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FEATURE PAPER

Estimates of seabird incidental catch by pelagic longline fisheries in the South Atlantic Ocean

Y-M. Yeh[1], H-W. Huang[2], K. S. Dietrich[3] & E. Melvin[4]

1 Department of Tourism Management Master Program of Leisure Environment Management, Nanhua University, Chiayi, Taiwan
2 Institute of Marine Affairs and Resources Management, Center of Excellence for Marine Bioenvironment and Biotechnology, National Taiwan Ocean University, Keelung, Taiwan
3 Fisheries Biologist, Seattle, WA, USA
4 School of Aquatic and Fishery Sciences, University of Washington, WA, USA

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Correspondence
Hsiang-Wen Huang, National Taiwan Ocean University, Institute of Marine Affairs and Resources Management, No. 2 Pei-Ning, Keelung 202, Taiwan. Tel: +886 2 2462 2192ex5608; Fax: +886 2 2463 3986
Email: julia@ntou.edu.tw

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Abstract

The mortality of seabirds in fisheries has had a serious negative impact on many seabird populations, yet the extent of fishery-derived seabird mortality in pelagic longline fisheries, remains poorly understood. In this study, we analyze fishing effort and catch data of the Taiwanese distant-water longline tuna fleet – the largest fleet in the Atlantic Ocean. These data collected by fishery observers over a 5-year span include 61 trips involving 6181 observed sets of over 20 million hooks, where 198 seabirds were caught (23 of which were released alive). Most birds were caught in the South Atlantic, with estimated seabird bycatch rates ranging from 0.026 birds per thousand hooks in the southwest Atlantic to 0.063 birds per thousand hooks in the southeast Atlantic. Black-browed, Atlantic yellow-nosed, and wandering albatrosses, as well as spectacled and southern giant petrels, were the most frequently caught species. Seabird bycatch hotspots were identified at 20°–40°S/10°W–15°E and 35°–45°S/45°–55°W. In the South Atlantic Ocean, generalized additive models indicated that fishing location and the number of birds sighted significantly influenced seabird bycatch rates. Extrapolating these spatially and temporally explicit seabird bycatch rates to the fishing effort data of other distant-water longline fleets and extrapolating the bycatch rates reported in the literature to the reported fishing effort of coastal nation fleets, we estimate the total seabird incidental mortality from pelagic longline fishing in the southern Atlantic Ocean to be between 3446 and 6083 birds per year from 2004 to 2008. These findings support proposals calling for the required use of best-practice mitigation measures by all pelagic longline vessels operating in seabird bycatch hotspots in the South Atlantic Ocean. International cooperation on research and data sharing is critical to ensure the sustainability of seabird populations and fisheries.

Introduction

The impact of longline fisheries on seabirds has drawn global attention since the 1990s (Brothers, 1991; Brothers, Gales & Reid, 1999; Lewison *et al*., 2004). In 1999, the Food and Agriculture Organization (FAO) developed the International Plan of Action for reducing seabird bycatch in longline fisheries (FAO, 1999) that called on longline nations to assess their impact and implement mitigation regulations where necessary. Since the development of that plan, best-practice guidelines have been developed to facilitate creation of national plans of action by individual countries and to provide a framework from which to implement the plans at the level of regional fisheries management organizations (FAO, 2008). The Agreement on the Conservation of Albatrosses and Petrels (ACAP) was established in 2001 to achieve and maintain favorable conservation status for albatrosses and petrels through research, monitoring, reduction of incidental mortality in fisheries, eradication of non-native species at breeding sites, reduction of disturbance and habitat loss, and reduction of pollution (ACAP, 2001).

Understanding the magnitude of seabird bycatch in all oceans could be useful for determining the need for appropriate conservation measures. Threats to seabirds are mainly from pelagic longline, demersal longline and trawl fisheries (Baker *et al*., 2007; Watkins, Petersen & Ryan, 2008; Anderson *et al*., 2011). The distribution of many seabird species significantly overlaps with longline fisheries (Tuck, Polacheck & Bulman, 2003; BirdLife International, 2004). In the Atlantic Ocean, fleets from 36 countries use pelagic longline to capture tuna, tuna-like species and sharks [International Commission for the Conservation of the Atlantic Ocean Tuna (ICCAT), 2010*c*)]. The ICCAT, which has jurisdiction over the largest area of the Atlantic Ocean, estimated that pelagic longline vessels fishing in the Atlantic Ocean deployed 315 million hooks annually from 2004 to 2008 (estimates ranged from 295 million hooks to 356 million hooks, http://www.iccat.int/en/accesingdb.htm). ICCAT identified 41 seabird populations of 28 species as being at serious risk from ICCAT longline fisheries (ICCAT, 2008). These included one critically endangered, seven endangered and nine vulnerable species [International Union for Conservation of Nature (IUCN) Red List http://www.redlist.org]. In response, the commission adopted a resolution [07-07] requesting that member countries provide seabird bycatch estimates to the Secretariat and requiring vessels to use mitigation measures to reduce their bycatch of seabirds (ICCAT, 2007).

There is strong evidence that seabird bycatch rates vary by fleet by area. In a summary of studies done in the Atlantic Ocean from 1987 to 2006, Tuck *et al.* (2011) reported that bycatch rates varied from 0.07 birds per thousand hooks in Canadian fisheries in 2001 to 4.7 per thousand hooks for the fisheries of Uruguay in 1993/1994. A lack of observer data from most member countries constrained the ICCAT Subcommittee on Ecosystems estimate of the annual seabird bycatch for the entire ICCAT area (ICCAT, 2010*a*). For the few countries providing data to ICCAT only Brazil, South Africa and Uruguay provided robust data consistently. Other countries, including Canada, Japan, Namibia, Spain and Taiwan, provided seabird bycatch data from limited sampling or the data were outdated, while China, Korea, the Philippines, St. Vincent and the Grenadines, provided no data (Tuck *et al.*, 2011). Consequently, the ICCAT assessment was considered incomplete because of a lack of reliable data on the incidental catch of seabirds stemming from low national observer coverage in the ICCAT area, as well as limited access to spatially or temporally detailed data from most nations (ICCAT, 2009, 2010*b*; Tuck *et al.*, 2011).

Understanding the factors influencing the rate of seabird mortality are important for effective fishery management, including taking action to require the use of seabird bycatch mitigation measures. Bycatch rates can be affected by many factors, including temporal, spatial, environmental, bait condition, mitigation measures and vessel-specific factors (Gales, Brothers & Reid, 1998; Stehn *et al.*, 2001; Tuck *et al.*, 2003; Dietrich, Parrish & Melvin, 2009; Jiménez, Domingo & Brazeiro, 2009; Jiménez *et al.*, 2010). Despite the millions of hooks deployed each year in the Atlantic Ocean by distant-water pelagic longline fishing nations, almost no seabird bycatch information is available from high seas fisheries (ICCAT, 2010*b*; Anderson *et al.*, 2011). Taiwan has the largest distant-water longline effort (hooks) in the Atlantic Ocean with highest level of observer coverage. This study aimed to (1) estimate the bycatch rate of the Taiwanese pelagic fleets for the entire high seas of Atlantic Ocean; (2) identify important factors, such as temporal, spatial, mitigation measures, and fisheries factors, affecting the incidental catch rates of seabirds; (3) estimate the total annual bycatch of seabirds by pelagic longline fleets operating in the Atlantic Ocean using spatially explicit fishing effort data reported to ICCAT for 2004–2008; (4) discuss the conservation implications of these analyses.

Materials and methods

Data sources

Catch and bycatch data were collected onboard Taiwanese vessels by fisheries observers through the scientific observer program started in 2002. For each set, observers recorded the fishing position (latitude and longitude), number of hooks deployed, times of setting and hauling, use of bird-scaring equipment, and bait types, catch information and bycatch information. Catch composition information included the number of all retained, discarded, and live-released catch brought aboard (including bycatch); the weight of the retained catch; and the depredation by sharks, cetaceans, and unknown animals. Data collected on incidentally caught seabirds, sea turtles and cetaceans includes species, number and status (dead/alive). Observers also recorded the number of birds flying and sea turtles/cetaceans swimming around the stern of the vessel during daylight. Digital photographs were taken for those individuals that could not be immediately identified.

The Taiwan Fisheries Agency (in collaboration with the Taiwan Tuna Association) deploy fishery observers in the Atlantic Ocean based on a quasi-lottery system to achieve 5% coverage in three longitudinal areas: north, tropical and south. In 2006, observer coverage was 100% in tropical areas in accordance with ICCAT Recommendation 05-02. The percentage of effort monitored by fisheries observers (observer coverage) increased from 0.2% in 2002 to 5.3% in 2008. In that observer coverage in 2002 and 2003 were low (Huang, 2011), data included in this study were from 2004 to 2008.

Data for 2004 to 2008 on total effort data by flag nation, publicly available from ICCAT, was used to estimate the number of seabirds caught in the Atlantic Ocean. The ICCAT database provides the most comprehensive effort data for pelagic longline effort throughout the entire Atlantic Ocean. Although the basic unit is hooks, the spatial units of reported effort varied by country (1 × 1-, 5 × 5-, 5 × 10-degrees grids). In that most countries provided pelagic longline fleets effort in 5 × 5-degree squares, the effort data in this study were standardized to 5 × 5 degrees for consistency.

Seabird bycatch rates and affecting variables

The rate of seabird bycatch (bycatch per unit effort, BPUE) was computed as the number of seabirds caught per 1000 hooks for each set. Given that previous studies revealed the spatio-temporal differences in seabird distributions and fisheries bycatch rates (BirdLife International, 2004; Baker

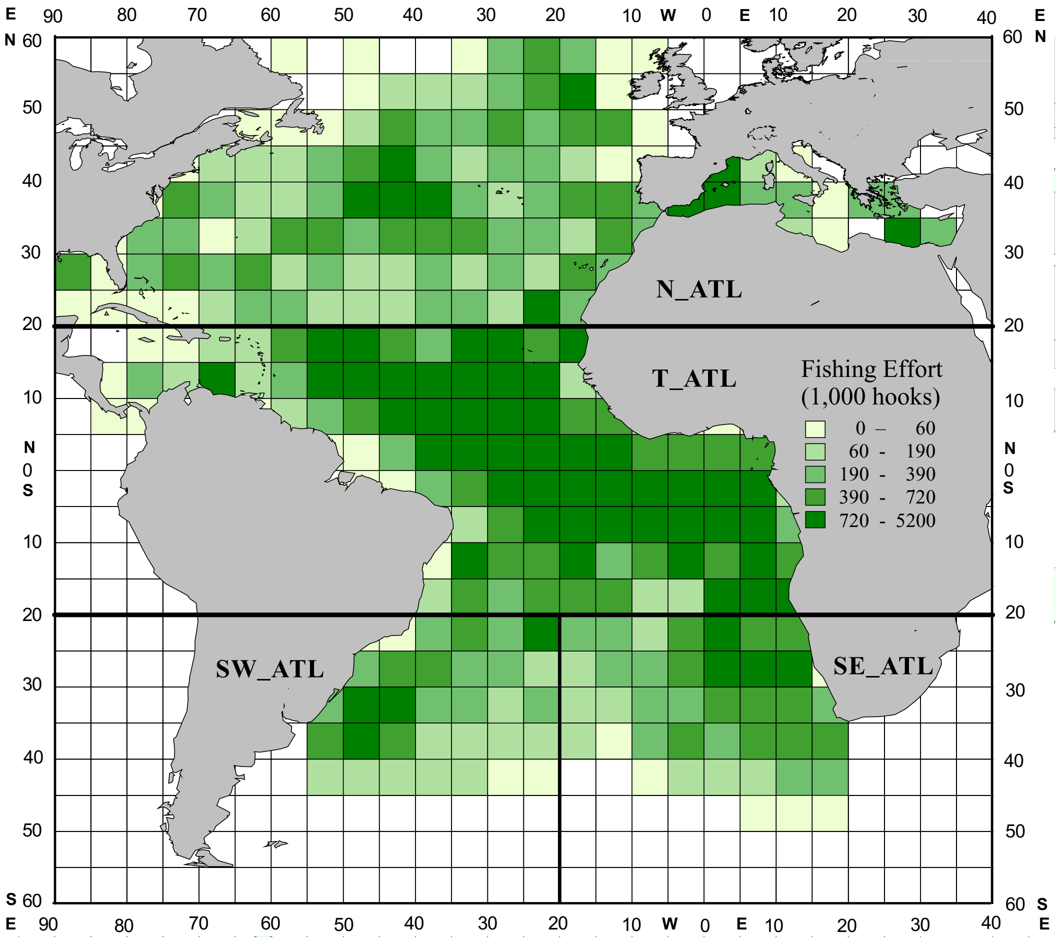

Figure 1 Aggregated pelagic longline fishing effort (thousands of hooks) reported to International Commission for the Conservation of the Atlantic Ocean Tuna and used in this analysis in each 5 × 5-degree square in the Atlantic Ocean from 2004 to 2008.The N_ATL included the area north of 20° N. The T_ATL included areas between 20° N and 20° S. The SE_ATL included areas south of 20° S and east of 20° W and the SW_ATL included areas south of 20° S and west of 20° W.

et al., 2007; Jiménez *et al.*, 2010), we calculated nominal bycatch rates by the four fishing grounds recognized by the fleets: the northern Atlantic Ocean (N_ATL, north of 20° N), the tropical Atlantic Ocean (T_ATL, between 20° N and 20° S), the southeast Atlantic Ocean (SE_ATL, south of 20° S, east of 20° W) and the southwest Atlantic Ocean (SW_ATL, south of 20° S, west of 20° W; Fig. 1).

In order to explore the variables that affect bycatch rates the most, we used catch data from the Taiwanese vessels operating in the south Atlantic, where birds were caught most often and at the highest rates. Variables included season, set position, presence or absence of a bird-scaring line, catch per unit effort (CPUE) of target tuna species and the number of seabirds sighted. Season and set position were the temporal and spatial factors. A bird-scaring line is the most common seabird bycatch mitigation measure used by the Taiwanese fleet. CPUE of target species was assumed to reflect the fishing operations. The number of seabirds sighted was assumed to be a measure of seabird abundance for a given set (see Table 1). In the model, the bycatch rates and number of seabirds sighted is not taxa-specific because not all bycatch seabirds are identified by species.

Table 1 Variables used in quasi-Poisson generalized additive models

Variable	Definition	Type
Season	1 – January to March 2 – April to June 3 – July to September 4 – October to December	Categorical
Set position	Latitude and longitude	Continuous
Bird-scaring lines	0 – none deployed 1 – one line deployed 2 – paired lines deployed	Categorical
Catch per unit effort (target)	Number of retained albacore or bigeye tuna	Continuous
Sightings	Number of seabirds counted during sighting observation	Continuous

In many studies of seabirds bycatch, the seabird bycatch rates were assumed to follow binomial (Gales *et al.*, 1998;

Brothers *et al.*, 1999; Gilman, Kobayashi & Chaloupka, 2008; Huang & Yeh, 2011), Poisson (Gilman *et al.*, 2008; Trebilco *et al.*, 2010) and negative binomial distributions (Hamel *et al.*, 2009). The effect of possible factors on bycatch rates were analyzed by generalized linear models (GLMs) and generalized additive models (GAMs; Gilman *et al.*, 2008; Dietrich *et al.*, 2009; Petersen *et al.*, 2009; Trebilco *et al.*, 2010). Both GLMs and GAMs allow for increased flexibility in assumptions compared with traditional regression techniques (i.e. normality and constant variance) as well as direct specification of error distribution (McCullagh & Nelder, 1989; Hastie & Tibshirani, 1990). GAMs supplement GLMs by allowing for the exploration of nonlinear functional relationships between the dependent and independent variables (Hastie & Tibshirani, 1990). Considering the inherent overdispersion in seabird bycatch data and lack of uniformity in sampling effort per set, we fitted quasi-Poisson GAM to the number of seabirds caught per set offset by the number of hooks per set {i.e. offset [ln (hooks)]} to standardize bycatch rates. An approximate *F*-test was used to evaluate variable significance ($P < 0.05$) (Chambers & Hastie, 1992). R version 2.10.1 was used for GAM model.

The ICCAT effort data by 5 × 5-degree square was input to the resulted GAM to obtain the predicted bycatch number for the South Atlantic. Then, the seabird bycatch rates were obtained by dividing the predicted bycatch number by thousand hooks in each 5 × 5-degree square. Besides, in order to overall understand, distribution fitting was performed to provide reasonable means and variances of BPUE for the whole South Atlantic, South-East Atlantic and South-West Atlantic Ocean. The fitting process was carried out by *fitdistr* R-function to fit parameters by maximum likelihood method.

Estimating total bycatch mortality in the South Atlantic

We generated seabird bycatch estimates for the Atlantic Ocean for two fleets, specifically: the distant-water fishing fleets operating on the high seas, and the coastal fishing fleets operating within national exclusive economic zones (EEZ).

Distant-water nations included: Taiwan, Japan, Spain, Korea, Belize, Vanuatu, St. Vincent and the Grenadines, and the Philippines. Taiwanese seabird bycatch rates from this study were used to extrapolate total bycatch for the high seas fleets because other countries did not provide seabird bycatch data to ICCAT (Anderson *et al.*, 2011). The seabird bycatch mortality was estimated for each 5 × 5-degree square in the area south of 20° S using the bycatch rate in each 5 × 5 grid estimated by the GAM multiplied by the effort data from ICCAT. We applied a bootstrap, with resampling 1000 times to calculate the 95% confidence interval for the estimation of seabird bycatch. For each bootstrap process, we resample the observed datasets to fit GAM model and input annual effort to the GAM model mentioned earlier, to get seabird mortality.

Coastal countries included South Africa and Namibia in the SE_ATL, and Brazil and Uruguay in the SW_ATL. Seabird bycatch rates reported in the recent literature were applied to the effort data reported to ICCAT by the coastal fleets from 2004 to 2008, to estimate the level of bycatch in coastal countries. Because of the lack of related detailed original data, only point estimates were calculated.

Results

Fishing operation patterns

The fishing effort of the pelagic longline fleets managed by ICCAT was distributed throughout the Atlantic Ocean from 2004 to 2008 (Fig. 1). During this period, 29 countries submitted effort data to ICCAT. One quarter (25.3%) of the total fishing effort in the Atlantic Ocean occurred in the N_ATL by the fleets of Spain, Japan, Taiwan, US and Cyprus. Most of the fishing effort (62.5%) occurred in the T_ATL, where Taiwan, Japan, China, St. Vincent and the Grenadines, and Panama operate. The least fishing effort was in the South Atlantic with 6.9% in the SE_ATL and 5.3% in the SW_ATL; Taiwan and Spain were the primary nations fishing in both areas, whereas Japan, South Africa and Namibia operated mostly in the southeast. Brazil, Uruguay, and St. Vincent and the Grenadines operated in the southwest Atlantic Ocean.

Taiwanese observers were onboard for 61 trips and monitored 6181 sets and 20 million hooks from April 2004 to February 2008. The distribution of observed effort is shown in Fig. 2. The observed coverage rate of Taiwanese fleets by effort was 3.4% of all sets made in the N_ATL, 7.6% in the T_ATL, 4.4% in the SE_ATL and 1.3% in the SW_ATL (Table 2).

Seabirds sighting records

Taiwanese fishery observers counted a total of 32.4 thousand seabirds, including 28 species (Table 3). The highest number of birds sighted during a single set was 300. The great shearwater *Puffinus gravis* was the only species observed in all three areas. Other species occurred in a single area (Table 3).

In the tropical areas, most seabird species were storm-petrels, boobies, terns and shearwaters. Albatrosses were sighted only in the South Atlantic Ocean; these included four endangered species, the northern royal albatross *Diomedea sanfordi*, the sooty albatross *Phoebetria fusca*, the Atlantic yellow-nosed albatross *Thalassarche chlororhynchos* and the black-browed albatross *Thalassarche melanophrys*. Petrels, including white-chinned petrel *Procellaria aequinoctialis*, spectacled petrel *Procellaria conspicillata*, cape petrel *Daption capense* and southern giant petrel *Macronectes giganteus*, were sighted throughout the south Atlantic; spectacled petrels and southern giant petrels were observed in SE_ATL and SW_ATL, others were sighted in SE_ATL only (Table 3).

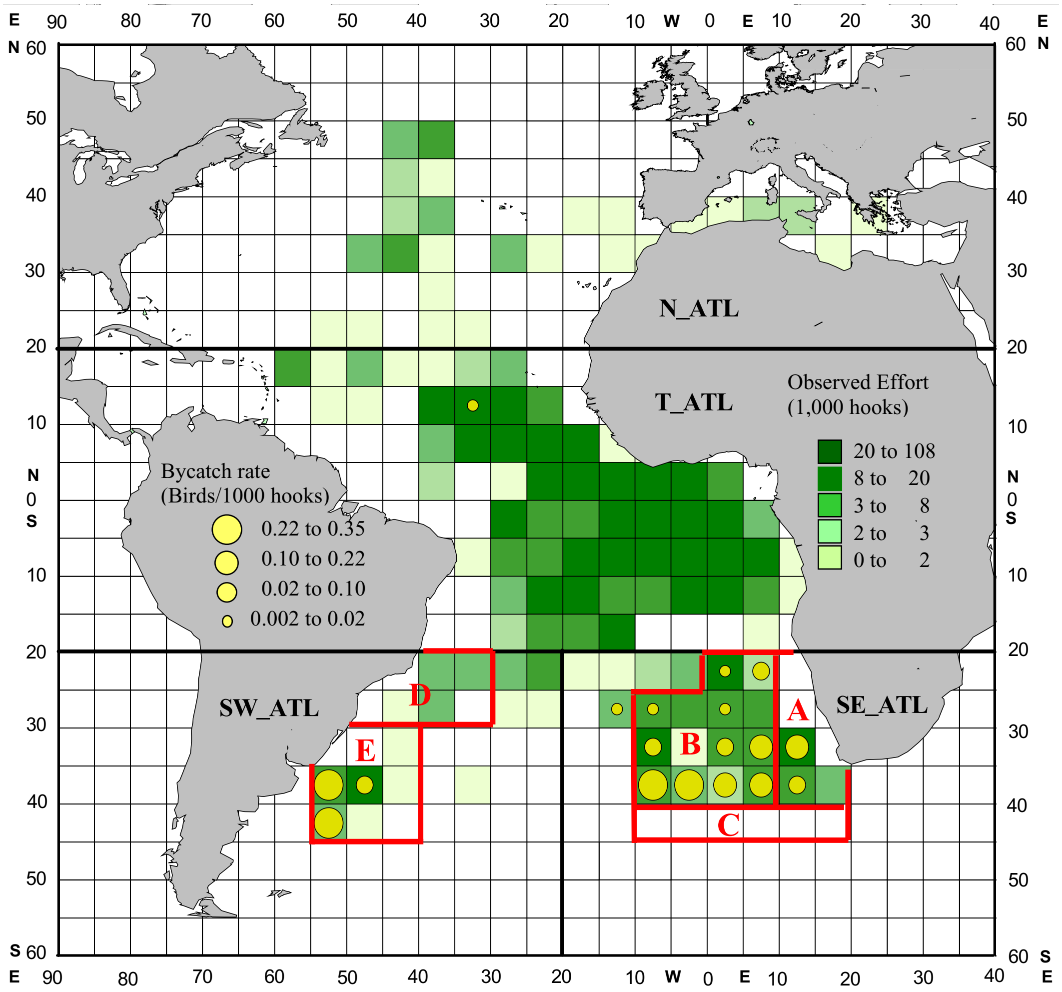

Figure 2 Observed effort distribution and average nominal bycatch rate (birds/1000 hooks) of Taiwanese pelagic longline fleets in 5 × 5-degree grid from 2004 to 2008. Five areas as seabird bycatch hotspots in the south Atlantic Ocean: (A) 10°–20° E/25°–35° S (Major bycatch by South Africa and Namibia fleets; Petersen *et al*., 2008; Petersen *et al*., 2009); (B) 10°–0° E/20°–40° S and 0°W–10° W, 25°–40° S, (Major bycatch by Taiwanese distant-water fleets); (C) 40°–45° S, 10° W–20° E, (Major bycatch by Japanese distant-water fleet, Inoue *et al*., 2011); (D) 30°–50° W, 20°–30° S, (Major bycatch by Brazil and Uruguayan fleets; Bugoni *et al*., 2008; Jiménez *et al*., 2010); and (E) 40°–55° W, 30°–45° S, (bycatch by Taiwanese distant-water and Uruguayan fleets; Jiménez *et al*., 2010).

Table 2 Total fishing effort, effort observed, and percent effort observed by fishery observers (coverage), number of seabirds sighted, number of seabirds caught, and bycatch rate by area for the Taiwanese pelagic tuna longline fleets in the Atlantic Ocean from 2004 to 2008

Area	Number of sets	Hooks (1000s)	Effort coverage rates	Number of sighted seabirds	Number of seabirds caught (dead/live)	Nominal bycatch rate (standard deviation) (birds/1000 hooks)
N_ATL	203	706	3.3%	7 071	0/0	0.000
T_ATL	5131	16 281	7.6%	6 591	0/1	0.000
SE_ATL	642	2 516	4.4%	6 049	140/22	0.070 (0.258)
SW_ATL	205	726	1.3%	12 686	35/0	0.047 (0.206)
Total	6181	20 230		32 397	175/23	0.010

The effort coverage rates are calculated by observed hooks divided by total hooks of Taiwanese fleets in each area.

Table 3 Seabird species sighted during the daytime and caught by area

IUCN status[a]	Species	Scientific name	Area[c]	Sighted(S)/caught(C)
LC	Northern fulmar	*Fulmarus glacialis*	N	S
LC	Great shearwater[b]	*Puffinus gravis*	N,T, S	S
LC	Cory's shearwater[b]	*Calonectris diomedea*	T	S
LC	South polar skua	*Catharacta maccormicki*	T	S
LC	Lesser frigatebird	*Fregata ariel*	T	S
LC	Wilson's storm-petrel	*Oceanites oceanicus*	T	S
LC	Madeiran storm-petrel	*Oceanodroma castro*	T	S
LC	Leach's storm-petrel	*Oceanodroma leucorhoa*	T	S
LC	Long-tailed jaeger	*Stercorarius longicaudus*	T	S
LC	Common tern	*Sterna hirundo*	T	S
LC	Arctic tern	*Sterna paradisaea*	T	S
LC	Masked booby	*Sula dactylatra*	T	S
LC	Brown booby	*Sula leucogaster*	T	S
LC	Red-footed booby	*Sula sula*	T	S
LC	Sabine's gull	*Xema sabini*	T	S
	Gannet	*Morus spp.*	T	S
CR	Tristan albatross[b]	*Diomedea dabbenena*	SE	S
VU	Southern Royal albatross	*Diomedea epomophora*	SE	S
VU	Wandering albatross[b]	*Diomedea exulans*	SE	S, C
EN	Northern Royal albatross[b]	*Diomedea sanfordi*	SE	S
EN	Sooty albatross[b]	*Phoebetria fusca*	SE	S, C
NT	Light-mantled albatross	*Phoebetria palpebrata*	SE	S
EN	Atlantic yellow-nosed albatross[b]	*Thalassarche chlororhynchos*	SE	S, C
EN	Black-browed albatross[b]	*Thalassarche melanophrys*	SE	S, C
VU	White-chinned petrel[b]	*Procellaria aequinoctialis*	SE	S
VU	Spectacled petrel[b]	*Procellaria conspicillata*	SE, SW	S, C
LC	Cape petrel[b]	*Daption capense*	SE	S, C
LC	Southern giant petrel[b]	*Macronectes giganteus*	SE, SW	S, C

[a] International Union for Conservation of Nature statuses downloaded from http://www.redlist.org on October 29, 2011.

[b] International Commission for the Conservation of the Atlantic Ocean Tuna priority species.

[c] N: North Atlantic (North of 20 N); T: Tropical Atlantic (between 20 N and 20 S); S: South Atlantic (South of 20 S).

CR, critically endangered; EN, endangered; LC, least concern; NT, near threatened; VU, vulnerable.

Bycatch rate and affecting variables

There were 198 seabirds caught incidentally over 4 years. Of these, 23 (11.6%) were released alive (Table 2). The bycatch of seabirds ranged from 0 to 12 birds per haul. No birds were caught in the N_ATL, only one bird was caught in the T_ATL; the remaining birds were caught in the SE_ATL and SW_ATL (Fig. 2). Most birds caught were albatrosses (61%): 16 black-browed, 14 Atlantic yellow-nosed, seven wandering, one sooty and 83 unidentified. Six southern giant petrels, three spectacled petrels and 68 unidentified seabirds were also taken.

The nominal bycatch rates were lowest in the N_ATL and T_ATL (0.000 birds per thousand hooks) and highest were in the South Atlantic Ocean (0.070 birds per thousand hooks in the SE_ATL and 0.047 in the SW_ATL; Table 2).

A gamma distribution best characterized BPUE by 5 × 5-degree grids (Fig. 3). A chi-squared goodness of fit indicates the estimated gamma distributions are acceptable. The BPUE for the entire South Atlantic Ocean followed a gamma distribution with mean of 0.048 and variance of 0.013. The BPUE for the SE_ATL followed a gamma distribution with a mean of 0.063 and variance of 0.01. The BPUE for the SW_ATL followed a gamma distribution with a mean of 0.026 and variance of 0.0065.

There were 847 observed sets in the South Atlantic Ocean. The number of seabird sightings and set position were significant effects in the GAM analysis, accounting for 50.3% of the model deviance; the model was a reasonable fit to the dataset ($r^2 = 0.43$). Season, bird-scaring lines and CPUE of target species showed no significant influence on seabird bycatch. Higher seabird catch rates occurred from 10°W to 20°E, with the highest rates from 10°W to 15°E, and from 35° to 40°S (Fig. 4a). The partial residual plot of this 2-D spatial effect on bycatch rate also hints at a more latitudinal effect in the southeast and a more longitudinal effect in the southwest. The number of seabirds sighted also resulted in a nonlinear effect; there was an apparent positive linear relationship between bycatch and the number of sighted birds within the range of 30–80 birds, which had an asymptotic response at higher sightings (Fig. 4b).

Bycatch number

No birds were caught in the North Atlantic Ocean where coverage by fishery observers was low. We considered this

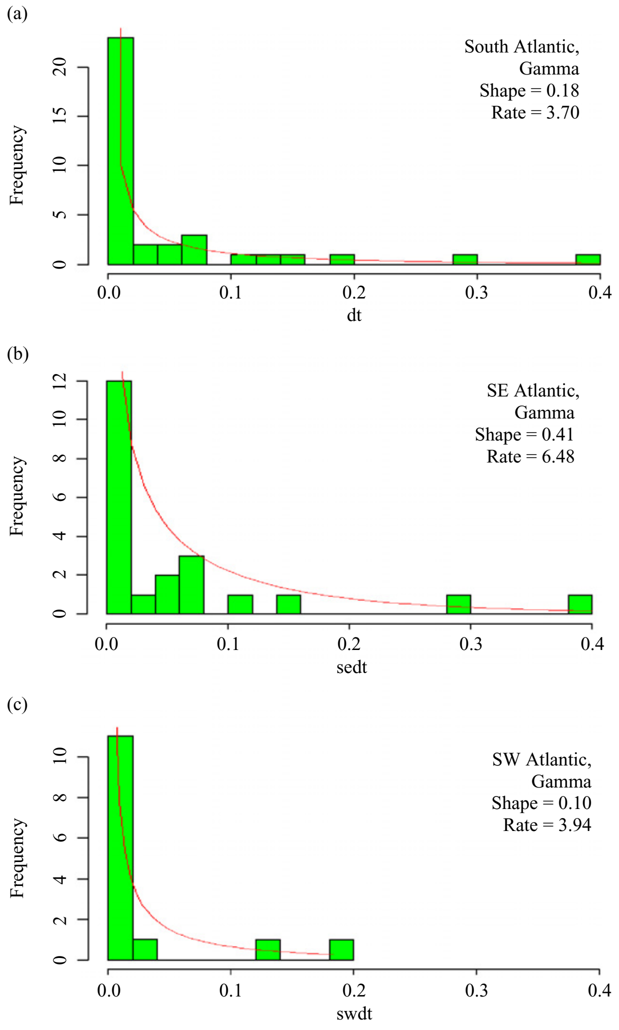

Figure 3 Gamma distribution for bycatch rates estimation in the (a) whole south Atlantic Ocean (b) SE Atlantic Ocean (c) SW Atlantic Ocean.

area too data-deficient for extrapolation to the Asia high seas fleets. For the tropical area, the estimated bycatch ranged from 6 to 10 birds annually in over 5000 observed sets. In the south Atlantic Ocean, because there was insufficient data regarding the birds sighted for the whole area, the location variable explained the most deviance (deviance = 43.6%) in our GAMs.

The estimated bycatch of distant-water longline fleets ranged from 2234 in 2007 to 4141 in 2006. More seabirds caught in SE_ATL (2255–3707) than SW_ATL (932–2376). Regarding seabird bycatch by coastal countries, country-specific rates from the literature were used to extrapolate mortality totals for Brazil, Uruguay, South Africa and Namibia (Bugoni *et al.*, 2008; Petersen, Honig & Nel, 2008; Petersen *et al.*, 2009; Jiménez *et al.*, 2010). This procedure yielded a total seabird bycatch estimates for coastal countries ranging from a low of 58 for Namibia in 2004 to a high of 798 for Uruguay in 2006. Coastal seabird bycatch showed an increasing trend in the SE_ATL and a decreasing trend in the SW_ATL.

From 2004 to 2008, our estimate of total seabird incidental catch by pelagic longline fleets operating in the South Atlantic Ocean ranged from 3446 to 6083 seabirds with 2255–3707 in the SE_ATL and 932–2376 in the SW_ATL (Table 4).

Discussion

Identify conservation concerns

This study is the first report of the extent of seabird incidental mortality by an Asian tuna fleet operating in the high seas of the Atlantic Ocean based on fishery observer data. The Taiwanese observer data, which included more than 6000 sets and 20 million hooks, came from the only comprehensive data submitted to and for the Atlantic Ocean distant-water pelagic longline fleets. Based on these results, ICCAT and related groups can gauge the spatial and temporal extent of the seabird incidental catch in Asian longline fleets operating throughout the Atlantic Ocean and make specific management recommendations.

Most species sighted in the N_ATL and T_ATL are not listed in the IUCN endangered species lists nor the ICCAT priority list (Table 3). In the N_ATL, the major species of concern is the Cory's shearwater in the Mediterranean Sea (Belda & Sanchez, 2001). Our analyses show that the Taiwanese fleet in the Mediterranean did not catch Cory's shearwater. They also show that the bulk of fishing by the Asian fleets occurred outside the Mediterranean Ocean in the north-central Atlantic Ocean. Based on available data, the greatest threat to seabirds in the north Atlantic stems from fleets from Spain: the Gran Sol Hake fishery operating in the Northeast Atlantic with 56 307 seabirds killed annually and its swordfish longline fisheries with 413 birds caught in eastern Mediterranean Sea between 2000 and 2008 (Anderson *et al.*, 2011). The US reported low seabirds bycatch rates: around 230 from 1992 to 2004 (Hata, 2006) and around 81 in 2008 (Winter, Jiao & Browder, 2011). The major species caught were unidentified seabirds, gulls and shearwaters. Continued collection and sharing of the bycatch information by Spain and Japan would improve assessments of the bycatch impacts on Cory's shearwaters in these areas.

The relatively low bycatch rate of seabirds in T_ATL compared with more temperate areas may be due to differences in the foraging behavior of tropical seabirds [e.g. most boobies and terns do not follow the longline vessels or feed on discards (Blaber *et al.*, 1995, 1998)]. This analysis shows that the total estimated bycatch was low (~10 birds) in tropical areas where observer coverage was highest (100% coverage rate in 2006 and 7.6% coverage rate overall with more than 5000 observed sets). This finding suggests that seabird bycatch avoidance measures are probably unnecessary in the tropical Atlantic.

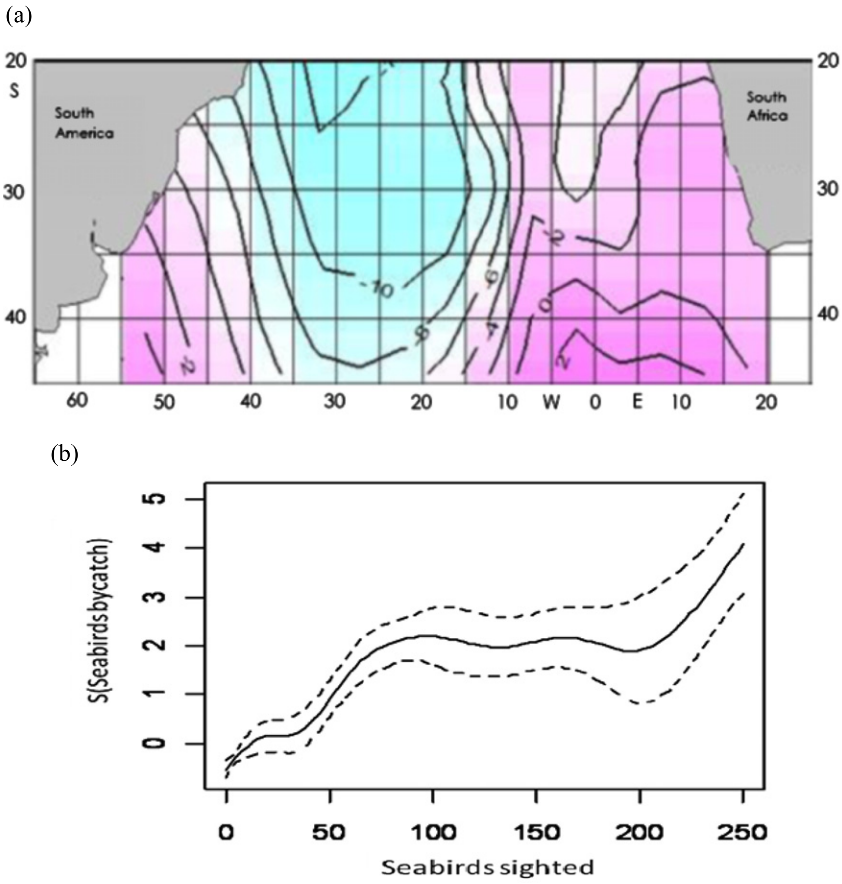

Figure 4 Partial residual plots of significant variables from the generalized additive model of the south Atlantic Ocean using sets observed in the Taiwanese longline tuna fishery during 2004–2008. (a) Two-dimensional spatial effect on catch rate. The color filled contour was on the response scale. Contours with smaller values (blue oriented) indicate lower rates, and contours with larger values (pink oriented) indicate higher rates. (b) Partial residual plot of the effect of seabirds sighted. The solid line is the model fit, and the dashed curve is the 95% pointwise confidence bands.

Table 4 Seabird bycatch rates and total mortality by area and year for distant water and coastal pelagic longline fleets in the South Atlantic Ocean

Area	Estimated bycatch rate (#/1000 hooks)	2004	2005	2006	2007	2008
SE_ATL		2527	2839	3707	2255	3604
DWLFs[a]	0.063[b]	2115	2372	3250	1637	3022
		(1096–3964)[c]	(1186–3270)	(1391–3976)	(997–2482)	(1150–3987)
South Africa	0.44[d]	354	359	320	470	497
Namibia	0.07[e]	58	108	137	148	85
SW_ATL		1317	1482	2376	1191	932
DWLFs[a]	0.026[b]	501	488	891	597	416
		(118–639)	(227–594)	(345–1300)	(227–819)	(131–517)
Brazil	0.229[f]	286	546	687	191	291
Uruguay	0.281[g]	530	448	798	403	225
Total		3844	4321	6083	3446	4536

[a] Distant-water tuna longline fleets (DWLFs) that provided effort data to ICCAT include Taiwan, Japan, Spain, the Philippines, Korea, Belize, St. Vincent and the Grenadines, Panama, and Vanuatu.

[b] The average bycatch rate estimated by Taiwanese pelagic tuna longline fleets observers data.

[c] Numbers in the parentheses are the 95% CI. Except for DWLFs, only point estimates of annually mortality were provided since lack of related detailed data.

[d] Bycatch rate from South African fleets (Petersen *et al.*, 2009).

[e] Bycatch rate from Namibian fleets (Petersen *et al.*, 2008).

[f] Bycatch rate from the Brazilian coastal fleet (Bugoni *et al.*, 2008).

[g] The observed bycatch rate from the Uruguayan coastal fleet (Jiménez *et al.*, 2010). The bycatch number is the sum of black-browed albatross, Atlantic yellow-nosed albatross and white-chinned petrel – the three major species from 2004 to 2007 (Jiménez *et al.*, 2010). The bycatch number in 2008 was calculated from the abovementioned bycatch rate and effort data from the ICCAT databank.

Most endangered seabird species are found south of 20°S (BirdLife International, 2004; Jiménez *et al.*, 2009; Tuck *et al.*, 2011). Twenty-two seabird populations were determined to be at serious risk from fishing mortality in the south Atlantic; South Georgia and Tristan de Cunha albatrosses had the highest risk scores (Tuck *et al.*, 2011). In this study, four (Atlantic yellow-nosed, black-browed, sooty and wandering albatrosses) of eight albatross species attending fishing operations were caught. These same species were also caught in Uruguayan and Brazilian fisheries (Bugoni *et al.*, 2008; Jiménez *et al.*, 2010; ICCAT, 2010*b*). This finding suggests that capture vulnerability varies by species and that these more vulnerable species should be a high priority for conservation action by fisheries managers. These results agree with those of Tuck *et al.* (2011), which suggest the conservation of Atlantic yellow-nosed, black-browed, sooty and wandering albatrosses should be a high priority for the ICCAT.

ICCAT's (2010*b*) estimate of total seabird bycatch for the Atlantic Ocean from 2003 to 2006 shows a declining trend from 16 568 seabirds in 2003, to 10 021 in 2004, 9879 in 2005, and 12 081 in 2006 because of decreasing fishing effort and shifts in effort among fishing grounds. However, there is a high degree of uncertainty associated with them because so few countries reported their seabird bycatch. Our estimated total seabird bycatch mortality focused on the South Atlantic Ocean was considerably lower than the ICCAT estimate (we estimated 3000–6000 annually). We found that the number of seabirds caught in the SE_ATL was higher than in SW_ATL, because of the higher effort and higher bycatch rate for distant-water and South African fleets. Total seabird bycatch peaked there in 2006 owning to a shift in effort to albacore fishing in south Atlantic Ocean because of quota limitation in the tropical bigeye fishery that year. In subsequent years, Taiwanese effort decreased after 2006; bycatch number decreased accordingly. At the other end of the spectrum, in the central South Atlantic observed seabird bycatch rates and total fishing effort were both low; consequently, this study provides little insight on seabird bycatch in this area.

In the South Atlantic Ocean, trawl fisheries and bottom longline fisheries are a major threat to seabirds. Estimated seabird mortality from South Africa deep-water hake trawling fisheries was around 18 000 (8000–31 000) annually (Watkins *et al.*, 2008); seabird take by Namibia hake fisheries were around 19 190 petrels and 606 albatross annually (Anderson *et al.*, 2011). Our study suggests that demersal longline fisheries are the primary concern in the South Atlantic, followed by trawl fisheries and pelagic longline fisheries.

Improvements in observer program and research

Klaer, Black & Howgate (2009) also attempted to estimate the number of seabirds taken in the Atlantic Ocean using the bycatch rates from fewer countries. However, because of the lack of data from higher latitudes in the north and coastal areas, they were forced to ignore temporal and spatial variability. In this study, incorporating data from the biggest Asian distant-water fleet (Taiwan) yielded more observation days than did previous studies, which enabled extrapolation within relatively small spatial cells (5 × 5-degree squares). It is likely that our estimate of bycatch mortality from coastal countries is an underestimate because not all coastal countries report their longline fishing effort to ICCAT.

The paucity of detailed seabird bycatch data limited this analysis. Seabird bycatch data should be submitted to ICCAT at the same spatial and temporal scales as fish catch. Specifically, ICCAT should implement minimum fishery observer standards for seabirds data collection, including increased observer coverage especially in 'hotspot' areas (5% is not enough for rare event species), specific criteria for vessel/trip selection, and how hooks within a set are randomly selected for observation. New action to require member nations to submit consistent and comparable data to the Secretariat routinely would allow sustainable management of all taxa under its purview. Although ICCAT adopted recommendations requiring members to submit seabird bycatch information, only one submitted data in 2010. In order to strengthen ICCAT regulations and improve bycatch evaluation, the major longline countries, such as Japan, Spain and China, should update their seabird bycatch information annually.

With regard to analysis tools, GAMs were our preferred choice to avoid the arbitrary classification of factors and to allow for nonlinear relationships between factors and response variables. However, they can be sensitive to extreme values, small sample sizes and missing values, such as our observation that seabird bycatch rates increased rapidly when more than 80 birds were sighted in the S_ATL. The actual number of large sighting events was low (only six sets with the number of sighted seabirds greater than 80), which is indicated by the larger confidence bands around the model fit. Therefore, the interpretation of the statistical analysis should be handled with caution.

The results showed the number of seabird sighted was significant in the model in the South Atlantic Ocean. This result suggests that if seabird tracking or distribution data were available, it would improve estimates of seabirds bycatch mortality based on number of seabirds and fishing effort in each location (Žydelis *et al.*, 2011). This could be achieved if ICCAT were to serve as data coordinator collecting effort data from fishing nations and seabirds tracking data from related researchers. In addition, better training to improve seabird species identification and a standardized protocol for collecting seabird abundance data by observers is also an important priority.

Considering the different behaviors, distributions and catchability of seabirds, if the species-specific or taxa-specific data could be collected, taxa-specific models and mortality estimates could yield considerably more insight for conservation actions. Most (76.3%) seabirds caught by Taiwanese vessels were not identified by species, either because of other priorities or the inability to identify, take photos or collect specimens; however, the percentage of birds correctly identified increased in recent years because of more training and accumulation of experience. Providing fishery observers with more information and increased training on seabird identification and distributions would undoubtedly improve the observers' ability to identify seabirds to species. Collection of consistent and high-quality species-specific bird-sighting data in a transparent protocol has the potential to improve investigations of the mechanics of seabird bycatch.

Conservation application

Temporal and spatial effects have been important in many analyses of seabird bycatch (Tuck *et al.*, 2003). Our results indicate that the spatial factor was the most influential predictor of seabird bycatch rates in the South Atlantic Ocean for pelagic longline fleets. Seasonal variation was not significant in any of our GAM models. Combining the results of this study with that of others, we identify the following five areas as seabird bycatch hotspots in the south Atlantic Ocean (Fig. 2): (1) 10°–20° E/25°–35° S (South Africa and Namibia fleets; Petersen *et al.*, 2008, 2009); (2) 10°–0° E/20°–40° S and 0°W–10° W, 25°–40° S, (Taiwanese distant-water fleets); (3) 40°–45° S, 10W–20E, Japanese distant-water fleet (Inoue *et al.*, 2011); (4) 30°–50° W, 20°–30° S, (Brazil and Uruguayan fleets; Bugoni *et al.*, 2008; Jiménez *et al.*, 2010); (5) 40°–55° W, 30°–45° S, Taiwanese distant-water and Uruguayan fleets (Jiménez *et al.*, 2010). These hotspots should be further considered for the highest level of best practice mitigation measures and heightened observer coverage to improve data collection and monitor compliance with mitigation measure requirements.

Bird-scaring lines are the most prescribed seabird bycatch mitigation measure in longline fisheries (Melvin *et al.*, 2004). However, in this research, we found no effect of the presence of bird-scaring lines on seabird bycatch rates probably because data collection was inadequate to show an effect. In some cases, vessels with many birds attending used bird-scaring lines, but caught birds, and vessels with no birds did not use bird-scaring lines and did not catch birds. In addition, some birds were caught during hauling, when bird-scaring lines are not used. Also, there were no standards for bird-scaring lines until 2008 and no protocol to judge if they were deployed properly. Standards for their use and fishery observer data reliably recording adherence to those standards would allow evaluation in future analyses.

Overall, this research strongly suggests that seabird bycatch mitigation is necessary to achieve seabird conservation and should be required, at the very least, in the seabird bycatch hotspots identified in this study. Melvin, Guy & Sato (2011) found that two hybrid streamer lines, together with double-weighted branch lines and night setting, constitute best-practice seabird bycatch mitigation for the joint-venture fleet operating in the South African EEZ and other fishing areas dominated by the white-chinned petrel. Following this research, ICCAT adopted Recommendation [11-09], requests members' longline fishing vessels to use at least two of the three measures: night setting with minimum deck lighting and bird-scaring lines and line weighting, when operating in the area south of 25 degrees south latitude. The standards are provided to ensure the effectiveness. In addition, these measures shall come into force by July 2013 (ICCAT, 2011).

The Taiwanese government has established many regulations on vessels fishing the high seas, including the installation of bird-scaring lines south of 20°S and other mitigation measures, to avoid the bycatch of seabirds in accordance with ICCAT-related recommendations (Huang, 2011). The Taiwanese government also requested that fishermen transmit photos of seabirds mitigation measures, such as bird-scaring lines for confirmation. These actions should be effective ways to limit and further reduce incidental catches. Improved monitoring and data collection is necessary to ensure sound conservation and management decisions.

Conclusions

This study identifies areas in the South Atlantic Ocean where the rate of seabird incidental mortality is high, and seabird bycatch mitigation should be implemented and strictly enforced to protect vulnerable seabird populations. Increased fishery observer coverage in these areas should be established as a high priority for ICCAT. In addition, outreach and conservation measures are required. For future research and conservation, more international cooperation on research and data sharing is critical to ensure the sustainability of marine ecosystems and fisheries.

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References

Agreement on the Conservation of Albatrosses and Petrels (ACAP) (2001). Battery Point, Australia.

Anderson, O.R.J., Small, C.J., Croxall, J.P., Dunn, E.K., Sullivan, B.J., Yates, O. & Black, A. (2011). Global seabird bycatch in longline fisheries. *Endangered Species Res.* **14**, 91–106.

Baker, G.B., Double, M.C., Gales, R., Tuck, G.N., Abbott, C.L., Ryan, P.G., Petersen, S.L., Robertson, C.J.R. & Alderman, R. (2007). A global assessment of the impact of fisheries-related mortality on shy and white-capped albatrosses: conservation implications. *Biol. Conserv.* **137**, 319–333.

Belda, E.J. & Sanchez, A. (2001). Sea bird mortality on longline fisheries in the western Mediterranean: factors affecting bycatch and proposed mitigating measures. *Biol. Conserv.* **98**, 357–363.

BirdLife International (2004). Tracking ocean wanderers: the global distribution of albatrosses and petrels. In *Results from the Global Procellariiform Tracking Workshop. Cambridge, UK*: 11–49. BirdLife International (Ed.). Gordon's Bay: BirdLife International.

Blaber, S.J.M., Milton, D.A., Farmer, M.J. & Smith, G.C. (1998). Breeding population sizes of seabirds of the far northern Great Barrier Reef, Australia: trends and influences. *Emu* **98**, 44–57.

Blaber, S.J.M., Milton, D.A., Smith, G.C. & Farmer, M.J. (1995). The importance of trawl discards in the diets of tropical seabirds of the northern Great Barrier Reef, Australia. *Mar. Ecol. Prog. Ser.* **127**, 1–13.

Brothers, N. (1991). Albatross mortality and associated bait loss in the Japanese longline fishery in the Southern Ocean. *Biol. Conserv.* **55**, 255–268.

Brothers, N., Gales, R. & Reid, T. (1999). The influence of environmental variables and mitigation measures on seabird catch rates in the Japanese tuna longline fisherry within the Australian Fishing Zone, 1991–1995. *Biol. Conserv.* **88**, 85–102.

Bugoni, L., Mancini, P.L., Monteiro, D.S., Nascimento, L. & Neves, T.S. (2008). Seabird bycatch in the Brazilian pelagic longline fishery and a review of capture rates in the south-western Atlantic Ocean. *Endangered Species Res.* **5**, 137–147.

Chambers, J.M. & Hastie, T. (1992). Statistical models in S.

Dietrich, K.S., Parrish, J.K. & Melvin, E.F. (2009). Understanding and addressing seabird bycatch in Alaska demersal longline fisheries. *Biol. Conserv.* **142**, 2642–2656.

Food and Agriculture Organization (FAO) (1999). *International Plan of Action for reducing incidental catch of seabirds in longline fisheries*. Rome: FAO.

Food and Agriculture Organization (FAO) (2008). *Report of the expert consultation on Best Practice Technical Guidelines for IPOA/NPOA-seabirds*. Rome: FAO.

Gales, R., Brothers, N. & Reid, T. (1998). Seabird mortality in the Japanese tuna longline fishery around Australia, 1988–1995. *Biol. Conserv.* **86**, 37–56.

Gilman, E., Kobayashi, D. & Chaloupka, M. (2008). Reducing seabird bycatch in the Hawaii longline tuna fishery. *Endangered Species Res.* **5**, 309–323.

Hamel, N.J., Burger, A.E., Charleton, K., Davidson, P., Lee, S., Bertram, D.F. & Parrish, J.K. (2009). Bycatch and beached birds: assessing mortality impacts in coastal net fisheries using marine bird strandings. *Mar. Ornithol.* **37**, 41–60.

Hastie, T.J. & Tibshirani, R.J. (1990). *Generalized additive models*. New York: Chapman and Hall.

Hata, D.N. (2006). *Incidental captures of seabirds in the US Atlantic pelagic longline fishery, 1986–2005*. Miami: NOAA Fisheries Service.

Huang, H.W. (2011). Bycatch of high sea longline fisheries and measures taken by Taiwan: actions and challenges. *Mar. Policy* **35**, 712–720.

Huang, H.W. & Yeh, Y.M. (2011). Impact of Taiwanese distant water longline fisheries on the Pacific seabirds: finding hotspots on the high seas. *Anim. Conserv.* **14**, 459–465.

International Commission for the Conservation of the Atlantic Ocean Tuna (ICCAT) (2007). Recommendation 07-07 by ICCAT on reducting incidental bycatch of seabirds in longline fisheries.

International Commission for the Conservation of the Atlantic Ocean Tuna (ICCAT) (2008). Report of the 2007 inter-sessional meeting of the sub-committee on ecosystems. February 19 to 23, 2007. *Collect. Vol. Sci. Pap. ICCAT* **62**, 1671–1720.

International Commission for the Conservation of the Atlantic Ocean Tuna (ICCAT) (2009). Report of the 2008 meeting of the sub-committee on ecosystems. *Collect Vol. Sci. Pap. ICCAT* **64**, 2295–2334.

International Commission for the Conservation of the Atlantic Ocean Tuna (ICCAT) (2010a). *Report for biennial period, 2008–2009*. Part II (2009) Vol. **2**. Madrid: SCRS.

International Commission for the Conservation of the Atlantic Ocean Tuna (ICCAT) (2010b). Report of the 2009 inter-sessional meeting of the sub-committee on ecosystems. *Collect Vol. Sci. Pap. ICCAT* **65**, 2209–2261.

International Commission for the Conservation of the Atlantic Ocean Tuna (ICCAT) (2010c). *Statistical bulletin*. Vol. **39** (1950-2008). Madrid: ICCAT.

International Commission for the Conservation of the Atlantic Ocean Tuna (ICCAT) (2011). Supplemental recommendation 11-09 by ICCAT on reducing incidental bycatch of seabirds in longline fisheries.

Inoue, Y., Yokawa, K., Minami, H. & Ochi, D. (2011). Preliminary view of bycatch hotspot: distribution of seabirds from tracking data, interaction map between seabird distribution and longline effort and bycatch distribution in the ICCAT conventional area of the southern hemisphere. ICCAT. SCRS/ 2011/198.

Jiménez, S., Abreu, M., Pons, M., Ortiz, M. & Domingo, A. (2010). Assessing the impact of the pelagic longline fishery on albatrosses and petrels in the southwest Atlantic. *Aquat. Living Resour.* **23**, 46–94.

Jiménez, S., Domingo, A. & Brazeiro, A. (2009). Seabird bycatch in the Southwest Atlantic: interaction with the Uruguayan pelagic longline Fishery. *Polar Biol.* **32**, 187–196.

Klaer, N.L., Black, A. & Howgate, E. (2009). Preliminary estimates of total seabird bycatch by ICCAT fisheries in recent years. *Collect. Vol. Sci. Pap. ICCAT* **64**, 2405–2414. ICCAT.

Lewison, R.L., Crowder, L.B., Read, A.J. & Freeman, S.A. (2004). Understanding impacts of fisheries bycatch on marine megafauna. *Trends Ecol. Evol.* **19**, 598–604.

McCullagh, P. & Nelder, J.A. (1989). *Generalized linear models*. New York: Chapman and Hall.

Melvin, E., Guy, T. & Sato, N. (2011). Preliminary Report of 2010 Weighted Branchline Trials in the Tuna Joint Venture Fishery in the South African EEZ Page 14 Fourth Meeting of the Seabird Bycatch Working Group, Agreement on the Conservation of Albatrosses and Petrels, Guayaquil, Ecuador.

Melvin, E., Sullivan, B., Robertson, G. & Wienecke, B. (2004). A review of the effectiveness of streamer lines as a seabird bycatch mitigation technique in longline fisheries and CCAMLR streamer line requirements. *CCAMLR Sci.* **11**, 189–201.

Petersen, S.L., Honig, M. & Nel, D.C. (2008). The impact of longline fisheries on seabirds in the Benguela current large marine ecosystem. *Collect. Vol. Sci. Pap. ICCAT* **62**, 1739–1756.

Petersen, S.L., Honig, M.B., Ryan, P.G. & Underhill, L.G. (2009). Seabirds bycatch in the pelagic longline fishery off southern Africa. *Afr. J. Mar. Sci.* **31**, 191–204.

Stehn, R.A., Rivera, K.S., Fitzgerald, S. & Wohl, K.D. (2001). Incidental catch of seabirds by longline fisheries in Alaska. in *Seabird bycatch: trends, roadblocks, and solutions*: 204. Melvin, E.F. & Parrish, J.K. (Eds). Blaine: University of Alaska Sea Grant.

Trebilco, R., Gales, R., Lawrence, E., Alderman, R., Robertson, G. & Baker, G.B. (2010). Characterizing seabird bycatch in the eastern Australian tuna and billfish pelagic longline fishery in relation to temporal, spatial and biological influences. *Aquat. Conservat. Mar. Freshwat. Ecosyst.* **20**, 531–542.

Tuck, G.N., Phillips, R.A., Small, C., Thomson, R.B., Klaer, N.L., Taylor, F., Wanless, R.M. & Arrizabalaga, H. (2011). An assessment of seabird–fishery interactions in the Atlantic Ocean. *ICES J. Mar. Sci.* **68**, 1628–1637.

Tuck, G.N., Polacheck, T. & Bulman, C.M. (2003). Spatio-temporal trends of longline fishing effort in the Southern Ocean and implications for seabird bycatch. *Biol. Conserv.* **114**, 1–27.

Watkins, B.P., Petersen, S.L. & Ryan, P.G. (2008). Interactions between seabirds and deep-water hake trawl gear: an assessment of impacts in South African waters. *Anim. Conserv.* **11**, 247–254.

Winter, A., Jiao, Y. & Browder, A. (2011). Modeling low rates of seabird bycatch in the US Atlantic longline fishery. *Waterbirds* **34**, 289–303.

Žydelis, R., Lewison, R.L., Shaffer, S.A., Moore, J.E., Boustany, A.M., Roberts, J.J., Sims, M., Dunn, D.C., Best, B.D., Tremblay, Y., Kappes, M.A., Halpin, P.N., Costa, D.P. & Crowder, L.B. (2011). Dynamic habitat models: using telemetry data to project fisheries bycatch. *Proc. Roy. Soc. Lond. Ser. B.* **278**, 3191–3200.