (Figure 6).

300 The dive feeding and scavenging behaviors failed to explain the majority of the
301 species effect on loss rate. Compared with the prior distribution (dotted line segments in
302 Figure 7) of the difference in loss rate between divers and non-divers, the posterior (solid
303 curve in Figure 7) only shifted slightly to the negative range, and on average, diving

304 species have a loss rate 7.26% lower in value than non-diving species. Similarly,
305 scavenging species on average have a loss rate 4.48% lower in value than non-scavenging
306 species (Figure 8).

307 4 Discussions and conclusion

308 Results from this study indicate that the loss component of seabird bycatch in
309 pelagic longline fisheries cannot be further ignored in assessing population impacts of
310 fishing on seabirds. The loss rate strongly depends on the species identity of the bycatch,
311 and for some species, species loss rate can well exceed average loss rate, which had a
312 medium value of 31.02% in this study and 50% in earlier studies (Anderson et al. 2011;
313 Brothers et al. 2010). Nevertheless, estimates based on average loss rate are an under-
314 estimate for some species. Notably, the posterior median loss rate of grey petrel is
315 77.84%. Species having a higher bycatch loss rate experience more impact from the
316 fishery than expected. Considering how little progress has been made to incorporate even
317 the average loss rate into seabird bycatch assessments, the first step forward would be to
318 recover lost bycatch using the average loss rate in order to gauge the approximate scale of
319 the total bycatch with the ultimate goal of species-specific loss-corrected assessments.

320 Estimated seabird species-specific bycatch loss rates provided here account for
321 fishery removals and are directly applicable to seabird conservation management. Efforts
322 to support bycatch loss observations are critically important given the high loss rate and
323 large variations among species found in this study. While the applicability of the study
324 results to data-deficient fisheries or regions remains open to question, use of indicative
325 information, such as the posterior average bycatch loss rate [see Zhou et al. (2019a) for

326 an example], is more appropriate from a seabird conservation perspective than to simply
327 ignore the fact of seabird bycatch losses entirely. This is increasingly important when
328 Potential Biological Removal methodology (Sharp et al. 2009) could be used to manage
329 fishery impacts and seabird populations.

330 It would be *wrong* to assume that, in general, the loss rate only rarely exceeds
331 54.19% (the upper boundary of the 95% credible interval of the average loss rate). By
332 itself, the average loss rate is misleading, and the only reason why it is presented here is
333 to accommodate data-poor scenarios where species identity of the bycatch is not available.
334 The estimated average bycatch loss rate is only *specific* to the experiment (Brothers et al.
335 2010), and in fact, it is the weighted average of all the seabird bycatches encountered
336 during the experiment. Thus, it does not represent the average bycatch loss rate in general.
337 Species identity plays a significant role in determining the actual average bycatch loss
338 rate for a particular fishery; whenever possible, the species-specific rates should be used
339 without making any unfounded assumptions on the sampling behavior. To incorporate the
340 bycatch loss process into assessment of the impact of bycatch on seabird populations, e.g.,
341 using the methods demonstrated in Zhou et al. (2019a), a species-specific approach is
342 recommended.

343 The primary forms of seabird bycatch are hooking in the bill/throat and
344 entanglement by the line (Brothers 1991). According to a recent study (Baker et al. 2019),
345 the retention rate is almost 100% for a hooked/entangled dead bird carcass. It is probable
346 that many birds caught that ultimately are lost successfully break loose while still alive.
347 Hooking and entanglement under stressful conditions may reduce successful escape
348 prospects. Even those that successfully escaped may have incurred injuries, e.g., a broken

349 lower bill, that can impact their long-term survival. Albatrosses have been observed that
350 have died on their nests from hook wounds (Weimerskirch and Jouventin 1987). Other
351 potential sources of hook wounds include discarded hooks in the offal and hooks
352 remaining on cut off branch lines attached to birds (Brothers 1995).

353 The loss of bycaught birds from fishing gear can be due to predation, currents and
354 other mechanical action during line soak and haul (Brothers et al. 2010; Gilman et al.
355 2003). Around one third of the seabird carcasses hauled aboard tuna fishing vessels in the
356 Australian Fishing Zone were damaged and partially eaten (Brothers et al. 1998; Gales et
357 al. 1999). Blue (*Prionace glauca*) and shortfin mako (*Isurus oxyrinchus*) sharks are
358 commonly caught as bycatch species on pelagic longlines (Gilman et al. 2008; Vega and
359 Licandeo 2009), and sharks in the vicinity, after the birds were hooked, including those
360 sharks later hooked themselves, may have caused removal of an entire seabird carcass
361 from a hook. In another study, , a large tear through the soft tissue in retrieved albatross
362 carcasses was often found in the region where the hook was lodged, suggesting that the
363 drag from currents might tear hooks free from the carcass (Trebilco et al. 2010). The
364 removal might also come from unobserved discarding of bycaught seabirds by the crew,
365 but it is not a factor in the current study due to the bycatch loss observations employed
366 (Brothers et al. 2010). Gales et al. (1998) found that the seabird catch rate in Tasmania
367 was 95% higher when accounting for the bycatch deliberately not hauled aboard due to
368 crew flicking or cutting the branch line along the side of the vessel.

369 The majority of the species effect remains unexplained. Some species, e.g., great-
370 winged petrel (Brothers et al. 2010), which is among the top three species with the
371 highest loss rate, are more skilled than others in successfully removing bait from hooks.

372 These species may be more likely to break free from otherwise fatal entanglement with
373 the fishing gear. Great-winged petrels, in particular, have a relatively small bill and gape,
374 which is likely to minimize their capture risk on the generally larger hook sizes in use by
375 pelagic longline vessels. Aggression and competition among individuals may be another
376 factor separating species according to successful outcomes and tendency to stay in place
377 once hooked. It has been observed that a seabird is capable of successfully removing bait
378 without being hooked or entangled in a relatively stress-free environment, e.g., when the
379 seabird is the only individual attempting to take the bait and the ocean is relatively calm.
380 When multiple individuals (possibly from multiple species) are competing for baits, a
381 higher number of individuals are caught (Brothers et al. 2010). Some species may
382 compete more aggressively for bait than others. In particular, northern royal albatross
383 often compete aggressively for baits already seized by other species (Brothers et al. 2010).
384 Such aggressive behavior may result in more secure capture circumstances and,
385 subsequently, relatively lower loss rate for this species (Figure 4).

386 This study did not find substantial evidence for divers having a different loss rate
387 from surface feeders and scavengers. Some proficient deep diving species are capable of
388 taking baits at even 200 m astern with an unweighted branchline (Keitt et al. 2000;
389 Weimerskirch and Cherel 1998), which is approaching the maximum reliable observation
390 distance across all sea state conditions under the current observation protocol, i.e., naked
391 eye with binocular assisted vision for more distant observations (Brothers et al. 2010). If
392 successful bait taking that can result in death was regularly occurring at depth beyond
393 observation distance, one would expect there to be a lot more inexplicable observed

394 bycatch, whereas the data contains few observed (carcasses hauled aboard) bycatch that
395 couldn't be ascribed to a particular interaction observation.

396 Geographically, the bait-taking observations in this study did not cover the West
397 Indian and Atlantic Ocean sectors, where the species composition of the bycatch is
398 substantially different from the regions covered in this study. Greater shearwater
399 (*Puffinus gravis*), northern gannet (*Morus bassanus*) and gulls (*Larus spp.*) dominate the
400 bycatch in the Western North Atlantic (Zhou et al. 2019b; Zhou et al. 2018), but none of
401 these species were bycaught in this study. Based on the strong species effect found in this
402 study, it is reasonable to suspect those bycatch species of the Atlantic may have a
403 different loss rate than explored here. It is therefore necessary to conduct a similar
404 experiment in the Atlantic (and elsewhere) to collect observations on seabird bait-taking
405 attempts in order to estimate the loss rate of additional species. Moreover, further
406 observations are needed for the seabird species (asterisked in Figure 4) that are already
407 covered in this study but with limited sample sizes.

408 The findings of the current study are consistent with previous studies on bycatch
409 loss rate (Baker et al. 2007; Brothers 1991; Brothers et al. 2010; Gilman et al. 2003;
410 Gilman et al. 2007; Zhou et al. 2019a), and the analysis of species-specific rates revealed
411 that the loss rate can reach as high as 70% for some species. An adequate bycatch
412 assessment should document the full impact of a fishery on seabird populations by trying
413 to recover the lost bycatch through the observation of both the set and haul. Continuing to
414 ignore bycatch loss in bycatch assessments may lead to eventual loss of biodiversity.

415 5 Acknowledgements

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534 longline fishery during 1992-2017 based on observer and logbook data. Virginia
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536

537 Tables and figures

538 *Table 1 Number of bait-taking interactions by the extent of confirmation of outcome and*
539 *whether or not carcass was retrieved*

Bait-taking attempts	Carcass retrieved	
	No	Yes
Observed caught	90	85
Possibly caught	65	14
Indeterminate	238	13
Successful	1152	2
Unsuccessful	1331	0

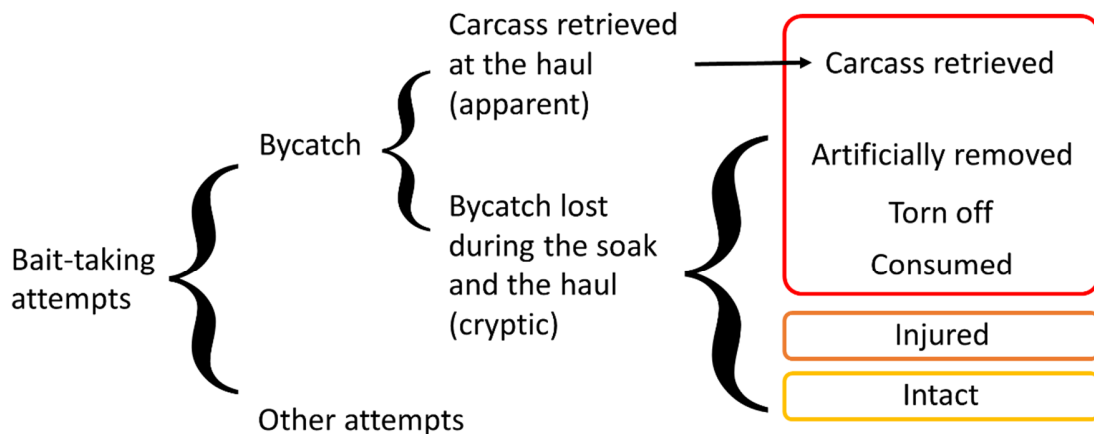
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541

542 *Table 2 Candidate models based on different hypothesis on the loss rate and the model*
 543 *selection results based on DIC. The selected model is marked in bold.*

Hypotheses	Covariates	Δ DIC
H0	-	8.6
H1	Fishing region	9.5
H2	Physical condition	8.9
H3	Bycatch risk score	11.1
H4	Species-specific effect	0
H5	Hierarchical species effect	2.5
H4e1	Diver or not	9.5
H4e2	Scavenger or not	10.1

544



545

Seabird-fishery interactions

Outcome

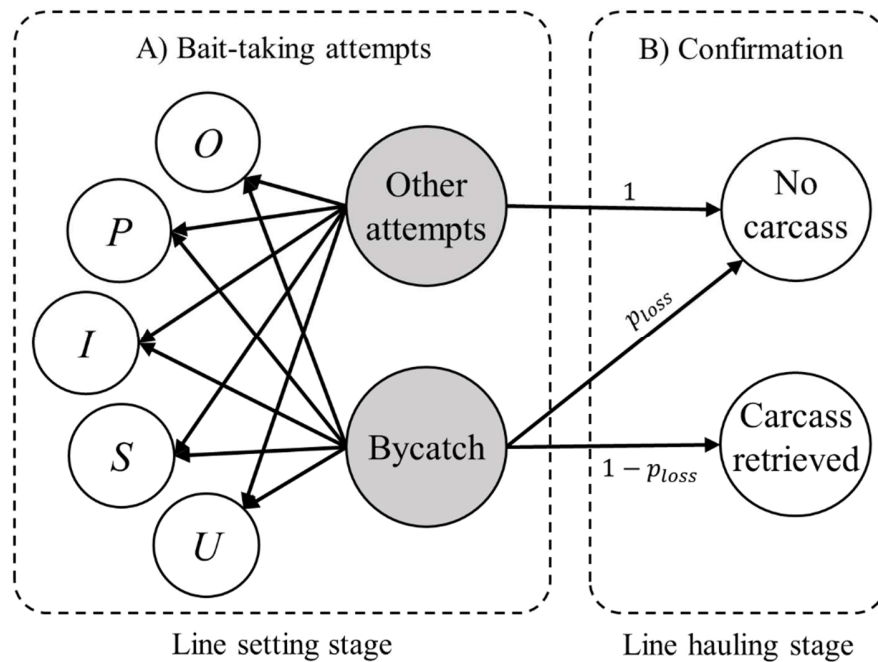
546 *Figure 1 Seabird-fishery interactions and the outcome of apparent and cryptic bycatch*
 547 *events in pelagic longline fisheries.*

548 *The outcome of the seabird-fishery interactions can be classified into three groups based*
 549 *on the severity of the impact. The high impact group (red) entails the immediate death of*
 550 *the seabird, and it includes carcasses retrieved, carcasses removed by cutting off the*
 551 *branch lines, those torn off the hook due to water pressure and those consumed whole by*
 552 *sharks or other predatory fish. The intermediate impact group (orange) and the low*
 553 *impact group (yellow) include those entangled seabirds that managed to escape with or*
 554 *without inflicting any injuries. Note that only the outcome of a retrieved carcass can be*
 555 *directly observed based on the existing observation protocol.*

556

557 [Production instructions: 1.5 or 2 columns; no color needed in print]

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559

560 *Figure 2 Observation of bait-taking interactions (A) at the line setting stage and outcome*
 561 *confirmation at the line hauling stage (B) with respect to a baited hook.*

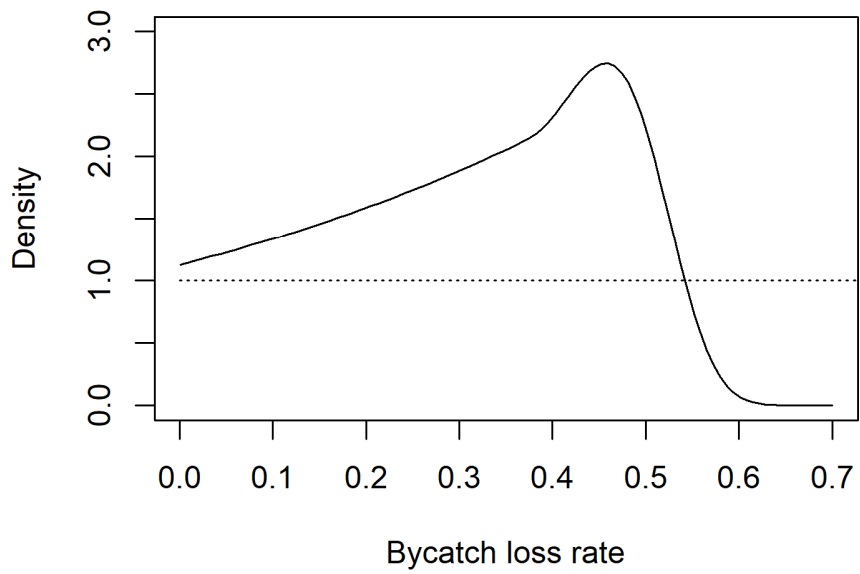
562 *There are two types of bait-taking attempts (Panel A), those leading to a bycatch (lower*
 563 *gray circle), either through hooking or entanglement, and other attempts (upper gray*
 564 *circle). An observer classifies the interactions into one of five types (white circles to the*
 565 *left), observed caught (O), possibly caught (P), indeterminate (I), successful (S) and*
 566 *unsuccessful (U).*

567 *Bycatch events (Panel A) have two possible outcomes at the line hauling stage (Panel B):*
 568 *Either the carcass is retrieved at the hauling stage (lower white circle) or the captured*
 569 *seabird may separate from the hook with probability p_{loss} and become unobservable to*
 570 *the observer at the hauling stage (upper white circle). All the other attempts (Panel A)*
 571 *lead to the event of no carcass retrieved (Panel B). The expressions on the arrows are the*
 572 *associated state transition probabilities.*

573

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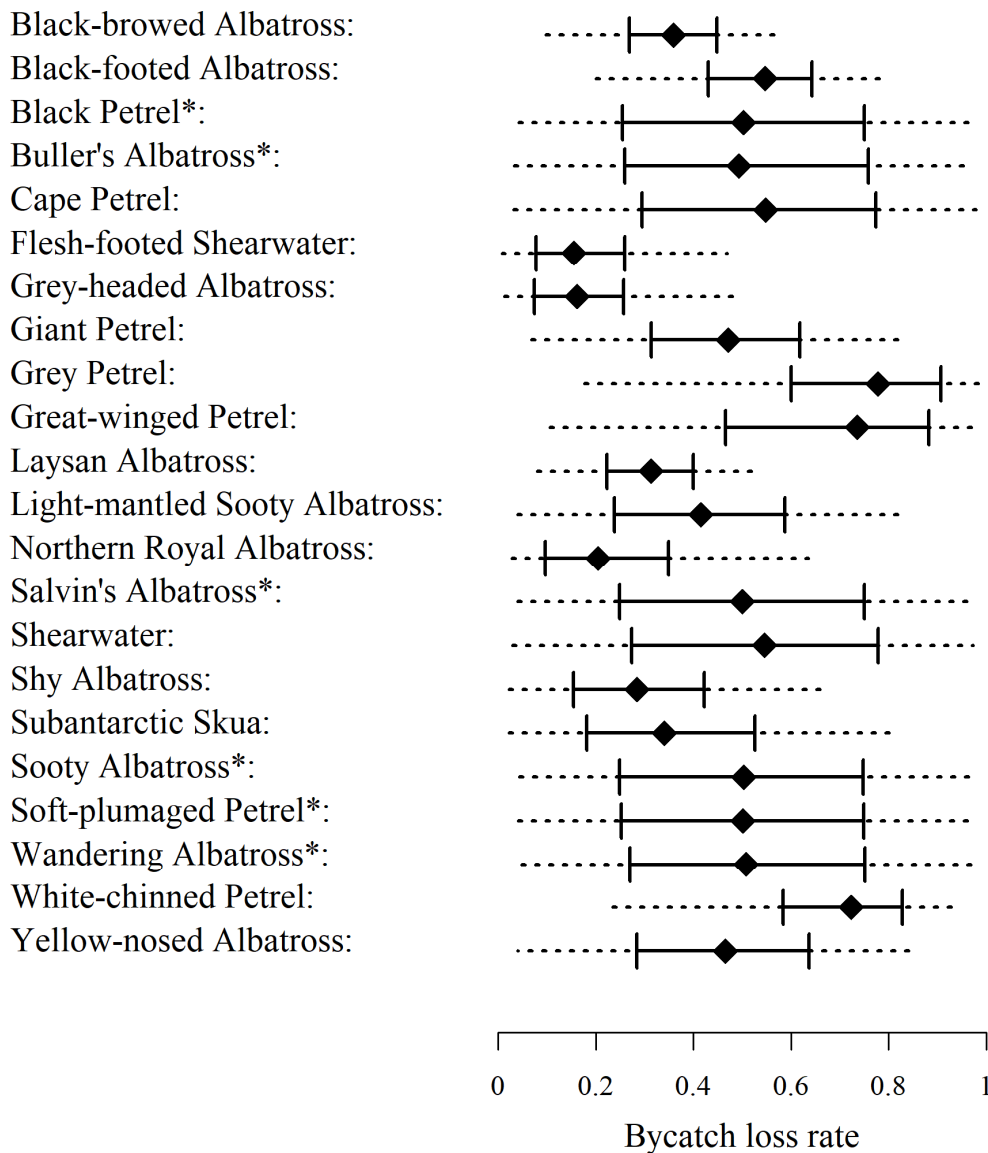
576

577 *Figure 3 Prior (dotted line) and posterior estimate (solid curve) of the average bycatch*
578 *loss rate based on model H0.*

579

580 [Production instructions: 1 or 1.5 columns; no color needed in print]

581

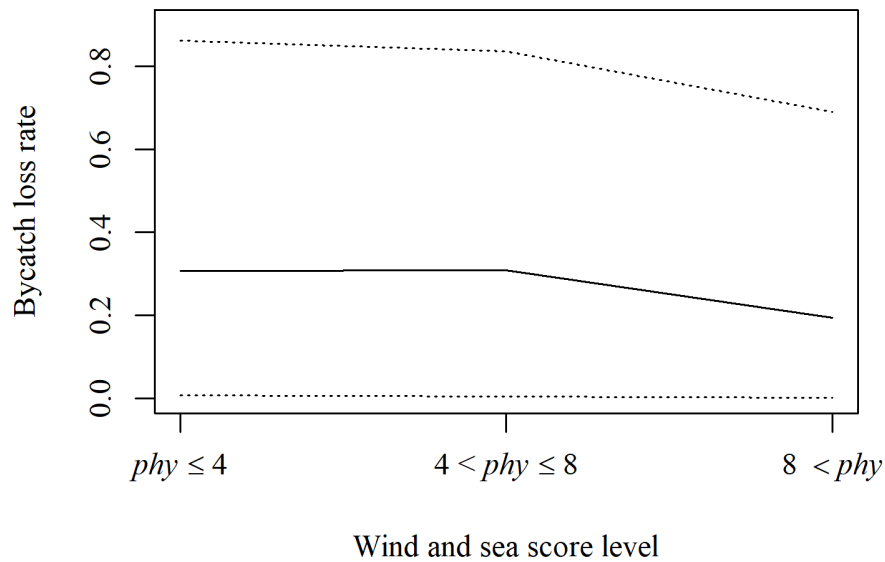


582

583 *Figure 4 Bycatch loss rates of common seabird species (groups) in pelagic longline*
 584 *fisheries. For each line, the solid diamond marks the median posterior estimate, the solid*
 585 *intervals mark the interquartile range of the posterior estimate, and the dashed line*
 586 *marks the 95% credible interval. Seabird species (groups) are ordered alphabetically.*
 587 *Black-browed albatross includes *Thalassarche melanophris* and *T. impavida*; Black*
 588 *petrel includes *Procellaria parkinsoni*, and *P. westlandica*; giant petrel includes*
 589 **Macronectes giganteus* and *M. halli*; shearwater includes *A. grisea*, *P. tenuirostris* and *P.**
 590 **pacificus*; shy albatross includes *T. cauta* and *T. steadi*; wandering albatross include*
 591 **Diomedea exulans*, *D. antipodensis*, *D. dabbenena* and *D. amsterdamensis* ; yellow-*
 592 *nosed albatross includes *T. chlororhynchos* and *T. carteri*. Species or species groups*
 593 *marked with * have no more than 10 observed records, and their results are inconclusive.*

594 [Production instructions: 1.5 or 2 columns; no color needed in print]

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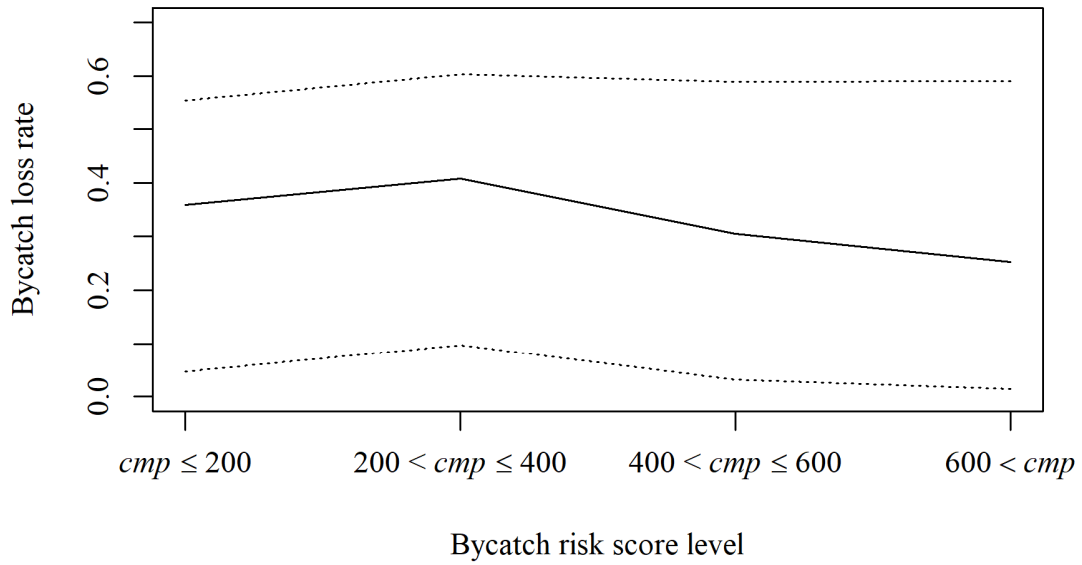
596

597 *Figure 5 Median (solid line) and 95% credible interval (dotted lines) of the posterior*
 598 *estimate of the bycatch loss rate at calm ($phy \leq 4$), intermediate ($4 < phy \leq 8$) and*
 599 *rough ($8 < phy$) physical conditions based on model H2.*

600

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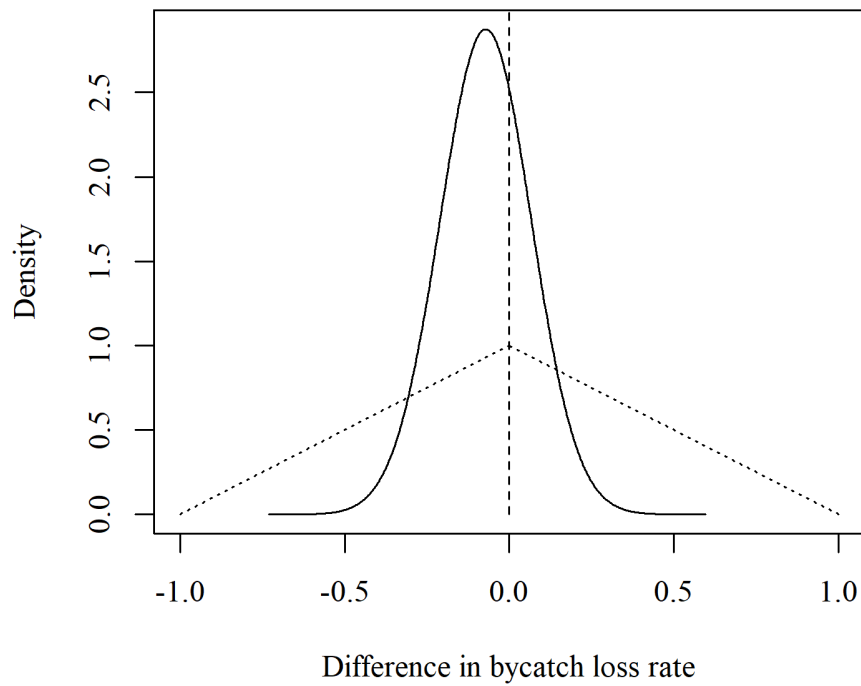
603

604 *Figure 6 Median (solid line) and 95% credible interval (dotted lines) of the posterior*
 605 *estimate of the bycatch loss rate at different levels of bycatch risk score based on model*
 606 *H3.*

607

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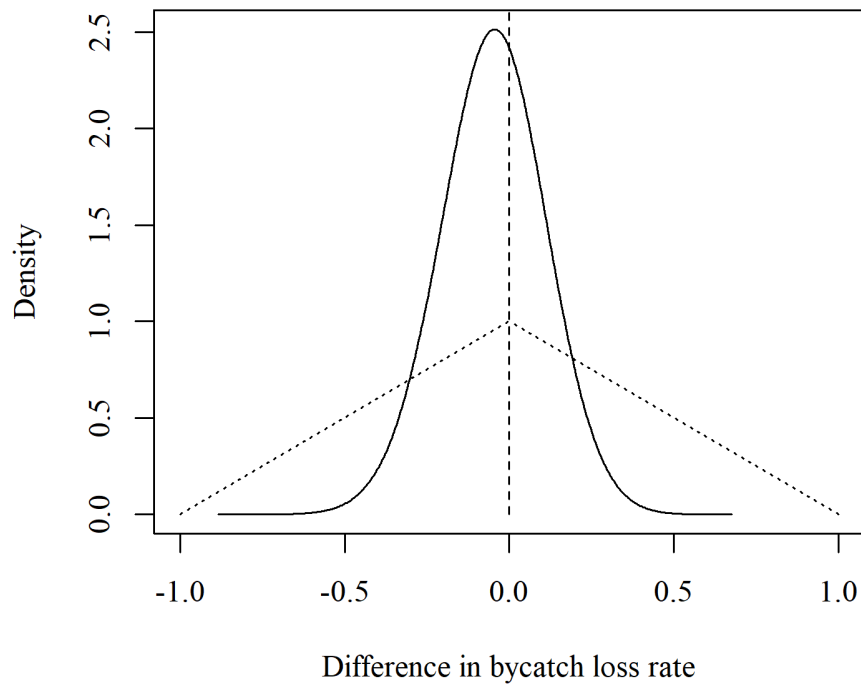
Difference in bycatch loss rate

611 *Figure 7 Prior (two dotted line segments) and posterior (solid curve) of the difference in*
612 *bycatch loss rate between divers and non-divers based on model H4e1. A negative value*
613 *indicates a lower loss rate for divers, and the vertical dashed line separates negative*
614 *values and positive ones.*

615

616 [Production instructions: 1 column; no color needed in print]

617



618

Difference in bycatch loss rate

619 *Figure 8 Prior (two dotted line segments) and posterior (solid curve) of the difference in*
620 *bycatch loss rate between scavengers and non-scavengers based on model H4e2. A*
621 *negative value indicates a lower loss rate for scavengers, and the vertical dashed line*
622 *separates negative values from positive ones.*

623

624 [Production instructions: 1 column; no color needed in print]