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

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ABSTRACT

Fisheries bycatch is a major threat to seabird populations, and understanding sex- and age-biases in bycatch rates is important for assessing population-level impacts. We analysed 44 studies to provide the first global assessment of seabird bycatch by sex and age, and used generalised models to investigate the effects of region and fishing method. Bycatch was highly biased by sex (65% of 123 samples) and age (92% of 114 samples), with the majority of samples skewed toward males and adults. Bycatch of adults and males was higher in subpolar regions, whereas there was a tendency for more immatures and females to be killed in subtropical waters. Fishing method influenced sex- and age-ratios only in subpolar regions. Sex- and age-biases are therefore common features of seabird bycatch in global fisheries that appear to be associated largely with differences in at-sea distributions. This unbalanced mortality influences the extent to which populations are impacted by fisheries, which is a key consideration for at-risk species. We recommend that researchers track individuals of different sex and age classes to improve knowledge of their distribution, relative overlap with vessels, and hence susceptibility to bycatch. This information should then be incorporated in ecological risk assessments of effects of fisheries on vulnerable species. Additionally, data on sex, age and provenance of bycaught birds should be collected by fisheries observers in order to identify regions and fleets where bycatch is more likely to result in population-level impacts, and to improve targeting of bycatch mitigation and monitoring of compliance.

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

1. Introduction

Fisheries are one of the primary threats to marine biodiversity, impacting ecosystems from the open ocean to the coast, and from the poles to the tropics (Halpern et al., 2008; Jackson et al., 2001). Commercial fishing has resulted in severe and widespread ecosystem disruption primarily as a result of over-harvesting, habitat degradation and the mortality of non-target species, also called bycatch (Hall et al., 2000; Halpern et al., 2008; Jackson et al., 2001). Populations of large marine vertebrates, such as sea turtles, sharks, marine mammals, and seabirds, are particularly susceptible to bycatch because of a combination of their attraction to fishery bait and discards, and their naturally slow reproductive rates rendering them sensitive to even small increases in mortality (Hall et al., 2000; Lewison et al., 2004). The impacts are so extensive 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 particularly at risk from fisheries, as they are bycaught in a wide range of gear types (Croxall et al., 2012; Montevecchi, 2002; Phillips at al., 2016). For example, drift nets set by Japanese, Korean and Taiwanese vessels are estimated to have killed up to 40 million sooty (*Ardenna grisea*) and short-tailed (*A. tenuirostris*) shearwaters 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 are estimated to have killed 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 trawls (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 al., 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, or younger birds of either sex, because they are better able to compete for discards and baits while attending fishing boats (Awkerman et al., 2007b; Bregnballe and Frederiksen, 2006; Croxall and Prince, 1990; Montevecchi, 2002). However, bycatch rates will also be influenced by region. Many studies have shown that females and immatures tend to travel further from their breeding sites, or to lower latitudes, compared with males and adults (Hedd et al., 2014; Phillips et al., 2005, 2004). Therefore, because the majority of seabirds breed at high latitudes (Schreiber and Burger, 2002) we broadly predict that bycatch in subpolar (sub-Arctic and sub-Antarctic) areas will tend to be skewed towards males and adults, whereas in subtropical regions, bycatch will be biased towards females and immatures.

2. Methods

2.1. Literature review

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

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

To aid comparison across regions, the global oceans were initially divided into five major zones: sub-Antarctic, subtropical southern hemisphere, tropical, subtropical northern hemisphere and sub-Arctic. For the purpose of this study, sub-Arctic and sub-Antarctic zones also included the adjacent temperate waters. Thus, sub-Antarctic and sub-Arctic regions mostly comprise waters between 60° and 40° of latitude (average sea surface temperature (SST) 0°–18° C), subtropical in both hemispheres between 40° and 20° of latitude (average SST 18°-24° C), and tropical between 20° S and 20° N (average SST >25° C). The exception was in the southern hemisphere, where cold water masses extend as far north as 30° S off the west coast of South America and to the south and south-west of Australia, which were included in sub-Antarctic waters (Figure 1). In modelling the regional effects on the sex- and age-ratios of seabird bycatch, sub-Antarctic and sub-Arctic areas were combined in “subpolar”, and subtropical waters of both hemispheres combined in “subtropical”.

We obtained data from a diverse range of fisheries, including pelagic and demersal longline, gillnet, trawl and pound net (shallow water nets attached to poles to create a funnel). Our sample, however, was dominated by two main gear types and variations therein: longline (pelagic and demersal) and gillnet. Longlines primarily kill surface-feeding birds attracted to baited hooks near the surface, while gillnets mainly entrap pursuit divers and bottom feeders (Anderson et al., 2011; Žydelis et al., 2013).

2.2.Data analysis

We first compared the number of biased with non-biased (sex and age, respectively) bycatch samples for each fishery type, region and category using contingency tables. We specifically used chi-squared tests with Yates's correction for continuity where there was only one degree of freedom. We then tested for the effects of region (subpolar vs subtropical) and fishery type (longline [demersal and pelagic combined] vs gillnet) on the age and sex ratios of seabird bycatch using linear models followed by analyse of variance (ANOVA). We first ran liner mixed models using the *lmer* function of the *lme4* package in R (R Core Development Team, 2011; Zuur et al., 2009), including species as a random effect to account for inclusion in multiple datasets. Then, after verifying that the random-effect was not significant, it was dropped and linear models applied instead, using the function *lm* of the same package in R. The proportion of males or adults was used as the response variable for sex and age-bias respectively, using a *Gaussian* error distribution. Due to the unbalanced geographical distribution of bycatch samples by fishery type, we also tested the effect of the four major gear types (pelagic longline, demersal longline, gillnet and trawl) within the subpolar region. This was the only region with sufficient datasets. All models were weighted by the sample size, which, for the purpose of this analysis, was the number of birds of each taxon caught in a particular gear type in each study. We tested the effect of region and fisheries on sex and age proportions separately. Models were compared using second-order Akaike Information Criterion (AICc), where the best model is taken to be that with the lowest AICc value. AICc differences of <2 are not considered to be meaningfully different (Zuur et al., 2009).

3. Results

We found 44 studies, published between 1990 and 2016, that reported sex and age composition of seabird bycatch in fisheries, of which 35 (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: 14 studies for pelagic longline (32%), nine for demersal longline (20%), nine for gillnet (20%), two for trawl (5%). Seven (16%) studies reported data for more than one fishery, separated according to gear type. In addition, two studies combined data from intentional catch, and bycatch in gillnet and longline (5%), and a single study (2%) reported data from pound nets.

Availability of data from each fishery type was not equally distributed, geographically. For example, 82% (n = 16) of the samples from demersal longline and 100% (n = 8) of those from trawl fisheries came from the sub-Antarctic region, 52% (n = 27) 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 18,389 individuals of 41 seabird taxa, including 15 which are globally threatened: 16 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 A).

3.1.Sex-specific bycatch

Of 123 samples of sex ratios in seabird bycatch, 43 (35%) were unbiased, 56 (46%) were male-biased (including 20 that were highly biased,), and 24 (19%) were female-biased (including five that were highly biased) (Figure 3-A, Appendix B). The number of sex-biased bycatch samples was significantly higher than the number of non-biased (χ^2_{Yates} = 10.537, P = 0.001), and the number of samples skewed towards males was significantly higher than that skewed towards females (χ^2_{Yates} = 12.013, 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 the interaction between region and fishery type on the sex ratios of seabirds killed in fisheries, with the regional effect influencing the sex ratio of seabirds bycaught in longlines but not in gillnets (Figure 5, Table 2). There was a higher proportion of males bycaught in fisheries in subpolar areas, whereas a trend towards female bycatch in subtropical waters (F = 38.464, P < 0.001) (Figure 6-A, Table 3). There was no significant difference in sex-ratios of seabird bycatch between gillnets and longlines (Figure 6-B, Table 3). However, when modelling the effect of the four major fishery gear-types within the subpolar region a significant effect was found (F = 10.556, P < 0.01), with a higher mortality of males in trawl fisheries (Figure 7-A, Table 4).

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 3-B, Appendix A). Age-biased bycatch was therefore widespread across global fisheries, accounting for 92% of reports (χ^2_{Yates} = 79.167, P < 0.001), with the frequency of adult-biased samples significantly larger than immature-biased (χ^2_{Yates} = 23.810, P < 0.001).

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 the interaction between region and fishery type on the age ratios of seabirds killed in fisheries, with the regional effect influencing the age ratio of seabirds bycaught in longlines but not in gillnets (Figure 5, Table 2). A higher proportion of adults was bycaught in subpolar regions whereas no difference was found in age-ratio of seabirds killed in subtropical areas (F = 6.262, P <0.05) (Figure 6-C, Table 3). More adults than immatures were bycaught in longline, but there was no age bias for seabirds bycaught in gillnets (F = 13.578, P < 0.001) (Figure 6-D, Table 3). Fishery type has a significant influence on the age ratio of seabirds bycaught in subpolar regions (F = 17.175, P < 0.001) (Table 4). Mortality of adults was significantly higher than of immatures in demersal longline and trawl fisheries than in other fishery types in these regions (Figure 7-B).

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., 2002a; 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 substantial variation in the sex and age ratios of bycaught seabirds, and that unbalanced sex and age proportions are the most common pattern. Additionally, we demonstrate that sex- and age-biases vary by region and, to a lesser extent 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 in the patterns of age- and sex-biased bycatch, as well as a disproportionately high number of studies from sub-polar waters (68%), indicating that foraging despotism alone does not explain the observed patterns. Nevertheless, there is a paucity of this data in the northern hemisphere (9 studies) compared with the southern hemisphere (35 studies). Possible mechanisms contributing to unbalanced age and sex mortality, as well as its demographic effects, and implications for management and conservation, are discussed below.

4.1. Sex-specific bycatch

4.1.1. Possible mechanisms contributing to sex-specific bycatch

Although offspring sex-ratios in seabirds can vary with age, quality and timing of breeding (Blanchard et al., 2007; Velando et al., 2002; Weimerskirch et al., 2005,), there is little evidence for any consistent sex-biases at hatching or recruitment at the population level (Awkerman et al., 2007a; Bregtanole and Thibault, 1995; Donald, 2007; Weimerskirch et al., 2005). Therefore, the patterns observed here indicate that sex-skewed bycatch is unlikely to be due to the underlying population sex-ratio. Hypotheses proposed to explain sex-related vulnerability to bycatch include sex-specific differences in at-sea distribution, and differential access to bait and discards related to sexual size-dimorphism and aggression (Barbraud et al., 2012; Bugoni et al., 2011; Nel et al., 2002a; Ryan and Box-Hinzen; 1999).

It has been suggested that the competitive advantage of males foraging behind 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 to have been a major contributor to the decline of both black-browed and grey-headed (*Thalassarche chrysostoma*) albatrosses 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 the most pervasive threat at sea (Croxall et al., 2012). Hence, given the frequency and magnitude of both sex- and age-biases 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 levels. The latter requires concerted and coordinated action by Regional Fishery Management Organisations (RFMOs). In addition to increased on-board observer effort, it is necessary to implement standardized protocols for retrieving carcasses and collecting biological samples to provide high quality information on seabird bycatch; this includes accurate information on sex (Bugoni and Furness, 2009; Fridolfsson and Ellekrer, 1999), age (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). These approaches are especially urgent in the northern hemisphere – despite high levels of seabird bycatch here, the number of studies reporting age and sex-specific totals is much lower than in the southern hemisphere. 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 (Jiménez et al., 2015a; Komorose and Lewison, 2015). Likewise, integrated population models testing the effects of fisheries on seabird demography, including analyses of Potential Biological Removal (PBR), must take sex- and age-specific differences in bycatch rates to avoid underestimation of the PBR and potentially instituting management actions that are insufficient (Dillingham and Fletcher, 2011; 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 where 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). However, because (1) there is low reliability of bycatch data globally, (2) populations are at risk from different fisheries across large areas, and (3) provenance of bycaught birds is often unknown, incorporating information on sex- and age-biased bycatch in seabird management and conservation remains challenging, and the data must be examined on a case-by-case basis.

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 colonies, whereas immatures and females were caught more frequently in subtropical waters. 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, or to naivety of young birds around fishing gear. There is clear evidence that differences in capture rates by sex and age 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 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.

Acknowledgments

We thank Stuart Bearhop for providing constructive comments on the manuscript, and Hanna Nevins and Peter Ryan for providing valuable literature. We also thank Fabio Olmos for providing pictures of some of the birds composing our figures. This work is part funded via a scholarship to DG from the Sciences Without Borders Program (CNPq/Brazil). The study represents a contribution to the Ecosystems component of the British Antarctic Survey Polar Science for Planet Earth Programme, funded by the Natural Environment Research Council.

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TABLES

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

Table 2. Candidate mixed effect models for proportion of males, and proportion of adults in seabird bycatch composition as influenced by region and type of fishery. 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 ~ 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

Table 3. Frequency of bycatch samples per fishery type and region not skewed and skewed toward 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]
Fishery								
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**
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	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.

Table 4. Candidate mixed effect models for proportion of males, and proportion of adults in seabird bycatch composition as influenced by fishery gear-type consider fisheries in the subpolar region only, which was the region with comparable sample sizes 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	**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

FIGURES

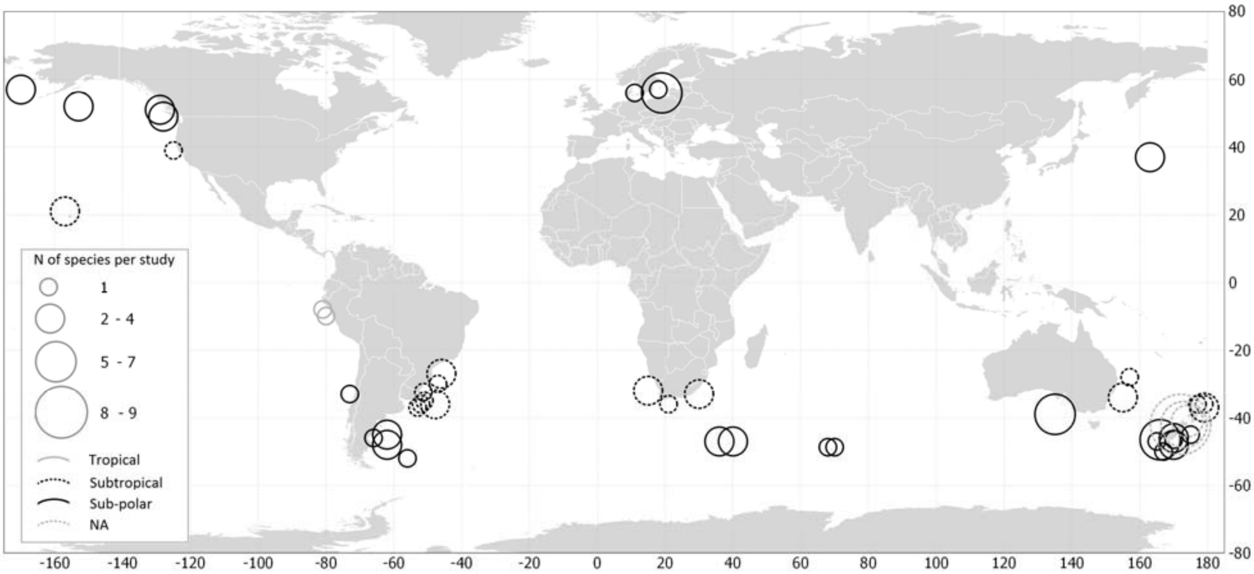
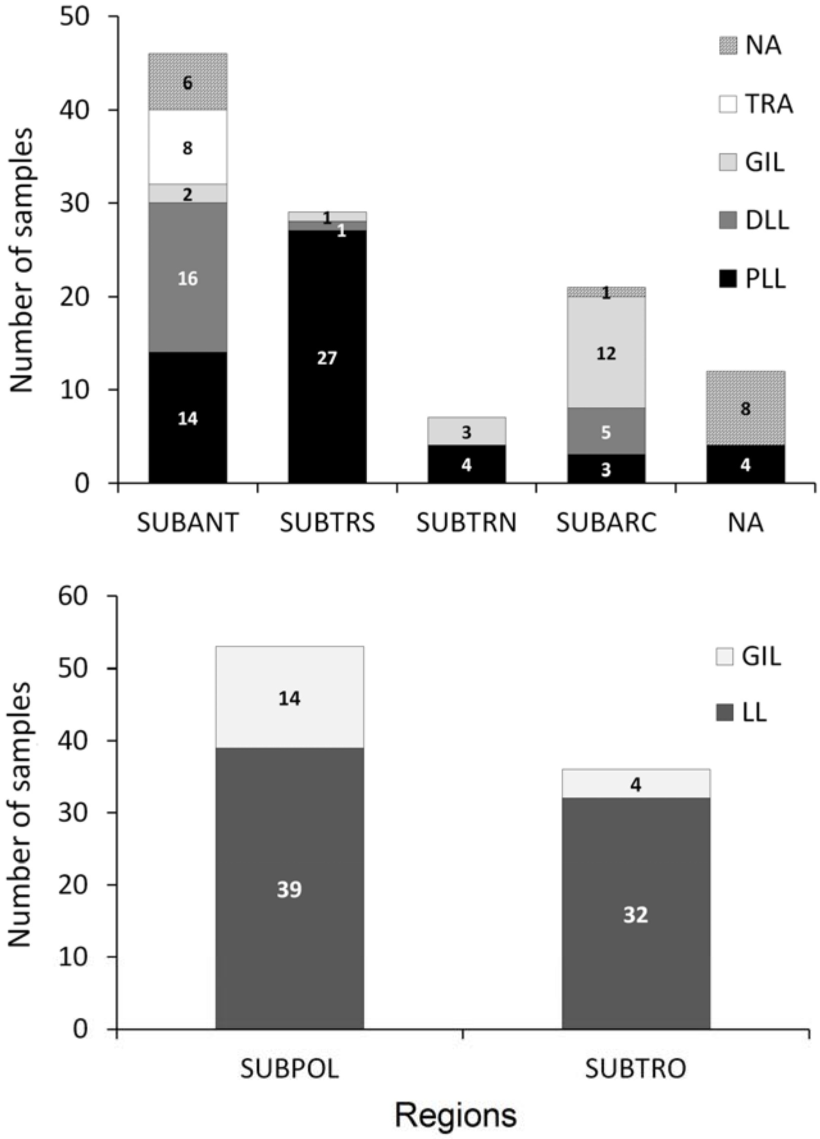


Figure 1. (Two columns fitting)



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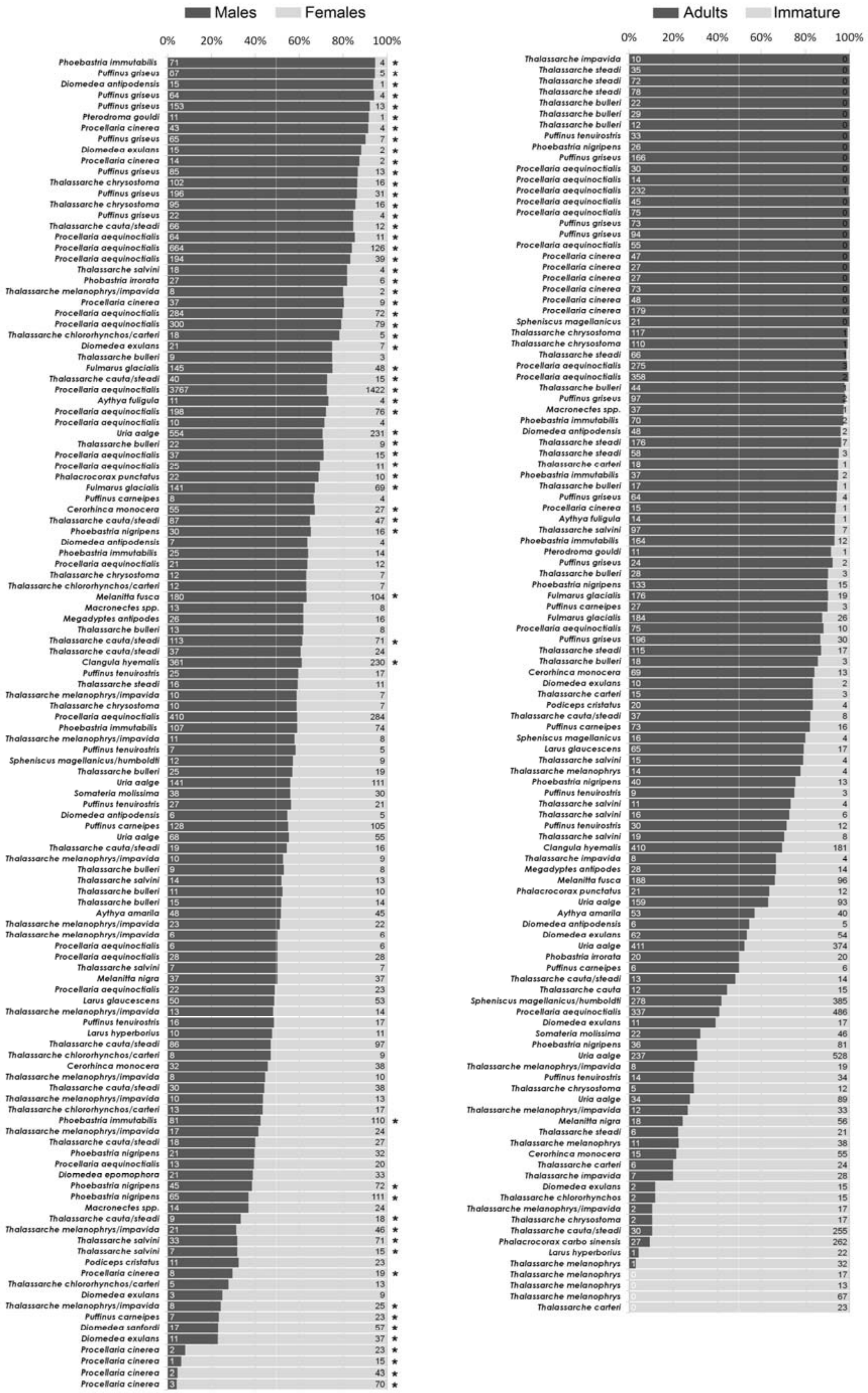

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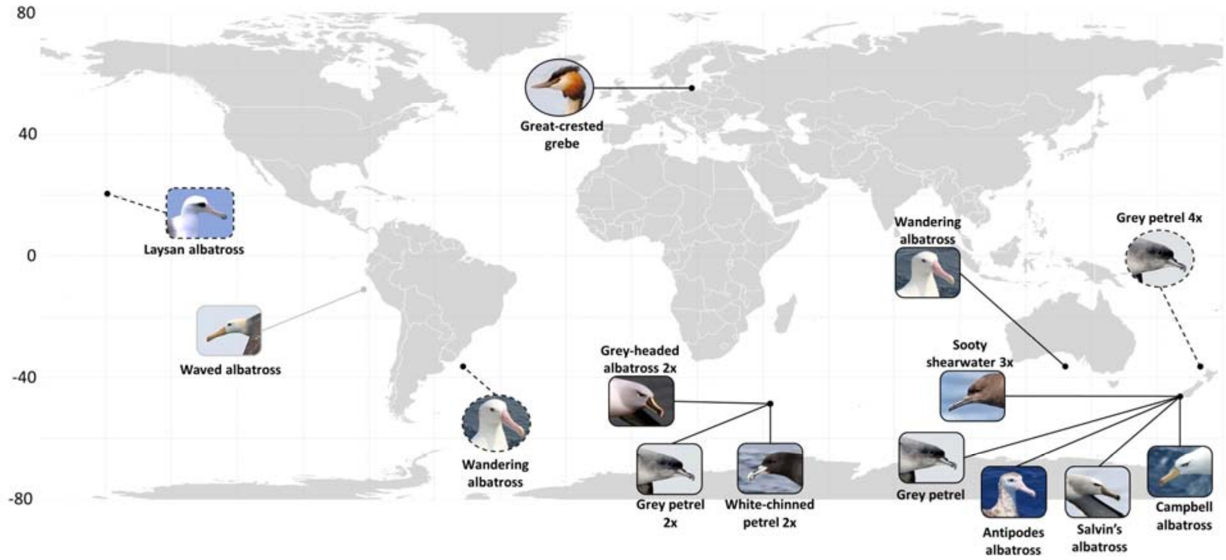

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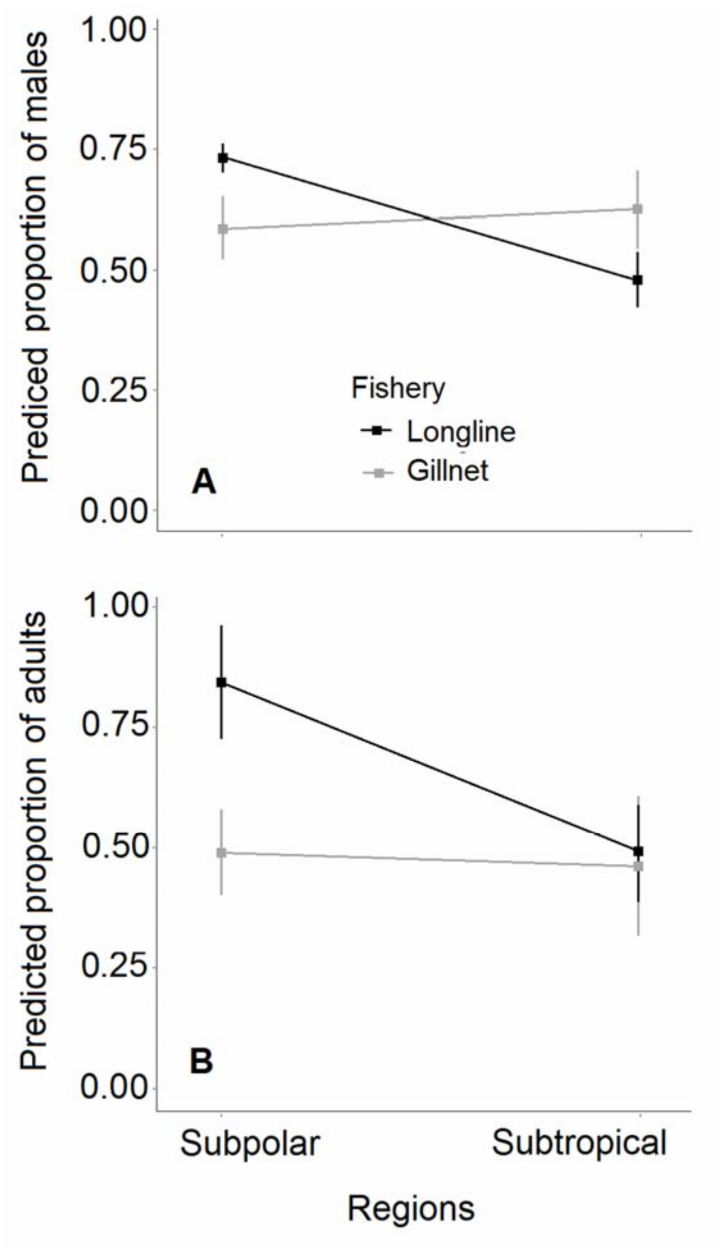

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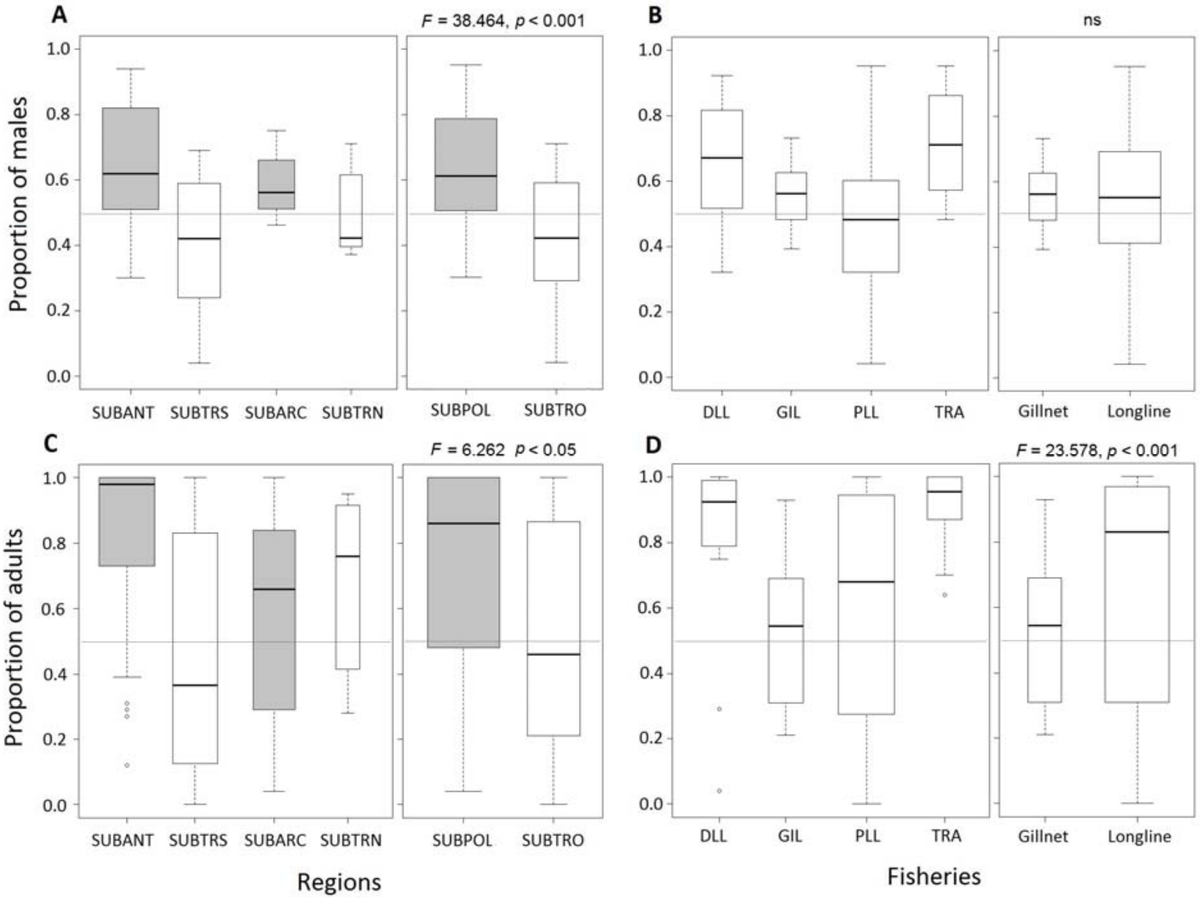
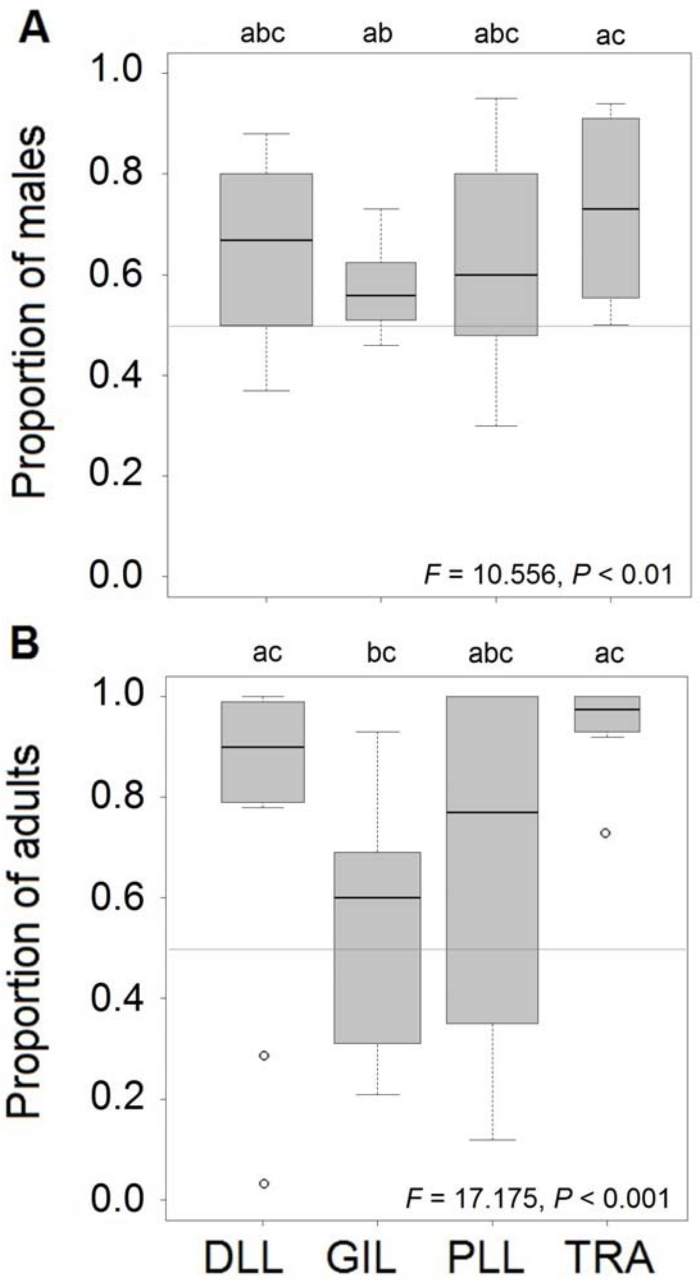


Figure 6. (1.5 column fitting)



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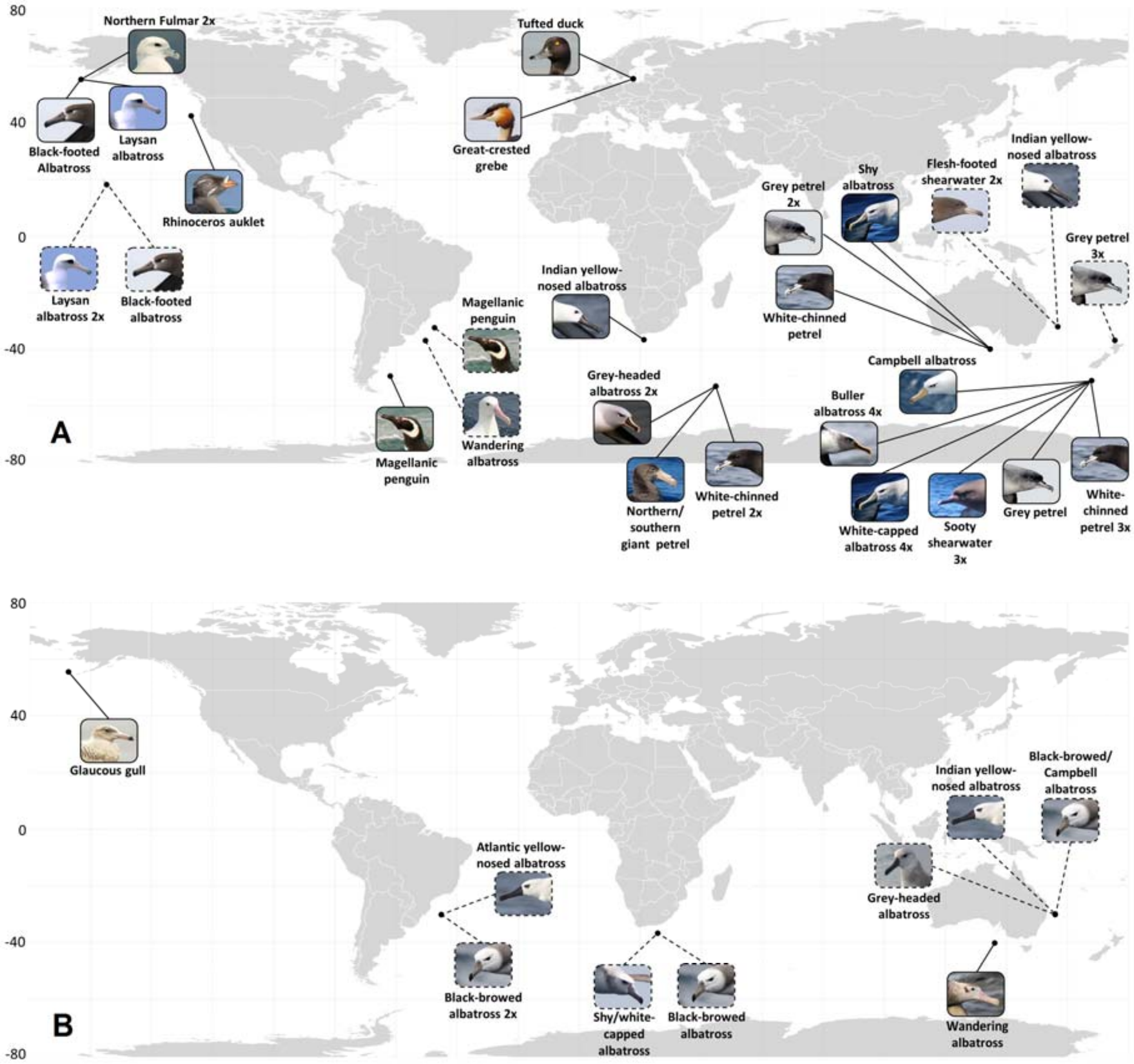

Figure 8. **(Two columns fitting)**

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

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**	$p\ \chi^2_{\text{Yates}}$	**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)

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)

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[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*.