Global patterns of sex- and age-specific variation in seabird bycatch

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54 ABSTRACT
55
56 Fisheries bycatch is a major threat to seabird populations, and understanding sex- and
57 age-biases in bycatch rates is important for assessing population-level impacts. We
58 analysed 44 studies to provide the first global assessment of seabird bycatch by sex and
59 age, and used generalised models to investigate the effects of region and fishing method.
60 Bycatch was highly biased by sex (65% of 123 samples) and age (92% of 114 samples),
61 with the majority of samples skewed toward males and adults. Bycatch of adults and males
62 was higher in subpolar regions, whereas there was a tendency for more immatures and
63 females to be killed in subtropical waters. Fishing method influenced sex- and age-ratios
64 only in subpolar regions. Sex- and age-biases are therefore common features of seabird
65 bycatch in global fisheries that appear to be associated largely with differences in at-sea
66 distributions. This unbalanced mortality influences the extent to which populations are
67 impacted by fisheries, which is a key consideration for at-risk species. We recommend that
68 researchers track individuals of different sex and age classes to improve knowledge of
69 their distribution, relative overlap with vessels, and hence susceptibility to bycatch. This
70 information should then be incorporated in ecological risk assessments of effects of
71 fisheries on vulnerable species. Additionally, data on sex, age and provenance of bycaught
72 birds should be collected by fisheries observers in order to identify regions and fleets
73 where bycatch is more likely to result in population-level impacts, and to improve
74 targeting of bycatch mitigation and monitoring of compliance.
75
76 Keywords: age ratio; incidental mortality; seabirds; fisheries management, sex ratio.
77
78 **1. Introduction**
79
80 Fisheries are one of the primary threats to marine biodiversity, impacting ecosystems
81 from the open ocean to the coast, and from the poles to the tropics (Halpern et al., 2008;
82 Jackson et al., 2001). Commercial fishing has resulted in severe and widespread ecosystem
83 disruption primarily as a result of over-harvesting, habitat degradation and the mortality
84 of non-target species, also called bycatch (Hall et al., 2000; Halpern et al., 2008; Jackson et
85 al., 2001). Populations of large marine vertebrates, such as sea turtles, sharks, marine
86 mammals, and seabirds, are particularly susceptible to bycatch because of a combination
87 of their attraction to fishery bait and discards, and their naturally slow reproductive rates
88 rendering them sensitive to even small increases in mortality (Hall et al., 2000; Lewison et
89 al., 2004). The impacts are so extensive that the recent declines of many large marine
90 vertebrates resulting from bycatch have been compared to the historical extirpations and
91 extinctions of terrestrial megafauna by human hunting (Lewison et al., 2014, 2004).
92
93 Seabirds are particularly at risk from fisheries, as they are bycaught in a wide
94 range of gear types (Croxall et al., 2012; Montevecchi, 2002; Phillips at al., 2016). For
95 example, drift nets set by Japanese, Korean and Taiwanese vessels are estimated to have
96 killed up to 40 million sooty (*Ardenna grisea*) and short-tailed (*A. tenuirostris*)
97 shearwaters in the North Pacific between 1952 and 2001 (Uhlmann et al., 2005). Coastal
98 gillnet fisheries are also a major source of mortality, with >400,000 seabirds killed
99 annually, worldwide (Žydelis et al., 2013). Global longline fisheries are estimated to have
100 killed at least 160,000, and potentially 320,000 seabirds annually, mainly albatrosses,
101 petrels and shearwaters (Anderson et al., 2011). Trawl fisheries are also a threat, with
102 about 9,300 birds, mostly albatrosses, estimated to be killed annually just in the waters off
103 South Africa by wet fish trawls (Maree et al., 2014; Sullivan et al., 2006; Waugh et al.,
104 2008). These levels of mortality have led to severe declines in many populations and are
105 clearly unsustainable (Croxall et al., 1998; Cuthbert et al., 2005; Delord et al., 2008;
106 Phillips at al., 2016; Piatt and Gould, 1994; Rolland et al., 2010; Žydelis et al., 2013, 2009).
107

108   The impact of bycatch depends not only on the number of individuals killed, but
109 also on the components of the population that are impacted (Bugoni et al., 2011; Lewison
110 et al., 2012). For example, because seabird life histories are characterised by delayed
111 maturation, high survival and low rates of reproduction, mortality of adults will have
112 greater population-level impacts than mortality of immatures (Lewison et al., 2014).
113 Moreover, because seabirds are monogamous, with obligate biparental care, sex-biased
114 mortality in fisheries can reduce the effective population size (Mills and Ryan, 2005;
115 Weimerskirch et al., 2005). Sex- and age-biases in seabird bycatch are reported in a
116 number of fisheries (Awkerman et al., 2006; Gales et al., 1998; Ryan and Box-Hinzen,
117 1999; Stempniewicz, 1994), and there has been a review of adult sex-ratios (ASR) in
118 bycatch of albatrosses and petrels (Bugoni et al., 2011). However, there has been no
119 comprehensive review of sex- and age-biases in bycatch of seabirds in general, even
120 though a better understanding of their nature and extent is required to determine the full
121 impact of bycatch on populations and communities. Indeed, this has been identified as one
122 of the highest priority research questions in the field of seabird ecology and conservation
123 (Lewison et al., 2012; Phillips et al., 2016).
124
125   Accordingly, the aim of the current study is to provide the first global review of
126 age- and sex-specific bycatch in seabirds. This will contribute towards a better
127 understanding of the frequency and magnitude of these effects across taxa, regions and
128 fishery gear-type, as well as the implications for management and conservation. We
129 predict that larger and more dominant individuals, usually adult males, will have higher
130 bycatch rates than adult females, or younger birds of either sex, because they are better
131 able to compete for discards and baits while attending fishing boats (Awkerman et al.,
132 2007b; Bregnballe and Frederiksen, 2006; Croxall and Prince, 1990; Montevecchi, 2002).
133 However, bycatch rates will also be influenced by region. Many studies have shown that
134 females and immatures tend to travel further from their breeding sites, or to lower
135 latitudes, compared with males and adults (Hedd et al., 2014; Phillips et al., 2005, 2004).
136 Therefore, because the majority of seabirds breed at high latitudes (Schreiber and Burger,
137 2002) we broadly predict that bycatch in subpolar (sub-Arctic and sub-Antarctic) areas
138 will tend to be skewed towards males and adults, whereas in subtropical regions, bycatch
139 will be biased towards females and immatures.
140
2. Methods
142
2.1. Literature review
144
145 We reviewed the literature for studies reporting sex and age composition of seabird
146 bycatch in fisheries from around the world. We searched *Thomson Reuters Web of Science*
147 and *Google Scholar* using the following search terms: Topic = (seabird* OR albatross* OR
148 petrel* OR penguin* OR shearwater*) AND (sex OR age OR female OR male OR adult OR
149 juvenile) AND (fishery* OR bycatch OR mortality) AND (bias); Timespan = All Years. To
150 ensure the best possible coverage of the bycatch literature, we supplemented this with
151 grey literature and contacted a number of experts directly to alert us to any missing
152 references and to access unpublished studies. Only the studies reporting sex or age
153 composition from samples of more than 10 individuals per species were included. We
154 used the term 'immature' to refer to birds of any age below age of first breeding.
155
156   Authors utilized different methods for sexing including examination of gonads
157 through necropsies (e.g. Petersen et al., 2010; Thompson et al., 2010a, b), molecular sexing
158 (e.g. Burg, 2008; Jiménez et al., 2015b) and ring recoveries of known-sex individuals (e.g.
159 Jiménez et al., 2015a). Birds were aged on the basis of plumage and bill morphology (e.g.
160 Cardoso et al., 2011; Jiménez et al., 2015b; Neves and Olmos, 1997), or ring details for
161 known-age individuals (Awkerman et al., 2006; Jiménez et al., 2015a; Österblom et al.,

162   2002). To aid interpretation, we classified each sample of seabird bycatch according to the
163   magnitude of sex- and age-bias: highly biased (≥80% belonging to one sex or age class);
164   biased (60% - 79%) and not biased (40% - 59%). The sampling unit for bycatch data
165   refers to the information for each taxon caught in a particular gear type in each study.
166   When possible, bycatch rates were separated by region and season (summer/winter).
167
168   To aid comparison across regions, the global oceans were initially divided into five
169   major zones: sub-Antarctic, subtropical southern hemisphere, tropical, subtropical
170   northern hemisphere and sub-Arctic. For the purpose of this study, sub-Arctic and sub-
171   Antarctic zones also included the adjacent temperate waters. Thus, sub-Antarctic and sub-
172   Arctic regions mostly comprise waters between 60° and 40° of latitude (average sea
173   surface temperature (SST) 0°–18° C), subtropical in both hemispheres between 40° and
174   20° of latitude (average SST 18°-24° C), and tropical between 20° S and 20° N (average SST
175   >25° C). The exception was in the southern hemisphere, where cold water masses extend
176   as far north as 30° S off the west coast of South America and to the south and south-west
177   of Australia, which were included in sub-Antarctic waters (Figure 1). In modelling the
178   regional effects on the sex- and age-ratios of seabird bycatch, sub-Antarctic and sub-Arctic
179   areas were combined in "subpolar", and subtropical waters of both hemispheres combined
180   in "subtropical".
181
182   We obtained data from a diverse range of fisheries, including pelagic and demersal
183   longline, gillnet, trawl and pound net (shallow water nets attached to poles to create a
184   funnel). Our sample, however, was dominated by two main gear types and variations
185   therein: longline (pelagic and demersal) and gillnet. Longlines primarily kill surface-
186   feeding birds attracted to baited hooks near the surface, while gillnets mainly entrap
187   pursuit divers and bottom feeders (Anderson et al., 2011; Žydelis et al., 2013).
188
189   *2.2. Data analysis*
190
191   We first compared the number of biased with non-biased (sex and age, respectively)
192   bycatch samples for each fishery type, region and category using contingency tables. We
193   specifically used chi-squared tests with Yates's correction for continuity where there was
194   only one degree of freedom. We then tested for the effects of region (subpolar vs
195   subtropical) and fishery type (longline [demersal and pelagic combined] vs gillnet) on the
196   age and sex ratios of seabird bycatch using linear models followed by analyse of variance
197   (ANOVA). We first ran liner mixed models using the *lmer* function of the *lme4* package in R
198   (R Core Development Team, 2011; Zuur et al., 2009), including species as a random effect
199   to account for inclusion in multiple datasets. Then, after verifying that the random-effect
200   was not significant, it was dropped and linear models applied instead, using the function
201   *lm* of the same package in R. The proportion of males or adults was used as the response
202   variable for sex and age-bias respectively, using a *Gaussian* error distribution. Due to the
203   unbalanced geographical distribution of bycatch samples by fishery type, we also tested
204   the effect of the four major gear types (pelagic longline, demersal longline, gillnet and
205   trawl) within the subpolar region. This was the only region with sufficient datasets. All
206   models were weighted by the sample size, which, for the purpose of this analysis, was the
207   number of birds of each taxon caught in a particular gear type in each study. We tested the
208   effect of region and fisheries on sex and age proportions separately. Models were
209   compared using second-order Akaike Information Criterion (AICc), where the best model
210   is taken to be that with the lowest AICc value. AICc differences of <2 are not considered to
211   be meaningfully different (Zuur et al., 2009).
212
213   **3. Results**
214

215   We found 44 studies, published between 1990 and 2016, that reported sex and age
216   composition of seabird bycatch in fisheries, of which 35 (79%) were in the southern
217   hemisphere and 9 (21%) in the northern hemisphere (Figure 1, Table 1). Data were
218   available from four main types of fishery: 14 studies for pelagic longline (32%), nine for
219   demersal longline (20%), nine for gillnet (20%), two for trawl (5%). Seven (16%) studies
220   reported data for more than one fishery, separated according to gear type. In addition, two
221   studies combined data from intentional catch, and bycatch in gillnet and longline (5%),
222   and a single study (2%) reported data from pound nets.
223
224   Availability of data from each fishery type was not equally distributed,
225   geographically. For example, 82% (n = 16) of the samples from demersal longline and
226   100% (n = 8) of those from trawl fisheries came from the sub-Antarctic region, 52% (n =
227   27) of the pelagic longline samples from subtropical waters of the southern hemisphere,
228   and 84% (n = 15) of the gillnet samples from sub-Arctic and adjacent subtropical waters
229   combined (Figure 2).
230
231   The bycatch data with information on sex and age composition comprised 18,389
232   individuals of 41 seabird taxa, including 15 which are globally threatened: 16 albatrosses
233   (Diomedeidae), nine petrels and shearwaters (Procellariidae), six sea ducks (Merginae),
234   three penguins (Spheniscidae), two gulls (Laridae), two alcids (Alcidae), one grebe
235   (Podicipedidae) and two cormorant/shags (Phalacrocoracidae) (Appendix A).
236
237
238   *3.1.Sex-specific bycatch*
239
240   Of 123 samples of sex ratios in seabird bycatch, 43 (35%) were unbiased, 56
241   (46%) were male-biased (including 20 that were highly biased,), and 24 (19%) were
242   female-biased (including five that were highly biased) (Figure 3-A, Appendix B). The
243   number of sex-biased bycatch samples was significantly higher than the number of non-
244   biased (χ^2_{Yates} = 10.537, P = 0.001), and the number of samples skewed towards males was
245   significantly higher than that skewed towards females (χ^2_{Yates} = 12.013, P < 0.001).
246
247   The geographical distribution of the highly sex-biased bycatch samples (≥80% of
248   one sex) is presented in Figure 4. There was a significant effect of the interaction between
249   region and fishery type on the sex ratios of seabirds killed in fisheries, with the regional
250   effect influencing the sex ratio of seabirds bycaught in longlines but not in gillnets (Figure
251   5, Table 2). There was a higher proportion of males bycaught in fisheries in subpolar
252   areas, whereas a trend towards female bycatch in subtropical waters (F = 38.464, P <
253   0.001) (Figure 6-A, Table 3). There was no significant difference in sex-ratios of seabird
254   bycatch between gillnets and longlines (Figure 6-B, Table 3). However, when modelling
255   the effect of the four major fishery gear-types within the subpolar region a significant
256   effect was found (F = 10.556, P < 0.01), with a higher mortality of males in trawl fisheries
257   (Figure 7-A, Table 4).
258
259
260   *3.2.Age-specific bycatch*
261
262   Of 114 samples reporting age composition of seabird bycatch, nine (8%) were unbiased,
263   78 (68%) were skewed towards adults (62 were highly biased) and 27 (24%) were biased
264   towards immatures (12 were highly biased) (Figure 3-B, Appendix A). Age-biased bycatch
265   was therefore widespread across global fisheries, accounting for 92% of reports (χ^2_{Yates} =
266   79.167, P < 0.001), with the frequency of adult-biased samples significantly larger than
267   immature-biased (χ^2_{Yates} = 23.810, P < 0.001).
268

269   The geographical distribution of the highly age-biased bycatch samples (≥80% of
270 one age class) is presented in Figure 8. There was a significant effect of the interaction
271 between region and fishery type on the age ratios of seabirds killed in fisheries, with the
272 regional effect influencing the age ratio of seabirds bycaught in longlines but not in gillnets
273 (Figure 5, Table 2). A higher proportion of adults was bycaught in subpolar regions
274 whereas no difference was found in age-ratio of seabirds killed in subtropical areas (F =
275 6.262, P <0.05) (Figure 6-C, Table 3). More adults than immatures were bycaught in
276 longline, but there was no age bias for seabirds bycaught in gillnets (F = 13.578, P < 0.001)
277 (Figure 6-D, Table 3). Fishery type has a significant influence on the age ratio of seabirds
278 bycaught in subpolar regions (F = 17.175, P < 0.001) (Table 4). Mortality of adults was
279 significantly higher than of immatures in demersal longline and trawl fisheries than in
280 other fishery types in these regions (Figure 7-B).
281
282
283   **4. Discussion**
284
285   Sex- and age-biases in seabird bycatch have been reported in a number of fisheries
286 (Delord et al., 2005; Gales et al., 1998; Nel et al., 2002a; Phillips et al., 2010; Ryan and Box-
287 Hinzen, 1999), and there is growing interest in both the underlying mechanisms and the
288 potential demographic consequences (Bugoni et al., 2011; Lewison et al., 2012). Here we
289 provide the first global synthesis of both sex and age-specific variation in seabird bycatch
290 rates by different fisheries and in diverse regions. Overall, our study shows substantial
291 variation in the sex and age ratios of bycaught seabirds, and that unbalanced sex and age
292 proportions are the most common pattern. Additionally, we demonstrate that sex- and
293 age-biases vary by region and, to a lesser extent by fishery type. Globally, male-biased
294 bycatch was significantly more frequent (47%) than female-biased bycatch (18%), and
295 adult-biased (68%) significantly more frequent than immature-biased (24%). These
296 results are consistent with our *a priori* prediction that the dominance of males and adults
297 foraging behind fishing vessels will lead to higher bycatch. However, there are regional
298 differences in the patterns of age- and sex-biased bycatch, as well as a disproportionately
299 high number of studies from sub-polar waters (68%), indicating that foraging despotism
300 alone does not explain the observed patterns. Nevertheless, there is a paucity of this data
301 in the northern hemisphere (9 studies) compared with the southern hemisphere (35
302 studies). Possible mechanisms contributing to unbalanced age and sex mortality, as well as
303 its demographic effects, and implications for management and conservation, are discussed
304 below.
305
306   *4.1. Sex-specific bycatch*
307
308   *4.1.1. Possible mechanisms contributing to sex-specific bycatch*
309
310   Although offspring sex-ratios in seabirds can vary with age, quality and timing of
311 breeding (Blanchard et al., 2007; Velando et al., 2002; Weimerskirch et al., 2005,), there is
312 little evidence for any consistent sex-biases at hatching or recruitment at the population
313 level (Awkerman et al., 2007a; Bregtanole and Thibault, 1995; Donald, 2007;
314 Weimerskirch et al., 2005). Therefore, the patterns observed here indicate that sex-
315 skewed bycatch is unlikely to be due to the underlying population sex-ratio. Hypotheses
316 proposed to explain sex-related vulnerability to bycatch include sex-specific differences in
317 at-sea distribution, and differential access to bait and discards related to sexual size-
318 dimorphism and aggression (Barbraud et al., 2012; Bugoni et al., 2011; Nel et al., 2002a;
319 Ryan and Box-Hinzen; 1999).
320
321   It has been suggested that the competitive advantage of males foraging behind
322 fishing vessels explains male-biased bycatch events (Awkerman et al., 2006; Ryan and

Box-Hinzen, 1999); however, there is little direct evidence to support this. Instead, in multi-species foraging aggregations, differences in body size between taxa are more important determinants of access to feeding opportunities than sex *per se* (Bugoni et al., 2011; Jimenez et al., 2012; Stauss et al., 2012; Votier et al., 2013). In contrast, sex-biased bycatch appears to be much better explained by sex-specific differences in distribution. For instance, in the southern hemisphere, our analysis showed a significantly higher frequency of male-biased bycatch in sub-Antarctic areas, but a trend towards the opposite pattern in subtropical waters; this is consistent with tracking and stable isotope results from a number of different sub-Antarctic seabird species during the breeding season, showing that females tend to forage farther from the colony and spend more time in subtropical waters compared with males (e.g. Hedd et al., 2014; Jiménez et al., 2015a; Nel et al. 2002b; Phillips et al., 2011, 2005, 2004; Thiers et al., 2014; Weimerskirch et al., 2014). In the northern hemisphere, where the bycatch data was more taxonomically heterogeneous and the sample size much smaller (15 species within 28 samples, 23%), overall patterns of sex-biased bycatch are less clear. Nevertheless, differential distribution at sea has also been identified as a cause of male-biased mortality of common guillemot (*Uria aalge*) in coastal gillnets of Monterrey Bay (California) (Nevins et al., 2004), and for the male-skewed bycatch of both Laysan (*Phoebastria immutabilis*) and black-footed (*P. nigripes*) albatrosses off Alaska compared with the relatively balanced or female-biased sex-ratios of birds bycaught in Hawaiian waters (Beck et al., 2013). In the Baltic Sea, the sex-ratios of diving ducks bycaught in gillnets largely reflects the sex proportions observed in their wintering grounds (Stempniewicz, 1994), supporting the hypothesis of differential distribution as the main driver of observed bycatch bias. Therefore, the overall predominance of males in seabird bycatch that we found in our study probably reflects the higher proportion of samples obtained in subpolar areas (68%), where the seabird mortality tend to be skewed toward males.

4.1.2. Demographic effects of sex-specific bycatch

The immediate effect of sex-biased bycatch could lead to skewed adult sex ratios and thus a reduction in effective population size (Donald, 2007; Millis and Ryan, 2005; Weimerskirch et al., 2005). For example, long-term demographic studies of wandering, black-browed (*Thalassarche melanophris*) and waved albatrosses (*Phoebastria irrorata*) all indicate sex-biases in survival that may be related to sex-specific bycatch (Arnold et al., 2006; Awkerman et al., 2006; Croxall et al., 1998; Weimerskirch and Jouventin, 1987). Nonetheless, it is very difficult to measure directly the demographic impact of sex-skewed mortality in fisheries because: (1) until now, there was a lack of systematic sex-specific seabird bycatch data across global fisheries; (2) there is often uncertainty about the provenance of bycaught birds, making it difficult to directly link events at sea with demographic monitoring on land; (3) there is a paucity of long-term demographic studies across multiple taxa and locations (Anderson et al., 2011; Lewison et al., 2012, 2004; Žydelis et al., 2013); and (4) there is uncertainty about other factors influencing sex differences in survival, such as relative predation risk, sex-specific costs of reproduction, variation in feeding strategies, or engagement in aggressive interactions (Donald, 2007; Weimerskirch et al., 2005). Mills and Ryan (2005) modelled the impact of sex-biased bycatch in wandering albatross and showed that even moderate increase in female mortality (2-4% per year) reduces fecundity by 9–27% compared with unbiased mortality. This effect may explain the steep decline in the wandering albatross at South Georgia (Croxall et al., 1998; Croxall and Prince, 1990; Jiménez et al., 2015a; Poncet et al., 2006). Population-level effects of sex-biased bycatch have been observed in situations where there is reliable information on both bycatch rates and demographic traits. For example, in the waved albatross, which breeds almost entirely on Española Island (Galápagos Islands), there is a skew in the adult population towards females as a result of the strongly male-biased mortality (82%) in artisanal fisheries off Peru and Ecuador

(Awkerman et al., 2007a, 2006). In the wandering albatross at Possession Island (Crozet), the lower survival of females, attributed to higher mortality in pelagic longline fisheries, has also led to a male-biased population (Weimerskirch et al., 2005), and the same is expected at South Georgia where females have a greater overlap with tuna fisheries in subtropical waters and consequently are bycaught more frequently than males (Jiménez et al., 2015a). Distorted sex ratios can also result in indirect effects on population dynamics, including unexpectedly high rates of extra-pair paternity in female-biased populations (Huyvaert et al., 2000), or reduced breeding success due to aggressive nest intrusions by unpaired males resulting in egg loss and infanticide in male-biased populations (Anderson et al., 2007; Taylor et al., 2001). These indirect effects, in tandem with the reduction of effective population size, can potentially increase the deleterious effects of bycatch on seabirds.

4.2. Age-specific bycatch

4.2.1. Possible mechanisms contributing to age-specific bycatch

Our review suggests that age-skewed seabird bycatch is common across global fisheries, with 68% of the bycatch samples skewed towards adults and 24% skewed towards immatures. The overall higher mortality of adults seems to agree with our initial prediction that dominant adults would outcompete immatures for foraging opportunities behind fishing vessels (Croxall and Prince, 1990). However, we must be cautious interpreting this result because the higher mortality of adults may largely reflect the typical age structure of seabird populations, which tend to be characterized by more adults than immatures (Nur and Sydeman, 1999). Detailed information on age-structure is lacking for most species and populations. Nevertheless, strong biases in both adult and immature bycatch suggest some extrinsic factors are in operation, and not that bycatch rates simply reflect the natural age ratios.

The degree to which different age classes interact with fisheries is not well understood (Lewison et al., 2012). However, some authors have proposed that juveniles may be more susceptible to bycatch because they favour scavenging over natural foods that may be more difficult to catch, or because of their naivety in avoiding fishing gear (Fayet et al., 2015; Lewison et al., 2012; Shealer, 2002,). Indeed, lack of experience while foraging around nets was considered to be the main reason for immature-biased mortality of pursuit-diving seabirds (Bregnballe and Frederiksen, 2006; Österblom et al., 2002). However, this is not a consistent pattern - in our study, 50% of the 12 samples of pursuit-diving seabirds of known age class drowned in nets were skewed towards adults, whereas 33% were skewed towards immatures. Naivety of young birds has also been suggested as the explanation for immature-skewed mortality in longlines, and potentially by trawls (Gales et al., 1998; Prince et al., 1994), but, again, this pattern was not supported by our data, which shows a large proportion of adults bycaught in these fisheries.

Based on the available data we suggest that a degree of spatial segregation at-sea by age is a better explanation for the observed age-specific susceptibility to bycatch, rather than differences in competitive capacity or experience in avoiding fishing gear. In the southern hemisphere, immature birds disperse further north and spend more time in subtropical waters, whereas adults (especially breeders) are more likely to stay in sub-Antarctic waters (Bugoni and Furness, 2009; Catry et al., 2013; Olmos, 1997; Phillips et al., 2005; Sullivan et al., 2004; Waugh et al., 1999; Weimerskirch et al., 2014, 2006). This pattern seems to be reflected in the significantly higher mortality of adults in subpolar areas in our analysis, which mainly resulted from the consistent adult-biased bycatch in diverse fisheries across sub-Antarctic waters (Bartle, 1991; Ryan and Box-Hinzen, 1999; Gales et al. 1998, Nel et al., 2002a; Robertson and Bell, 2002; Gandini et al., 1999; Seco-Pon

et al., 2007; Thompson, 2010a, b). On the other hand, in subtropical areas, where there are often more immatures (Copello et al. 2013, Phillips et al., 2006, 2005; Weimerskirch et al., 2014), our analyses indicated more samples biased to this younger age class (43%) in comparison to fisheries in sub-Antarctic waters (17%). Although the proportion of immatures bycaught in subtropical areas is highest during summer (up to 100%), when most adults return to their breeding areas (Petersen at al., 2010; Ryan et al., 2002), immatures can also predominate in bycatch during winter (Gales et al., 1998; Murray et al., 1993; Neves and Olmos, 1997; Roma et al., 2009). The significantly higher bycatch of adults in trawl and demersal longline fisheries within the subpolar region is likely to reflect the same large-scale pattern, since those fisheries operate in shelf and slope waters closer to colonies (Bartle, 1991; Gandini at al., 1999; Nel et al. 2002a; Robertson et al. 2003, 2004), whereas pelagic longliners operate in much more pelagic waters and at lower latitudes of the subpolar region (Beck et al., 2013, Gales et al. 1998; Thompson 2010a). This age-specific mortality associated with differential distribution at sea is not exclusive to albatrosses and petrels of the southern hemisphere. A range of other species in both hemispheres, including diving ducks, penguins, alcids, fulmars and gulls showed regional and seasonal patterns of age-specific bycatch likely to reflect differential overlap with fisheries; these seem to be linked to age-related differences in distribution as a consequence of breeding constraints, moult cycles, migration or age-specific foraging strategies (Cardoso et al., 2011; Gandini et al., 1999; Nevins et al., 2004; Phillips et al., 2010; Stempniewicz, 1994; Thompson et al., 1998; Votier et al. 2011). The significant effect of region on age ratios of seabirds bycaught on longlines but not in gillnets may be related to the characteristics of the affected seabird. It is unclear whether the taxa that are at greatest risk from gillnets (alcids, diving ducks) show large-scale age-segregation by latitude, or even if they do, they may not be killed in gillnets in some parts of their range.

4.2.2. Demographic effects of age-specific bycatch

Globally, mortality of adults in fisheries is thought to have deleterious effects not just on albatrosses and petrels, but also diving ducks, alcids and penguins (Cardoso et. al, 2011; Darby and Dawson 2000, Smith and Morgan, 2005, Thompson et al., 2010a, 2010b, 1998; Žydelis et al., 2009). In many cases, there is insufficient data on bycatch rates of different age classes to accurately estimate the impacts of, or predict the response to, potential management regimes (including changes in fishing effort distribution, or bycatch mitigation). These problems are exacerbated in the absence of robust data on demographic rates, particularly given the difficulties of disentangling effects of mortality in fisheries from other factors affecting breeding populations, such as environmental changes, depletion of prey stocks, introduced predators, habitat deterioration etc.

Although adult mortality has the most immediate and pronounced negative effect, chronic mortality of immatures can reduce recruitment below the minimum level needed to maintain population stability (Nur and Sydeman, 1999; Prince et al., 1994, Sherley et al. 2015). Juvenile survival in seabirds is normally lower than adults (Nur and Sydeman, 1999), but there is evidence that fisheries can reduce immature survival rates of some species even further. For example, negative trends in juvenile survival of black-browed albatross from South Georgia are correlated with the increase in pelagic longline fishing effort off South Africa (Arnold et al., 2006; Croxall et al., 1998; Tuck et al., 2003), which is the primary destination of young birds from that population (Phillips et al. 2005). Therefore, the higher susceptibility of juveniles to bycatch in pelagic longline fisheries, which are the most widespread and largest-scale of those operating in subtropical waters of the southern hemisphere (Anderson et al., 2011; Tuck et al., 2003), may be contributing to the low immature survival of black-browed and other albatross populations in the Southern Ocean (ACAP 2010b, a, 2009; Croxall et al., 1998; Prince et al., 1994). Indeed, high mortality of immatures in fisheries resulting in depressed recruitment levels appears

485 to have been a major contributor to the decline of both black-browed and grey-headed
486 (*Thalassarche chrysostoma*) albatrosses at South Georgia (Prince et al., 1994).
487
488 **4.3. Implications for management and conservation**
489
490   Seabirds are the most threatened group of birds; nearly half of the 346 species are
491 known or suspected to be in decline, with one third threatened with extinction, including
492 17 critically endangered, 35 endangered, 49 vulnerable and 37 near threatened (Croxall et
493 al., 2012), and there has been a 70% decline in monitored populations between 1950 and
494 2010 (Paleczny et al., 2015). Bycatch was identified as one of the two greatest threats, and
495 the most pervasive threat at sea (Croxall et al., 2012). Hence, given the frequency and
496 magnitude of both sex- and age-biases in seabird bycatch, and the demographic
497 implications, we strongly recommend much improved data collection on the age and sex of
498 birds killed by fisheries in on-board observing programs at national and international
499 levels. The latter requires concerted and coordinated action by Regional Fishery
500 Management Organisations (RFMOs). In addition to increased on-board observer effort, it
501 is necessary to implement standardized protocols for retrieving carcasses and collecting
502 biological samples to provide high quality information on seabird bycatch; this includes
503 accurate information on sex (Bugoni and Furness, 2009; Fridolfsson and Ellekrer, 1999),
504 age (Bugoni and Furness, 2009; Thompson et al., 2010), and improved attempts to identify
505 provenance (Abbot et al., 2006; Gómez-Díaz & González-Solís, 2007; Abbot et al., 2014).
506 These approaches are especially urgent in the northern hemisphere – despite high levels
507 of seabird bycatch here, the number of studies reporting age and sex-specific totals is
508 much lower than in the southern hemisphere. Moreover, tracking studies that map the
509 distributions and hence overlap with specific vessels of birds of different age class and sex,
510 throughout the year, will greatly improve ecological risk assessments (Jiménez et al.,
511 2015a; Komorose and Lewison, 2015). Likewise, integrated population models testing the
512 effects of fisheries on seabird demography, including analyses of Potential Biological
513 Removal (PBR), must take sex- and age-specific differences in bycatch rates to avoid
514 underestimation of the PBR and potentially instituting management actions that are
515 insufficient (Dillingham and Fletcher, 2011; Lewison et al., 2012). Together, this
516 information can then be used by regional (i.e. national action plans) and international
517 conservation initiatives (including the Agreement on the Conservation of Albatrosses and
518 Petrels, ACAP), as well as local fisheries management organizations and RFMOs to identify
519 regions and fleets where more prescriptive mitigation measures should be applied, and
520 where monitoring of compliance needs to be more intensive to prevent severe impacts of
521 bycatch on seabird populations (Croxall et al., 2013; Phillips, 2013; Phillips et al., 2016).
522 However, because (1) there is low reliability of bycatch data globally, (2) populations are
523 at risk from different fisheries across large areas, and (3) provenance of bycaught birds is
524 often unknown, incorporating information on sex- and age-biased bycatch in seabird
525 management and conservation remains challenging, and the data must be examined on a
526 case-by-case basis.
527
528 **5. Conclusion**
529
530   Sex and age biases in seabird bycatch are common features across global fisheries,
531 mainly related to differential at-sea distributions. Overall, bycatch of adults and males was
532 higher in subpolar regions and closer to colonies, whereas immatures and females were
533 caught more frequently in subtropical waters. We found no compelling evidence that
534 differences in sex and age ratios are related to the competitive advantage of males and
535 adults foraging at fishing vessels, or to naivety of young birds around fishing gear. There is
536 clear evidence that differences in capture rates by sex and age have implications for
537 populations that differ from those of unbiased mortality. Despite this, the need to ensure
538 information is obtained on sex and age of bycaught birds has been largely neglected by on-

board observer programs in national and international fisheries. Given the ubiquity and population-level consequences of such biases, we believe that global efforts to map bycatch and understand their impacts (e.g. Lewison et al., 2014) should include age and sex information wherever possible.

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References

Abbott, C.L., Millikin, R.L., Hipfner, M.J., Hatch, S., Ito, M., Watanuki, Y., Burg, T.M., 2014. Genetic structure of rhinoceros auklets, *Cerorhinca monocerata*, breeding in British Columbia, Alaska and Japan. Mar. Biol. 161: 275–283. http://dx.doi.org/10.1007/s00227-013-2333-2

Abbott, C.L., Double, M.C., Gales, R., Baker, G.B., Lashko, A., Robertson, C.J.R., Ryan, P.G., 2006. Molecular provenance analysis for shy and white-capped albatrosses killed by fisheries interactions in Australia, New Zealand, and South Africa. *Conserv. Genet.* 7: 531–542. http://dx.doi.org/10.1007/s10592-005-9064-y

ACAP - Agreement on the Conservation of Albatrosses and Petrels, 2009. ACAP Species assessment: Campbell Albatross *Thalassarche impavida*. http://www.acap.aq/acap-species

ACAP - Agreement on the Conservation of Albatrosses and Petrels, 2010a. ACAP Species assessment: Black-browed Albatross *Thalassarche melanophris*. http://www.acap.aq/acap-species

ACAP - Agreement on the Conservation of Albatrosses and Petrels, 2010b. ACAP Species assessment: Grey-headed Albatross *Thalassarche chrysostoma*. http://www.acap.aq/acap-species

Anderson, O.R.J., Small, C.J., Croxall, J.P., Dunn, E.K., Sullivan, B.S., Yates, O., Black, A., 2011. Global seabird bycatch in longline fisheries. Endanger. Species Res. 14, 91-106. http://dx.doi.org/10.3354/esr00347

Arnold, M.J., Brault, S., Crowall, J.P., 2006. Albatross population in peril: a population trajectory for black-browed albatrosses at South Georgia. Ecol. Appl. 16, 419-432. http://www.jstor.org/stable/40061809

Awkerman, J.A., Huyvaert, K.P., Mangel, J., Shigueto, J.A., Anderson D.J., 2006. Incidental and intentional catch threatens Galápagos waved albatross. Biol. Conserv. 133, 483-489. http://dx.doi.org/10.1016/j.biocon.2006.07.010

Anderson, D. J., Porter, E. T., Ferre, E. D., 2077. Non-breeding Nazca boobies (*Sula Granti*) show social and sexual interest in chicks: behavioural and ecological aspects. Behav. 141, 959-977. http://dx.doi.org/10.1163/1568539042360134

Awkerman, J.A., Westbrock, M.A., Huyvaert, K.P., Anderson D.J., 2007a. Female-biased sex ratio arises after parental care in the sexually dimorphic waved albatross (*Phoebastria irrorata*). Auk 124, 1336-1346. http://www.jstor.org/stable/25150393

Awkerman, J.A., Hobson, K.A., Anderson, D.J., 2007b. Isotopic (d15N and d13C) evidence for intersexual foraging differences and temporal variation in habitat use in waved albatrosses. Can. J. Zool. 85, 273–279. http://dx.doi.org/10.1139/Z06-202

592 Barbraud, C., Rolland, V., Jenouvrier, S., Nevoux, M., Delord, K., Weimerskirch, H., 2012.
593   Effects of climate change and fisheries bycatch on Southern Ocean seabirds: a
594   review. Mar. Ecol. Prog. Ser. 454, 285–307. http://dx.doi.org/10.3354/meps09616
595 Barnes, K.N., Ryan, P.G., Boix-Hinzen, C., 1997. The impact of the Hake *Merluccius* spp.
596   longline fishery off South Africa on procellariiform seabirds. Biol. Conserv. 82,
597   227–234. http://dx.doi.org/10.1016/S0006-3207(97)00020-7
598 Bartle, J.A., 1990. Sexual segregation of foraging zones in procellariiform birds:
599   implications of accidental capture on commercial fishery longlines of Grey Petrels
600   (*Procellaria cinerea*). Notornis 37, 146–150.
601   http://notornis.osnz.org.nz/system/files/Notornis_37_2_146.pdf
602 Bartle, J.A., 1991. Incidental capture of seabirds in the New Zealand subantarctic squid
603   trawl fishery, 1990. Bird Conserv. Int. 1, 351–359.
604   http://dx.doi.org/10.1017/S0959270900000708
605 Beck J., Nevins, H., Hester, M., 2013. Necropsy findings from Seabird Bycatch in Hawaii and
606   Alaska Longline Fisheries: Examinations conducted in 2013. Final 2013 Report:
607   Oikonos - Ecosystem Knowledge. NOAA Order No. AB133F-10-SE-3805. 11 p.
608 Blanchard, P., Hanuise, N., Dano, S., Weimerskirch, H., 2007. Offspring sex ratio in relation
609   to parental structural size and body condition in the long-lived wandering
610   albatross (*Diomedea exulans*). Behav. Ecol. Sociobiol. 61, 767-773.
611   http://dx.doi.org/10.1007/s00265-006-0307-9
612 Bretagnole, V., Thibault, J., 1995. Method for Sexing Fledglings in Cory's Shearwaters and
613   Comments on Sex-Ratio Variation. Auk 112, 785-790.
614   http://www.jstor.org/stable/4088700
615 Bregnballe, T., Frederiksen, M., 2006. Net-entrapment of great cormorants *Phalacrocorax*
616   *carbo sinensis* in relation to individual age and population size. Wildl. Biol.. 12, 143-
617   150. http://dx.doi.org/10.2981/0909-6396(2006)12[143:NOGCPC]2.0.CO;2
618 Burg, T., 2008. Genetic analysis of Wandering Albatrosses killed in longline fisheries off the
619   east coast of New Zealand. Aquat. Conserv. 17, S93–S101.
620   http://dx.doi.org/10.1002/aqc.907
621 Bugoni, L., Furness, R.W., 2009. Age composition and sexual size dimorphism of
622   albatrosses and petrels off Brazil. Mar. Ornithol. 37, 253–260.
623   http://www.marineornithology.org/PDF/37_3/37_3_253-260.pdf
624 Bugoni, L., Griffiths, K., Furness, R.W., 2011. Sex-biased incidental mortality of albatrosses
625   and petrels in longline fisheries: differential distributions at sea or differential
626   access to baits mediated by sexual size dimorphism? J. Ornithol. 152, 261-268.
627   http://dx.doi.org/10.1007/s10336-010-0577-x
628 Cardoso, L.G., Bugoni, L., Mancini, P.L., Haimovici, M., 2011. Gillnet fisheries as a major
629   mortality factor of Magellanic penguins in wintering areas. Mar. Pollut. Bull. 62,
630   840-844. http://dx.doi.org/10.1016/j.marpolbul.2011.01.033
631 Catry, P., Lemos, R., Brickle, P., Phillips, R.A., Matias, R., Granadeiro, J.P., 2013. Predicting
632   the distribution of a threatened albatross: the importance of competition, fisheries
633   and annual variability. Prog. Oceanogr. 110, 1-10.
634   http://dx.doi.org/10.1016/j.pocean.2013.01.005
635 Cuthbert, R., Hilton, G., Ryan, P., Tuck, G.N., 2005. At-sea distribution of breeding Tristan
636   albatrosses *Diomedea dabbenena* and potential interactions with pelagic longline
637   fishing in the South Atlantic Ocean. Biol. Conserv. 121, 345–355.
638   http://dx.doi.org/10.1016/j.biocon.2004.05.007
639 Copello, S., Seco-Pon, J.P., Favero, M., 2013. Use of marine space by Black-browed
640   albatrosses during the non-breeding season in the Southwest Atlantic Ocean.
641   Estuar. Coast. Shelf Sci. 123, 34-38. doi: 10.1016/j.ecss.2013.02.016
642 Croxall, J.P., Prince, P.A., 1990. Recoveries of Wandering Albatrosses *Diomedea exulans*
643   ringed at South Georgia 1958–1986. Ringing Migr. 11, 43–51. http://dx.doi.org/
644   10.1080/03078698.1990.9673960

645 Croxall, J.P., Butchart, S.H.M., Lascelles, B., Stattersfield, A.J., Sullivan, B., Symes, A., Taylor,
646   P., 2012. Seabird conservation status, threats and priority actions: a global
647   assessment. Bird Conserv. Int. 22: 1–34.
648   http://dx.doi.org/10.1017/S0959270912000020
649 Croxall, J., Small, C., Sullivan, B., Wanless, R., Frere, E., Lascelles, B., Ramirez, I., Sato, M.,
650   Yates, O., 2013. Appropriate scales and data to manage seabird-fishery
651   interactions: comment on Torres et al. 2013. Mar. Ecol. Prog. Ser. 493: 297-300.
652   http://dx.doi.org/10.3354/meps10600
653 Croxall, J.P., Prince, P.A., Rothery, P., Wood, A.G., 1998. Population changes in albatrosses at
654   South Georgia, in: Robertson, G., Gales, R., (Eds.), Albatross Biology and
655   Conservation, Surrey Beatty and Sons, Chipping Norton, pp. 69-83.
656 Darby , J.T., Dawson, M.S., 2000. Bycatch of yellow-eyed penguins (*Megadyptes antipodes*)
657   in gillnets in New Zealand waters 1979-1997. Biol. Conserv. 93, 327-332.
658   http://dx.doi.org/10.1016/S0006-3207(99)00148-2
659 Delord, K., Gasco, N., Weimerskirch, H., Barbraud, C., Micol, T., 2005. Seabird mortality in
660   the Patagonian Toothfish longline fishery around Crozet and Kerguelen Islands,
661   2001-2003. CCAMLR Science. 12, 53–80.
662   http://www.ccamlr.org/en/system/files/science_journal_papers/04delord-
663   etal.pdf
664 Delord, K., Besson, D., Barbraud, C., Weimerskirch, H., 2008. Population trends in a
665   community of large Procellariiforms of Indian Ocean: Potential effects of
666   environment and fisheries interactions. Biol. Conserv. 141, 1840-1856.
667   http://dx.doi.org/10.1016/j.biocon.2008.05.001
668 Delord, K., Barbraud, C., Weimerskirch, H., 2010. Multivariate effects on seabird bycatch in
669   the legal Patagonian Toothfish longline fishery around Crozet and Kerguelen
670   Islands. Polar Biol. 33,367-378. http://dx.doi.org/10.1007/s00300-009-0713-3
671 Dillinghan, P.W., Fletcher, D., 2011. Potential biological removal of albatrosses and petrels
672   with minimal demographic information. Biol. Conserv. 144: 1885-1894.
673   http://dx.doi.org/10.1016/j.biocon.2011.04.014
674 Donald, P.F., 2007. Adult sex ratios in wild bird populations. Ibis 149: 671–692.
675   http://dx.doi.org/ 10.1111/j.1474-919X.2007.00724.x
676 Fayet, A. L., Freeman, R., Shoji, A., Padget, O., Perrins, C. M., Guilford, T., 2015. Lower
677   foraging efficiency in immatures drives spatial segregation with breeding adults in
678   a long-lived pelagic seabird. Anim. Behav. 110: 79-89.
679   http://dx.doi.org/10.1016/j.anbehav.2015.09.008
680 Fridolfsson, A. K., Ellegren, H., 1999. A simple and universal method for molecular sexing
681   of non-ratite birds. *J. Avian Biol.* 30, 116–121.
682   http://www.jstor.org/stable/3677252
683 Gales, R., Brothers, N., Reid, T., 1998. Seabird mortality in the Japanese tuna longline
684   fishery around Australia, 1988–1995. Biol. Conserv. 86, 37-56.
685   http://dx.doi.org/10.1016/S0006-3207(98)00011-1
686 Gandini, P.A., Frere, E., 2006. Spatial and temporal patterns in the bycatch of seabirds in
687   the Argentinean longline fishery. Fish. Bull. 104, 482–485. URL:
688   http://fishbull.noaa.gov/1043/gandini.pdf
689 Gandini, P.A., Frere, E., Pettovello, A.D., Cedrola, P.V., 1999. Interaction between Magellanic
690   Penguins and Shrimp Fisheries in Patagonia, Argentina. Condor. 101, 783-789.
691   http://www.jstor.org/stable/1370065
692 Gómez-Díaz, E., González-Solís, J. 2007. Geographic assignment of seabirds to their origin:
693   combining morphologic, genetic, and biogeochemical analyses. *Ecol. Appl.* 17,
694   http://dx.doi.org/1484-1498./doi/10.1890/06-1232.1
695 Hall, M.A., Alverson, D.L., Metulzas, K.I., 2000. By-Catch: Problems and Solutions. Mar.
696   Pollut. Bull., 41: 204-219. http://dx.doi.org/10.1016/S0025-326X(00)00111-9
697 Halpern, B.S., Walbridge, S., Selkoe, K.A., Kappel, C.V., Micheli, F., D'Grosa, C., Bruno, J.F.,
698   Casey, K.S., Ebert, C., Fox, H.E., Fugita, R., Heinemann, D., Lenihan, H.S., Madin,

699   E.M.P., Perry, M.T., Selig, E.R., Spalding, M., Steneg, R., Watson, R., 2008. A global
700   map of human impact on marine ecosystem. Science 319, 948-952.
701   http://dx.doi.org/ 10.1126/science.1149345
702 Hedd, A., Montevecchi, W.A., Phillips, R.A., Fifield, D.A., 2014. Seasonal Sexual Segregation
703   by Monomorphic Sooty Shearwaters *Puffinus griseus* Reflects Different
704   Reproductive Roles during the Pre-Laying Period. PLoS ONE 9,
705   e85572. http://dx.doi.org/ 10.1371/journal.pone.0085572
706 Huyvaert, K.P., Anderson, D.J., Jones, T.C., Duan, W., Parker, P.G., 2000. Extra-pair paternity
707   in waved albatrosses. Mol. Ecol. 9, 1415–1419. http://dx.doi.org/10.1046/j.1365-
708   294x.2000.00996.x
709 Jackson, J.B.C., Kirby, M.X., W.H. Berger, Bjorndal, K.A., Botsford, L.W., Bourque, B.J.,
710   Bradbury, R.H., Cooke, R., Erlandson, J., Estes, J.A., Huges, T.P., Kidwell, S., Lange,
711   C.B., Lenihan, H.S., Pandolfi, J.A., Peterson, C.H., Steneck, R.S., Tegner, M.J., Warner,
712   R.R., 2001. Historical overfishing and the recent collapse of coastal ecosystems.
713   Science 293, 629-637. http://dx.doi.org/10.1126/science.1059199
714 Jiménez-Uzcátegui, G., Mangel, J., Alfaro-Shigueto, J., Anderson, D., 2006. Fishery bycatch of
715   the Waved Albatross *Phoebastria irrorata*, a need for implementation of
716   agreements. Galapagos Res. 64: 7-9.
717   http://www.darwinfoundation.org/datazone/media/pdf/64/GR_64_2006_%20Ji
718   menez-Uzcategui_et_al_Waved_Albatross.pdf
719 Jiménez, S., Domingo, A., Abreu, M., Brazeiro, A., 2012. Bycatch susceptibility in pelagic
720   longline fisheries: are albatrosses affected by the diving behaviour of medium-
721   sized petrels? Aquat. Conserv. 22, 436-445.
722   http://dx.doi.org/doi/10.1002/aqc.2242
723 Jiménez, S., Domingo, A., Abreu, M., Brazeiro, Defeo, O., Wood, A.G., Froy, H., Xavier, J.C.,
724   Phillips, R.A., 2015a. Sex-related variation in the vulnerability of wandering
725   albatrosses to pelagic longline fleets. Anim. Conserv. 19: 281-295.
726   http://dx.doi.org/ 10.1111/acv.12245
727 Jiménez, S., Alejandro, M., Abreu, M., Forselledo, R., Pereira, A., Domingo, A., 2015b.
728   Molecular analysis suggests the occurrence of Shy Albatross in the south-western
729   Atlantic Ocean and its by-catch in longline fishing. Emu 115, 58–62.
730   http://dx.doi.org/ 10.1071/MU13105
731 Jiménez, S., Domingo, A., Brazeiro, A., Defeo, O., Abreu, M., Forselledo, R., Phillips, R.A.,
732   2016. Sexual size dimorphism, spatial segregation and sex-biased bycatch of
733   southern and northern royal albatrosses in pelagic longline fisheries. Antarct. Sci.,
734   *First view*. http://dx.doi.org/10.1017/S0954102016000493
735 Langston, N.E., Rohwer S., 1995. Unusual pattern of incomplete primary moult in Laysan
736   and Black-footed albatrosses. Condor 97, 1-19.
737   http://www.jstor.org/stable/1368978
738 Komoroske, L.M., Lewison, R.L., 2015. Addressing fisheries bycatch in a changing world.
739   Front. Mar. Sci. 2, 83. http://dx.doi.org/10.3389/fmars.2015.00083
740 Lewison, R.L., Crowder, L.B., Wallace, B.P., Moore, J.E., Cox, T., Zydelis, R., MacDonald, S.,
741   DiMatteo, A., Dunn, D.C., Cot, C.Y., Bjorkland, R., Kelez, S., Soykan, C., Stewart, K.R.,
742   Sims, M., Boustany, A., Read, A.J., Halpin, P., Nichols, W.J., Safina, C., 2014. Global
743   patterns of marine mammal, seabird, and sea turtle bycatch reveal taxa-specific
744   and cumulative megafauna hotspots. Proc. Natl. Acad. Sci. USA 111, 5271-5276.
745   http://dx.doi.org/10.1073/pnas.1318960111
746 Lewison, R.L., Crowder, L.B., Read, A.J., Freeman, S.A., 2004. Understanding impacts of
747   fisheries bycatch on marine megafauna. Trends Ecol. Evol. 19, 598-604.
748   http://dx.doi.org/10.1016/j.tree.2004.09.004
749 Lewison, R.L., Oro, D., Godley, B.J., Underhill, L., Bearhop, S., Wilson, R.P., Ainley, D., Arcos,
750   J.M., Boersma, P.D., Borboroglu, P.G., Boulinier, T., Frederiksen, M., Genovart, M.,
751   González-Solís, J., Green, J.A., Grémillet, D., Hamer, K.C., Hilton, G.M., Hyrenbach,
752   K.D., Martínez-Abraín, A., Montevecchi, W.A., Phillips, R.A., Ryan, P.G., Sagar, P.,

753   Sydeman, W.J., Wanless, S., Watanuki, Y., Weimerskirch, H., Yorio, P., 2012.
754   Research priorities for seabirds: improving conservation and management in the
755   21st century. Endanger. Species Res. 17, 93-121.
756   http://dx.doi.org/10.3354/esr00419
757 Maree, B.A, Wanless, R,M, Fairweather, T.P., Sullivan, B.J., Yates, O., 2014. Significant
758   reductions in mortality of threatened seabirds in a South African trawl fishery.
759   Anim. Conserv. 17: 520-529. http://dx.doi.org/ 10.1111/acv.12126
760 Mills, M.S. L., Ryan, P.G., 2005. Modelling impacts of long-line fishing: what are the effects
761   of pair-bond disruption and sex-biased mortality on albatross fecundity? Anim.
762   Conserv. 8, 359-367. http://dx.doi.org/10.1017/S1367943005002386
763 Montevecchi, W.A., 2002. Interactions between fisheries and seabirds, in: Schreiber, E.A.,
764   Burger, J. (eds.), Biology of Marine Birds, CRC Press, Boca Raton, pp. 527-558.
765 Murray, T.E., Battle, J.A., Kalish, S.R., Taylor, P.R., 1993. Incidental capture of seabirds by
766   Japanese Southern Bluefin Tuna longline vessels in New Zealand waters, 1988–
767   1992. Bird Conserv. Int. 3, 181-210. http://dx.doi.org/
768   http://dx.doi.org/10.1017/S0959270900000897
769 Nel, D.C., Ryan, P.G., Watkins, B.P., 2002a. Seabird mortality in the Patagonian Toothfish
770   longline fishery around Prince Edward Island, 1996–2000. Antarct. Sci. 14, 151–
771   161. http://dx.doi.org/10.1017/S0954102002000718
772 Nel, D.C., P.G. Ryan, Nel, J.L., Klages, N.T.W., Wilson, R.P., Robertson, G., Tuck, J.N., 2002b.
773   Foraging interactions between Wandering Albatrosses *Diomedea exulans* breeding
774   on Marion Island and long-line fisheries in the southern Indian Ocean. Ibis 144,
775   E141–E154. http://dx.doi.org/10.1046/j.1474-919X.2002.00092.x
776 Neves, T., Olmos, F., 1998. Albatross mortality in fisheries off the coast of Brazil, in:
777   Robertson, G., Gales, R., (Eds.), Albatross Biology and Conservation, Surrey Beatty
778   and Sons, Chipping Norton, pp. 214–219.
779 Nevins, H.N., 2004. Diet, demography and behaviour of Common Murre (*Uria aalgae*) in
780   Central California, Master Thesis, San Francisco State University, San Francisco.
781 Nur, N., Sydeman, W.J., 1999. Demographic Processes and Population Dynamic Models of
782   Seabirds. Curr. Ornithol. 15, 149-188. http://dx.doi.org/10.1007/978-1-4757-
783   4901-4_4
784 Olmos, F., 1997. Seabirds attending bottom long-line fishing off Southeastern Brazil. Ibis
785   139, 685–691. http://dx.doi.org/10.1111/j.1474-919X.1997.tb04692.x
786 Österblom, H., Fransson, T., Olsson, O., 2002. Bycatches of common guillemot (*Uria aalge*)
787   in the Baltic Sea gillnet fishery. *Biol. Conserv.* 105, 309-319.
788   http://dx.doi.org/10.1016/S0006-3207(01)00211-7
789 Petersen, S.L., Honig, M.B., Ryan, P.G., Underhill, L.G., 2010. Seabird bycatch in the pelagic
790   longline fishery off southern Africa. Afr. J. Mar. Sci. 31, 191-204.
791   http://dx.doi.org/10.2989/AJMS.2009.31.2.7.879
792 Paleczny, M., Hammill, E., Karpouzi V, Pauly, D., 2015. Population Trend of the World's
793   Monitored Seabirds, 1950-2010. PLoS ONE 10(6), e0129342.
794 Phillips, R.A., Gales, R., Baker, G.B., Double, M.C., Favero, M., Quintana, F., Tasker, M.L.,
795   Weimerskirch, H., Uhart, M., Wolfaardt, A., 2016. The conservation status and
796   priorities for albatrosses and large petrels. Biol. Conserv. 201, 169-183.
797   http://dx.doi.org/10.1016/j.biocon.2016.06.017 0006-3207
798 Phillips, R., 2013. Requisite improvements to the estimation of seabird by-catch in pelagic
799   longline fisheries. *Anim. Conserv.* 16: 157-158.
800   http://dx.doi.org/10.1111/acv.12042
801 Phillips, R.A., McGill, R., Dawson, D., Bearhop, S., 2011. Sexual segregation in distribution,
802   diet and trophic level of seabirds: insights from stable isotope analysis. Mar. Biol.
803   158, 2199–2208. http://dx.doi.org/10.1007/s00227-011-1725-4
804 Phillips, E.M., Nevins, H.M., Hatch, S.A., Ramey, A.M., Miller, M.A., Harvey, J.T., 2010. Seabird
805   bycatch in Alaska demersal longline fishery trials: A demographic summary. Mar.

806   Ornithol. 38, 111-117. http://marineornithology.org/PDF/38_2/38_2_111-
807   117.pdf
808 Phillips, R.A., Silk, J.R.D., Croxall, J.P., Afanasyev, V., 2006. Year-round distribution of white-
809   chinned petrels from South Georgia: Relationships with oceanography and
810   fisheries. *Biol. Conserv.* 129, 336-334.
811   http://dx.doi.org/10.1016/j.biocon.2005.10.046
812 Phillips, R.A., Silk, J.R.D., Croxall, J.P., Afanasyev, V., Bennett, V.J., 2005. Summer
813   distribution and migration of nonbreeding albatrosses: individual consistencies
814   and implications for conservation. Ecology 81, 2386-2396.
815   http://dx.doi.org/10.1890/04-1885
816 Phillips R.A., Silk, J.R.D., Phalan, B., Catry, P., Croxall, J.P., 2004. Seasonal sexual segregation
817   in two *Thalassarche* albatross species: competitive exclusion, reproductive role
818   specialization or foraging niche divergence? Proc. R. Soc. B 271, 1283–1291.
819   http://dx.doi.org/10.1098/rspb.2004.2718
820 Piatt, J.F., Gould, P.J., 1994. Dispersal and drift-net mortality of endangered Japanese
821   murrelets. Auk 111: 953-961. http://dx.doi.org/10.2307/4088827
822 Poncet, S., Robertson, G., Phillips, R.A., Lawton, K., Phalan, B., Trathan, P.N., Croxall, J.P.,
823   2006. Status and distribution of wandering, black-browed and grey-headed
824   albatrosses breeding at South Georgia. Polar Biol. 29, 772-781.
825   http://dx.doi.org/10.1007/s00300-006-0114-9
826 Prince, P.A., Rothery, P., Croxall, J.P., Wood, A.G., 1994. Population dynamics of Black-
827   browed and Grey-headed Albatrosses at Bird Island, South Georgia. Ibis 136, 50–
828   71. http://dx.doi.org/10.1111/j.1474-919X.1994.tb08131.x
829 R Development Core Team, 2011. R: A Language and Environment for Statistical
830   Computing, The R Foundation for Statistical Computing, Vienna. http://www.R-
831   project.org/
832 Reid, T.A., Sullivan, B.J., Pompert, J., Enticott, J.W., Black, A.D., 2004. Seabird mortality
833   associated with Patagonian Toothfish (*Dissostichus eleginoides*) longliners in
834   Falkland Islands waters. Emu 104, 317-325.
835   http://dx.doi.org/10.1071/MU030020158-4197/04/040317
836 Robertson, C.J.R., 2000. Autopsy report for seabirds killed and returned from New Zealand
837   fisheries, 1 January 1998 to 30 September 1998. Conservation Advisory Science
838   Notes No. 294, Department of Conservation, Wellington.
839   http://www.doc.govt.nz/Documents/science-and-technical/casn294.pdf
840 Robertson, C.J.R., Bell. C., 2002. Autopsy report for seabirds killed and returned from New
841   Zealand fisheries, 1 October 1998 to 30 September 1999: Birds returned by
842   Ministry of Fisheries observers to the Department of Conservation, DOC Science
843   Internal Series 28, Department of Conservation, Wellington.
844   http://www.doc.govt.nz/documents/science-and-technical/DSIS28.pdf
845 Robertson, C.J.R., Bell, E., Scofield, P., 2004. Autopsy report for seabirds killed and returned
846   from New Zealand fisheries, 1 October 2001 to 30 September 2002: Birds returned
847   by Ministry of Fisheries observers to the Department of Conservation, DOC
848   Science Internal Series 155, Department of Conservation, Wellington.
849   http://www.doc.govt.nz/documents/science-and-technical/dsis155.pdf
850 Robertson, C.J.R., Bell, E., Scofield, P., 2003. Autopsy report for seabirds killed and returned
851   fromNew Zealand fisheries, 1 October 2000 to 30 September 2001: Birds returned
852   by Ministry of Fisheries observers to the Department of Conservation, DOC Science
853   Internal Series 96, Department of Conservation, Wellington.
854   http://doc.govt.nz/documents/science-and-technical/DSIS96.pdf
855 Rolland, V.,H. Weimerskirch, H., Barbraud, C. 2010. Relative influence of fisheries and
856   climate on the demography of four albatross species. Glob. Chang. Biol. 16,
857   1910–1922. http://dx.doi.org/10.1111/j.1365-2486.2009.02070.x
858 Roma, C.R., 2009. Composição sexual e etária do Albatroz-de-sobrancelha-negra
859   *Thalassarche melanophrys* [sic] e da Pardela-preta *Procellaria aequinoctialis*

860   (Ordem: Procellariiformes) do Sul-Sudeste do Brasil. Master dissertation,
861   Unimonte, Santos.
862 Ryan, P.G., Boix-Hinzen, C., 1999. Consistent male-biased seabird mortality in the
863   Patagonian Toothfish longline fishery. Auk 116, 851-854.
864   http://www.jstor.org/stable/4089350
865 Ryan, P.G., Keith, D.G., Kroese, M., 2002. Seabird bycatch by tuna longline fisheries off
866   Southern Africa, 1998-2000. S. Afr. J. mar. Sci. 24, 103-110.
867   http://dx.doi.org/10.2989/025776102784528565
868 Schreiber, E. A., Burger, J. 2002. Biology of Marine Birds, CRC Press, Boca Raton.
869 Shealer, D.A. 2002. Foraging behaviour and food of seabird. in: Schreiber, E. A., Burger J.
870   (eds.), Biology of Marine Birds, CRC Press, Boca Raton, pp. 137-178.
871 Sherley, R.B., Winkwer, J., Altwegg, van der Lingen, C.D., Votier, S.C., Crawford, R.J.M., 2015.
872   Bottom-up effects of a no-take zone on endangered penguin demographics. Biol.
873   Lett. 11(7), 20150237. http://dx.doi.org/10.1098/rsbl.2015.0237
874 Seco-Pon, J.P., Gandini, P.A., Favero, M., 2007. Effect of longline configuration on seabird
875   mortality in the Argentine semi-pelagic Kingclip *Genypterus blacodes* fishery. Fish.
876   Res. 85, 101-105. http://dx.doi.org/10.1016/j.fishres.2007.01.002
877 Simeone, A., Bernal, M., Meza, J., 1999. Incidental mortality of Humboldt Penguins
878   *Spheniscus humboldti* in gillnets, Central Chile. Mar. Ornithol. 27, 157–161.
879   http://www.marineornithology.org/PDF/27/27_19.pdf
880 Smith, J.L., Morgan, H.K., 2005. An assessment of seabird bycatch in longline and net
881   fisheries in British Columbia. Technical Report Series No. 401, Pacific and Yukon
882   Region, Canadian Wildlife Service, Delta, URL:
883   http://birdsmith.ca/papers/SmithMorgan_2005.pdf
884 Stauss, C., Bearhop, S., Bodey, T.W., Garthe, S., Gunn, C., Grecian, W.J., Inger, R., Knight, M.E.,
885   Newton, J., Patrick, S.C., Phillips, R.A., Waggitt, J.J., Votier, S.C., 2012. Sex-specific
886   foraging behaviour in northern gannets *Morus bassanus*: Incidence and
887   implications. Mar. Ecol. Prog. Ser. 457, 151-162. http://dx.doi.org/
888   10.3354/meps09734
889 Stempniewicz, L., 1994. Marine birds drowning in fishing nets in the Gulf of Gdańsk
890   (Southern Baltic): numbers, species composition, age and sex structure. Ornis
891   Svecica 4, 123-132.
892 Sullivan, B., Reid, T., Huin, N., Neves, T., Warlich, R., 2004. Colour marking of fledgling
893   black-browed albatross on Steeple Jason Island, Falklands Conservation.
894   http://www.falklandsconservation.com/news/54-colour-marking-of-fledgling-
895   black-browed-albatross
896 Sullivan, B., Reid, T., Bugoni, L., 2006. Seabird mortality on factory trawlers in the Falkland
897   Islands and beyond. Biol. Conserv. 131, 495-504.
898   http://dx.doi.org/10.1016/j.biocon.2006.02.007
899 Taylor, S.S., Leonard, M., 2001. Aggressive nest intrusions by male Humboldt penguins.
900   Condor 103, 162-165. http://dx.doi.org/10.1650/0010-
901   5422(2001)103[0162:ANIBMH]2.0.CO;2
902 Thiers, L., Delord, K., Barbraud, C., Phillips, R.A., Pinaud, D., Weimerskirch, H., 2014.
903   Foraging zones of the two sibling species of giant petrels in the Indian Ocean
904   throughout the annual cycle: implication for their conservation. Mar. Ecol. Prog.
905   Ser. 499, 233-248. http://dx.doi.org/10.3354/meps10620
906 Thompson, D.R., 2010a. Autopsy report for seabirds killed and returned from observed
907   New Zealand fisheries: 1 October 2006 to 30 September 2007. DOC Marine
908   Conservation Services 3. Department of Conservation, Wellington.
909   http://www.doc.govt.nz/Documents/science-and-technical/dmcs3entire.pdf
910 Thompson, D.R., 2010b. Autopsy report for seabirds killed and returned from observed
911   New Zealand fisheries: 1 October 2008 to 30 September 2009. DOC Marine
912   Conservation Services Series 6. Department of Conservation, Wellington.
913   http://www.doc.govt.nz/Documents/science-and-technical/dmcs6entire.pdf

914 Thompson, D.R., 2009. Autopsy report for seabirds killed and returned from observed
915   New Zealand fisheries: 1 October 2005 to 30 September 2006. DOC Marine
916   Conservation Services 2. Department of Conservation, Wellington.
917 Thompson, C.W., Wilson, M.L., Pierce, D.J., DeGhetto, D., 1998. Population characteristics of
918   Common Murres and Rhinoceros Auklets entangled in gillnets in Puget Sound,
919   Washington, from 1993 to 1994. Northwest. Nat. 79, 77-91.
920   http://www.jstor.org/stable/3536837
921 Trebilco, R., Gales, R., Lawrence, E., Alderman, R., Robertson, G., Baker, G.B., 2011.
922   Characterizing seabird bycatch in the eastern Australian tuna and billfish pelagic
923   longline fishery in relation to temporal, spatial and biological influences. Aquat.
924   Conserv. 20, 531-542. http://dx.doi.org/10.1002/aqc.1115
925 Tuck, G.N., Polacheck, T., Bulman, C.M., 2003. Spatio-temporal trends of longline fishing
926   effort in the Southern Ocean and implications for seabird bycatch. Biol. Conserv.
927   114, 1-27. http://dx.doi.org/10.1016/S0006-3207(02)00378-6
928 Uhlmann, S., Fletcher, D., Moller, H., 2005. Estimating incidental takes of shearwaters in
929   driftnet fisheries: lessons for the conservation of seabirds. Biol. Conserv. 123, 151-
930   163. http://dx.doi.org/10.1016/j.biocon.2004.11.003
931 Velando, A., Graves, J. Ortega-Ruano, J.E., 2002. Sex ratio in relation to timing of breeding,
932   and laying sequence in a dimorphic seabird. Ibis 144, 9-16. http://dx.doi.org/
933   10.1046/j.0019-1019.2001.00002.x
934 Votier, S.C., Grecian, W.J., Patrick, S., Newton J., 2011 Inter-colony movements, at-sea
935   behaviour and foraging in an immature seabird: results from GPS-PPT tracking,
936   radio-tracking and stable isotope analysis. Mar. Biol.158, 355–362.
937   http://dx.doi.org/10.1007/s00227-010-1563-9
938 Votier S.C., Bicknell A., Cox, S.L., Scales, K.L., Patrick, S.C., 2013. A Bird's Eye View of Discard
939   Reforms: Bird-Borne Cameras Reveal Seabird/Fishery Interactions. PLoS ONE 8,
940   e57376. http://dx.doi.org/10.1371/journal.pone.0057376
941 Waugh, S.M., Sagar, P.M., Cossee, R.O., 1999. New Zealand Black-browed Albatross
942   *Diomedea melanophrys impavida* and Grey-headed Albatross *D-chrysostoma*
943   banded at Campbell Island: Recoveries from the South Pacific region. Emu 99, 29-
944   35.
945 Waugh, S.M., MacKenzie, D.I., Fletcher, D., 2008. Seabird bycatch in New Zealand trawl and
946   longline fisheries, 1998–2004. Pap. proc. R. Soc. Tasmania 142, 45–66.
947   https://www.stats.otago.ac.nz/webdata/resources/david_fletcher/Waugh_et_al_2
948   008.pdf
949 Weimerskirch, H., Jouventin, P., 1987. Population dynamics of the wandering albatross,
950   *Diomedea exulans*, of the Crozet Islands: causes and consequences of the
951   population decline. Oikos 49, 315-322. URL: http://www.jstor.org/stable/35657
952 Weimerskirch. H., Akesson, S., Pinaud, D., 2006. Postnatal dispersal of wandering
953   albatrosses *Diomedea exulans*: implications for the conservation of the species. J.
954   Avian Biol. 37, 23–28. http://dx.doi.org/10.1111/j.2006.0908-8857.03675.x
955 Weimerskirch, H., J. Lallemand, Martin, J. 2005. Population sex ratio variation in a
956   monogamous long-lived bird, the wandering albatross. *J. Anim. Ecol.* 74, 285-291.
957   http://dx.doi.org/10.1111/j.1365-2656.2004.00922.x
958 Weimerskirch, H., Cherel, Y., Delord, K., Jaeger, A., Patrick, S.C., Riotte-Lambert, L., 2014.
959   Lifetime foraging patterns of the wandering albatross: Life on the move! J. Exp.
960   Mar. Biol. Ecol. 450, 68-78. http://dx.doi.org/10.1016/j.jembe.2013.10.021
961 Žydelis, R., Bellebaum, J., Österblom, H., Vetemaa, M., Schirmeister, B., Stipniece, A., M.,
962   Dagys, van Eerden, M., Garthe, S., 2009. Bycatch in gillnet fisheries – An overlooked
963   threat to waterbird populations. Biol. Conserv. 142, 1269-1281.
964   http://dx.doi.org/10.1016/j.biocon.2009.02.025
965 Žydelis, R., Small, C., French, G., 2013. The incidental catch of seabirds in gillnet fisheries: A
966   global review. Biol. Conserv. 162: 76-88.
967   http://dx.doi.org/10.1016/j.biocon.2013.04.002

968   Zuur, A.F., Ieno, E.N., Walker, N.J., Saveliev, A.A., Smith, G., 2009. Mixed Effects Models and
969   Extensions in Ecology with R, Springer, New York.
970
971
972
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976
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1023 **TABLES**

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1025 **Table 1.** List of the studies (n = 44) reporting sex and age composition of seabird bycaught
1026 in fisheries, with information on the number of taxa with data (N), type of fishery (PLL,
1027 pelagic longline; DLL, demersal longline; TRA, trawl; GIL, gillnet; PND, pound net; INT,
1028 intentional), region (SUBANT: sub-Antarctic; SUBARC: sub-Arctic; SUBTRS, subtropical
1029 southern; SUBTRN, subtropical northern; TROPIC, tropical), area, and year of the bycatch.

Reference	N species	N sexed	N aged	Fishery	Region	Area	Bycatch year
Jiménez et al., 2016	2	128	0	PLL	SUBTRS	Uruguay	2004-2012
Jiménez et al., 2015a	1	49	116	PLL	SUBTRS	Uruguay	1999-2012
Jiménez et al., 2015b	1	28	28	PLL	SUBTRS	Uruguay	2008-2011
Beck et al., 2013	4	822	694	DLL, PLL	SUBARC, SUBTRN	Hawaii, Alaska	2007-2013
Trebilco et al., 2011	1	233	89	PLL	SUBTRS	Australia	2001-2006
Cardoso et al., 2011	1	0	20	GIL	SUBTRS	Brazil	2009
Phillips et al., 2010	4	365	348	DLL	SUBARC	Alaska	2005
Petersen et al., 2010	3	935	1175	PLL	SUBTRS	South Africa	1998-2005
Delord et al., 2010	1	5189	0	DLL	SUBANT	Kerguelen	2003-2006
Thompson, 2010a	7	312	327	PLL, TRA	SUBANT, SUBTRS	New Zealand	2006-2007
Thompson, 2010b*	7	361	367	PLL, TRA	SUBANT, SUBTRS	New Zealand	2008-2009
Thompson et al., 2009	4	308	311	DLL, PLL, TRA	SUBANT	New Zealand	2005-2006
Roma, 2009	1	100	67	PLL	SUBTRS	Brazil	2006-2008
Burg, 2008	1	27	0	PLL	SUBANT, SUBTRS	New Zealand	1997
Seco-Pon et al., 2007	2	74	18	DLL	SUBANT	Argentina	2005
Gandini and Frere, 2006	2	31	0	DLL	SUBANT	Argentina	200-2001
Awkerman et al.. 2006	1	33	0	PLL, GIL, INT	TROPIC	Peru	2005
Bregnballe and Frederiksen, 2006	1	0	289	PND	SUBARC	North Sea	1983-1992
Jiménez-Uzcátegui et al., 2006	1	0	40	PLL, GIL, INT	TROPIC	Peru	1998-2006
Delord et al., 2005	1	379	0	DLL	SUBANT	Kerguelen	2001-2003
Smith and Morgan, 2005	2	205	205	GIL	SUBARC	NE Pacific	1995-2001
Nevins, 2004	1	785	785	GIL	SUBTRN	California	1999-2000
Robertson et al., 2004*	5	643	646	DLL, PLL, TRA	SUBANT, SUBTRS	New Zealand	2001-2002
Robertson et al., 2003*	9	898	1033	DLL, PLL, TRA	SUBANT, SUBTRS	New Zealand	2000-2001
Reid et al., 2004	1	17	0	DLL	SUBANT	Falklands	2001-2002
Ryan et al., 2002	2	0	50	PLL	SUBTRS	South Africa	1998-2000
Nel et al., 2002a	4	962	241	DLL	SUBANT	Prince Edward	1996-2000
Osterblom et al., 2002	1	0	765	GIL	SUBARC	Baltic Sea	1972-1999
Darby and Dawson, 2000	1	42	42	GIL	SUBANT	New Zealand	1979-1997
Robertson, 2000*	4	161	161	PLL,TRA	SUBANT, SUBTRS	New Zealand	1998
Robertson and Bell, 2002	4	150	153	BLL, PLL, TRA	SUBANT, SUBTRS	New Zealand	1998-1999
Ryan and Box-Hinzen, 1999	4	388	367	DLL	SUBANT	Prince Edward	1996-1997
Gandini et al., 1999	1	31	0	TRA	SUBANT	Argentina	1995-1997
Simeone et al., 1999	1	0	663	GIL	SUBANT	Chile	1991-1996
Thompson et al., 1998	2	322	322	GIL	SUBARC	NE Pacific	1994-1994
Gales at al., 1998	8	407	407	PLL	SUBANT, SUBTRS	Australia	1988-1995
Barnes et al., 1997	1	33	0	DLL	SUBTRS	South Africa	1994
Neves and Olmos, 1997	2	50	50	PLL	SUBTRS	Brazil	1994-1995
Langston and Rohwer, 1995	2	308	308	GIL	SUBTRN	North Pacific	1990-1991
Stempniewicz, 1994	7	1149	1149	GIL	SUBARC	Baltic Sea	1972-76,

							86-90
Murray et al., 1993	4	100	105	PLL	SUBANT, SUBTRS	New Zealand	1988-1992
Bartle, 1991	1	35	35	TRA	SUBANT	New Zealand	1990
Bartle, 1990	1	16	16	PLL	SUBANT	New Zealand	1989
Croxal and Prince, 1990	1	12	12	PLL	SUBTRS	N Argentina, Uruguay, Brazil	1984-1986

* Bycatch in subtropical and sub-Antarctic areas of New Zealand was pooled.

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1078 **Table 2**. Candidate mixed effect models for proportion of males, and proportion of adults in seabird
1079 bycatch composition as influenced by region and type of fishery. All models included species as a
1080 random effect. Best models are highlighted in bold.

Model	df	AICc	ΔAICc	Deviance	Resid df
Sex (y <- proportion of males)					
y ~ Region * Fishery	**5**	**-37.17**	**0**	**142.2**	**79**
Y ~ Region	3	-22.37	14.8	211.98	95
y ~ 1	2	-18.27	18.9	183.5	80
y ~ Region + Fishery	4	12.17	49.34	381.34	122
y ~ Fishery	3	18.65	55.82	310.4	90
Age (y <- Proportion of adults)					
y ~ Region * Fishery	**5**	**48.4**	**0.0**	**35.1**	**68**
y ~ Region + Fishery	4	55.5	7.1	44.6	69
y ~ Fishery	3	72.1	23.7	63.3	79
Y ~ Region	3	83.3	34.9	74.8	85
y ~ 1	2	109.9	61.5	103.7	112

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1123 **Table 3**. Frequency of bycatch samples per fishery type and region not skewed and skewed toward
1124 males (M) or females (F), and toward adults (A) or immatures (I); per fishery type and regions.

	Sex				Age			
	Not skewed	M	F	p (χ^2)	Not skewed	A	I	p (χ^2_{Yates}): A vs I[a]
<u>Fishery</u>								
Pelagic longline	18	14	16	0.779	5	27	15	0.090
Demersal longline	**9**	**15**	**2**	**0.008**	0	**14**	**4**	**0.034**
Gillnet	7	6	2	na[b]	3	8	7	1.000
Trawl	**5**	**12**	**1**	**0.006**	0	**17**	**0**	**<0.001**
Longlines combined	27	29	18	0.249	5	**41**	**19**	**0.007**
<u>Region</u>								
Sub-Antarctic	**18**	**26**	**3**	**<0.001**	2	**29**	**7**	**<0.001**
Sub-Arctic	**8**	**8**	**1**	**0.056**	1	11	7	0.479
Subtropical South	8	5	12	0.228	3	10	10	1.000
Subtropical North	2	2	3	na	1	4	2	na
Sub-polar	**26**	**34**	**4**	**<0.001**	3	**41**	**15**	**<0.001**
Subtropical	10	7	13	0.407	4	14	12	0.844

[a] Comparisons were made only between the frequency of adult- and immature-skewed samples since unbalanced age ratios are expected in wild populations; [b] "na" (not available) refers to frequencies not compared due to small sample sizes.

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1159 **Table 4**. Candidate mixed effect models for proportion of males, and proportion of adults in seabird
1160 bycatch composition as influenced by fishery gear-type consider fisheries in the subpolar region
1161 only, which was the region with comparable sample sizes among fisheries. All models included
1162 species as a random effect. Best models are highlighted in bold.

Model	df	AICc	ΔAICc	Deviance	Resid df
Sex (y <- proportion of males)					
y ~ Fishery, subpolar only	**4**	**-40.1**	**0.0**	**75.9**	**54**
y ~ 1	1	12.17	5.2	381.3	122
Age (y <- Proportion of adults)					
y ~ Fishery, subpolar only	**4**	**14.4**	**0.0**	**188.4**	**47**
y ~ 1	1	95.6	81.2	1033.9	114

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1207 **FIGURES**
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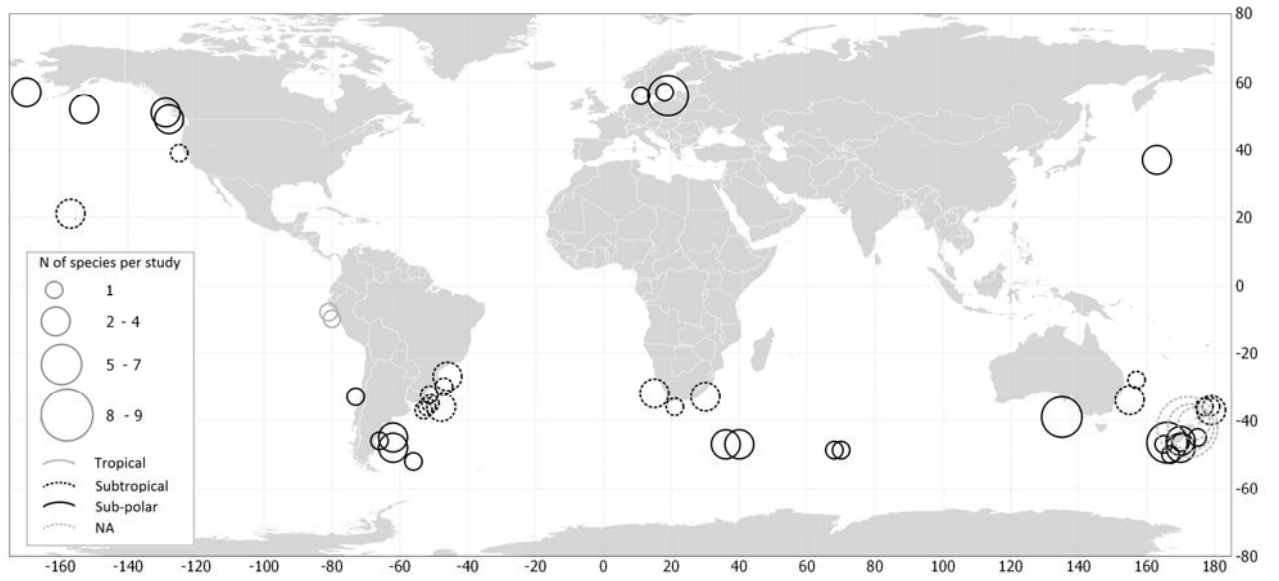
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1211 **Figure 1. (Two columns fitting)**
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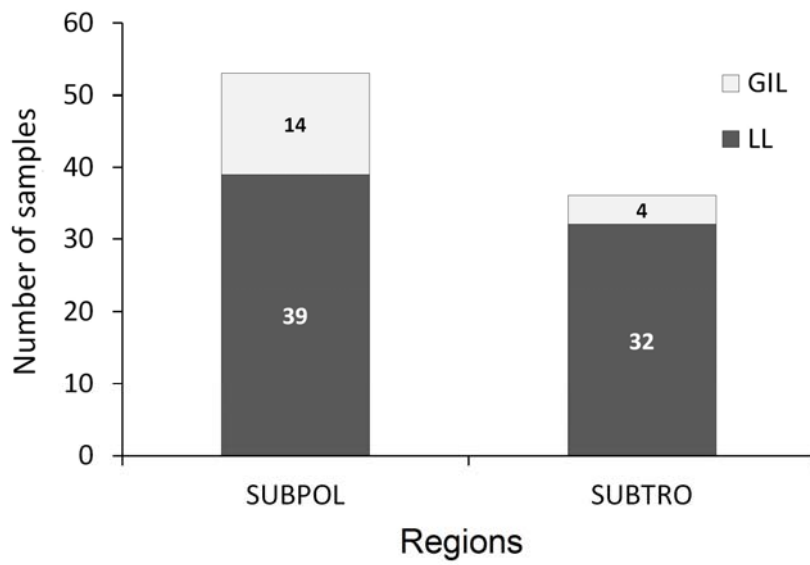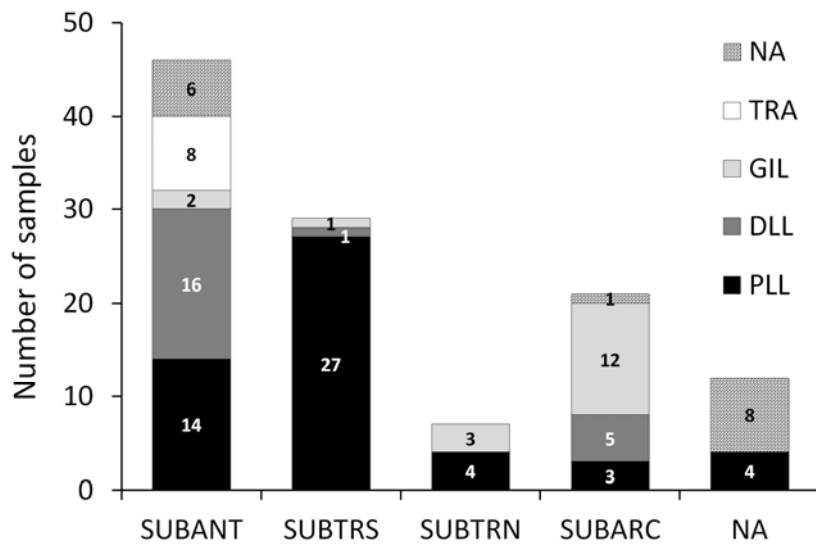
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1233   **Figure 2. (Single column fitting)**
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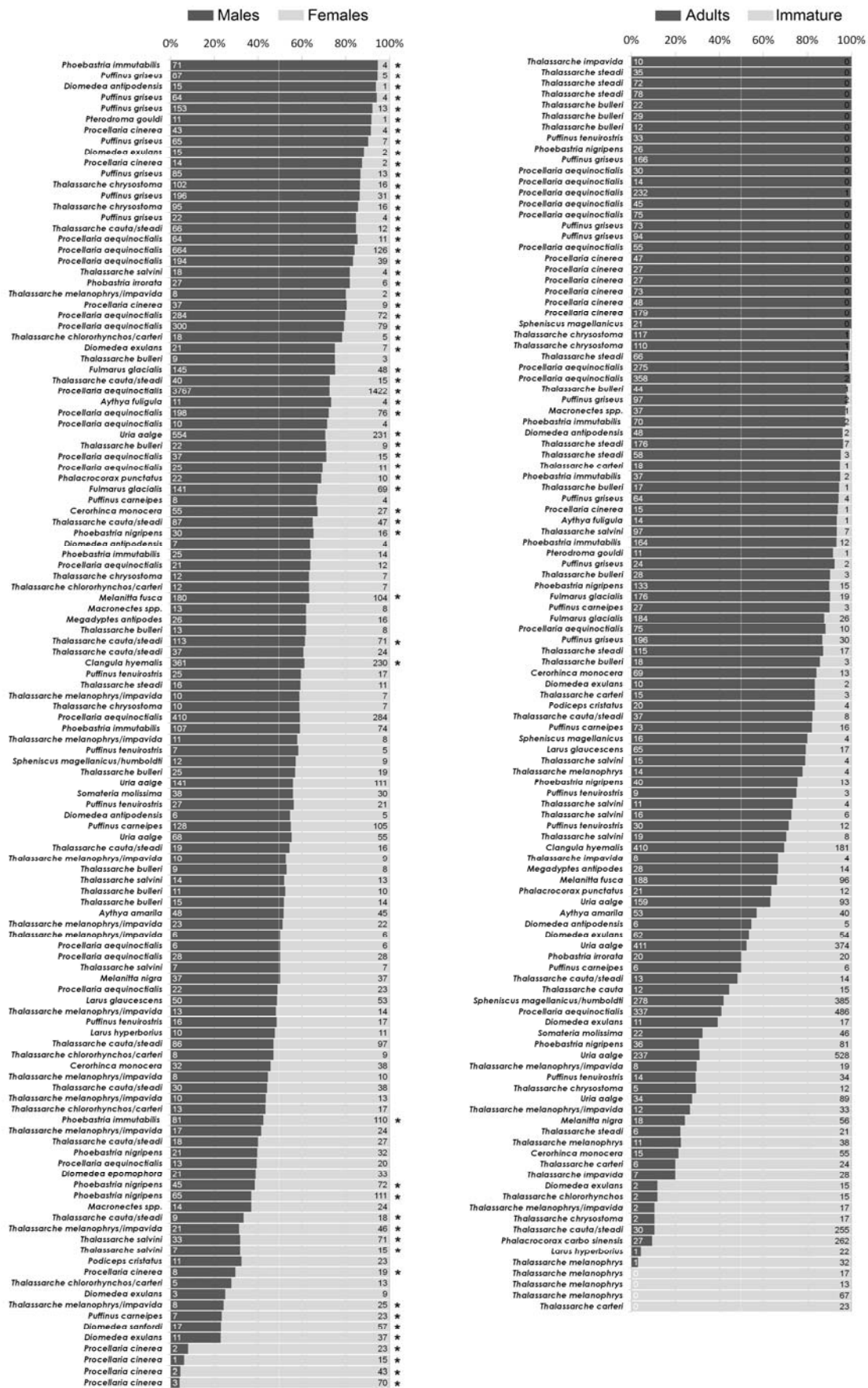
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1236 **Figure 3**. **(Two columns fitting)**
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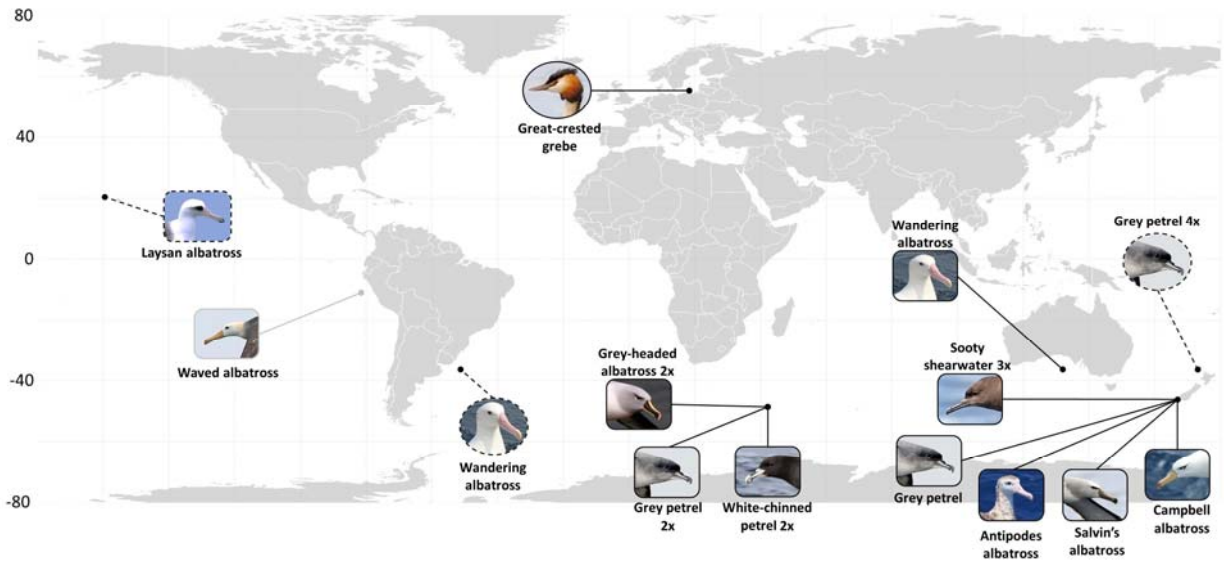
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1240 **Figure 4**. **(Two columns fitting)**
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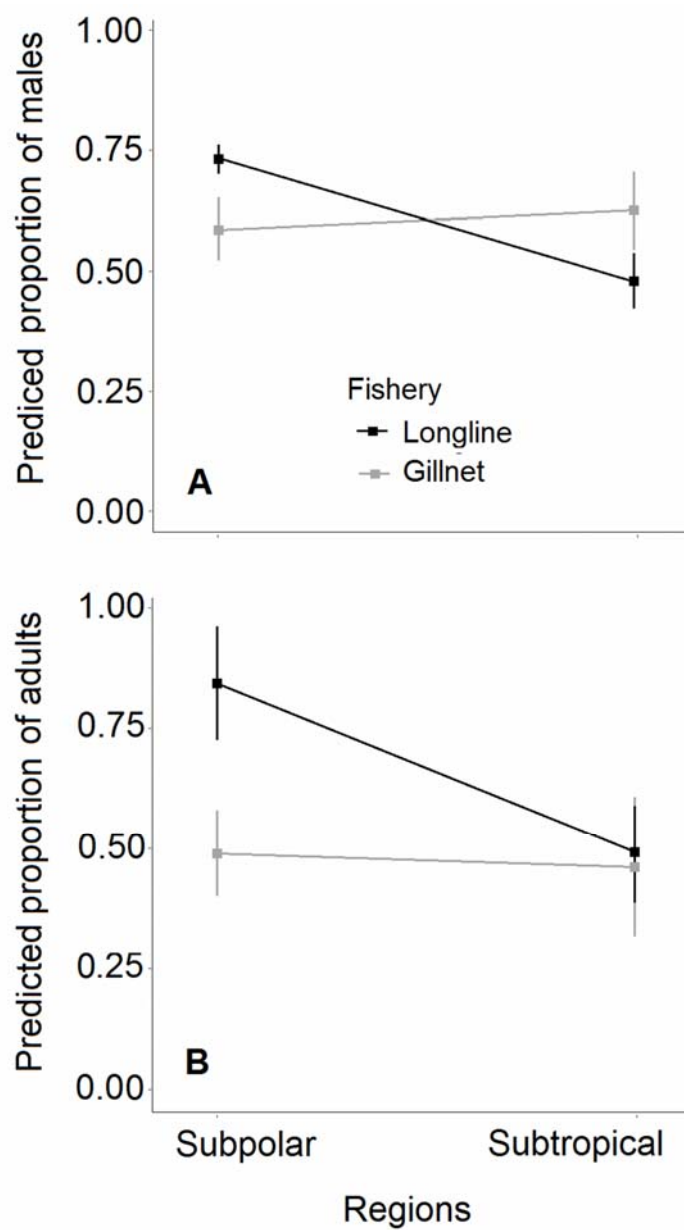
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1261 **Figure 5. (Single column fit)**
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A $F = 38.464, \ p < 0.001$
B   ns
C $F = 6.262 \ \ p < 0.05$
D $F = 23.578, \ p < 0.001$
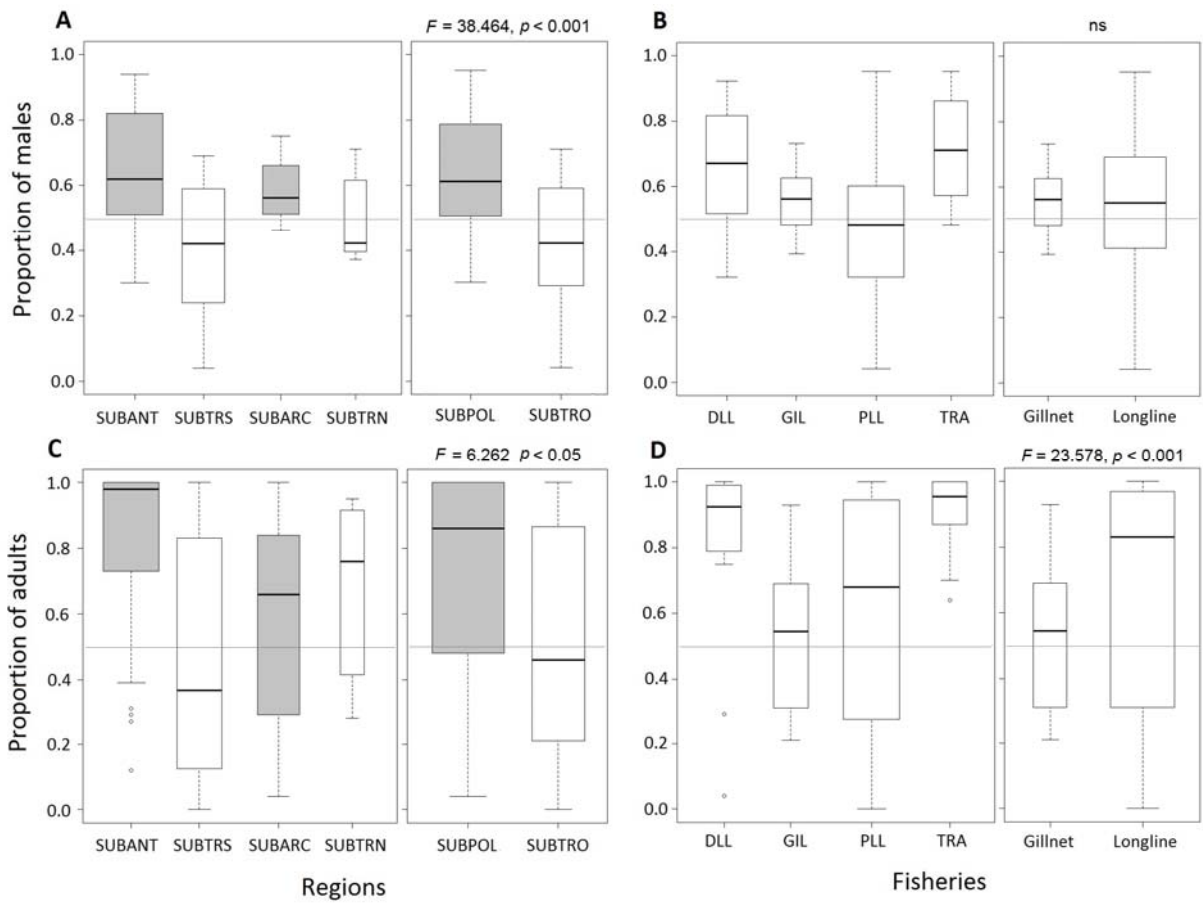
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1264   **Figure 6. (1.5 column fitting)**

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abc   ab   abc   ac

$F = 10.556, P < 0.01$

B

ac   bc   abc   ac

$F = 17.175, P < 0.001$

DLL   GIL   PLL   TRA
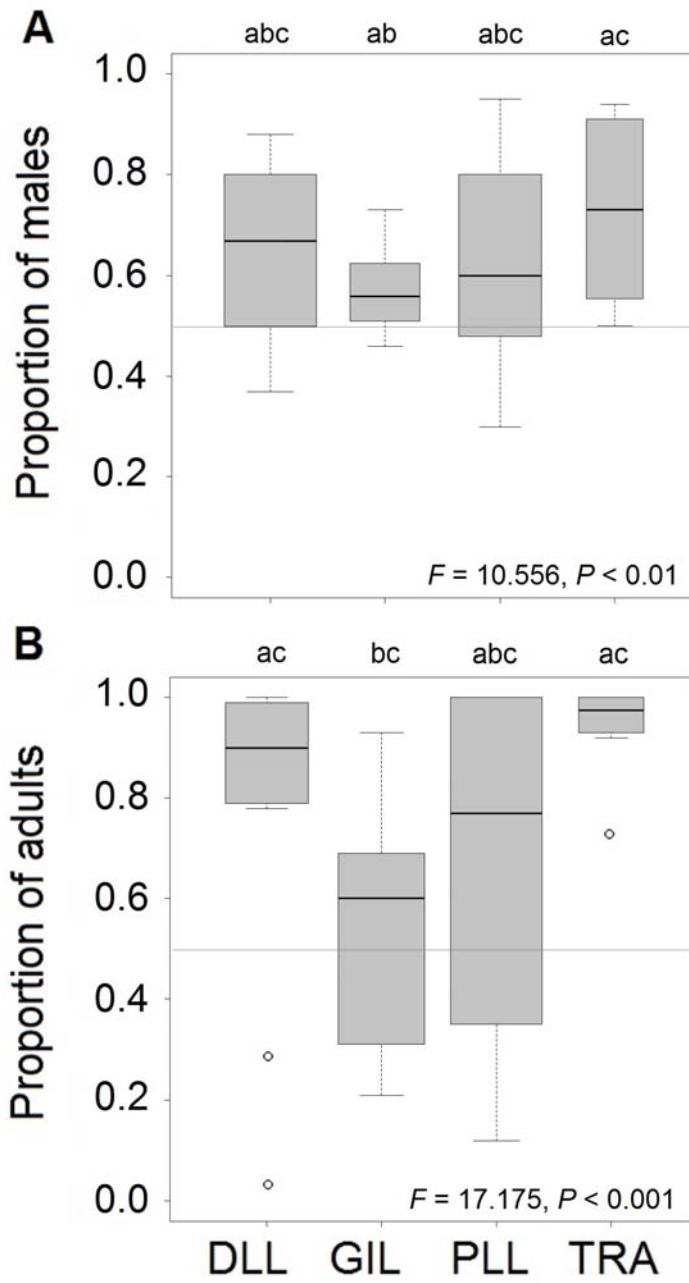
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1266   Figure 7. (Single column)
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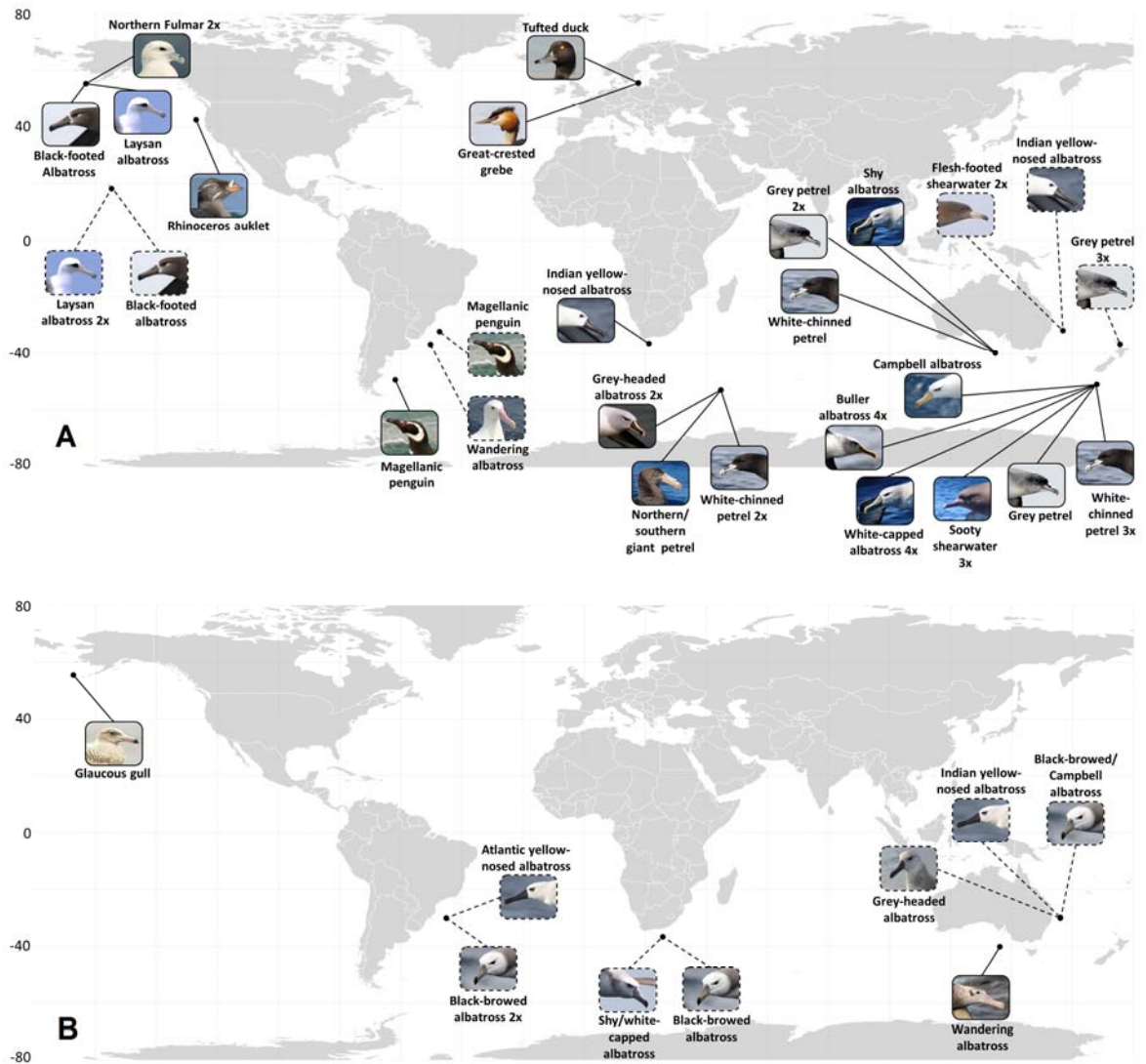
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1271 **Figure 8**. **(Two columns fitting)**
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FIGURE LEGENDS

Figure 1. Spatial distribution of seabird bycatch studies with data on sex and age composition. The size of the circles indicates the number of species per study. Black solid and dotted circles indicate subpolar and subtropical regions, respectively. Light grey solid circles show studies in the tropics (Peru), and light grey dotted circles correspond to studies from New Zealand without detailed information on region (NA), which were therefore excluded from the analysis of regional effects. **(Two columns fitting)**

Figure 2. Number of bycatch samples by main fishery type and regions, reflecting (A) the original data, and (B) fisheries categories collapsed for the purposes of modelling. Abbreviations: SUBANT, sub-Antarctic; SUBARC, sub-Arctic; SUBTRS, subtropical southern; SUBTRN, subtropical northern; SUBPOL, subpolar; SUBTRO, subtropical; PLL, pelagic longline; DLL, demersal longline; GIL, gillnet; TRA, trawl; LL, longline; NA, detailed data per fishery type or region was not available. **(Single column fitting)**

Figure 3. Sex (A) and age ratios (B) of seabird species reported as bycatch in global fisheries. The number of individuals in each sample is shown inside the bars, and asterisks indicate sex compositions that deviated statistically from the expected sex ratio of 1:1 (χ^2_{Yates}, P < 0.05). Deviation from a 1:1 ratio age ratios were not tested because equal proportions of adults and immatures are not expected in wild populations. **(Two columns fitting)**

Figure 4. Geographical distribution of the highly sex-biased bycatch samples (≥80% of one sex). Squared figures refer to male and circled figures refer to female-biased samples. Black solid, black dotted and grey lines denote bycatch events in subpolar, subtropical and tropical regions respectively. Highly sex-biased samples from studies that subtropical and sub-Antarctic areas of New Zealand were pooled are not shown. The numbers follow common names indicate the number of sex-biased samples for that taxon in the given location. **(Two columns fitting)**

Figure 5. Interaction effect of region (subpolar vs subtropical) and fishery type (longline [demersal and pelagic combined] vs gillnet) on the proportion of males (A) and adults (B) in seabird bycatch. **(Single column fit)**

Figure 6. Proportion of males (top) and of adults (bottom) in seabird bycatch samples by region (left) and fishery type (right). Box plots show the median and the 25th and 75th percentiles, whiskers indicate values within 1.5 times of the interquartile range, circles

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represent outliers, and box plot width varies with the sample size, and the horizontal grey line indicates the 0.5 mark. Abbreviations: SUBANT, sub-Antarctic; SUBARC, sub-Arctic; SUBTRS, subtropical southern; SUBTRN, subtropical northern; SUBPOL, subpolar; SUBTRO, subtropical; PLL, pelagic longline; DLL, demersal longline; GIL, gillnet; TRA, trawl. Grey boxes in A and C indicate subpolar regions. *F-statistic* and *P-value* from ANOVA comparing the effect of region (subtropical vs subpolar) and fishery type (longline [demersal and pelagic combined] vs gillnet) are shown inside the graph area **(Two columns fitting)**

F**igure 7.** Proportion of males (A) and of adults (B) in seabird bycatch samples compared among the four major gear types using only data from subpolar regions. Box plots show the median and the 25th and 75th percentiles, whiskers indicate values within 1.5 times of the interquartile range, circles represent outliers, box plot width varies with the sample size, and the horizontal grey line indicates the 0.5 mark. Abbreviations: PLL, pelagic longline; DLL, demersal longline; GIL, gillnet; TRA, trawl. *F-statistic* and *P-value* from ANOVA comparing the effect of fishery type are shown inside the graph area. Box-plots not sharing the same lower case letters are statistically distinct ($P < 0.05$) according to Tukey post-hoc test. **(Single column)**

Figure 8. Geographical distribution of bycatch samples highly skewed towards adult (A) or towards immature (B) (≥80% of one age class). Solid and dotted lines denote bycatch events in subpolar and subtropical regions respectively. The numbers following common names indicate the number of highly age-biased samples for that taxon in the given location. **(Two columns fitting)**

Appendix A. List of the species included in this study.

Family	Common name	Specie	IUCN*
Albatrosses (Diomedeidae)	Wandering albatross	*Diomedea exulans*	VU
	Antipodean albatross	*Diomedea antipodensis*	VU
	Northern royal albatross	*Diomedea sanfordi*	EN
	Southern royal albatross	*Diomedea epomophora*	VU
	Black-browed albatross	*Thalassarche melanophris*	NT
	Campbell albatross	*Thalassarche impavida*	VU
	White-capped albatross	*Thalassarche steadi*	NT
	Shy albatross	*Thalassarche cauta*	NT
	Salvin's albatross	*Thalassarche salvini*	VU
	Grey-headed albatross	*Thalassarche chrysostoma*	EN
	Buller's albatross	*Thalassarche bulleri*	NT
	Atlantic yellow-nosed albatross	*Thalassarche chlororhynchos*	EN
	Indian yellow-nosed albatross	*Thalassarche carteri*	EN
	Laysan albatross	*Phoebastria immutabilis*	NT
	Black-footed albatross	*Phoebastria nigripes*	NT
	Waved albatross	*Phoebastria irrorata*	CR
Petrels (Procellaridae)	Southern giant petrel	*Macronectes giganteus*	LC
	Northern giant petrel	*Macronectes halli*	LC
	Northern fulmar	*Fulmarus glacialis*	LC
	Flesh-footed shearwater	*Puffinus carneipes*	LC
	White-chinned petrel	*Procellaria aequinoctialis*	VU
	Short-tailed shearwater	*Puffinus tenuirostris*	LC
	Sooty shearwater	*Puffinus griseus*	NT
	Grey petrel	*Procellaria cinerea*	LC
	Grey-faced petrel	*Pterodroma gouldi*	LC
Sea ducks (Merginae)	Tufted duck	*Aythya fuligula*	LC
	Greater scaup	*Aythya marila*	LC
	Long-tailed duck	*Clangula hyemalis*	VU
	Velvet scoter	*Melanitta fusca*	EN
	Common scoter	*Melanitta nigra*	LC
	Common eider	*Somateria mollissima*	LC
Penguins (Spheniscidae)	Yellow-eyed penguin	*Megadyptes antipodes*	EN
	Magellanic penguin	*Spheniscus magellanicus*	NT
	Humboldt penguin	*Spheniscus humboldti*	VU
Auks (Alcidae)	Common guillemot	*Uria aalge*	LC
	Rhinoceros auklet	*Cerorhinca monocerata*	LC
Gulls (Laridae)	Glaucous-winged gull	*Larus glaucescens*	LC
	Glaucous gull	*Larus hyperboreus*	LC
Cormorants (Phalacrocoracidae)	Great cormorant	*Phalacrocorax carbo*	LC
	Spotted shag	*Phalacrocorax punctatus*	LC
Grebes (Podicipodidae)	Great crested grebe	*Podiceps cristatus*	LC

* IUCN Status: LC, Least concern; NT, Near threat; VU, Vulnerable; EN, Endangered; CR, Critically endangered.

Apendix B. Detailed information of each bycatch report comprised for the present study, including specie, number of birds sexed (N sexed), number of males (M) and females (F), proportion of males (P_M), number of birds aged (N aged), number of adults (A) and immature (I), proportion of adults (P_A), fishery type (Fishery), location, region, period of study and reference. Abbreviations: SUBANT, sub-Antarctic; SUBARC, sub-Arctic; SUBTRS, subtropical southern; SUBTRN, subtropical northern; SUBPOL, subpolar; SUBTRO, subtropical; TROPIC, tropical; PLL, pelagic longline; DLL, demersal longline; GIL, gillnet; TRA, trawl; POU, pound net; INT, intentional catch.

Specie[1]	N sexed	M	F	P_M	$p\,\chi^2$ Yates	N aged	A	I	P_A	Fishery	Area	Region	Period of study	Reference
DIEXU	12	3	9	0.25	ns	12	10	2	0.83	PLL	SW Atlantic	SUBTRS	1984-1986	Croxall & Prince (1990)
DIEXU	28	21	7	0.76	<0.05	28	11	17	0.39	PLL	Australia	SUBANT	1988-1995	Gales at al. (1998)
DIEXU	17	15	2	0.86	<0.005	17	2	15	0.12	PLL	Australia	SUBANT	1988-1995	Gales at al. (1998)
DIEXU	48	11	27	0.23	<0.05	116	62	54	0.53	PLL	Uruguay	SUBTRS	1999-2012	Jiménez et al. (2015a)
DIANT	11	6	5	0.55	ns	na	na	na	na	PLL	New Zealand	SUBTRS	1997	Burg (2008)
DIANT	11	7	4	0.63	ns	11	6	5	0.54	PLL	New Zealand	SUBTRS, SUBANT	1988-1992	Murray et al. (1993)
DIANT	16	15	1	0.94	0.001	na	na	na	na	PLL	New Zealand	SUBANT	1997	Burg (2008)
DIANT	50	24	26	0.48	ns	50	48	2	0.96	PLL	New Zealand	SUBTRS, SUBANT	1998	Robertson (2000)
DISAN	74	17	57	0.23	<0.01	na	na	na	na	PLL	Uruguay	SUBTRS	2004-2012	Jiménez et al. (2016)
DIEPO	54	21	33	0.39	ns	na	na	na	na	PLL	Uruguay	SUBTRS	2004-2012	Jiménez et al. (2016)
THMEL	19	10	9	0.53	ns	na	na	na	na	DLL	Argentina	SUBANT	200-2001	Gandini and Frere (2006)
THMEL	33	8	25	0.24	<0.001	33	1	32	0.03	PLL	Brazil	SUBTRS	1994-1995	Neves and Olmos (1998)
THMEL	17	10	7	0.59	ns	17	0	17	0.00	DLL	Falklands	SUBANT	2001-2002	Reid et al. (2004)
THMEL	18	8	10	0.44	ns	18	14	4	0.78	DLL	Argentina	SUBANT	2005	Seco-Pon et al. (2007)
THMEL	41	17	24	0.41	ns	49	11	38	0.22	PLL	South Africa	SUBTRS	1998-2005	Petersen et al. (2010)

THIMP	12	6	6	0.50	ns	12	8	4	0.67	PLL	New Zealand	SUBTRS, SUBANT	1998	Robertson (2000)
THIMP	10	8	2	0.80	ns	10	10	0	1.00	PLL	New Zealand	SUBANT	2006-2007	Thompson (2010a)
THIMP	23	10	13	0.43	ns	25	7	28	0.28	PLL	New Zeland	SUBTRS	1988-1992	Murray et al. (1993)
THMEL/THIMP	19	11	8	0.60	ns	19	2	17	0.13	PLL	Australia	SUBTRS	1988-1995	Gales at al. (1998)
THMEL/THIMP	45	23	22	0.51	ns	45	12	33	0.27	PLL	Australia	SUBANT	1988-1995	Gales at al. (1998)
THMEL/THIMP	27	13	14	0.47	ns	27	8	19	0.31	PLL	Australia	SUBANT	1988-1995	Gales at al. (1998)
THMEL	na	na	na	na	na	13	0	13	0.00	PLL	South Africa	SUBTRS	1998-2000	Ryan et al. (2002)
THMEL	67	21	46	0.31	<0.005	67	0	67	0.00	PLL	Brazil	SUBTRS	2006-2008	Roma (2009)
THCHR	118	102	16	0.86	<0.0001	118	117	1	0.99	DLL	Prince Edward	SUBANT	1996-2000	Nel et al. (2002a)
THCHR	111	95	16	0.86	<0.0001	111	110	1	0.99	DLL	Prince Edward	SUBANT	1996-1997	Ryan and Box-Hinzen (1999)
THCHR	19	12	7	0.64	ns	19	2	17	0.09	PLL	Australia	SUBTRS	1988-1995	Gales at al. (1998)
THCHR	17	10	7	0.60	ns	17	5	12	0.29	PLL	Australia	SUBANT	1988-1995	Gales at al. (1998)
THCAU/THSTE	183	86	97	0.47	ns	285	30	255	0.11	PLL	South Africa	SUBTRS	1998-2005	Petersen et al. (2010)
THCAU/THSTE	45	18	27	0.41	ns	45	37	8	0.83	PLL	Australia	SUBANT	1988-1995	Gales at al. (1998)
THCAU/THSTE	27	9	18	0.32	ns	27	13	14	0.48	PLL	Australia	SUBANT	1988-1995	Gales at al. (1998)
THSTE	27	16	11	0.59	ns	27	6	21	0.22	PLL	Uruguay	SUBANT	2008-2011	Jimenez et al. (2015b)
THSTE	35	19	16	0.54	ns	35	35	0	1.00	TRA	New Zeland	SUBANT	1990	Bartle (1991)
THSTE	55	40	15	0.73	<0.005	67	66	1	0.99	TRA	New Zeland	SUBTRS, SUBANT	2008-2009	Thompson (2010b)
THSTE	68	30	38	0.44	ns	72	72	0	1.00	PLL, TRA	New Zeland	SUBANT	2006-2007	Thompson (2010a)
THSTE	184	113	71	0.61	<0.005	183	176	7	0.96	TRA	New Zealand	SUBTRS, SUBANT	2000-2001	Robertson et al. (2003)

Species	N					N				Method	Country	Zone	Years	Reference
THSTE	134	87	47	0.65	<0.001	132	115	17	0.87	TRA	New Zealand	SUBTRS, SUBANT	2001-2002	Robertson et al. (2004)
THSTE	61	37	24	0.61	ns	61	58	3	0.95	TRA	New Zealand	SUBANT	1998-1999	Robertson and Bell (2002)
THSTE	78	66	12	0.85	<0.0001	78	78	0	1.00	TRA	New Zealand	SUBANT	2005-2006	Thompson et al. (2009)
THCAU	na	na	na	na	na	37	12	15	0.32	PLL	South Africa	SUBTRS	1998-2000	Ryan et al. (2002)
THSAL	22	18	4	0.82	<0.001	22	15	4	0.68	PLL	New Zealand	SUBANT	2006-2007	Thompson (2010a)
THSAL	14	7	7	0.50	ns	15	11	4	0.73	TRA	New Zealand	SUBANT	1998-1999	Robertson and Bell (2002)
THSAL	27	14	13	0.52	ns	27	19	8	0.70	TRA	New Zealand	SUBTRS, SUBANT	2008-2009	Thompson (2010b)
THSAL	104	33	71	0.32	<0.001	104	97	7	0.93	DLL	New Zealand	SUBTRS, SUBANT	2000-2001	Robertson et al. (2003)
THSAL	22	7	15	0.32	ns	22	16	6	0.73	PLL,TRA	New Zealand	SUBTRS, SUBANT	2001-2002	Robertson et al. (2004)
THCHL	17	5	13	0.29	ns	17	2	15	0.12	PLL	Brazil	SUBTRS	1994-1995	Neves and Olmos (1997)
THCAR	23	18	5	0.78	ns	23	0	23	0.00	DLL	Prince Edward	SUBANT	1996-1997	Ryan and Box-Hinzen (1999)
THCAR	17	8	9	0.45	ns	18	15	3	0.83	PLL	South Africa	SUBTRS	1998-2005	Petersen et al. (2010)
THCAR	30	13	17	0.44	ns	30	6	24	0.20	PLL	Australia	SUBTRS	1988-1995	Gales at al. (1998)
THCAR	19	12	7	0.62	ns	19	18	1	0.94	PLL	Australia	SUBTRS	1988-1995	Gales at al. (1998)
THBUL	21	11	10	0.52	ns	22	22	0	1.00	PLL	New Zealand	SUBANT	1988-1992	Murray et al. (1993)
THBUL	29	15	14	0.52	ns	29	29	0	1.00	PLL,TRA	New Zealand	SUBANT	1998-1999	Robertson and Bell (2002)
THBUL	44	25	19	0.57	ns	45	44	1	0.98	PLL	New Zealand	SUBANT	2006-2007	Thompson (2010a)
THBUL	31	22	9	0.71	<0.05	31	28	3	0.90	PLL,TRA	New Zealand	SUBTRS, SUBANT	2008-2009	Thompson (2010b)
THBUL	17	9	8	0.53	ns	18	17	1	0.94	PLL,TRA	New Zealand	SUBTRS, SUBANT	2000-2001	Robertson et al. (2003)
THBUL	21	13	8	0.62	ns	21	18	3	0.86	PLL,TRA	New Zealand	SUBTRS, SUBANT	2001-2002	Robertson et al. (2004)

THBUL	12	9	3	0.75	ns	12	12	0	1.00	na	New Zealand	SUBANT	2005-2006	Thompson et al. (2009)
PHIMM	191	81	110	0.42	<0.05	191	54	137	0.28	GIL	North Pacific	SUBTRN	1990-1991	Langston and Rohwer (1995)
PHIMM	39	25	14	0.64	ns	39	37	2	0.95	PLL	Hawaii	SUBTRN	2013	Beck et al. (2013)
PHIMM	181	107	74	0.59	<0.05	176	164	12	0.93	PLL	Hawaii	SUBTRN	2007-2012	Beck et al. (2013)
PHIMM	75	71	4	0.95	<0.0001	72	70	2	0.97	PLL	Alaska	SUBARC	2007-2012	Beck et al. (2013)
PHNIG	117	45	72	0.39	<0.05	117	36	81	0.31	GIL	North Pacific	SUBTRN	1990-1991	Langston and Rohwer (1995)
PHNIG	53	21	32	0.40	ns	53	40	13	0.76	PLL	Hawaii	SUBTRN	2013	Beck et al. (2013)
PHNIG	176	65	111	0.37	<0.001	148	133	15	0.90	PLL	Hawaii	SUBTRN	2007-2012	Beck et al. (2013)
PHNIG	46	30	16	0.65	0.0553	26	26	0	1.00	PLL	Alaska	SUBARC	2007-2012	Beck et al. (2013)
PHIRR	33	27	6	0.82	<0.01	na	na	na	na	PLL,GIL,INT	Peru	TROPIC	2005	Awkerman et al. (2006)
PHIRR	na	na	na	na	na	40	20	20	0.50	PLL,GIL,INT	Peru	TROPIC	1998-2006	Jiménez- Uzcátegui et al. (2006)
MAGIG	21	13	8	0.62	ns	na	na	na	na	DLL	Prince Edward	SUBANT	1996-1997	Ryan and Box-Hinzen (1999)
MAGIG/MAHAL	38	14	24	0.37	ns	38	37	1	0.97	DLL	Prince Edward	SUBANT	1996-2000	Nel et al. (2002a)
FUGLA	193	145	48	0.75	<0.0001	195	176	19	0.90	DLL	Alaska	SUBARC	2005	Phillips et al. (2010)
FUGLA	210	141	69	0.67	<0.0001	210	184	26	0.88	DLL	Alaska	SUBARC	2013	Beck et al. (2013)
ARCAR	233	128	105	0.55	ns	89	73	16	0.82	PLL	Australia	SUBTRS	2001-2006	Trebilco et al. (2011)
ARCAR	30	7	23	0.24	<0.01	30	27	3	0.91	PLL	Australia	SUBTRS	1988-1995	Gales at al. (1998)
ARCAR	12	8	4	0.69	ns	12	6	6	0.46	PLL	Australia	SUBTRS	1988-1995	Gales at al. (1998)
ARTEN	48	27	21	0.56	ns	48	14	34	0.29	DLL	Alaska	SUBANT	2005	Phillips et al. (2010)

ARTEN	12	7	5	0.58	ns	12	9	3	0.75	DLL	New Zealand	SUBTRS, SUBANT	2000-2001	Robertson et al. (2003)
ARTEN	42	25	17	0.60	ns	42	30	12	0.71	PLL	Alaska	SUBANT	2013	Beck et al. (2013)
ARTEN	33	16	17	0.48	ns	33	33	0	1.00	TRA	New Zealand	SUBTRS, SUBANT	2000-2001	Robertson et al. (2003)
ARGRI	68	64	4	0.94	<0.0001	68	64	4	0.94	TRA	New Zealand	SUBANT	2006-2007	Thompson (2010a)
ARGRI	72	65	7	0.90	<0.0001	73	73	0	0.92	TRA	New Zealand	SUBANT	2006-2007	Thompson (2010a)
ARGRI	26	22	4	0.85	<0.001	26	24	2	0.92	TRA	New Zealand	SUBTRS, SUBANT	1998	Robertson (2000)
ARGRI	92	87	5	0.95	<0.0001	94	94	0	1.00	TRA	New Zealand	SUBTRS, SUBANT	2008-2009	Thompson (2010b)
ARGRI	227	196	31	0.86	<0.0001	226	196	30	0.87	TRA	New Zealand	SUBTRS, SUBANT	2000-2001	Robertson et al. (2003)
ARGRI	98	85	13	0.87	<0.0001	99	97	2	0.98	PLL, TRA	New Zealand	SUBTRS, SUBANT	2001-2002	Robertson et al. (2004)
PUGRI	166	153	13	0.92	<0.0001	166	166	0	1.00	TRA	New Zealand	SUBANT	2005-2006	Thompson et al. (2009)
PRAEQ	36	25	11	0.69	<0.05	36	30	0	0.83	PLL, TRA	New Zeland	SUBANT	2006-2007	Thompson (2010a)
PRAEQ	14	10	4	0.71	ns	14	14	0	1.00	DLL, TRA	New Zealand	SUBANT	1998-1999	Robertson and Bell (2002)
PRAEQ	33	21	12	0.64	ns	na	na	na	na	DLL	South Africa	SUBTRS	1994	Barnes et al. (1997)
PRAEQ	379	300	79	0.79	<0.0001	na	na	na	na	DLL	Kerguelen	SUBANT	2001-2003	Delord et al. (2005)
PRAEQ	12	6	6	0.50	ns	na	na	na	na	DLL	Argentina	SUBANT	2000-2001	Gandini and Frere (2006)
PRAEQ	5189	3767	1422	0.73	<0.0001	na	na	na	na	DLL	Kerguelen	SUBANT	2003-2006	Delord et al. (2010)
PRAEQ	790	664	126	0.84	<0.0001	85	75	10	0.88	DLL	Prince Edward	SUBANT	1996-2000	Nel et al. (2002a)
PRAEQ	233	194	39	0.83	<0.0001	233	232	1	1.00	DLL	Prince Edward	SUBANT	1996-1997	Ryan and Box-Hinzen (1999)
PRAEQ	56	28	28	0.50	ns	na	na	na	na	DLL	Argentina	SUBANT	2005	Seco-Pon et al. (2007)
PRAEQ	694	410	284	0.59	ns	823	337	486	0.41	PLL	South Africa	SUBTRS	1998-2005	Petersen et al. (2010)

PRAEQ	45	22	23	0.48	ns	45	45	0	1.00	PLL	Australia	SUBANT	1988-1995	Gales at al. (1998)
PRAEQ	33	13	20	0.39	ns	na	na	na	na	PLL	Brazil	SUBTRS	2006-2008	Roma (2009)
PRAEQ	75	64	11	0.85	<0.0001	75	75	0	1.00	TRA	New Zealand	SUBTRS, SUBANT	2008-2009	Thompson (2010b)
PRAEQ	274	198	76	0.72	<0.0001	278	275	3	0.99	PLL, TRA	New Zealand	SUBTRS, SUBANT	2000-2001	Robertson et al. (2003)
PRAEQ	356	284	72	0.80	<0.0001	360	358	2	0.99	DLL	New Zealand	SUBTRS, SUBANT	2001-2002	Robertson et al. (2004)
PRAEQ	52	37	15	0.71	<0.005	55	55	0	1.00	PLL, TRA	New Zealand	SUBANT	2005-2006	Thompson et al. (2009)
PRCIN	16	1	15	0.06	<0.0001	16	15	1	0.94	PLL	New Zeland	SUBTRS	1989	Bartle (1990)
PRCIN	45	2	43	0.04	<0.0001	47	47	0	1.00	PLL	New Zeland	SUBTRS	1988-1992	Murray et al. (1993)
PRCIN	16	14	2	0.88	<0.01	na	na	na	na	DLL	Prince Edward	SUBANT	1996-2000	Nel et al. (2002a)
PRCIN	27	8	19	0.30	0.0500	27	27	0	1.00	PLL	Australia	SUBANT	1988-1995	Gales at al. (1998)
PRCIN	27	2	23	0.07	<0.0001	27	27	0	1.00	PLL	New Zealand	SUBTRS	2006-2007	Thompson (2010a)
PRCIN	73	3	70	0.04	<0.0001	73	73	0	1.00	PLL	New Zealand	SUBTRS, SUBANT	1998	Robertson (2000)
PRCIN	46	37	9	0.80	<0.0001	48	48	0	1.00	DLL	New Zealand	SUBANT	1998-1999	Robertson and Bell (2002)
PRCIN	47	43	4	0.91	<0.0001	179	179	0	1.00	DLL	New Zealand	SUBTRS, SUBANT	2000-2001	Robertson et al. (2003)
PTGOU	12	11	1	0.92	<0.01	12	11	1	0.92	DLL	New Zealand	SUBTRS, SUBANT	2000-2002	Robertson et al. (2004)
LAGLA	103	50	53	0.49	ns	82	65	17	0.79	DLL	Alaska	SUBARC	2005	Phillips et al. (2010)
LAHYP	21	10	11	0.48	ns	23	1	22	0.04	DLL	Alaska	SUBARC	2005	Phillips et al. (2010)
AYFUL	15	11	4	0.73	ns	15	14	1	0.93	GIL	Baltic Sea	SUBARC	1972-76, 1986-90	Stempniewicz (1994)
CLHYE	591	361	230	0.61	<0.0001	591	410	181	0.69	GIL	Baltic Sea	SUBARC	1972-76, 1986-90	Stempniewicz (1994)
MEFUS	284	180	104	0.63	<0.0001	284	188	96	0.66	GIL	Baltic Sea	SUBARC	1972-76, 1986-90	Stempniewicz (1994)
AYAMA	93	48	45	0.52	ns	93	53	40	0.57	GIL	Baltic Sea	SUBARC	1972-76, 1986-90	Stempniewicz (1994)

MENIG	74	37	37	0.50	ns	74	18	56	0.24	GIL	Baltic Sea	SUBARC	1972-76, 1986-90	Stempniewicz (1994)
SOMOL	68	38	30	0.56	ns	68	22	46	0.32	GIL	Baltic Sea	SUBARC	1972-76, 1986-90	Stempniewicz (1994)
POCRI	24	11	23	0.46	ns	24	20	4	0.83	GIL	Baltic Sea	SUBARC	1972-76, 1986-90	Stempniewicz (1994)
MEANT	42	26	16	0.62	ns	42	28	14	0.67	GIL	New Zeland	SUBANT	1979-1997	Darby and Dawson (2000)
SPMAG	21	12	9	0.57	ns	21	21	0	1.00	TRA	Argentina	SUBANT	1995-1997	Gandini et al. (1999)
SPMAG	na	na	na	na	na	20	16	4	0.80	GIL	Brazil	SUBTRS	2009	Cardoso et al. (2011)
SPMAG/SPHUM	na	na	na	na	na	663	278	385	0.42	GIL	Chile	SUBANT	1991-1996	Simeone et al. (1999)
URAAL	252	141	111	0.56	ns	252	159	93	0.63	GIL	NE Pacific	SUBARC	1994-1994	Thompson et al. (1998)
URAAL	123	68	55	0.55	ns	123	34	89	0.28	GIL	NE Pacific	SUBARC	1995-2001	Smith and Morgan (2005)
URAAL	na	na	na	na	na	765	237	528	0.31	GIL	Baltic Sea	SUBARC	1972-1999	Osterblom et al. (2002)
URAAL	785	554	231	0.71	<0.0001	785	411	374	0.52	GIL	NE Pacific	SUBTRN	1999-2000	Nevins et al. (2004)
CEMON	70	32	38	0.46	ns	70	15	55	0.21	GIL	NE Pacific	SUBARC	1994-1994	Thompson et al. (1998)
CEMON	82	55	27	0.67	<0.01	82	69	13	0.84	GIL	NE Pacific	SUBARC	1995-2001	Smith and Morgan (2005)
PHCAR	na	na	na	na	na	289	27	262	0.09	POU	North Sea	SUBARC	1983-1992	Bregnballe and Frederiksen (2006)
PHPUN	32	22	10	0.69	0.0518	33	21	12	0.64	TRA	New Zealand	SUBTRS, SUBANT	2008-2009	Thompson (2010b)

[1]Abbreviation for species is composed by the two first characters of the generic epithet and the three first of the specific epithet: DIEXU, *Diomedea exulans*; DIANT, *Diomedea antipodensis*; THMEL, *Thalassarche melanophris*; THIMP, *Thalassarche impavida*; THSTE, *Thalassarche steadi*; THCAU, *Thalassarche cauta*; THSAL, *Thalassarche salvini*, THCHR, *Thalassarche chrysostoma*, THBUL, *Thalassarche bulleri*, THCHL, *Thalassarche chlororhynchos*; THCAR, *Thalassarche carteri*; PHIM, *Phoebastria immutabilis*; PHNIG, *Phoebastria nigripes*; PHIRR, *Phoebastria irrorata*, MAGIG, *Macronectes giganteus*; MAHAL, *Macronectes halli*; FUGLA, *Fulmarus glacialis*; LAGLA, *Larus glaucescens*; LAHIP, *Larus hiperboreus*; PUCAR, *Ardenna carneipes*; PRAEQ, *Procellaria aequinoctialis*; ARTEN, *Ardenna tenuirostris*, ARGRI, *Ardenna grisea*; PRCIN, *Procellaria cinerea*; POCRI, *Podiceps cristatus*; PTGOU, *Pterodroma gouldi*; MEANT, *Megadyptes antipodes*; SPMAG, *Spheniscus magellanicus*; SPHUM, *Spheniscus humboldti*; URALG, *Uria aalge*; CEMON, *Cerorhinca monocerata*; AYFUL, *Aythya fuligula*; CLHYE, *Clangula hyemalis*; MEFUS, *Melanitta fusca*; AYMAR, *Aythya marila*; MENIG, *Melanitta nigra*; PHCAR, *Phalacrocorax carbo*; PHPUN, *Phalacrocorax punctatus*; SOMOL, *Somateria mollissima*.