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

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37   ABSTRACT

38   Fisheries bycatch is a major threat to seabird populations, and understanding sex- and age-

39   biases in bycatch is important for assessing population-level impacts of this incidental

40   mortality. We analysed the peer-reviewed and grey literature to provide the first global

41   assessment of seabird bycatch by sex and age, and used generalised mixed models to

42   investigate the effects of region and fishing method. Sex- and age-biased bycatch was

43   significantly more frequent than unbiased ratios, with the majority skewed toward males

44   and adults. Bycatch of adults and males was significantly higher in subpolar regions,

45   whereas there was a tendency for more immatures and females to be killed in subtropical

46   waters. Fishing method did not appear to influence sex and age-specific bycatch. Sex- and

47   age-biases are therefore common features of seabird bycatch in global fisheries that appear

48   to be associated largely with differences in at-sea distributions. This unbalanced mortality

49   influences the extent to which populations are impacted by fisheries, which is a key

50   consideration for at-risk species. We recommend that researchers track individuals of

51   different sex and age classes to improve knowledge of their distribution, relative overlap

52   with vessels, and hence susceptibility to bycatch; this information should then be

53   incorporated in ecological risk assessments of effects of fisheries on vulnerable species.

54   Additionally, data on sex, age and provenance of bycaught birds should be collected by

55   fisheries observers in order to identify regions and fleets where bycatch is more likely to

56   result in population-level impacts, and to improve targeting of bycatch mitigation and

57   monitoring of compliance.

58   Keywords: age ratio; incidental mortality; seabirds; fisheries management, sex ratio.

59

60   **1. Introduction**

61   Fisheries are one of the primary threats to marine biodiversity, impacting ecosystems from

62   the open ocean to the coast, and from the poles to the tropics (Halpern et al., 2008; Jackson

63   et al., 2001). Commercial fishing has resulted in severe and widespread ecosystem

64   disruption primarily as a result of over-harvesting, habitat degradation and the mortality of

65   non-target species, also called bycatch (Hall et al., 2000; Halpern et al., 2008; Jackson et al.,

66   2001). Populations of large marine vertebrates, such as sea turtles, sharks, marine

67   mammals, and seabirds, are particularly susceptible to bycatch because of a combination of

68   their attraction to fishery bait and discards and their naturally slow reproductive rates

69   rendering them sensitive to even small increases in mortality (Hall et al., 2000; Lewison et

70   al., 2004). So much so that, the recent declines of many large marine vertebrates resulting

from bycatch have been compared to the historical extirpations and extinctions of terrestrial megafauna by human hunting (Lewison et al., 2014, 2004).

Seabirds are especially impacted, by becoming bycatch in a wide range of fishery gear-types (Croxall et al., 2012; Montevecchi, 2002). For example, drift nets set by Japanese, Korean and Taiwanese vessels were estimated to kill up to 40 million sooty (*Ardenna grisea*) and short-tailed shearwaters (*A. tenuirostris*) in the North Pacific between 1952 and 2001 (Uhlmann et al., 2005). Coastal gillnet fisheries are also a major source of mortality, with >400,000 seabirds killed annually, worldwide (Žydelis et al., 2013). Global longline fisheries were estimated to kill at least 160,000, and potentially 320,000 seabirds annually, mainly albatrosses, petrels and shearwaters (Anderson et al., 2011). Trawl fisheries are also a threat, with about 9,300 birds, mostly albatrosses, estimated to be killed annually just in the waters off South Africa by wet fish trawlers (Maree et al., 2014; Sullivan et al., 2006; Waugh et al., 2008). These levels of mortality have led to severe declines in many populations and are clearly unsustainable (Croxall et al., 1998; Cuthbert et al., 2005; Delord et a., 2008; Phillips at al., 2016; Piatt and Gould, 1994; Rolland et al., 2010; Žydelis et al., 2013, 2009).

The impact of bycatch depends not only on the number of individuals killed, but also on the components of the population that are impacted (Bugoni et al., 2011; Lewison et al., 2012). For example, because seabird life histories are characterised by delayed maturation, high survival and low rates of reproduction, mortality of adults will have greater population-level impacts than mortality of immatures (Lewison et al., 2014). Moreover, because seabirds are monogamous, with obligate biparental care, sex-biased mortality in fisheries can reduce the effective population size (Mills and Ryan, 2005; Weimerskirch et al., 2005). Sex- and age-biases in seabird bycatch are reported in a number of fisheries (Awkerman et al., 2006; Gales et al., 1998; Ryan and Box-Hinzen, 1999; Stempniewicz, 1994), and there has been a review of adult sex-ratios (ASR) in bycatch of albatrosses and petrels (Bugoni et al., 2011). However, there has been no comprehensive review of sex- and age-biases in bycatch of seabirds in general, even though a better understanding of their nature and extent is required to determine the full impact of bycatch on populations and communities. Indeed, this has been identified as one of the highest priority research questions in the field of seabird ecology and conservation (Lewison et al., 2012; Phillips et al. 2016).

Accordingly, the aim of the current study is to provide the first global review of age- and sex-specific bycatch in seabirds. This will contribute towards a better understanding of the frequency and magnitude of these effects across taxa, regions and fishery gear-type, as well as the implications for management and conservation. We predict that larger and more dominant individuals, usually adult males, will have higher bycatch rates than adult females,

107 or younger birds of either sex, because they are better able to compete for discards and bait
108 while attending fishing boats (Bregnballe and Frederiksen, 2006; Croxall and Prince, 1990;
109 Montevecchi, 2002). However, bycatch rates will also be influenced by region. Many studies
110 have shown that females and immatures tend to travel further from their breeding sites, or
111 to lower latitudes, compared with males and adults (Hamer et al., 2002; Hedd et al., 2014;
112 Phillips et al., 2005, 2004). Therefore, because the majority of seabirds breed at high
113 latitudes (Burger, 2002) we broadly predict that bycatch in subpolar (sub-Arctic and sub-
114 Antarctic) areas will tend to be skewed towards males and adults, whereas in subtropical
115 regions, bycatch will be biased towards females and immatures.

2. Methods

2.1. Literature review

119 We reviewed the literature for studies reporting sex and age composition of seabird bycatch
120 in fisheries from around the world. We searched *Thomson Reuters Web of Science* and *Google*
121 *Scholar* using the following search terms: Topic = (seabird* OR albatross* OR petrel* OR
122 penguin* OR shearwater*) AND (sex OR age OR female OR male OR adult OR juvenile) AND
123 (fishery* OR bycatch OR mortality) AND (bias); Timespan = All Years. To ensure the best
124 possible coverage of the bycatch literature, we supplemented this with grey literature and
125 contacted a number of experts directly to alert us to any missing references and to access
126 unpublished studies. Only the studies reporting sex or age composition from samples of
127 more than 10 individuals per species were included. We used the term 'immature' to refer
128 to birds of any age below age of first breeding.

129 Authors utilized different methods for sexing including examination of gonads
130 through necropsies (e.g. Petersen et al., 2010; Thompson et al., 2010), molecular sexing (e.g.
131 Burg, 2008; Jiménez et al., 2015b) and ring recoveries of known-sex individuals (e.g.
132 Jiménez et al., 2015a). Birds were aged on the basis of plumage and bill morphology (e.g.
133 Cardoso et al., 2011; Jiménez et al., 2015b; Neves and Olmos, 1997), or ring details for
134 known-age individuals (Awkerman et al., 2006; Jiménez et al., 2015a; Österblom et al.,
135 2002). To aid interpretation, we classified each sample of seabird bycatch according to the
136 magnitude of sex- and age-bias: highly biased (≥80% belonging to one sex or age class);
137 biased (60% - 79%) and not biased (40% - 59%). The sampling unit for bycatch data refers
138 to the information for each taxon caught in a particular gear type in each study. When
139 possible, bycatch rates were separated by region and season (summer/winter).

140 To aid comparison across regions, the global oceans were initially divided into five
141 major zones: sub-Antarctic, subtropical southern hemisphere, tropical, subtropical
142 northern hemisphere and sub-Arctic. For the purpose of this study, sub-Arctic and sub-

143   Antarctic zones also included the adjacent temperate waters. Thus, sub-Antarctic and sub-

144   Arctic regions mostly comprise waters between 60° and 40° of latitude (average sea surface

145   temperature (SST) 0°–18° C), subtropical in both hemispheres between 40° and 20° of

146   latitude (average SST 18°-24° C), and tropical between 20° S and 20° N (average SST >25°

147   C). The exception was in the southern hemisphere, where cold water masses extend as far

148   north as 30° S off the west coast of South America and to the south and south-west of

149   Australia, which were included in sub-Antarctic waters (Figure 1). In modelling the regional

150   effects on the sex- and age-ratios of seabird bycatch, sub-Antarctic and sub-Arctic areas

151   were combined in "subpolar", and subtropical waters of both hemispheres combined in

152   "subtropical".

153   We obtained data from a diverse range of fisheries, including pelagic and demersal

154   longlines, gillnets, trawlers and pound nets (shallow water nets attached to poles to create

155   a funnel). Our sample, however, was dominated by two main gear types and variations

156   therein: longline (pelagic and demersal) and gillnet. Longlines primarily kill surface-feeding

157   birds attracted to baited hooks near the surface, while gillnets mainly entrap pursuit divers

158   and bottom feeders (Anderson et al., 2011; Žydelis et al., 2013).

159

160   *2.2. Data analysis*

161   We first compared the number of biased with non-biased (sex and age, respectively)

162   bycatch samples using contingency tables, specifically, chi-squared tests with Yate's

163   correction for continuity due to only one degree of freedom. We then tested for the effects

164   of region (subpolar vs subtropical) and fishery type (longline vs gillnet) on the age and sex

165   ratios of seabird bycatch with generalised linear mixed models, using the *lmer* function of

166   the *lme4* package in R (R Core Development Team, 2011; Zuur et al.. 2009). The proportion

167   of males or adults was used as the response variable for sex and age-bias respectively, using

168   a *Gaussian* error distribution. Due to the unbalanced geographical distribution of fishery

169   type data we also tested the effect of the four major fishery gear-types (pelagic longlines,

170   demersal longlines, gillnets and trawlers) within the subpolar region – this was the only

171   region with comparable data among fisheries. All models included species as a random

172   effect to account for inclusion in multiple datasets, and were weighted by the sample size,

173   which, for the purpose of this analysis, was the number of birds of each taxon caught in a

174   particular gear type in each study. We tested the effect of region and fisheries on sex and

175   age proportions separately. Models were compared using second-order Akaike Information

176   Criterion (AICc), where the best model is taken to be that with the lowest AICc value. AICc

177   differences of <2 are not considered to be meaningfully different (Zuur et al., 2009). In this

178   case, the model with the fewest parameters was selected through parsimony.

179

3. Results

We found 43 studies, published between 1990 and 2015, that reported sex and age composition of seabird bycatch in fisheries, of which 34 (79%) were in the southern hemisphere and 9 (21%) in the northern hemisphere (Figure 1, Table 1). Data were available from four main types of fishery: 13 studies for pelagic longline (30%), nine for demersal longline (21%), nine for gillnet (21%), two for trawlers (5%), two for intentional catch, gillnet and longline combined (5%), and a single study (2%) reported data from pound nets. In addition, seven (16%) studies reported data for more than one fishery, separated according to gear type (trawler, demersal and pelagic longline, and gillnet).

Availability of data from each fishery type was not equally distributed, geographically. For example, 82% (n = 16) of the demersal longline and 100% (n = 8) of the trawl fisheries samples came from the sub-Antarctic region, 50% (n = 25) of the pelagic longline samples from subtropical waters of the southern hemisphere, and 84% (n = 15) of the gillnet samples from sub-Arctic and adjacent subtropical waters combined (Figure 2).

The bycatch data with information on sex and age composition comprised 18,263 individuals of 39 seabird taxa, including 13 which are globally threatened: 14 albatrosses (Diomedeidae), nine petrels and shearwaters (Procellariidae), six sea ducks (Merginae), three penguins (Spheniscidae), two gulls (Laridae), two alcids (Alcidae), one grebe (Podicipedidae) and two cormorant/shags (Phalacrocoracidae) (Appendix B).

3.1. Sex-specific bycatch

Of 121 samples of sex ratios in seabird bycatch, 43 (35%) were unbiased, 56 (47%) were male-biased (including 20 that were highly biased,), and 22 (18%) were female-biased (including five that were highly biased) (Figure 3A, Appendix A). The number of sex-biased bycatch samples was significantly higher than the number of non-biased (χ^2_{Yates} = 10.208, P = 0.001), and the number of samples skewed towards males was significantly higher than that skewed towards females (χ^2_{Yates} = 13.299, P < 0.001).

The geographical distribution of the highly sex-biased bycatch samples (≥80% of one sex) is presented in Figure 4. There was a significant effect of region on the sex ratios (Tables 2 and 3), with a higher mean proportion of males caught in fisheries in subpolar areas, and the opposite pattern (i.e. more females caught) in subtropical waters (Figure 5-A). There was no significant difference in sex-ratios of seabird bycatch in gillnets or longlines (Figure 5-B, Tables 2 and 3). However, when modelling the effect of the four major fishery gear-types within the subpolar region only, there was a significantly higher mortality of males in trawl fisheries (Figure 6-B, Table 4).

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3.2. Age-specific bycatch

Of 114 samples reporting age composition of seabird bycatch, nine (8%) were unbiased, 78 (68%) were skewed towards adults (62 were highly biased) and 27 (24%) were biased towards immatures (12 were highly biased) (Figure 3B, Appendix A). Age-biased bycatch was therefore widespread across global fisheries, accounting for 92% of reports (χ^2_{Yates} = 79.167, P < 0.0001), with the frequency of adult-biased samples significantly larger than immature-biased (χ^2_{Yates} = 23.810, P < 0.0001).

The geographical distribution of the highly age-biased bycatch samples (≥80% of one age class) is presented in Figure 8. There was a significant effect of region on the age ratios of seabirds killed in fisheries (Tables 2 and 3); a higher proportion of adults were bycaught in subpolar regions, and a higher proportion of immatures bycaught in subtropical waters, although the latter difference was non-significant (Figure 5-C, Tables 2 and 3). In terms of fishery type effects, there was a higher mortality of adults in longline fisheries but no difference in age ratios of seabird bycaught in gillnets (Figure 5-D, Table 3). There was also a significant interaction between region and fishery method, with the regional effect influencing the sex-ratio of seabird bycaught in longlines but not in gillnets (Table 2, Figure 7). When modelling the effect of the four major fishery types in subpolar region only, there was a significantly higher mortality of adults in demersal longline and trawl fisheries compared with other gears (Figure 6-D, Table 4).

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4. Discussion

Sex- and age-biases in seabird bycatch have been reported in a number of fisheries (Delord et al., 2005; Gales et al., 1998; Nel et al., 2002; Phillips et al., 2010; Ryan and Box-Hinzen, 1999), and there is growing interest in both the underlying mechanisms and the potential demographic consequences (Bugoni et al., 2011; Lewison et al., 2012). Here we provide the first global synthesis of both sex and age-specific variation in seabird bycatch rates by different fisheries and in diverse regions. Overall, our study shows that there is strong variation in the sex and age ratios of bycatch, but that unbalanced sex and age proportions are the most common pattern. Additionally, we demonstrate that sex- and age-biases vary by region but, apparently, not by fishery type. Globally, male-biased bycatch was significantly more frequent (47%) than female-biased bycatch (18%), and adult-biased (68%) significantly more frequent than immature-biased (24%). These results are consistent with our *a priori* prediction that the dominance of males and adults foraging behind fishing vessels will lead to higher bycatch. However, there are regional differences

251   in the patterns of age- and sex-biased bycatch, as well as a disproportionately high number

252   of studies from sub-polar waters (68%), indicating that foraging despotism alone does not

253   explain the observed patterns. Possible mechanisms contributing to unbalanced age and sex

254   mortaility, as well as its demographic effects, and implications for management and

255   conservation, are discussed below.

256

257   **_4.1. Sex-specific bycatch_**

258   Although offspring sex-ratios in seabirds can vary with age, quality and timing of

259   breeding (Blanchard et al., 2007; Velando et al., 2002; Weimerskirch et al., 2005,), there is

260   little evidence for any consistent sex-biases at hatching or recruitment at the population

261   level (Awkerman et al., 2007a; Bregtanole and Thibault, 1995; Donald, 2007; Weimerskirch

262   et al., 2005). Therefore, the patterns observed here indicate that sex-skewed bycatch is

263   unlikely to be due to the underlying population sex-ratio. Hypotheses proposed to explain

264   sex-related vulnerability to bycatch include sex-specific differences in at-sea distribution,

265   and differential access to bait and discards related to sexual size-dimorphism and

266   aggression (Barbraud _et al._, 2012; Bugoni _et al._, 2011; Nel et al., 2002; Ryan and Box-Hinzen;

267   1999).

268   It has been suggested that the competitive advantage of males foraging behind

269   fishing vessels explains male-biased bycatch events (Awkerman et al., 2006; Ryan and Box-

270   Hinzen, 1999); however, there is little direct evidence to support this. Instead, in multi-

271   species foraging aggregations, differences in body size between taxa are more important

272   determinants of access to feeding opportunities than sex _per se_ (Bugoni et al., 2011; Jimenez

273   et al., 2012; Stauss et al., 2012; Votier et al., 2013). In contrast, sex-biased bycatch appears

274   to be much better explained by sex-specific differences in distribution. For instance, in the

275   southern hemisphere, our analysis showed a significantly higher frequency of male-biased

276   bycatch in sub-Antarctic areas, but the opposite pattern in subtropical waters; this is

277   consistent with tracking and stable isotope results from a number of different sub-Antarctic

278   seabird species during the breeding season, showing that females tend to forage farther

279   from the colony and spend more time in subtropical waters compared with males (e.g. Hedd

280   et al., 2014; Jiménez et al., 2015; Phillips et al., 2011, 2005, 2004; Thiers et al., 2014;

281   Weimerskirch et al., 2014). In the northern hemisphere, where the bycatch data was more

282   taxonomically heterogeneous and the sample size much smaller (15 species within 28

283   samples, 23%); overall patterns of sex-biased bycatch are less clear. Nevertheless,

284   differential distribution at sea has also been identified as a cause of male-biased mortality

285   of common guillemot (_Uria aalge_) in coastal gillnets of Monterrey Bay (California) (Nevis et

286   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.

4.1.1. 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) uncertainty about other factors influencing sex differences in survival, such as relative predation risk, or 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 increases 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., 2004; 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

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 population. 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 adult, 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 trawlers

358 (Gales et al., 1998; Prince et al., 1994), but, again, this pattern was not supported by our
359 data, which shows a large proportion of adults bycaught in these fisheries.

360   Based on the available data we suggest that a degree of spatial segregation at-sea by
361 age is a better explanation for the observed age-specific susceptibility to bycatch, rather
362 than differences in competitive capacity or experience in avoiding fishing gear. In the
363 southern hemisphere, immature birds disperse further north and spend more time in
364 subtropical waters, whereas adults (especially breeders) are more likely to stay in sub-
365 Antarctic waters (Bugoni and Furness, 2009; Catry et al., 2013; Olmos, 1997; Phillips et al.,
366 2005; Sullivan et al., 2004; Waugh et al., 1999; Weimerskirch et al., 2014, 2006). This pattern
367 seems to be reflected in the significantly higher mortality of adults in subpolar areas in our
368 analysis, which mainly resulted from the consistent adult-biased bycatch in diverse
369 fisheries across sub-Antarctic waters (Bartle, 1991; Box-Hinzen, 1999; Gales et al. 1998, Nel
370 et al., 2002; Robertson and Bell, 2002; Ryan and Gandini, 1999; Seco-Pon et al., 2007;
371 Thompson, 2010). On the other hand, in subtropical areas, where there are often more
372 immatures (Copello et al. 2013, Phillips et al., 2006, 2005; Weimerskirch et al., 2014), our
373 analyses indicated more samples biased to this younger age class (43%) in comparison to
374 fisheries in sub-Antarctic waters (17%). Although the proportion of immatures bycaught in
375 subtropical areas is highest during the summer (up to 100%), when most adults return to
376 their breeding areas (Ryan et al., 2002; Petersen at al., 2010), immatures can also
377 predominate in bycatch during winter (Gales et al., 1998; Murray et al., 1993; Neves and
378 Olmos, 1997; Roma et al., 2009). The significantly higher bycatch of adults in trawlers and
379 demersal longline among fisheries within the subpolar region is likely to reflect the same
380 large scale pattern, since those fisheries operate on shelf and slope waters closer to colonies
381 (Bartle, 1991; Gandini at al., 1999; Nel et al. 2002; Robertson et al. 2003, 2004), while
382 pelagic longline operates in much more pelagic waters and at lower latitudes of the subpolar
383 region (Beck et al., 2013, Gales et al. 1998; Thompson 2010). This age-specific mortality
384 associated with differential distribution at sea is not exclusive to albatrosses and petrels of
385 the southern hemisphere. A range of other species in both hemispheres, including diving
386 ducks, penguins, alcids, fulmars and gulls showed regional and seasonal patterns of age-
387 specific bycatch likely to reflect differential overlap with fisheries; these seem to be linked
388 to age-related differences in distribution as a consequence of breeding constraints, moult
389 cycles, migration or age-specific foraging strategies (Cardoso et al., 2011; Gandini et al.,
390 1999; Nevins et al., 2004; Phillips et al., 2010; Stempniewicz, 1994; Thompson et al., 1998;
391 Votier et al. 2011).

392

393 *4.2.1. 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). Even though juvenile survival in seabirds is normally lower than adults (Nur and Sydeman, 1999), there is evidence that fisheries have reduced immature survival rates of some species. For example, negative trends in juvenile survival of black-browed albatross from South Georgia are correlated with 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 (Birdlife International, 2004; 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 several other albatross species in the Southern Ocean (ACAP, 2010a, 2010b, 2009; Prince et al., 1994; Croxall et al., 1998). Indeed, high mortality of immatures in fisheries resulting in depressed recruitment levels appears to have been a major contributor to the decline of both black-browed and grey-headed albatrosses *Thalssarche chrystoma* at South Georgia (Prince et al., 1994).

4.3. Implications for Management and Conservation

Seabirds are the most threatened group of birds; nearly half of the 346 species are known or suspected to be in decline, with one third threatened with extinction, including 17 critically endangered, 35 endangered, 49 vulnerable and 37 near threatened(Croxall et al., 2012) and there has been a 70% decline in monitored populations between 1950 and 2010 (Paleczny et al. 2015). Bycatch was identified as one of the two greatest threats, and

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the most pervasive threat at sea (Croxall et al., 2012). Hence, given the frequency and magnitude of both sex- and age-bias in seabird bycatch, and the demographic implications, we strongly recommend much improved data collection on the age and sex of birds killed by fisheries in on-board observing programs at national and international level. The latter requires concerted and coordinated action by Regional Fishery Management Organisations (RFMOs). In addition to increased onboard observation effort, it is necessary to implement standardized protocols for retrieving carcasses and collecting biological samples to provide high quality information on seabird bycatch; including accurate information on sex (Fridolfsson and Ellekrer 1999, Bugoni and Furness 2009), ageing (Bugoni and Furness 2009, Thompson et al. 2010), and improved attempts to identify provenance (Abbot et al. 2006, Gómez-Díaz & González-Solís 2007, Abbot et al. 2014). Moreover, tracking studies that map the distributions and hence overlap with specific vessels of birds of different age class and sex, throughout the year, will greatly improve ecological risk assessments (Komorose and Lewison 2015). Likewise, integrated population models testing the effects of fisheries on seabird demography must take sex- and age-specific differences in bycatch rates into account (Lewison et al. 2012). Together, this information can then be used by regional (i.e. national action plans) and international conservation initiatives (including the Agreement on the Conservation of Albatrosses and Petrels, ACAP), as well as local fisheries management organizations and RFMOs to identify regions and fleets where more prescriptive mitigation measures should be applied, and monitoring of compliance needs to be more intensive, to prevent severe impacts of bycatch on seabird populations (Croxall et al., 2013; Phillips, 2013; Phillips et al. 2016).

5. Conclusion

Sex and age biases in seabird bycatch are common features across global fisheries, mainly related to differential at-sea distributions. Overall, bycatch of adults and males was higher in subpolar regions and closer to the colonies, whereas immatures and females were more frequent caught in and subtropical waters, confirming our predictions. Moreover, we found no compelling evidence that differences in sex and age ratios are related to the competitive advantage of males and adults foraging at fishing vessels. We found clear evidence that such differences have implications for populations that differ from those of unbiased mortality. Despite this, the need to ensure information is obtained on sex and age of bycaught birds has been largely neglected by on-board observing programs in national and international fisheries. Given the ubiquity and population-level consequences of such

465 biases, we believe that global efforts to map bycatch and understand their impacts (e.g.
466 Lewison et al., 2014) should include age and sex information wherever possible.
467

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476

477 **References**
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906 **Table 1.** List of the studies (n = 43) reporting sex and age composition of seabird bycaught

907 in fisheries, with information on the number of taxa with data (N), type of fishery (PLL,

908 pelagic longline; DLL, demersal longline; TRA, trawler; GIL, gillnet; PND, pound net; INT,

909 intentional), region (SUBANT: sub-Antarctic; SUBARC: sub-Arctic; SUBTRS, subtropical

910 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. (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. (2002)	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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943 **Table 2**. Candidate mixed effect models for proportion of males, and proportion of adults in seabird

944 bycatch composition as influenced by region and type of fishery. All models included species as a

945 random effect. Best models are highlighted in bold.

Model	df	AICc	ΔAICc	Deviance	Resid df
Sex (y <- proportion of males)					
y ~ Region * Fishery	6	-42.1	0.0	-55.3	75
Y ~ Region	**4**	**-40.6**	**1.5**	**-49.0**	**91**
y ~ 1	3	-33.0	9.1	-39.2	118
y ~ Region + Fishery	5	-32.3	9.8	-43.1	76
y ~ Fishery	4	-7.8	34.3	-16.3	86
Age (y <- Proportion of adults)					
y ~ Region * Fishery	**6**	**48.4**	**0.0**	**35.1**	**68**
y ~ Region + Fishery	5	55.5	7.1	44.6	69
y ~ Fishery	4	72.1	23.7	63.3	79
Y ~ Region	4	83.3	34.9	74.8	85

$y \sim 1$		3	109.9	61.5	103.7	112

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

	Sex				Age			
Fishery	Not skewed	M	F	p (χ^2)	Not skewed	A	I	p (χ^2_{Yates}): A vs I[a]
Pelagic longline	18	14	16	0.789	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
Trawler	**5**	**12**	**1**	**0.006**	0	**17**	**0**	**<0.001**
Longlines combined	27	29	18	0.249	5	**41**	**19**	**0.007**
Region								
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	10	0.439	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

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990 **Table 4**. Candidate mixed effect models for proportion of males, and proportion of adults in seabird
991 bycatch composition as influenced by region and fishery type. The analyses of regional effects
992 compared bycatch only in pelagic longline fisheries (PLL), which was the fishery gear-type best
993 represented between regions (subpolar vs subtropical), while the analyses of the fishery gear-type
994 consider fisheries in the subpolar region only, which was the region with comparable sample sizes
995 among fisheries. All models included 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	**6**	**-38.2**	**0.0**	**-51.8**	**52**
Y ~ 1	3	-33.0	5.2	-39.2	118
y ~ Region, PLL only	4	-16.6	21.6	-25.6	40
Age (y <- Proportion of adults)					
y ~ Fishery, subpolar only	**6**	**14.4**	**0.0**	**0.5**	**45**
y ~ Region, PLL only	4	27.4	13.0	18.4	39
y ~ 1	3	95.6	81.2	89.4	112

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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 regions (NA), which were therefore excluded from the analysis of regional effects. **(Two columns fitting)**

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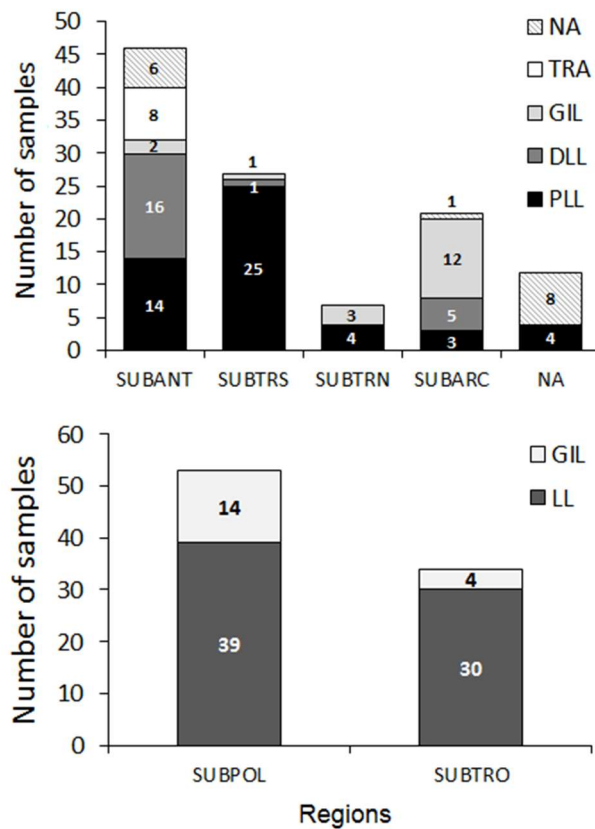
Figure 2. Number of bycatch samples by main fishery type and regions, reflecting (A) the original data, and (B) fisheries categories collapsed for the purposes of modelling. Abbreviations: SUBANT, sub-Antarctic; SUBARC, sub-Arctic; SUBTRS, subtropical southern; SUBTRN, subtropical northern; SUBPOL, subpolar;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

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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)**

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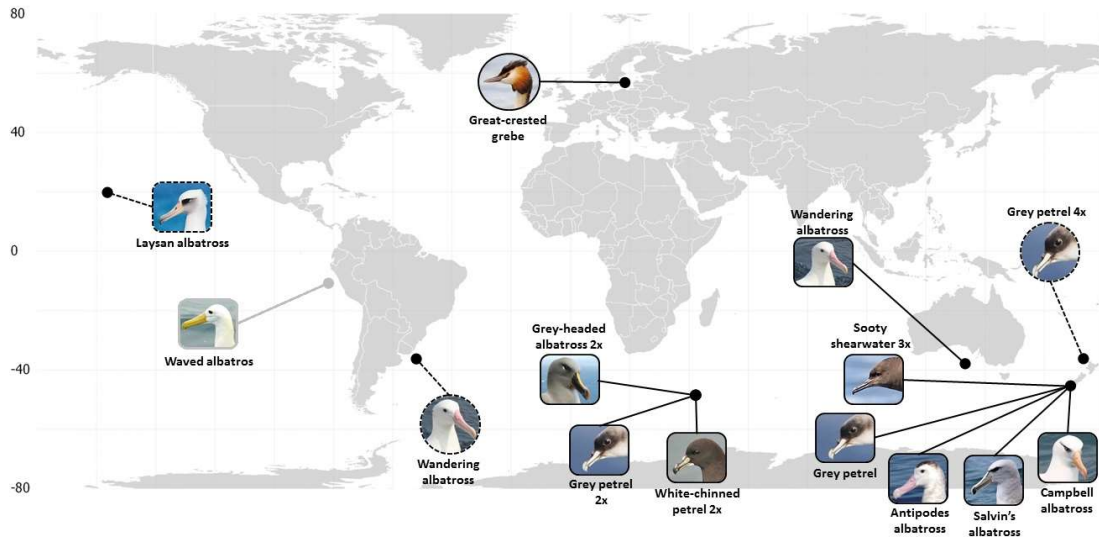
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1062 **Figure 4**. Geographical distribution of the highly sex-biased bycatch samples (≥80% of one

1063 sex). Squared figures refer to male and circled figures refer to female-biased samples. Black

1064 solid, black dotted and grey lines denote bycatch events in subpolar, subtropical and

1065 tropical regions respectively. Highly sex-biased samples from studies that subtropical and

1066 sub-Antarctic areas of New Zealand were pooled are not shown. The numbers follow

1067 common names indicate the number of sex-biased samples for that taxon in the given

1068 location. **(Two columns fitting)**

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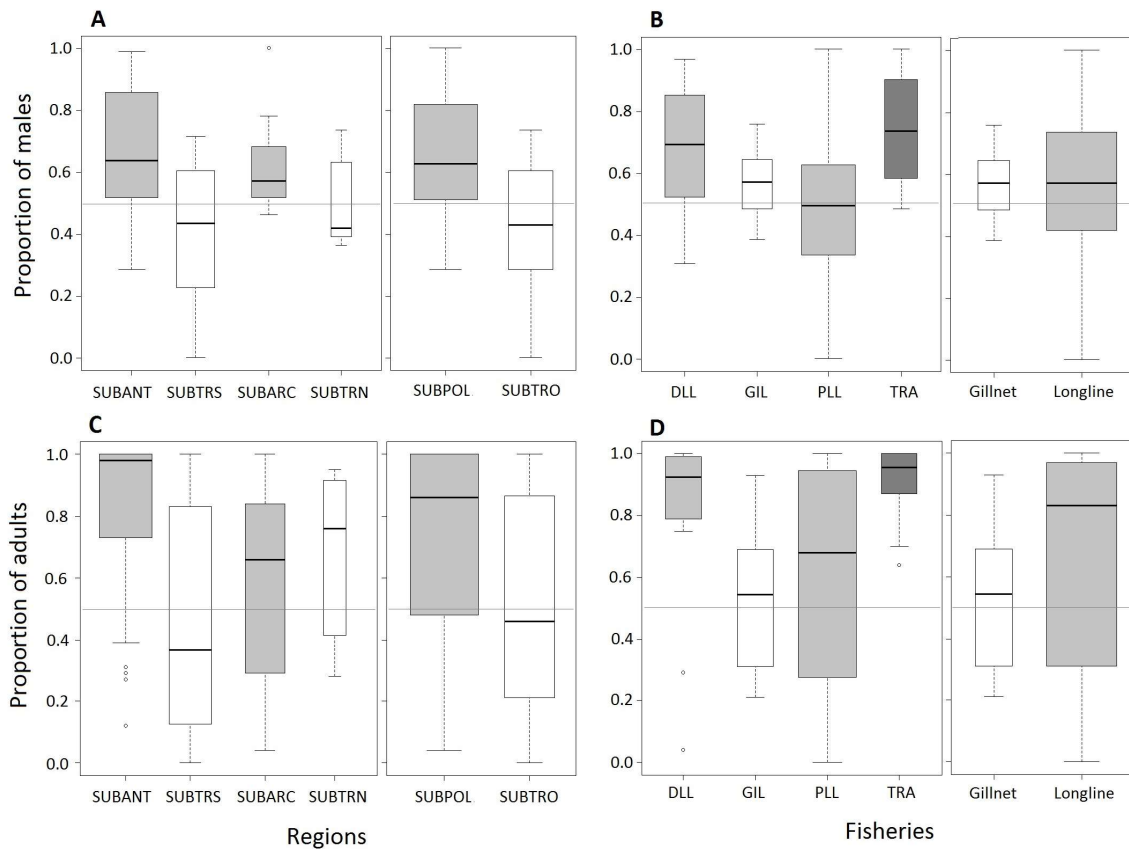
Figure 5. Proportion of males (top) and of adults (bottom) in seabird bycatch samples by region (left) and fishery type (right). Box plots show the median and the 25th and 75th percentiles, whiskers indicate values within 1.5 times of the interquartile range, circles represent outliers, and box plot 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, trawler. **(Two columns fitting)**
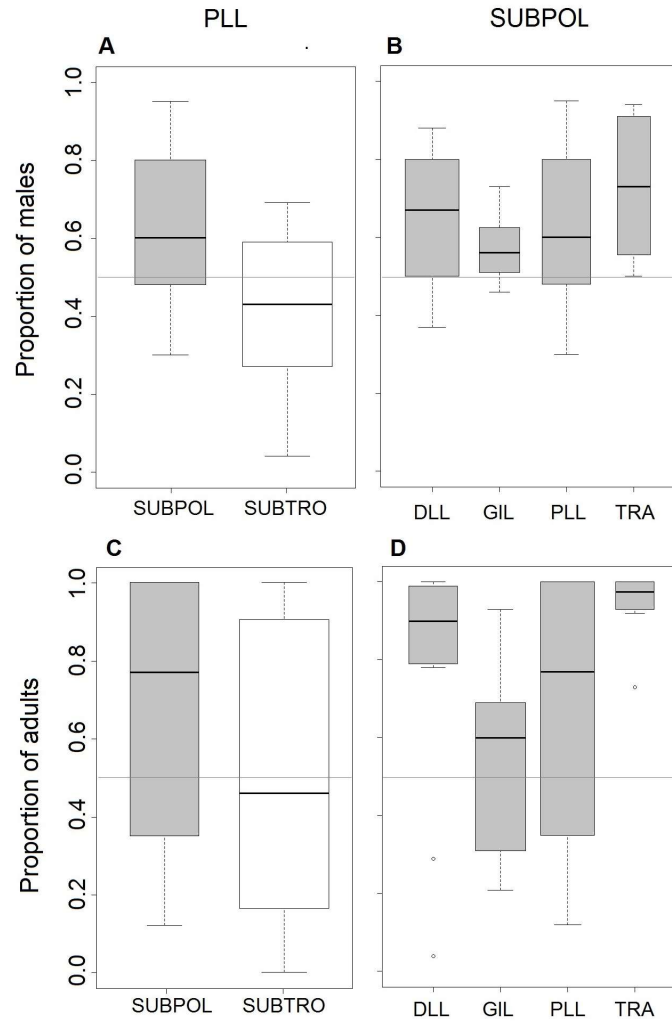
Figure 6. Proportion of males (top) and of adults (bottom) in seabird bycatch samples compared between regions using only bycatch data from pelagic longline fisheries (left), and compared among the four major fishery-gear types using only data from subpolar regions (right). Box plots show the median 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 sampl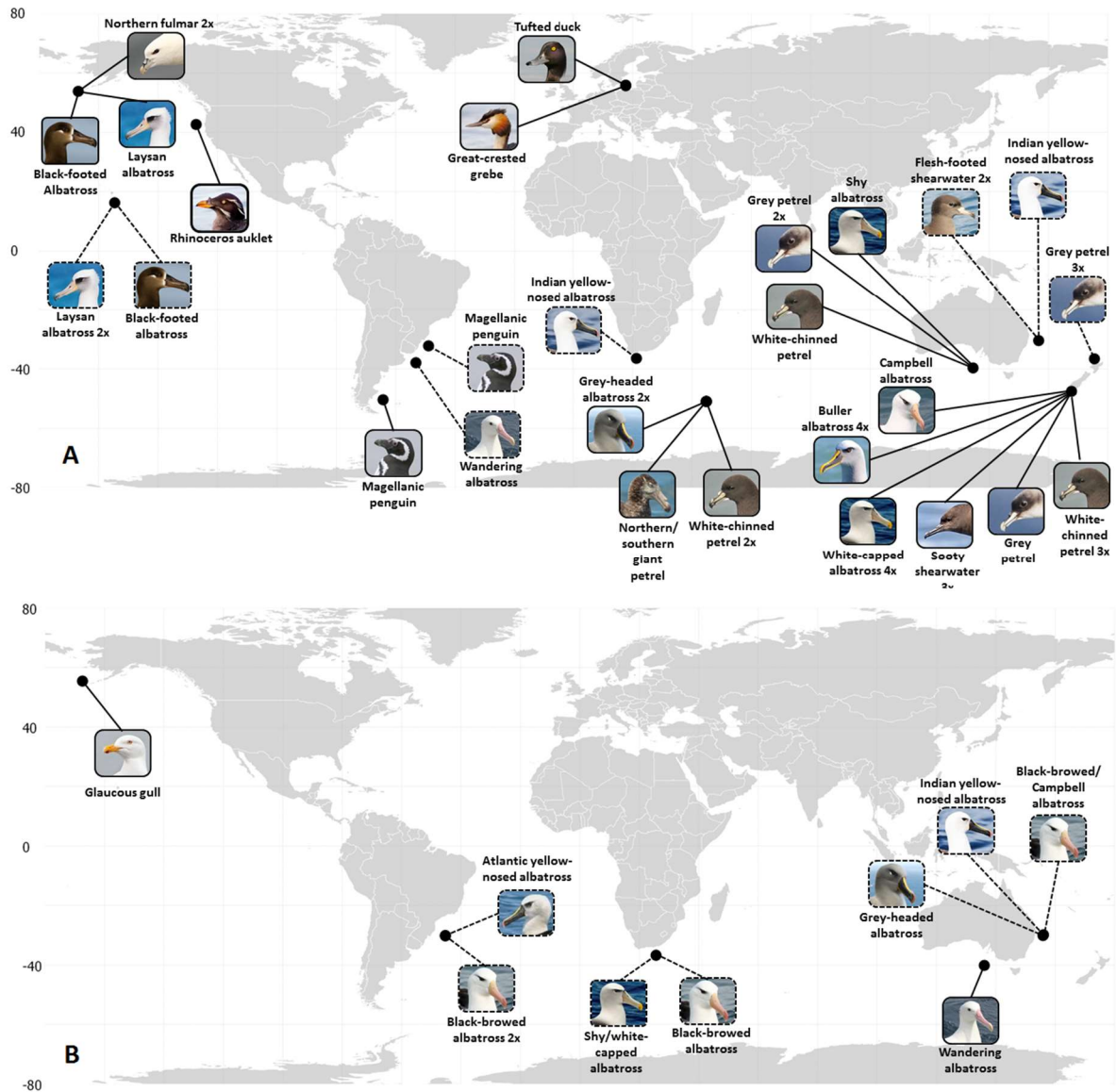e size, and the horizontal grey line indicates the 0.5 mark. Abbreviations: SUBPOL, subpolar; SUBTRO, subtropical; PLL, pelagic longline; DLL, demersal longline; GIL, gillnet; TRA, trawler. **(Single column)**
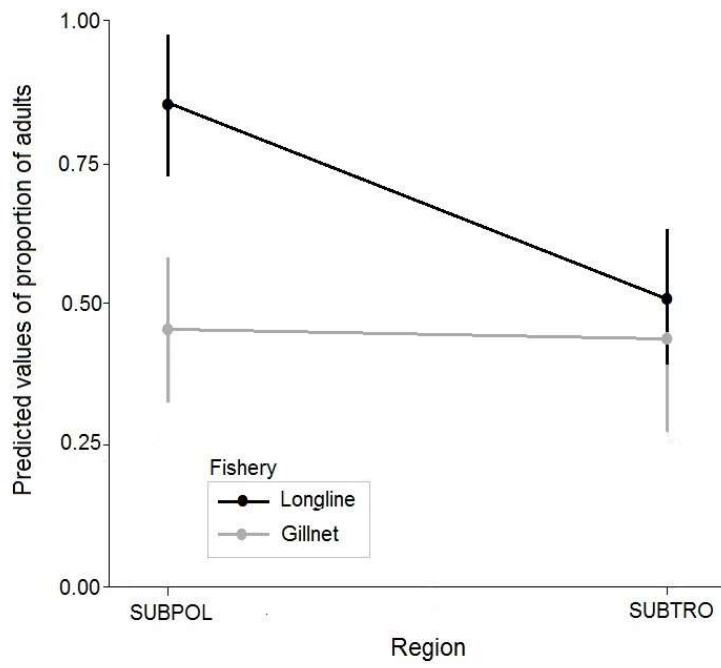
Figure 7. Interaction effect of region and fishery type on the proportion of adults in seabird bycatch. SUBPOL, subpolar; SUBTRO, subtropical.

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)**