Great shearwater *Ardenna gravis* attendance at commercial fisheries in the Argentine economic fishing zone

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ABSTRACT: The great shearwater *Ardenna gravis* is a pelagic seabird that forages in waters of the southwestern Atlantic Ocean mainly during the pre-laying and chick-rearing periods. There, the species has been reported in the bycatch of longline and trawl fisheries. The aim of this study was to evaluate the effect of fishing effort on the foraging behavior of shearwaters, analyzing the distribution and behavior of birds and fishing effort and using evidence from isotope analysis to assess their use of fishery discards and facilitated prey. Tracking data of immature and adult shearwaters and fishing effort of different Argentine commercial fishing fleets were used to determine the effect of fishing effort on the foraging behavior of the species through generalized additive mixed models. Adult and immature shearwaters are more likely to forage when the fishing effort of demersal high-seas ice-trawlers increases and that of coastal demersal ice-trawlers decreases (and midwater ice-trawlers for immatures). The isotope analysis showed higher contribution of zooplanktonic species and mid-water fish, followed by demersal species (which can be only available through the consumption of discards and offal). These results are related to the common use of highly productive waters and the attraction of shearwaters generated by prey captured in nets and by discards as a predictable source of food. Understanding the impact of fisheries on seabird behavior is essential for implementing measures aimed at reducing the incidental capture of seabirds by fishing fleets.

KEY WORDS: Seabirds · Fisheries · Discards · Tracking data · Foraging behavior · Stable isotope analysis

1. INTRODUCTION

Incidental mortality in fisheries (bycatch) is one of the biggest threats to marine megafauna like seabirds, marine mammals and sea turtles (Moore & Reid 2009, Wallace et al. 2013, Phillips et al. 2023). Seabirds such as albatrosses, petrels and shearwaters travel 1000s of km when foraging at sea, where they interact with a range of fisheries that operate in the same highly productive areas (Petersen et al. 2008, Copello et al. 2014). About half of seabird species are listed as threatened with extinction by the International Union for Conservation of Nature (IUCN), with fisheries bycatch, the presence of invasive species in breeding areas and climate change as the main causes of their worsening conservation status (Dias et al. 2019, Phillips et al.

2023). The Southwest Atlantic Ocean concentrates one of the largest seabird biomasses in the world (Falabella et al. 2009, Carneiro et al. 2020), hosting some 40 procellariiform species, including breeders and long-distance migrants (Favero & Silva Rodriguez 2005, Seco Pon et al. 2015). These species share this marine ecosystem with human activities, including commercial fisheries as one of the main economic activities. Current fishing effort in the Argentine exclusive economic zone (EEZ) comprises ca. 800 vessels operating throughout the year, using a wide range of fishing gear, to catch some 800 000 t annually (Argentine NPOA—Seabirds 2010, Secretaría de Agricultura Ganadería y Pesca 2022). Seabird attendance and interactions have been reported in a range of fleets including longliners as well as coastal and offshore trawlers (e.g. González-Zevallos & Yorio 2006, Favero et al. 2013, Seco Pon et al. 2015, 2023, Paz et al. 2018). The interactions primarily arise from seabirds attempting to feed on discarded fish and/or offal generated by fishing fleets, often resulting in entanglements of strikes with fishing gear leading to severe injuries or incidental mortality (i.e. bycatch) (Favero & Seco Pon 2014).

Within this group of threatened seabirds, 10 petrel species are known to interact with fisheries operating in the Argentine EEZ and the fishing zone shared with Uruguay, particularly divers such as *Procellaria* petrels and *Ardenna* shearwaters, including the great shearwater *A. gravis*, which is globally listed as Least Concern (BirdLife International 2023) and locally as 'not threatened' (Ministerio de Ambiente y Desarrollo Sustentable y Aves Argentinas 2017). However, this species faces several threats including predation by introduced mice on Gough Island (Wanless et al. 2007, Dilley et al. 2015), the harvest of eggs/chicks on Nightingale Island (Rowan 1952, Richardson 1984), plastic ingestion (Ryan 1987, Pierce et al. 2004) and incidental mortality in a range of fisheries (Barnes et al. 1997, Glass et al. 2000, Bugoni et al. 2008, Jiménez et al. 2009, Paz et al. 2018, Seco Pon et al. 2020). Locally, great shearwaters have been recorded in seabird assemblages attending demersal and mid-water trawl fleets (coastal and offshore), as well as longline fleets (Seco Pon et al. 2007, 2020, 2023, Favero et al. 2011, Paz et al. 2018, Tamini et al. 2021, 2023). This species has been also reported in the bycatch of longliners and demersal freezer and ice-trawlers (Favero et al. 2011, 2013, Tamini et al. 2015, 2021, Seco Pon et al. 2023), and in some fleets showing high bycatch rates, for example in the mid-water trawl fishery (Paz et al. 2018, Seco Pon et al. 2020).

Great shearwaters breed at 3 main sites in the Tristan da Cunha archipelago, namely Nightingale, Inac-cessible and Gough islands, where the total population is estimated to be some 5 million pairs (Carboneras 1992, Snow et al. 1998, Ryan 2007). The species was also recorded in 1987 as a breeder (albeit with fewer than 15 pairs) in the Malvinas Islands (Woods 1988). Adults begin a trans-equatorial migration in April, moving north-west to South America, up to Canada, past Greenland and onto the northeast Atlantic, before returning south from late September to November to their breeding grounds (Harrison 1983, Powers et al. 2022). Tracking data indicate that the southwestern Atlantic Ocean is an important foraging area for the species during all phases of the breeding period (pre-laying, incubation and post-breeding) (Ronconi et al. 2010, 2018, Schoombie et al. 2018). During the non-breeding period in the north Atlantic, the diet of shearwaters includes fish such as *Clupea harengus* and *Scomber scombrus*, squid *Illex illecebrosus* and krill *Meganyctiphanes norvegica* (Ronconi et al. 2010). The knowledge about the diet during breeding is limited, with sparse information available at the prey species level. Data from stomach contents suggest that chicks and adults primarily feed on squid, with occasional consumption of fish and crustaceans (Hagen 1952, Rowan 1952).

The spatial and temporal overlap between seabirds and fisheries has been used extensively as a proxy of risk of bycatch (Copello & Quintana 2009, Yorio et al. 2010, 2021, Tuck et al. 2011, Copello et al. 2014). In addition, the analysis of stable isotopes has been used as a proxy of dietary information and to better understand the importance and contribution of fishery target species and discards (Bugoni et al. 2010, Mariano-Jelicich et al. 2014, 2017). Although the use of fishery discards and offal by seabirds could be seen as a food subsidy, the literature shows negative impacts on the life history traits and population dynamics of seabirds, with incidental mortality as the main threat worsening the conservation status of many procellariiforms (Favero & Seco Pon 2014, Louzao et al. 2020). In general, studies focused on spatial overlap with fisheries and the effect of fishing effort on the foraging behavior of seabirds have been conducted at a single fishery scale. Despite the importance of conducting a multi-gear/fisheries assessment of possible impact, no such attempt has been made so far within the Argentine EEZ and adjacent areas. This study assesses the spatial association of adult and immature great shearwaters with commercial fisheries in the Argentine EEZ and in the Argentine—Uruguayan Common Fishing Zone (ZCPAU), analyzing the effect of fishing effort on the foraging behavior of the species. In addition, the study provides evidence of the

importance of mid-water fish and demersal prey in the diet of shearwaters. The information supplied here is relevant for use in the design, development and implementation of marine protected areas in Argentina, aimed at achieving the objective of protecting 10% of the marine areas (Ministerio de Ambiente y Desarrollo Sostenible Resolution 356/2022; https://www.boletinoficial.gob.ar/detalleAviso/primera/268717/20220817), as envisioned in the United Nations Convention on Biological Diversity Strategic Plan for Biodiversity 2021−2024 (https://www.cbd.int/sp; ratified in Argentina for 2021−2024).

2. MATERIALS AND METHODS

2.1. Tracking data

Great shearwaters *Ardenna gravis* were tagged at different sites during breeding (incubation and post-breeding) and pre-laying periods between 2006 and 2015. Between 2006 and 2009, 24 birds were captured in the Bay of Fundy, Canada (44.47−44.87° N, 66.52−66.82° W), most of which were considered to be 'immature' birds (Powers et al. 2017, Ronconi et al. 2018). In 2009, 42 birds were caught in their burrows at breeding colonies on Gough Island (40.35° S, 9.88° W; population size: 1 million pairs) and Inaccessible Island (37.29° S, 12.70° W; 2 million pairs) (Ronconi et al. 2018). The tracking devices used were battery-powered platform terminal transmitters (PTTs). In addition, data from 2 GPS-tracked individuals from Gough and Nightingale islands (37.42° S, 12.47° W) in 2014 and 2015 were used to analyze the general distribution of shearwaters in the study area. To summarize, a total of 66 birds were tracked using PTTs, with an additional 2 tracked via GPS. However, only data from individuals within the study area were considered, totaling 41 birds (Table S1 in Supplement 1 at www.int-res.com/articles/suppl/m751p173_supp.pdf, both supplements). The locations and techniques used to capture and deploy these tracking devices are described by Ronconi et al. (2018) and Schoombie et al. (2018), respectively.

2.2. Data analysis

Analyses were conducted using all shearwater locations where the commercial Argentine-flagged fisheries operate, hereafter referred to as the 'Argentine fishing zone', comprising the Argentine EEZ and the ZCPAU (Table S1, Fig. S1 in Supplement 1). The kernel utilization distribution of birds by age class

(adults from 2009 to 2015 and immatures from 2006 to 2010) was estimated using the 'kernelUD' function in the 'adehabitatHR' package in R (Calenge 2006, 2021) with a reference bandwidth smoothing parameter (Worton 1989). Kernel analysis enables the prediction of a volume representing the estimated probability distribution across a surface defined by (x, y) coordinates. In this study, quantiles were employed to identify the upper 50%, as well as 75% and 95% of that volume (Copello et al. 2014), indicating the probability of a particular individual being within a specific cell (x, y). Subsequently, contours (polygons) were delineated to represent the minimum area where the probability of relocating the animal equals a specified value. For example, the 95% home range corresponds to the smallest area where the probability of relocating the animal equals 0.95 (Copello et al. 2014).

Treatment of tracking data are summarized here and fully described in Ronconi et al. (2018). Tracking data were fitted to a Bayesian switching state-space model (SSSM) using the 'bsam' package in R (Jonsen et al. 2005, 2013). These models provide improved location estimates (using statistical processes to estimate positions which account for inaccuracy from different Argos location classes, Jonsen et al. 2005), evenness in the sampling (Reid et al. 2014, Jodice et al. 2015) and an inferred behavior state as a probability that any bird position is in 1 of 2 states: transiting (1) or foraging (2), thus representing transiting or area-restricted search (i.e. foraging), respectively (Jonsen et al. 2013, Powers et al. 2017). Estimated locations were derived using the hierarchical first-difference correlated random walk with switching, which was run in batches on groups of 4 birds (running larger batches would have taken several days of work for the processor), keeping batches separate for Fundy and Gough/Inaccessible birds. The modeling approach used a Markov chain Monte Carlo method with 10 000 iterations (thinned by every 10th record) after a burn-in of 40 000 iterations to eliminate the effects of initial values. The model was run with a 6 h time step so that estimated locations were normalized in time over a regular interval (6 h) for the entire tracking period. While a 3 h time step has been previously modeled with these data, the results were qualitatively similar when modeled with a 6 h time step (see the supplementary materials in Powers et al. 2017), although we opted for a 6 h time step to produce a more generalized track due to the longer 'off' period of these tag deployments, which were duty-cycled at 8 h on and 16 h off (Ronconi et al. 2018). Moreover, the long distance and duration of foraging trips from their colonies (Ronconi et al. 2018,

Schoombie et al. 2018) suggest that behavior-state models at 6 h time intervals would be sufficient to differentiate between foraging and long-distance movements. Foraging and transiting behaviors were determined by investigating the value of b from the SSSM, with $b > 1.7$ defining foraging behavior and $b < 1.3$ as transit behavior. Behavior was uncertain and not defined for b values between 1.31 and 1.69 (Jonsen et al. 2013, Powers et al. 2017); the duty-cycle of the tags and the positional inaccuracy of Argos data (compared to GPS data) may have contributed to the uncertainty in behavior inference; therefore, these data were omitted from the analyses rather than considering the modeling of additional behavior states.

A range of commercial Argentine fisheries operate in the Argentine fishing zone throughout the year (see Argentine NPOA—Seabirds 2010, Copello et al. 2014, Seco Pon et al. 2015). Trawl fleets consiste of vessels preserving the entire fish in ice within plastic cubes (i.e. ice-trawlers) operating in coastal or high-seas areas and those freezing the catch after processing onboard (freezer trawlers) operating mainly in high-seas. These fleets are different both in length and number of vessels operating. Both types of vessels discard part of the catch lacking commercial value, but freezer trawlers also generate offal as a product of the processing, consisting of heads, fins and guts that are released back to the sea (Copello et al. 2014). Trawlers were classified according to their fishing gear: bottom otter trawl (e.g. targeting Patagonian scallop *Zygochlamys patagonica*; consistent catches throughout the year), demersal trawl (e.g. targeting common hake *Merluccius hubbsi*, southern hake *M. australis* and Patagonian grenadier *Macruronus magellanicus*; consistent catches throughout the year), mid-water trawl (e.g. targeting Argentine anchovy *Engraulis anchoita*; higher catches from July to November) and double beam trawl (targeting Patagonian shrimp *Pleoticus muelleri*; higher catches from July to September) (Navarro et al. 2019, Prodocimi 2020). Two demersal longline fleets also operate in the area, chiefly targeting Patagonian toothfish *Dissostichus eleginoides* and kingklip *Genypterus blacodes*. For the study period, the number of operative trawlers was on average higher (n = 265) than that of longliners (n = 5) (Favero et al. 2013, Bertolotti et al. 2017). The following fleets were considered in this study for the overlap analyses: (1) freezer bottom trawlers, (2) freezer demersal trawlers, (3) demersal longliners, (4) freezer double beam trawlers, (5) coastal demersal ice-trawlers mainly fishing common hake or without a specific target species, locally known as 'coastal mixed catch', (6) mid-water ice-

trawlers, (7) coastal demersal ice-trawlers mainly fishing for common hake or Patagonian shrimp (operating from Rawson fishing harbor), (8) demersal high-seas ice-trawlers and (9) coastal semi-industrial ice-trawlers (small-scale vessels ranging from 9 to 18 m in length). The distribution of fishing vessels in the Argentine fishing zone was obtained from a satellite vessel monitoring system (VMS) database, supplied by the Undersecretariat of Fisheries (Ministerio de Agricultura, Ganadería y Pesca de la Nación). This information was coincident with the study period per age class (see next paragraph) and provides hourly GPS positions of each vessel. VMS data were filtered by speed and time to obtain only fishing locations and discard navigation positions (Martinez Puljak et al. 2018).

The shearwaters—fisheries overlap analysis was conducted using locations from PTTs, since the 2 GPS data sets available did not match with the PTT tracking period (GPS data were only used for the analysis of shearwater distribution in the study area). Adult and immature birds were analyzed separately and by period (i.e. for adults from October 2009 to June 2010, and for immatures from September 2008 to February 2009, and September 2009 to June 2010; Table S1). The same periods were selected for fisheries. The data from 2006 for immature individuals were not considered, as they represent a different time frame from that obtained for adults, thereby introducing variability into future comparisons. The overlap between the distribution of selected fisheries and great shearwaters (adults 2009—2010 and immatures 2008—2010) was estimated with the kernel overlap function in 'adehabitatHR' using the utilization distribution overlap index (UDOI), following (Fieberg & Kochanny 2005). The UDOI method assumes space use independently between groups (Hurlbert 1978), with values ranging from 0 (no overlap) to 1 (100% overlap) but can be >1 if both UDs are non-uniformly distributed and have a high degree of overlap. The fleets that had a UDOI ≥0.2 were selected to be used in the statistical models. This cut-off value was arbitrarily chosen to select fleets that are most spatially associated with the species' distribution areas, avoiding selecting variables that may lead to convergence errors in the statistical modelling.

2.3. Statistical models

The effect of fishing effort on shearwater behavior was determined through statistical modeling. Fishing effort was estimated by summing the number of

fishing points per hour per 4 × 4 km grid cell (Fig. S2 in Supplement 1). Subsequently, in order to discard multicollinearity between fishing effort of different fleets, a Pearson correlation analysis was performed for each age class using the 'ggpairs' function in the R package 'GGally' (Emerson et al. 2013). There was no significant correlation between fishing fleets (Fig. S3 in Supplement 1).

Generalized additive mixed models (GAMMs) for each age class were applied using the 'bam' function in the package 'mgcv' (Wood 2023). The advantage of 'bam' is a much lower memory footprint than 'gam,' but it can also be much faster for large data sets. The response variable was presence (1) or absence (0) of foraging behavior per point (subsequently the fishing effort of each cell was extracted). The absences were represented by transiting positions; in addition, a set of random pseudo-absences was generated for each individual. This was done because transiting positions constituted a lower proportion (approximately 10%) of the total data set compared to foraging positions, thus making convergence and model fitting challenging. The pseudo-absences were generated within the 95% kernel area of each individual (ID) in the study area, and their number was the same as the difference between original foraging and transiting positions per ID. A binomial distribution was used with a 'logit' link function since it is the one that best fits for response variables with binary outcome (0 [transit positions and pseudo-absences] vs. 1 [foraging positions]) (Zuur et al. 2009). The explanatory variables were the fishing effort of each fleet; these covariates were transformed towards normal using an optimized Box-Cox transformation factor (Box & Cox 1964), derived using the package EnvStats (Millard & Kowarik 2023). In adults, individual ID was included as a random effect, while for immatures it was not included because it did not show a significant effect during the explorations of the models. As a consequence of the spatial autocorrelation evaluated by a Moran test (p < 0.001 for both age classes) using the 'ape' package (Paradadis et al. 2024), a Gaussian process fixed term with the coordinates was added to the models (Bivand et al. 2013, Wood 2017). The adjustment of each global model was made from a visual inspection of the residual graphs, and the goodness of fit of the final model was determined by the area under the receiver operating characteristic curve (Zuur et al. 2009). Model selection was based on Akaike's information criterion (AIC) using the 'dredge' function in the 'MuMIn' package (Bartoń 2023). Candidate models were compared using the difference between the AIC for each respective model and the lowest observed value (measured as ΔAIC, where ΔAIC = 0 represents the best model, and those within the range of ΔAICc ≤ 2 are considered plausible models). In addition to the ΔAICc value, the Akaike weight (w_i) was used (Burnham & Anderson 2002).

2.4. Stable isotope analysis

Blood samples (n = 5) were obtained from adult birds captured alive in April 2013 with nets from recreational fishing boats sailing in waters of the northern Argentine fishing zone. Breeding status of individuals was not determined. Blood of shearwaters integrates dietary information up to 8 wk before sampling (Vander Zanden et al. 2015, Hong et al. 2019). Hence, in this study, we assumed that blood samples provided information on the species' diet during the late austral summer and early austral autumn (Hong et al. 2019). Stable isotope ratios were determined by mass spectrometry and were compared among potential prey categories (taken from the literature, as described in Table S2 in Supplement 2) through a permutational multivariate analysis of variance (PERMANOVA) (Anderson 2001, Anderson et al. 2008) in PRIMER 6 (Clarke & Gorley 2006) and pairwise post hoc comparisons. To assess the importance of different prey as food sources, we used the 'MixSIAR' Bayesian stable isotope mixing model in the R environment (Stock et al. 2018). Convergences of mixing models were evaluated using the Gelman-Rubin and Geweke diagnostics (Stock et al. 2018). Results from the isotope mixing models are expressed as mode and 95% credibility intervals (CI). Means are provided ±SD unless otherwise stated. More methodological procedures of sample preparation and analysis are detailed in Text S1 in Supplement 2.

The data management and analysis were conducted using R (R Core Team 2021) and QGIS 3.14 (QGIS Development Team 2020).

3. RESULTS

In general terms, the area used by great shearwaters *Ardenna gravis* covered waters from southern Brazil (~32° S) to southern Argentina (~49° S) (Fig. 1). The distribution of adult shearwaters was wider than the area used by immatures (kernel 95%), with a large core area (ca. 167 000 km²) chiefly running between the 50 and 200 m isobaths east and south of the mouth of the Río de la Plata and a small one (ca. 6000 km²) located at the northern boundary of San Jorge Gulf
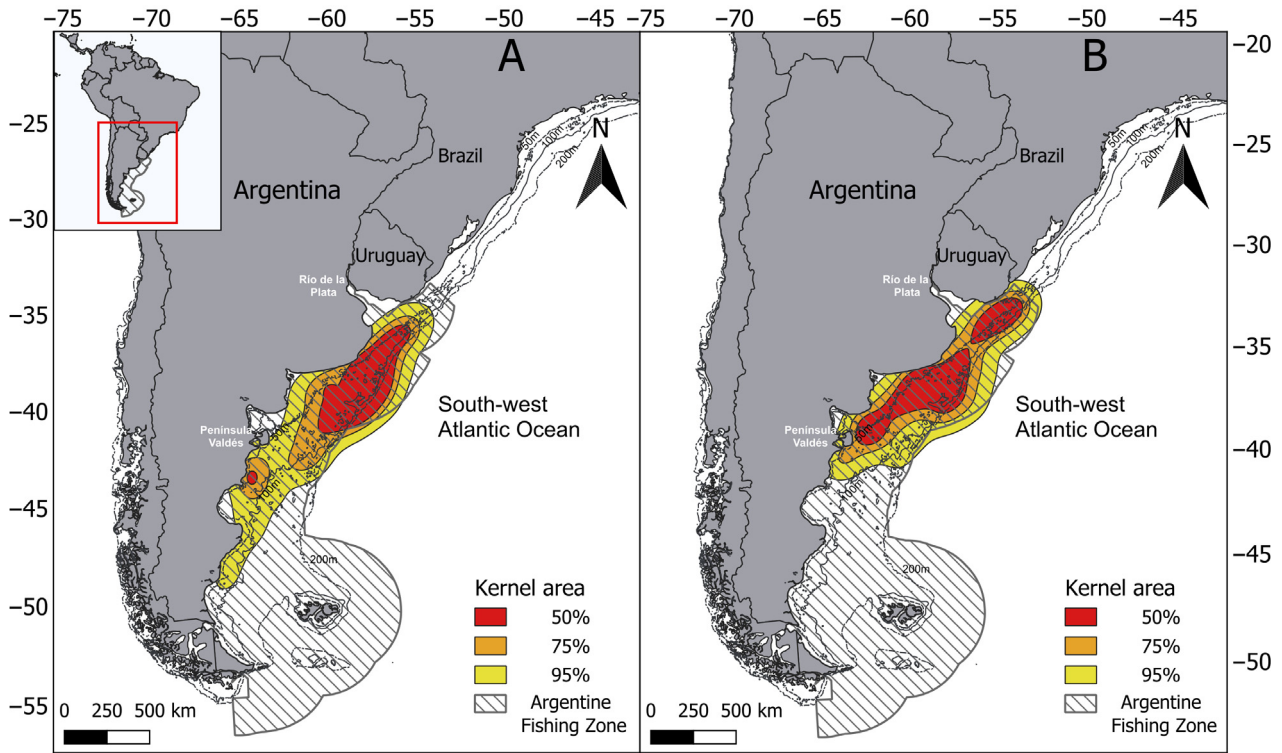
Fig. 1. Marine areas used by (A) adult and (B) immature great shearwaters in the study area during 2006–2015

(~43° S). Immature shearwaters used waters slightly farther north than adults, from southern Brazil (~32° S) to northern Argentine Patagonia (~42° S), showing 2 core areas, one off the mouth of the Río de la Plata (ca. 45 000 km^2) and a larger one (ca. 153 000 km^2) from south-east Buenos Aires province (~36° S) to Valdés peninsula (Fig. 1). The overlap analysis showed that coastal demersal ice-trawlers, mid-water ice-trawlers and demersal high-seas ice-trawlers highly over-lapped with shearwaters of both age classes. In addition, immatures showed high overlap with de-mersal longliners and coastal semi-industrial ice-trawlers (Table 1, Fig. 2).

The Box-Cox transformation factors used in models for adult shearwaters were 0.24, 0.16 and 0.16 for demersal high-seas ice-trawlers, mid-water ice-trawlers and coastal demersal ice-trawlers, respec-tively. Those used for immature individuals were 0.20, 0.12, 0.19, 0.05, 0.09 for demersal high-seas ice-trawlers, mid-water ice-trawlers, coastal demersal ice-trawlers, demersal longliners and coastal semi-indus-trial ice-trawlers, respectively. When analyzing the effect of fishing effort on the behavior of great shear-waters, global models for each age class showed a deviance explained of 6.40% for adults and 6.53% for immatures. The selected model for adult birds included a significant association with the demersal

high-seas ice-trawlers and the coastal demersal ice-trawlers (Table 2). The prediction plots showed that adults were more likely to forage when the effort of demersal high-seas ice-trawlers increased, and then it remained constant at high effort. In the case of the variable coastal demersal ice-trawlers, adults initially did not seem to respond to changes in fishing effort; however, once the effort began to increase signifi-cantly, they became less likely to forage (Fig. 3). In immatures, there were different selected models

Table 1. Utilization distribution overlap indices (UDOI) be-tween great shearwaters and studied fishing fleets per age class (fleets selected to be used in statistical models, with UDOI ≥0.2, are highlighted in **bold**)

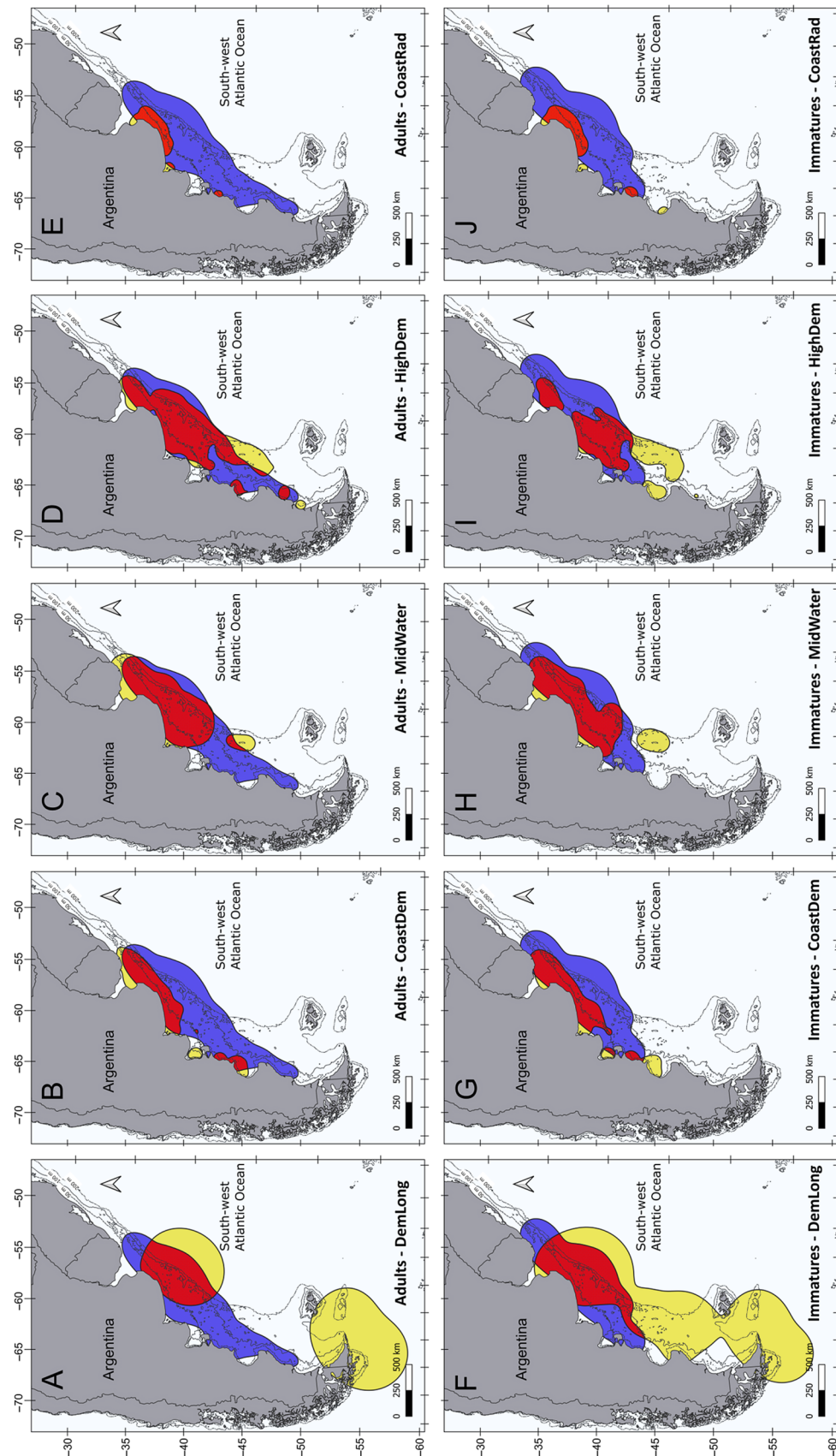| Fleet	Adults	Immatures
Freezer demersal trawlers	0.16	0.05
Demersal longliners	0.12	**0.22**
Freezer double beam trawlers	0.03	0.00
Freezer bottom trawlers	0.16	0.13
Coastal demersal ice-trawlers	**0.28**	**0.38**
Mid-water ice-trawlers	**0.59**	**0.60**
Coastal demersal ice-trawlers of Rawson	0.01	0.01
Demersal high-seas ice-trawler	**0.61**	**0.29**
Coastal semi-industrial ice-trawlers	0.17	**0.20**

Fig. 2. Overlap areas (red) between 95% kernel areas of (A–E) adult and (F–J) immature great shearwaters (blue) and fisheries (yellow). DemLong: demersal longliners; CoastDem: coastal demersal ice-trawlers; MidWater: mid-water ice-trawlers; HighDem: demersal high-seas ice-trawler; CoastRad: coastal semi-industrial ice-trawlers. Only those fisheries with UDOI ≥ 0.2 are shown

Table 2. Generalized additive models that explain the probability of foraging behavior of adult and immature great shearwaters in relation to the fishing effort. The best and the plausible models (according to differences in Akaike's information criterion [ΔAIC] ≤ 2 and Akaike weight [w_i]) are shown. Estimated degrees of freedom (edf) represent the complexity of the model term, while χ^2 represents the effect the term has on the model output. A p-value of <0.05 is considered significant. The models highlighted in **bold** best explain the foraging behavior of the species. See Fig. 2 for variable abbreviations

| Age class	Period	Model	AIC	ΔAIC	w_i	Variable	edf	χ^2	p
Adults	2009–2010	1	**19113.3**	**0**	**0.934**	**CoastDem**	**4.313**	**164.61**	**<0.001**
						HighDem	**6.516**	**258.02**	**<0.001**
Immatures	2008–2010	1	4400.86	0	0.43	CoastDem	2.908	12.939	0.009
						MidWater	2.425	10.717	0.010
						HighDem	1.347	18.659	<0.001
						CoastRad	1.884	4.475	0.136
		2	4402.13	1.27	0.23	CoastDem	2.865	12.066	0.013
						MidWater	2.425	10.69	0.010
						HighDem	1.318	18.679	<0.001
						CoastRad	1.925	5.097	0.107
						DemLong	1.725	2.16	0.365
		3	**4402.16**	**1.3**	**0.22**	**CoastDem**	**2.866**	**13.41**	**0.007**
						MidWater	**2.413**	**11.35**	**0.008**
						HighDem	**1.548**	**22.4**	**<0.001**
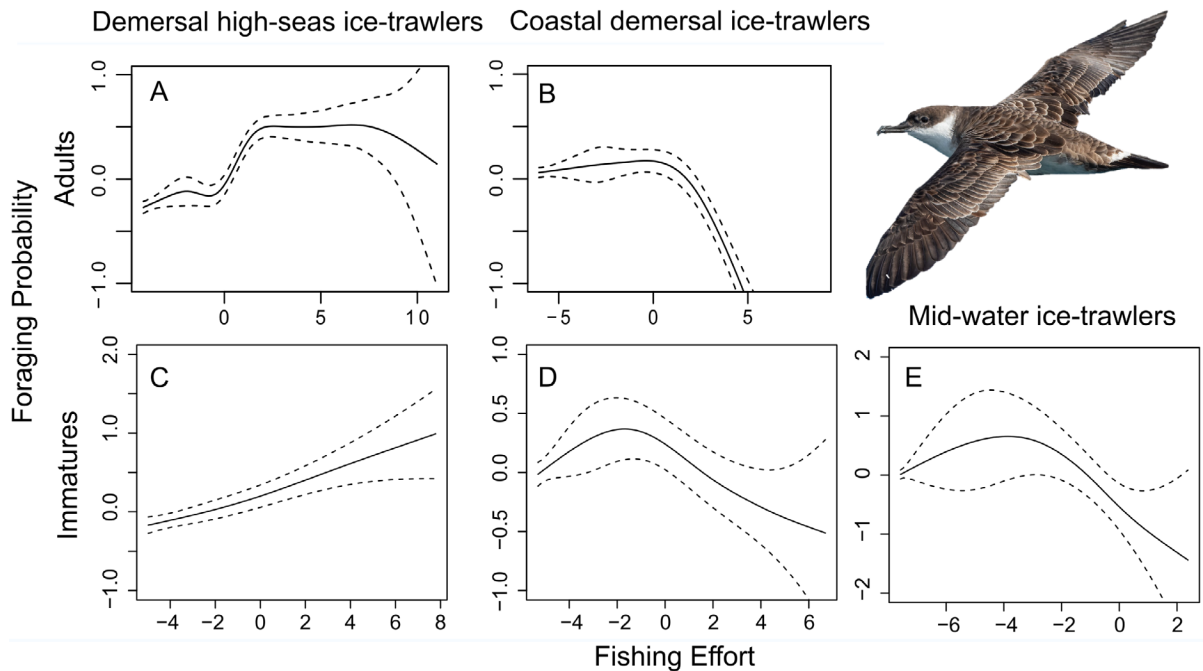
Fig. 3. Marginal effects of each model covariate on the foraging probability prediction in (A,B) adult and (C–E) immature great shearwaters. Dotted lines represent 95% confidence intervals. The explanatory variables on the x-axis are expressed in values resulting from Box-Cox transformations (see Section 2)

according to the ΔAIC criterion; however, the model chosen here included only the variables that had a significant effect on the foraging behavior of immature individuals: demersal high ice-trawlers, coastal demersal ice-trawlers and mid-water ice-trawlers (Table 2). The immature individuals were more likely to forage with increased fishing effort of demersal high ice-trawlers, while for the other fisheries, initially the foraging probabilities increased as fishing effort began to rise. However, this trend reversed, and they became less likely to forage with increased fishing effort, although with greater associated variability (Fig. 3). The goodness of fit of the final models was 0.67 for both age classes.

Isotope ratios for great shearwaters were −17.9 ± 0.2 for carbon and 16.8 ± 0.3 for nitrogen. Isotope ratios of potential food sources ranged from −18.8 to −15.5‰ in $\delta^{13}C$ and from 12.6 to 16.9‰ in $\delta^{15}N$ (Table S2). Significant differences were found in $\delta^{13}C$ and $\delta^{15}N$ values among species considered as potential prey (PERMANOVA $F_{7,52}$ = 21.71, p < 0.001) allowing the prey to be pooled into 5 functional categories from the Argentine fishing zone (Table S2): demersal fish (*Merluccius hubbsi* and *Nototenia patagonothen*, part of demersal ice-demersal trawler discards), mid-water fish (*Engraulis anchoita*), demersal crustacea (*Pleoticus muelleri*) and 2 components of local zooplankton, calanoid copepods (Gaitán 2012) and the lobster krill *Munida gregaria* (Funes et al. 2018). The isotopic signatures of mid-water cephalopods from the Argentine fishing zone (including *Illex argentinus* and *Doryteuthis gahii*) did not differ from demersal fish species; nevertheless, they are shown as a discrete category (Fig. 4). Given the high values observed in the isotopic composition of Patagonian shrimp *Pleoticus muelleri*, this category was excluded from the mixing model analysis. As a result, the model included demersal fish, mid-water fish, calanoid copepods and *M. gregaria* as potential food sources for great shearwaters in the Argentine fishing zone. Mixing polygon sensitivity analyses showed that isotopic ratios of most individual samples, given the trophic discriminant factor and food sources values used (see Text S1), were included in more than 70% of the simulated mixing polygons, validating the proposed mixing models. The distributions

resulting from the MixSIAR showed, for individuals sampled during austral autumn, similar higher contribution of zooplanktonic species, particularly calanoid copepods (mode: 34%; 95% CI: 13−51%) and mid-water fish (30%, CI: 5−56%), followed by demersal species (20%, CI: 3−38%) and other abundant components of the zooplankton such as *M. gregaria* (15%, CI: 2−39%).

4. DISCUSSION

This study investigates the association and effect of commercial fishing activities on the distribution and foraging behavior of great shearwaters *Ardenna gravis* during their pre-laying, incubation and post-breeding periods in the Southwest Atlantic Ocean. Core distribution areas of great shearwaters were concentrated at the northern Patagonian Shelf, mainly at the mouth of the Río de la Plata estuary, the shelf break and the convergence zone of the Malvinas—Brazil Currents, a highly productive region (Acha et al. 2004, 2015, Lucas et al. 2005). Oceanographic features such as high surface temperature gradients, neritic zones, convergence areas and river discharges, coupled with the abundance of prey, make these areas important foraging grounds and migratory routes for seabirds and other marine megafauna, including turtles, sea lions and whales (Phillips et al. 2006, Falabella et al. 2009, Zerbini et al. 2015, González Carman et al. 2016, Carneiro et al. 2020, Mariano-Jelicich et al. 2021).

The high overlap observed between great shearwaters and different commercial fishing fleets in the Argentine fishing zone was in line with previous studies based on onboard observations in a range of fleets, where high abundances of great shearwaters have been observed throughout the year (González-Zevallos & Yorio 2006, 2011, Favero et al. 2011, González-Zevallos et al. 2011, Paz et al. 2018, Seco Pon et al. 2020). However, onboard observations did not consider the effect of fishing effort and spatial scales analyzed in this study. The overlap with the anchovy fishery was high in both age classes. High bycatch rates were also reported in this fishery, with mortalities mainly due to net entanglements while shearwaters were feeding on discards or prey captured during hauling opera-
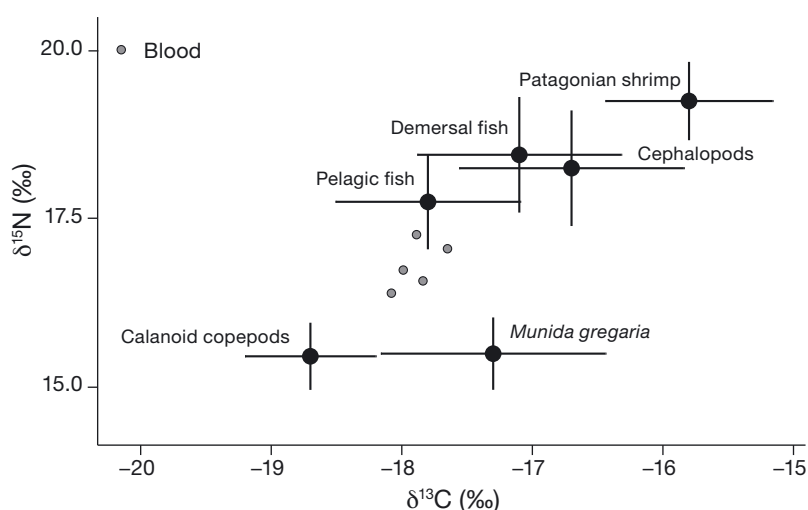

Fig. 4. Carbon and nitrogen stable isotope ratios of great shearwater blood samples (grey circles). Black circles correspond to mean isotopic ratios of Argentine fishing zone potential food sources. Error bars show standard deviation. The isotopic signatures of cephalopods did not differ from demersal fish species; nevertheless, they are shown as a discrete category

tions (Paz et al. 2018, Seco Pon et al. 2020). Studies in other trawl fisheries such as coastal and offshore ice-trawlers have also reported interactions (i.e. contacts with fishing gear) and incidental mortality of great shearwaters (González-Zevallos & Yorio 2006, 2011).

An increase in fishing effort in demersal high-seas ice-trawlers was associated with a high probability of foraging behavior in adult and immature shearwaters, similar to the response of black-browed albatrosses *Thalassarche melanophris* foraging in neighboring waters closed to common hake fishing (Copello et al. 2016, Paz et al. 2019). Such increased foraging behavior can be attributed to the attraction generated by the availability of important volumes of discards, offal and facilitated prey as a predictable source of food (like in high-seas ice-trawlers, see Favero et al. 2011, Bovcon et al. 2013). Great shearwaters may show dominant behavior offshore over other species when feeding on fishery discards (for example dominating the zone in close proximity to the vessel), which may even lead to higher risks of incidental mortality through heavy strikes or entanglement (Cianchetti-Benedetti et al. 2018, Carvalho et al. 2020). Contrary to the above effect, an increase in fishing effort in coastal demersal ice-trawlers was associated with a decreased probability of foraging behavior in shearwaters of both age classes, and in mid-water ice-trawlers for immatures. This opposite effect could be attributed to the existence of density-dependent processes or interspecific competition with coastal and very abundant species, such as the kelp gull *Larus dominicanus*, identified as a dominant species attending Argentine coastal fleets (González-Zevallos & Yorio 2006, Seco Pon et al. 2012, 2013). Another important aspect to be considered is that coastal demersal ice-trawlers concentrate their fishing efforts in areas very close to the coastline not frequently used by shearwaters preferring to forage in pelagic waters (Ronconi et al. 2018), hence reducing the likelihood of encounters with those vessels and causing lower foraging probability when fishing effort increases. Instead, they might be attracted to offshore fleets with larger fishing efforts (e.g. catches in offshore demersal high-seas ice-trawlers is ca. 40 times greater than that reported by coastal demersal ice-trawlers; Navarro et al. 2014) and generating higher levels of discards (Favero et al. 2011, Seco Pon et al. 2015, Paz et al. 2018).

The results from isotopic analysis supported, at least partially, the important role that Argentine anchovy *Engraulis anchoita* and other mid-water resources play in the diet of adult shearwaters in the Argentine sea (Table S2). This finding becomes even more relevant when considering the high overlap between the mid-water ice-trawlers and the distribution of great shearwaters. The isotopic analysis also showed the contribution of demersal fish species like common hake *Merluccius hubbsi* (Table S2), which is a primary target species for a significant portion of the offshore demersal trawl fleet and is present in the discards and offal (González-Zevallos & Yorio 2006, Favero et al. 2011, Bovcon et al. 2013). This kind of prey is not naturally available and could only be obtained through association with other subsurface predators or fisheries. However, considering that the stable isotope ratios of mid-water cephalopods were similar to those of demersal fish in the Argentine fishing zone, we cannot rule out the possibility that these results are related to the consumption of cephalopods (i.e. *Illex argentinus, Doryteuthis gahii*). Hard parts like cephalopod beaks can be over-represented in stomach contents (Barrett et al. 2007), and a previous study reported a high occurrence of cephalopods in stomachs of shearwaters (Petry et al. 2008). We are aware of the limited number of individuals sampled, and so these results should be considered with caution. A larger sample size could more accurately represent the diet during the breeding and pre-laying period. Nevertheless, these results are in line with other approaches in southern South America (Bugoni et al. 2010). Coupled with high-resolution distribution records of shearwaters and long-term tracking of the same individuals (for example, through captures and recaptures in colonies), this would provide crucial information to identify changes in behavior over time and assess the direct impact of resources provided by fishing fleets on the species' long-term diet.

Several studies highlight the positive and negative effects of fishery discards and the importance of food quality, as well as abundance and availability, on seabird reproduction, survival and population dynamics (Oro et al. 1999, Hüppop & Wurm 2000, Bartumeus et al. 2010, Mariano-Jelicich et al. 2017, Church et al. 2019). 'White' fish (like hake) and some offal discards (such as intestines) have little nutritional value, while 'blue' fish (like anchovies) present a much higher nutritional value. In this regard, the consumption of discarded hake by shearwaters may only be beneficial in the short term, whereas anchovies (whether caught naturally or associated with trawlers through discards or facilitated prey) could represent high-quality prey meeting the nutritional requirements during the breeding period (Navarro et al. 2009, Montevecchi 2023). However, this benefit of accessing discards and prey facilitated by fishing operations results in a greater seabird attendance, increasing the likelihood

of negative direct interactions leading to incidental mortality (Montevecchi 2001, 2023).

The present study is an approximation of the behavioral response of shearwaters to commercial fishing effort in Argentine waters; however, data at finer spatial and temporal resolution is necessary to visualize changes in the species' behavior at the time of the encounters with vessels, taking into account different moments of the fishing operation and discard processes (for example, through the use of GPS devices that provide more precise data, see Collet et al. 2015, 2017, Ouled-Cheikh et al. 2020). Nevertheless, this study allowed us to better understand the effect of fisheries on seabird behavior, which is essential for developing and implementing measures aimed at reducing the incidental capture of seabirds by fishing fleets, including the design of discard management strategies.

Argentina has developed regulations promoting the implementation of the ecosystem approach to fisheries management, including the adoption in 2010 of the National Plan of Action for Seabirds (and other National Plans for other marine megafauna), aimed at minimizing the detrimental effects of fishing operations on seabirds (Argentine NPOA—Seabirds 2010). More recently, Argentina and Uruguay have adopted a Regional Plan of Action—Seabirds to address bycatch in fisheries operating in a common fishing zone, which is largely used by great shearwaters, among other marine megafauna (Domingo et al. 2022). The incidental mortality of seabirds in the Argentine demersal longline fishery has decreased significantly from the 1990s, mainly due to a significant reduction in fleet size and fishing effort (Favero et al. 2013). Regulations have been developed to mitigate the impact of longliners and trawlers (Federal Fisheries Council Resolutions 08/2008 and 03/2017), calling for the use of methods endorsed internationally (ACAP 2024a,b). However, the effective implementation of mitigation measures and regulations remains largely uncertain in the majority of Argentine net fisheries (Favero et al. 2011, 2013, Favero & Seco Pon 2014, Tamini et al. 2023). The South Atlantic Ocean represents a crucial highly productive marine ecosystem extremely valuable for great shearwaters and many other local and distant migrant species (Phillips et al. 2006, González Carman et al. 2016, Krüger et al. 2017), holding international significance for the conservation of marine biodiversity. Argentina has recently created (through Law 27 490) 3 large southern offshore marine protected areas, namely Yaganes and Namuncurá—Banco Burdwood I and II, which favor the conserva-

tion of marine biodiversity. However, the full implementation of these marine protected areas and the establishment of new areas is still needed to achieve the objective of protecting 10% of the marine areas in the region, as envisioned in the National Strategic Plan for Biodiversity (Resolution 356/2022). The existence of other well-regulated areas with permanent or temporary fishing closures in the Argentine EEZ and in the ZCPAU surely benefit seabirds and the overall marine ecosystem. The results presented in this study may help decision makers in the identification of key waters for the further delimitation of important areas to be protected.

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