

Ecología de forrajeo e interacciones con pesquerías de los grandes albatros (*Diomedea* spp.) en el Atlántico sudoccidental

Foraging ecology and fisheries interactions of great albatrosses (*Diomedea* spp.) in the southwest Atlantic

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Resumen

Uno de los beneficios directos más relevantes proporcionados por las pesquerías a las aves marinas es el suministro de una fuente de alimento alternativa, a menudo superabundante, constituida por los descartes pesqueros. A pesar de este beneficio, muchas aves marinas, y en particular los albatros, se encuentran consideradas dentro de las más amenazadas a nivel global, como consecuencia de la captura incidental en pesquerías. Las pesquerías de palangre pelágico en el Atlántico sudoccidental son una amenaza importante para la conservación de varias especies, incluyendo cuatro especies de grandes albatros (Diomedea spp.): el albatros errante (D. exulans), el albatros de Tristán (D. dabbenena), el albatros real del sur (D. epomophora) y el albatros real del norte (D. sanfordi). Esta tesis aborda diversos aspectos de la ecología de estas especies, con un foco general en la segregación inter e intra-específica y su relación con las pesquerías. El objetivo general de esta tesis es caracterizar la captura incidental de los grandes albatros en la pesca con palangre pelágico en el Atlántico sudoccidental y comprender el rol de los descartes, incluyendo su influencia en la competencia y segregación espacial. Mediante el uso de aves capturadas incidentalmente en la pesca con palangre pelágico, se combinaron análisis convencionales de dieta y de isótopos estables para evaluar la importancia de los descartes pesqueros en la dieta de los grandes albatros y otras especies de Procellariiformes relacionadas (albatros y petreles). La captura incidental de los grandes albatros en las pesquerías de palangre pelágico fue examinada a partir de datos obtenidos por observadores a bordo en buques uruguayos durante 2004-2011 y en buques japoneses que operaron bajo licencia de pesca experimental en Uruguay durante 2009-2011. Adicionalmente, se utilizó una base de datos extensa de albatros errantes de South Georgia (1990-2012) rastreados durante la estación reproductiva, para investigar su solapamiento con el esfuerzo de pesca reportado por las flotas de palangre pelágico a la Comisión Internacional para la Conservación del Atún Atlántico (ICCAT). Los grandes albatros exhibieron repartición interespecífica de nicho en su distribución espacial, uso de hábitats y dieta. Sin embargo, se obtuvo evidencia convincente de que la pesca de arrastre en la plataforma continental, al proveer una fuente de alimento superabundante y artificial (descartes), permite la coexistencia de especies cercanamente relacionadas, relajando la repartición del nicho trófico. Esto fue evidente en las dos especies neríticas de grandes albatros (albatros real del sur y del norte), las cuales presentaron

dietas sorprendentemente similares compuestas de peces demersales y calamares, provenientes de los descartes de la pesca de arrastre. Los descartes de las pesquerías de palangre pelágico y demersal fueron relativamente poco importantes para la dieta todas las especies. Los grandes albatros mostraron segregación espacial entre sexos, donde en promedio las hembras se distribuyeron más al norte que los machos, dentro y fuera de la estación reproductiva. Sin embargo, tanto la segregación inter como intra-específica, exponen de forma diferencial a los grandes albatros a la captura incidental en palangre pelágico en el Atlántico sudoccidental. Las dos especies más oceánicas (albatros errante y de Tristán) son vulnerables a un mayor número de flotas (incluyendo a Belice, Brasil, Japón, Filipinas, Portugal, España, San Vicente y Granadinas, Taiwán, Uruguay y Vanuatu) que operan en aguas internacionales, donde ocurre el mayor esfuerzo pesquero. Las especies neríticas están expuestas a altos niveles de mortalidad principalmente sobre el talud continental, dentro de las Zonas Económicas Exclusivas, donde opera un número limitado de flotas. Sin embargo, también son vulnerables a la pesca de arrastre, cuyo impacto es menos conocido. La pesca con palangre pelágico en la región produce una mortalidad incidental sesgada hacia las hembras, lo que agravaría el impacto en sus poblaciones. Otra amenaza detectada en grandes albatros fue la ingestión de plásticos. Esto complementaría al impacto negativo de la captura incidental en pesquerías. Para proteger a estas especies altamente amenazadas, se deben implementar medidas de mitigación en las flotas de palangre pelágico manejadas por ICCAT en una amplia región del Atlántico sudoccidental (25°-45° S), con un mayor control entre mayo y diciembre en los 30°-40° S. Se determinó que una serie de prácticas operativas de los buques de pesca y de variables relacionadas al hábitat afectan a las tasas de captura incidental, entre las cuales la hora del calado del palangre, la fase lunar, el área y la estación del año son útiles en términos de análisis del riesgo y en el desarrollo de medidas de conservación más efectivas.

Abstract

One of the most important direct benefits provided by fisheries to seabirds is the provision of an alternative food source, often superabundant, comprised by fisheries discards. Despite this benefit, many seabirds, and particularly albatrosses, are considered among the most globally threatened species, as a result of bycatch in fisheries. Pelagic longline fisheries in the southwest Atlantic are a major conservation concern for multiple species, including four species of great albatrosses (Diomedea spp.): wandering albatross (D. exulans), Tristan albatross (D. dabbenena), southern royal albatross (D. epomophora) and northern royal albatross (D. sanfordi). This thesis deals with various aspects of their ecology, with a general focus on inter- and intra-specific segregation and its relation to fisheries. The overall objective was to characterise the bycatch of great albatrosses in the pelagic longline fishery operating in the southwest Atlantic and to understand the role of fisheries discards, including their influence on competition and spatial segregation. Using bycaught birds from pelagic longline fisheries, conventional diet and stable isotope analyses were combined to assess the importance of fishing discards in the diet of great albatrosses and other related Procellariiformes (albatrosses and petrels). Bycatch of great albatrosses in pelagic longline fisheries was examined using data collected by observers on board Uruguayan vessels in 2004-2011, and on Japanese vessels operating in Uruguay under an experimental fishing license in 2009–2011. Additionally, extensive tracking data (1990–2012) from breeding wandering albatrosses at South Georgia were used to investigate overlap with longline fishing effort reported to the International Commission for the Conservation of Atlantic Tunas (ICCAT). The great albatrosses exhibit interspecific niche partitioning in their spatial distribution, habitat use and diet. However, there was convincing evidence that trawl fisheries on the continental shelf, by providing a superabundant and artificial source of food (discards), allow the coexistence of closely-related species and relax trophic niche partitioning. This was evident in the two neritic species of great albatrosses (southern and northern royal albatrosses), which had surprisingly similar diets composed of demersal fish and squids discarded from trawl fisheries. Discards from pelagic and demersal longline fisheries were considerably less important for all species. The species of great albatrosses exhibited spatial sexual segregation, with females on average distributed further north than males, and this occurs both in breeding and nonbreeding

birds. However, both inter- and intra-specific segregation have negative effects on great albatrosses, exposing species and sexes differentially to pelagic longline fishing in the southwest Atlantic. The two most oceanic species (wandering and Tristan albatrosses) are exposed to a greater number of fleets (including Belize, Brazil, Japan, Philippines, Portugal, Spain, St. Vincent and Grenadines, Taiwan, Uruguay and Vanuatu) operating in international waters, where the greatest fishing effort is deployed. The neritic species are exposed to high levels of mortality mainly on the shelf break within the Exclusive Economic Zones, where a limited number of fleets are allowed to operate. However, they are also exposed to trawl fisheries, the impact of which is less known. The pelagic longline fishing in the region produces female-biased mortality, exacerbating the impact of bycatch on populations. Another anthropogenic threat detected for great albatrosses in this region was plastic ingestion. This may compound the negative impact of fisheries bycatch. In order to protect these highly threatened species, mitigation measures on ICCAT pelagic longline fleets should be implemented in a wide region of the southwest Atlantic (25°-45° S), with greater compliance-monitoring in May-December and in 30°-40° S. A range of vessel operational practices and habitat variables affected bycatch rates, among which setting time, moon phase, area and season are useful in terms of risk assessment, and in the development of more effective conservation measures.

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Capítulo 1

Introducción General

LOS GRANDES ALBATROS

Las aves marinas son frecuentemente definidas como aquellas especies de aves que se alimentan en el mar, ya sea cerca de la costa o en alta mar (Schreiber & Burger 2002). Éstas incluyen a todos los miembros de los órdenes Sphenisciformes y Procellariiformes, y parte de los Pelecaniformes y Charadriiformes. Los Procellariiformes incluyen a los petreles (Procellariidae), los albatros (Diomedeidae), los petreles de las tormentas (Hydrobatidae) y los petreles zambullidores (Pelecanoididae); aves verdaderamente pelágicas que desarrollan su vida en altamar, yendo a tierra (generalmente a islas oceánicas) únicamente para reproducir (Onley & Scofield 2007). Los albatros son en general las aves marinas de mayor tamaño, con una masa corporal y envergadura que varía entre 1.7 y 11.9kg y entre 1.9 y 3.23m, respectivamente (Tickell 2000). Dentro de los Procellariiformes, sólo las dos especies de petreles gigantes (Macronectes spp.) exceden la masa corporal de las especies más pequeñas de albatros. El vuelo de los albatros, efectuado casi exclusivamente mediante planeo, tiene un costo energético excepcionalmente bajo, lo que les permite cubrir enormes distancias en busca de alimento (Pennycuick 1982, Tickell 2000, Wakefield et al. 2009). El dimorfismo sexual en tamaño varía entre las especies de Procellariiformes, y en los albatros, así como en petreles, los machos son de mayor tamaño que las hembras. En algunas especies estas diferencias son conspicuas, pero en otras es solo aparente luego de análisis estadísticos (Tickell 2000).

Se reconocen actualmente cuatro géneros de albatros: los albatros del Pacífico Norte (*Phoebastria*), los albatros oscuros (*Phoebetria*), los "mollymawks" (*Thalassarche*) y los grandes albatros (*Diomedea*); los últimos tres sólo se reproducen en los océanos del hemisferio Sur (Tickell 2000). La taxonomía de los albatros ha estado en debate (Robertson & Nunn 1998,

Penhallurick & Wink 2004, Penhallurick 2012), incluyendo la de los grandes albatros. Actualmente, en base a las recomendaciones de su grupo de trabajo sobre taxonomía (Taxonomy Working Group), el Acuerdo sobre la Conservación de Albatros y Petreles (ACAP) reconoce seis especies de grande albatros (Phillips et al. 2016; Tabla 1).

Tabla 1. Especies existentes de grandes albatros (*Diomedea* spp.), principales poblaciones, estatus IUCN de conservación y tamaño de poblacional global. Las especies y poblaciones en negrita son aquellas que están ampliamente distribuidas el Atlántico sudoccidental.

Especies	Nombre común	Nombre inglés	Poblaciones/Archipiélagos de reproducción	IUCN	Tamaño de la población global (parejas anuales)*
Diomedea epomophora	Albatros Real del Sur	Southern Royal Albatross	Islas Campbell y Auckland** (Pacífico)	VU	7900
Diomedea sanfordi	Albatros Real del Norte	Northern Royal Albatross	Isla Chatham , Taiaroa Head** (Pacífico)	EN	5200
Diomedea exulans	Albatros Errante	Wandering Albatross	Islas South Georgia (Atlántico), Crozet, Kerguelen, Marion, Prince Edward (Índico) y Macquarie (Pacífico)	VU	6107
Diomedea dabbenena	Albatros de Tristán	Tristan Albatross	Islas Gough , Tristan da Cunha** (Atlántico)	CR	1698
Diomedea antipodensis	Albatros de las Antípodas	Antipodean Albatross	Islas Antipodes, Chatham, Campbell y Auckland (subespecie <i>D. a. gibsoni</i>)	VU	8050
Diomedea amsterdamensis	Albatros de Ámsterdam	Amsterdam Albatross	Isla Amsterdam (Índico)	CR	26

* La estimación corresponde al número de parejas que reproducen por año, aunque todas las especies reproducen de forma bienal. Esto significa que un gran parte de la población reproductora se encuentra en su año sabático cada año. ** Se distribuyen en el Atlántico sudoccidental pero la población es pequeña (< 1% de la población global) y por lo tanto muy poco abundantes en esta región.

La mayoría de las aves marinas comparten rasgos demográficos característicos de animales estrategas K, incluyendo altas tasas de supervivencia de adultos, madurez tardía y baja fecundidad (Furness 2003). Los Procellariiformes, y en particular los grandes albatros, representan el ejemplo extremo; además de exhibir el tamaño corporal más grande de todas las aves marinas, son

monógamos, muestran una madurez sexual altamente tardía (> 10 años), una fecundidad muy baja (reproducción bienal, posturas de un único huevo) y tasas de supervivencia (> 90%) y de longevidad (varias décadas) muy altas (Tickell 2000). Como resultado, son altamente sensibles a cambios en la supervivencia de adultos. Por ejemplo, para mantener una población estable, un declive de sólo un 1% por año en la tasa de supervivencia de adultos en grande albatros debería ser compensado por un adelantamiento de 6,5 años en la edad media de la primera reproducción (Weimerskirch & Jouventin 1987). Por lo tanto, cualquier mortalidad adicional producida por las actividades humanas tiene fuertes efectos negativos sobre las tendencias poblacionales de estas especies.

INTERACCIÓN ENTRE ALBATROS Y PESQUERÍAS

En los años 1950 – 1960, las pesquerías en el hemisferio norte crecieron enormemente y comenzaron a desplazar su esfuerzo hacia el hemisferio sur, alcanzando la cobertura global casi completa de los stocks de peces comerciales que vemos hoy (Pauly 2008). Las pesquerías de palangre pelágico dirigidas a la captura de atunes (*Thunnus* spp.) y otros grandes peces pelágicos se expandieron hacia el hemisferio sur desde los 1960s (Tuck et al. 2003), y las pesquerías de palangre demersal, en particular las de merluza negra *Dissostichus eleginoides*, comenzaron en el Atlántico sur a fines de los 1980s, y se expandieron rápidamente dentro de aguas sub-Antárticas (Brothers et al. 1999). Las pesquerías industriales de arrastre han operado de forma continua en las plataformas continentales del hemisferio Sur desde hace varias décadas. Por ejemplo, la capturas de merluza *Merluccius hubbsi* con arrastre de fondo en el Atlántico sudoccidental se expandieron desde mediados de 1970s (Csirke 1987, Lorenzo & Defeo 2015, Lorenzo 2016).

Las pesquerías pueden tener efectos adversos o positivos en las poblaciones y comunidades de aves marinas (Furness 2003). Uno de los beneficios directos más relevantes proporcionados por las pesquerías es la provisión de una fuente de alimento alternativa, a menudo superabundante, constituida por los descartes (la proporción de la captura no retenida a bordo compuesta generalmente por peces de tallas menores a las comercializadas, especies de bajo interés comercial y restos del procesado a bordo de las capturas). Sin embargo, a pesar de este beneficio, muchas aves marinas, y en particular los albatros, se encuentran consideradas dentro de los taxa

más amenazados a nivel global como consecuencia de la captura incidental en pesquerías (Croxall et al. 2012, Phillips et al. 2016). La mayor amenaza es la mortalidad incidental en la pesca con palangre pelágico, palangre de fondo y de arrastre, pero las pesquerías artesanales entre otras también son de preocupación para algunas especies. Otras amenazas incluyen la ingestión de plásticos en el mar, mientras que en las colonias, el impacto de la enfermedades, como el cólera aviar, y la depredación por especies introducidas, son graves para algunas poblaciones (Phillips et al. 2016). Sin embargo, todas estas amenazas suelen afectar a menos especies que la captura incidental. No es de sorprender que algunas poblaciones de albatros en el hemisferio sur que han sido monitoreadas desde el inicio de la expansión del esfuerzo pesquero, hayan mostrado evidencia de declives a causa de los impactos de las pesquerías (Weimerskirch & Jouventin 1987, Croxall et al. 1998, Poncet et al. 2006).

El Atlántico sudoccidental es una región de importancia mundial para los albatros y otras especies de Procellariiformes (Croxall & Wood 2002, Nicholls et al. 2002). Esto es principalmente debido a las grandes colonias de las Islas Malvinas/Falkland, South Georgia, Tristan da Cunha y Gough; archipiélagos de importancia global para la reproducción de albatros y petreles. La gran productividad biológica también hace a esta zona atractiva para muchas especies migrantes que llegan desde regiones remotas (e.g. Nueva Zelanda). Esta región también es considerada de relevancia global para el manejo debido a la preocupación por la conservación de varias especies de albatros capturadas incidentalmente en gran número en las pesquerías de palangre pelágico (Bugoni et al. 2008, Jiménez et al. 2009) y de arrastre (Sullivan et al. 2006, Favero et al. 2011). Dentro de la distribución de los albatros (principalmente al Sur de los 30° S), el mayor esfuerzo de la pesca con palangre pelágico se da sobre la región influenciada por la Confluencia Brasil-Malvinas/Falkland (Tuck et al. 2003, Jiménez et al. 2012), mientras que el arrastre de altura dirigido a merluza ocurre a lo largo de la plataforma continental de Uruguay y Argentina (Favero et al. 2011, Lorenzo 2016). Las principales especies capturadas en palangre son el albatros de ceja negra (Thalassarche melanophris) y el albatros de pico amarillo (Thalassarche chlororhynchos) (Bugoni et al. 2008, Jiménez et al. 2010), mientras que en arrastre la mayor mortalidad es de la primera especie (Favero et al. 2011, Tamini et al. 2015). Sin embargo, otras especies con poblaciones más pequeñas también son capturadas, aunque con menor frecuencia, particularmente en palangre pelágico (Bugoni et al. 2008, Jiménez et al. 2010). Éstas incluyen las cuatro especies de grandes albatros que ocurren en la región: el albatros errante (Diomedea

exulans), el albatros de Tristán (*Diomedea dabbenena*), el albatros real del sur (*Diomedea epomophora*) y el albatros real del norte (*Diomedea sanfordi*). Estas especies están globalmente amenazadas de acuerdo con la Unión Internacional para la Conservación de la Naturaleza (IUCN) (<u>http://www.birdlife.org/datazone/home</u>), y pertenecen a pequeñas poblaciones (Tabla 1).

La población regional del albatros errante y la global del albatros de Tristán reproducen en South Georgia (Atlántico sur) e isla Gough (Atlántico sur central), respetivamente, y ambas están disminuyendo (Poncet et al. 2006, Cuthbert et al. 2014). Éstas son consideradas dentro de las especies más afectadas por la pesquería de palangre pelágico en el Atlántico sudoccidental (Jiménez et al. 2012). Por otro lado, se sabe muy poco acerca de las interacciones con pesquerías en esta región de los albatros reales del norte y del sur migrantes de Nueva Zelanda (Robertson et al. 2003). Por lo tanto, es extremadamente importante obtener información precisa sobre la captura de estas cuatro especies de albatros. También hay una necesidad urgente de estudios dirigidos a la comprensión de los factores, incluyendo el comportamiento, preferencias de hábitat y las interacciones intra e inter-específicas, que afectan a la ecología de forrajeo, su dieta y su distribución, y por lo tanto que hacen a los grandes albatros susceptibles a las interacciones con la pesca.

SEGREGACIÓN DE ALBATROS EN EL MAR

Segregación espacial entre sexos

La segregación de hábitat describe las diferencias entre clases de animales (e.g. machos y hembras, subadultos y adultos, o individuos grandes y pequeños) en su distribución espacial y, por lo tanto, en el uso del ambiente físico (Conradt 2005). Las causas de la segregación de hábitat pueden variar. El dimorfismo en el tamaño corporal parece ser un posible candidato para explicar las diferencias entre sexos en ecología, y potencialmente para la segregación de hábitat. El dimorfismo en el tamaño corporal podría resultar en divergencias en los requerimientos nutricionales y energéticos, en las estrategias reproductivas, en los presupuestos de actividades y en las relaciones sociales (Ruckstuhl & Clutton-Brock 2005). Dos hipótesis principales, no mutuamente excluyentes, buscan explicar la segregación sexual en las aves (revisado en Catry et al. 2005). La hipótesis de dominancia social propone que la segregación surge de la exclusión de

individuos subordinados de aquellas zonas favorables por parte los individuos dominantes de la especie. Por otro lado, la hipótesis de especialización sugiere que los machos y las hembras se segregan en diferentes áreas debido a que los sexos tienen distintas preferencias de hábitats, difieren en la tolerancia a factores ecológicos o en restricciones específicas vinculadas el sexo que surgen de la especialización de roles y de las presiones competitivas durante la reproducción.

En las especies más grandes de Procellariiformes, aquellas que exhiben un pronunciado dimorfismo sexual en tamaño, tienden a mostrar una segregación sexual más prominente en el mar, con los machos (el sexo más grande) siendo comunes en áreas más al sur que las hembras (Phillips et al. 2009). Esto parecer ser el caso en las poblaciones del albatros errante (Diomedea exulans sensu lato), mientras que es menos claro para otras especies de grandes albatros, la cuáles también muestran un dimorfismo sexual prominente (Shaffer et al. 2001, Cuthbert et al. 2003, Xavier & Croxall 2005). Ambos sexos se alimentan en promedio en diferentes áreas geográficas tanto en la estación reproductiva, como en la estación no reproductiva (Weimerskirch et al. 1993, Prince et al. 1998, Jaeger et al. 2009, Phillips et al. 2009, Froy et al. 2015). En el albatros errante de South Georgia, por ejemplo, las hembras son más propensas que los machos a forrajear en áreas más al norte fuera de la temporada reproductiva (Phillips et al. 2009) y durante la incubación y las etapas posteriores de la cría de pichones de la estación reproductiva (Prince et al. 1998, Froy et al. 2015). Esta segregación sexual se atribuye a dos hipótesis, ambas mediadas por el dimorfismo sexual en tamaño. La primera es la competencia, donde los machos más grandes excluyen a las hembras más pequeñas del acceso a los recursos cercanos, forzándolas a viajar más lejos de la colonia (Weimerskirch et al. 1993, Phillips et al. 2008). La relación entre el dimorfismo sexual en tamaño y el desempeño del vuelo (Shaffer et al. 2001, Phillips et al. 2004), por otro lado, propone que debido a que la carga alar determina la velocidad de vuelo, las regiones sub-antárticas y antárticas con mayores vientos son más óptimas para los machos, que tienen una mayor carga alar, mientras que las hembras y los volantones están mejor adaptados para la explotación de los vientos más ligeros de las regiones subtropicales.

Segregación inter-específica y repartición de nicho

La competencia inter-específica se produce cuando dos o más especies utilizan los mismos recursos y cuando estos recursos son escasos (Pianka 2011). Se considera que las especies ecológicamente similares que potencialmente compiten por el mismo recurso, son capaces de coexistir si particionan el uso del mismo. Los Procellariiformes, en particular, han sido utilizados frecuentemente para estudiar la repartición de recursos entre especies estrechamente relacionadas, morfológicamente similares y/o que se reproducen simpátricamente (Weimerskirch et al. 1988, Phillips et al. 2004, Phillips et al. 2005, González-Solís et al. 2007, Navarro et al. 2013, Connan et al. 2014). Durante la temporada reproductiva, las demandas de la reproducción limitan las distancias que pueden recorrerse desde las colonias, y por lo tanto, se considera que la competencia por los recursos cercanos entre las especies que se reproducen simpátricamente es intensa (Phillips et al. 2008). Después de la reproducción, estas especies dejan las colonias para migrar hacia zonas distantes, por lo que se reduce la competencia entre especies que se reproducen simpátricamente. En estas áreas, a menudo enormes, las oportunidades de forrajeo son mayores y, junto con la disminución en la densidad de competidores, la competencia parece relajarse (Bodey et al. 2014). Sin embargo, hay una mayor posibilidad de solapamiento entre especies estrechamente relacionadas provenientes de distintos grupos de islas de reproducción (Phillips et al. 2008). De hecho, se ha propuesto repartición de nicho durante la estación reproductiva tanto en especies estrechamente relacionadas y morfológicamente similares se reproducen tanto en simpatría (González-Solís et al. 2007, Navarro et al. 2009, Connan et al. 2014, Navarro et al. 2015, Quillfeldt et al. 2015) como en alopátria (Nicholls et al. 2002, Quillfeldt et al. 2013, Ramos et al. 2016).

Las especies de albatros cercanamente relacionadas parecen reducir la competencia por recursos evitando el solapamiento espacial, lo que se supone que influencia en la composición de la dieta (Nicholls et al. 2002, Connan et al. 2014). En grandes albatros, por ejemplo, hay evidencia de cierto grado de repartición inter-específica de nicho, principalmente en las preferencias relativas por áreas de forrajeo sobre aguas de la plataforma continental, del talud o de aguas profundas (Nicholls et al. 2002). Las dos especies de albatros reales tienden a forrajear en la plataforma continental, y los albatros errantes en el talud y aguas profundas. El albatros de Tristán forrajea en

aguas profundas pero principalmente en el área subtropical, en aguas cálidas, y por lo tanto se solapa con la parte norte de la distribución del albatros errante (Nicholls et al. 2002, Cuthbert et al. 2005, Moore & Bettany 2005, Reid et al. 2013).

PREGUNTAS, HIPÓTESIS Y OBJETIVOS

La segregación inter-específica e intra-específica en los grandes albatros tiene potenciales efectos en el solapamiento con el esfuerzo pesquero, y por lo tanto en las interacciones entre aves y pesquerías (con efectos negativos o positivos en sus poblaciones). Por otra parte, es factible suponer que los cambios iniciados hace varias décadas atrás en términos de disponibilidad de alimento a causa de las pesquerías, hayan tenido efectos sobre la distribución de estas aves oceánicas, sus interacciones ecológicas, e incluso en la estructura comunitaria. Sin embargo, poco de esto ha sido abordado. En el Atlántico sudoccidental, la duración (varias décadas) e intensidad de monitoreo del albatros errante de Bird Island, South Georgia, es inusual. Estudios previos de esta población han abordado la segregación en el mar entre sexos durante la estación reproductiva y su relación con el solapamiento con pesquerías, además de reunir evidencia de su captura incidental (Croxall & Prince 1990, Prince et al. 1992, Prince et al. 1998, Xavier et al. 2004).

A nivel intra-específico por lo tanto, cabe preguntarse: ¿Puede ésta segregación espacial entre sexos generalizarse para todos los grandes albatros?; ¿ocurre en otras especies de grande albatros también durante la estación no reproductiva, cuando ambos sexos no forrajean desde un lugar central, y por lo tanto la accesibilidad a hábitats y recursos distantes no está restringida? Si esto ocurre, inmediatamente surgen implicancias importantes para las amenazas que sufren estas especies en el mar. Desde un punto de vista de la conservación, la mortalidad incidental en pesquerías sesgada hacia un sexo en especies monógamas, donde se asume un relación entre sexos de 1:1, produce no sólo efectos directos inmediatos en el tamaño poblacional, sino también indirectos, que disminuyen la fecundidad (Mills & Ryan 2005). Por lo tanto, es relevante evaluar si la mortalidad en pesquerías sesgada hacia un sexo en grandes albatros es un efecto de la segregación espacial entre sexos. En otras palabras, lleva la segregación entre sexos en el mar a un solapamiento relativamente mayor entre un sexo y una pesquería, y es esto reflejado en una mortalidad incidental sesgada hacia ese sexo? En base a la región de mayor esfuerzo de la pesca

con palangre pelágico (ver arriba), y el patrón de segregación propuesto con las hembras en promedio distribuidas más al norte que machos, se plantea la siguiente hipótesis:

• La segregación espacial entre sexos en grandes albatros ocurre durante la estación reproductiva y no reproductiva, y lleva a una mayor exposición y mortalidad sesgada hacia las hembras en la pesca en áreas subtropicales.

A nivel inter-específico, la segregación espacial o las preferencias por distintos tipos de hábitats tiene implicancias tanto en la ecología trófica como en el solapamiento con el esfuerzo pesquero. Con respecto a lo primero, se pone a prueba la siguiente hipótesis:

• La segregación espacial en grandes albatros afecta la composición de su dieta.

Es de esperar que las especies experimenten una exposición diferencial a las distintas pesquerías. Considerando el patrón propuesto de repartición inter-especifica de nicho (ver arriba), las especies más oceánicas, como los albatros errante y de Tristán, deberían interactuar en mayor grado con la pesca de palangre pelágico, la cual se realiza generalmente desde el talud hacia aguas profundas, abarcando todas las aguas internacionales del Atlántico sudoccidental (Jiménez et al. 2010). Un razonamiento análogo aplica a las especies más neríticas, como los albatros reales, con la pesca de arrastre que se efectúa sobre la plataforma continental (Favero et al. 2011). De nuevo, desde el punto de vista de las implicancias para la conservación es necesario determinar cuáles son las áreas y épocas donde cada especie se encuentra más expuesta a la captura incidental.

Los descartes pesqueros suplementan las fuentes naturales de alimento de los grandes albatros y por tanto podrían aumentar el solapamiento espacio-temporal entre especies, las cuales de otra manera se encontrarían segregadas en el mar. Cabe preguntarse, ¿son los descartes pesqueros importantes en la dieta de estas especies? Si lo son, ¿permiten éstos un solapamiento mayor al esperado en la dieta de estas especies cercanamente relacionadas? Debido a que la teoría predice que en situaciones en que los recursos son superabundantes las especies ecológicamente similares pueden coexistir, es relevante preguntarse si los descartes pesqueros permiten un aumento en el solapamiento del nicho trófico de estas especies. No todas las pesquerías proporcionan una fuente superabundante de alimento. Por ejemplo, se estima que gran parte de los descartes globales

provienen de la pesca de arrastre (Kelleher 2005). Por lo tanto, ¿Hay diferencias en la contribución relativa de cada pesquería a la dieta de éstas especies? Esto lleva a la siguiente hipótesis:

 Los descartes pesqueros permiten un solapamiento en la dieta y el nicho trófico de las especies de grande albatros, siendo evidente en aquellas especies más neríticas expuestas a la pesca de arrastre.

Objetivos

El objetivo general de esta tesis es caracterizar la captura incidental de los grandes albatros en la pesca con palangre pelágico en el Atlántico sudoccidental y comprender el rol de los descartes, y su influencia en la competencia y segregación espacial, en estas especies cercanamente relacionadas.

Los objetivos específicos son los siguientes:

(1) evaluar la segregación y el solapamiento en la dieta en cuatro especies de grandes albatros estrechamente relacionadas, con especial énfasis en la influencia de descartes en su dieta y nicho trófico.

(2) determinar la variación espacio-temporal y la contribución de las variables relacionadas al hábitat y a la operativa de pesca en la captura incidental de los grandes albatros en la pesca con palangre pelágico en el Atlántico sudoccidental.

(3) determinar el solapamiento espacio-temporal relativo entre hembras y machos de albatros errantes de South Georgia durante la estación reproductiva, con las flotas de palangre pelágico que operan en el Atlántico sudoccidental.

(4) determinar si hay segregación espacial entre sexos en albatros reales durante la estación no reproductiva.

(5) determinar si la mortalidad sesgada hacia un sexo es un patrón general que ocurre en grandes albatros a causa de la segregación espacial parcial relacionada al sexo.

(6) identificar otras amenazas de origen antrópico (distintas a pesquerías) que puedan afectar a los grandes albatros de forma diferencial debido a su segregación inter e intra-específica en el mar.

(7) discutir las principales implicancias para la conservación de los resultados de esta tesis, en particular para abordar las deficiencias críticas en el conocimiento de las especies estudiadas a nivel internacional.

ESTRUCTURA DE LA TESIS

La tesis está estructurada en siete capítulos: Una Introducción General (este Capítulo), cinco capítulos (Capítulos 2-6) que constituyen investigaciones originales, y finalmente una Discusión General y Conclusiones (Capítulo 7). Los capítulos 2-6 abordan diversos aspectos de la ecología de estas especies, con un foco general en la segregación inter e intra-específica y su relación con las pesquerías.

El Capítulo 2 tiene como objetivo determinar la segregación y el solapamiento en la dieta y el nicho trófico de especies de albatros (incluyendo los grandes albatros) y petreles estrechamente relacionadas, con especial énfasis en la influencia de los descartes en su distribución y en la ecología trófica. Mediante análisis de contenidos estomacales y análisis de isótopos estables usados de forma complementaria, se aborda la influencia relativa de los descartes de distintas pesquerías (arrastre de altura, palangre pelágico y palangre de fondo) en la composición de la dieta, y se evalúa la influencia potencial de los mismos en la estructura comunitaria. Los capítulos 3-5 analizan las interacciones de los grandes albatros con la pesca de palangre pelágico, para la cual existe mayor evidencia del impacto negativo de la captura incidental. El Capítulo 3 caracteriza la captura incidental de los albatros grandes en la pesca con palangre pelágico en el Atlántico sudoccidental. Las tasas de capturas son analizadas con respecto a factores potencialmente relacionados con las preferencias de hábitat de las especies, así como los factores relacionados a la operación de pesca. Se evalúan los patrones espacio-temporales de las capturas, con énfasis en similitudes o diferencias inter-especificas útiles para el manejo y la conservación. Los capítulos 4 y 5 evalúan directa o indirectamente la segregación espacial entre sexos y sus consecuencias en la captura incidental. El Capítulo 4, en base a datos de rastreo del albatros errante durante la estación reproductiva, examina diferencias en la distribución de hembras y machos y las consecuencias en el solapamiento espacio-temporal, y en la captura incidental, con las distintas flotas palangreras que operan en el Atlántico. El Capítulo 5 utiliza datos de aves capturados incidentalmente, para poner a prueba el dimorfismo sexual en tamaño en albatros reales del sur y del norte. Mediante una muestra grande de aves capturadas incidentalmente, se evaluó si existía mortalidad incidental sesgada hacia un sexo, proporcionando una prueba indirecta de la segregación entre sexos para ambas especies durante la estación no reproductiva. El Capítulo 6 investiga otra amenaza de origen antrópico en estas especies: la contaminación por plásticos. Se analiza la ocurrencia de plásticos en base al análisis de contenidos estomacales de varias especies de albatros (incluyendo los grandes albatros) capturadas en pesquerías. Se compara las diferencias entre especies y sexos.

El último capítulo (Capítulo 7) presenta la Discusión General y Conclusiones, donde se discute la contribución de los capítulos 2-6 para responder los objetivos generales de la tesis. A su vez, se exploran las implicancias para la conservación de las especies, especialmente para abordar las deficiencias críticas en el conocimiento en un contexto internacional.

Chapter 1

General Introduction

GREAT ALBATROSSES

Seabirds are frequently considered to be those birds that feed at sea, either nearshore or offshore (Schreiber & Burger 2002). These include all members of the orders Sphenisciformes and Procellariiformes, and some of the Pelecaniformes and Charadriiformes. The Procellariiformes include petrels (Procellariidae), albatrosses (Diomedeidae), storm petrels (Hydrobatidae) and diving petrels (Pelecanoididae); truly pelagic birds that spend the majority of their lives at sea and only come to land (usually to oceanic islands) in order to breed (Onley & Scofield 2007). The albatrosses are the largest seabirds, with a body mass and wingspan ranging from 1.7 to 11.9kg and 1.9 to 3.23m, respectively (Tickell 2000). Among the Procellariiformes, only the two species of giant petrels (*Macronectes* spp.) exceed the body mass of the smallest albatross species. The flight of albatrosses, largely involving gliding, has an exceptionally low energy cost, allowing them to cover vast distances in search of food (Pennycuick 1982, Tickell 2000, Wakefield et al. 2009). The sexual size dimorphism varies between species of Procellariiformes, and in albatrosses and petrels, the males are larger than females. In some species, these sex differences are conspicuous, but in others are only apparent after statistical analyses (Tickell 2000).

Four genera of albatrosses are currently recognised: the North Pacific albatrosses (*Phoebastria*), the sooty albatrosses (*Phoebetria*), the mollymawks (*Thalassarche*) and the great albatrosses (*Diomedea*); the latter three breed only in the southern hemisphere (Tickell 2000). The taxonomy of albatrosses has been debated (Robertson & Nunn 1998, Penhallurick & Wink 2004, Penhallurick 2012), including that of the great albatrosses. Currently, based on the recommendations of its Taxonomy Working Group, the Agreement on the Conservation of Albatrosses and Petrels (ACAP) recognises six species of great albatrosses (Phillips et al. 2016; Table 1).

Table 1. Species of great albatrosses (*Diomedea* spp.), major breeding populations, IUCN conservation status and global population sizes. Species and populations in bold are those that are widely distributed in the southwest Atlantic.

Species	English names	Spanish names	Breeding populations/ archipelagos	IUCN	Global population size (annual
					breeding pairs)*
Diomedea epomophora	Southern Royal Albatross	Albatros Real del Sur	Campbell and Auckland islands ** (Pacific)	VU	7900
Diomedea sanfordi	Northern Royal Albatross	Albatros Real del Norte	Chatham Islands , Taiaroa Head** (Pacific)	EN	5200
Diomedea exulans	Wandering Albatross	Albatros Errante	South Georgia (Atlantic), Crozet, Kerguelen, Marion, and Prince Edward islands (Indian Ocean) and Macquarie (Pacific)	VU	6107
Diomedea dabbenena	Tristan Albatross	Albatros de Tristán	Gough , Tristan da Cunha** (Atlántico)	CR	1698
Diomedea antipodensis	Antipodean Albatross	Albatros de las Antípodas	Antipodes, Chatham, Campbell and Auckland islands (subspecies <i>D. a.</i> <i>qibsoni</i>)	VU	8050
Diomedea amsterdamensis	Amsterdam Albatross	Albatros de Ámsterdam	Amsterdam Island (Indian Ocean)	CR	26

* The estimate corresponds to the number of breeding pairs that reproduce per year, although all the species breed biennially. This means that a major part of the breeding population is on sabbatical each year. ** These are distributed at sea in the southwest Atlantic but the population is tiny (<1% of the global population) and therefore their abundance in this region is very low.

Most seabirds share values for demographic traits that are characteristic of K-selected animal, including high adult survival rates, deferred maturity and low fecundity (Furness 2003). Procellariiformes, and particularly great albatrosses, represent extreme examples; they exhibit the largest body size of all seabirds, are monogamous, show long-deferred sexual maturity (> 10 years), very low fecundity (biennial breeders, single egg clutches) and very high survival rates (>90%) and longevity (several decades)(Tickell 2000). As a result, they are very sensitive to changes in the adult survival. For example, to maintain a stable population, a decline of only 1% per year in adult survival rate of great albatrosses would need to be compensated by an

advancement of 6.5 yr in the mean age at first breeding (Weimerskirch & Jouventin 1987). Therefore, any additional mortality produced by human activities has strong negative effects on population trends of these species.

INTERACTION BETWEEN ALBATROSSES AND FISHERIES

In the 1950s – 1960s, fisheries in the northern hemisphere grew enormously and then began to shift their efforts into the southern hemisphere, reaching the near complete global coverage of commercial fish stocks that we see today (Pauly 2008). Pelagic longline fisheries targeting tuna (*Thunnus* spp.) and other large pelagic fishes expanded into the southern hemisphere from the 1960s (Tuck et al. 2003), and demersal longline fisheries, particularly those for Patagonian toothfish *Dissostichus eleginoides* began in the southern Atlantic in the late 1980s, and expanded rapidly into sub-Antarctic waters (Brothers et al. 1999). Industrial trawl fisheries have operated continuously for decades in the continental shelves of the southern hemisphere. For example, the catches of hake *Merluccius hubbsi* by bottom trawling in the southwest Atlantic expanded from the mid-1970s (Csirke 1987, Lorenzo & Defeo 2015, Lorenzo 2016).

Fisheries may have adverse or positive effects on seabird populations and communities (Furness 2003). One of the most important direct benefits provided by fisheries is the provision of an alternative food source, often superabundant, comprised by discards (the proportion of the catch not retained on board, and generally composed of non-target and undersized fish, and offal from onboard processing). However, despite this benefit, many seabirds, and particularly albatrosses are considered among the most globally threatened of all taxa, as a result of bycatch in fisheries (Croxall et al. 2012, Phillips et al. 2016). The main threat is the incidental mortality in pelagic longline, demersal longline and trawl fisheries, but artisanal and other fisheries are also of concern for some species. Other threats include ingestion of plastics at sea, while in the colonies, the impact of diseases such as avian cholera, and predation by introduced species, are serious for some populations (Phillips et al. 2016). However, all these threats tend to affect fewer species than bycatch. Not surprisingly, some populations of albatrosses in the southern hemisphere that have been monitored since the widespread expansion of fishing effort, have shown evidence of declines

as a result of fisheries impacts (Weimerskirch & Jouventin 1987, Croxall et al. 1998, Poncet et al. 2006).

The southwest Atlantic is a region of global significance for albatrosses and other Procellariiformes (Croxall & Wood 2002, Nicholls et al. 2002). This is principally due to the large colonies at the Falkland Islands, South Georgia, Tristan da Cunha and Gough Island, archipelagos of global importance for the breeding albatrosses and petrels. The high biological productivity also makes this region attractive for several migratory species from remote areas (e.g. New Zealand). This region is also a global management focus because of conservation concern for several albatross species killed in large numbers in pelagic longline (Bugoni et al. 2008, Jiménez et al. 2009) and trawl fisheries (Sullivan et al. 2006, Favero et al. 2011). Within the distribution of albatrosses (mainly south of 30° S), the greatest effort by the pelagic longline fishery is in the region influenced by the Brazil-Falkland Confluence (Tuck et al. 2003, Jiménez et al. 2012), while bottom trawling for hake occurs all along the continental shelf of Uruguay and Argentina (Favero et al. 2011, Lorenzo 2016). The main bycaught species in longline fisheries are the black-browed albatross (Thalassarche melanophris) and the Atlantic yellow-nosed albatross (Thalassarche chlororhynchos) (Bugoni et al. 2008, Jiménez et al. 2010), while in the trawl fishery the greatest mortality is of the former species (Favero et al. 2011, Tamini et al. 2015). However, other species with smaller populations are also captured, albeit less frequently, particularly in pelagic longline fishing (Bugoni et al. 2008, Jiménez et al. 2010). These include the four species of great albatrosses that occur in the region: the wandering albatross (Diomedea exulans), Tristan albatross (Diomedea dabbenena), southern royal albatross (Diomedea epomophora) and northern royal albatros (Diomedea sanfordi). These species are globally threatened according to the International Union for Conservation of Nature (IUCN) (http://www.birdlife.org/datazone/home), and belong to small populations (Table 1).

The regional and the global populations of wandering albatross and Tristan albatross, breeding in South Georgia (south Atlantic) and Gough Island (central south Atlantic), respectively, are declining (Poncet et al. 2006, Cuthbert et al. 2014). They are considered to be among the most affected species by the pelagic longline fishery in the southwest Atlantic (Jiménez et al. 2012). On the other hand, very little is known about fisheries interactions in this region of the migrant northern and southern royal albatrosses from New Zealand (Robertson et al. 2003). Therefore, it is extremely important to obtain precise information on the capture of these four albatross species. There is also a pressing need for studies aimed at understanding the factors, including behavior, habitat preferences and intra and inter-specific interactions, which affect their foraging ecology, diet and distribution, and hence make the great albatrosses susceptible to fisheries interactions.

SEGREGATION IN ALBATROSSES AT SEA

Spatial sexual segregation

Habitat segregation describes differences between animal classes (e.g., males and females, subadults and adults, or large and small individuals) in their spatial distribution and, thus, in their use of the physical environment (Conradt 2005). The causes of habitat segregation may vary. Body size dimorphism seems a likely candidate as an explanation for sex differences in ecology, and potentially for habitat segregation. Dimorphism in body size could result in divergent nutritional and energetic requirements, reproductive strategies, activity budgets and social affinities (Ruckstuhl & Clutton-Brock 2005). Two main hypotheses, not mutually exclusive, seek to explain the sexual segregation in birds (reviewed in Catry et al. 2005). The social dominance hypothesis proposes that segregation arises from the exclusion of subordinate individuals from favoured areas by dominant conspecifics. On the other hand, the specialization hypothesis suggests that males and females segregate in different areas because of sex-specific habitat preferences, differential tolerance to ecological factors or sex specific constraints arising from breeding role specialization and competitive pressures in reproduction.

In larger species of Procellariiformes, those with pronounced sexual size dimorphism tend to display more obvious sexual segregation at sea, with males (the larger sex) more common in southern areas than females (Phillips et al. 2009). This appears to be the case in populations of wandering albatross (*Diomedea exulans sensu lato*), but is less clear for the other great albatrosses, which also show substantial sexual size dimorphism (Shaffer et al. 2001, Cuthbert et al. 2003, Xavier & Croxall 2005). Both sexes tend towards foraging segregation throughout both the breeding and non-breeding seasons (Weimerskirch et al. 1993, Prince et al. 1998, Jaeger et al. 2009, Phillips et al. 2009, Froy et al. 2015). In wandering albatrosses from South Georgia, for example, females are more likely than males to forage in northern areas outside the breeding

season (Phillips et al. 2009) and also during the incubation and post-brood (chick-rearing) stages of the breeding season (Prince et al. 1998, Froy et al. 2015). This sexual segregation is attributed to two hypotheses that are mediated by sexual size dimorphism. The first is competition, where larger males exclude the smaller females from access to nearby resources, forcing them to travel further from the colony (Weimerskirch et al. 1993, Phillips et al. 2008). The relationship between sexual size dimorphism and flight performance (Shaffer et al. 2001, Phillips et al. 2004), on the other hand, proposes that as wing loading determines flight speed, the windier regions of the sub-Antarctic and Antarctic are more optimal for males, which have higher wing loading, whereas females and fledglings are better adapted for exploiting the lighter winds of subtropical regions.

Interspecific segregation and niche partitioning

Interspecific competition occurs when two or more species use the same resources and when those resources are in short supply (Pianka 2011). Ecologically-similar species that potentially compete are considered to be able to co-exist if they partition their use of resources. The Procellariiformes in particular, have been studied frequently to understand resource partitioning between closely-related, morphologically-similar and often sympatric species (Weimerskirch et al. 1988, Phillips et al. 2004, Phillips et al. 2005, González-Solís et al. 2007, Navarro et al. 2013, Connan et al. 2014). During the breeding season, reproductive demands limited their travel distances from the colonies, and thus the competition for nearby resources between sympatric breeding species is thought to be intense (Phillips et al. 2008). After breeding, these species migrate to distant nonbreeding areas and competition among species that breed sympatrically is reduced. The potential foraging opportunities over these areas, often vast, are broader and together with the diminished density of competitors, competition appears to be relaxed (Bodey et al. 2014). However, there is increased potential for overlap among closely-related species from other island groups (Phillips et al. 2008). Indeed niche partitioning during the nonbreeding season have been proposed for closely-related and morphologically-similar species that breed in sympatry (González-Solís et al. 2007, Navarro et al. 2009, Connan et al. 2014, Navarro et al. 2015, Quillfeldt et al. 2015) or allopatry (Nicholls et al. 2002, Quillfeldt et al. 2013, Ramos et al. 2016).

Closely-related species of albatrosses appear to reduce competition for resources by avoiding spatial overlap, which is presumed to influence diet composition (Nicholls et al. 2002, Connan et al. 2014). In great albatrosses, for example, there is evidence for some degree of inter-specific niche partitioning, particularly in the relative preference for foraging over continental shelves, shelf-slope or deep waters (Nicholls et al. 2002). The two species of royal albatrosses tend to forage on the continental shelf, and wandering albatross on the slope and deep waters. Tristan albatross also forage in deep water but mainly in the subtropical area, in warm waters, and therefore overlap with the northern part of the distribution of wandering albatross (Nicholls et al. 2002, Cuthbert et al. 2005, Moore & Bettany 2005, Reid et al. 2013).

QUESTIONS, HYPOTHESES AND OBJECTIVES

The intra and interspecific segregation in great albatrosses has potential effects on the overlap with fishing effort and therefore in the interactions between birds and fisheries (with negative or positive effects on populations). Additionally, it is also feasible to assume that the changes begiining several decades ago in terms of food availability from fisheries have had an impact on the distribution of these oceanic birds, their ecological interactions, and even in the structure of the community. However, little of this has been addressed. In the southwest Atlantic, the wandering albatross is unusual in terms of the length (several decades) and intensity of monitoring at Bird Island, South Georgia. Past studies of this population have addressed sexual segregation at sea during the breeding season and its relationship with fisheries overlap, in addition to gathering information on sex-ratio of bycaught birds (Croxall & Prince 1990, Prince et al. 1992, Prince et al. 1998, Xavier et al. 2004).

At the intraspecific level, therefore, several questions arise: Can this spatial sexual segregation be generalised for all the great albatrosses?; Does it occur in other species of great albatrosses also during the nonbreeding season, when both sexes do not forage from a central place, and therefore accessibility to distant habitats and resources is not restricted? If this occurs, there are important implications for the threats facing these species at sea. From the perspective of conservation, in monogamous species, where a sex ratio of 1 : 1 is assumed, incidental mortality in fisheries biased towards one sex produces not only immediate direct effects on population size, but also indirect

effects that decrease fecundity (Mills & Ryan 2005). Therefore, it is important to assess whether the sex-biased mortality in fisheries in great albatrosses is an effect of the spatial sexual segregation. In other words, does the spatial segregation between sexes at sea lead to a relatively greater overlap between one sex and a specific fishery, and is this reflected in sex-biased bycatch? Based on the region of highest effort of the pelagic longline fishery (see above), and the proposed pattern of spatial segregation in females, on average distributed farther north than males, the following hypothesis is proposed:

• That spatial sexual segregation in great albatrosses occurs during the breeding and the non-breeding seasons, and leads to greater exposure to fisheries in subtropical areas and bycatch biased to females.

At the interspecific level, the spatial segregation or the preferences for different habitat types have implications for both trophic ecology and in the overlap with fishing effort. With respect to the former, the following hypothesis is tested:

• That spatial segregation in great albatrosses affects the diet composition.

The species of great albatrosses should experience differential exposure to the various fisheries. Considering the proposed pattern of inter-specific niche partitioning (see above), the more oceanic species, such as the wandering and Tristan albatrosses, should interact to a greater extent with pelagic longline fishing, which is usually carried out from the shelf break to deeper waters, covering all the international waters of the southwest Atlantic (Jiménez et al. 2010). An analogous argument applies to the neritic species such as royal albatrosses in terms of bottom trawl fisheries, which take place on the continental shelf (Favero et al. 2011). Again, from a conservation viewpoint, the detection of areas and seasons where these species are more exposed to bycatch is necessary in order to implement effective mitigation measures.

Fisheries discards supplement the natural food sources of great albatrosses; therefore they may increase the spatio-temporal overlap between species that would otherwise be segregated at sea. It is important to determine whether fisheries discards are important in the diet of these species. If they are, is there a higher overlap than expected in the diet of these closely-related species?

Because theory predicts that ecologically-similar species can coexist in situations where resources are superabundant, it is also relevant to ask whether fisheries discards allow an increase in trophic niche overlap among species. Not all fisheries provide a superabundant source of food. For example, it is estimated that much of the global discards come from trawl fisheries (Kelleher 2005). Therefore, are there differences in the relative contribution of each fishery to diet composition of these scavenging species? This leads to the following hypothesis:

• That fisheries discards allow an overlap in the diet and the trophic niche of great albatrosses, and that this will be most evident in the neritic species exposed to the trawl fishery.

Objectives

The general objective of this thesis is to characterise the bycatch of great albatrosses in the pelagic longline fishery operating in the southwest Atlantic and to understand the role of fisheries discards, and their influence on competition and spatial segregation among these closely related species.

The specific objectives are as follows:

(1) to assess the segregation and the overlap in diet of four closely related species of great albatrosses, with particular emphasis on the influence of fisheries discards on their diet and trophic niche.

(2) to determine the spatio-temporal variation and the contribution of habitat and fishing operational variables in the bycatch of great albatrosses in the pelagic longline fisheries of the southwest Atlantic.

(3) to quantify spatio-temporal and sex-related variation in the overlap of wandering albatross from South Georgia with the pelagic longline fleets operating in waters of the southwest Atlantic.

(4) to determine whether there is spatial segregation between the sexes in royal albatrosses during the non-breeding season.

(5) to determine whether the sex-biased mortality in fisheries is a general pattern that occurs in great albatrosses because of spatial sexual segregation.

(6) to identify other anthropogenic threats (other than fisheries) which may differentially affect great albatrosses because of their inter and intraspecific segregation at sea.

(7) to discuss the main conservation implications of the results in this thesis, particularly for addressing critical gaps in knowledge of the study species in an international context.

THESIS STRUCTURE

The thesis is arranged into seven chapters: A General Introduction (this Chapter), five chapters (Chapters 2-6) that constitute original research papers, and finally a General Discussion and Conclusions (Chapter 7). Chapters 2-6 deal with various aspects of the ecology of these species, with a general focus on inter- and intraspecific segregation and its relation to fisheries.

Chapter 2 aims to determine the segregation and overlap in the diet and trophic niche of closely related species of albatrosses (including great albatrosses) and petrels, with particular emphasis on the influence of fisheries discards on their distribution and trophic ecology. In this Chapter, conventional diet and stable isotope analyses are combined to assess the importance of discards from various fisheries (pelagic longline, demersal longline and bottom trawl fisheries) in diet composition. Additionally, the potential influence of discards on the community structure is evaluated. Chapters 3-5 analyse the interactions of great albatrosses with the pelagic longline fishery for which there is growing evidence of a negative impact of bycatch. Chapter 3 characterises the bycatch of great albatrosses in the pelagic longline fisheries of the southwest Atlantic. Bycatch rates are analysed with respect to factors potentially related to habitat preferences, as well as factors related to fishing operations. The spatio-temporal patterns in captures are evaluated, with emphasis on determining interspecific similarities or differences useful for management and conservation. Chapters 4 and 5 either directly or indirectly evaluate the spatial sexual segregation and its consequences for bycatch. Chapter 4, based on extensive tracking data of breeding wandering albatrosses, examines differences in the distribution of males and females and consequences for spatio-temporal overlap with, and bycatch by, the various longline fleets operating in the Atlantic. Chapter 5 uses data from bycaught birds to test for sexual
size dimorphism in southern and northern royal albatrosses. Using a large sample of bycaught birds of both species, evidence for sex-biased mortality is assessed, providing an indirect test of sexual segregation during the non-breeding season. Chapter 6 investigates another anthropogenic threat for these species: plastic pollution. The occurrence of plastics is addressed based on stomach contents analyses of several species of albatrosses (including great albatrosses) caught in fisheries. Differences between species and sexes are compared.

The last chapter (Chapter 7) presents the General Discussion and Conclusions, where the contributions of the Chapters 2-6 to meet the overall objectives of the thesis are discussed. In addition, the implications for the conservation of these species are explored, particularly for addressing critical gaps in knowledge in an international context.

Capítulo 2 | Chapter 2

Partición y superposición inter-específica de nicho en albatros y petreles: divergencia en la dieta y el rol de los descartes pesqueros

Inter-specific niche partitioning and overlap in albatrosses and petrels: dietary divergence and the role of fishing discards

Article: Jiménez, S., Xavier, J.C., Domingo, A., Brazeiro, A., Defeo O., Viera, M., Lorenzo, M.I. & Phillips, R.A. (under review). Inter-specific niche partitioning and overlap in albatrosses and petrels: dietary divergence and the role of fishing discards.

Abstract

Although fisheries discards are recognized as a key food source for many seabirds, there have been few thorough assessments of their importance relative to natural prey, and of the influence on the trophic structure of pelagic seabird communities during the non-breeding period. Competition for resources in Procellariiformes appears to be reduced mainly by avoiding spatial overlap, which is presumed to influence diet composition. However, artificial food sources provided by fisheries might relax niche partitioning, increasing trophic niche overlap. Using bycaught birds from pelagic longline fisheries, we combined conventional diet and stable isotope analyses to assess the importance of fishing discards in the diet of eight species of Procellariiformes. Both methods revealed the high contribution of trawl discards to the nonbreeding diet of three neritic species and a moderate considerably less important. There was a clear contrast in diets of neritic vs. oceanic species, which are closely-related taxonomically, but segregate at sea. Niche partitioning was less clear among neritic species. They showed an unexpectedly high level of diet overlap, presumably related to the large volume of trawl discards available. Ours is the first study combining conventional diet and stable isotope analyses to quantify the importance of fishery discards for a community of non-breeding seabirds, and demonstrates how the super-abundance of supplementary food can produce high levels of overlap in diets and permit the coexistence of species.

KEY WORDS: Seabirds, Mixing models, Isotopic Niche, Diet assessment, Trophic segregation

Introduction

Seabirds are important consumers of global marine resources with an estimated annual consumption comparable to total fisheries landings (Brooke 2004; Karpouzi et al. 2007). Fisheries discards, which include non-target and undersized fish, squid and other invertebrates, used bait, and offal from onboard processing, are a key food source for many scavenging seabirds, including gulls, skuas, gannets, albatrosses and petrels (Garthe et al. 1996; Oro et al. 1996; Montevecchi 2002). The negative aspects of interactions with fisheries are particularly obvious for albatrosses and large petrels (Procellariiformes), which are recorded as bycatch in substantial numbers (Anderson et al. 2011; Jiménez et al. 2014). However, in the provision of discards as a potentially major dietary component, fisheries may also have a major role in the structuring of seabird communities, with implications for marine food webs in general.

During the breeding season, seabirds are central-place foragers and competition among sympatric species is thought to be intense (Phillips et al. 2008). As many seabirds disperse during the nonbreeding period, competition among species from the same breeding location is much reduced (Bodey et al. 2014); however, there is increased potential for overlap among closely-related species from populations (Phillips et al. 2008; Quillfeldt et al. 2013). Niche partitioning has been proposed as the main mechanism explaining the coexistence of closely-related species of seabirds, as competition for resources is reduced by the avoidance of spatial overlap (Nicholls et al. 2002; Frere et al. 2008; Navarro et al. 2009a; Quillfeldt et al. 2013), use of different habitats (i.e. oceanographic features; Waugh and Weimerskirch 2003; Bugoni et al. 2009) and consumption of different prey (Cherel et al. 2002; Connan et al. 2014). Very productive areas with high levels of environmental heterogeneity can facilitate coexistence in closely-related species that exhibit some degree of niche divergence (Waugh and Weimerskirch 2003). Fisheries also tend to concentrate in highly productive areas and are known to affect seabird distributions (Ryan and Moloney 1988; Garthe 1997). Because the discards provided by vessels supplement natural food sources, they could be a cause, rather than a consequence, of spatio-temporal overlap in species that might otherwise segregate at sea. Hence, this abundant and predicable source of supplementary food could be the major determinant of trophic structure.

Trawl fisheries account for over 50% of total estimated global discards (Kelleher 2005). Therefore, in continental shelf regions with both high trawl fishing activity and high abundance of scavenging seabirds, we could anticipate very high levels of consumption (Oro et al. 1997). Other fishing techniques that provide fewer discards (e.g. pelagic longlining) might also attract birds, particularly highly pelagic species foraging over extensive, but less productive, ocean regions where prey patches are less predictable. Communities of scavenging seabirds tend to be most speciose in the Southern Hemisphere, and for example, there are globally-important populations of many albatrosses and petrels in the southwest Atlantic Ocean which aggregate around different fisheries to feed on discards (Bugoni et al. 2008; Favero et al. 2011; Jiménez et al. 2011). Over shelf waters, 1000s of birds may feed behind demersal trawl vessels targeting Argentine hake (Merluccius hubbsi) off Argentina and Uruguay, which produce large amounts of discards (Favero et al. 2011; Dirección Nacional de Recursos Acuáticos - DINARA - unpublished data). The oceanic region from the shelf break to high seas influenced by the Brazil-Falkland Confluence is fished extensively by several pelagic longline fleets targeting swordfish (Xiphias qladius), tuna (Thunnus spp.) and sharks (Huang 2011; Jiménez et al. 2016), which produce fewer discards (pieces of large fish, including viscera, and used baits) and vessels attract at most a few 100 seabirds (Bugoni et al. 2008; Jiménez et al. 2011). Over the shelf break and slope, seabirds also feed also on discards from the demersal longline fishery for Patagonian toothfish (Dissostichus eleginoides) (Favero et al. 2013; DINARA unpublished data).

Many species, including great albatrosses (*Diomedea* spp.), mollymawks (*Thalassarche* spp.) and medium-sized petrels (e.g. *Procellaria* spp.), some of which are closely-related, overlap in the southwest Atlantic. Tracking data indicate some segregation in at-sea distribution and habitat use; northern royal albatrosses (*D. sanfordi*) tend to forage on continental shelves, and wandering albatrosses (*D. exulans*) on the shelf slope and deeper waters, whereas Tristan albatrosses (*D. dabbenena*) mainly forage in warm subtropical areas, and so overlap only with the northern part

of the distribution of the wandering albatross (Nicholls et al. 2002; Xavier et al. 2004; Cuthbert et al. 2005; Reid et al. 2013). Ring recoveries and data from fishing vessels suggest that southern royal albatrosses (*D. epomophora*), like northern royal, also prefer shelf waters (Moore and Bettany 2005; Jiménez et al. 2014). White-chinned petrels (*P. aequinoctialis*) are distributed mainly in shallow continental shelf and highly productive regions (Phillips et al. 2006), whereas spectacled petrels (*P. conspicillata*) prefer warm tropical and subtropical oligotrophic and mesotrophic waters (Bugoni et al. 2009). Despite this evidence of niche partitioning, these species overlap extensively in the Brazil-Falkland Confluence region. They are commonly observed feeding on fisheries discards (Jiménez et al. 2011), yet its importance relative to natural prey, and the potential influence on niche overlap, is poorly understood.

Separating prey captured naturally from those obtained through fisheries discards is not always possible, as the same species or groups may be obtained by either means. The importance of fishing discards for seabird species has been addressed using several methods, including conventional and isotopic studies (Hudson and Furness 1988; Colabuono and Vooren 2007; Navarro et al. 2009b, Bugoni et al. 2010; González-Zevallos and Yorio 2011; Mariano-Jelicich et al. 2014). Each approach has advantages and disadvantages: conventional assessment allows the identification of many prey species but provides only a brief snapshot of diet and tends to underestimate the importance of easily-digested items. The use of stable isotope analysis (SIA) avoids the biases of conventional diet assessments and reflects prey assimilated over different timescales depending on the tissue, but provides limited taxonomic resolution (Barrett et al. 2007; Inger and Bearhop 2008; Karnovsky et al. 2012). In this study, we combined conventional diet and stable isotope analyses to determine the degree of dietary segregation in albatrosses and petrels in a major resource and biodiversity hot-spot, the southwest Atlantic, and in particular to assess the relative importance of fishing discards during the non-breeding period. It was hypothesized that fishery discards allowed overlap in the diet of the different seabirds. Based on the reported spatial and habitat segregation for albatrosses and petrels and the quantity of food supplied by longline vs. demersal trawl fisheries, we also predicted higher trophic niche overlap among species feeding mainly on discards from the latter fishery.

Materials and Methods

Conventional diet assessment

Samples were obtained from albatrosses and petrels caught incidentally during pelagic longline fishing by Uruguayan commercial and research vessels in 2005-12, and 2009-13, respectively, and Japanese commercial vessels in 2009-11 operating off Uruguay under an experimental fishing license (Jiménez et al. 2010, 2014, 2015a).

The digestive tracts (esophagus, proventriculus and ventriculus) of 126 and 27 specimens of six species of albatrosses and two of petrels, respectively, were examined. These included four great albatrosses (*Diomedea* spp.): northern royal (n = 36), southern royal (n = 23), wandering (n = 12) and Tristan albatrosses (n = 6); two species of mollymawks: black-browed (*Thalassarche melanophris*, n = 32) and white-capped albatrosses (*T. steadi*, n = 17); and white-chinned (n = 19) and spectacled petrels (n = 8). Birds were captured on the shelf break and deeper waters off Uruguay and in adjacent international waters, and a few in international waters off southern Brazil (details in Appendix S1, Fig. S1). All the *Thalassarche* and *Procellaria* spp. were bycaught during the non-breeding season (April-November). Because the breeding season of great albatrosses lasts almost a year and adults take a sabbatical year before breeding again, both breeding and non-breeding birds and a wandering albatrosses and two spectacled petrels were about to breed (see Appendix S1).

The cephalopod beaks were identified using Xavier and Cherel (2009) and checked against reference collections held at the University of Coimbra or the Centre d'Etudes Biologiques de Chizé. The lower rostral length (LRL) and the lower hood length (LHL) of the squid and octopod beaks (except those highly eroded), respectively, were measured to \pm 0.01 mm, and allometric equations used to predict mantle length and mass (Xavier and Cherel 2009). Wet mass was reconstructed separately from all measurable lower beaks (fresh and old) and then only for fresh beaks. The former was used to compare the cephalopod diet between species, and the latter to estimate the proportion by fresh mass represented by each cephalopod species and the cephalopod component in the overall diet, including fish.

Fish prey were identified in almost all cases from otoliths using the available literature, online catalogues and fish samples collected from different fisheries by DINARA (see Appendix S1). The number of fish present in each sample was estimated from the number of paired otoliths of similar sizes, and often from unpaired otoliths. Otolith length and width were measured to \pm 0.01 mm and fish standard length and mass estimated using regression equations (see Detailed methods in Appendix S1). In some stomachs, remains of fresh fish (skeletal material with attached flesh, etc.) were found, but no otoliths or other distinctive structures to enable identification.

The analyses of conventional diet took account of the time scales represented by different types of sample. The overall species composition of the cephalopod and fish components was determined separately. The frequency of occurrence, number and reconstructed mass of all accumulated beaks (fresh and old) were considered to represent the cephalopod diet during the non-breeding period (few breeding birds were sampled). In contrast, fish species identified from otoliths (including eroded) were considered to represent the fish component of the diet in the last week. Data just from the fresh cephalopod beaks and fish remains (including whole prey and all otoliths, except those heavily eroded; see Detailed methods in Appendix S1) were assumed to represent the diet in recent days, and used to estimate the relative contribution of each component and species, reducing the biases caused by different digestion rates. Reconstructions of fresh mass were performed for all but one species with at least 12 stomachs sampled. This exception was the black-browed albatross because the stomachs held a considerable number of unidentified fresh fish remains (see below), and two crustaceans for which the original wet mass could not be assessed, and hence, any reconstruction of the overall diet would have led to an overestimation of the importance of cephalopods.

We employed hierarchical cluster and non-metric multidimensional scaling (MDS) analyses in the software Primer (version 6) to analyse similarities in the diet between seabird species (Clarke and Gorley 2006). These were based on the Bray-Curtis similarity index and used the default parameters for the software. Results of the cluster analyses were integrated in the MDS output to produce ellipses of similarities. We set two similarity thresholds: > 50% and > 75%, which would represent a moderate or high overlap in diet among species. This procedure was conducted three times, first with a matrix of presence-absence of all the identified prey by species to compare the non-breeding diet using as many prey as possible. Second and third, we conducted the analyses with the percentage of wet mass reconstructed from fresh prey (see above) both by species and by component (cephalopod, demersal fish, pelagic fish), respectively.

Stable isotope analysis

As tissue samples were not available for all individuals for which stomach contents were examined, these were also taken from birds captured incidentally during the same trips and in the same fishing area (see Appendix S1, Fig. S2; Jiménez et al. 2014, 2015b). Stable isotope ratios were analysed in eight birds per species (except for Tristan Albatross; see below). Samples from southern royal, northern royal, white-capped and black-browed albatrosses and most white-chinned petrels were selected at random from birds incidentally captured in the same year (April-November 2009). Spectacled petrels and wandering albatrosses are captured incidentally in low numbers, and so samples for SIA were from four and five birds from the conventional diet analysis and an additional four samples from 2011 and three from 2008-2009, respectively. The only four samples available for Tristan albatross were from the non-breeding birds included in the conventional diet assessment. Overall, 33% of the birds from the conventional diet assessment were represented in the isotopic analysis.

Seabirds usually replace feathers during the non-breeding season, and the isotopic ratios of nitrogen (^{15}N / ^{14}N ; $\delta^{15}N$) and carbon (^{13}C / ^{12}C ; $\delta^{13}C$) in feathers are fixed after formation (Thompson and Furness 1995; Cherel et al. 2000, 2013; Phillips et al. 2009). Not all body plumage is replaced annually and so includes feathers that may have been grown in multiple non-breeding seasons (Ginn and Melville 1983). In order to focus on the diet in the southwest Atlantic, we sampled growing feathers from the head (new feathers less than two-thirds grown, with remains of waxy sheath at its base; scores 2-4 of Ginn and Melville 1983); isotope ratios should therefore represent those in prey consumed within the last few weeks. Material from 2-4 (albatrosses) and 4-8 (petrels) growing feathers was pooled for each bird. Feathers were cleaned of surface contaminants (details in Appendix S1).

SIA was also carried out on fish and squid tissues obtained from stomach contents or from fishing vessels (see Appendix S₂, Table S_{2.1}). This included samples of muscle from large pelagic fishes, including tuna (*Thunnus alalunga* = 6, *T. albacares* = 4), swordfish (*Xiphias gladius*=5) and blue shark (*Prionace glauca* = 4), small pelagic fishes (*Scomber* sp = 1, *Trachurus* sp = 2), demersal fishes (*Merluccius hubbsi* = 3, *Bassanago albescens* = 5, *Macrourus carinatus* = 2), and from squid

baits (Illex argentinus = 3), and of squid beaks (fresh or slightly eroded) from Histioteuthis eltaninae (n = 5), Histioteuthis atlantica (n = 5), Histioteuthis macrohista (n = 3) and Illex argentinus (n = 3). All prey, except large pelagic fishes, were represented in the conventional diet samples. Identifiable remains from large pelagic fishes are unlikely to be represented in stomach contents because scavenging birds feed mainly on soft body parts and viscera, and are unable to swallow the head (hence the absence of otoliths). Squid beaks and muscle samples were ovendried over 24h at 60°C and ground to a fine powder. For analysis of δ^{13} C, lipids were extracted from subsamples of muscle (see Appendix S1). Muscle subsamples of prey with and without the lipids extracted were analysed separately at the Stable Isotope Laboratory of Facultad de Agronomía (Universidad de la República, Uruguay). Carbon and nitrogen isotope ratios for seabird feathers and prey (i.e. beaks and muscle) samples (~0.7mg weighed within tin capsules) were measured by isotope ratio mass spectrometry using a Flash EA 112 elemental analyzer coupled with a Delta Plus isotope ratio mass spectrometer (Finnigan MAT). Stable isotope values are presented in delta (δ) notation in units of parts per thousand (∞), δX = [(Rsample/Rstandard) - 1], where R is the ratio of the heavy to the light isotope of element X. Standards for this equation were the stable isotope values of Pee Dee belemnite and atmospheric nitrogen for δ^{13} C and δ^{15} N, respectively. Analytical error based on repeated measurements of internal standards was of 0.2% (SD) for both nitrogen and carbon.

A Bayesian multisource stable isotope mixing model (SIAR: Stable Isotope Analyses in R; Parnell et al. 2010) was used to estimate the ranges of probable contributions of each prey group to the diet of each seabird species. Diet-tissue enrichment factors for albatross or petrel feathers have not been published (see Bond and Jones 2009). However, Caut et al. (2009) reviewed trophic enrichment factors for various taxa, including birds, and calculated mean values in bird feathers of 2.16 \pm 1.52‰ (SD) for ¹³C and 2.37 \pm 1.13‰ for ¹⁵N, which were therefore the values we assumed in all our models. The δ ¹⁵N values from our samples of lower beaks were converted into those expected for mantle tissue (see Appendix S1). After this correction, lower beaks of *Illex argentinus* showed similar isotope ratios to those in the mantle of longline bait of this species; therefore, they were pooled as a single group for further analyses. Bayesian mixing models were employed using a non-informative Dirichlet prior distribution, with zero concentration dependencies, and 5 × 10⁵ iterations, thinned by 15, with an initial discard of 5 × 10⁴ interactions in the MCMC estimation. A total of six potential prey sources were included in the model: *Histioteuthis* spp., *Illex*, small

pelagic fish, pelagic longline fish (including all large pelagic fishes), demersal trawl fish (Merluccius hubbsi and Bassanago albescens) and demersal longline fish (Macrourus carinatus). The species from the last three groups are known to be the discards from the respective fisheries. The trawl fishery produces the largest amount of discards, comprising undersized hake, nontarget demersal fish (in Uruguay and northern Argentina, this includes Bassanago albescens and other species that can be fully discarded; and Helicolenus dactylopterus, Cheilodactylus bergi and other species that may be retained), squid (mainly *Illex argentinus*, which is largely retained), and other invertebrates, and offal from onboard processing (DINARA unpublished data). Both longline fisheries provide substantially fewer discards. In the pelagic longline fishery, the discards comprise pieces of swordfish, tuna and sharks, including their viscera, and parts or whole individuals of other large fishes, and the used baits. Discards from the demersal longline fishery are mainly non-target demersal fish, including Macrouridae, and offal. None of these demersal and large pelagic fishes are expected to be obtained naturally in substantial amounts. The cephalopods, including Histioteuthis spp., are thought to be taken directly by the seabirds (either caught close to the surface, or scavenged postmortem) (Croxall and Prince 1996; Cherel and Klages 1998), but *I. argentinus* may also be made available to surface predators either as a discard from the trawl fishery (see above and Discussion) or as used baits discarded from pelagic longline vessels. Some of the small pelagic fishes could also be used baits (see Results), although they are also naturally available. Similar cluster hierarchical and MDS analyses to those conducted for the conventional diet analyses were performed using the mean values of raw δ^{13} C and δ^{15} N values for seabirds, and the median values for the contribution of each prey for the different albatross and petrel species.

Bayesian ellipses (SIBER: Stable Isotope Bayesian Ellipses in R, Jackson et al. 2011) were used to describe the isotopic niche space occupied by the different seabird species during the nonbreeding season. The Standard Ellipse Area (SEA) encompassing 40% of the data after small sample size correction (SEAc) was used to estimate the percentage overlap (regarding the smaller SEAc of each species pair) among isotopic niches. The posterior estimates of the Bayesian Standard Ellipse Area (SEAB) were used to compare isotopic niche widths between species.

Results

Dietary analysis

A total of 40 prey species were identified in 153 stomachs of the eight species of albatrosses and petrels: at least 28 species of cephalopods (squid and Octopoda), 12 of fishes and one of crustaceans. Crustacea were only found in a black-browed albatross (remains of two *Chaceon notialis*) and two northern royal albatross (fragments of unidentified exoskeleton).

Cephalopod component of the diet

At least nine species of squid were identified among 31 accumulated beaks in the stomachs of six Tristan albatrosses, representing those ingested in recent weeks or months of the non-breeding period. The most important family by number (61.3%) and mass (78.2%) was Histioteuthidae (mainly *Histioteuthis bonnellii corpuscula*), followed by Chiroteuthidae (19.4% by number, 10.2% by mass) (Table 1). Thirteen species of squid were determined in 12 stomachs of wandering albatrosses, of which the most important by number were Histioteuthidae (61.4%) and Ommastrephidae (13.6%) and by mass were Onychoteuthidae (53.8%), represented by just two individual Kondakovia longimana, and Histioteuthidae (27.6%), of which H. eltaninae and H. atlantica, were the most important (Table 1). A total of 10 and 12 species of squid were found in the diet of 23 southern and 36 northern royal albatrosses, respectively, of which Illex argentinus (Ommastrephidae) was by far the most important species (83.2% by number and 60.9% by reconstructed mass of 161 cephalopods found in southern royal albatrosses, and 61.3% by number and 70.8% by mass of the 137 squid found in northern royal albatrosses; Table 2). The second most important by mass were Onychoteuthidae (27.3%), represented by a few individual Moroteuthis spp. in southern royal albatross, and Histioteuthidae (21.9% by number, 17.7% by mass) in northern royal albatross (Table 2). Octopoda were only recorded in the diet of southern and northern royal albatrosses (Table 2).

Thirty-six and eight individual squid from at least six and three species were found in the 32 and 17 stomachs, respectively, from black-browed and white-capped albatrosses (Table 3). Similar to the royal albatrosses, the most important squid for white-capped albatross was *Illex argentinus*, both by numbers (72.5%) and mass (84.2%), whereas Histioteuthidae were the most common squid (52.8% by number, 61.9% by mass; mainly *Histioteuthis atlantica*) consumed by black-

browed albatrosses (Table 3). Very large numbers of lower squid beaks were found in the 19 and 8 stomachs analysed, respectively, from white-chinned and spectacled petrels, of which 69.3% (of 192), and 48.9% (of 92) were highly eroded (Table 4). A total of eight species were identified for white-chinned petrels, of which the most important were Histioteuthidae (22.4% by number, 77.7% by mass). Nine squid species were present in spectacled petrel stomachs, with *Lycoteuthis lorigera* (Lycoteuthidae) the most abundant (23.9%), but representing just 4.3% of wet mass, partly because almost all beaks were eroded, preventing mass reconstruction. In contrast, five of six lower beaks of *I. argentinus* were measurable, and hence this squid was the most important by reconstructed mass (45.4%).

Fish component of the diet

No fish was recorded in Tristan albatross stomachs, and just one unidentified fish was found in a spectacled petrel. Most of the identified fish species in the other albatrosses and petrels were demersal, and a few were pelagic and small; some of the latter were confirmed to be longline baits (fresh, and located at the esophagus or attached to a hook). Only two Macrouridae and a bait fish, *Sardinops sagax*, were found in wandering albatrosses. The main fish species eaten by the two royal albatross species were *Bassanago albescens* and *Merluccius hubbsi*, which represented 48.0% and 18.0% by number, respectively, in northern royal, and 34.4% and 31.3%, respectively in southern royal albatross. Macrouridae and a few *Urophycis cirratus* were also found in both albatrosses. Only three (one Macrouridae, one *M. hubbsi* and one *Scomber* sp. bait) of the 17 fish found in black-browed albatross were identified. The fish diet of white-capped albatross was dominated by *B. albescens* (61.5% by number). Finally, *M. hubbsi* and *B. albescens* were the most important fish by number (54.5% and 13.6%) for white-chinned petrel, which had also consumed the demersal fish *Cynoscion guatucupa* and *Helicolenus dactylopterus*, and some pelagic fishes that were longline baits.

Dietary overlap and segregation

Using only fresh material, we were able to reconstruct the fresh mass of each component in the diet of five seabird species. The diets of all species, except wandering albatross (reconstructed mass: cephalopods 80.2%, fish 19.8%), were dominated in mass by fish (Table 6). The relative importance of fish (~80%) and cephalopods (20%) was similar in the closely-related southern and

northern royal albatrosses; in the former, these were largely the demersal fishes *Bassanago albescens*, *Merluccius hubbsi* and Macrouridae species. Fish were even more important for whitecapped albatross and white-chinned petrel (91.2% and 89.6%, respectively), of which the main species by mass were *B. albescens*, or both *M. hubbsi* and *B. albescens*, respectively (Table 6). *Illex argentinus* was usually the most important fresh cephalopod in diets (Table 6).

The cluster and MSD results underlined the similarity in diet between some species, particularly the royal albatrosses (Fig. 1). Based on the presence-absence of each prey species, northern and southern royal albatrosses showed the greatest, and Tristan albatross and spectacled petrel showed the least overlap among species pairs (Fig. 1a). Based on reconstructed wet mass (Fig. 1b), there was extensive dietary overlap between the two royal albatross species, and a moderate overlap between these species and white-capped albatross. However, the diet of both royal albatrosses showed greater overlap with white-capped albatross and white-chinned petrel if comparing the reconstructed wet mass by component (fish *vs.* squid; Fig. 1c). The most distinct diet using these various metrics was that of the wandering albatross because of the predominance of squid (Fig. 1c).

Stable isotope analyses

Isotopic ratios of growing feathers ranged from the mean (\pm SD) values of both δ^{13} C and δ^{15} N of -16.67 \pm 0.67 ‰ and 15.14 \pm 0.67 ‰, respectively, in spectacled petrel, to -15.55 \pm 0.98 ‰ and 18.47 \pm 1.09‰ in northern royal albatross (see Appendix 2, Table S2.1). There were significant differences among species in feather δ^{13} C and δ^{15} N values using a multivariate ANOVA (Wilks' λ , $F_{14,102} = 5.29$, P < 0.05), but in univariate tests, the differences were significant in δ^{15} N (ANOVA, $F_{7.52} = 10.99$, P<0.05), but not in δ^{13} C (ANOVA, $F_{7.52} = 1.862$, P>0.05). Post-hoc tests (Tukey tests <0.05) indicated several pairwise differences in δ^{15} N values: northern royal albatross > all species, except southern royal and black-browed albatrosses; southern royal and black-browed albatrosses > spectacled petrel and wandering albatross; black-browed albatross > Tristan albatross; whitecapped albatross > spectacled petrel.

Niche overlap and segregation

Levels of niche overlap also varied between the seabird species (Table 7, Fig. 2a). Excluding Tristan albatross because of the small sample size, the corrected Standard Ellipse Area (SEAc) ranged between 0.914 $\%^2$ in wandering albatross and 3.380 $\%^2$ in white-capped albatross (Table 7). The overlap between isotopic niches of the great albatross species (from SEAc estimates) was low (southern royal overlapped with 10% of the SEAc of northern royal) or null (wandering vs. both northern and southern royal albatross). Additionally, wandering albatross showed a significantly narrower niche width (SEAB, P < 0.05) than either royal albatross species, whereas these two species showed similar niche widths (Fig. 2b). White-capped and black-browed albatrosses showed considerable niche overlap (52%, Table 7) and similar niche widths according SEAB (p>0.05; Figs. 2a and 2b). The isotope niches of the *Procellaria* petrels differed substantially; there was little overlap (15%, Table 7), and the niche width of white-chinned petrel was significantly wider than in spectacled petrel (Fig. 2b). Relative differences between species appeared to reflect habitat preferences; the two most oceanic species (wandering albatross and spectacled petrel) showed the narrowest niche widths (Fig. 2b) and least overlap (Fig. 2a, Table 7) with most of the neritic species. No differences were detected between the niche width of blackbrowed albatross and any other species (Fig. 2b). Furthermore, the isotopic niches of all neritic species overlapped extensively with the SEAc of black-browed albatross (35% to 78%, Table 7, Fig. 2a).

Mixing model

The results of the Bayesian stable isotope mixing model showed some differences in the contribution of each of the six prey groups to the diet, although credibility intervals overlapped in most cases (Fig. 3; Appendix 2, Table S2.2). Prey groups overlapped to some extent in their δ^{13} C and δ^{15} N values, particularly demersal trawl fish and *Illex* (Appendix 2, Table S2.1). According to the Bayesian mixing model, the most important prey groups in the diet of southern royal, northern royal and black-browed albatrosses were demersal trawl fish and *Illex*, with mean proportions ranging from 0.23 to 0.27. The next most important prey for the three albatrosses were demersal longline fish, *Histioteuthis* and pelagic longline fish (mean proportions ranging from 0.12 to 0.15), followed by small pelagic fish (Fig. 3, Appendix 2, Table S2.2). Results for white-capped albatross were similar in some respects, with the diet dominated by both demersal fish

and *Illex* (mean proportions of 0.20 and 0.19, respectively) but with somewhat higher proportions of the remaining groups, particularly pelagic and demersal longline fishes (Fig. 3, see Appendix 2, Table S2.2). In contrast with the remaining species, the diets of wandering albatross and spectacled petrel were dominated by *Histioteuthis* (mean of 0.30 and 0.31, respectively) and small pelagic fish (0.26 and 0.29), followed by demersal longline fish and then pelagic longline fish (Fig. 3, see Appendix 2, Table S2.2). Demersal trawl fish and *Illex* were of little relevance, as expected for these two predominately oceanic seabirds. *Histioteuthis* (mean proportion of 0.23) was the most important item for white-chinned petrel. However, in obvious contrast to the spectacled petrel, white-chinned petrels consumed substantially more demersal trawl fish and *Illex* (means of 0.17) (Fig. 3, see Appendix 2, Table S2.2). Finally, the diet of Tristan Albatross was based on very few birds sampled and thus the mixing model output should be viewed with caution. They suggest a diet similar in some respects to the wandering albatross but with greater contributions of *Histioteuthis* and small pelagic fish (means of 0.19), followed by demersal and pelagic longline fishes (means of 0.17), and *Illex* and demersal trawl fish (both 0.14; Fig. 3, see Appendix 2, Table S2.2).

The results of the cluster and MSD analyses from both stable isotope outputs (i.e. mean δ^{13} C and δ^{15} N values, and posterior estimates of the Bayesian model) indicated similarities in diet among some species pairs (Figs. 4a and b). The highest overlap was in the diets of both royal albatrosses and black-browed albatross, which clearly contrasted with the diets of wandering albatross and spectacled petrel (Figs. 4a and b). The diets of white-capped albatross and white-chinned petrel were similar to each other, and most like the diets of the royal and black-browed albatrosses. The diet of Tristan albatross was closest to white-capped albatross and white-chinned petrel (Figs. 4a and b).

Discussion

To our knowledge, this is the first study to use a combination of conventional diet and stable isotope analyses to examine the role of fishing discards in structuring trophic relationships within a seabird community. The conventional diet assessment provided a robust taxonomic identification of the prey consumed by several albatross and petrel species in the southwest Atlantic, including, for the first time, migrants from colonies in the New Zealand region (whitecapped, northern royal and southern royal albatrosses). The conventional and isotopic approaches provided complementary information, overcoming some of the biases or limitations of the individual methods, to reveal the major importance of trawl discards in the non-breeding diet of three species (southern and northern royal, and black-browed albatrosses), moderate importance in two species (white-capped albatross and white-chinned petrel) and minor relevance in two others (wandering albatross and spectacled petrel). Although the study was of birds killed on pelagic longliners, discards from this type of fishery, or from demersal longlining, contributed substantially less than other sources to their diets, according to the stable isotope mixing model. This indicates that our sample was not biased to birds specialised in pelagic longline discards. Moreover, the mean and range of stable isotope ratios measured in feathers were the same as in random samples of these same seabird species taken at colonies (see below), and therefore there is no reason to consider that the birds we sampled were atypical of these populations. Segregation in the diet and isotopic niche between neritic and oceanic species was confirmed. The availability of abundant resources in shelf waters, partly supplied by trawl fishing, appear to reduce the degree of segregation among neritic species-pairs; this was especially evident for both royal albatrosses, which had similar diets based on stomach contents, although their isotopic niches were more distinctive. Our results applied to the non-breeding season, which are of particular relevance as most natural mortality in seabirds occurs during the winter, when the diet of pelagic species, such as the Procellariiformes, is much more difficult to study than when they attend colonies during breeding

Relevance of fishing discards

In this study, conventional analysis of stomach contents proved to be effective for accurately identifying prey species, but not for quantifying the importance of large pelagic fishes obtained as discards. However, use of the Bayesian stable isotope mixing model with these fish included as a potential food source revealed their importance relative to other prey groups. Bayesian stable mixing models are sensitive to the initial inputs, especially to the trophic enrichment factors (TEFs) (Bond and Diamond 2011). Due to the lack of TEF values for Procellariiformes, we used TEFs for bird feathers that are an average across many different taxa and a wide SD to allow for the uncertainty (Caut et al. 2009). Therefore, we acknowledge that caution is required when interpreting our estimates of the contribution of prey groups. Additionally, this method may not provide reliable estimates of the relative contribution of groups with similar isotopic signatures

(*Illex vs.* demersal fish, see below), for which stomach contents provided better resolution. We acknowledge the small sample size for stable isotope ratios of some prey groups, and overlap in the credibility intervals between groups in the mixing model. Given these biases, similar results were not expected from the two methods of quantifying the number of prey groups consumed and their proportion in the diet. Indeed, the estimates for the proportions of each prey group varied between methods (Fig. 5, see below). However, the combined results from the conventional and isotopic approaches provide a compelling indication of the main prey in the diet of the study species, with the possible exception of Tristan albatross for which sample sizes were smallest. The diet of wandering albatross and potentially that of spectacled petrel (see below) included the highest contributions of prey that are likely to be taken naturally (*Histioteuthis* spp. and probably many of the small pelagic fish). However, the diet of northern royal, southern royal, black-browed and white-capped albatrosses, and white-chinned petrel were dominated by prey obtained artificially, i.e., from fisheries discards.

Based on reconstructed wet mass from conventional diet, fishing discards from trawl fisheries are a major food source for four of our study species in the southwest Atlantic during their nonbreeding season (southern and northern royal, and white-capped albatrosses, and white-chinned petrel). There is a major trawl fishery for Argentinean hake operating over the Argentinean and Uruguayan shelf (mainly from 50 to 200m isobaths), where these seabirds are relatively abundant (Favero et al. 2011; Jiménez et al. 2015c; DINARA unpublished data). Undersized hake (landing of hake <35cm is not allowed) are the most likely source of food, which is also supported by the length of the hake estimated from otoliths found in stomach contents of the bycaught birds (mean \pm SD of reconstructed hake length = 25 \pm 8 cm, n = 32; this study). Bassanago albascens is highly abundant in deep shelf waters from 35° to 42°S (Figueroa and Ehrlich 2006; García et al. 2010), is discarded only in trawl fisheries, and is more buoyant than other discarded demersal fish so will remain closer to the surface and more accessible to birds behind vessels (Seco Pon 2014). Another prey likely to be obtained as discards is *Ilex argentinus*; this is the most important squid captured by fisheries in the shelf waters off southern Brazil, Uruguay and Argentina, is abundant in our study area mainly during winter (Sacau et al. 2005), and discarded in large amounts from the trawl fishery for hake (Seco Pon 2014). However, it can also be obtained naturally, and so the proportions that are taken directly by the seabirds (either caught close to the surface, or

scavenged postmortem), obtained as pelagic longline baits, or as trawl discards, are unknown, although this last source is likely to be major.

Stable isotope analyses supported that both demersal trawl fish (Merluccius hubbsi and Bassanago albescens) and Illex argentinus were major items in the diet, particularly of southern and northern royal albatrosses, but also white-capped albatross and white-chinned petrel (see below). Furthermore, although we could not reconstruct the diet of black-browed albatross by wet mass because of the unidentified fish, the stable isotope results suggested that its diet was close to that of both royal albatross species and that discards from the trawl fishery were a main food source. This is supported by the high abundance of black-browed albatrosses, which in winter can reach >1000 birds behind a single trawler (Favero et al. 2011; Jiménez et al. 2015c). It should be noted that two sources might have the same contribution in a stable isotope mixing model if they occupy the same isotope space. Hence, the similarity in isotopic signatures of demersal trawl fish and Illex (see Appendix 2, Table S2.1.) could explain the differences in relative importance between conventional diet and Bayesian mixing models. Nevertheless, demersal trawl fish and Illex are clearly of major importance to both species of royal albatrosses and black-browed albatross, as supported by the Bayesian mixing model including demersal trawl fish and Illex combined as a source (Fig. 5; Appendix 2, Fig. S2.1), and by a previous study of black-browed albatrosses (Mariano-Jelicich et al. 2014). Note that this mixed source - demersal fish and Illex encompasses the bulk of the discards of this particular fishery.

The Bayesian mixing model output indicated that discards from pelagic and demersal longline fisheries did not predominate in the diet of any species. Across the study area, discards from the demersal longline fishery for toothfish consist of offal from onboard processing, and non-target demersal fish, including *Macrourus* spp. For the species for which we reconstructed the fresh mass, *Macrourus* spp. were eaten by wandering albatross, southern and northern royal albatrosses, and white-capped albatross (16.5% to 30.6%). These values matched very well with the mean proportions estimated by the mixing model (equivalent to 15% to 18%, Fig. 5; see Appendix 2, Table S2.2) based on stable isotope ratios of muscle samples of *M. carinatus* obtained from this fishery within the Argentinean–Uruguayan Common Fishing Zone (ZCPAU). Although there was some difference between these two percentages in the diet of southern royal albatross, this resulted mainly from the reconstructed mass of two large *Macrourus holotrachys*.

The Bayesian stable isotope mixing models suggested that discards from pelagic longline fishing were of low to moderate importance in all species. However, some Illex and small pelagic fish used as pelagic longline baits are undoubtedly ingested by scavenging seabirds (see Table 6). All the birds in our study were bycaught on pelagic longliners, so the relatively low importance of this fishery might indicate that vessels are not attended by birds for prolonged periods, as suggested from vessel-based observations of those that are banded or have diagnostic external marks (Bugoni et al. 2010). Spectacled petrel and particularly wandering albatross are the two most oceanic of our study species known to overlap extensively with pelagic longline fishing (Bugoni et al. 2009, Jiménez et al. 2016). Histioteuthis spp. and small pelagic fish dominated their diet according to the mixing models. The predominance of *Histioteuthis* spp. in the diet of wandering albatross was confirmed by the conventional diet analysis of fresh prey only (Table 6), or fresh and old material combined (Table 1). These species are also important in the diet during the breeding season (Xavier et al. 2003) along with other squid (e.g. Kondakovia longimana and Taonius sp. B (Voss)), and fish discarded from the demersal longline fishery for toothfish (Xavier et al. 2003; Ceia et al. 2012). Although we analysed few stomachs of spectacled petrel, almost half of the squid beaks were highly eroded, and so remained undetermined. The most important squid identified was Lycoteuthis lorigera, but the lower beaks were eroded and thus excluded from isotopic analyses as they were potentially consumed outside the study area. Although Histioteuthis was recorded, its importance remained unclear. However, stomach analysis of seven bycaught birds in southern Brazil found that Histioteuthidae was the main squid family targeted by spectacled petrel (Colabuono and Vooren 2007), suggesting that may be important prey. The isotopic signatures of small pelagic fish used in the mixing model were from Scomber spp. and Trachurus spp., which are often used as baits by pelagic longliner and are consumed by both seabird species (Jiménez et al. 2011, 2012). Therefore, the provenance of this dietary component could be as discards; however, no evidence for either prey was found in the stomach contents of wandering albatross or spectacled petrel.

A study in southern Brazil found that discards from pelagic longline fishery was the main dietary source for the community of Procellariiformes (Bugoni et al. 2010). This used stable isotope ratios of muscle from blue shark as a proxy of pelagic longline fishing discards, as birds frequently feed on shark liver. We generated an additional Bayesian mixing model for wandering albatross and spectacled petrel that included four potential sources: *Histioteuthis*, small pelagic fish, blue shark

(see Appendix 2, Table S2.1 for isotopic values) and demersal longline fish. *Illex* and demersal fish from the trawl fishery were excluded as they were of minor relevance for these seabirds (see above). The model again supported the higher importance of *Histioteuthis* and small pelagic fish than either blue shark or demersal longline fish for spectacled petrel (Appendix 2, Fig. S2.2a). For wandering albatross, *Histioteuthis* was the most important prey, followed closely by both small pelagic fish and demersal longline fish; however, blue shark was least important (Fig. 5, Appendix 2, Fig. S2.2b). This latter scenario is closest to our stomach content analysis and previous studies of diet of wandering albatross at the breeding site (Xavier et al. 2004; Ceia et al. 2012). Hence, our results do not support the suggestion that discards from pelagic longline fishing are a major diet component for wandering albatross, spectacled petrel, or indeed any of the species sampled in our study.

Niche overlap and segregation

The stable isotope ratios measured in growing head feathers in our study matched those in body feathers of the same albatross species sampled at colonies (Cherel et al. 2013); of our species, northern royal albatross exhibited the highest, and wandering albatross the lowest values of both δ^{15} N and δ^{13} C. An individual body feather is presumed to take at least 2-3 weeks to grow 6-10 cm long (Jaeger et al. 2010), therefore our sample of growing feathers from head (from several mm in petrels to few cm in some albatrosses) might represent the diet over a shorter period. The δ^{13} C values in these feathers were as expected for a region influenced by the Brazil-Falkland confluence, i.e., typical of subtropical, or a mixture of subtropical, subantarctic and continental shelf waters (Phillips et al. 2009; Cherel et al. 2013). The exception was the value for a single southern royal albatross (δ^{13} C = -18.65), which may have been a recent arrival from a more southerly or oceanic region. Therefore, our results indicate that SI values in small, growing feathers provide a good proxy of the foraging ecology of highly mobile seabirds while using a relatively well-defined region.

Although direct evidence is lacking, it is usually assumed that population sizes of large marine predators are limited by resources (Nicholls et al. 2002; Lewis et al. 2006; Conners et al. 2015). Foraging competition in Procellariiformes appears to be reduced by avoiding spatial overlap, which is presumed to lead to the targeting of different prey (Cherel et al. 2002; Nicholls et al. 2002; Connan et al. 2014). Our comparison between closely-related species supported this

hypothesis. The diets of the neritic southern and northern royal albatrosses were well differentiated from the more oceanic wandering albatross, as of the neritic white-chinned petrel from the predominantly oceanic spectacled petrel. Over shelf waters, the super-abundant and artificial food source provided by trawl fishing seems to relax niche partitioning, allowing coexistence, and thus high trophic niche overlap among closely-related species. Indeed, niche partitioning was less apparent between the neritic congeners - black-browed and white-capped albatrosses, which fed mainly on demersal trawl fish and *Illex* (Fig. 3). Isotopic niches of both albatrosses overlapped and did not differ statistically in isotopic niche width, although the latter tended to be wider in white-capped albatross (Fig. 2a), suggesting some level of niche partitioning. Both northern and southern royal albatrosses showed surprising similarity in diets, dominated by discards from the trawl fishery (Table 6, Figs. 1 and 4), and exhibited similar niche widths. However, they showed low isotopic niche overlap (Fig. 2a). This is unlikely to be caused either by dietary divergence (Table 6, Figs. 1 and 4) or small sample size, as Cherel et al. (2013) also found higher values of δ^{15} N in feathers of northern royal than southern royal albatross. A plausible explanation is that both species coexist in the area and feed on the same abundant resources provided by fishing, but on a finer scale they overlap little on space or time when feeding at trawlers. The slightly lower $\delta^{15}N$ and $\delta^{13}C$ in southern royal albatross (albeit not significant possibly due to the constrained study area) might suggest feeding on average in shelf waters slightly to the south or further offshore than northern royal albatross. Nevertheless, the unprecedented high levels of dietary overlap among these closely-related species of albatrosses highlight the key influence of fisheries discards.

In summary, this study confirmed the expectation that ecologically-similar species should avoid spatial overlap (neritic *vs.* pelagic) or show divergent diets, suggesting that niche partitioning reduces competition. However, there was also convincing evidence that closely-related species of neritic albatross can show high levels of trophic overlap when feeding on a super-abundant resource. Although supported by all the evidence gathered in this paper, the lack of a control study of a similar community without fisheries discards (e.g. Oro et al. 1996), does not allow us to conclude explicitly that the availability of trawl fishery discards increases niche overlap. Niche overlap as a consequence of super-abundant resources will also occur if natural resources are superabundant. However, in that case, the diet of neritic species should mainly consist of natural prey, including squid (e.g. *Histioteuthis* spp.), epipelagic fish and carrion (Cherel and Klages

1998), for which there was little evidence (with the exception of some of the *Illex argentinus*). It therefore appears that the availability of trawl fishery discards on the continental shelf can produce high levels of dietary overlap and permit the coexistence of species within communities of non-breeding seabirds.

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Family	Species	Tr	istan	albatross	(n=6)	War	nderin	g albatros	s (n=12)
		%FO	Ν	%N	% Mass	%FO	Ν	%N	% Mass
Batoteuthidae	Batoteuthis skolops	16.7	1	3.2	2.1	8.3	2	4.5	0.5
Chiroteuthidae	Chiroteuthis sp	33.3	4	12.9	8.5				
	Chiroteuthis sp F (Imber)	33.3	2	6.5	1.7				
Cranchiidae	Galiteuthis glacialis					8.3	1	2.3	0.7
	<i>Taonius</i> sp B (Voss)	16.7	1	3.2	6.1	8.3	2	4.5	4.6
Histioteuthidae	Histioteuthidae	33.3	3	9.7					
	Histioteuthis miranda					8.3	1	2.3	4.0
	Histioteuthis arcturi	33.3	3	9.7	9.5				
	Histioteuthis atlantica	33.3	4	12.9	22.0	41.7	7	15.9	10.1
	Histioteuthis bonnellii corpuscula	33.3	7	22.6	38.4	25.0	3	6.8	3.9
	Histioteuthis eltaninae					25.0	14	31.8	6.6
	Histioteuthis macrohista	33.3	2	6.5	8.3	16.7	2	4.5	3.0
Mastigoteuthidae	Mastigoteuthis A (Clarke)					16.7	2	4.5	0.9
Neoteuthidae	Alluroteuthis antarcticus					8.3	2	4.5	6.4
	Nototeuthis dimegacotyle	16.7	2	6.5	3.5				
Ommastrephidae	Illex argentinus •					16.7	3	6.8	3.4
	Illex argentinus*					16.7	2	4.5	2.0
	Martialia hyadesi					8.3	1	2.3	
Onychoteuthidae	Kondakovia longimana					8.3	2	4.5	53.8
	Moroteuthis sp B (Imber)	16.7	1	3.2					
Unknown	Squid Unknown	16.7	1	3.2					
Total			31	100.0	100.0		44	100.0	100.0

Table 1. Frequency of occurrence, numbers and reconstructed wet mass for all the cephalopods ingested (fresh and old material combined) by Tristan and wandering albatrosses.

* confirmed longline baits are presented separately. • mixed source: prey that are likely to be obtained from trawl discards, naturally, or as longline baits (see Methods and Discussion).

ingested (fresh a	nd old material combine	d) by s	outhe	rn and	northern ro	oyal albat	trosse	es.	
Family	Species	South	ern roy	al albatr	oss (n=23)	North	ern ro	yal albatr	oss (n=36)
		%FO	Ν	%N	% Mass	%FO	Ν	%N	% Mass
Batoteuthidae	Batoteuthis skolops					2.8	1	0.7	0.2
Chiroteuthidae	Chiroteuthis veranyi					2.8	1	0.7	0.5
Cranchiidae	Galiteuthis glacialis	4.3	1	0.6	0.6	2.8	1	0.7	0.5
	<i>Taonius</i> sp B (Voss)	4.3	1	0.6	1.0				
Gonatidae	Gonatus antarcticus	4.3	1	0.6	1.5				
Histioteuthidae	Histioteuthidae					8.3	3	2.2	
	Histioteuthis atlantica					11.1	7	5.1	8.7
	Histioteuthis eltaninae					8.3	9	6.6	2.9
	Histioteuthis macrohista	13.0	3	1.9	1.4	19.4	11	8.0	6.1
Loliginidae	Loligo gahi	4.3	1	0.6	2.6				
	<i>Loligo</i> sp	4.3	1	0.6	0.5				
Lycoteuthidae	Lycoteuthis lorigera					2.8	1	0.7	0.3
Mastigoteuthidae	Mastigoteuthis A (Clarke)	8.7	2	1.2	2.1	2.8	1	0.7	0.7
Neoteuthidae	Alluroteuthis antarcticus	4.3	1	0.6	2.2				
Ommastrephidae	Illex argentinus ●	60.9	130	80.7	54.9	58.3	81	59.1	67.9
	Illex argentinus*	17.4	4	2.5	5.9	8.3	3	2.2	2.9
Onychoteuthidae	Moroteuthis ingens	8.7	2	1.2	17.9	2.8	1	0.7	
	Moroteuthis robsoni	4.3	1	0.6	9.4	2.8	1	0.7	8.9
	Notonykia africanae					2.8	1	0.7	0.4

Table 2. Frequency of occurrence, numbers and reconstructed wet mass for all the cephalopoc	S
ingested (fresh and old material combined) by southern and northern royal albatrosses.	

Unknown	Squid Unknown	21.7	11	6.8		22.2	12	8.8	
Octopodidae	Octopodidae	4.3	2	1.2		2.8	3	2.2	
Total			161	100.0	100.0		137	100.0	100.0

* confirmed longline baits are presented separately. • mixed source: prey that are likely to be obtained from trawl discards, naturally, or as longline baits (see Methods and Discussion).

Table 3. F	Frequency of occurrence,	numbers ar	nd reconstructe	ed wet mass for	all the cephalopods
ingested	(fresh and old material co	ombined) by	black-browed	and white-cap	ped albatrosses.

Family	Species	Bla	ck-br	owed al (n=32)	batross	White-capped albatross (n=17)					
		%FO	Ν	%N	% Mass	%FO	Ν	%N	% Mass		
Gonatidae	Gonatus antarcticus	3.1	1	2.8	4.8						
Histioteuthidae	Histioteuthidae	3.1	1	2.8							
	Histioteuthis atlantica	21.9	13	36.1	53.7	5.9	1	12.5	6.4		
	Histioteuthis macrohista	9.4	5	13.9	8.2	5.9	1	12.5	9.4		
Ommastrephidae	Illex argentinus •	6.3	4	11.1	5.1	17.6	4	50.0	63.5		
	Illex argentinus*	9.4	3	8.3	6.1	5.9	1	12.5	20.7		
	Ommastrephidae	3.1	4	11.1	1.8						
Onychoteuthidae	Moroteuthis robsoni	3.1	1	2.8	20.3						
	Moroteuthis sp B (Imber)	3.1	1	2.8							
Unknown	Squid Unknown	9.4	3	8.3		5.9	1	12.5			
Total			36	100	100.0		8	100.0	100.0		

* confirmed longline baits are presented separately. • mixed source: prey that are likely to be obtained from trawl discards, naturally, or as longline baits (see Methods and Discussion).

Table 4. Frequency of occurrence, numbers and reconstructed wet mass for all the cephalopod
ingested (fresh and old material combined) by white-chinned and spectacled petrels.

Family	Species	Whit	e-chinr	ned petre	el (n=19)	Spe	Spectacled petrel (n=8)				
		%FO	Ν	%N	% Mass	%FO	Ν	%N	% Mass		
Chiroteuthidae	Chiroteuthis veranyi					25.0	2	2.2	2.0		
Cranchiidae	Taonius sp (Clarke)					25.0	2	2.2	4.9		
	<i>Taonius</i> sp B (Voss)	5.3	2	1.0		12.5	1	1.1			
Gonatidae	Gonatus antarcticus	10.5	3	1.6	2.8	12.5	7	7.6	19.9		
Histioteuthidae	Histioteuthidae	15.8	14	7.3		12.5	1	1.1			
	Histioteuthis atlantica	10.5	3	1.6	14.5						
	Histioteuthis bonnellii corpuscula	10.5	2	1.0	14.6						
	Histioteuthis macrohista	52.6	24	12.5	48.7	12.5	4	4.3	23.5		
	Histioteuthis meleagroteuthis					12.5	1	1.1			
Lycoteuthidae	Lycoteuthis lorigera					50.0	22	23.9	4.3		
Mastigoteuthidae	Mastigoteuthis A (Clarke)	5.3	1	0.5	1.4						
Octopoteuthidae	Octopoteuthis sp					12.5	1	1.1			
Ommastrephidae	Illex argentinus ●	21.1	8	4.2	16.1	37.5	5	5.4	45.4		
	Illex argentinus*	5.3	1	0.5	1.9	12.5	1	1.1			
Onychoteuthidae	Moroteuthis ingens	5.3	1	0.5							
Unknown	Squid Unknown	100.0	133	69.3		75.0	45	48.9			
Total			192	100.0	100.0		92	100.0	100.0		

* confirmed longline baits are presented separately. • mixed source: prey that are likely to be obtained from trawl discards, naturally, or as longline baits (see Methods and Discussion).

Table 5. Frequency of occurrence and percentage of the total numbers of fishes found in the stomach content analysis of wandering (WA), southern royal (SRA), northern
royal (NRA), black-browed (BBA) and white-capped (WCA) albatrosses and white-chinned petrel (WCP).

Family	Species	W	/A (n=	:12)	SF	SRA (n=23)		NF	NRA (n=36)			BBA (n=32)			CA (n=	=17)	WCP (n=19)		
		%FO	Ν	%N	%FO	Ν	%N	%FO	Ν	%N	%FC	N	%N	%FO	Ν	%N	%FO	Ν	%N
Demersal																			
Cheilodactylidae	Cheilodactylus bergi ●●							2.8	1	1.6									
Congridae	Bassanago albescens $ullet ullet$				21.7	24	48.0	25.0	22	34.4				23.5	8	61.5	10.5	3	13.6
Macrouridae	Coelorinchus spp ●●●				4.3	1	2.0	2.8	1	1.6	3.1	1	5.9						
Macrouridae	Macrourus carinatus ●●●	8.3	1	33.3	4.3	4	8.0	5.6	3	4.7									
Macrouridae	Macrourus holotrachys •••	8.3	1	33.3	8.7	2	4.0	2.8	1	1.6				5.9	1	7.7			
Merlucciidae	Merluccius hubbsi 🔸				17.4	9	18.0	25.0	20	31.3	3.1	1	5.9				10.5	12	54.5
Phycidae	Urophycis cirratus 🔸				4.3	1	2.0	5.6	3	4.7									
Sciaenidae	Cynoscion guatucupa $ullet ullet$																5.3	1	4.5
Sebastidae	Helicolenus dactylopterus ••																5.3	1	4.5
Pelagic																			
Carangidae	Trachurus sp							5.6	2	3.1							5.3	1*	4.5
Clupeidae	Sardinops sagax*	8.3	1	33.3													10.5	2	9.1
Scombridae	Scomber sp				4.3	1	2.0				3.1	1*	5.9						
Unknown	Fish Unknown				30.4	8	16.0	27.8	11	17.2	40.6	14	82.4	23.5	4	30.8	10.5	2	9.1
Total			3	100.0		50	100.0		64	100.0		17	100.0		13	100.0		22	100.0

3 * confirmed longline baits. •• prey that are likely to be obtained from the trawl fishery. ••• prey that are likely to be obtained from the demersal longline fishery.

4

5 **Table 6.** Fresh cephalopod and fish contribution in the dietary analysis of wandering (WA), southern royal (SRA), northern royal (NRA), and white-capped (WCA) albatrosses

and white-chinned petrel (WCP). Percentage by numbers and reconstructed mass (g) are presented for the two main components (Fish: from otoliths (categories 1-3, see
methods) and fresh fish; Cephalopods: from fresh lower beaks and fresh squid) and for each prey identified species.

Species		W	A (n=12)			SF	A (n=23)			N	RA (n=36)			W	CA (n=17)		WC	CP (n=19)	
	Ν	%N	Mass	%Mass	Ν	%N	Mass	%Mass	Ν	%N	Mass	%Mass	Ν	%N	Mass	%Mass	Ν	%N	Mass	%Mass
Total Squid	10	83.3	2386	80.2	25	37.9	2773	20.2	22	34.4	3032	20.1	5	35.7	383	8.8	2	10.5	186	10.4
Taonius sp B (Voss)	1	8.3	370	12.5																
Histioteuthis miranda	1	8.3	606	20.4																
Histioteuthis atlantica	1	8.3	276	9.3					1	1.6	403	2.7	1	7.1	60	1.4				
Histioteuthis bonnellii corpuscula	1	8.3	87	2.9																
Histioteuthis macrohista	1	8.3	240	8.1									1	7.1	89	2.0	1	5.3	104	5.8
Mastigoteuthis A (Clarke)									1	1.6	134	0.9								
Illex argentinus •	3	25.0	504	17.0	21	31.8	1757	12.8	17	26.6	1966	13.0	2	14.3	39	0.9				
Illex argentinus*	2	16.7	301	10.1	4	6.1	1015	7.4	3	4.7	529	3.5	1	7.1	195	4.5	1	5.3	82	4.6
Total Fish	2	16.7	587	19.8	41	62.1	10980	79.8	42	65.6	12074	79.9	9	64.3	3993	91.2	17	89.5	1600	89.6
Demersal																				
Cheilodactylus bergi ●●									1	1.6	187	1.2								
Bassanago albescens ●●					23	34.8	4555	33.1	18	28.1	4640	30.7	8	57.1	3096	70.8	3	15.8	398	22.3
Coelorinchus spp ●●●					1	1.5	121	0.9	1	1.6	16	0.1								
Macrourus carinatus ●●●	1	8.3	497	16.7	4	6.1	1446	10.5	3	4.7	1645	10.9								
Macrourus holotrachys ●●●					2	3.0	2766	20.1	1	1.6	845	5.6	1	7.1	897	20.5				
Merluccius hubbsi 🔸					9	13.6	1400	10.2	13	20.3	2890	19.1					9	47.4	754	42.2
Urophycis cirratus ●●					1	1.5	542	3.9	3	4.7	1694	11.2								
Cynoscion guatucupa $ullet ullet$																	1	5.3	6	0.4
Helicolenus dactylopterus 🔸																	1	5.3	98	5.5
Pelagic																				
Trachurus sp									2	3.1	159	1.1					1	5.3	121	6.8
Sardinops sagax*	1	8.3	90	3.0													2	10.5	223	12.5
Scomber sp					1	1.5	150	1.1												
Total	12	100	2973	100	66	100	13752	100	64	100	15105	100	14	100	4376	100	19	100	1786	100

8 * confirmed longline baits. • mixed source: prey that are likely to be obtained from trawl discards, naturally, or as longline baits (see Methods and Discussion). • prey that are likely to be obtained from the trawl

9 fishery. ••• prey that are likely to be obtained from the demersal longline fishery.

		SRA	NRA	BBA	WCA	WCP	SP	WA
					‰ ²			
SRA		-	0.226	1.392	1.974	2.050	0.000	0.000
NRA		10	-	0.625	0.000	0.216	0.000	0.000
BBA		78	35	-	0.927	1.070	0.000	0.000
WCA	%	62	0	52	-	2.106	0.223	0.321
WCP		64	9	60	64	-	0.176	0.558
SP		0	0	0	19	15	-	0.499
WA		0	0	0	35	61	55	-
SEAc		3.203	2.284	1.795	3.380	3.286	1.190	0.914

Table 7. Corrected Standard Ellipse Area (SEAc; ‰²) and overlap of SEAc between species pairs in ‰² and percentage of the smaller SEAc of the species pair. Species codes showed in Fig. 1.

Figure 1 Right: Non-metric multidimensional scaling (MDS) with superimposed clusters at similarity levels of 50% (grey) and 75% (black). Left: Hierarchical clustering (Bray-Curtis similarity). **a**) Presence-absence data of all squid and fish species identified in the stomach content analysis of eight species of albatross and petrels. **b**) Percentage of reconstructed wet mass of squid and fish species found in the stomach content analysis of the five main species. **c**) Percentage of reconstructed wet mass for the three main components (squid, demersal fish and pelagic fish) found in the stomach content analysis of the five main species. SRA = southern royal albatross, NRA = northern royal albatross, BBA = black-browed albatross, WCA = white-capped albatross, WCP = white-chinned petrel, SP = spectacled petrel, WA = wandering albatross and TA =Tristan albatross.

Figure 2 a) Stable carbon and nitrogen values of re-growing feathers and Standard Ellipse Area (SEA) estimated using Stable Isotope Bayesian Ellipses in R (SIBER, Jackson et al. 2011) for seven species of albatross and petrels (eight sample per species). b) Density plots of the Bayesian Standard Ellipse Area (SEAB, mean [black dots] and their credibility intervals 50%, 75% and 95%). Species codes are showed in Fig. 1.

Figure 3 Range of possible proportions of six prey groups in the diet of eight species of albatrosses and petrels. *Histioteuthis* spp. are likely to be obtained naturally (mostly), *Illex argentinus* as trawl discards, natural prey or longline baits, small pelagic fishes as natural prey or longline baits. Decreasing bar widths represent 5%, 50%, 75% and 95 % Bayesian credibility intervals computed by Stable Isotope Analysis in R. Species codes are showed in Fig. 1.

Figure 4 Right: Non-metric multidimensional scaling (MDS). Left: Hierarchical clustering (Bray-Curtis similarity). (a) Mean values of δ^{13} C and δ^{15} N. (b) Mean posterior estimates of the Bayesian stable isotope mixing model for the proportion of the six prey groups (*Histioteuthis* spp., *Illex argentinus*, pelagic longline fish, small pelagic fish, demersal trawl fish and demersal longline fish) in the diet of eight species of albatross and petrels. Superimposed clusters in MDS are at similarity levels of 98% (grey) and 99% (black) in (a) and 75% (grey) and 95% (black) in (b). Species codes are showed in Fig. 1.

Figure 5 Comparison of the conventional analysis of stomach contents (% of the reconstructed fresh mass, see Table 6) and the Bayesian stable isotope mixing model for the five species in which we could reconstruct the wet mass of the prey. Mixing models outputs are the range of possible proportions of four and five prey groups in the diet of each study species. Blue shark was used as pelagic longline fish (marked with an asterisk) and demersal trawl fish and *Illex* were pooled as a single source in the models with four and five prey groups, respectively (see Discussion for specifications). Decreasing bar widths represent 5%, 50%, 75% and 95% Bayesian credibility intervals computed by Stable Isotope Analysis in R. Sources of the prey groups are explained in Fig. 3 and species codes showed in Fig. 1.



Figure 1.







Figure 3.


Figure 4.



Figure 5.

Appendix S1. Detailed methods

Separating prey captured naturally from those obtained through fisheries discards is not always possible, as the same species or groups may be obtained by either means. The importance of fishing discards for seabird species has been addressed using several methods, including conventional and isotopic studies (Hudson and Furness 1988, Colabuono and Vooren 2007, Navarro et al. 2009, Bugoni et al. 2010, González-Zevallos and Yorio 2011, Mariano-Jelicich et al. 2014). Each approach has advantages and disadvantages: conventional assessment allows the identification of many prey species but provides only a brief snapshot of diet and tends to underestimate the importance of easily-digested items. The use of stable isotope analysis (SIA) has increased considerably in recent years, and works on the principle that stable isotope ratios measured in consumer tissues can be linked to those in their diet in a predictable way. This avoids the biases of conventional diet assessments, reflects prey assimilated over different timescales depending on the tissue, but provides limited taxonomic resolution (Barrett et al. 2007, Inger & Bearhop 2008, Karnovsky et al. 2012). Stable isotope data can also be used to estimate two important attributes of niche space of species in the same community; breadth and overlap (Bearhop et al. 2004, Newsome et al. 2007, Jackson et al. 2011). This is because the stable isotope ratios within tissues can be considered descriptors of key axes of the Hutchinson's hypervolume of the consumer, providing data on environmental and trophic components of the niche at the individual, population or community level (Newsome et al. 2007, Jackson et al. 2011). The ratios of the heavy to light stable isotope of nitrogen (${}^{15}N/{}^{14}N$; $\delta^{15}N$), increase by ~3-5 % between each trophic level in marine systems (Barrett et al. 2007), and thus is analogous to a trophic axis. Although carbon isotope ratios (${}^{13}C/{}^{12}C$; $\delta^{13}C$) change less between trophic levels, they reflect the primary carbon source within a food web; in marine environments δ^{13} C provides a general idea of the oceanographic region or different gradients, including latitudinal, offshore-inshore or benthic-pelagic (Barrett et al. 2007, Newsome et al. 2007, Phillips et al. 2009), and therefore it provides information analogous to both the biotic and environmental axes of the niche (Newsome et al. 2007).

Conventional diet assessment

Samples were obtained from albatrosses and petrels caught incidentally during pelagic longline fishing by Uruguayan commercial and research vessels in 2005-12, and 2009-13, respectively, and Japanese commercial vessels in 2009-11 operating off Uruguay under an experimental fishing license (Jiménez et al. 2010, 2014, 2015a). All vessels fished in shelf break, slope and deeper waters off Uruguay, and Uruguayan commercial vessels also operated in international waters (Jiménez et al. 2014).

The digestive tracts (esophagus, proventriculus and ventriculus) of 126 and 27 specimens of six species of albatrosses and two of petrels, respectively, were examined. The albatross species included four great albatrosses (*Diomedea* spp.): northern royal (n = 36), southern royal (n = 23), wandering (n = 12) and Tristan albatrosses (n = 6); and two species of mollymawks: black-browed (*Thalassarche melanophris*, n = 32) and white-capped albatrosses (*T. steadi*, n = 17). Species of great albatrosses were identified in the laboratory; northern royal and southern royal albatrosses were distinguished by their plumage, and wandering albatrosses were separated from Tristan albatrosses by a morphometric discriminant function (Cuthbert et al. 2003). White-capped albatrosses were identified by molecular analysis (Jiménez et al. 2015b). The petrel species were white-chinned petrel (n = 19) and spectacled petrel (n = 8). Birds were captured on the shelf break and deeper waters off Uruguay and in adjacent international waters, with a few individuals captured in international waters off southern Brazil (Fig. S1; see also Jiménez et al. 2015a). All the Thalassarche and Procellaria spp. were bycaught during the non-breeding season (April-November). Because the breeding season of great albatrosses lasts almost a year and adults take a sabbatical year before breeding again, both breeding and non-breeding seasons overlap temporally. Only two Tristan albatrosses (with unfeathered brood patches captured in January) and two wandering albatrosses (ringed birds caught in late July and early September; late chickrearing) were breeding birds. Based on gonad examination, a few other birds (a wandering albatross and two spectacled petrels) were about to breed.

Frozen bycatch specimens were thawed and the digestive tract removed. Food items found in the esophagus, proventriculus and ventriculus were examined separately. Few undigested or partially digested prey were found, so most of the data on diet composition are from the identification of cephalopod beaks and fish otoliths. The beaks were identified using Xavier and Cherel (2009) and

checked against reference collections held at the University of Coimbra or the Centre d'Etudes Biologiques de Chizé. As the ratio of upper:lower beaks frequently differs from unity (Xavier et al. 2011), the number and species identification of individual squid was determined from the 709 lower beaks (611 upper beaks were also collected). The lower rostral length (LRL) and the lower hood length (LHL) of the squid and octopod beaks (except those highly eroded), respectively, were measured to \pm 0.01 mm with a digital vernier calliper, and allometric equations used to predict mantle length and mass (Xavier & Cherel 2009). Wet mass was reconstructed separately from all measurable lower beaks (fresh and old) and then only for fresh beaks (see below). The former was used to compare the cephalopod diet between species, and the latter to estimate the proportion by fresh mass represented by each cephalopod species and the cephalopod component in the overall diet, including fish (see Results). Fresh beaks were those with beak wings and lateral walls in near perfect condition, often with buccal muscle attached (Xavier & Cherel 2009). Because squid and octopod beaks can accumulate in the stomach (mainly the ventriculus) for long periods (Furness et al. 1984), the abundance and reconstructed mass of these accumulated beaks represent cephalopods ingested in previous weeks or months. In contrast, fresh beaks represent cephalopods ingested in the last few days (Spear et al. 2007).

Fish prey were identified in almost all cases from otoliths using the available literature (Reid 1996, Volpedo & Echeverría 1999, Rossi-Wongtschowski et al. 2014, DINARA unpublished), online catalogues (http://www.cmima.csic.es/aforo/) and fish samples collected from different fisheries by DINARA. The number of fish present in each sample was estimated from the number of paired otoliths of similar sizes, and often from unpaired otoliths. Otolith length and width were measured to ± 0.01 mm and fish standard length and mass estimated using regression equations; where no relationships were available, regression equations were used from closely-related species or subspecies (Wohler 1997, Waessle et al. 2003, Morley & Belchier 2002, Xavier et al. 2003, González-Zevallos et al. 2010, Crec'hriou et al. 2015). Otoliths are digested faster than squid beaks by seabirds and the level of erosion depends on their shape, size, thickness and time since ingestion. Experiments in captivity (Furness 1984, Casaux et al. 1995) and dedicated stomach content analyses (Spear et al. 2007) show that otoliths can be completely digested from within one to several days. Thus, otoliths were classified into four categories of erosion: (1) no sign of wear or digestion, (2) slight, with some signs of smoothing of margins (3) moderate, and (4) heavily eroded with margins rounded or broken, or with a considerable part of the otolith missing

after fracture. Otoliths in categories 1 to 3 were measured to reconstruct the fish mass. A correction factor was applied to compensate for erosion: 10% for otoliths from category 2 and 20% for those in category 3 (Reid 1995, Arata et al. 2004). In some stomachs, remains of fresh fish (skeletal material with attached flesh, etc.) were found, but otoliths or other distinctive structures to identify the species were absent, in which cases, the occurrence of one unknown fish was assumed.

The analyses of conventional diet data took account of the time scales represented by different types of sample. The overall species composition of the cephalopod and fish components was determined separately. The frequency of occurrence, number and reconstructed mass of all accumulated beaks (fresh and old) were considered to represent the cephalopod diet of each seabird species during the non-breeding period (few breeding birds were sampled). In contrast, similar data on fish species identified from otoliths (including eroded) were considered to represent the fish component of the diet in the last week. Data just from the fresh cephalopod beaks and fish remains (including whole prey and otoliths in categories 1-3) were assumed to represent the diet in recent days, and used to estimate the relative contribution of each component and species, reducing the biases caused by different digestion rates. Reconstructions of fresh mass were performed for all but one species with at least 12 stomachs sampled. This exception was the black-browed albatross because the stomachs held a considerable number of unidentified fresh fish remains (see below), and two crustaceans for which the original wet mass could not be assessed, and hence, any reconstruction of the overall diet would have led to an overestimation of the importance of cephalopods.

We employed hierarchical cluster and non-metric multidimensional scaling (MDS) analyses in the software Primer (version 6) to analyse similarities in the diet between seabird species (Clarke & Gorley 2006). These were based on the Bray-Curtis similarity index and used the default parameters for the software. Results of the cluster analyses were integrated in the MDS output to produce ellipses of similarities. We set two similarity thresholds: > 50% and > 75%, which would represent a moderate or high overlap in diet among species. This procedure was conducted three times, first with a matrix of presence-absence of all the identified prey by species to compare the non-breeding diet using as many prey species as possible, but reducing the over-represented abundance of the accumulated squid. Second and third, we conducted the analyses with the

percentage of wet mass reconstructed from fresh prey (see above) both by species and by component (cephalopod, demersal fish, pelagic fish), respectively. Only one fresh beak belonging to a deep-sea squid (fam. Mastigoteuthidae) was recorded, so the cephalopod component was not classified according to depth preference.

Stable isotope analysis

As tissue samples were not available for all individuals for which stomach contents were examined, these were also taken from birds captured incidentally during the same trips and in the same fishing area (Fig. S2; Jiménez et al. 2014, 2015b). Stable isotope ratios were analysed in eight birds per species (except for Tristan Albatross; see below). Samples from southern royal, northern royal, white-capped and black-browed albatrosses and most white-chinned petrels were selected at random from birds incidentally captured in the same year (April-November 2009). Spectacled petrels and wandering albatrosses are captured incidentally in low numbers, and so samples for SIA were from four and five birds from the conventional diet analysis and an additional four samples from 2011 and three from 2008-2009, respectively. The only four samples available for Tristan albatross were from the birds included in the conventional diet assessment. Overall, 33% of the birds from the conventional diet assessment were represented in the isotopic analysis.

Seabirds usually replace their feathers during the non-breeding season, and the isotopic ratios of nitrogen (^{15}N / ^{14}N ; $\delta^{15}N$) and carbon (^{13}C / ^{12}C ; $\delta^{13}C$) in feathers are fixed after formation (Thompson & Furness 1995, Cherel et al. 2000, 2013, Phillips et al. 2009). Not all body plumage is replaced annually and so includes feathers that may have been grown in multiple non-breeding seasons (Ginn & Melville 1983). As we were interested in the feeding ecology while these species were exclusively in the southwest Atlantic, we sampled growing feathers from the head (new feathers less than two-thirds grown, with remains of waxy sheath at its base; scores 2-4 of Ginn & Melville 1983); isotope ratios should therefore represent those in prey consumed within the last few weeks. Material from 2-4 (albatrosses) and 4-8 (petrels) growing feathers was pooled for each bird. Feathers were cleaned of surface contaminants using 2:1 chloroform:methanol followed by a methanol rinse, air dried and then homogenized by cutting into small fragments with stainless steel scissors.

SIA was also carried out on fish and squid tissues obtained from the bird stomach content analyses or from fishing vessels (see Appendix S2, Table S2.1). This included samples of muscle

from large pelagic fishes, including tuna (Thunnus alalunga = 6, Thunnus albacares = 4), swordfish (Xiphias gladius=5) and blue shark (Prionace glauca = 4), small pelagic fishes (Scomber sp = 1, Trachurus sp = 2), demersal fishes (Merluccius hubbsi = 3, Bassanago albescens = 5, *Macrourus carinatus* = 2), and from squid baits (*Illex argentinus* = 3), and of squid beaks (fresh or slightly eroded) from Histioteuthis eltaninae (n = 5), Histioteuthis atlantica (n = 5), Histioteuthis macrohista (n = 3) and Illex argentinus (n = 3). All prey, except large pelagic fishes, were represented in the conventional diet samples. Identifiable remains from large pelagic fishes are unlikely to be represented in stomach contents because scavenging birds feed mainly on their soft body parts and viscera, and are unable to swallow the head (hence the absence of otoliths). Squid beaks and muscle samples were oven-dried over 24h at 60°C and ground to a fine powder. For analysis of δ^{13} C, lipids were extracted from subsamples of muscle (~50 mg) placed in filter paper envelopes using 2:1 chloroform:methanol and ultrasound for one hour. This procedure was repeated twice and then subsamples were oven-dried at 40°C for 24 h (Colabuono et al. 2014). Muscle subsamples of prey with and without the lipids extracted were analysed separately. Stable isotope analysis was carried out at the Stable Isotope Laboratory of Facultad de Agronomía (Universidad de la República, Uruguay). Carbon and nitrogen isotope ratios for seabird feathers and prey (i.e. beaks and muscle) samples (~0.7mg weighed within tin capsules) were measured by isotope ratio mass spectrometry using a Flash EA 112 elemental analyzer coupled with a Delta Plus isotope ratio mass spectrometer (Finnigan MAT). Stable isotope values are presented in delta (δ) notation in units of parts per thousand (‰), $\delta X = [(Rsample/Rstandard) - 1]$, where R is the ratio of the heavy to the light isotope of element X. Standards for this equation were the stable isotope values of Pee Dee belemnite and atmospheric nitrogen for δ^{13} C and δ^{15} N, respectively. Analytical error based on repeated measurements of internal standards was of 0.2% (SD) for both nitrogen and carbon.

A Bayesian multisource stable isotope mixing model (SIAR: Stable Isotope Analyses in R; Parnell et al. 2010) was used to estimate the ranges of probable contributions of each prey group to the diet of each seabird species. Diet-tissue enrichment factors for albatross or petrel feathers have not been published (see Bond & Jones 2009). However, Caut et al. (2009) reviewed trophic enrichment factors for various taxa, including birds, and calculated mean values in bird feathers of 2.16 \pm 1.52% (SD) for ¹³C and 2.37 \pm 1.13% for ¹⁵N. Therefore, we assumed in all our models that consumer tissue (raw feather isotope data for each seabird species) were enriched by these values

compared with their prey (mean and SD of δ^{13} C and δ^{15} N in muscle of each prey group). Soft parts, which represent the bulk of the squid consumed by birds (mainly mantle and arms), are consistently highly enriched in ¹⁵N over beaks, but slightly depleted in ¹³C (Hobson & Cherel 2006). Thus δ^{15} N values from our samples of lower beaks were converted into those expected for mantle tissue. For *Illex argentinus*, the values of δ^{15} N and δ^{13} C in muscle were assumed to be 5.2% higher and 0.8‰ lower than lower beaks, respectively, based in data from *Illex coindetii* (Hobson & Cherel 2006). For *Histioteuthis* spp we assumed that soft body parts were enriched by 4.8% in ¹⁵N and depleted by 0.8‰ in ¹³C over lower beaks by using an average estimate for several cephalopod species (Hobson & Cherel 2006). After this correction, lower beaks of Illex argentinus showed similar isotope ratios to those found in the mantle of longline bait of this species; therefore, they were pooled as a single group for further analyses. Bayesian mixing models were employed using a non-informative Dirichlet prior distribution, with zero concentration dependencies, and 5×10^5 iterations, thinned by 15, with an initial discard of 5×10^4 interactions in the MCMC estimation. A total of six potential prey sources were included in the model: *Histioteuthis* spp, *Illex*, small pelagic fish, pelagic longline fish (including all large pelagic fishes), demersal trawl fish (Merluccius hubbsi and Bassanago albescens) and demersal longline fish (Macrourus carinatus). The species from the latter three groups are known to be the discards from the respective fisheries. The trawl fishery produces the largest amount of discard, comprised by undersized hake, non-target demersal fish (in Uruguay and northern Argentina they include Bassanago albescens and other species that can be fully discarded; and Helicolenus dactylopterus, Cheilodactylus bergi and other species that can be also retained), squids (mainly Illex argentinus, which is also largely retained), and other invertebrates, and offal from onboard processing (DINARA unpublished data). Both longline fisheries produce substantially lower levels of discard. In the pelagic longline fishery the discards are comprised by pieces of swordfish, tuna and sharks, including their viscera, and parts or whole individuals of other large fishes, and the used baits. Discards from the demersal longline fishery are mainly non-target demersal fish, including Macrouridae, and offal. None of these demersal and large pelagic fishes are expected to be naturally eaten in a substantial amount. The species of cephalopods, as *Histioteuthis* spp., are thought to be taken directly by the seabirds (either caught close to the surface, or scavenged postmortem) (Croxall & Prince 1996, Cherel & Klages 1998), but Illex argentinus can also become artificially available to surface predators either as discard from the trawl fishery (considered a relevant source; see above and Discussion) or as used baits discarded from pelagic longline vessels. The provenance of at least part of the small pelagic fishes (epipelagic species) could be from the latter source (see Results), although they are naturally available (Cherel & Klages 1998). Similar cluster hierarchical and MDS analyses to those conducted for the conventional diet analyses were performed using the mean values of raw δ^{13} C and δ^{15} N values for seabirds, and the median values for the contribution of each prey for the different albatross and petrel species.

Bayesian ellipses (SIBER: Stable Isotope Bayesian Ellipses in R, Jackson et al. 2011) were used to describe the isotopic niche space occupied by the different seabird species during the nonbreeding season. The Standard Ellipse Area (SEA) encompassing 40% of the data after small sample size correction (SEAc) was used to estimate the percentage overlap (regarding the smaller SEAc of each species pair) among isotopic niches. The posterior estimates of the Bayesian Standard Ellipse Area (SEAB) were used to compare isotopic niche widths between species.



Figure S1. Distribution of sampled birds for conventional diet assessment. (A) All bycaught albatrosses, (B) albatrosses bycaught within the Uruguayan Economic Exclusive Zone, and (C) all bycaught petrels. The 200 m isobath is represented.



Figure S2. Distribution of sampled birds for stable isotope analysis (SIA). (A) All bycaught albatrosses and petrels, and (B) albatrosses and petrels bycaught within the Uruguayan Economic Exclusive Zone (EEZ). The 200 m isobath is represented.

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Appendix S2. Supplementary data on stable isotope analysis

Species	Code	,	Sex	δ13C (‰)		δ15N (‰)	
·		n	Males : Females	Mean	± SD	Mean	± SD
			(unknown)				
southern royal albatross	SRA 8		1:7	-15.57	1.34	17.27	1.01
northern royal albatross	NRA	8	2:6	-15.55	0.98	18.47	1.09
black-browed albatross	BBA	8	(8)	-15.65	0.76	17.57	0.69
white-capped albatross	; WCA		3 : 4 (1)	-15.65	1.08	16.73	1.18
white-chinned petrel	WCP	8	(8)	-16.20	0.99	16.64	1.14
spectacled petrel	SP	8	4 : 0 (4)	-16.67	0.67	15.14	0.67
wandering albatross	WA	8	2:6	-16.65	0.51	15.59	0.53
Tristan albatross	ТА	4	0:4	-16.16	1.38	15.96	0.69
Histioteuthis		13		-20.06	1.80	13.52	1.41
Histioteuthis atlantica *		5		-18.29	0.48	14.58	1.31
Histioteuthis eltaninae *		5		-22.06	0.64	12.19	0.51
Histioteuthis macrohista *		3		-19.68	0.06	13.98	0.60
		-					
Illex		6		-17.17	1.26	15.34	0.96
Illex argentinus (beaks)*		3		-17.67	1.48	15.34	1.31
Illex argentinus (muscle)	Illex argentinus (muscle)			-16.66	1.01	15.34	0.76
			Fish length (cm)				
Pelagic longline fish		19		-17.55	0.70	13.49	1.22
Prionace glauca		4	110 - 183	-17.78	1.02	13.55	0.92
Thunnus alalunga		6	76 - 113	-17.56	0.41	12.73	0.75
Thunnus albacares		4	117 – 129	-16.93	0.50	15.35	0.55
Kiphias gladius		5	190 – 263	-17.83	0.68	12.88	0.57
Small pelagic fish		3		-17.99	1.21	12.47	0.53
Trachurus sp		2	~ 20	-17.34	0.67	12.33	0.67
Scomber sp		1	-	-19.3	-	12.75	-
Demersal trawl fish		8		-16 92	0.46	15 33	1.86
Merluccius hubbsi		3	14 - 31	-17.38	0.43	16.88	2.31
Bassanaao alhescens		5	37 – 56	-16 64	0.14	14.40	0.71
2000 and 200		5		10.04	0.14	11.40	0.7 1
Demersal longline fish		2		-17.96	0.08	13.71	0.10
Macrourus carinatus		2	<40	-17.96	0.08	13.71	0.10

Table S2.1. Stable isotope ratios (mean and standard deviation) and samples size for albatross, petrels (growing feathers from the head) and prey (muscle and/or beaks).

* Stable isotope ratios for squid beaks were corrected for those expected for mantle (see Methods).

Species		Histioteuthis	Illex	Pelagic	Small	Demersal	Demersal
-				Longline Fish	Pelagic Fish	Trawl Fish	Longline Fish
SRA	Mean	0.14	0.23	0.14	0.11	0.24	0.15
	5th	0.01	0.05	0.01	0.01	0.06	0.01
	95th	0.29	0.42	0.31	0.26	0.42	0.31
NRA	Mean	0.13	0.23	0.14	0.12	0.23	0.15
	5th	0.01	0.05	0.01	0.01	0.05	0.01
	95th	0.27	0.43	0.31	0.28	0.41	0.32
BBA	Mean	0.14	0.27	0.12	0.08	0.26	0.13
	5th	0.02	0.08	0.01	0.01	0.07	0.01
	95th	0.27	0.48	0.28	0.23	0.43	0.30
WCA	Mean	0.15	0.19	0.16	0.14	0.20	0.16
	5th	0.02	0.04	0.02	0.01	0.04	0.02
	95th	0.30	0.35	0.32	0.29	0.35	0.32
WCP	Mean	0.23	0.17	0.15	0.14	0.17	0.15
	5th	0.07	0.02	0.01	0.01	0.02	0.02
	95th	0.37	0.33	0.31	0.29	0.32	0.31
SP	Mean	0.31	0.06	0.14	0.29	0.06	0.15
	5th	0.16	0.00	0.01	0.08	0.00	0.01
	95th	0.45	0.17	0.33	0.51	0.16	0.33
WA	Mean	0.30	0.06	0.15	0.26	0.06	0.18
	5th	0.17	0.00	0.01	0.08	0.00	0.02
	95th	0.42	0.16	0.32	0.44	0.16	0.36
ТА	Mean	0.19	0.14	0.17	0.19	0.14	0.17
	5th	0.03	0.01	0.02	0.03	0.01	0.02
	95th	0.35	0.29	0.33	0.35	0.29	0.33

Table S2.2. Posterior estimates of the Bayesian stable isotope mixing model for the proportion of each prey group in the diet of eight species of albatross and petrels. Seabird species codes in Table S2.1. For the definition of the prey groups see main text.



Figure S2.1. Range of possible proportions of five prey groups (*Histioteuthis* spp., pelagic longline fish, small pelagic fish, demersal trawl fish and *Illex argentinus* combined and demersal longline fish) in the diet of five species of albatrosses and petrels. Decreasing bar widths represent 5, 50, 75 and 95 % Bayesian credibility intervals computed by Stable Isotope Analysis in R. Seabird species codes in Table S2.1.



Figure S2.2. Range of possible proportions of four prey groups (*Histioteuthis* spp., pelagic longline fish (blue shark), small pelagic fishes and demersal longline fish in the diet of spectacled petrel (SP) and wandering albatross (WA). Decreasing bar widths represent 5, 50, 75 and 95 % Bayesian credibility intervals computed by Stable Isotope Analysis in R.

Capítulo 3 | Chapter 3

Captura incidental de los grandes albatros en pesquerías de palangre pelágico en el Atlántico sudoccidental: factores que contribuyen e implicancias para el manejo

Bycatch of great albatrosses in pelagic longline fisheries in the southwest Atlantic: contributing factors and implications for management

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Abstract

Pelagic longline fisheries in the southwest Atlantic are a major conservation concern for several threatened seabirds, including four species of great albatrosses: wandering albatross (*Diomedea exulans*), Tristan albatross (*D. dabbenena*), southern royal albatross (*D. epomophora*) and northern royal albatross (*D. sanfordi*). The aim of this study was to examine the spatial and temporal variation in bycatch rates of these species, and to identify the contributing environmental and operational factors. We used data collected by observers on board pelagic longliners in the Uruguayan fleet in 2004-2011, and on Japanese vessels operating in Uruguay under an experimental fishing license in 2009-2011. Bycatch rates for northern and southern royal albatrosses were higher than expected based on previous reports, particularly over the shelf break. Wandering and Tristan albatrosses were caught predominantly in pelagic waters, where there are numerous fishing fleets from other flag states. Bycatch of great albatrosses was highest in April-November, with the peak for royal albatrosses in June-July, and for wandering and Tristan

albatrosses in September-November. A range of vessel operational practices and habitat variables affected bycatch rates, among which setting time, moon phase, area and season are useful in terms of risk assessment, and in the development and improvement of conservation measures for these highly threatened species.

Keywords: Incidental mortality, Fisheries Impacts, Non-target species, Seabirds, Fishery Management

1. Introduction

Incidental mortality (bycatch) in fisheries is one of the major threats facing many populations of seabirds (Croxall et al., 2012; Žydelis et al., 2013). The global extent of seabird bycatch in commercial longline fisheries alone is likely to be at least 160,000 birds per year (Anderson et al., 2011). A high proportion of this bycatch is albatrosses (family Diomedeidae) (Brothers, 1991; Anderson et al., 2011). Particularly in the southwest Atlantic, pelagic longline fisheries appear to be a major conservation problem for several species, including great albatrosses (*Diomedea* spp.) (Jiménez et al., 2009a, 2012a). Although captured in very low numbers (Bugoni et al., 2008; Jiménez et al., 2009a, 2010), the great albatrosses originate from small breeding populations and, given these are biennially breeding species, the naturally low productivity means there is limited capacity for recovery following depletion (Croxall and Gales 1998).

The great albatrosses caught incidentally by the pelagic longline fishery in the southwest Atlantic include wandering albatrosses from the South Georgia population (*Diomedea exulans*), Tristan albatrosses (*D. dabbenena*) that are endemic to Gough Island, and southern royal albatross (*D. epomophora*) and northern royal albatross (*D. sanfordi*) from New Zealand (Jiménez et al., 2012a). These are all globally threatened according to the World Conservation Union (IUCN) (http://www.birdlife.org/datazone/home). The first two populations number ca. 1500 breeding pairs each year, and are declining dramatically because of incidental capture in longline fisheries (Croxall et al., 1998; Poncet et al., 2006), exacerbated for the Tristan albatross by predation of chicks by invasive mammals (Cuthbert et al., 2004; Cuthbert and Hilton, 2004; Wanless et al., 2007, 2009). The population trend for northern royal albatross in the Chatham Islands is unknown, and southern royal albatrosses at Campbell Island appear to be stable (ACAP, 2009a;

2009b). Birds breeding at these two archipelagos account for > 99% of the respective global populations (ca. 5,800 and 7,800 annual breeding pairs, respectively; ACAP, 2009a and ACAP, 2009b). Despite the parlous conservation status of these four species and the potentially major impact of pelagic longline fishing, very little attention has been directed at understanding the factors that make the great albatrosses susceptible to fisheries interaction. Even the overall bycatch rates are uncertain because these species are caught in low numbers, only a small proportion of fishing effort is observed, bycatch rates vary a great deal by fleet, vessel, season, location, time of day etc., and very often *Diomedea* albatrosses are not identified to species level (Jiménez et al., 2009a).

Because of the patchy nature of the marine resources upon which albatrosses depend, they should disproportionally target particular habitats or suites of environmental conditions where prey are more abundant or predictable (Pinaud and Weimerskirch 2005; Wakefield et al., 2009; 2011; Louzao et al., 2011). Such areas are usually highly productive and as a result are often exploited by commercial fisheries. Seabirds are opportunistic foragers, and so are attracted to discards provided by fishing vessels (Tasker et al., 2000; Furness, 2003). An overlap between the distributions of fishing effort and seabirds is an obvious prerequisite for bycatch; however, broad-scale spatio-temporal overlap does not necessarily indicate interaction, as not all birds follow vessels (Granadeiro et al., 2002; Torres et al., 2013), and those that do will only be injured or killed if they have a close encounter with fishing gear, which in longline fisheries involves access to baited hooks (Jiménez et al., 2012a). Great albatrosses can dive to <1 m (Prince et al. 1994), and so on their own can only access baited hooks at the sea surface. However, they easily and routinely displace smaller species, and so the risk of bycatch is much greater where they co-occur with petrels and *Thalassarche* albatrosses that can reach hooks at greater depths and return them to the surface (Brothers 1991; Jiménez et al., 2012b).

Past studies indicate that a number of aspects of fishing operations, including time of setting in relation to daylight, twilight and moon phase, and the use of mitigation measures, influence access to baited hooks and hence the bird bycatch rate (Brothers 1991; Brothers et al., 1999; Jiménez et al., 2009a; Trebilco et al., 2010). In addition, particular environmental conditions may lead to aggregation of birds around vessels, increasing the likelihood of interaction. These factors presumably explain some of the high inter-specific variation in susceptibility to bycatch.

Identifying such factors could be useful for preventing seabird bycatch, by highlighting specific areas and operations where mitigation needs to be particularly effective. Within this framework, and given the broad similarity in the behaviour of great albatross species around vessels, we hypothesized that operational variables affect their bycatch likelihoods in a similar way. On the other hand, environmental variables could lead to differences in bycatch rates because of speciesspecific preference for particular habitats, which is likely to affect the relative overlap of birds with fisheries operations and potentially increase the likelihood of bird-vessel interactions (see Table 1). These species show some degree of inter-specific niche partitioning, particularly in the relative preference for foraging over continental shelves, shelf-slope or deep waters (Nicholls et al., 2002; Xavier et al., 2004; Cuthbert et al., 2005; Reid et al., 2013). In addition, the northern and southern royal albatrosses occurring in the southwest Atlantic are migrants from New Zealand, whereas the wandering and Tristan albatrosses include both breeding and nonbreeding birds, with the relative proportions depending on the time of year. Therefore, bycatch rates are likely to be temporally and spatially heterogeneous. Here, we used the largest data set available on the incidental capture of great albatrosses in pelagic longline fisheries in the southwest Atlantic, including information on specimens collected for further examination, to determine the spatial and temporal variation in bycatch rates of each species, and the contributing environmental and operational variables. The results are discussed in the context of developing effective strategies for mitigating bycatch of these highly threatened species.

2. Methods

2.1. Fishery and study area

The analyses were of observer data from the "Programa Nacional de Observadores a bordo de la flota atunera uruguaya" (PNOFA) of the "Dirección Nacional de Recursos Acuáticos" (DINARA), collected on board Uruguayan pelagic longline vessels in 2004-2011, and on Japanese vessels operating in Uruguay under an experimental fishing license in 2009-2011 (see Appendix A for details). The Uruguayan pelagic longline fleet targets swordfish (*Xiphias gladius*), yellow-fin tuna (*Thunnus albacares*), bigeye tuna (*T. obesus*), albacore (*T. alalunga*), and pelagic sharks (mainly *Prionace glauca*). Most of these vessels (20-37m length) employed an American-style longline (monofilament mainline), and the remainder (two freezer vessels) used a Spanish-style longline (multifilament mainline). Both types of fishing gear are described in Jiménez et al. (2009a) and

Domingo et al. (2012). The hook depth during soak time rarely exceeds 80 m for the Uruguayan vessels (DINARA unpublished data). During the study period the fishing area encompassed between 19-47°S and 20-60°W (Fig. 1). Vessels using American-style longlines operated mainly in Uruguayan waters (92% of sets), and those using Spanish-style longlines mostly (91% of sets) in deeper, international waters (Appendix A). The Japanese vessels (48-52 m length) targeted bigeye tuna and albacore with a Japanese-style longline (see Domingo et al. 201a). The fishing area was between 34-37°S and 49-54°W, and vessels concentrated their effort in Uruguayan waters (99.1% of the sets) near the shelf break (Fig. 2, Appendix A). The average hook depth for Japanese vessels was 133m (range = 75-210m; Miller et al., 2012). The main oceanographic influence on the region is the confluence of the Brazil and Malvinas currents, which includes complex frontal systems and the simultaneous presence of warm and cold eddies (Olson et al., 1988; Acha et al., 2004; Ortega and Martínez, 2007).

2.2. Fishing operations

During the study period, longline vessels operating in Uruguay were required to use a single tori (streamer or bird-scaring) line and night setting as seabird mitigation measures; however, implementation took several years (see below). There were no regulations regarding the use of weighted branch lines (a minimum weight within a specified distance from the hook).

In the Uruguayan fleet, the longline is set over the stern, usually around sunset, and setting is generally completed before midnight. A single tori line was first used as a seabird bycatch mitigation measure in 2008, and by 2010 all the trips with observers used tori lines. During the study period, the longline set effort varied between 400 and 2000 hooks (mean = 1117 hooks, SD = 299 hooks) for American longlines, and between 360 and 3740 hooks (mean = 2570 hooks, SD = 647 hooks) for Spanish longlines. The mean distance between the start and end locations of the longline set involving these gear types was 46.9 km (SD= 15.7 km, range 0-94.3 km) and 68.9 Km (SD= 21.5 km, range 8.0-135.3 km), respectively. The baits were squid (*Illex argentinus*) or mackerel (*Scomber* spp., *Trachurus* spp.) thawed a few hours before line setting, and occasionally shark belly.

On Japanese vessels the longline was set over the stern, mainly after midnight, and the set completed before sunrise. Night setting was practiced to reduce seabird bycatch, with the exception of the initial fishing period from March to late April 2009 when some sets were in daylight, and the occasional set thereafter that began during darkness and was not completed until after sunrise. Japanese vessels used tori lines on all trips; however, the original design was replaced by the Uruguayan style (see below) on 31 April 2009. In total, 1000 to 3360 hooks were set per day (mean \pm SD = 2329 \pm 275 hooks). The mean distance between the start and end of the set was 71.0 km (SD= 14.8 km, range 9.4-116.0 km). The baits were squid, mackerel and other small pelagic fishes (*Sardinops sagax, Decapterus macrosoma*), usually mixed along the same set.

2.3. Observer data

A total of 1599 sets and 3,311,113 hooks were observed during 81 commercial fishing trips by Uruguayan vessels from January 2004 to November 2011 (Appendix A). The temporal distribution of the observed fishing effort for the period 2004-2007 is detailed in Jiménez et al. (2010). Data were available from all months except November and December 2004. Additionally, observer data from two trips in 2007 were included, one in June-August and another in September-November. In the later years (2008-2011), data were available for all months except January and February in 2008, February and October in 2009, January, February and May-July in 2010, and March-April, June, August and December 2011. Over the entire study period, observed effort was 989,881 hooks, 833,925 hooks, 993,254 hooks and 494,043 hooks, in the first (January-March), second (April-June), third (July-September) and fourth (October-December) quarters, respectively. These values represent a substantial proportion of the total fishing effort by quarter (28%-55% of hooks). For Japanese vessels, a total of 1114 sets and 2,589,465 hooks were observed in 26 trips in 2009-2011, during March-September, May-September and April-August in 2009, 2010 and 2011, respectively (Appendix A).

A substantial proportion of annual fishing effort (26%-75% of hooks) by the Uruguayan fleet, and all trips and sets by the Japanese fleet during 2009-2011 were observed. The variables recorded during setting were as follows: date, position and several operational and environmental variables (time, type of gear, number of hooks, moon phase and sea surface temperature). A proportion of each haul was observed (100% coverage on Uruguayan and 60-100% on Japanese vessels). The observer identified and classified all species as catch, discard, bycatch (retained or released), or lost, and recorded biological information; they were tasked specifically to record the total number of birds caught per set, identify the species and collect samples (head and tarsus, or entire specimens) and any bird rings. If a great albatross was captured incidentally, the entire carcass was collected. All bycaught albatrosses were identified in the laboratory by analysis of the retained whole or part specimens. Some birds recorded alive were identified by combination of photos, videos and measurements taken by observers. The species of royal albatross were distinguished by their plumage according to Onley and Bartle (1999) and Onley and Scofield (2007). Wandering albatrosses were separated from Tristan albatrosses by a morphometric discriminant function (Cuthbert et al., 2003). Ringing authorities or groups confirmed species identifications for all ringed birds, including 15, 2, and 2 wandering, Tristan, and northern royal albatrosses, respectively.

2.4. Operational and habitat variables

A number of operational and habitat (static and dynamic) variables (see Table 1) were included in analyses of bycatch rates. These were selected either because they are important predictors of habitat preference of albatrosses (Louzao et al., 2009, 2011; Kappes et al., 2010; Wakefield et al., 2011; Žydelis et al., 2011) or because they influenced bycatch rates in other studies (Murray et al., 1993; Klaer and Polacheck, 1998; Brothers et al., 1999; Gandini and Frere 2006; Jiménez et al., 2009a; Trebilco et al., 2010). Variables obtained from observer data included: latitude and longitude at the start of the set, date and moon phase (i.e. new moon, first quarter, full moon and last quarter; following Jiménez et al., 2009a). Operational variables included the time of the set (day vs. night setting), presence and type of tori line, and fishing effort (numbers of hooks). Given the differences in the fishing operation between fleets (see above), all sets by Uruguayan vessels that started before sunset were considered as day sets (even though some finished in darkness) following Jiménez et al. (2009a), and for Japanese vessels, daytime sets were considered to be those that finished after sunrise; otherwise, sets were classified as night. Details of the tori lines used by the different fleets are included in Appendix A.

Satellite remote-sensed and other environmental variables were extracted automatically using custom-written scripts in R (R Development Core Team, 2012) for the start position of each set as follows: sea surface temperature (SST; MODIS sea surface temperature product, 4 km resolution, 8 day grids, <u>http://oceancolor.gsfc.nasa.gov/</u>), chlorophyll a concentration (CHLOa; MODIS Chlorophyll product, 4km resolution, 8 day grids, <u>http://oceancolor.gsfc.nasa.gov/</u>), ocean surface wind speed (wind) and eddy kinetic energy (EKE). The dataset (5 day datasets, 0.25 degree x 0.25

degree grid resolution) combines multiple instrument data (scatterometers and microwave radiometers,

http://podaac.jpl.nasa.gov/dataset/CCMP_MEASURES_ATLAS_L4_OW_L3_5A_5DAY_WIND_VE_CTORS_FLK) and cross calibration (Atlas et al., 2011) to produce a homogenous dataset for a long time series. The zonal and meridional geostrophic currents derived from satellite altimetry products were used to calculate EKE using the following formula: EKE=1/2 (U^2+V^2), where U and V are zonal and meridian geostrophic currents components, respectively (Kappes et al., 2010). Data were supplied by AVISO (http://www.aviso.oceanobs.com/) on 7 day grids at 0.33 x 0.33 degree resolution. Data on bathymetry were from GEBCO – 30 arc second grid, http://www.gebco.net/). In addition, we estimated the spatial gradients of SST (SSTG), CHLOa (CHLOaG) and BAT (BATG) by estimating their proportional change (PC) within a surrounding 3 × 3 cell grid (12km x 12km for SSTG and CHLOaG; 90x90 arc seconds [~ 3km x 3km] for BATG) using a moving window as follows: PC = [(maximum value –minimum value) × 100]/maximum value (Louzao et al., 2009). Finally, the distances between longline sets and the shelf break (200 m isobath) and the coast were calculated.

2.5. Data analysis

The seabird bycatch data in longline fisheries are characterized by a large proportion of zero catch observations (Delord et al., 2010; Jiménez et al., 2010; Trebilco et al., 2010; Winter et al., 2011). Great albatrosses have very small populations and therefore the proportion of zeros is much greater than with abundant species captured in longline fisheries (e.g. black browed albatross *Thalassarche melanophris*). In the present study, the bycatch of great albatrosses was modelled at species level and by fleet using generalized linear mixed models (GLMMs). Sets during one trip or from one particular vessel could be more similar (e.g. observer, specific gear configurations) than those on other trips or by other vessels, respectively. Therefore, for each case (see below) we alternatively fitted three GLMMs using "fishing trip", "vessel" or the fishing trip nested in vessel as a random factor to model bycatch as a function of the explanatory variables. Considering the few captures of most species, this type of analysis was restricted to bycatch of wandering albatross by the Uruguayan fleet and both species of royal albatross by Japanese vessels. Best fit (applying the Likelihood Ratio Test) included "fishing trip" as a random factor for wandering and southern royal, and "vessel" for northern royal albatross. Therefore, only these scenarios are presented.

2.5.1. Explanatory variables

Records with incomplete variable information (e.g. remotely sensed data were not available because of cloud cover) were removed. This eliminated 12.4 % and 20.6% of the Uruguayan and Japanese datasets, respectively. In order to maximise sample sizes, any explanatory variable that was unavailable for >10% of captures was excluded. This applied to CHLO and CHLOG for the Uruguayan and Japanese fleets. Additionally, the variables year and use of a tori line were dropped for both fleets either because no species was caught every year (by Uruguayan vessels) or the analyses were unbalanced. Wind data were unavailable for the last half of 2011, resulting in the removal of many longline sets from the analysis, but only one capture of a northern royal albatross. However, given the potential of wind speed to explain albatross distribution and bycatch rates (Brothers et al., 1999; Shaffer et al., 2001; Phillips et al., 2004), this variable was retained but the time factor (year) was removed.

For all the remaining explanatory variables, the effects of outliers and collinearity were investigated, the latter by examining variance inflation factors (VIF; Zuur et al., 2010, 2012). After dropping highly correlated variables, the following candidate covariates were standardized to have a mean of o and an SD of 1, and included in the model to explain the bycatch of great albatrosses in the Uruguayan pelagic longline fishery: SST, SSTG, BATG, EKE and wind. The same covariates and latitude were included in the model to explain bycatch by Japanese vessels. Models also included other potentially important categorical covariates, including season (May-November and December-April; Jiménez et al., 2009a), moon phase and time of set (day vs. night). The interaction between time of the set and moon was also considered.

2.5.2. Bycatch modelling

Because bycatch of great albatross species in the Uruguayan fishery was a very rare event and in most cases only one bird was caught per set, the bycatch of wandering albatross was modelled using a GLMM with a logit link function, assuming a binomial distribution. Longline set was the sampling unit. In contrast, several birds (particularly northern royal albatross) were often caught in the same set by Japanese vessels. Bycatch for this fleet was therefore modelled initially using a binomial GLMM as for Uruguayan vessels, and subsequently for sets in which at least one northern royal albatross was caught, by using a Poisson distribution with fishing effort (log transformed) included as an off-set variable, and using a canonical log link function. The same set of explanatory variables was used in both models. A likelihood Ratio Test was used to test the significance of each covariate. Sequential deletions of non-significant terms were conducted until only significant covariates remained in the model. All the analyses were carried out in R using lme4 (Bates et al., 2011) for the GLMMs and AED (http://www.highstat.com/Book2/AED_1.o.zip) to calculate the VIF values based on the *corvif* function (Zuur et al., 2009).

2.5.3. Independent comparisons

The effect of including or excluding certain variables on bycatch rates (i.e. bird capture per unit of effort, BCPUE; birds/1000 hooks) of royal albatrosses was explored independently for the Japanese fleet because: 1) night setting was implemented as a mitigation measure and the Uruguayan toriline replaced the Japanese style after mid-2009 (see above), and; 2) some variables had a potential influence (year, type of tori line, time of the set and moon phase; Jiménez et al., 2009a) on the BCPUE, but not necessarily on bycatch occurrence as explored in the logistic models. The effect of tori line (considering three categories: without tori line and each of the two tori line types; see Appendix A) on the BCPUE of wandering albatross was also tested using Kruskal-Wallis (with post hoc Mann-Whitney test comparisons, Bonferroni corrected) and Mann-Whitney U tests in R (R Development Core Team, 2012).

3. Results

3.1. Bycatch of great albatrosses

A total of 193 great albatrosses (0.033 albatrosses/1000 hooks) were recorded as bycatch during the study period, 71 of which (0.0214 albatrosses/1000 hooks) were caught by Uruguayan vessels in 2004-2011, and 122 (0.0471 albatrosses/1000 hooks) by Japanese vessels in 2009-2011. Because only a proportion of each haul was observed on Japanese vessels (see Methods), overall bycatch values for this fleet should be interpreted as minimum numbers. Additionally, an unknown proportion of great albatrosses could have been detached from fishing gear and not hauled on board vessels (see Brothers et al. 2010; Jiménez et al. 2012b) in both fleets. Of the great albatrosses recorded as bycatch, just 4 and 13 birds were recorded alive for the respective fleets, all of which were entangled in the branch lines by their wings or hooked at the bill, probably during hauling. The

condition at release for most of these birds was unknown and some may die subsequently from their injuries.

In the Uruguayan fishery, the most common great albatross recorded as bycatch was the wandering albatross (38.0%; n=27 birds; 0.0082 albatrosses/1000 hooks), followed by southern royal albatross (21.1%; n=15 birds; 0.0045 albatrosses/1000 hooks), Tristan albatross (16.9%; n=12 birds; 0.0036 albatrosses/1000 hooks) and northern royal albatross (5.6%; n=4 birds; 0.0012 albatrosses/1000 hooks). However, 13 great albatrosses could not be identified to species, at least eight of which were either northern or southern royal albatrosses. Thus, the relative BCPUE of the two royal albatrosses is slightly greater than indicated by the breakdown at species level. Results for Japanese vessels contrasted both in terms of numbers and proportions of each species, with bycatch of great albatrosses dominated by royal albatrosses, more than half of which were northern royal (52.5%, n=64 birds; 0.0247 albatrosses/1000 hooks), followed by southern royal (25.4%; n=31 birds; 0.0120 albatrosses/1000 hooks), with very few captures of wandering and Tristan albatrosses (4.9%, n=6, 0.0023 albatrosses/1000 hooks and 0.8%, n=1, 0.0004 albatrosses/1000 hooks, respectively). Of the 20 great albatrosses not identified to species level for the Japanese fleet, at least 15 were royal albatrosses, which is very similar to the overall proportion among those identified.

3.2. Spatial and temporal variation

Wandering albatrosses were caught by Uruguayan vessels in both Uruguayan and international waters between 28° and 46° S (Fig. 1A). With one exception, all captures of Tristan albatross occurred in international waters between 28° and 37° S. This was the most frequent species caught in the eastern portion of the fishing range; indeed, it was the only species caught east of 42° W (Fig. 1B), and on average was captured further from the shore that any of the other great albatrosses (Appendix A). Tristan albatrosses were also caught further from the shelf break than wandering albatrosses (Appendix A). Southern royal albatrosses were caught over the shelf slope off Uruguay and in international waters (34°-41° S; Fig. 1C). Finally, all captures of northern royal albatrosses were over the shelf-break (Fig. 1D). Moreover, there was a significant effect of bathymetry and distance to the shelf break on the incidence of bycatch of this albatross compared with that of the other three species (Appendix A).

All captures of great albatrosses by Japanese longliners were west of 51° W, over the shelf break and slope of Uruguay, where fishing effort by this fleet was concentrated (Fig. 2). Only a few wandering albatrosses (n=6; Fig. 2A) and one Tristan albatross (Fig. 2B) were caught over the slope. However, captures of both royal albatross species were common and widely distributed in this area (Fig. 2C and 2D). The single capture of a Tristan albatross was over waters that were relatively deep and far from the shelf break and shore, again underlining the more pelagic range of this species (Appendix A).

For the Uruguayan fleet, bycatch rates varied between years for all species (Fig. 3). No species was captured in every year, highlighting the extreme rarity of bycatch events. The highest BCPUE of wandering albatross was observed in 2009. The BCPUE of southern royal albatross was low in most years except 2008 and 2010. In the three years (2009-2011) where there are comparable data, catch rates of wandering and Tristan albatrosses were lower on Japanese than Uruguayan vessels. In contrast, royal albatrosses (particularly northern) were caught much more frequently by Japanese vessels in 2009 (Fig. 3). The BCPUE of both royal albatrosses decreased dramatically from 2009 to 2011 (Fig. 3). Result of independent comparisons showed that catch rate varied significantly between years for southern (Kruskal-Wallis = 15.5, d.f. = 2, p < 0.01, n=1108) and northern royal albatrosses (Kruskal-Wallis = 12.7, d.f. = 2, p < 0.01, n=1108).

Great albatrosses were caught during all months from April to November by Uruguayan pelagic longliners (Fig. 4). Additionally, a few captures of wandering and Tristan albatrosses were recorded in January, towards the south and east, respectively, of the fishing area, which included some of the closest sets to the breeding sites at South Georgia or Gough islands (Figs. 1A and 1B). During April-November, wandering albatross was the most frequently captured species, with records in all months and a peak in BCPUE in November (Fig. 4). Tristan albatrosses were caught mainly in July-November, particularly in September-November (Fig. 4). The highest BCPUE of southern royal albatross was observed in July, whereas no monthly pattern was obvious for northern royal albatrosses given the low number observed. On Japanese vessels, great albatrosses were captured in all fishing months with the exception of March. During April-August, the incidental catch of great albatrosses was dominated by royal albatrosses, peaking in June (Fig. 4). The only capture of a Tristan albatross occurred in April, whereas wandering albatrosses were caught from June to September (Fig. 4). It is important to note that in September, Japanese vessels set only 8 longlines yet caught two wandering and two northern royal albatrosses, resulting in a BCPUE per species for that month of 0.1036 albatrosses/1000 hooks (Fig. 4). This value is an order of magnitude higher than the catch rates observed in other months by either fleet, but should not be considered representative of the general pattern because of the small sample.

3.3. Factors affecting bycatch

The bycatch of a great albatross was an extremely rare event, occurring during only 3.33% and 5.30% of the sets observed on Uruguayan and Japanese vessels, respectively. The average percentage of positive sets among species on Uruguayan vessels was 0.73%, the highest proportion of which involved wandering albatross (1.38%) and the lowest involved northern royal albatross (0.25%). For Japanese vessels, this average was 1.39%, with the highest incidence for northern royal albatross (i.e. 2.96%) and the lowest for Tristan albatross (i.e. 0.09%).

Results of the modeling are summarized in Table 2 (for details on model selection see Appendix A). For wandering albatross in the Uruguayan fishery, the final model (binomial GLMM) included time of the set, wind speed and SST. Most of the captures of wandering albatross (25 from 27 birds) occurred in sets during daylight (Fig. 5). The rate of change in odds showed that the chance of a wandering albatross being caught during night setting was much lower (7%, 95% confidence limit=1-48%) than during sets in daylight. Coefficient estimates indicated that bycatch occurrence increased significantly with wind speed, and decreased (although marginally significant) with increasing SST (Table 2). For captures of southern royal albatross by Japanese vessels, the final model (binomial GLMM) included moon phase, latitude, SST and EKE. The estimated coefficients indicated that bycatch occurrence increased with latitude and showed a declining trend, albeit non-significant, with SST and EKE (Table 2). For northern royal albatross, the final model (binomial GLMM) included moon phase, SST and time of the set. The rate of change in odds showed that the chance of a northern albatrosses being caught during night setting is 30% (95% confidence limit=3 - 77%) of that during daylight sets. Bycatch occurrence also decreased with increasing SST (Table 2). Considering only sets with captures (Poisson GLMM), the only significant covariate was SST, which was negatively associated with the number of birds caught (coefficient = -0.42, SE=0.14, p<0.01).

Independent comparisons showed that bycatch rate varied significantly with the time of the set for both southern (Mann-Whitney, p=0.036, n=1108) and northern royal albatrosses (Mann-Whitney, p=0.031, n=1108), and was higher in daylight (Fig. 5). However, several individuals were caught during night setting (Fig. 5). For those sets, the BCPUE varied strongly with the moon phase in southern (Kruskal-Wallis, df=3, p<0.001, n=926) and northern royal albatrosses (Kruskal-Wallis, df=3, p<0.001, n=926). For both species, the BCPUE was higher during the full moon (Fig. 6). There was no significant effect on BCPUE of the type of tori line for both royal albatrosses species (Kruskal-Wallis, df=2, p > 0.05, n=1108) caught by Japanese vessels. Nor was there a significant differences in the BCPUE of wandering albatrosses between sets with (including both types, see Methods) and without a tori line by the Uruguayan fleet (Kruskal-Wallis, df=2, p > 0.05, n=1491).

4. Discussion

This is the first detailed study of variation in bycatch rates of great albatrosses by pelagic longline fisheries in the southwest Atlantic. It also identifies the main contributing operational and environmental factors, and provides the first bycatch assessment for Japanese vessels operating under license in Uruguayan waters. High bycatch levels of northern and southern royal albatrosses were recorded for the first time in this region, particularly over the shelf break. Previously, very few captures of royal albatrosses had been reported over the Patagonian shelf in demersal longline (Favero et al., 2003) or trawl fisheries (Favero et al., 2011), or in Brazilian waters in the pelagic longline fishery (Bugoni et al., 2008 and references therein). This result is therefore both a major conservation concern and a demonstration of the importance of this habitat for nonbreeding birds of both species. Similarly, the consistently high bycatch of wandering and Tristan albatrosses in pelagic waters is a major issue, particularly because many other fleets also operate in this region. These include vessels flagged to Belize, Brazil, Chinese Taipei, Spain, Portugal, Japan, Philippines, St. Vincent and Grenadines, and Uruguay, which reported to the International Commission for the Conservation of Atlantic Tunas (ICCAT) a total of 15.5.-21 million hooks annually in 2004-2009 from 20°-45°S and 20°-55°W (Jiménez et al. 2012a; http://iccat.int/Data/t2ce.rar). Vanuatu also reported fishing effort within this region in 2010-2011.

4.1. Spatial and temporal patterns in bycatch

Despite the differences in fishing effort distribution between fleets, there was clear temporal and spatial heterogeneity in bycatch rates of the four great albatross species. Much of this seems to reflect differences in at-sea distribution of each species, providing new evidence to support the reported niche segregation among these species (Nicholls et al., 2002; Cuthbert et al., 2005; Reid et al., 2013). Bycatch was influenced by bathymetry, distance to the shelf break and distance to the shore (Appendix A). Tristan albatross was the most pelagic species, followed by wandering albatross, reflected in the spatial pattern in bycatch by both fleets. These species were captured in very low numbers by Japanese vessels, which concentrated their fishing effort near the shelf break. However, these vessels captured a high number of northern royal albatrosses, suggesting that this species is widely distributed over the shelf break. This is supported by the data from Uruguayan vessels, which only captured northern royal albatrosses in this area even though this fleet operated over a much wider region of the southwest Atlantic. Finally, although bycatch rates of southern royal albatross were highest for both fleets over the shelf break and slope, suggesting those are the habitats in which this species is most abundant, some birds were caught in deeper Uruguayan and international waters indicating that they also exploit oceanic waters. This is supported by a few ring recoveries reported from vessels in international waters (Moore and Bettany, 2005).

Analysis of the observer data showed that the bycatch of great albatrosses was highest from April to November. Together the data from both longline fleets indicate a peak in bycatch of northern and southern royal albatrosses in June or July, and of wandering and Tristan albatrosses from September to November. The latter was clearest for the Uruguayan fleet, as this has the greatest overlap between the fishing area and the pelagic waters used by wandering and Tristan albatrosses. Clearly, the peaks in bycatch rates are likely to be explained largely by the time of greatest spatial overlap between the species and fishery in question. Northern royal albatross prebreeders and failed breeders migrate from New Zealand to the southwest Atlantic in February and have departed by September (Nicholls et al., 2002). Analysis of ring recoveries of southern royal albatross, visit the southwest Atlantic over a broadly similar period, February to October (Moore and Bettany, 2005). However, at-sea observations of both species in December indicate that some birds remain for

longer in the region (Jiménez et al., 2011). Over the Uruguayan shelf break and slope, where northern and southern royal albatrosses were mainly captured by both fleets, they are more abundant from May/June to August (Jiménez et al., 2011), perhaps because prior to this time, the bulk of the birds are concentrated in colder, more southerly latitudes (Nicholls et al., 2005) and so do not overlap with this fleet.

Wandering and Tristan albatrosses are more difficult to differentiate at sea and thus are usually pooled in counts from vessels (Bugoni et al. 2008, Jiménez et al., 2009b, 2011). This would suggest that abundance of both species attending vessels is highest over the Uruguayan shelf slope from August to November (Jiménez et al., 2011). However, bycatch specimens (this study) and ring recoveries (Croxall and Prince, 1990; and see Jiménez et al., 2012a), indicate that the majority of birds in these waters during this particular period are wandering albatrosses. This species is highly migratory, and most birds from South Georgia spend much of the nonbreeding period in the Indian or Pacific oceans (Mackley et al., 2010). The last visit to the colony by successful breeders is in November - December when the chick fledges, and by immatures and breeders that fail in incubation is in April - May (Tickell, 2000). As this is a biennial breeder that lays in December, the number of birds in the southwest Atlantic will peak in November, to include both breeders from the current year still provisioning well-grown chicks, and birds about to breed in the coming season. Tristan albatross appears to remain for much of the year in warmer deeper waters, and towards the east and north of Uruguay. The number of breeding and nonbreeding adults should peak in the southwest in late winter to spring (Cuthbert et al., 2005; Dénes et al., 2007; Reid et al., 2013; this study). Therefore the period of highest bycatch for both wandering and Tristan albatrosses coincides with the highest abundances expected for both species in the southwest Atlantic.

The dramatic decrease in the bycatch of both royal albatross species by Japanese vessels from 2009 to 2011 is more difficult to explain. However, it probably relates partly to the introduction of night setting as a mitigation measure in 2009, which led to a significant decline in BCPUE. In addition, the replacement of the Japanese by the Uruguayan design of tori line in 2009 standardised the use of this mitigation measure thereafter. Several captures occurred during winter after the implementation of these measures. However, the only factor that had a significant effect on the bycatch of northern royal albatross in the Japanese fishery was SST, which
suggests that the reduction in the number of birds captured from 2009 to 2010-11 may largely reflect a shift in bird distribution in response to water temperature rather than a change in operational practices on board vessels. An alternative explanation would be local population depletion following the high bycatch levels experienced in 2009; however, this is less probable since these are highly mobile species and this area is part of the main winter range (Robertson et al., 2003; Nicholls et al., 2002; Moore and Bettany, 2005).

4.2. Effect of habitat and operational variables

Results of the modeling indicated that operational variables (time of the set) affected the bycatch likelihood of the great albatross species in a similar way. The evidence for an influence of variables related to habitat use was weaker; however, each species might nevertheless show strong habitat preferences that affect their overall at-sea range, even if distributions overlap.

The time of the set was an important determinant of bycatch occurrence (as observed for wandering and northern royal albatrosses on Uruguayan and Japanese vessels, respectively; see Table 2) as well as the BCPUE (see Fig. 5). Both bycatch occurrence and rates were higher in daylight than night-time sets, probably because albatrosses detect prey largely by sight, although they might also use olfactory cues at this small scale (Nevitt, 2008). They fly less and have lower foraging success at night because prey are more difficult to locate, and so active searching on the wing is less effective (Phalan et al., 2007). However, wandering albatrosses during the night significantly increase their activity (e.g. time in flight) with a brighter moon (Phalan et al., 2007). This explains the bycatch of great albatrosses during the night, particularly during the full moon, followed by the first quarter (and none during the new moon phase), for both royal albatross species (Fig. 6, Table 2). Of the eight captures of wandering albatross recorded at night by the two fleets, seven were during the first quarter. Higher seabird bycatch rates during the brightest moon phases are consistent with the patterns observed in previous studies (Vaske, 1991; Gandini and Frere, 2006; Jiménez et al., 2003).

Sea surface temperature and wind also influenced the bycatch likelihood and could be associated mainly with habitat use by the great albatrosses. It is important to note that the preference of each species for particular habitat characteristics could be masked by the much stronger effect of operational practices (e.g. time of the set) on bycatch rates. Typically, seabird bycatch data are zero-inflated because birds do not overlap with vessels (i.e. they are not present in that type of habitat at that time of year), or they overlap but are not caught. The latter is often the case; on 13-41% of seabird counts conducted during setting and hauling in 2005-2008, one or more of the four species of great albatross were associated with a Uruguayan vessel (Jiménez et al. 2012a), yet on only a small minority of sets was a bird caught in this fishery (this study). Similar results were obtained in previous studies (Weimerskirch et al., 2000; Bugoni et al., 2008). This is because hooks can only be accessed for a limited time, largely determined by the activity of other birds (including small species that are more proficient divers) and by the type of fishing gear, use of tori lines, available light levels etc. (Brothers, 1991; Robertson et al., 2010; Jiménez et al., 2012b).

Sea surface temperature is indicative of water mass. For the three species with sufficient captures for analysis, bycatch occurrence decreased with increasing SST (although marginally significant in two cases). Uruguayan vessels fished over a wide area, as far as 19°S. A relationship between bycatch rate and SST is expected for the wandering albatross, since this species in the southwest Atlantic prefers oceanic waters from the sub-Antarctic to the subtropics and is rare in tropical waters north of 30° S (Prince et al., 1998; Xavier et al., 2004; Phillips et al., 2009). Both royal albatrosses occur in the area where bycatch is highest (the Uruguayan slope; Jiménez et al., 2011) and the oceanography of this region is dominated by an influx of sub-Antarctic waters (Ortega and Martínez, 2007). Bycatch of these species by Japanese vessels occurred mainly over the southern Uruguayan slope (Fig. 2), where colder waters ingress during winter (Ortega and Martínez, 2007). Over the Uruguayan slope, increased bycatch occurrence towards the south was also evident for the southern royal albatross (Table 2). This species is common during winter in the colder shelf waters of Argentina and southern Uruguay around trawlers (Favero et al., 2011; Jiménez pers. obs.). The only significant factor explaining the bycatch (Poisson GLMM) of northern royal albatross by Japanese vessels was SST, increasing with colder temperatures, denoting again a preference for sub-Antarctic waters.

Wind may affect bycatch at different scales (Table 1). Firstly, it may reflect favourable habitat; flight speed is determined mainly by wing loading, and thus windier regions are more optimal for large albatrosses (Shaffer et al., 2001; Phillips et al., 2004) where they may overlap more with the fishery. Indeed, this seems a plausible explanation for the pattern observed in our study.

Secondly, wind speed (and also direction) could influence access to baited hooks by changing the effectiveness of tori lines, affecting flight maneuverability, or the energetic cost of take-offs and landings by birds. Unfortunately, the resolution of the remote sensed data used here is too low for an analysis at a sufficiently fine scale to test the latter.

The edges of mesoscale meanders and eddies (where EKE values are highest) exhibit increased levels of marine productivity and zooplankton biomass, and lead to prey aggregation (see Bost et al., 2009). Several studies have found evidence supporting the association of albatrosses with these features (Nel et al., 2001; Petersen et al., 2008; Wakefield et al., 2011; but see Kappes et al., 2010), including in the oceanic waters of the Brazil–Malvinas Confluence (Wakefield et al., 2011). We found only limited evidence of such relationships from the bycatch analysis; although there was a weak negative relationship between EKE and bycatch of southern royal albatross, this was of marginal statistical significance and would need to be confirmed by further studies.

4.3. Implications for management

Great albatrosses are among the species most affected by pelagic longline fishing in the southwest Atlantic (Bugoni et al., 2008; Jiménez et al., 2012a). Therefore, any measure that could reduce or eliminate negative interactions between birds and vessels in this region should be considered a high priority for fisheries management organizations. This paper identified key factors affecting their bycatch, which are extremely useful for developing or improving conservation measures of these highly threatened species. Firstly, we determined the areas and seasons where the interaction between great albatrosses and pelagic longliners is most intense. Considering the time of year in which recorded bycatch rates are highest (with conservative temporal bounds of ± 1 month), bycatch of both royal albatross species could be reduced by the strict use of mitigation measures (see below) in May-August in the region of the Uruguayan shelf break. Bycatch of wandering and Tristan albatrosses was less restricted spatially, but highest in pelagic areas from the shelf break to international waters, mainly around the Brazil-Malvinas confluence. Efforts to implement and ensure compliance with mitigation measures for these species should occur throughout this region, and be focused during August to December.

Secondly, restriction on longline setting only to the hours of darkness is unambiguously a key mitigation measure for reducing the bycatch of great albatrosses in the Uruguayan, Japanese and

indeed all other pelagic longline fisheries in this region. The effectiveness of this approach to mitigation has strong scientific support (see reviews in Bull, 2007 and Løkkeborg, 2011), and reflects the lower seabird bycatch rates reported for night than daylight sets in a wide range of pelagic and demersal longline fisheries (Murray et al., 1993; Brothers et al., 1999; Gómez-Laich et al., 2006; Jiménez et al., 2009a). However, our results also indicate that BCPUE increases during bright moon phases, in line with previous studies (Vaske, 1991; Brothers et al., 1999; Gandini and Frere, 2006; Jiménez et al., 2009a). Indeed, bycatch by Japanese vessels in sets during full moon was higher than those in daylight for both royal albatross species (Fig. 5 and 6). However, these daytime sets were conducted mostly in April 2009 before many migrant royal albatrosses had returned to the study area, and the implementation of night setting by Japanese vessel in May-July coincided with the peak in arrival, which probably explains the higher BCPUE during the full moon.

We found no evidence that the use of a tori line by Uruguayan vessels reduced bycatch of wandering albatross. However, comparisons were made between lines set in different years, which may make the effect difficult to detect if bycatch varies for other reasons. A controlled study on Uruguayan vessels showed a significant reduction in bycatch of all seabirds associated with tori line usage (Domingo et al., 2011b), but these data are not sufficient to draw conclusions for individual species. Nor did we detect an effect of tori line use or type on bycatch of either royal albatross species by Japanese vessels, but again the comparisons of the two designs involved data from different periods. In addition, the Uruguayan design of tori line was not adopted until late May 2009 after which the abundance of great albatrosses in the area increases.

Current mitigation measures recommended for pelagic longline fisheries include the combined use of night setting, tori line and appropriate weighting in the branch-lines (Løkkeborg, 2011). The ICCAT recommendation 11-09 (http://www.iccat.int/en/RecsRegs.asp) stipulates that in the area south of 25° S, ICCAT members shall ensure that all longline vessels use at least two of these mitigation measures, including minimum technical standards and specifications. Strict night setting is useful to reduce bycatch of great albatrosses (this study) and tori lines demonstrably reduce bycatch of seabirds in pelagic longline fisheries (Brother, 1991; Murray et al., 1993; Domingo et al., 2010; Melvin et al., 2013). Despite this, our results (Fig. 6) suggest that the combined use of night setting and tori line are not sufficient to reduce the bycatch of great albatrosses during the full moon. At least during this period of the lunar cycle, a precautionary approach for these highly threatened species would be the combined used of all three mitigation measures (ACAP, 2013; Melvin et al., 2014). Current mitigation research and advice on branch-line weighting are focused on determining the effects of different weights and distances of the point of attachment from the hook (see Robertson et al., 2010; ACAP, 2013). By incorporating this information into the development and updating of best practice guidelines, international initiatives such as those of the Agreement on the Conservation of Albatrosses and Petrels (ACAP) can promote the implementation of effective branch-line weighting regimes that, along with tori lines and night setting, would greatly reduce bycatch rates in ICCAT and other fisheries. Because great albatrosses obtain pelagic longline baits mainly through secondary interaction, an effective mitigation regime must also reduce access to baited hooks by medium sized petrels (*Procellaria* and *Puffinus* spp.) and, to a lesser extent, *Thalassarche* albatrosses (Jiménez et al. 2012b).

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Table 1. Explanatory variables used in models to characterise the bycatch of great albatrosses (*Diomedea* spp.) in the southwest Atlantic. Variables dropped prior to analyses are indicated with an asterisk (see text section 2.5.1.).

Variables (Unit or categories)	Process and hypothesized link with habitat preference or bycatch likelihood
Habitat covariates	Dynamic variables
Sea surface temperature, SST (º C)	Indicative of water mass distribution, affects the distribution of albatrosses.
SST gradient, SSTG	Indicative of frontal systems, potential prey aggregation and increased seabird density.
Chlorophyll a *, CHL, (mg m ⁻³)	Indicative of ocean productivity domains, may affect the distribution of albatrosses.
CHL gradient *, CHLG	Indicative of frontal systems, potential prey aggregation and increased seabird density.
Wind Speed (m s ⁻¹)	Effect on albatross flight, and therefore on their abundance in the area. Potential effect on tori line performance or access to baits, affecting great albatrosses (mostly as secondary species).
Eddy kinetic energy, EKE (cm ² s ⁻²)	Increased local enhancement of productivity or prey aggregation, and therefore potential increase in seabird density.
Moon phase (New, First quarter, Full, Last quarter)	Moon light facilitates the access to bait for seabirds, affecting great albatrosses (mostly as secondary species).
	Static variables
Latitude (degree and minutes in decimal scale)	May affect the distribution of albatrosses.
Longitude (degree and minutes in decimal scale)	May affect the distribution of albatrosses.
Bathymetry (m)	Spatial usage of albatrosses may vary because bathymetric regimes are characterized by different levels of productivity (e.g. neritic mesotrophic vs. oceanic oligotrophic domains).
Bathymetry gradient	Usage of albatrosses may vary because the presence of topographic features (shelf break, seamounts).
Distance from the shelf break, i.e. 200m isobath (km)	Proximity with shelf break, slope currents, vertical mixing and prey concentration, potential increase in seabird density.
Distance from the shore (km)	Spatial usage of albatrosses may vary according onshore-offshore distribution patterns.
Operational covariates	
Tori line * (see main text for categories)	The presence of this mitigation measure could reduce access to bait for seabirds, affecting great albatrosses (mostly as secondary species).
Time of the set (Day, Night)	Daylight facilitates the access to bait for seabirds, affecting great albatrosses (mostly as secondary species).
Vessel/Fishing trip	Some factors are intrinsically linked to vessels throughout the entire trip (e.g. observer, specific gear configurations), therefore, either "vessel" or "fishing trip" were considered as a random factor in GLMMs.
Fishing effort (Hooks)	Including as part of the response variable, as off set in the models formulation, when Poisson model was fitted.
Temporal covariates	
Year * (from 2004 to 2011 and from 2009 to 2011 for Uruguayan and Japanese vessels, respectively)	Annual variation in either distribution of albatrosses or vessels may affect their overlap.
Season (May-November and December-April)	Seabird bycatch seasons reported for longliners in the study region. Variation in distribution and abundance of albatrosses due to breeding phenology and migration patterns may affects bycatch rates.

Table 2. Estimated coefficients and standard errors (SE) of the GLMM (Binomial) for wandering albatross captured by Uruguayan vessels, and southern and northern royal albatrosses captured by Japanese vessels. The rate of change in the odds is presented for categorical variables. EKE= eddy kinetic energy; SST= sea surface temperature.

Species	Fixed Effects	Coefficient	SE	Z	р	Rate of	95%
						change in	confidence
						odds (%) ¹	limits (%)
Wandering albatross	(Intercept)	-5.32	0.58	-9.115	0.0000	-	-
	SST	-0.94	0.49	-1.912	0.0559	-	-
	wind	0.85	0.30	2.824	0.0048	-	-
	Time Set Night	-2.68	0.98	-2.716	0.0066	7	1 - 48
Southern Royal Albatross	(Intercept)	-4.17	0.61	-6.886	0.0000	-	-
	Latitude	0.64	0.29	2.217	0.0267	-	-
	SST	-0.39	0.25	-1.596	0.1105	-	-
	EKE	-0.91	0.65	-1.396	0.1626	-	-
	Moon Full	1.00	0.61	1.650	0.0989	272	82 - 901
	Moon Last Quarter	-2.07	1.19	-1.737	0.0824	13	1 - 134
	Moon New	-16.81	2097.25	-0.008	0.9936	0	-
Northern Royal Albatross	(Intercept)	-2.05	0.51	-3.990	0.0001	-	-
	SST	-0.68	0.21	-3.190	0.0014	-	-
	Moon Full	0.48	0.41	1.172	0.2414	161	72 - 363
	Moon Last Quarter	-2.95	1.08	-2.742	0.0061	5	1 - 44
	Moon New	-16.71	1261.33	-0.013	0.9894	0	-
	Time Set Night	-1.21	0.48	-2.537	0.0112	30	3 - 77

Variance and standard deviation values of the random variable "Trip" were 3.48 and 1.87 for wandering, 0.39 and 0.62 for southern royal. These values for the random variable "Vessel" was 0.26 and 0.51 for northern royal albatross. ¹The rate of change in the odds is calculated as the exponent of the parameter estimate, and is a measure of the change of catching an albatross under one condition compared with the change of catching an albatross under another condition. The 95% confidence limits are calculated using the exponent of the parameter plus or minus 1.96 times the standard error and presented as a percentage.



Figure 1. Spatial distribution of the observed fishing sets and incidental captures of great albatrosses (circles) observed in the Uruguayan pelagic longline fishery (2004-2011). A = wandering albatross; B = Tristan albatross; C = southern royal albatross; D = northern royal albatross. The 200m isobath is represented by a black line.



Figure 2. Spatial distribution of the observed fishing sets and incidental captures of great albatrosses (circles) observed on board Japanese longline vessels operating in Uruguay (2009-2011). A = wandering albatross; B = Tristan albatross; C = southern royal albatross; D = northern royal albatross. The 200 m isobath is represented by a black line.



Figure 3. Annual variation in the observed bird capture per unit of effort (BCPUE, birds/1000 hooks) for great albatross species incidentally captured and for the observed fishing effort. Left column: Uruguayan pelagic longline fleet in 2004-2011; Right Column: Japanese pelagic longline vessels operating in Uruguay and adjacent waters under an experimental fishing license in 2009-2011. WA = wandering albatross, TA= Tristan albatross, SRA=southern royal albatross and NRA= northern royal albatross.



Figure 4. Monthly variation in the observed bird capture per unit of effort (BCPUE, birds/1000 hooks) for great albatross species incidentally captured and for the observed fishing effort. Left column: Uruguayan pelagic longline fleet in 2004-2011; Right Column: Japanese pelagic longline vessels operating in Uruguay and adjacent waters under an experimental fishing license in 2009-2011. These vessels operated from March to September. Species codes as in Fig. 3.



Figure 5. Bird capture per unit of effort (birds/1000 hooks) of great albatross species incidentally captured during day and night sets. The number above the bar indicates the number of birds captured. Wandering albatross (WA) captured in the Uruguayan pelagic longline fleet during 2004-2009. Southern (SRA) and northern royal (NRA) albatrosses captured in Japanese pelagic longline vessels (2009-2011) operating in Uruguay and adjacent waters under an experimental fishing license.



Figure 6. Bird capture per unit of effort (birds/1000 hooks) of southern (SRA) and northern (NRA) albatrosses according to the moon phase for night sets conducted in Japanese pelagic longline vessels (2009-2011) operating in Uruguay and adjacent waters under an experimental fishing license. The number above the bar indicates the number of birds incidentally captured.

Appendix A. Supplementary material

Observed fishing effort

The changes over time for the active fishing vessels operating in Uruguayan and adjacent waters are presented in Figure A1. Number of Uruguayan pelagic longline vessels decreased from 13 in 2004 to 2 in 2011. Between 2 and 5 Japanese vessels operated in Uruguay under an experimental fishing licence in 2009-2011. Details on observed fishing effort per fleet are presented in Table A1.



Figure A1. Number of pelagic longline vessels operating in Uruguayan and adjacent waters of the Southwest Atlantic during 2004-2011. Vessels are differentiated by flag: Uruguayan vessels and Japanese vessels. The latter comprise those that operated in Uruguay under an experimental fishing licence.

Table A1. Details of the observed fishing effort on board Uruguayan and Japanese pelagic longline vessels, the latter operating in Uruguayan waters under an experimental fishing licence.

Year	Uruguayan vessels				Jaj	panese ve	ssels		Totals		
	# Trips	# Sets	# Hooks	_	# Trips	# Sets	# Hooks	# Trips	# Sets	# Hooks	
2004	9	312	764 918					9	312	764 918	
2005	15	244	511 954					15	244	511 954	
2006	9	196	473 232					9	196	473 232	
2007	16	313	573 894					16	313	573 894	
2008	9	158	250 376					9	158	250 376	
2009	9	184	368 011		13	514	1 221 025	22	698	1 589 036	
2010	9	102	177 132		5	189	432 327	14	291	609 459	
2011	6	90	191 586		8	411	936 113	14	501	1 127 699	
	0.2.*	4 500	2 244 402	•	26		2 500 465	100	2740	E 000 E 00	
Total	82*	1 599	3 311 103	0	26	1 1 1 4	2 589 465	108	2713	5 900 568	

* One trip started in 2008 and finished in 2009 but the purposes of analysis was considered as two trips.

Distribution of the fishing effort and bycatch of great albatrosses related to bathymetry and distance to the shelf break and shore

The fishing effort of the Uruguayan vessels was widely distributed in the southwest Atlantic (see main text). Considering the start position of the sets, Uruguayan vessels operated on a median distance of 454 km (range 127-2051km) and 302 km (range 0-1847km) from the shore and the shelf-break (i.e. 200m isobath), respectively (Fig. A2). The median depth was 3679 m (range = 31-6195 m; Fig. A2). Vessel operating with American-style longline operated closer to the shore (i.e. median =207km; range = 127-501 km) and shelf break (i.e. median =40 km; range = 0-375 km) than those using Spanish-style longline. For the later vessels, the median for the respective distances was 564 km (range = 180-2051 km) and 404 km (range = 3-1847km). The median operation depth was 1673 m (range = 31-4404m) and 4294 m (range = 362-6195m, - m), for vessels using Americanstyle and Spanish-style longline, respectively. Only 8.22% of the sets conducted by vessels using American-style longline were in international waters (i.e. outside of the 200nm), while an opposite trend was observed for vessels using Spanish-style longline with 90.56% of the sets deployed in international water. Japanese vessels concentrated their fishing effort within Uruguayan waters (see main text). Most of the effort was over the shelf break and slope. The median operation depth was 1257 m (range=53-4713m; Fig.A2). These vessels operated on a median distance of 204 km (range 104-469km) and 25 Km (range 0-312km) from the shore and the shelf-break, respectively (Fig. A2).

Comparisons between sets with presence of albatross bycatch for the four species according to bathymetry, distance from the shelf-break and distance from the shore are presented in Figure A2. ANOVA (and Tukey HSD pairwise comparison) or Kruskal-Wallis (Mann-Whitney Test, Bonferroni corrected) were conducted after normality and homogeneity assumptions been tested. For those sets, variation between species was recorded for all these variables (Bathymetry: ANOVA F = 8.77, P < 0.05; Shelf-break: Kruskal-Wallis H=16.41, p < 0.05; Shore: ANOVA H=5.60, p < 0.05) in the Uruguayan fleet. Pairwise comparisons (Tukey HSD) indicated a significant difference (p< 0.05) in the bathymetry between set with captures of northern royal albatross and those with the other three species. When the distance to the shelf-break was considered, pairwise comparisons (Mann-Whitney Test, Bonferroni corrected) indicated a significant difference (p< 0.05) between set with captures of northern royal albatross and those with the other three species. The difference between wandering and Tristan albatross was also significant (p< 0.05). Finally,

pairwise comparisons (Tukey HSD) indicated a significant difference (p< 0.05) in the distance to the shore between set with captures of Tristan albatross and those with the other three species. Considering the longline sets with captures of great albatrosses for the Japanese vessels, no differences were observed in the catch distribution between species (excluding Tristan albatross) according bathymetry, distance to the shelf-break and distance to the shore (Kruskal-Wallis >> 0.5 in all cases). For the single capture of Tristan albatross, the values for these spatial variables were close to the upper range of the other species (Fig. A2).



Figure A.2. Boxplots of 3 spatial explanatory variables (bathymetry, distance from the shelf-break and distance from the shore) for the sets with bycatch occurrence of great albatrosses (numbers represent *n* of sets) and for the total (T) sets observed in the Uruguayan pelagic longline fleet (above) during 2004-2011 and Japanese longline vessels (below) during 2009-2011. WA=wandering albatross, TA=Tristan albatross, SRA=southern royal albatross, NRA=northern royal albatross. The hinges represent the 25% (Q_{25}) and 75% (Q_{75}) quartiles and the black band the median. Whiskers represent 1.5 times the spread or difference between hinges (i.e. Q_{75} - Q_{25}) and the dots are values out these intervals.

Tori line description

Details on the design of the "Uruguayan toriline" are presented in Domingo et al. (2011b). Briefly, this toriline, from its start to the end, consisted of a backbone of 100m polyamide monofilament line with long and short streamers (i.e. aerial section), a 20m polyamide monofilament line (connection section) and a 30m polyethylene multifilament line (towing object) with 0.80m polypropylene strapping bands placed every 0.20m (approx.) by a central knot. The aerial section contains nine doubled long streamers (red plastic tubes or strips) whose length are reduced from the first one of 5.80m (placed at 10m from the start of the line) to ninth long streamer of 1,70m. Long streamers are spaced at intervals of 5m, with the exception of those placed in position 1 and 2, which are spaced at 10m. Short streamers consist of three 1m nylon/plastic ribbons of different colours (red, blue, yellow, green) placed double in the tori line. Between the first 15m and the 55m of the aerial section, the short streamers were placed every meter and interlaced with the long streamers, four short per one long. After 55m only short streamers were used up to 75m and thereafter only spaced every 2m.

Other types of toriline were used by the vessels, which varied in length, material, types and number of used streamers and in the presence/absence of the connection section and/or towing object. No specific details were recorded for these toriline, and therefore, all of them were grouped and named for the analysis purpose as "Uruguayan toriline B".

Two groups of Japanese toriline were recorded; the first one and the most used, was a group of toriline with a polyester backbone and doubled long streamers (red rubber tubes) with a small lead weight attached at their free end. The total length of the toriline, the number of paired streamer and their length, and the spacing between them was highly variable, and not always recorded by observers. No towed devices were recorded. This group of toriline was named "Japanese toriline". The second group, named "Japanese toriline B", consisted of a line (70-200m long) with doubled streamers made of polypropylene strapping bands (white or yellow). This group of toriline have short steamers of equal length (lees than 1m) or long streamers whose length decrease from the first one (7m length) towards the end. From May 31th of 2009, all Japanese vessels changed the toriline type and used the Uruguayan toriline. The use of a polyester multifilament instead of a polyamide monofilament as the backbone was noted.

Model selection (GLMM)

Considering only the longline sets with a complete suite of independent variables, after applying single term deletions from the full models and the Likelihood Ratio Test (LRT), several covariates were significant predictors of bycatch probability. For wandering albatross in the Uruguayan fishery, the full model (binomial GLMM) was significantly better than models without time of the set (LRT, $\chi_2 = 15.41$, degrees of freedom (df)= 1, p<0.001), wind speed (LRT, $\chi_2 = 9.41$, df= 1, p=0.002) and SST (LRT, $\chi_2 = 4.80$, df= 1, p=0.028), respectively. After removing the remaining covariates, the model including time of the set, wind speed and SST was significantly better than the three models constructed by single term deletions (LRT, p<0.05 in all cases). For captures of southern royal albatross by Japanese vessels, the full model (binomial GLMM) was significantly better than the models without moon phase ($\chi_2 = 26.29$, df=3, p<0.001), latitude ($\chi_2 = 5.49$, df=1, p=0.019), SST (χ_2 =4.15, df=1, p=0.042) and EKE (χ_2 =3.90, df=1, p=0.048). The model including these four variables was significantly better than the models without moon phase ($\chi_2 = 29.18$, df=3, p<0.001) and latitude (χ_2 =5.86, df=1, p=0.016). Non-significant differences were found between this model and the models without SST and EKE (LRT, p>0.05 in both cases). However, a slight increase in the AIC (Akaike's Information Criterion) value was observed between these two models; therefore, both variables were retained in the final model. For northern royal albatross, the full model (binomial GLMM) was significantly better than the models without moon phase (LRT, $\chi_2 = 41.14$, df=3, p<0.001) and SST (LRT, $\chi_2 = 4.60$, df=1, p=0.032). Although the LRT did not indicate any statistical differences between the full model and the model without the time of setting, the latter had a slightly greater AIC value. With serial deletion of single terms, including moon phase, SST and time of the set, this model was significantly better (LRT, p<0.05 in both cases) than the three possible sub models; therefore, no further term was removed. Considering only sets with captures (Poisson GLMM), the only significant covariate was SST (full model better than sub model without SST; $\chi_2 = 8.74$, df=1, p=0.003).

Capítulo 4 | Chapter 4

Variación relacionada al sexo en la vulnerabilidad de los albatros errantes a las flotas de palangre pelágico

Sex-related variation in the vulnerability of wandering albatrosses to pelagic longline fleets

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Abstract

The population of wandering albatrosses (*Diomedea exulans*) at South Georgia is decreasing because of bycatch in longline fisheries. Until at least the early 1990s, the survival rate of females was lower than males, consistent with the adult female-biased bycatch reported for fisheries operating around the Brazil-Falklands Confluence (BFC). Here we use extensive tracking data (1990-2012) from breeding birds at South Georgia to investigate overlap with longline fishing effort reported to the International Commission for the Conservation of Atlantic Tunas (ICCAT). Using data from multiple years, we conclude that breeding females are at higher risk than males from all the main pelagic longline fleets in the southwest Atlantic. Our overlap index (based on fishing effort and bird distributions) correlated positively with numbers of ringed birds reported dead on longliners, indicating that the metric was a good proxy of bycatch risk. The consistent sex-bias in overlap across years, and the likely resulting sex-biased mortality, could account for lower adult female survival rate at the colony. The risk from fisheries changed seasonally; both sexes overlapped with pelagic longline effort during incubation (January-March), and particularly during post-brood chick-rearing (May-December), whereas overlap was negligible during

brooding (April). The highest percentage of overlap was with the Taiwanese fleet, then vessels flagged to Brazil, Uruguay, Spain, Japan and Portugal. Females were consistently at greatest risk in the BFC region, whereas males showed lower and more variable levels of overlap with fisheries from 35° to 45°S. Our results have important implications for management of ICCAT longline fisheries and conservation of this highly threatened albatross population.

Keywords: Fisheries impacts; Ecological risk assessment; seabirds; satellite-transmitters; GPS loggers; Southwest Atlantic; Regional Fisheries Management Organisation

Introduction

Fisheries bycatch represents a major concern in the conservation of marine biodiversity, given the risk posed to large marine predators (Hall *et al.*, 2000; Lewison *et al.*, 2004). Pelagic seabirds are wide-ranging, interact with many fisheries and are captured incidentally in a wide range of fishing gears (Anderson *et al.*, 2011; Favero *et al.*, 2011; Žydelis *et al.*, 2013). Albatrosses are the seabird family most affected by bycatch (Croxall *et al.*, 2012), with the greatest impact in the southern hemisphere, where most species are exposed to numerous longline and trawl fisheries (Baker *et al.*, 2007; Jiménez *et al.*, 2010; Favero *et al.*, 2011). The situation appears to be particularly serious in the South Atlantic, with very high bycatch reported for pelagic longline (Jiménez *et al.*, 2009; Petersen *et al.*, 2009), demersal longline (Barnes *et al.*, 1997; Favero *et al.*, 2003) and trawl fisheries (Sullivan *et al.*, 2006; Watkins *et al.*, 2008), and long-term monitoring indicates severe declines in several globally-important albatross populations (Poncet *et al.*, 2006; Cuthbert *et al.*, 2014).

The wandering albatross (*Diomedea exulans*) provides a clear example of regional variation in the effect of fisheries. In total, an estimated ca 8,000 pairs breed each year at four main island groups (ACAP, 2009). Populations in the Indian Ocean are recovering after rapid decreases in the 1970s to 1980s linked to longline bycatch (Weimerskirch *et al.*, 1997; Nel *et al.*, 2002a; ACAP, 2009). In contrast, at South Georgia (South Atlantic), a long-term decline from the early 1960s accelerated to >4% per year from the mid 1990s to mid 2000s (Poncet *et al.*, 2006), and although numbers stabilized subsequently, as yet there is no sign of a recovery (British Antarctic Survey, unpublished data). Formerly the second, and now the third largest breeding population, the South Georgia population represents ca 19% of the global total (ACAP, 2009). This is also considered to be the seabird species most affected by pelagic longline fishing in the southwest

Atlantic (Jiménez *et al.*, 2012, 2014). The small population size and very low fecundity (adults may not recruit until aged \geq 10 years, and at most fledge one chick every two years; Croxall *et al.*, 1998), make this species highly vulnerable even to the low recorded bycatch rates (Bugoni *et al.* 2008; Jiménez *et al.*, 2009, 2014).

An increase in the use of satellite and archival tracking devices in recent decades has greatly improved our understanding of the exposure of seabirds to anthropogenic threats, including overlaps in distribution with fisheries and hence potential bycatch risk (Phillips *et al.*, 2006, 2007). As central-place foragers during breeding, seabird foraging strategies can change substantially depending on constraints associated with each breeding stage (Weimerskirch *et al.*, 1993; Phillips *et al.*, 2004; Phalan *et al.*, 2007). The fasting capability of adults is high, and trips during incubation can last several weeks. After hatching, both adults alternate brooding with feeding at sea, and potential trip duration is much reduced. Then, once the chick is thermally independent and better able to defend itself from predation, both parents forage simultaneously; not only does potential feeding range increase, but twice the number of breeding adults are at sea. Sex-related variation in distribution is also apparent; females often travel farther north than males, which makes them more vulnerable to fisheries operating in subtropical regions (Prince *et al.*, 1992; Nel *et al.*, 2004).

An early study of ring recoveries of wandering albatrosses from South Georgia indicated that adult females in particular interacted with pelagic longline fisheries around the Brazil-Falklands Confluence (BFC) (Croxall & Prince, 1990). This matched with subsequent tracking data which revealed sex differences in foraging range (Prince *et al.*, 1992; 1998), and lower survival of adult females than males in the 1980s and early 1990s (Croxall *et al.*, 1990, 1998). This sex difference in mortality is still evident (British Antarctic Survey, unpublished data), consistent with female-biased bycatch of adult wandering albatrosses reported for the Uruguayan pelagic longline fishery (Jiménez *et al.*, 2008). Although previous assessments suggested that sex-biased bycatch rates in seabirds reflect behavioral factors (e.g. dominance hierarchy behind vessels; Ryan & Boix-Hinzen, 1999), a recent review considered that the underlying cause was probably sex differences in distribution rather than susceptibility *per se* (Bugoni *et al.*, 2011). On this basis, relative overlap with fishing effort should provide an effective proxy for bycatch risk.

For seabirds in general, the risk posed by particular fisheries varies depending on movements between water masses (reflecting fluctuations in natural food availability, seasonal reproductive constraints, weather conditions etc.), and shifts in fishing effort. In addition, as different fleets (vessels from a particular flag state) differ in operational practises which affect bycatch rates (e.g. recommended mitigation measures and degree of compliance), overall bycatch risk reflects the contribution of each fleet to the total fishing effort that overlaps with bird distributions. Hence, coastal countries or leased fleets using Economic Exclusive Zones and adjacent waters (Bugoni et al., 2008; Jiménez et al., 2014), and high-seas fleets fishing over vast regions (Huang, 2011), may have quite distinct impacts. Given the severity of the population decline for wandering albatrosses, better information on seasonal and annual changes in relative risk may provide valuable details for targeting of conservation efforts. In this study, we use extensive tracking data from breeding birds at South Georgia to quantify overlap with pelagic longline fisheries in the southwest Atlantic. Our aims were: (1) to examine seasonal, annual and sex-related variation in fisheries overlap; (2) to determine whether breeding females are consistently at greater overall risk than males, and; (3) to partition the bycatch risk posed by each fleet to each sex. Because the overlap of bird distributions and fishing effort does not necessarily indicate interaction, and a direct correlation with bycatch rate cannot be assumed (nor easily tested, given the limitations of current vessel-based bycatch estimation; Phillips, 2013), we also (4) test whether albatrossfisheries overlap metrics reflect bycatch risk using ring recoveries as a proxy. The results are discussed in the context of mitigating the risk that fisheries pose to this highly threatened population.

Materials and Methods

Tracking data

An extensive tracking program on wandering albatrosses has been carried out at Bird Island (54°00'S, 38°03'W), South Georgia, since the early 1990s. Analyses were of data from 263 breeding albatrosses of known age and sex (142 males and 121 females) tracked during 399 complete foraging trips (205 by males and 194 by females) either with Argos satellite-transmitters (Platform Terminal Transmitters or PTTs) from 1990 to 2004 (Prince *et al.*, 1992, 1998; Xavier *et al.*, 2003, 2004; Phillips *et al.*, 2009) or global positioning system (GPS) loggers from 2003 to 2012 (Phalan *et*

al., 2007; Phillips *et al.*, 2009; Ceia *et al.*, 2012; Froy *et al.*, 2015) (for more details see Appendix S1, Table S1).

Overlap with longline fishing effort

Overlap of breeding males and females with longline fishing effort was determined separately for each breeding stage: incubation, brood and chick-rearing (see Appendix Sı). Overlap analyses were restricted to years where ≥8 foraging trips per sex were tracked (mean: females=13 trips, males=14 trips). Although a small proportion of birds were tracked for more than one trip, these were rarely to the same area and so multiple tracks from the same individual were included in our analyses to increase sample size and explore overlap in different years. Data for incubation were available in 2004 and 2012, for brood in 1998, 2003 and 2004, and for chick-rearing in 1999, 2000, 2002, 2004, 2006 and 2009 (see Appendix S1, TableS1, for sample sizes). In order to match with fishing effort, breeding stages were considered to approximate to the following months: incubation = January-March, brood = April and chick-rearing = May-December.

We used the proportion of time spent per unit area (days per each 5x5° cell) for each breeding stage as the albatross density metric. To quantify bird-fisheries overlap, this was multiplied by the number of hooks (Tuck *et al.*, 2011) obtained from the International Commission for the Conservation of Atlantic Tunas (ICCAT) to produce an overlap index which accounts for the proportion of time spent by the females / males in a given breeding stage and the potential number of hooks which may be encountered in a given cell (for more details see Appendix S1).

Factors affecting overlap and contribution by the main fleets during chick-rearing

For each year, we estimated the total fishing effort (number of hooks) deployed in those 5x5° cells used by each sex during chick-rearing, which was multiplied by the sum of the albatross density metric (see above) to produce an overall index of overlap with the ICCAT pelagic longline fishery (hereafter termed "ICCAT overlap index"). This analysis was then repeated for each longline fleet of the main ICCAT flag states (hereafter termed "fleet overlap index") to estimate their percentage contribution to the overlap with males and females in chick-rearing. The ICCAT and fleet overlap indices are for the Atlantic sector used by birds, but do not account for spatial variation. Therefore, another dataset was constructed with all the possible overlap index values for the principal fleets in the 5x5° cells, by sex and year (for more details see Appendix S1).

The effect of the sex on the ICCAT overlap index was analyzed using a Linear Model (LM). Additionally, the effects of sex, year and fleet on the fleet overlap indices and the overlap at 5x5° cell level during chick-rearing were analyzed using Generalized Linear Models (GLM) for the. Best fit in both cases included a two-step analysis: 1) the occurrence of overlap was modeled using a binomial distribution; then 2) overlap index values different from zero were modeled assuming a Gaussian distribution (for more details see Appendix S1). All statistical analyses were conducted in R (http://www.r-project.org/).

Correlation between overlap and bycatch risk

Ring recoveries of wandering albatrosses from Bird Island, South Georgia, reported to the British Trust for Ornithology or directly to the British Antarctic Survey, were used to test whether the bird-fisheries overlap metric was a useful proxy of bycatch risk. Adults and chicks have been ringed intermittently at Bird Island since the late 1950s, and annually since the mid 1970s (Croxall *et al.*, 1990; Croxall & Prince, 1990). We examined all reported recoveries of dead birds in fisheries (longline, trawl or unknown gear) between 1999 and 2012 from the southwest Atlantic. Birds were classified as breeders or non-breeders, based on the last sighting as a breeder at the colony. For each sex, we determined the number of rings recovered from birds killed incidentally in each 5x5° cell during the chick-rearing months for all albatrosses (breeding and non-breeding), and separately just for breeding albatrosses. The correlation between average overlap index for chick-rearing birds (1999-2009) and the number of recoveries (1999-2012; note the slightly larger year range to increase sample sizes) was tested using the Spearman correlation coefficient (r), including values for all 5x5° cells with fishing effort.

Results

During breeding, wandering albatrosses from South Georgia were distributed widely in the southwest Atlantic as far north as 28°S and east to 15°W (Fig. 1). A few birds travelled through the Drake Passage to the southeast Pacific, and some as far south as the Antarctic Peninsula during incubation (both sexes) and chick-rearing (only males). Constraints imposed by breeding were evident in distributions, with a very restricted range apparent during brooding compared with the other two stages (Fig. 1).

Overlap with pelagic longline fisheries in terms of effort

Vessels from Taiwan accounted for a higher proportion of reported pelagic longline fishing effort than any other fleet in the area used by the tracked albatrosses during 1990-2012 (Fig. 2). Other important fleets, ordered by decreasing number of hooks reported, were Spain, Brazil, Uruguay, Japan and Portugal. The distribution of the ICCAT fishing effort during the incubation, brood and chick-rearing periods in the years with ≥ 8 trips tracked per sex is shown in Figures 3, 4 and 5, respectively.

There was no overlap with pelagic longline fisheries during brood in 1998, 2003 and 2004. If the analysis is expanded to include all complete trips during brood (see Appendix S1, Table S1), i.e., from every year in which data are available, only two tracked males overlapped with fishing effort in one of the southernmost 5 x 5 °cells, in 1992, where < 10,000 hooks were reported (Fig. 4). Brooding females were tracked to two cells in which fishing has occurred, but in years without reported effort. In contrast, both males and females overlapped with pelagic longline effort during incubation (Fig. 3) and, particularly, during chick-rearing (Fig. 5). During incubation in 2004 and 2012, females showed greater overlap with ICCAT longline effort than males; indeed, the overlap with reported effort was nil for males in 2004 (Fig. 3).

There were sufficient tracking data from males and females for a more detailed analysis of annual variation in fisheries overlap during chick-rearing. Overall, the overlap of chick-rearing females with ICCAT fishing effort was considerably higher than that of males (LM, R² = 0.46, F= 8.65, d.f=1, p= 0.015, n=12, Table 1). The fleet overlap index (binomial GLM) also varied significantly with sex, and was lower for males (Table 2). Considering only cells in which tracked birds overlapped with vessels, the overlap index (ln transformed) varied significantly (Gaussian GLM) with fleet (% of explained deviance =56.0, χ^2 test <0.01, n=44), and sex (% of explained deviance =44.0, χ^2 test <0.01, n=44). Coefficient estimates indicated significantly greater overlap with the Taiwanese than any other fleet, and lower fisheries overlap overall for males than females (Table 2). There were no significant differences among years in the overlap index.

Across all pelagic longline fleets, the overlap index was always higher for females (Fig. 6A). On average, by far the greatest overlap for both sexes was with the Taiwanese fleet, then, in descending order, Brazil (again for both sexes), followed by Uruguay, Spain, Japan and Portugal

for females, and Spain, Japan, Uruguay and Portugal for males (Fig. 6A). The highest percentage contribution was by the Taiwanese fleet in every year for females (mean = 70.4%, range = 54.1 – 90.5%) and in most years for males except 2009 (68.0%, o - 94.1%; Fig. 6B, see Appendix S2, Fig. S2). The other fleets in terms of decreasing contribution to the overlap index for females were Brazil (13.2%, o.4 - 32.4%), Uruguay (7.0%, o.2 - 19.8%), Spain (5.0%, o - 13.9%), Japan (4.0%, o.1 - 21.8%) and Portugal (2.6%, only data for 2009), and for males (excluding 2009), were Spain (14.4%, o - 59.0%), Japan (2.0%, o - 9.7%), Brazil (1.7%, o - 4.8%) and Uruguay (0.3%, o - 1.2%). In 2009, only two fleets overlapped with the distribution of males, vessels from Portugal accounted for 78.2% of the index, and from Uruguay for the remainder (Fig. 6B).

Spatial differences in overlap during chick-rearing

On average, the greatest overlap index was for females in the region of the BFC ($_{30}$ – $_{40}$ °S, and up to 40°W; Fig. 5). Overlap index values were also the most consistent across years for females in this area, according to the coefficients of variation (Fig. 5). During chick-rearing, males showed less spatial overlap with fisheries than females both in terms of total number of cells (Table 1) and overlap index values (Fig. 5). Males mainly overlapped with longline fishing effort from 35-45°S, and off southern Brazil (30-35°S). The overlap index for each 5x5° cell was highly variable (Fig. 5); fleet, sex and year explained the most deviance in occurrence in the binomial GLM, followed by the sex-by-year interaction, and latitude was least important (Table 3). Based on the coefficient, the greatest contribution to overlap was by the fleet of Taiwan, followed by Brazil, Uruguay, Spain and Japan (Table 4). The occurrence of overlap varied between years (coefficient only significant for 2009), and the sex-by-year interaction indicated that males had a significantly lower overlap than females, decreasing over time from 2004 (marginally non-significant) to 2009. Finally, the occurrence of overlap increased toward the north, as expected given the high concentration of pelagic longline effort around the BFC (see above). For cells in which overlap occurred, there were significant effects (Gaussian GLM) of, in order of importance, fleet, the sex-by-year interaction, and year (Table 3). The only fleet with a significant coefficient was Taiwan, which showed a strong positive relationship with the overlap index (Table 4). Similar to the binomial model, the interaction between sex and year indicated negative relationships with the overlap index in the Gaussian model for some of the regression parameters (Table 4).

Relationship between overlap and ring recoveries

A total of 167 ringed wandering albatrosses were recovered at sea during 1999-2012, with 134 reported killed on longliners. Remaining records included birds captured on vessels, mostly in trawl or unknown fishing gear (n=24), or in unknown circumstances (n=9). Of the 134 birds killed by longliners, 89 (66.4%), 36 (26.9%) and 7 (5.2%) were reported from fisheries in the Atlantic, Indian and Pacific oceans, respectively. Overall, 85.4% (n=76 birds) of the captures in the Atlantic were in the southwest, i.e., the area in which we focus the overlap analyses (see Appendix S₃, Fig. S8). A total of 116 albatrosses (86.6% of those caught by longliners) were killed during the months of chick-rearing (May-December), 54 of which were unknown sex (birds that fledged from Bird Island but had yet to return). Amongst the remaining 62 birds, the sex ratio was strongly biased to females (females=46, males=16; χ^2_{Yates} = 13.56, d.f. = 1, p<0.01). Fifty of these birds were captured by longliners in the region where breeding wandering albatrosses overlap with ICCAT fishing effort, of which two were excluded from further analysis as the recovery location was unavailable. Within this region, these reports of ringed birds as bycatch were strongly female-biased (females=37, males=11; χ^2_{Yates} = 13.02, d.f. = 1, p<0.01), including if the sample is split into birds killed while breeding (females=21, males=9; χ^2_{Yates} = 4.03, df = 1, p<0.05), or as non-breeders (females=16, males=2; χ^2_{Yates} = 9.39, d.f. = 1, p<0.01). Restricting the analyses to females (because there are so few data for males), the correlation between the average overlap index and the number of ringed adults reported killed on longliners in each cell in May-December was marginally non-significant for all females (breeding and non-breeding) (r = 0.34; p = 0.058; n =32), and significant just for breeding females (r = 0.46; p < 0.01; n = 32) (Appendix S₃, Fig. S₉).

Discussion

This is the first detailed quantitative assessment of overlap between pelagic longline fisheries and wandering albatrosses that examines both sex-related variation across breeding stages, and the contribution of individual longline fleets to the bycatch risk. Based on extensive tracking and fisheries data, breeding females showed consistently higher overlap than males with pelagic longline fisheries in the southwest Atlantic, including all the main fleets. The correlations between the overlap index and number of ringed females reported killed by longliners in each 5x5° square provided strong evidence that the degree of overlap is reflected in the bycatch rate. Hence, the consistently high overlap of females with these longline fisheries, and the resulting

sex-biased mortality, would account for the lower adult female survival rate observed at South Georgia since the 1970s (Croxall *et al.*, 1990, 1998; BAS unpublished, data).

Sex-related differences in overlap with pelagic longline fishing

Breeding female wandering albatrosses were at greater risk of bycatch in pelagic longline fisheries than males, except during brooding when both sexes feed closer to South Georgia (see Fig. 4). Around South Georgia, of the order of 10s of wandering albatrosses were killed each year during the mid to late 1990s in demersal longline fisheries for Patagonian toothfish (Dissostichus eleginoides) (Moreno et al., 1996); however, bycatch has been far lower in this fishery since the early 2000s (Waugh et al., 2008). Only when reproductive constraints are reduced, i.e., during incubation and post-brood chick-rearing, can seabirds routinely reach more distant waters where fleets from a range of flag states target tunas, swordfish and sharks. However, during incubation, wandering albatrosses still remain mostly in southern areas (Fig. 1), and birds of both sexes are commonly sighted from demersal longliners at the southern Patagonian shelf (Croxall et al., 1999; Otley et al., 2007). Hence in terms of the number of 5x5° cells occupied, and the overlap index, overlap with pelagic longliners is considerably higher during chick-rearing when not only are breeding adults spending most of their time at sea, increasing densities in each cell, but females in particular visit northern areas (Figs. 1, 3 and 5). Our fine-scale spatial analysis confirmed that females were consistently at greatest risk around the BFC, whereas males showed a lower and more variable level of overlap with fisheries in the area from 35°-45°S. Moreover, fishing effort is consistently highest in the north (Fossette et al., 2014) (see Fig. 5). These results are supported further by the distribution of ring recoveries (this study) and previous bycatch assessments (Jiménez et al., 2014); most incidental captures of wandering albatrosses by the Uruguayan fleet, and a Japanese fleet operating under license in the Uruguayan EEZ, occurred between May and November.

The female-biased mortality in the north is unlikely to be counterbalanced by bycatch of males in southern areas, given the general reduction in bycatch rates in demersal longline fisheries reported since the early 2000s (see above) and the low incidence of ring recoveries in trawl fisheries (see Results). Females might be expected to recruit at younger ages to buffer the expected skew in the sex ratio. Indeed, in the early 1990s there was a significant trend towards a lower mean age at first breeding in females in particular; however, the small reduction (by <1

year) in age at recruitment had a minimal effect on the overall population trend, and did not compensate for the increase in mortality of adult females (Croxall *et al.*, 1998).

Overlap with individual longline fleets

We found that for all longline fleets, the highest overlap with breeding female wandering albatrosses was during chick-rearing, underlining that they were at greatest risk. Based on the contribution of each longline fleet to the overlap indices, the highest overlap with females and males was with the Taiwanese fleet, which deploys by far the most hooks (Fig. 2), followed to a lesser extent by a few other fleets (Brazil, Uruguay, Spain, Japan and Portugal). The importance of the Taiwanese fleet was evident both at large (the southwest Atlantic) and fine (5x5° cells) scales (see Table 2 and 4). The variation in overlap related to sex (see above) and fleet was also apparent at the 5° scale, reflecting annual variation both in the proportion of time spent by albatrosses, and in the number of hooks deployed by each fleet in each cell (Fig. 5, and see Appendix S2, Figs. S2-S7). Changes in order of importance of fleets by year were slight. Perhaps the most noteworthy was the greater overlap of Brazilian and Uruguayan fleets with females than males, presumably reflecting the preference of females for shelf-slope waters in the region of the BFC (Prince *et al.*, 1998).

Relationship between overlap and bycatch risk

Ecological risk assessments of the effects of fishing on seabirds often make the assumption that the overlap between fishing effort and distribution of a given population provides a reasonable proxy of vulnerability to bycatch (Tuck *et al.*, 2011; Small *et al.*, 2013). Ideally, this would be validated by comparing estimated overlap with bycatch data collected on board fishing vessels (Croxall *et al.*, 2013). However, few wandering albatrosses are recorded in observer programs (Bugoni *et al.*, 2008; Jiménez *et al.*, 2014), largely because the population is so much smaller than that of other species. Moreover, bird bycatch data for most fleets is unavailable, poorly representative both spatially and temporally, or of dubious reliability (Phillips, 2013). However, we were able to analyse the recoveries of ringed birds from South Georgia that were killed in fisheries to assess the relationship between overlap calculated from the distribution of fishing effort and of males and females of known breeding status, and likely bycatch risk.

There are caveats associated with the interpretation of ring recovery data, which reflect biases arising from differences in reporting effort and practices (Croxall & Prince, 1990). Vessel-based studies of seabird bycatch in the southwest Atlantic started in the late 1980s (Vaske, 1991), but fisheries observer programs were not established until the late 1990s and early 2000s (Jiménez et al., 2009; Pons et al., 2010; Yeh et al., 2013). In addition, the variability in observer coverage influences recovery rates, and in particular, ringed birds are much less likely to be reported from vessels without observers. Some national fishery bodies and NGOs actively encourage fishermen to collect and report bird rings, for example on vessels from Uruguay (Jiménez et al., 2008, 2012) and other states that use the port of Montevideo. In addition, recoveries have been reported from the late 1980s onwards by fishermen on Brazilian vessels (Olmos, 2002). While acknowledging that there may be inequalities in reporting rates, these should tend towards Type 2 rather than Type 1 errors in terms of our analyses. We therefore interpret the positive correlations (one significant, one marginally non-significant) between the overlap index and number of ringed adult female wandering albatrosses reported killed on longliners as evidence that our overlap metric was a good proxy of the bycatch risk. Although overlap analyses are often used to estimate bycatch risk for seabirds (Tuck et al., 2011; Croxall et al., 2013; Small et al., 2013), our study is a rare example where the assumption of a direct relationship with capture rates has been corroborated by independent evidence.

Implications for conservation

The six species of great albatrosses (*Diomedea* spp.) are all listed as globally threatened by the International Union for Conservation of Nature and Natural Resources (IUCN; http://www.birdlife.org/datazone/home); Tristan (*D. dabbenena*) and Amsterdam (*D. amsterdamensis*) albatrosses are Critical, northern royal albatross (*D. sanfordi*) is Endangered, and wandering, southern royal (*Diomedea epomophora*) and Antipodean (*D. antipodensis*) albatrosses are Vulnerable. However, the substantial wandering albatross population from South Georgia is at particularly high risk from pelagic longline fisheries (Jiménez *et al.*, 2012, 2014; Tuck *et al.*, 2011). Between 1984 and 2004, numbers dropped from 2,230 to only 1,553 breeding pairs, and at a particularly high rate (4% per year) since 1997 (Poncet *et al.*, 2006). The longer time-series of counts at Bird Island, which holds 60% of the South Georgia population, indicate a drop from 1,922 pairs in 1962 to 948 pairs in 2004 (Croxall *et al.*, 1990; Poncet *et al.*, 2006). At a regional and

biogeographic level, this sustained decline meets IUCN criterion A₂ for Endangered (an estimated population size reduction of \geq 50% over three generations, where the reduction or its causes may not have ceased), based on sub criteria b (an appropriate index of abundance, i.e. breeding pairs) and d (actual or potential levels of exploitation, i.e. bycatch) (for full definitions see http://www.iucnredlist.org/static/categories_criteria_3_1). For the *Diomedea* species that occur in the southwest Atlantic (see Table 5), this decline for wandering albatross is comparable with the annual decrease of 3% estimated for Tristan albatross, which is considered to be Critical because of the negative impact of longline fishing exacerbated by predation of chicks by invasive rodents (Cuthbert *et al.*, 2014).

Although our study provides further evidence of the risk from ICCAT-registered pelagic longline fleets in the southwest Atlantic, we were unable to account for potential Illegal, Unreported and Unregulated (IUU) fishing, the extent of which is entirely unknown. Nevertheless, this study provides a breakdown of the contribution of fleets from each flag state to the overall bycatch risk, which is extremely useful for focusing efforts within the framework of existing international conservation initiatives (including the Agreement on the Conservation of Albatrosses and Petrels; ACAP), and in sub-groups of fisheries management organizations which have delegated responsibility for providing advice to minimise bycatch or wider ecosystem-level impacts. So far, monitoring of bycatch of wandering albatrosses and other seabirds on pelagic longline vessels operating in the southwest Atlantic has been largely limited to observer programmes for the Brazilian and Uruguayan fleets (Bugoni et al., 2008; Jiménez et al. 2009, 2014), and recently for Japanese vessels operating in Uruguay under an experimental fishing licence (Jiménez et al., 2014). No bycatch data with sufficient information on species composition are available to properly assess bycatch at the species level for the other 11 fleets that reported fishing effort to ICCAT in the southwest Atlantic in the last two decades. This includes the fleets of Taiwan, which showed the greatest overlap with wandering albatrosses, and of Spain and Portugal, which also operate on the high seas. The Taiwanese longline fleet is the largest in the Atlantic; an observer program was established in the 2000s, data from which were recently included in the first assessment for this fleet of seabird bycatch for the entire Atlantic Ocean (Yeh et al., 2013). No wandering albatrosses were reported as bycatch for the southwest sector; however, this was presumed to reflect the very small percentage (1.3%) of fishing effort that was observed (Phillips, 2013).
It is imperative for this population that effective mitigation measures be enforced on all ICCATregistered longline vessels in the southwest Atlantic, with appropriate monitoring of compliance. Based on the overlap index, mitigation actions are required most urgently during the chickrearing period (May-December) in waters from 25° to 45° S, and particularly, because of the risk to adult females, around the BFC (30°- 40°S and east to 35°W). The implementation of measures to reduce the mortality of this highly threatened population would directly benefit all species of albatrosses and petrels at risk from longline fishing in the southwest Atlantic, which are caught in many of the same areas and seasons (Table 5).

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Table 1. Metrics of overlap between breeding female and male wandering albatrosses tracked from South Georgia, and pelagic longline fishing effort in the southwest Atlantic during the post-brood chickrearing period in different years. N of cells = number of $5x5^{\circ}$ cells with overlap; Proportion of time spent = overall proportion of time spent by each sex in the $5x5^{\circ}$ cells with fishing effort; Millions of hook = total reported for the $5x5^{\circ}$ cells within the albatross distributions; Overlap index = proportion of time spent x no. of hooks.

		Fem	ales		Males						
Year	N of cells	Proportion of time spent	Millions of hooks	Overlap index	N of cells	Proportion of time spent	Millions of hooks	Overlap index			
1999	13	0.16	6.40	1,000,061	11	0.18	8.52	1,569,505			
2000	10	0.22	6.01	1,345,617	8	0.22	0.36	77,355			
2002	11	0.20	10.47	2,053,823	8	0.09	8.43	757,956			
2004	10	0.34	6.46	2,182,667	4	0.03	0.68	19,122			
2006	13	0.21	7.83	1,608,181	2	0.00	0.30	907			
2009	6	0.20	3.11	607,860	1	0.01	0.12	1,248			
Average	10.50	0.22	6.71	1,466,368	5.67	0.09	3.07	404,349			

Table 2. Estimated coefficients and standard errors (SE) for the factors affecting the overall overlap between tracked wandering albatrosses and pelagic longline fleets in the southwest Atlantic. Results for the Binomial and Gaussian (In transformed response) GLM are presented. Note that for every factor, one category is fixed (intercept), which serves as the standard for comparisons with other levels. Significant coefficients are highlighted in bold. JAP=Japan, SPA=Spain, TAI=Taiwan, URU=Uruguay.

Model		Coefficients	SE	Z	р
Binomial	(Intercept)	3.258	1.019	3.197	0.001
	Sex Males	-2.565	1.098	-2.336	0.019
Gaussian (ln)					
	(Intercept)	10.992	0.751	14.638	< 0.001
	Sex Males	-2.745	0.663	-4.141	<0.001
	Fleet JAP	-0.982	1.202	-0.817	0.419
	Fleet SPA	-0.239	1.018	-0.235	0.816
	Fleet TAI	2.458	0.971	2.531	0.016
	Fleet URU	-1.478	0.990	-1.492	0.144

Table 3. Percentage of the deviance explained by each factor affecting the overlap between tracked wandering albatrosses and pelagic longline fleets in each 5x5° cell in the southwest Atlantic. Results for the Binomial and Gaussian (In transformed response) GLM are presented. Significant factors are highlighted in bold.

Model		Df	Deviance	Residual Df	Residual deviance	р	% Deviance explained
Binomial	NULL			1735	1280.6		
	Sex	1	43.117	1734	1237.5	<0.001	28.5
	Fleet	5	52.114	1729	1185.4	<0.001	34.5
	Year	5	33.639	1724	1151.8	<0.001	22.2
	Latitude	1	5.084	1723	1146.7	0.024	3.4
	Sex:Year	5	17.266	1718	1129.4	0.004	11.4
Gaussian (ln)	NULL			209	1046.3		
	Year	5	47.869	204	998.4	0.028	15.5
	Fleet	5	196.956	199	801.5	<0.001	63.9
	Year:Sex	6	63.279	193	738.2	0.011	20.5

Table 4. Estimated coefficients and standard errors (SE) for the factors affecting the overlap between tracked wandering albatross and pelagic longline fleets in each 5x5° cells in the southwest Atlantic. Results for the binomial and Gaussian (In transformed response) GLM are presented. Note that for every factor, one category is fixed (intercept), which serves as the standard for comparisons with other levels. Significant coefficients are highlighted in bold. JAP=Japan, POR=Portugal, SPA=Spain, TAI=Taiwan, URU=Uruguay.

Model		Coefficients	SE	Z	р
Binomial	(Intercept)	-1.013	0.250	-4.048	<0.001
	Sex Males	-0.576	0.328	-1.757	0.079
	Fleet JAP	-0.878	0.360	-2.436	0.015
	Fleet POR	-0.382	0.668	-0.572	0.568
	Fleet SPA	-0.646	0.248	-2.608	0.009
	Fleet TAI	0.580	0.203	2.862	0.004
	Fleet URU	-0.538	0.241	-2.227	0.026
	Year 2000	-0.601	0.320	-1.878	0.060
	Year 2002	-0.210	0.302	-0.698	0.485
	Year 2004	-0.400	0.318	-1.257	0.209
	Year 2006	-0.345	0.315	-1.094	0.274
	Year 2009	-0.958	0.342	-2.801	0.005
	Latitude	-0.175	0.078	-2.245	0.025
	Sex Males:Year 2000	-0.327	0.521	-0.627	0.530
	Sex Males:Year 2002	0.129	0.456	0.283	0.777
	Sex Males:Year 2004	-1.157	0.612	-1.893	0.058
	Sex Males:Year 2006	-1.745	0.711	-2.454	0.014
	Sex Males:Year 2009	-1.803	0.822	-2.195	0.028
Gaussian (ln)					
	(Intercept)	4.599	0.409	11.239	<0.001
	Year 2000	0.447	0.561	0.797	0.426
	Year 2002	1.362	0.504	2.704	0.007
	Year 2004	2.306	0.548	4.206	<0.001
	Year 2006	0.935	0.534	1.753	0.081
	Year 2009	1.411	0.607	2.323	0.021
	Fleet JAP	0.782	0.683	1.145	0.253
	Fleet POR	1.493	1.334	1.120	0.264
	Fleet SPA	0.881	0.461	1.911	0.057
	Fleet TAI	2.382	0.357	6.681	<0.001
	Fleet URU	0.127	0.457	0.277	0.782
	Year 1999:Sex Males	0.681	0.562	1.211	0.227
	Year 2000:Sex Males	-0.613	0.754	-0.813	0.417
	Year 2002:Sex Males	-0.506	0.557	-0.909	0.365
	Year 2004:Sex Males	-2.648	0.969	-2.732	0.007
	Year 2006:Sex Males	-2.967	1.203	-2.466	0.015
	Year 2009:Sex Males	-0.574	1.549	-0.371	0.711

Table 5. Populations of albatrosses and petrels that are most affected by pelagic longline fishing in the southwest Atlantic (see Jiménez *et al.*, 2012) and the areas and seasons of highest bycatch risk (peaks in bycatch rates in parentheses).

Species	Global status *	Population: Islands or island groups	Main bycatch areas	Main bycatch seasons (peak)
Diomedea exulans	VU	South Georgia	28° S to 46° S and shelf-break to 43° W ¹ ; 25° S to 46° S and shelf-break to 30° W ²	Abril-November (November) ¹ ; May-December ² ; July- November (October- November) ³
Diomedea dabbenena	CR	Gough	28° S to 37° S and international and deep Uruguayan waters ¹ ; 29° S to 35° S and 45° W to 52° W ⁴	July-November (September– November) ¹ ; May-January ⁴
Diomedea epomophora	VU	Campbell	34° S to 41° S and shelf-break to 49° W ¹	April-November (June–July) ¹
Diomedea sanfordi	EN	Chatham	34° S to 37° S and shelf-break to 51° W ¹	April-November (June–July) ¹
Thalassarche melanophris	NT	Falklands & South Georgia	27° S to 37° S and shelf-break to 40° W ⁵ ; 27° S to 46° S and shelf-break to 39° W ⁶	March-December (July) ⁵
Thalassarche chlororhynchos	EN	Tristan da Cunha & Gough	22° S to 37° S and shelf-break to 33° W ⁵ ; 22° S to 40° S and shelf-break to 30° W ⁶	May-November (September) ⁵
Thalassarche steadi	NT	Auckland Islands	shelf-break off Uruguay ⁷ and off southern Brazil ⁸	April-November (?) ⁷
Procellaria aequinoctalis	VU	South Georgia	27° S to 37° S and shelf-break to 41° W ⁵ ; 27° S to 42° S and shelf-break to 39° W ⁶	May-November (August) ⁵
Procellaria conspicillata	VU	Tristan da Cunha	27° S to 37° S and shelf-break to 41° W ⁶	April-December (?) ⁶
All seabirds			27° S to 37° S and shelf-break to 28° W ⁹ ; 24° S to 36° S and shelf-break to 42° W ¹⁰	(May-November) ⁹ ; (June- October) ¹⁰ ; (June-November) ¹¹

* <u>http://www.birdlife.org/datazone/species/search</u>. 1: Jiménez *et al.*, 2014; 2: this study; 3: Jiménez *et al.*, 2008; 4: Dénes *et al.*, 2007; 5: Jiménez *et al.*, 2010; 6: DINARA, unpublished data; 7: Jiménez *et al.*, 2015; 8: Gianuca *et al.*, 2011; 9: Jiménez *et al.*, 2009; 10: Neves & Olmos, 1998; 11: Bugoni *et al.*, 2008

Figure 1. Distribution of breeding female and male wandering albatrosses tracked using satellitetransmitters (PTTs) and GPS loggers from Bird Island, South Georgia, during incubation (1992, 1996, 2004, 2006 and 2012), brood (1991, 1992, 1998, 2000, 2003 and 2004) and post-brood chick-rearing (1990-1992, 1995-2002, 2004, 2006 and 2009) (details about sample sizes in Appendix S1, Table S1). Tracks were linearly interpolated at 30 min intervals. The 200 m isobath is represented by a black line.

Figure 2. ICCAT fishing effort reported in number of hooks for the southwest Atlantic (south to 25°S and east to 15°W) used by breeding wandering albatrosses tracked from Bird Island, South Georgia in 1990-2012. The category "Others" includes fleets from Belize, St Vincent and Grenadines, Vanuatu, Philippines, Panama, South Korea, China and Namibia (in decreasing order of hooks reported).

Figure 3. (A) ICCAT longline fishing effort (number of hooks) reported for January-March (corresponding to the incubation period = Inc) and its overlap with the distribution of (B) breeding females and (C) breeding male wandering albatrosses from South Georgia in 2004 and 2012. Overlap index = $\frac{1}{2}$ x proportion of time spent x no. of hooks * N of hooks (see definitions in Methods).

Figure 4. Overlap of breeding male and female wandering albatrosses tracked from South Georgia during brooding, and mean pelagic longline fishing effort (number of hooks) reported to ICCAT for the same period (in 1991, 1992, 1998, 2000, 2003 and 2004).

Figure 5. Mean (for 1999, 2000, 2002, 2004, 2006 and 2009) and coefficient of variation (CoV) of (A) ICCAT longline fishing effort (number of hooks) reported for May-December (corresponding to the postbrood chick-rearing period = Post brood) and overlap with the distribution of (B) breeding females and (C) breeding male wandering albatrosses from South Georgia. Overlap index = proportion of time spent * N of hooks (see definitions on Methods and annual overlaps in Appendix S2, Fig S1). In panels showing the CoV, darker cells represent lower variation (i.e. higher inter-annual consistency).

Figure 6. A) Mean (± SE) overlap index (proportion of time spent x no. of hooks) for male and female wandering albatrosses during post-brood chick-rearing (May-December) in 1999, 2000, 2002, 2004, 2006 and 2009 with the six main pelagic longline fleets operating in the southwest Atlantic. B) Relative contribution of each longline fleet by year to the overlap index. TAI=Taiwan, SPA=Spain, BRA= Brazil, URU=Uruguay, JAP=Japan and POR=Portugal. Note that the reduced overlap of males with the fleet of Taiwan and increased overlap with the Portuguese fleet in 2009 reflects a shift in the distribution of birds (based on tracking data) rather than in the fishing effort (see Appendix S2, Figs S1, S2 and S7).

Appendix S1. Tracking data and overlap analyses

Breeding cycle and tracking data

On South Georgia, wandering albatrosses lay their eggs in late December. During incubation (ca 72 days), the parents alternate shifts on the egg with foraging trips to sea, which last on average 8-12 days. The egg hatches around mid-March and during the brood period (ca 32 days), parents attend the chick continuously by alternating one to a few days at the nest with foraging trips. The rest of the breeding period (post-brood chick-rearing; hereafter termed chick-rearing) lasts ca 245 days, during which time both parents feed at sea, returning at intervals varying from one day to several weeks to feed the chick, which usually fledges in November (although the range is from late October to January) (Tickell, 2000). Biparental care is maintained at least until shortly before fledging.

Analyses were of data from 263 breeding albatrosses of known age and sex (142 males and 121 females) tracked during 399 complete foraging trips (205 by males and 194 by females) either with Argos satellite-transmitters (Platform Terminal Transmitters or PTTs) from 1990 to 2004 or by global positioning system (GPS) loggers from 2003 to 2012 (Table S1). Birds with PTTs were usually fitted concurrently with a 17 g radio transmitter attached to a plastic band on one tarsus, allowing the exact arrival and departure times to be determined using a remote radio-receiver logger system (Televilt) (Berrow & Croxall, 2001); otherwise, arrival and departure times were estimated from satellite or GPS fixes and visual observations (Phillips et al., 2009). PTTs weighed up to 180 g in the early 1990s (Prince et al., 1992), and 20-30 g in the late 1990s to early 2000s (Phillips et al., 2009; Xavier et al., 2004). GPS loggers weighed between 19.5 g (Ceia et al., 2012) and 68 g (Fukuda et al., 2004). Instrument loads (0.2 to 2.0% of body mass) were well below the threshold where deleterious effects might be expected (Phillips et al., 2003). All satellitetransmitter locations in ARGOS System Location Class 3,2,1,0, A and B were filtered using an iterative forward/backward averaging filter (McConnell et al., 1992) to remove any that indicated unrealistic flight speeds (filter velocity >90 km h^{-1} to allow for occasional rapid flights) (Phillips *et* al., 2009). The mean sampling frequencies for the foraging trips with PTTs and GPS loggers were 122 and 29 minutes, respectively.

Table S1. Number of birds and foraging trips tracked of wandering albatrosses breeding at Bird Island, South Georgia. F= females, M = males. The overlap between breeding stage and fishing effort was restricted to years with at least 8 tracked trips per sex (indicated by numbers in italic and bold). All albatrosses from 1990 to 2002, plus a male in 2004, were equipped with a Platform Terminal Transmitter (PTT); the remaining birds were equipped with Global Positioning System (GPS) loggers.

Year		Breeding stage												Breeding season				
	Incubation					Brood			Post-brood									
	F	Trips	М	Trips	F	Trips	М	Trips	F	Trips	Μ	Trips	F	Trips	Μ	Trips	Birds	Trips
1990		-		-		-		-	1	3	1	2	1	3	1	2	2	5
1991		-		-	4	9	4	5	4	5	8	15	6*	14	8*	20	14	34
1992	3	3	2	2	2	5	3	4	1	2	2	2	6	10	7	8	13	18
1995		-		-		-		-		-	1	1	0	0	1	1	1	1
1996		-		-		-		-	1	2	1	3	1	2	1	3	2	5
1997		-		-		-		-		-	2	3	0	0	2	3	2	3
1998	4	4	3	3	8	9	9	9	2	4	4	11	14	17	14*	23	28	40
1999		-		-		-		-	9	10	9	9	9	10	9	9	18	19
2000		-		-	4	4	5	5	10	13	10	11	14	17	15	16	29	33
2001		-		-		-		-	1	1		-	1	1	0	0	1	1
2002		-		-		-		-	13	24	13	24	13	24	13	24	26	48
2003		-		-	8	8	16	16		-		-	8	8	16	16	24	24
2004	7	8	8	8	8	10	8	9	9	15	10	12	24	33	26	29	50	62
2006	1	1	1	1		-		-	8	23	4	15	9	24	5	16	14	40
2009		-		-		-		-	14	14	13	13	14	14	13	13	27	27
2012	15	17	20	22		-		-		-		-	15	17	20	22	35	39
Total	30	33	34	36	34	45	45	48	65*	116	73*	121	121*	194	142*	205	263*	399

*Note that in some cases the total number of tracked birds do not match the sum of the annual number of birds tracked as a few birds were tracked in two or three years. Similarly, in few cases, birds were tracked in two breeding stages in the same year.

Overlap with longline fishing effort

We used the proportion of time spent per unit area (days per each 5x5° cell) for each breeding stage, after linear interpolation of PTT or GPS locations on each foraging trip at 30 min intervals using the R package *trip* version 1.1-10 (Sumner, 2011) as the albatross density metric to overlap with fishing effort distribution. Because only half of the breeding birds are at sea during incubation and brood, the proportions calculated as above should be divided by 2. However, wandering albatross distribution overlaps very little with pelagic longline fisheries during brood (see Results), and therefore this correction was only applied for incubation. Pelagic longline fishing effort for the southwest Atlantic (number of hooks at 1x1° and 5x5° cells, by month) was obtained from the International Commission for the Conservation of Atlantic Tunas (ICCAT) available at <u>http://iccat.int/en/accesingdb.htm</u>. To quantify bird-fisheries overlap, the albatross

density metric was multiplied by the number of hooks (Tuck *et al.*, 2011). This produces an overlap index which accounts for the proportion of time spent by the females / males in a given breeding stage and the potential number of hooks which may be encountered in a given cell. Because we were concerned with differences between males and females within each breeding stage, it was not necessary to account for the unequal duration of each stage.

Factors affecting overlap and contribution by the main fleets during chick-rearing

For each year, we estimated the total fishing effort (number of hooks) deployed in those 5x5° cells used by each sex during chick-rearing, which was multiplied by the sum of the albatross density metric (see above) to produce an overall index of overlap with the ICCAT pelagic longline fishery (hereafter termed "ICCAT overlap index"). This produced 12 separate index values (six for each sex). This analysis was then repeated for each longline fleet of the main ICCAT flag states in the study area, obtaining for each year as many overlap index values as fleets (hereafter termed "fleet overlap index"), multiplied by two (males and females), and resulting in 54 overlap index values (44 distinct from zero, with Portugal excluded; see below). This allows estimation of the percentage contribution of each fleet to the overall overlap with males and females in chickrearing. Note that the ICCAT and fleet overlap indices are for the southwest Atlantic sector used by wandering albatrosses, but do not account for the spatial variation. Therefore, another dataset was constructed with all the possible overlap index values for the principal fleets at $5x5^{\circ}$ cells, by sex and year. Excluding cells not used by either sex, there were 1776 values for the overlap index, of which 210 were distinct from zero. Only four fleets (Brazil, Spain, Taiwan and Uruguay; see Results) operated in all six years of the study; however, the Japanese and Portuguese fleets showed considerable overlap with tracked wandering albatrosses in three or one of the six years, respectively. The Japanese fleet was included in all analyses, whereas that of Portugal was sometimes excluded to fit models.

The effect of the categorical variable, sex, on the ICCAT overlap index was analyzed using a Linear Model (LM). Additionally, the effects of sex, year and fleet on overlap during chick-rearing were analyzed using Generalized Linear Models (GLM) for the dataset of fleet overlap index and for the other dataset at 5x5° cells. Both datasets showed a strongly skewed distribution (particularly the second dataset, with 88% zero values). Best fit in both cases included a two-step analysis: 1) the occurrence of overlap was modeled using a GLM with a logit link function, assuming a binomial

distribution; then 2) Overlap Index values different from zero were modeled using GLM assuming a Gaussian error distribution, with a canonical identity link function. The response variable (overlap index) was natural log (ln) transformed. For the dataset of fleet overlap index, only the categorical variable sex was included in the binomial sub-component, and sex, year and fleet in the Gaussian sub-component. However, in the largest dataset at 5x5° scale, the categorical variables sex, year and fleet, and the first order interactions between sex and fleet and sex and year were included in both binomial and Gaussian models. Additionally, we included latitude and longitude (at the centre of each 5x5° cell) as continuous variables. The best model was selected using AIC with a forward selection algorithm using R's default AIC statistics via the step function. Deviance analyses were used to test the significance (χ^2 test) of each explanatory factor and first order interaction. Additionally, the percent of deviance explained by each factor and first order interactions with respect to the total deviance of our resulting final model was estimated.

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Appendix S₂. Overlap distributions of wandering albatross with pelagic longline fishing effort during the post-brood chick-rearing period.



Figure S1. Overlap distributions of breeding females and males of wandering albatross with ICCAT pelagic longline fishing effort during the post-brood chick-rearing period.

Figure S1. (continued).



Figure S2. Overlap distributions of breeding females and males of wandering albatross with the reported pelagic longline fishing effort of Taiwan (TAI) the post-brood chick-rearing period.



Figure S2. (continued).



Figure S3. Overlap distributions of breeding females and males of wandering albatross with the reported pelagic longline fishing effort of Spain (SPA) during the post-brood chick-rearing period.



Figure S3. (continued).



Figure S4. Overlap distributions of breeding females and males of wandering albatross with the reported pelagic longline fishing effort of Brazil (BRA) the post-brood chick-rearing period.



Figure S4. (continued).



Figure S5. Overlap distributions of breeding females and males of wandering albatross with the reported pelagic longline fishing effort of Uruguay (URU) during the post-brood chick-rearing period.



Figure S5. (continued).



Figure S6. Overlap distributions of breeding females and males of wandering albatross with the reported pelagic longline fishing effort of Japan (JAP) during the post-brood chick-rearing period.



Figure S7. Overlap distributions of breeding females and males of wandering albatross with the reported pelagic longline fishing effort of Portugal (POR) during the post-brood chick-rearing period.



Appendix S₃. Distribution of the ringed birds reported dead on longliners in the southwest Atlantic

Figure S8. Distribution of the ringed birds reported dead on longliners in the southwest Atlantic region where pelagic longline fishing is regulated by ICCAT.



Figure S9. Mean overlap index (1999-2009) for post-brooding females (see details on Fig. 5 of the main text) and distribution of the ringed adult females reported killed on longliners (1999-2012) in the southwest Atlantic region regulated by ICCAT during May-December (corresponding to the post-brood chick-rearing period). (A) Recoveries of breeders and non-breeders (B and N-B). (B) Recoveries of breeders.

Capítulo 5 | Chapter 5

Dimorfismo sexual en tamaño, segregación espacial y captura incidental sesgada hacia un sexo en los albatros reales del sur y del norte en pesquerías de palangre pelágico

Sexual size dimorphism, spatial segregation and sex-biased bycatch of southern and northern royal albatrosses in pelagic longline fisheries

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Abstract

Bycatch in longline fisheries is a major cause of global declines of albatrosses. Sexual segregation at sea often leads to unequal overlap with different fisheries, resulting in sex-biased bycatch, exacerbating impacts at the population level. In great albatrosses (*Diomedea* spp.), males (the larger sex) tend to spend more time at higher latitudes than females, attributed to competitive exclusion or differences in flight performance, mediated by the pronounced sexual size dimorphism (SSD). Consequently, females are often caught in larger numbers by pelagic longline fisheries in subtropical and temperate areas. Although known for *Diomedea exulans*, this has not been generalised for all great albatrosses. Here we examined the degree of SSD, and developed discriminant functions to determine species and sex in *Diomedea epomophora* and *D. sanfordi*, which are killed in several fisheries in the southern hemisphere. Based on a large sample of bycaught albatrosses caught off Uruguay, both species showed substantial SSD. Discriminant functions assigned species and sexes to otherwise indeterminate individuals with 90-100%

accuracy. Based on all birds identified (n=128), bycatch in the pelagic longline fishery was femalebiased, indicating sexual segregation at sea. These discriminant functions allow species and sexes to be separated, providing critical data for future bycatch assessments.

Key words: Discriminant Analysis, Sexual segregation, Seabirds, Southwest Atlantic

Introduction

Bycatch in commercial fisheries represents one of the main conservation threats to albatrosses and other seabirds (Croxall et al. 1998, Gales 1998). Albatross life-history strategies (i.e. delayed maturity, low reproductive output and great longevity) make these species particularly vulnerable to any additional source of mortality. Adult survival is the most important demographic parameter influencing population trends (Weimerskirch et al. 1987, Gales 1998). As such, population declines at some colonies associated with reduced adult survival rates have been attributed to bycatch in longline fisheries (Weimerskirch et al. 1987, Croxall et al. 1998). Albatrosses are monogamous and sex ratio in the breeding population is expected to be 1:1. Sexual segregation at sea can therefore have implications for conservation, as sex-specific overlap with fisheries can produce sex-biased mortality (Jiménez et al. 2015); this translates both to an immediate, direct effect on the total number of potential breeders, as well as an indirect effect on fecundity because it affects availability of one sex as partners (Mills & Ryan, 2005).

Sexual segregation in at-sea distribution has been reported in great albatrosses (*Diomedea* spp.), particularly in the wandering albatross (*Diomedea exulans* Linnaeus; Prince et al. 1992, Jiménez et al. 2015), a species that, like others in the genus, exhibits noticeable sexual size dimorphism (SSD) (Shaffer et al. 2001, Cuthbert et al. 2003). On average, males have longer bills (ca. 4%, 170 vs 164 mm) and greater wing span (ca. 4%, 311 vs 299 cm), with ca. 7% more wing area (6260 vs 5860 cm²), and are also 20% heavier (9.4 vs 7.8 kg) than females (Shaffer et al. 2001). Female wandering albatrosses typically forage in sub-Antarctic and subtropical waters, whereas males usually forage further south, in sub-Antarctic and Antarctic zones (Xavier & Croxall 2005, Froy et al. 2015). This partial sexual segregation is attributed either to competition, with larger males excluding the smaller females from access to nearby resources, forcing them to travel further from the colony (Phillips et al. 2008), or the relationship between sexual size dimorphism and flight performance

(Shaffer et al. 2001). The latter hypothesis is that as wing loading determines flight speed, the windier regions of the sub-Antarctic and Antarctic are more optimal for males, which have ca. 12% higher wing loading than females, whereas females and fledglings are better adapted for exploiting the lighter winds of subtropical regions. Consequently, bycatch of wandering albatrosses in pelagic longline fisheries, which mainly operate in subtropical regions, is female-biased (Jiménez et al. 2015). Because both hypotheses explaining this latitudinal segregation are mediated by SSD, similar processes and consequences (female-biased bycatch in pelagic longline fisheries) are expected for the other *Diomedea* species.

Large proportions of the global populations of two great albatross species from New Zealand migrate to the southwest Atlantic; the southern royal albatross *Diomedea epomophora* (Lesson) and the northern royal albatross *Diomedea sanfordi* (Murphy) (Nicholls et al. 2002, Robertson et al. 2003, Moore and Bettany 2005). Separation of these two species was proposed by Robertson and Nunn (1998), and adopted subsequently by both BirdLife International (the listing authority for the World Conservation Union, IUCN) and the Agreement for the Conservation of Albatross and Petrels (ACAP). Northern and southern royal albatrosses are globally threatened according to the IUCN (Endangered and Vulnerable, respectively), and >99% of breeding pairs nest at the Chatham Islands and Campbell Island, respectively. The global population trend for southern royal albatross appears to be stable, and for northern royal albatross is unknown (ACAP 2009a, b). During breeding, both species are distributed in New Zealand continental shelf waters (Nicholls et al. 2002, Waugh et al. 2002), while during the non-breeding season, they occur in the southern Pacific, Atlantic and Indian oceans (Nicholls et al. 2002, Robertson et al. 2003, Moore and Bettany 2005). They winter mainly in the southern continental shelf waters of South America, both on the Pacific and Atlantic coasts, and particularly off Argentina and Uruguay (Nicholls et al. 2002, Robertson et al. 2003, Jiménez et al. 2014). This preference for continental shelf habitat contrasts with the wandering albatross, which remains mainly oceanic (Froy et al. 2015). The limited data on body size of southern and northern royal albatrosses suggest that males are larger than females (Westerskov 1960, Tickell 2000), but the size dimorphism has not been tested statistically. In this paper, we use data from royal albatrosses of both species bycaught in pelagic longline fisheries in the southwest Atlantic to first test for sexual size dimorphism, and then apply discriminant analyses to assign sex and species in indeterminate birds. Most of these birds were partially eaten by scavengers, which is common in bycatch studies. We then tested for a biased sex ratio in the

complete sample of bycaught birds, and discuss the potential conservation implications. Despite the difference in foraging habitats from the wandering albatross, we predicted comparable latitudinal segregation among sexes in the two royal albatross species, and hence a biased sex ratio in bycatch in pelagic longline fisheries in the north of their ranges.

Materials and Methods

This work used data from seabird carcasses collected on pelagic longline vessels by the "Programa Nacional de Observadores a bordo de la flota atunera uruguaya" (PNOFA) of the "Dirección Nacional de Recursos Acuáticos" (DINARA). These specimens were caught incidentally by Uruguayan commercial and research vessels in 2004-12, and 2009-12, respectively, and Japanese commercial vessels in 2009-11 operating off Uruguay under an experimental fishing license. All vessels fished in shelf break, slope and deeper waters off Uruguay, and Uruguayan commercial vessels also operated in international waters. The temporal distribution of fishing effort, and the captures of royal albatrosses until 2011, are presented in Jiménez et al. (2014). A total of 1599 sets and 3 311 113 hooks were observed during 81 commercial fishing trips by Uruguayan vessels from January 2004 to November 2011. For Japanese vessels, a total of 1114 sets and 2 589 465 hooks were observed in 26 trips in 2009-11. During these sets of observations, a total of 137 royal albatrosses were captured; 68 northern royal albatrosses (NRA), 46 southern royal albatrosses (SRA), and 23 undetermined. We also include data from 10 individuals (three NRA, five SRA and two undetermined) captured incidentally by a Uruguayan research vessel during three surveys (October 2010, July 2011 and July 2012) to assess large pelagic fishes on the shelf break off Uruguay, and 10 individuals (one SRA and nine undetermined) caught incidentally during three commercial fishing trips observed by PNOFA on Uruguayan vessels during May-June, July and September 2012.

Each albatross carcass was referenced and kept frozen in a labelled plastic bag for subsequent analysis in land. Most bycaught birds could be identified as northern or southern royal albatrosses in the laboratory by their plumage. Northern royal albatross has an entirely black upper wing, whereas southern royal has a black upper wing that becomes progressively whiter with age; this white plumage develops first at the leading edge and progresses backwards across the wing towards the trailing edge (Marchant & Higgins 1990, Nicholls et al. 2007, Onley & Scofield 2007). Some bycaught birds were in poor condition, with ruffled feathers or damaged plumage, and species could not be distinguished. The sex was determined directly, where possible, by examining the gonads, unless these were missing as a result of scavengers. Morphometric data were taken from 133 royal albatrosses, including 96, 17 and 20 birds of known species and sex, species only and sex only, respectively. Eighty four, 39 and 10 of these birds were measured by SJ, RF and MA, respectively. Each observer followed the same protocol and has extensive experience with hundreds of bycaught seabirds sampled. All were supervised initially by SJ, reducing the variability among observers. The remaining 24 birds, excluded from analyses, were released alive (2 NRA, 6 SRA and 4 undetermined), not landed (1 NRA and 10 undetermined) or not sampled (1 undetermined). A total of 19 measurements were taken: bill length (Culmen), basal bill depth (BBD), minimum bill depth (MBD), bill depth at unguis (BDU), basal bill width (BBW), basal bill width at commissures (BBWb), head length (HL), maximum head width (MHW), tarsus, middle toe with claw (MTCLAW), middle toe without claw (MTnoC), claw, total length (TL), wing length (WL) and wing cord (WC) from both right and left wings, tail length (Tail) and wing span (WS). Full definitions for all these measurements, and pictures (Fig. S1) of several of them, are shown in the Supplementary Material. Total length, tail length, wing length and cord and wing span were measured with metal rules to the nearest 1 mm. All other measurements were made with a Vernier caliper to the nearest 0.1 mm.

Comparison of mean values between species and sexes were conducted using one-way ANOVA or Student t-tests, after testing for normality (Kolmogorov–Smirnov test) and homogeneity of variance (Levene test). Otherwise, Kruskal-Wallis and Mann–Whitney test were used. Measurements with sample sizes ≤ 8 in one or both groups were not compared statistically. The percentage of dimorphism between sexes in each measurement was calculated as: $[(X_m - X_f)/X_f]$ ×100, where X_m and X_f are mean values for males and females, respectively (Cuthbert et al. 2003). Discriminant function analysis (DFA; Phillips and Furness 1997, Cuthbert et al. 2003) was used to assign species and sex. Nine measurements were initially considered for all functions: Culmen, BBD, MBD, BDU, BBW, HL, MHW, Tarsus and MTNoCL. These were available for 98 birds of known species (58 NRA and 40 SRA), 88 of which were of known sex (females: 42 NRA and 23 SRA, males: 11 NRA and 12 SRA). Therefore, separate DFAs were used to assign species and sex. Eight measurements were excluded: BBWb had low repeatability; MTCLAW and claw were not always available, as the claw was often worn or broken, and MTCLAW was highly correlated with MTNoCL (see below); WL, WC and WS and LT and Tail, as P10 or central rectrices, respectively, were sometimes unreliable because feathers were very worn, broken, missing or re-growing, resulting in small sample sizes (particularly for males). However, some of these were included in the paired comparisons (see Results, Tables I-III). As the right wing of some birds was damaged, measurements from the left wing were used for WL and WC, to maximise sample sizes. Fourteen (12 SRA and 2 NRA) and 71 (21 SRA and 50 NRA) out of these 98 birds were assigned to first-year juveniles (no replacement primaries or rectrices) and immature-adults (moulting primaries or rectrices), respectively. The states of the gonads were noted in 30 of these latter birds, and 27 birds (6 SRA and 21 NRA) were assigned to old immature or adult (granular ovary or enlarged testes).

Backward stepwise DFA was used to establish which characters contribute the most to species and sex classification. In this analysis, characters that contribute least to species or sex discrimination are determined according to a threshold of F values (4.0; significance level of α = 0.05) and successively removed from the analysis until the least number of characters remains. Analyses included all birds for which all nine measurements were available. Each bird was reclassified by calculating the score for each of the two classification groups (e.g. SRA or NRA) and the associated probability, assuming an equal *a priori* probability of belonging to each group. Prior to each backward stepwise DFA, collinearity was investigated by examining variance inflation factors (VIF), and one variable was removed from each pair of highly correlated variables (≥0.9, following Zuur et al. 2007 for DFA). This only occurred in the analysis to assign species; Tarsus and MTOENOCL were highly correlated (0.91) and the latter was removed. The performance of each backward stepwise DFA was also compared with that of a DFA using a jackknifed classification. This classifies each individual using the coefficients derived from all the other birds, eliminating bias and providing a more rigorous estimate of the ability of the functions to separate groups (Phillips and Furness 1997, Thalmann et al. 2007). To separate species (because sample sizes were larger), a second backward DFA based on a random sample of 60 birds (training set) was also performed. The resulting discriminant function was then used to predict the species of the remaining 38 birds. In some cases an alternative DFA was constructed based on
fewer measurements than those included in the backward stepwise DFA, particularly when a measurement is not commonly taken by observers, or is difficult to take consistently. However, in order to assign species and sex for the analysis of bycatch composition, those discriminant functions with a higher correct assignment rate were used. Deviations of the sex-ratio from 1 : 1 were tested using Chi square tests with Yates' correction for continuity. All statistical analyses were conducted in R 2.13.1.

Results

Both southern and northern royal albatrosses showed sexual dimorphism, with males larger on average than females in all body measurements tested statistically, although there was always some overlap (Tables I and II). In both species, MBD and MDU, and then HL, showed a higher degree of dimorphism. Southern royal albatrosses were larger, on average, than northern royal albatrosses, but there was considerable overlap between species and sexes (Table III). Pairwise comparisons of mean values showed that male SRA were larger than female NRA in all measurements, but differences between female SRA and male NRA were not significant, with the exception of MBD, BDU and MHW (Table III). There were significant differences between species in mean values for most measurements in comparisons of birds of the same sex, except MBD and BBW (both sexes), BDU (females) and BBW2 (males) (Table III).

The backward stepwise DFA including all 98 birds (58 NRA and 40 SRA) with eight of the nine characters (MTnoC excluded because of collinearity), correctly assigned 95% of the birds to species using a combination of Culmen, BDU and Tarsus (DF1, Table IV). The five misclassified birds included a SRA of unknown sex and four NRAs (three males and one female). After the jackknifing procedure, 94% of birds were assigned correctly. In a backward stepwise DFA including a random sample of 60 birds (36 NRA and 24 SRA), again with eight of the nine characters, the same three characters were retained and 90% of birds were assigned correctly to species (88% after jackknifing). When this equation was applied to the remaining 38 birds (22 NRA and 16 SRA), 89.5% of them were assigned correctly.

Because Culmen and Tarsus are frequently measured by observers, we constructed another backward stepwise DFA including the original 98 birds, but excluding BDU. The equation (DF2,

Table IV) correctly assigned 92% of the birds. Eight NRA (seven males and one female) were misclassified as SRA. After the jackknifing classification, the correct species allocation was again 92%.

For SRA, the analysis including the nine characters measured in 35 sexed birds (23 females and 12 males) showed that a combination of the BDU and HL (DF3, Table IV) correctly assigned sex to 100% of individuals (100% again after the jackknifing classification). A similar analysis based on 53 sexed birds (42 females and 11 males) showed that a combination of BDU and MTnoC (DF4, Table IV) correctly assigned 98% of the birds (also 98% again after jackknifing). Because measuring MTnoC can be problematic (e.g. in living birds), we conducted another backward stepwise DFA based only on head measurements. A combination of three measurements (Culmen, BDU and HL; DF5, Table IV) correctly assigned 98% of the birds as a male NRA classified as female, and *vice versa* in the other DFA.

By including results obtained with the DFAs, both species and sex were determined for 128 (54 SRA and 74 NRA) of the 133 royal albatrosses caught in the fishery under study. For the remaining five birds (3 NRA and 2 SRA) measurements for applying discriminant functions for sex determination were missing. Bycatch of both species was female-biased; however, the difference from a 1:1 ratio was highly statistically significant in NRA ($\chi^2_{Yates} = 20.55$, d.f. = 1, p < 0.01, 57 females and 17 males), but not significant in SRA ($\chi^2_{Yates} = 2.24$, d.f. = 1, p > 0.05, 33 females and 21 males).

Discussion

Sexual size dimorphism in both southern and northern royal albatrosses was apparent in all body measurements. The measurements with higher size dimorphism (MBD, BDU and HL) follow the general patterns for the species of Procellariiformes with marked size differences among sexes, such as albatrosses and giant petrels (*Macronectes* spp.), where males often have noticeably bigger bills and heads (Warham 1996). Similar to other species of great albatrosses, such as wandering, Tristan (*Diomedea dabbenena*, Mathews; Cuthbert et al. 2003) and Antipodean (Gibson's) albatross (*Diomedea antipodensis gibsoni*, Robertson & Warham; Walker & Elliott

1999), and mollymawks (*Thalassarche* spp.; Hedd et al. 1998, Ryan et al. 1999, Gandini et al. 2009), measurements of the depth of the bill (MBD and BDU) of both royal albatross species showed higher dimorphism values. Cuthbert et al. (2003) also found high sexual size dimorphism in the total head length (from the bill tip to the occiput at the rear of the skull), but not culmen, in Tristan albatross, which is comparable to our results for the royal albatrosses.

Interspecific differences in the biogeography of albatrosses have been ascribed to aerodynamic features (Suryan et al. 2008); the hypothesis relating wing loading and wind patterns to sexual segregation (see Introduction) may also explain interspecific segregation at sea. Although there was considerable overlap between species and sexes, SRA was on average larger in body measurements than NRA. Although not measured in the present study, a lower wing loading is expected for NRA, in which case this species might be better adapted for exploiting the lighter winds of subtropical regions. This is supported by our findings, with higher numbers of NRA, particularly females (the smaller sex), bycaught in the northern part of the distribution of royal albatrosses. However, NRA has a considerably lower global population than SRA (ca. 5800 and 7800 annual breeding pairs, respectively; ACAP 2009a, b), and hence the inference that different bycatch rates relate to wing loading would need to be confirmed by analysis of habitat preferences and better data on densities of each species at sea during the non-breeding period.

Assessing the effect of fisheries on seabird populations requires bycaught birds to be identified to species, and provenance (except for endemics), sex and age to be determined (Alexander et al. 1997). An age bias towards young birds is less of a concern than if all bycatch were of adults. Sexbiased mortality in fisheries has reproductive costs beyond the immediate reduction of breeding population, because widowed individuals of the more abundant sex may have difficulties in securing a new partner. Therefore, the impact of the skewed sex ratio on fecundity (mean number of offspring produced per adult) is additive and may persist once bycatch ceases (Mills & Ryan, 2005). The present study provides a valuable tool for onboard scientific observers to separate species and sexes of bycaught royal albatrosses using combinations of two or three morphometric measurements (with accuracies ranging from 90 to 100%), two of which are standard (Culmen and Tarsus) and two are unusual but easy to take (BDU and HL). These discriminant functions were based on birds of a range of ages (see Methods), which can be considered broadly representative of the age structure in the southwest Atlantic; ring recoveries and tracking data

indicate that first-year birds are more abundant off Chile, and immatures and adults in the southwest Atlantic (Nicholls et al. 2002, Moore & Bettany 2005, Thomas et al. 2010). Nevertheless, as our analyses included juveniles or younger immatures, which may not have completed growth in skeletal traits (Ryan 1999), it would be useful to confirm the wider application of these DFAs to identify species and sex of royal albatrosses outside the southwest Atlantic by applying them to birds measured at breeding sites. We have done this to some extent, but involving few individuals (see below).

Based on a small sample, Westerskov (1960) suggested that Tarsus may be useful for discriminating royal albatross species. We found overlap among species in this measurement, but it had the greatest standardised discriminant coefficient in both functions based on three (Culmen = 0.448, BDU = -0.484, Tarsus = 0.859) or two (Culmen = 0.372, Tarsus = 0.704) measurements. The power of our discriminant functions for species identification was lower for NRA, particularly males (see results). This is because of the high overlap in measurements of male NRA and female SRA (see Tables I-III). Misidentification in the opposite direction between these two groups may be expected. We applied our DFAs to discriminate species from Culmen and Tarsus (DF2, Table IV) to published data from 10 SRA (5 males and 5 females) from Campbell Island (Westerskov 1960), and sexed nine (90%) correctly. This performance is similar to that within our own sample, either by cross-validation or jackknifing (92%). In addition, two of the bycaught female NRA in our study were ringed (one from Middle Sister Island, Chathams and another from Taiaroa Head), and both were correctly assigned using our two DFAs for species, and the two DFAs for sexing NRA, respectively (Table IV).

Based on the complete dataset of birds identified and sexed by necropsy or discriminant analysis, we showed that both species have female-biased mortality (although not significant in SRA) in pelagic longline fisheries operating in the northern range of their distribution in South America. In subtropical regions, female-biased mortality in seabird bycatch is common, contrasting with male-biased mortality in subpolar regions, a pattern explained by differential at-sea distributions of the two sexes (Bugoni et al. 2011). Therefore, our results strongly suggest that non-breeding NRA and SRA segregate at sea, with females in more northern areas than males. These results have implications for conservation of these globally threatened species. Not only are females likely to be caught in greater numbers in pelagic longline fisheries in other regions, but males are

potentially more susceptible to bycatch in fisheries operating in southern regions. However, little is known about the bycatch rates of either royal albatross species and the magnitude of their global bycatch is completely unknown. Both species have been captured incidentally in longline (Gales et al. 1998, Jiménez et al. 2014, this study) and trawl fisheries (Favero et al. 2011, Waugh et al. 2008). Usually few individuals are captured, with the exception of Australian waters in early 1990s (Gales et al. 1998) and recently in the southwest Atlantic (Jiménez et al. 2014), where the bycatch rates for both species in pelagic longline were very high. However, bycatch observer coverage of most fishing fleets is very poor (Phillips 2013). More data are required on fisheries bycatch throughout the at-sea ranges of these and other vulnerable species, and there is a pressing need to determine not only the species, but also the sex and, where possible, the age of captured individuals in order to improve our understanding of impacts of global fishing on their populations.

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Table I. Measurements (mean, S.D. and range, in mm) of female and male southern royal albatrosses, and sexual size dimorphism. BBD = basal bill depth; MBD = minimum bill depth; BDU = bill depth at ungis; BBW = basal bill width; BBWb = basal bill width at commissures; HL = head length; MHW = maximum head width; MTnoC = middle toe without claw; TL = total length; WL = wing length; WC = wing cord; Tail = tail length; WS = wing span.

			Females					Males			% males larger	t-value	Р
	Mean	SD	Min.	Max.	n	Mean	SD	Min.	Max.	n			
Culmen	171.0	3.7	163.4	177.5	24	179.1	4.7	171.5	186.0	13	4.7	-5.80	< 0.001
BBD	62.6	1.7	59.9	66.5	25	66.3	2.6	61.8	70.1	13	5.9	-5.27	< 0.001
MBD	34.3	1.6	30.8	36.8	25	37.9	1.9	34.9	41.0	13	10.4	-6.09	< 0.001
BDU	39.4	1.2	36.7	41.4	24	43.6	1.4	41.2	46.2	13	10.6	-9.51	< 0.001
BBW	42.0	1.6	39.3	45.1	25	43.9	1.7	40.9	46.5	13	4.5	-3.43	0.002
BBWb	55.6	2.0	52.1	58.5	24	59.1	4.1	53.0	64.2	13	6.2	-3.49	0.001
HL	92.3	2.3	87.9	96.8	25	101.5	3.3	96.5	105.9	12	9.9	-9.81	< 0.001
MHW	79.7	1.9	76.3	82.8	25	85.4	2.1	82.7	88.6	13	7.0	-8.24	< 0.001
Tarsus	123.6	2.0	119.4	126.9	24	130.9	3.9	125.2	137.5	13	5.9	-7.57	< 0.001
MTnoC	146.3	3.5	137.9	152.0	25	156.2	3.9	151.5	164.3	13	6.8	-8.03	< 0.001
TL	1109	35	1029	1149	19	1176	35	1138	1235	10	6.1	-4.88	< 0.001
WL	649	15	618	674	14	674	18	639	696	7	3.9		
WC	626	17	595	650	14	646	15	620	665	7	3.2		
Tail	198	7	190	214	19	206	8	193	219	11	4.3	-3.16	0.004
WS	2969	71	2855	3079	13	3119	80	3010	3220	7	5.0		

Table II. Measurements (mean, S.D. and range, in mm) of females and males northern royal albatrosses, and sexual size dimorphism. For details of abbreviations see Table I.

			Females					Males			% males larger	t-value	Р
	Mean	SD	Min.	Max.	n	Mean	SD	Min.	Max.	n			
Culmen	160.4	4.7	151.4	173.7	44	168.9	4.0	163.2	176.7	11	5.3	-5.56	< 0.001
BBD	59.7	1.8	56.7	63.8	45	63.1	1.9	60.0	66.6	12	5.7	-5.80	< 0.001
MBD	34.1	1.3	31.1	37.0	45	36.8	2.0	33.2	40.2	12	8.0	-5.72	< 0.001
BDU	38.9	1.2	36.0	41.0	44	42.3	1.6	39.4	45.7	11	9.0	-7.82	< 0.001
BBW	40.8	1.5	37.7	44.1	45	42.8	1.1	41.2	45.0	12	4.9	-4.24	< 0.001
BBWb	52.9	2.2	48.6	58.5	44	56.4	2.6	50.7	59.9	12	6.6	-4.65	< 0.001
HL	87.6	2.8	82.2	100.6	45	93.9	3.5	88.9	103.6	13	7.1	-6.76	< 0.001
MHW	77.7	1.5	75.0	81.5	45	81.9	1.5	79.8	83.8	13	5.5	-8.80	< 0.001
Tarsus	115.4	2.5	110.3	121.0	44	121.6	1.8	119.2	126.3	13	5.4	-8.22	< 0.001
MTnoC	137.6	3.0	131.2	144.1	45	145.9	3.3	140.4	149.6	13	6.1	-8.65	< 0.001
TL	1057	43	957	1180	32	1116	13	1092	1134	8	5.6		
WL	630	15	599	647	13	649	4	645	652	3	3.1		
WC	604	15	576	620	11	628	8	620	635	3	4.1		
Tail	190	6	180	202	27	200	9	190	217	9	5.1	-3.58	0.001
WS	2874	86	2673	2971	11	3010	6	3005	3016	3	4.8		

Table III. Comparison of body size between northern royal albatrosses (NRA) and southern royal albatrosses (SRA). For details of abbreviations see Table I. Significant values are highlighted in bold.

	AN	OVA	Between-species pairwise comparisons (P)							
	F <i>P</i>		Females	Males	Females SRA vs	Males SRA vs				
			VS	VS	Males NRA	Females NRA				
			Females	Males						
Culmen	74.83	< 0.001	< 0.001	< 0.001	0.488	< 0.001				
BBD	45.14	< 0.001	< 0.001	< 0.001	0.828	< 0.001				
MBD	26.58	< 0.001	0.977	0.180	< 0.001	< 0.001				
BDU	57.65	< 0.001	0.583	0.027	< 0.001	< 0.001				
BBW	16.89	< 0.001	0.793	0.129	0.425	< 0.001				
BBWb	37.00*	< 0.001	< 0.001	0.182	0.196	< 0.001				
HL	81.39	< 0.001	< 0.001	< 0.001	0.348	< 0.001				
MHW	73.81	< 0.001	0.003	< 0.001	0.001	< 0.001				
Tarsus	142.40	< 0.001	< 0.001	< 0.001	0.093	< 0.001				
MTnoC	121.10	< 0.001	< 0.001	< 0.001	0.990	< 0.001				
TL	28.15	< 0.001	0.004			< 0.001				
Tail	15.10	< 0.001	0.034	0.097	0.856	< 0.001				

* Kruskal-Wallis test and Mann–Whitney post hoc comparisons were used.

Table IV. Discriminant functions for species and sex determination in southern and northern royal albatrosses. For species determination, scores >0 indicate SRA and <0 NRA. For sex determination, scores >0 indicate male and <0 female.

Species determination

D1 = - 31.385213 + (0.0830137 * Culmen) + (-0.225838 * BDU) + (0.218976 * Tarsus) D2 = - 33.361657 + (0.0689926 * Culmen) + (0.179565 * Tarsus) Sex determination Southern royal D3 = - 51.595711 + (0.611952 * BDU) + (0.269481 * HL) Northern royal D4 = - 55.805479 + (0.52554 * BDU) + (0.242787 *MTnoC) D5 = - 53.541313 + (0.139945 * Culmen) + (0.463007 * BDU) + (0.128741 * HL)

Appendix 1. Description of measurements

The 19 measurements taken in albatrosses included: bill length (Culmen; exposed culmen, Fig. S1A), basal bill depth (BBD; measured at the base of the culmen, Fig. S1B), minimum bill depth (MBD; measured roughly halfway along the bill, Fig. S₁C), bill depth at unguis (BDU; the greatest depth from the dorsal surface of the unguis to the angle of the gonys, Fig. S1D), basal bill width (BBW; measured at the base of the maxilla, Fig. SiE), basal bill width at commissures (BBWb, see Fig. S₁F), head length (HL; from the base of the culmen to the occiput at the rear of the skull, Fig. SIG), maximum head width (MHW; measured at the widest part of the skull, behind the eyes, Fig. S1H), tarsus (from the back of the joint between the tibiotarsus and tarsometatarsus to the front edge of the bent foot, at the joint between the tarsometatarsus and the middle toe, Fig. S1), middle toe with claw (MTCLAW; on the upper side from the tip of the claw to the joint between the toe and the tarsus, Fig. SIJ), middle toe without claw (MTnoC; on the upper side from the base of the claw to the joint between the toe and the tarsus, Fig. SiK), claw (from the base to the tip of the claw, Fig. S1L), total length (TL; measured from the back, from the tip of the culmen to the tip of the central rectrices, with the back of the bird on a flat surface and the bill parallel to it), wing length (WL; from the carpal joint to the tip of the longest primary, Pio, and stretching the curve of the primary) and wing cord (WC; similar to WL but without stretching the wing) from both right and left wings, tail length (Tail; with a metal ruler inserted parallel between the two central rectrices, measuring from the base to the tip of them) and wing span (WS; between the wing tips when the wing were stretched maximally, measured from the back and with the bird lying on its back on a flat surface). Total length, wing length, tail length and cord and wing span were measured with metallic rules to the nearest 1 mm. All other measurements were made with a Vernier caliper to the nearest 0.1 mm.



Fig. S1. Pictures from bycaught *Diomedea* birds showing the main measurements taken to royal albatrosses. A) Bill length (Culmen). B) Basal bill depth (BBD). C) Minimum bill depth (MBD). D) Bill depth at unguis (BDU). E) Basal bill width (BBW). F) Basal bill width at commissures (BBWb), G) Head length (HL). H) Maximum head width (MHW). I) Tarsus. J) Middle toe with claw (MTCLAW). K) Middle toe without claw (MTnoC). L) Claw.

Capítulo 6 | Chapter 6

Ingestión de desechos marinos por albatros en el Océano Atlántico sudoccidental

Marine debris ingestion by albatrosses in the southwest Atlantic Ocean

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Abstract

Plastics and other marine debris affect wildlife through entanglement and by ingestion. We assessed the ingestion of marine debris by seven albatross species in the southwest Atlantic by analysing stomach contents of birds killed in fisheries. Of the 128 specimens examined, including four *Diomedea* species (n=78) and three *Thalassarche* species (n=50), 21 (16.4%) contained 1-4 debris items, mainly in the ventriculus. The most common type was plastic fragments. Debris was most frequent in *Diomedea* species (25.6%) and, particularly, *D. sanfordi* (38.9%) and very rare in *Thalassarche* species (2.0%), presumably reflecting differences in foraging behavior or distribution. Frequency of occurrence was significantly higher in male than female *Diomedea* albatrosses (39.3% vs. 18.0%). Although levels of accumulated debris were relatively low overall, and unlikely to result in gut blockage, associated toxins might nevertheless represent a health risk for *Diomedea* albatrosses, compounding the negative impact of other human activities on these threatened species.

Keywords: Seabirds, Procellariiformes, Pollution, Plastics

1. Introduction

Plastics and other marine debris are increasing in the oceans worldwide and can be found even in the most remote and isolated regions (Barnes et al. 2009; Cózar et al. 2014). Plastic pollution affects marine wildlife by entanglements and ingestion. The latter can result in digestive tract blockage or ulceration, or poisoning from toxins adsorbed onto the debris surface or released after digestion, leading to reduced body condition and even to death (Azzarello and Van Vleet 1987; Ryan 1988; Ryan et al. 1988; Teuten et al. 2009; Tanaka et al. 2013).

There are many published studies on the ingestion of marine debris by seabirds (Ryan 1987; Colabuono et al. 2009; Codina-García et al. 2013), and very often these species are used as indicators of marine pollution (Robards et al. 1995; Ryan 2008; Ryan et al. 2009; Bond et al. 2013; Elliott and Elliott 2013). Among seabirds, species in the order Procellariiformes (albatrosses and petrels) seem to be the most vulnerable to effects of plastic ingestion (Ryan 1987). This is due to their smaller ventriculus (gizzard), and often a limited ability to regurgitate ingested plastics (Azzarello and Van Vleet 1987). The latter is a particular problem for most petrels (except giant petrels *Macronectes* spp.), as the narrow, angled junction between the proventriculus and ventriculus prevents the passage of material back up to the mouth (Furness 1985b; Ryan 1987; Spear et al. 1995). To some extent, this must also be an issue for albatrosses; although they do regurgitate plastic and other debris (Huin and Croxall 1996; Imber 1999; Phillips et al. 2010), there is a higher frequency of plastics in the ventriculus than proventriculus (Colabuono et al. 2009).

Albatrosses are among the seabirds that are most susceptible to bycatch in fisheries, and some face other major threats at breeding sites, including predation by alien invasive mammals (Croxall et al. 2012). Given their status as the most threatened of any bird family according to the World Conservation Union (IUCN), it is important to assess the relative risk from plastic ingestion for different species. In this study, we assess the ingestion of marine debris by seven species of albatrosses in the southwest Atlantic, through the analysis of stomach contents from carcasses recovered as fisheries bycatch.

2. Methods

Samples were obtained from albatross carcasses collected on pelagic longline vessels. These specimens were caught incidentally by Uruguayan commercial and research vessels in 2005-12,

and 2009-13, respectively, and Japanese commercial vessels in 2009-11 operating off Uruguay under an experimental fishing license (Jiménez et al. 2010, 2014, 2015). All vessels fished in shelf break, slope and deeper waters off Uruguay, and Uruguayan commercial vessels also operated in international waters (Jiménez et al. 2014).

The digestive tract (esophagus, proventriculus and ventriculus) of 128 specimens of seven species of albatrosses were examined (Table 1). These were of two genera; four species of great albatrosses (Diomedea spp.) and three species of mollymawks (Thalassarche spp.). Species of great albatrosses were identified in the laboratory; Northern royal Diomedea sanfordi and Southern royal *D. epomophora* albatrosses were distinguished by their plumage, and Wandering albatrosses D. exulans were separated from Tristan albatrosses D. dabbenena by a morphometric discriminant function (Cuthbert et al. 2003). White-capped albatrosses *Thalassarche steadi* were identified by molecular analysis (Jiménez et al. 2015). The sex was determined by examining the gonads. Both royal albatross species (Jiménez et al. 2014) and White-capped albatrosses (Jiménez et al. 2015) were captured on the shelf break off Uruguay. Black-browed T. melanophris and Wandering albatrosses were captured on the shelf break and deeper waters off Uruguay $(34^{\circ}-36^{\circ} \text{ S}, 51^{\circ}-53^{\circ}\text{W})$ and in adjacent international waters (35°-38° S, 48°-50°W). Two of the Tristan albatrosses were captured in deep waters off Uruguay (35°28'S-51°20'W and 37°29'S-51°57'W), two others in international waters off Brazil (28°38'S-42°41'W and 30°25'S-43°47'W) and two breeding birds (with unfeathered brood patches) were captured at 35°28'S-29°30'W. The only Atlantic yellownosed albatross *T. chlororhynchos* was caught in Uruguayan waters (35°41'S-51°25'W) (Fig. 1).

All debris items found in each part of the digestive tract were counted and categorized as follows: plastic fragments (rigid plastics, usually pieces of larger objects); plastic pellets (raw material); nylon line; hooks; and wood. For each species, the relative frequency of occurrence (FO%) of each plastic category was estimated. Because almost all debris were found in great albatrosses, and mainly Northern royal albatrosses (see Results), we first used a χ_2 test to evaluate whether there was an effect of sex on plastic incidence in these species. Subsequently, a generalized linear model (GLM), using a binomial error distribution and the log link function, was fitted to the data for Northern royal albatross; sex was included as a categorical variable and its significance examined using a Likelihood Ratio Test (LRT). Analyses were conducted in R (http://www.r-project.org/).

3. Results

Of the 128 albatross specimens analyzed, 21 (FO%=16.4) had one to four items of marine debris in their digestive tracts. Almost all debris items were located in the ventriculus; only two birds also had debris in their proventriculus (Table 1). Debris types were dominated by plastic fragments (Fig. 2). Fisheries-related items were also found, including a hook and pieces of nylon line. There was a single debris item (a small white plastic pellet) in the stomach of only one of the 50 mollymawks examined, a Black-browed albatross (overall FO%=2.0). The great majority of the debris items were found in great albatrosses (FO%=25.6). Plastics were found mainly in the two royal albatross species, with a higher FO% in Northern royal albatross (Table 1). No plastic or other marine debris were found in the Wandering albatrosses.

The presence of debris varied significantly between sexes in the great albatrosses ($\chi^2 = 4.27$, d.f. = 1, P < 0.05); the FO% was significantly higher in males (39.3% of 28 birds examined) than females (18.0% of 50 birds examined). This was also the case in the analyses restricted to Northern royal albatrosses (binomial GLM; LRT, $\chi^2 = 4.39$, d.f.= 1, p<0.05), with a higher incidence of debris in males. Based on the rate of change in odds, the probability of occurrence of debris was 4.5 times higher (453%, 95% confidence limit = 104–1970%) in males than females.

4. Discussion

Previous studies have quantified the occurrence of marine debris ingested by albatrosses in the southwest Atlantic, including Wandering, Black-browed and Grey-headed (*Thalassarche chrysostoma*) albatrosses breeding at South Georgia (Huin and Croxall 1996), Atlantic yellow-nosed, Sooty (*Phoebetria fusca*) and Tristan albatrosses breeding at Gough Island (Furness 1985a), and Black-browed and Atlantic yellow-nosed albatrosses wintering off southern Brazil (Petry et al. 2007; Barbieri 2009; Colabuono et al. 2009; Tourinho et al. 2010). Presence of plastic particles has also been noted for two Southern royal albatrosses found dead in Brazil (Petry et al. 2001). In addition, there is a study on the incidence of plastics in Northern and Southern royal albatrosses breeding at New Zealand colonies (Imber 1999). Plastics were common in the breeding birds sampled at South Georgia and New Zealand, but absent at Gough Island. The numbers of birds examined at Gough Island were small, however, and so our study provides a robust quantification of the occurrence of plastic and other debris in a wide range of albatross species in the southwest

Atlantic, including, for the first time, wintering birds from the New Zealand region (Whitecapped, Northern royal and Southern royal albatrosses).

Almost all plastic items found were in the ventriculus, as in previous studies (Colabuono et al. 2009). This suggests that most ingested debris, including large items such as the hook and line that were found in one proventriculus (Fig. 2), or smaller items that do not enter a full ventriculus, tend to be regurgitated. Indeed, the relatively small ventriculus (mean values and range in mm; this study) of great albatrosses (length = 35.5, 27.3-43.0; width = 26.6, 19.9-34.3; n=69 birds) and mollymawks (length = 29.3, 20.2-40.2; width = 20.6, 13.7-33.6; n=46 birds) probably limits the number of plastic fragments that are retained, and explains the lower number of items found in comparison with medium-sized petrels and shearwaters in other studies (Furness 1983; Furness 1985a; Ryan 2008; Colabuono et al. 2009). The latter often accumulate smaller items than those reported in our study (Ryan 1987; Colabuono et al. 2009), which may reflect a ventriculus (mean length x mean width = 29.7 x 21.8 mm in *Procellaria* petrels, n=26; 36.5 x 24.6 mm in great shearwater *Puffinus gravis*, n=1; unpublished data) that is relatively large given their markedly smaller body size.

The previous studies in southern Brazil were of Black-browed and Atlantic yellow-nosed albatrosses incidentally caught in fisheries (Colabuono et al. 2009) and beach-stranded birds collected from the mid 1990s to mid 2000s (Petry et al. 2007; Barbieri 2009; Colabuono et al. 2009; Tourinho et al. 2010). The reported frequency of occurrence of marine debris in Black-browed albatrosses was between 12% and 73% (sample size range: 26-59 birds), excluding a study of only two birds which both had debris (Tourinho et al. 2010). As in our study, plastics always accounted for the majority of the ingested debris, followed by fishing-related items, such as nylon lines and hooks. The type and number of plastics varied, but plastic fragments were the most common, followed by nylon lines and plastic pellets (Petry et al. 2007; Barbieri 2009; Colabuono et al. 2009; Tourinho et al. 2010). For Atlantic yellow nosed albatrosses, the frequency of occurrence of marine debris in previous studies was 7% (Colabuono et al. 2009) and 44% (Barbieri 2009), with sample sizes of 29 and 9 birds, respectively. Similar to Black-browed albatross, the plastics were mainly fragments, and fishing lines and plastic pellets were recorded infrequently. In the present study we found a low frequency of plastic in Black-browed albatross (FO% = 3.1). For Atlantic yellow-nosed albatross, we had only one sampled individual, precluding interpretation, but we

also analyzed 17 White-capped albatrosses and failed to find any plastic item. It is important to note that most studies of plastic ingestion by mollymawk species in the southwest Atlantic are of beach-stranded birds (see references above), which have often starved and are in poor body condition compared with birds incidentally caught in fisheries (Colabuono et al. 2012). A proportion of the beached birds may have died due to complications associated with plastic ingestion, and if so, would provide a biased representation of plastic retention by the wider population (Ryan 1987; Codina-García et al. 2013). Although a study in southern Brazil found no significant differences between the number of plastic items in bycaught and beach-stranded Procellariiformes (Colabuono et al. 2009), the sampling included several species of petrel which are well known to ingest and retain plastics at higher frequencies than albatrosses. As birds caught incidentally in fisheries are more likely to provide a random sample, the low frequency of plastics found in mollymawks in our study indicates a lower rate of plastic retention than that suggested by previous studies of beach-stranded albatrosses, which seem likely to have been overestimates.

Contrasting with the mollymawks, a higher frequency of plastics was found in great albatrosses in our study, although varying among species; FO% ranged from o in Wandering albatrosses to 38.9% in Northern royal albatrosses. The greater incidence in wintering royal albatrosses is consistent with the large number of plastic items found regurgitated on the ground near nests at breeding sites of this species in New Zealand; 16 and 72 plastic items were found in 34 and 151 samples from Northern royal albatrosses at Chatham Islands and Taiaroa Head, respectively, and 81 plastic items were found in 79 samples from Southern royal albatrosses at Campbell Island (Imber 1999). Although we found no marine debris in the Wandering albatrosses, studies at Bird Island, South Georgia, have reported plastic and fishing-related items (including rubber, hooks and line) in diet samples and regurgitated on the ground by both adults and chicks (Huin and Croxall 1996; Phillips et al. 2010). However, these are often large items and for example, during 1993/1994 the reported incidence of plastics was low; 11 items at 1329 nests checked (Huin and Croxall 1996). Together, these results can be explained if Wandering albatrosses do ingest marine debris but these tend to be large items that are later regurgitated, and hence it would be rare for small plastic items to be retained in the ventriculus. In contrast, possibly because of differences in diet and foraging strategies, the two royal albatrosses, and potentially Tristan albatross (33% of the six birds sampled had ingested plastic fragments, nylon lines or wood) may have a greater

tendency to ingest and retain small plastic items. However, some caution should be exercised in interpreting our results from Wandering, and particularly Tristan albatrosses due to low sample size, and so this hypothesis would need to be tested further.

Differences in densities of floating plastic in the main foraging areas of great albatrosses could also explain the variability in plastic incidence between species and sexes. Wandering and Tristan albatrosses breed in South Georgia and Tristan da Cunha, respectively, and both breeding and nonbreeding birds use the southwest Atlantic; Wandering albatrosses forage over an extensive region from oceanic waters to the shelf break, whereas Tristan albatrosses forage almost exclusively in oceanic waters in the subtropical region (Nicholls et al. 2002; Cuthbert et al. 2005; Reid et al. 2013). The reported plastic accumulation area for the subtropical south Atlantic gyre (Cózar et al. 2014; Ryan 2014) matches very well with the distribution of Tristan albatross, at least during breeding, suggesting a greater susceptibility in this species to plastic ingestion. On the other hand, plastic also tends to accumulate over the shelf-break and continental shelf areas of the southwest Atlantic because of the density of fishing vessels, the main source of marine debris for seabirds in the region (Copello and Quintana 2003, 2008), and the occurrence of numerous oceanographic fronts (Acha et al. 2004). This may at least partially explain the greater frequency of plastic in royal albatrosses, which forage extensively over the continental shelf and shelf-slope (Nicholls et al. 2002; Jiménez et al. 2014) and interact with large number of fishing vessels, including trawlers, longliners and others, mainly off Uruguay and Argentina (Favero et al. 2011; Jiménez et al. 2014). However, it is also probable that some of birds sampled in our study had retained plastic particles in their ventriculus from the Pacific Ocean. Differences in at-sea distribution in relation to sex have also been noted in great albatrosses, with females foraging in more northern areas than males (Prince et al. 1998). The significantly higher frequency of plastic in male Northern royal albatrosses could indicate greater availability of floating plastics in their foraging areas in the southern continental shelf of South America.

The striking differences among great albatross and mollymawk species in the incidence of plastic debris seem likely to also reflect differences in distribution or foraging behavior. Similar to royal albatrosses, White-capped and Black-browed albatrosses are also distributed over shelf areas and the shelf-break (but the latter also in coastal and oceanic waters) (Phillips et al. 2005; Jiménez et al. 2010, 2015; Copello et al. 2013). A plausible explanation is that individual royal albatrosses

spend a higher proportion of the time in frontal zones in these areas where there is more floating plastic, or following vessels (picking up the rubbish thrown overboard) than mollymawks. Alternatively, most plastic ingestion by royal albatrosses could be in areas other than Uruguay; again, the southern shelf of South America or around breeding colonies in the Pacific Ocean.

Given their small breeding populations and low productivity, great albatrosses are likely to be the species most affected by pelagic longline fisheries in the southwest Atlantic Ocean (Jiménez et al. 2012), with royal albatrosses probably also killed in small numbers by trawlers (Favero et al. 2011). Recently, high levels of bycatch in the pelagic longline fishery were reported for both royal albatross species in Uruguayan and adjacent waters (Jiménez et al. 2014). We have found evidence that Northern royal albatrosses also interact with demersal longliners, as a hook often used in fisheries for Patagonian toothfish *Dissostichus eleginoides* or other demersal target species was found in the proventriculus of a male. In addition, our study showed that royal albatrosses accumulated plastic in their digestive tract at a higher frequency than other common albatross species occurring in the southwest Atlantic. Although overall, levels of accumulated debris were relatively low and unlikely to result in digestive tract blockage, the associated toxins might nevertheless represent a health risk for the great albatrosses. This may compound the negative impact of other human activities, including fishing, on these threatened species.

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Species	Sampled stomachs		Stomachs with debris			Number of debris items					
	Ν	F/M	Ν	F/M	FO%	Plastic fragments	Pellet	Nylon Line	Hook	Wood	Total
Great Albatrosses											
Tristan Albatross Diomedea dabbenena	6	5/1	2	1/1	33.3	4	0	2	0	1	7
Wandering Albatross Diomedea exulans	12	8/4	0	-	0.0	0	0	0	0	0	0
Northern Royal Albatross Diomedea sanfordi	36	23 / 13	14	6/8	38.9	25	0	0	1	0	26
Southern Royal Albatross Diomedea epomophora	23	13 / 10	4	2/2	17.4	5	0	0	0	0	5
Royal Diomedea spp.	1	1/0	0	-	0.0	0	0	0	0	0	0
Mollymawks											
White-capped Albatross Thalassarche steadi	17	9/8	0	-	0.0	0	0	0	0	0	0
Black-browed Albatross Thalassarche melanophris	32	20/11*	1	0/0*	3.1	0	1	0	0	0	1
Atlantic yellow-nosed Albatross Thalassarche											
chlororhynchos	1	0/1	0	-	0.0	0	0	0	0	0	0
All Species	128	79 / 48 *	21	9/11*	16.4	34	1	2	1	1	39

Table 1. Sample size, sex ratio (F: females; M: males), relative frequency of occurrence (FO%) and types of marine debris found in the digestive tract of albatrosses caught in the southwest Atlantic Ocean.

* The sex of one bird was unknown.



Figure 1. Distribution of the sampled bycaught *Diomedea* (A) and *Thalassarche* (B) albatrosses. The Uruguayan Economic Exclusive Zone (EEZ; dotted line) and the 200 m isobath (dashed line) are represented.



Figure 2. Marine debris found in great albatrosses (southwest Atlantic). The codes are the species [Dd=*Diomedea dabbenena* (first row); De= *D. epomophora* (second row); Ds= *D. sanfordi* (remaining rows)] plus the reference number. There are two samples from a small number of individuals. All items were from the ventriculus, except for two individuals where those from the pro-ventriculus (p) and ventriculus (v), are labelled accordingly. Db 413: nylon lines, Db413: wood; Ds543 hook with multifilament line; remaining items are plastic fragments. Black line = 1cm scale.

Capítulo 7

Discusión General y Conclusiones

En la presente tesis por primera vez se caracterizó la captura incidental de grandes albatros (*Diomedea* spp.) en la pesca con palangre pelágico en el Atlántico sudoccidental (Capítulos 3 y 5) y se determinó la importancia relativa de los descartes de diversas pesquerías en la ecología trófica de estas especies (Capítulo 2). Las tasas de captura incidental variaron espacio-temporalmente, reflejando la distribución y estacionalidad de las especies. También se determinaron varios factores relacionados a las preferencias de hábitat y de la operativa de pesca que afectan su captura incidental (Capítulo 3). El análisis de la segregación espacial entre sexos en grandes albatros permitió determinar que la misma ocurre dentro y fuera de la estación reproductiva, y que produce una mayor exposición para la hembras, además de mortalidad sesgada hacia este sexo, en la pesca con palangre pelágico en esta región (Capítulos 4 y 5).

El análisis de su ecología trófica aportó evidencia del grado de repartición inter-específica de nicho entre estas especies (Capítulo 2). Se apoyó la hipótesis de que la segregación espacial lleva a una variación en la composición de la dieta. Las pesquerías fueron una fuente importante de alimento en la dieta, en particular la pesquería de arrastre de altura para las dos especies de albatros reales. De hecho, se observó un solapamiento sorprendentemente alto en la dieta de estas dos especies altamente relacionadas, aunque sus nichos isotópicos mostraron una leve divergencia. La evidencia reunida en grandes albatros, pero también en otras especies de albatros y petreles relacionadas, permitió concluir que los descartes de la pesca de arrastre en la plataforma continental pueden aumentar el solapamiento en las dietas y permitir la coexistencia de las especies dentro de las comunidades de aves marinas.

Al estudiar la ecología trófica de estas especies se detectó otra amenaza de origen antrópico: la contaminación por plásticos, los cuales fueron registrados acumulados en sus tractos digestivos (Capítulo 6). Los grandes albatros, y en particular los albatros reales, presentaron mayor

ocurrencia de plásticos que las especies de albatros del género *Thalassarche* spp. También se observaron diferencias entre sexos. De esta manera, se reunió evidencia adicional de que la segregación inter e intra-específica en grandes albatros los expone de forma diferencial a las distintas amenazas.

SEGREGACIÓN DE ALBATROS EN EL MAR

Segregación inter-específica y repartición de nicho

La repartición inter-específica de nicho en grandes albatros en el Atlántico sudoccidental fue propuesta a través de datos de rastreo del albatros real del norte y del albatros errante (Nicholls et al. 2002). Subsecuentes estudios en el albatros de Tristán (Cuthbert et al. 2005, Reid et al. 2013) confirmaron diferentes grados de segregación espacial o uso de hábitats entre especies. La recuperación de anillos del albatros real del sur permite suponer que los individuos se distribuyen principalmente sobre plataforma continental (Moore & Bettany 2005). En la presente tesis, la distribución de las capturas incidentales en palangre pelágico de estas especies, sus nichos isotópicos, así como los valores de δ^{13} C en plumas, aportaron nueva evidencia sobre la repartición de la dieta de las especies, estimada tanto por análisis convencionales de contenidos estomacales, como a través de modelos de mezcla de isótopos estables.

La ocurrencia de capturas incidentales de las cuatro especies de grandes albatros en palangre pelágico en el Atlántico sudoccidental (analizado para las flotas de Uruguay y de Japón) varió con la batimetría, distancia al talud y distancia a la costa. Las capturas de albatros de Tristán fueron registradas en promedio en aguas más profundas y distantes a la costa que las otras especies, mientras que en el albatros real del norte, las capturas ocurrieron más cercanas al talud y en menores profundidades. La ocurrencia de capturas del albatros errante tendió a aumentar hacia aguas oceánicas y las del albatros real del sur en dirección opuesta, hacia el talud y costa (Capítulo 3). Esto confirma los patrones de segregación propuestos; las dos especies de albatros reales son las más neríticas, distribuyéndose principalmente sobre la plataforma y talud, mientras que el albatros errante, y particularmente el albatros de Tristán, explotan aguas más oceánicas. También se determinaron algunos factores que reflejan las preferencias de hábitat de estas especies. En

ambas especies de albatros reales, las mayores capturas registradas sobre la región del talud de Uruguay ocurrieron en aguas frías, reflejando sus preferencias por aguas sub-antárticas (Capítulo 3). Las capturas incidentales del albatros errante ocurrieron principalmente en la flota Uruguaya que operó en una amplia región del Atlántico sudoccidental desde aguas tropicales en los 19° S hacia al sur. Las capturas hacia aguas más frías y en zonas con mayores vientos (Capítulo 3) reflejan sus preferencias por aguas subtropicales y sub-antárticas (Capítulo 4), los cuales son hábitats favorables en términos del desempeño del vuelo en grandes albatros (Shaffer et al. 2001, Capítulo 5).

Excluyendo al albatros de Tristán debido al bajo tamaño de muestra, los análisis del solapamiento y de la amplitud de los nichos isotópicos durante la estación no reproductiva (estimada a partir de δ^{13} C y δ^{15} N en plumas en crecimiento de la cabeza) confirmaron la divergencia de nicho entre el albatros errante y las dos especies de albatros reales (Capítulo 2). En los ambientes marinos, los valores de δ^{13} C pueden proporcionar una idea general de la región oceanográfica o de determinados gradientes (Forero et al. 2004, Barrett et al. 2007, Phillips et al. 2009). Por ejemplo, el uso relativo de regiones costeras, de bajas latitudes o de zonas demersales se refleja en valores enriquecidos en ¹³C con respecto a los de regiones oceánicas, altas latitudes y zonas pelágicas, respectivamente. Aunque los valores no fueron significativos, posiblemente debido a que los δ^{13} C en plumas en muda reflejaron una región restringida (ver Capítulo 2), las dos especies de albatros reales mostraron valores de 13C más altos que el albatros errante. Esto concuerda con la preferencia de estas especies por la plataforma continental y por aguas oceánicas, respectivamente.

La tesis permitió a su vez apoyar la hipótesis de que la segregación espacial lleva a diferencias en la composición de la dieta (Capítulo 2). La dieta de las especies neríticas de albatros reales contrastó con la del albatros errante de hábitos oceánicos. En los albatros reales, los contenidos estomacales reflejaron una mayor proporción de peces demersales (dominados por *Bassanago albascens* y *Merluccius hubbsi*), seguido por el calamar *Illex argentinus*. Esta composición fue atribuida al descarte de la pesca de arrastre de altura (ver abajo). En cambio, la dieta del albatros errante estuvo dominada por calamares del género *Histioteuthis*. Estos resultados fueron confirmados mediante modelos de mezcla de isótopos estables, en base a los δ^{15} N y δ^{13} C de las plumas en crecimiento de los albatros y los tejidos (músculo y picos de calamares) de diversas potenciales presas.

A su vez, la tesis puso a prueba y apoyó la hipótesis de que los descartes pesqueros permiten un solapamiento en la dieta y en el nicho trófico de las especies de grande albatros, siendo evidente en aquellas especies más neríticas expuestas a la pesca de arrastre. El uso complementario de los análisis de contenidos estomacales y de isótopos estables demostró la importancia de los descartes de la pesca de arrastre en varias especies neríticas de albatros y petreles. Los ejemplos más evidentes fueron las dietas excepcionalmente similares de las dos especies de albatros reales, ambas dominadas por descartes de esta pesquería. Los resultados obtenidos fueron interpretados como pruebas convincentes de que en aguas de la plataforma continental el alimento superabundante y artificial proporcionado por la pesca de arrastre permite la coexistencia, y por lo tanto un alto solapamiento del nicho trófico entre especies estrechamente relacionadas.

Segregación espacial entre sexos

En albatros errante, varios estudios principalmente basados en datos de rastreo durante la estación reproductiva indicaron que los machos tienden a pasar mayor tiempo en latitudes más alta que la hembras (Weimerskirch et al. 1993, Prince et al. 1998, Xavier & Croxall 2005, Froy et al. 2015). Las recuperaciones de anillos de albatros errantes en pesquerías sugieren que esta segregación también ocurre durante el periodo no reproductivo (Croxall & Prince 1990, Prince et al. 1998). Debido a que las plumas de las aves son mudadas, y por lo tanto sintetizadas, fuera de la estación reproductiva (Ginn & Melville 1983), los análisis de isótopos estables de estos tejidos también han sido útiles para confirmar esta segregación entre sexos en el albatros errante durante la estación no reproductiva (Phillips et al. 2009). Los datos de captura incidental de aves en pesquerías también pueden ser informativos; debido a que se espera una mayor proporción de hembras en latitudes más al norte, las mismas estarían más expuestas a la captura incidental que los machos en las pesquerías que operan en estas zonas (Capítulo 5, y ver abajo).

En la tesis se demostró como la segregación varió entre sexos en los distintos estadios de la estación reproductiva del albatros errante de South Georgia, exponiendo consistentemente a las hembras a un mayor riesgo de captura incidental en las pesquerías de palangre pelágico (y a cada

una de las flotas) que operan en el Atlántico sudoccidental (Capítulo 4). De hecho, los análisis de las recuperaciones de anillos de aves capturadas en esta pesca indicaron que esta mayor exposición llevó a una mayor mortalidad incidental (Capítulo 4). Esta relación permitió una evaluación indirecta, por primera vez, de la segregación espacial entre sexos de las otras dos especies de grandes albatros durante el periodo no reproductivo: los albatros reales del sur y del norte (Capítulo 5). Las dos hipótesis que explican la segregación espacial entre sexos; exclusión competitiva o diferencias en el desempeño del vuelo, son mediadas por la existencia de un pronunciado dimorfismo sexual en tamaño (ver Capítulos 1 y 5). En base a una muestra de aves capturadas incidentalmente en palangre pelágico en el Atlántico sudoccidental, identificadas a nivel de especies y sexo, se determinó que ambas especies de albatros presentan dimorfismo sexual en tamaño (capítulo 5). Este resultado significa que la segregación espacial entre sexos puede ser generalizada dentro de los grandes albatros, y aporta nueva evidencia de que ocurre fuera de la estación reproductiva.

CAPTURA INCIDENTAL E IMPLICANCIAS PARA LA CONSERVACIÓN

Las cuatro especies de grandes albatros que se distribuyen en el Atlántico sudoccidental se encuentran globalmente amenazadas según la Unión Internacional para la Conservación de la Naturaleza, IUCN (ver Tabla 1 en Capítulo 1). Aunque estas especies están consideradas dentro de las más afectadas por la pesquería de palangre pelágico en el Atlántico sudoccidental (Jiménez et al. 2012), hasta ahora existía muy poca información sobre su interacción con pesquerías (incluyendo su captura incidental) en esta región, particularmente para los albatros reales del norte y del sur (Robertson et al. 2003). La presente tesis constituye el primer estudio detallado a nivel de especies sobre la captura incidental de los grandes albatros en palangre pelágico (Capítulo 3). Se determinó la variación espacio-temporal de las tasas de captura incidental en dos flotas: la de Uruguay operando en una amplia región del océano Atlántico sudoccidental (19–47°S y 20–60°W) durante 2004-2011 y la de Japón con permiso de pesca dentro de aguas de Uruguay en 2009-2011. Esto último representa a su vez la primera evaluación sobre la mortalidad de aves marinas en la flota de Japón en el Atlántico sudoccidental. La situación registrada en ambas flotas debe considerarse como casos de estudio en el contexto de todas las flotas que operan en el

Atlántico sudoccidental, las cuales son reguladas por la Comisión Internacional para la Conservación del Atún Atlántico (ICCAT). De hecho, el solapamiento de datos de rastreo del albatros errante con el esfuerzo de todas las flotas de ICCAT confirmó que las áreas y épocas de mayor riesgo de captura incidental coinciden con las tasas relativas de captura de las flotas de Uruguay y Japón (Capítulo 4).

Cabe destacar los altos niveles de captura incidental registrados por primera vez para los albatros reales del norte y del sur, sobre la región del talud (Capítulo 3). Para interpretar este resultado es importante considerar la distribuciones relativas del esfuerzo de pesca de todas las flotas que operan en la región (Capítulo 4), que en gran parte se desarrolla en aguas internacionales sobre la confluencia Brasil/Malvinas-Falkland, principalmente por Taiwán, pero también Brasil, España, Uruguay, Japón y Portugal, entre otros. La región del talud donde se distribuyen los albatros (principalmente al sur de los 30°S) y que opera esta pesquería, se encuentra principalmente dentro de la Zona Económica Exclusiva (ZEE) de Brasil y de Uruguay y por tanto estas aguas son usadas por estos países y eventualmente por otros con permiso de pesca, como fue mostrado para Japón en la presente tesis. Debido a los hábitos más oceánicos, los albatros errante y de Tristán se encuentran expuestos a la mortalidad incidental tanto en el talud (principalmente la primera especie), como en una amplia región del Atlántico sudoccidental que incluye el área de mayor esfuerzo de pesca (Capítulos 3 y 4). Por lo tanto, es de suponer un mayor impacto de la pesca con palangre pelágico en estas dos especies (Jiménez et al. 2012). Para especies de albatros amenazadas, una estimación conservativa sugiere que una mortalidad anual (en número de individuos) superior al 1.5% del número de parejas, es suficiente para generar un declive poblacional (Dillingham & Fletcher 2011). Esto significa la muerte de pocas decenas de aves al año para la población de South Georgia del albatros errante y para el albatros de Tristán, y varias decenas de aves en las dos especies de albatros reales (Dillingham & Fletcher 2011, Jiménez et al. 2012). Para las dos primeras poblaciones, estos valores posiblemente sean superados sólo en el palangre pelágico en el Atlántico sudoccidental durante la mayoría de los años (Jiménez et al. 2012, Klaer 2012). Esto está de acuerdo con las disminuciones dramáticas experimentadas por estas dos poblaciones en décadas recientes (Poncet et al. 2006, Cuthbert et al. 2014). La situación no es tan clara para el albatros real del norte y el albatros real del sur; sus tendencias poblacionales son desconocida o presumiblemente estable, respectivamente.
Los grandes albatros son afectados por otras pesquerías y, debido a que son altamente migratorios, también en otras regiones (Gales et al. 1998, Waugh et al. 2008a, Petersen et al. 2009, Brothers et al. 2010). En el Atlántico sudoccidental, también existen escasos registros de mortalidad de grandes albatros con palangre de fondo (Favero et al. 2003), aunque actualmente el nivel de mortalidad incidental de estas especies parece ser bajo o nulo (Favero et al. 2013, Jiménez et al. 2015). Sin embargo, como fue determinado a través del estudio de su dieta en la presente tesis (Capítulo 2), las dos especies de albatros reales se encuentran altamente expuestas en esta región a la pesca de arrastre de altura, donde existe evidencia reciente de mortalidad incidental (Favero et al. 2011). Por lo tanto, la suma de los impactos negativos generados por las distintas pesquerías, principalmente las de palangre pelágico y de arrastre de altura, tanto en el Atlántico sudoccidental como en otras regiones del Pacífico e Indico, podría una amenaza considerable para estas especies altamente migratorias.

Los albatros son vulnerables a cambios en la fecundidad y sobrevivencia, siendo esta última el parámetro demográfico más importante que influye en las tendencias poblacionales (Weimerskirch & Jouventin 1987, Gales 1998). Como fue discutido en la tesis (Capítulos 1, 4 y 5), la mortalidad sesgada hacia un sexo agrava el impacto de la captura incidental, reduciendo inmediatamente la población efectiva, pero también la fecundidad. El efecto de un sesgo entre la proporción de sexos es acumulativo y, a diferencia de una disminución en la supervivencia, su impacto sobre la demografía de los albatros persiste aun después de que cesa la mortalidad en palangre (Mills & Ryan 2005). Excluyendo al albatros de Tristán a causa del bajo tamaño de muestra, se confirmó que la captura incidental de grandes albatros en palangre pelágico en el Atlántico sudoccidental produce una mortalidad sesgada hacia las hembras (Capítulos 4 y 5, ver arriba Sección sobre Segregación espacial entre sexos). Para el caso del albatros errante de South Georgia, se considera que la mortalidad actual en pesquerías que operan en regiones al sur, donde los machos son más abundantes, es relativamente baja (Waugh et al. 2008b, ver Capítulo 4). Esto sugiere que el impacto del palangre pelágico en las hembras no es contrarrestado (ver Capítulo 4). Por lo tanto, el solapamiento consistentemente alto de las hembras adultas con el esfuerzo pesquero de todas las flotas de palangre pelágico y la asociada mortalidad sesgada hacia este sexo, podrían explicar las menores tasas de sobrevivencia de hembras adultas observadas desde los 1970's en esta población (Croxall et al. 1990, Croxall et al. 1998). Para los albatros reales se conoce bastante poco sobre la mortalidad en otras regiones, incluyendo en los océanos Pacífico e Índico.

Una evaluación de la mortalidad global en pesquerías de estas especies, con información del sexo y edad de las aves capturadas, debería considerarse de alta prioridad.

El Acuerdo sobre la Conservación de Albatros y Petreles (ACAP) es un tratado que busca conservar los albatros y petreles mediante la coordinación de actividades internacionales con el objetivo de mitigar las amenazas conocidas en sus poblaciones (Cooper et al. 2006, Phillips et al. 2016). Actualmente, este acuerdo multilateral tiene 13 países miembros y un listado de 31 especies de albatros y petreles (http://www.acap.aq/). La presente tesis reúne nueva información sobre la ecología (dieta, distribución y preferencias de hábitats) y amenazas en el mar (captura incidental en palangre pelágico, contaminación por plásticos) para algunas de las poblaciones listadas en ACAP. Además, el trabajo proporcionó información útil para el manejo de las pesquerías de palangre pelágico de ICCAT en el Atlántico sudoccidental. Para cada una de las flotas de sus países miembros, se cuantificó su contribución al solapamiento entre el esfuerzo pesquero y la distribución de la población del albatros errante de South Georgia. La flota de Taiwán, seguida en menor grado por unas pocas flotas (Brasil, Uruguay, España, Japón y Portugal), mostró el mayor solapamiento con esta especie. Sin embargo, poco o nada se sabe sobre la captura incidental de grandes albatros y de otras especies para algunas de estas flotas, incluyendo Taiwán. Por lo tanto, es necesario fortalecer la cooperación internacional, especialmente entre estos países, para estandarizar métodos de recolección de datos, mejorar la identificación de especies, poner medidas de mitigación en prácticas y evaluar sus desempeños, con el objetivo de mitigar los efectos adversos de la pesca en estas y otras especies relacionadas.

Actualmente, se recomienda el uso combinado de calado nocturno, líneas espantapájaros y regímenes específicos de pesos en las brazoladas del palangre como mejores prácticas para mitigar la mortalidad de aves marinas en las pesquerías de palangre pelágico (ACAP 2016). La recomendación 11-09 de ICCAT (http://www.iccat.int/en/Recs-Regs.asp) estipula que en el área al sur de los 25°S, los miembros de ICCAT deben asegurar que todos los barcos de palangre usen al menos dos de estas medidas de mitigación. Similar a lo reportado en estudios previos (Murray et al. 1993, Jiménez et al. 2009, Løkkeborg 2011), en la tesis se confirmó que el calado nocturno disminuyó de forma significativa la mortalidad de grande albatros (Capítulo 3), por lo que el calado diurno debe evitarse bajo cualquier circunstancia. Sin embargo, en los calados nocturnos efectuados durante las fases más luminosas de la luna se produjeron altos niveles de captura

incidental, aun con líneas espantapájaros. Es posible que mejoras en el desempeño de esta última medida, en combinación con el calado nocturno estricto, puedan contribuir a reducir de forma importantes las capturas. El uso simultáneo de las tres medidas arriba mencionadas podría, sin duda, disminuir aún más esta mortalidad. En base a los resultados de los Capítulos 3 y 4, deberían implementarse de forma urgente medidas de mitigación efectivas entre los 25° y 45° S, con un control estricto de su uso entre mayo y diciembre y particularmente entre los 30° y 40° S y al oeste de los 35° W. Esto sería de gran utilidad para proteger a las cuatro especies de grandes albatros, pero también a las restantes principales especies afectadas por esta pesquería en el Atlántico sudoccidental (*Thalassarche chlororhynchos, T. melanophris, T steadi, Procellaria conspicillata y P. aequinoctialis*, ver Capítulo 4).

CONCLUSIONES

La presente tesis presentó evidencia de que los grandes albatros que se distribuyen en el Atlántico sudoccidental exhiben una repartición inter-especifica de nicho, siendo principalmente evidente en su distribución espacial, en su uso de hábitats y también en su dieta. Sin embargo, las dos especies neríticas (albatros real del sur y del norte) también presentaron alto grado de solapamiento en la dieta.

Se demostró que las especies también muestran segregación espacial entre sexos, donde en promedio las hembras se distribuyen más al norte que los machos, dentro y fuera de la estación reproductiva.

Se obtuvo evidencia convincente de que la fuente de alimento superabundante y artificial dada por los descartes generados por la pesca de arrastre en la plataforma continental, permite la coexistencia de especies cercanamente relacionadas y relajan la repartición del nicho trófico.

No obstante, tanto la segregación inter e intra-específica tiene efectos negativos, exponiendo de forma diferencial a los grandes albatros a la pesca con palangre pelágico en el Atlántico sudoccidental. Las dos especies más oceánicas (albatros errante y de Tristán) se encuentran más vulnerables a un mayor número de flotas que operan en aguas internacionales y por lo tanto al mayor esfuerzo pesquero. Las neríticas, están expuestas a altos niveles de mortalidad en palangre pelágico principalmente sobre el talud continental, aunque esta interacción ocurría

principalmente con un número limitado de flotas que operan dentro de las ZEE. También están expuestas a la pesca de arrastre, cuyo impacto es menos conocido.

La evidencia reunida indica que la pesca con palangre pelágico en la región produce una mortalidad incidental sesgada hacia las hembras, lo cual agravaría el impacto de la captura incidental en sus poblaciones.

La ingestión de plásticos fue detectada como una amenaza adicional que podría agravar el impacto negativo de la captura incidental en pesquerías, la cual constituye la amenaza más generalizada en estas especies.

Para proteger a estas especies altamente amenazadas, se deben implementar medidas de mitigación en las flotas de palangre pelágico manejadas por ICCAT en una amplia región del Atlántico sudoccidental (25°-45° S), con un mayor control entre mayo y diciembre en los 30°-40° S. Esto protegería a su vez a todas las especies que son afectadas por esta pesquería.

Chapter 7

General Discussion and Conclusions

This thesis addressed for the first time the variation in bycatch rates of great albatrosses (*Diomedea* spp.) in pelagic longline fisheries in the southwest Atlantic (Chapters 3 and 5) and the relative importance of discards from various fisheries for their trophic ecology (Chapter 2). Bycatch rates varied in space and time, reflecting the distribution and seasonality of the species. Several factors related to habitat preferences and fishing operations that affect their bycatch rates were also determined (Chapter 3). The spatial sexual segregation in great albatrosses was analysed, determining that it occurs during both the breeding and non-breeding seasons, and produces greater exposure for females, and sex-biased mortality towards this sex, in the pelagic longline fisheries in this region (Chapters 4 y 5).

The analysis of the trophic ecology of great albatrosses provided evidence of the degree of interspecific niche partitioning (Chapter 2). The hypothesis that the spatial segregation leads to variation in diet composition was supported. Fisheries discards were an important source of food in the diet, particularly those from the trawl fishery for both species of royal albatrosses. In fact, the overlap between the diets of these two closely related species was surprisingly high, although their isotopic niches showed a slight divergence. The evidence gathered in great albatrosses, but also in other related species of albatrosses and petrels, led to the conclusion that discards from trawl fisheries on the continental shelf may increase the diet overlap and allow the coexistence of species within seabird communities.

In studying the trophic ecology of these species, another anthropogenic threat was detected: plastic pollution (Chapter 6). The great albatrosses and particularly both species of royal albatrosses, accumulated plastics in their digestive tracts to a greater extent than the mollymawk albatrosses (*Thalassarche* spp.). Sex-related differences were also recorded. Consequently, this

constitutes further evidence that inter and intraspecific segregation exposes great albatrosses to different threats.

SEGREGATION IN ALBATROSSES AT SEA

Interspecific segregation and niche partitioning

Interspecific niche partitioning in great albatrosses in the southwest Atlantic was first proposed from tracking data from northern royal and wandering albatrosses (Nicholls et al. 2002). Subsequent studies of the Tristan albatross (Cuthbert et al. 2005, Reid et al. 2013) confirmed different degrees of spatial segregation and habitat use between species. Ring recoveries of southern royal albatross suggest that individuals are distributed mainly on the continental shelf (Moore & Bettany 2005). In this thesis, the distribution of the incidental captures in pelagic longline fisheries of these species, their isotopic niches and δ^{13} C value in feathers, provided new evidence on interspecific niche partitioning. This was also particularly evident when the diet composition was assessed both by conventional analysis of stomach contents, and through stable isotope mixing models.

The occurrence of bycatch of great albatrosses in pelagic longline fisheries in the southwest Atlantic (analysed for the fleets of Uruguay and Japan) varied with bathymetry, and distance to the shelf break and to the coast. The captures of Tristan albatross were recorded on average in deeper waters and further offshore than those of the other species, while in northern royal albatross, the captures occurred at shallower depths and were the nearest to the shelf break. The captures of wandering albatross tended to increase in more oceanic waters whereas the relationship for southern royal albatross was in the opposite direction, toward the shelf break and the coast (Chapter 3). This confirms the proposed patterns of segregation; the two royal albatross species are the most neritic, distributed mainly on the shelf and slope, while wandering albatross and particularly the Tristan albatross exploit more oceanic waters. Some factors reflecting habitat preferences of these species were also determined. In both species of royal albatrosses, most captures occurred in the shelf break region off Uruguay in cold waters, reflecting their preference for sub-Antarctic waters (Chapter 3). The bycatch of wandering albatross was mainly by the Uruguayan fleet, which operated in a wide region of the southwest Atlantic from tropical waters at 19° S towards the south. Captures in colder waters and over areas with higher winds (Chapter 3) reflected their preference for subtropical and sub-Antarctic waters (Chapter 4), which are favoured habitats in terms of the flight performance of great albatrosses (Shaffer et al. 2001, Chapter 5).

Excluding Tristan albatross due to low sample size, the analyses of the overlap and breadth of isotopic niches during the non-breeding season (estimated from δ^{13} C and δ^{15} N in growing head feathers) confirmed the niche divergence between the wandering albatross and the two species of royal albatrosses (Chapter 2). In marine environments, δ^{13} C values can provide a general idea of oceanographic region or certain gradients (Forero et al. 2004, Barrett et al. 2007, Phillips et al. 2009). For example, the relative use of coastal regions, low latitudes or demersal habitats is reflected in enrichment of ¹³C compared to oceanic regions, high latitudes and pelagic habitats, respectively. Although the differences were not significant, possibly because the δ^{13} C in actively molting feathers reflected a relatively well-defined region (see Chapter 2), the two species of royal albatrosses showed higher δ^{13} C values than the wandering albatross. This is consistent with the preference of these species for the continental shelf and oceanic waters, respectively.

The thesis also included a test of the hypothesis that spatial segregation leads to differences in diet composition (Chapter 2). The diet of the neritic royal albatross species contrasted with that of the wandering albatross. In the royal albatrosses, the stomach contents reflected a higher proportion of demersal fish (dominated by *Bassanago albascens* and *Merluccius hubbsi*), followed by the squid *Illex argentinus*. This composition was attributed to the discards from trawl fisheries (see below). In contrast, the wandering albatross diet was dominated by squid of the genus *Histioteuthis*. These results were confirmed by stable isotope mixing models, based on δ^{15} N and δ^{13} C of growing feathers from the albatrosses, and tissues (muscle and squid beaks) of various potential prey.

In turn, the thesis included a test of the hypothesis that fisheries discards allow an overlap in diet and trophic niche of great albatross species: this was especially evident in neritic species exposed to trawl fisheries. The combined use of conventional diet and stable isotope analyses demonstrated the importance of discards from trawl fisheries for various neritic species of albatrosses and petrels. The most obvious examples were the remarkably similar diets of the two royal albatross species, both dominated by discards from this fishery. The results were interpreted as convincing evidence that in continental shelf waters the superabundant and artificial food provided by trawl fisheries permits coexistence and therefore a high trophic niche overlap between closely-related species of seabirds.

Spatial sexual segregation

In the wandering albatross, several tracking studies of breeding birds indicate that males tend to spend more time in higher latitudes than females (Weimerskirch et al. 1993, Prince et al. 1998, Xavier & Croxall 2005, Froy et al. 2015). The ring recoveries of wandering albatrosses in fisheries also suggest that this segregation occurs during the non-breeding season (Croxall & Prince 1990, Prince et al. 1998). Because bird feathers are molted, and therefore synthesised outside the breeding season (Ginn & Melville 1983), the stable isotope analysis of these tissues have also been useful to confirm sexual segregation in the wandering albatross during the non-breeding season (Phillips et al. 2009). Data from seabirds bycaught in fisheries may also be informative; because a higher proportion of females are expected in northern latitudes, they should be more exposed to bycatch than males in fisheries operating in these areas (Chapter 5, and see below).

In the thesis, I demonstrated how segregation of wandering albatross from South Georgia varied among sexes in the different breeding stages, consistently exposing females to increased risk of bycatch in pelagic longline fisheries, including each fleet of the main flag states operating in the southwest Atlantic (Chapter 4). In fact, analysis of ring recoveries of bycaught birds from this fishery indicated that this increased exposure led to an increased incidental mortality (Chapter 4). This relationship allowed an indirect assessment, for the first time, of the spatial sexual segregation of the other two species of great albatrosses during the nonbreeding season: the southern and northern royal albatrosses (Chapter 5). The two hypotheses that explain the spatial sexual segregation; competitive exclusion or differences in flight performance, are mediated by the existence of a pronounced sexual size dimorphism (see Chapters 1 and 5). Based on a sample of bycaught birds from pelagic longline in the southwest Atlantic identified to species and sex, it was determined that both southern and northern royal albatrosses exhibit sexual size dimorphism in various body measurements, and the prediction of female-biased mortality was confirmed (Chapter 5). This result means that spatial sexual segregation can be generalised among the great albatrosses, and provides further evidence that it occurs outside the breeding season.

BYCATCH AND IMPLICATIONS FOR CONSERVATION

The four species of great albatrosses that are distributed in the southwest Atlantic are globally threatened according to the International Union for Conservation of Nature, IUCN (see Table 1 in Chapter 1). Although these species are considered among the most affected by the pelagic longline fishery in the southwest Atlantic (Jiménez et al. 2012), until now there was little information on interaction with fisheries (including bycatch) in this region, particularly for northern and southern royal albatrosses (Robertson et al. 2003). This thesis presented the first detailed study on bycatch of great albatrosses at the species level in pelagic longline fisheries (Chapter 3). The spatio-temporal variation of bycatch rates was determined for two fleets: that of Uruguay operating in a wide region of southwest Atlantic $(19-47^{\circ}S \text{ and } 20-60^{\circ}W)$ during 2004-2011, and of Japan, fishing under license in Uruguayan waters during 2009-2011. The latter in turn represents the first seabird bycatch assessment for the Japanese fleet in the southwest Atlantic. The situation for both fleets should be considered as case studies in the context of all fleets operating in the southwest Atlantic which are regulated by the International Commission for the Conservation of Atlantic Tunas (ICCAT). In fact, the overlap of tracking data from wandering albatross with the fishing effort of ICCAT fleets confirmed that the areas and seasons of higher bycatch risk coincided with the relative bycatch rates by the Uruguayan and Japanese vessels (Chapter 4).

High bycatch levels of northern and southern royal albatrosses were recorded for the first time in the southwest Atlantic, particularly over the shelf break (Chapter 3). In order to interpret this result, the relative distributions of the fishing effort of all fleets operating in the region need to be considered (Chapter 4); these largely operate in international waters at the Brazil-Falkland Confluence, and the highest effort is by Taiwan, but also by Brazil, Spain, Uruguay, Japan and Portugal, among others. The shelf break region within the distribution range of albatrosses (mainly south of 30°S) and used by these fisheries is principally within the Exclusive Economic Zone (EEZ) of Brazil and Uruguay, therefore these waters are used by these countries and occasionally by others with fishing license, as was shown for Japan in this thesis. Because of their oceanic habits, wandering and Tristan albatrosses are exposed to bycatch in the shelf break (mainly the former species) and in a wide region of the southwest Atlantic which includes the area with the greatest fishing effort (Chapters 3 and 4). Therefore, a greater impact of pelagic longline fishing is presumed for these two species (Jiménez et al. 2012). For threatened albatrosses, a conservative estimate suggests that an annual mortality higher than 1.5% of birds breeding each year is sufficient to produce a population decline (Dillingham & Fletcher 2011). This amounts to the death of a few tens of birds a year for the South Georgia wandering albatross population and for the Tristan albatross, and several tens of birds for the two species of royal albatrosses (Dillingham & Fletcher 2011, Jiménez et al. 2012). For the first two populations, these values may be exceeded during most years only in the pelagic longline fisheries of the southwest Atlantic (Jiménez et al. 2012, Klaer 2012). This agrees with the dramatic declines experienced by these two populations in recent decades (Poncet et al. 2006, Cuthbert et al. 2014). The impact of this fishery is not as clear for southern and northern royal albatrosses; their population trends are unknown or presumed stable, respectively.

The great albatrosses are affected by other fisheries and, because they are highly migratory, in other regions (Gales et al. 1998, Waugh et al. 2008a, Petersen et al. 2009, Brothers et al. 2010). In the southwest Atlantic, there are few records of bycatch of great albatrosses in demersal longline fisheries (Favero et al. 2003), but currently the level of mortality is low or nil (Favero et al. 2013, Jiménez et al. 2015). However, as confirmed by the diet composition (Chapter 2), the two species of royal albatrosses are highly exposed to trawl fisheries in this region, in which there is recent evidence of bycatch (Favero et al. 2011). Therefore, the sum of the negative impacts generated by the various fisheries, and especially the pelagic longline and trawl fisheries in the southwest Atlantic and other regions of the Pacific and Indian Oceans, could represent a major threat to these highly migratory species.

Albatrosses are vulnerable to changes in fecundity and survival, with the latter the most important demographic parameter influencing population trends (Weimerskirch & Jouventin 1987, Gales 1998). As discussed in the thesis (Chapter 1, 4 and 5), sex-biased mortality exacerbates the impact of bycatch, immediately reducing the effective population, but also indirectly affecting fecundity. The effect of a sex bias is cumulative and, unlike a decrease in survival, its impact on the demography of albatrosses persists even after mortality in longlines ceases (Mills & Ryan 2005). Excluding the Tristan albatross because of the small sample size, I confirmed that the bycatch of great albatrosses in the pelagic longline fisheries of the southwest Atlantic produces female-biased mortality (Chapters 4 and 5; see above the section: Spatial sexual segregation). The

current mortality levels of wandering albatrosses from South Georgia in demersal longline and trawl fisheries operating in southern regions, where males are more abundant, are thought to be relatively low (Waugh et al. 2008, see Chapter 4) and hence unlikely to be counterbalanced the impact of pelagic longline fisheries in females (see Chapter 4). Therefore, the consistently high overlap of adult females with the fishing effort of all pelagic longline fleets, and the resulting sexbiased mortality, would account for the lower adult female survival rate observed at South Georgia since the 1970s (Croxall et al. 1990, Croxall et al. 1998). Very little is known about the incidental mortality of southern and northern royal albatrosses in other regions, including in the Pacific and Indian oceans. A global assessment of the mortality in fisheries for these species, and if possible with information of sex and age of birds caught, should be considered a high priority.

The Agreement on the Conservation of Albatrosses and Petrels (ACAP) is a treaty which seeks to conserve albatrosses and petrels by coordinating international activity to mitigate known threats to their populations (Cooper et al. 2006, Phillips et al. 2016). Currently, this multilateral agreement has 13 country members and 31 listed species of albatrosses and petrels (http://www.acap.aq/). This thesis brings together new information on the ecology (diet, distribution and habitat preferences), and threats at sea (bycatch in pelagic longline fisheries, plastic ingestion), for some of the populations listed by ACAP. Additionally, the work provides useful information for managing ICCAT pelagic longline fisheries in the southwest Atlantic. For each of the flag state fleets member of ICCAT, its contribution to the overall overlap between the fishing effort and the distribution of the population of wandering albatross from South Georgia was quantified. The fleet of Taiwan, followed to a lesser extent by a few other fleets (including Brazil, Uruguay, Spain, Japan and Portugal), showed the greatest overlap with this species. However, very little or nothing is known about the bycatch of great albatrosses and other species for some of these fleets, including Taiwan. Therefore, it is necessary to strengthen international cooperation, especially between these countries, to standardize methods of data collection, to improve species identification and to put in practice and evaluate the performance of mitigation measures, in order to mitigate the adverse effects of fishing in these and other related species.

Currently, recommended best-practice to mitigate seabird mortality in pelagic longline fisheries is the combined use of night setting, bird scaring lines and specific weighting regimes in branch lines (ACAP 2016). The ICCAT recommendation 11-09 (http://www.iccat.int/en/Recs-Regs.asp) stipulates that in the area south of 25°S, ICCAT members shall ensure that all longline vessels use at least two of these mitigation measures. Similar to that reported in previous studies (Murray et al. 1993, Jiménez et al. 2009, Løkkeborg 2011), in this thesis I confirmed that night setting decreases significantly the mortality of great albatrosses (Chapter 3), so daylight setting should be avoided under all circumstances. However, in night sets made during the brighter moon phases high levels of bycatch are recorded even if bird scaring lines were used. It is possible that improvements in the performance of the latter measure, in combination with the strict night setting, may help to reduce these captures significantly. The simultaneous use of the above three measures would undoubtedly further reduce this mortality. Based on the results of Chapters 3 and 4, effective mitigation measures between 25° and 45° S should be implemented urgently, with strict compliance monitoring between May and December and principally between 30° and 40° S and west of 35° W. This would be useful to protect the four species of great albatrosses, but also all the other species affected by this fishery in the southwest Atlantic (*Thalassarche chlororhynchos, T. melanophris, T steadi, Procellaria conspicillata* and *P. aequinoctialis,* see Chapter 4).

CONCLUSIONS

This thesis presented evidence that the species of great albatrosses distributed in the southwest Atlantic exhibit interspecific niche partitioning, which was especially evident in their spatial distribution, habitat use and diet. However, the two neritic species (southern and northern royal albatrosses) also showed a high degree of overlap in their diet.

The species of great albatrosses also exhibited spatial sexual segregation, with females on average distributed further north than males, and this occurs both in breeding and nonbreeding birds.

There was convincing evidence that trawl fisheries on the continental shelf, by providing a superabundant and artificial source of food in the form of discards, allow the coexistence of closely-related species and relax trophic niche partitioning.

However, both inter and intraspecific segregation had negative effects on great albatrosses, exposing species and sexes differentially to pelagic longline fishing in the southwest Atlantic. The two most oceanic species (wandering and Tristan albatrosses) are vulnerable to a greater number

of fleets operating in international waters and to the greatest fishing effort. The neritic albatrosses are exposed to high levels of mortality in pelagic longline fisheries mainly over the shelf break, although this interaction may occur with a limited number of fleets operating within the EEZs. They are also exposed to trawl fisheries whose impact is less known.

The evidence gathered here indicates that pelagic longline fishing in the region produces femalebiased mortality. This would exacerbate the impact of bycatch on their populations.

Another anthropogenic threat detected for great albatrosses in this region was plastic ingestion. This may compound the negative impact of the most pervasive threat, fisheries bycatch.

In order to protect these species, mitigation measures on ICCAT pelagic longline fleets should be implemented in a wide region of the southwest Atlantic ($25^{\circ}-45^{\circ}$ S), with greater compliance monitoring in May-December and in the $30^{\circ}-40^{\circ}$ S. This in turn would protect all the seabird species that are affected by this fishery.

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