



The importance of pelagic longline fishery discards for a seabird community determined through stable isotope analysis

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ARTICLE INFO

Article history:

Received 22 December 2009

Received in revised form 18 June 2010

Accepted 25 June 2010

Keywords:

Albatross

Community disruption

Diet overlap

Longline fishery discards

Petrels

Wintering

ABSTRACT

Seabird species within a community are expected to have distinct trophic niches according to foraging methods and body size, but some seabirds exploit fishery waste which can be quite distinct from natural foods. Even in the presence of fishery discards we hypothesize that a pelagic seabird community is structured according to body size, feeding methods, and access to discards. We measured carbon and nitrogen stable isotopes in whole blood of seabirds from the offshore wintering community of Procellariiformes (albatrosses, petrels, shearwaters and storm-petrels) in the SW Atlantic Ocean. We compared this with isotope values of potential prey items and fishery discards, to investigate the importance of discards from the tuna-shark pelagic longline fishery in the diet of these birds. Despite contrasting body masses and feeding techniques, there was extensive overlap in the range of isotopic ratios for different species. Carbon isotope values were typical of the subtropical offshore region. Nitrogen values also showed a high degree of overlap among species and clearly signify that the birds are feeding on fishery waste (especially shark liver). Recently arrived migrants from the Antarctic and sub-Antarctic, and species still rearing chicks when sampled (e.g. wandering albatross *Diomedea exulans*) had carbon isotopic values indicative of Antarctic and sub-Antarctic regions. All species breeding at more southerly latitudes underwent a marked shift (increase) in carbon and nitrogen isotopes, indicating a change in diet between breeding and wintering seasons. Cory's shearwater (*Calonectris diomedea*), the only sampled species not attending vessels, had low nitrogen values reflecting a diet of flying fish which occur naturally in the area and showed no change in isotope values between breeding and wintering grounds. Mixing models demonstrate the need to include an external food source (Antarctic krill) to recreate the isotope values obtained from seabird blood: this corresponds to the blood of wintering migrants retaining a minor component from their diet in the southern breeding grounds. The stable isotope results suggest that the availability of discards from pelagic fisheries in the SW Atlantic Ocean lead to an artificially and poorly structured seabird community, with most species utilizing the same food resource. The balance between population benefits obtained from feeding upon otherwise unavailable discards, and the costs from incidental mortality on longline fishing hooks is likely to differ among species, with positive effects for small-sized species and negative effects on albatrosses and *Procellaria* petrels.

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1. Introduction

About 7.3 million tonnes of discards from marine fisheries are released globally every year, of which 506,481 tonnes are from pelagic longline fisheries (Kelleher, 2005). This fishery targets top marine predators (tuna, billfishes and sharks) and has been demonstrated to have profound effects on the food web structure (Kitchell et al., 2002; Heithaus et al., 2008). Discards from fisheries in the form of undersized fish, commercially unattractive species or offal have been recognized as a key food source for many scavenging seabird

species around the world (Montevecchi, 2002; Furness, 2003; Votier et al., 2004).

Fishing activities could have a beneficial effect on seabirds, by bringing them otherwise unavailable food in the form of offal or discarded demersal fish, and by removing competitors (Montevecchi, 2002; Furness, 2003). The importance of fishing discards for seabirds is usually difficult to assess at the population level, and is traditionally inferred from direct observations of birds attending fishing vessels or dietary studies in colonies (e.g. Hudson and Furness, 1988; Thompson and Riddy, 1995).

Conversely, discards could have adverse effects, when fisheries deplete stocks of prey used by seabirds, drown them in nets or on longline hooks (Montevecchi, 2002; Furness, 2003). Discards have been demonstrated to be detrimental for some species, for example skuas increase predation upon other seabirds when discard levels decline

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(Votier et al., 2004), poor quality discards affect chick development in gannets (Grémillet et al., 2008) and discards from demersal fisheries increase pollutant intake by seabirds (Arcos et al., 2002).

The pelagic longline fishery, targeting large predatory fishes and sharks off the coast of Brazil, is an important food source for offshore albatrosses and petrels in the form of discarded offal (Bugoni et al., 2008c), but at the same time it causes the death of a large number of albatrosses and petrels (Bugoni et al., 2008a). The balance between positive and negative effects of this fishery on seabirds is likely to vary according to species.

In this study we analyzed stable isotopes in whole blood of Procellariiformes (albatrosses, petrels, shearwaters and storm-petrels) attending pelagic longline fishing vessels off southern Brazil, and in tissues of potential prey and discards from the fishery. We hypothesize that if discards from longline fishery are the main food source for the community, trophic levels (TL) would be similar and overlapping amongst bird species, and that isotopic values indicative of discard use would be identified in bird tissues. In contrast, if species rely heavily on 'naturally' available prey, given the wide range of body sizes from storm-petrels to greater albatrosses, and given the diverse foraging strategies employed by these birds, a multi-level trophic-structured seabird community should be anticipated.

Wide differences in stable isotope signatures have been found between seabird species in a suite of studies, reflecting wide differences in diets (e.g. Rau et al., 1992; Buckman et al., 2004; Kojadinovic et al., 2008), and indicating the classical pattern of distinct ecological niches of species. However, in the Patagonian region, the coastal seabird community shows considerable overlap in diet among species (Foreiro et al., 2004), as in Antarctica, where tissues of top predators (fish, seabirds and seals) show great overlap in carbon and nitrogen isotope values, because they rely on a few abundant prey (Hodum and Hobson, 2000). These studies suggested that coexistence of species in the community is possible as a consequence of superabundance of food or species diversification in morphology and foraging strategies. Furthermore, because the community comprises migrants from southern latitudes (e.g. Patagonia, Antarctica, sub-Antarctic islands) which feed on prey with characteristic low carbon signatures and low TL during the breeding period (summer – from September to March for most species, and throughout the year for large albatrosses *Diomedea* spp.) (Quillfeldt et al., 2005; Cherel and Hobson, 2007), a considerable change in values

of stable isotopes of carbon and nitrogen (or TL) in seabird blood could be expected if discards from longline fisheries are an important food source.

The use of stable isotope techniques is particularly relevant in this case because it integrates dietary information during a medium-term period rather than a snapshot of the diet provided by direct observations of feeding birds or stomach content methods (Barrett et al., 2007). A number of recent studies have inferred winter diet of seabirds based on stable isotopes in feathers grown during this period, and sampled afterwards in breeding grounds (e.g. Cherel et al., 2000, 2006; Quillfeldt et al., 2005). We used a different approach, namely direct at sea sampling of blood for stable isotope analysis coupled with observations on the behaviour of feeding seabirds during the wintering period and by this we aim to contribute to a better understanding of seabird ecology during this poorly-studied period of their life-cycle. Therefore, behaviour and biochemistry were integrated in order to clarify the organization of the seabird community in relation to food sources, with implications for conservation of threatened albatrosses and petrels.

2. Material and Methods

2.1. Study area

In the SW Atlantic Ocean the cold Falkland/Malvinas Current flowing northward meets the warm Brazilian Current (Garcia, 1998; Fig. 1). The presence of highly productive waters from the Falkland/Malvinas Current in winter sustains an important pelagic longline fishery in southern Brazil (Castello, 1998), as well as the most abundant and diverse seabird community in Brazil (Neves et al., 2006).

In Brazil, sharks are an important target of pelagic longliners, with meat sold for the domestic market and fins exported, and frequently compose the bulk of captures (Bugoni et al., 2008a; Montealegre-Quijano and Vooren, 2010). The domestic Brazilian pelagic longline fleet operated with about 60 vessels in 2006, mainly over the continental shelf break and adjacent international waters, with fishing trips lasting up to one month (Bugoni et al., 2008a). Sharks are headed and gutted at sea, which results in viscera being discarded overboard and available for seabirds (Bugoni et al., 2008c). Shark livers are soft, very edible to seabirds, lipid-rich, large in size, and float in sea water,

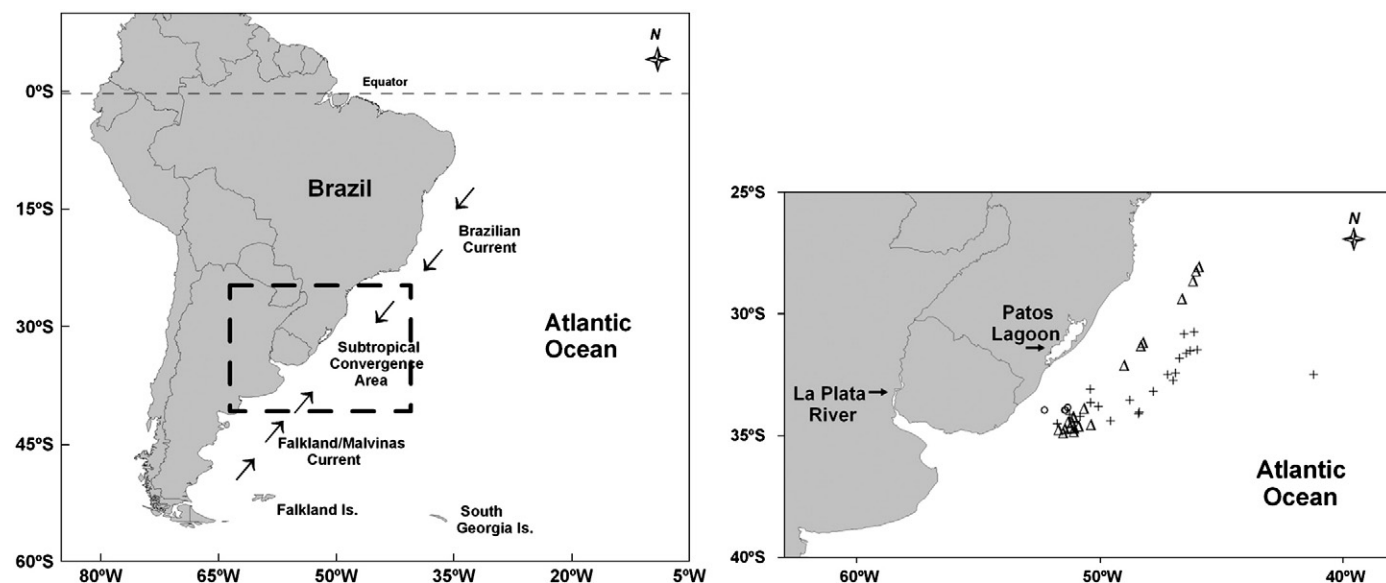


Fig. 1. Map of the Atlantic Ocean off southern Brazil where seabirds were sampled in summer – February (○), autumn – April/May/early June (Δ) and winter – July/August/early September (+). A single location usually represents several sampled birds. The approximate location of the Subtropical Convergence Area, breeding grounds of some seabird species and the flow of continental waters is shown.

making them the preferred food for scavenging seabirds attending longline fishing vessels, swallowed whole or in big chunks by the large seabirds or in small pieces by small ones (Bugoni et al., 2008c). The pelagic longline fishery is the main fishery overlapping spatially with seabirds in the offshore waters of southern and southeastern Brazil (Bugoni et al., 2008a). The other main fisheries which could potentially provide discards for seabirds, in the form of undersized fish, are a large bottom-trawling fleet for fish and shrimps, and the gillnet fishery for bottom fish species, both operating over the continental shelf (Haimovici et al., 1998).

2.2. Bird capture and sampling

Birds close to the vessel were captured using a cast net (Bugoni et al., 2008c) on 58 trapping days from February to June 2006 and July to September 2007. Captures occurred during six cruises from 25 to 35°S from vessels targeting tuna (*Thunnus* spp.), sharks (mainly the blue shark *Prionace glauca*) and swordfish (*Xiphias gladius*). Whole blood was

collected from the tarsal vein, stored in Merck® absolute ethanol and birds were ringed to avoid resampling the same individual.

Samples of potential foods were collected onboard, during these cruises, and included squids and fish captured opportunistically by the vessel crew; baits used for longline fishing (sardines, mackerel and squid); the tuna, sharks and swordfish targeted by the vessels and whose remains were discarded. For prey samples we collected white muscle from the lateral region of fish and the mantle of squids. Seabirds feed on shark liver but we sampled shark muscle. This is primarily because we expect liver and muscle to give similar isotope ratios after lipid removal by solvents (Hussey et al., 2010). Lipids are ¹³C depleted relative to whole tissue and lipid extraction reduces carbon isotope variability due to varying lipid content in different tissues (Sotiropoulos et al., 2004). Also, white muscle is regarded as the best tissue for ecological work as individual variation is less (Pinnegar and Polunin, 1999). The inventory of potential prey was supplemented by sampling demersal and coastal species from trawlers, and frozen pelagic fish collected during research cruises in the area (Table 1). Tissues were also

Table 1
Stable-carbon and nitrogen isotope values (mean ± 1 SD, range) of Procellariiform seabirds and their potential food sources (prey, baits and fish discards) sampled at sea off Brazil.

Species	n	δ ¹³ C (‰)	δ ¹⁵ N (‰)	Trophic level
		mean ± SD (range)	mean ± SD (range)	mean ± SD
<i>Seabirds</i>				
Cory's shearwater <i>Calonectris diomedea</i>	2	-17.4 ± 0.0 (-17.4 -17.3)	9.6 ± 1.2 (8.8 -10.4)	3.4 ± 0.4
Wilson's storm-petrel <i>Oceanites oceanicus</i>	3	-18.9 ± 1.1 (-20.1 -18.2)	12.8 ± 1.7 (11.3 -14.7)	4.3 ± 0.5
Southern fulmar <i>Fulmarus glacialis</i>	10	-18.5 ± 0.7 (-19.7 -17.1)	14.0 ± 0.9 (12.9 -16.0)	4.7 ± 0.3
Wandering albatross <i>Diomedea exulans</i>	9	-19.3 ± 0.7 (-20.3 -18.2)	14.2 ± 0.5 (13.5 -15.1)	4.8 ± 0.2
Great shearwater <i>Puffinus gravis</i>	37	-16.9 ± 0.5 (-18.5 -16.2)	14.4 ± 1.7 (11.0 -17.0)	4.9 ± 0.5
Cape petrel <i>Daption capense</i>	31	-19.4 ± 1.2 (-23.5 -17.9)	14.5 ± 1.5 (9.5 -16.3)	4.9 ± 0.5
Northern giant petrel <i>Macronectes halli</i>	1	-18.8	14.6	4.9
Spectacled petrel <i>Procellaria conspicillata</i>	38	-16.6 ± 0.9 (-18.3 -14.8)	15.1 ± 1.0 (13.8 -17.1)	5.1 ± 0.3
White-chinned petrel <i>Procellaria aequinoctialis</i>	30	-18.0 ± 1.8 (-21.5 -15.9)	15.1 ± 1.9 (11.3 -18.2)	5.1 ± 0.6
Atlantic yellow-nosed albatross <i>Thalassarche chlororhynchus</i>	33	-17.0 ± 0.5 (-17.8 -15.9)	15.4 ± 1.3 (13.9 -18.9)	5.2 ± 0.4
Sooty shearwater <i>Puffinus griseus</i>	2	-15.6 ± 0.3 (-15.9 -15.4)	15.5 ± 0.4 (15.3 -15.8)	5.2 ± 0.1
Tristan albatross <i>Diomedea dabbenena</i>	4	-17.6 ± 0.6 (-18.3 -16.9)	15.6 ± 0.6 (14.8 -16.0)	5.2 ± 0.2
Black-browed albatross <i>Thalassarche melanophris</i>	33	-17.2 ± 0.6 (-18.2 -16.0)	16.3 ± 0.9 (14.7 -17.6)	5.4 ± 0.3
Southern giant petrel <i>Macronectes giganteus</i>	11	-17.4 ± 0.4 (-18.0 -16.8)	16.4 ± 1.3 (14.1 -17.7)	5.5 ± 0.4
<i>Large pelagics (fishes and sharks)</i>				
Swordfish <i>Xiphias gladius</i>	2	-15.6 ± 1.9 (-16.9 -14.2)	13.4 ± 1.1 (12.6 -14.2)	4.5 ± 0.4
Yellowfin tuna <i>Thunnus albacares</i>	4	-16.5 ± 0.1 (-16.6 -16.4)	13.9 ± 0.8 (12.7 -14.5)	4.7 ± 0.3
Bigeye tuna <i>Thunnus obesus</i> (large)	7	-16.9 ± 0.2 (-17.3 -16.6)	12.0 ± 1.1 (10.4 -13.5)	4.0 ± 0.3
Bigeye tuna <i>Thunnus obesus</i> (small)	4	-16.5 ± 0.6 (-17.1 -15.8)	10.2 ± 1.2 (8.8 -11.6)	3.5 ± 0.4
Skipjack tuna <i>Katsuwonus pelamis</i>	3	-16.7 ± 0.5 (-17.2 -16.3)	12.4 ± 1.3 (11.0 -13.5)	4.2 ± 0.4
Blue shark <i>Prionace glauca</i> (small and large)	14	-17.4 ± 0.5 (-18.1 -16.3)	12.9 ± 0.5 (12.4 -14.2)	4.4 ± 0.1
Mako shark <i>Isurus oxyrinchus</i>	1	-15.6	16.6	5.5
Dolphinfish <i>Coryphaena hippurus</i>	1	-17.2	13.4	4.5
<i>Small pelagics (fishes and squid)</i>				
Flying fish <i>Cypselurus</i> sp.	6	-18.1 ± 0.4 (-18.6 -17.6)	8.5 ± 0.8 (7.0 -9.5)	3.0 ± 0.3
Brazilian sardine <i>Sardinella brasiliensis</i> (bait)	7	-17.6 ± 0.6 (-18.3 -16.7)	11.4 ± 1.0 (10.5 -13.3)	3.9 ± 0.3
Rough scad <i>Trachurus lathami</i>	9	-16.1 ± 0.1 (-16.4 -15.9)	16.1 ± 1.1 (14.6 -17.1)	5.4 ± 0.3
Cutlassfish <i>Trichiurus lepturus</i>	16	-16.0 ± 0.4 (-17.0 -15.6)	16.8 ± 0.9 (14.9 -18.0)	5.6 ± 0.3
Chub mackerel <i>Scomber japonicus</i> (bait)	16	-18.5 ± 0.3 (-18.9 -17.8)	10.9 ± 0.4 (10.1 -11.4)	3.8 ± 0.1
Almaco jack <i>Seriola rivoliana</i>	5	-16.8 ± 0.3 (-17.3 -16.4)	6.5 ± 0.9 (5.8 -8.0)	2.4 ± 0.3
Argentine anchovy <i>Engraulis anchoita</i>	14	-16.5 ± 0.5 (-17.5 -15.9)	14.7 ± 0.5 (13.9 -15.9)	4.9 ± 0.2
Filefish <i>Aluterus monoceros</i>	6	-16.6 ± 0.3 (-17.0 -16.3)	6.4 ± 1.0 (5.0 -7.5)	2.4 ± 0.3
Mullet <i>Mugil</i> sp.	10	-12.4 ± 1.3 (-14.3 -10.6)	13.0 ± 0.9 (11.5 -14.3)	4.4 ± 0.3
Short-finned squid <i>Illex argentinus</i> (bait)	21	-17.2 ± 0.6 (-18.1 -15.8)	14.2 ± 1.6 (8.8 -15.9)	4.8 ± 0.5
Squid <i>Ommastrephes bartrami/Illex argentinus</i>	8	-16.7 ± 0.4 (-17.1 -16.0)	9.3 ± 0.8 (8.5 -10.7)	3.3 ± 0.2
<i>Demersal fish</i>				
White croaker <i>Micropogonias furnieri</i>	11	-15.1 ± 0.6 (-15.9 -14.0)	16.5 ± 0.4 (15.9 -17.2)	5.5 ± 0.1
Striped weakfish <i>Cynoscion guatucupa</i>	10	-16.1 ± 0.4 (-16.8 -15.8)	15.8 ± 0.8 (14.8 -16.8)	5.3 ± 0.2
King weakfish <i>Macrodon ancylodon</i>	10	-16.6 ± 0.3 (-17.2 -16.1)	15.6 ± 1.1 (13.7 -16.7)	5.2 ± 0.3
Argentine croaker <i>Umbrina canosai</i>	10	-15.5 ± 0.3 (-15.9 -15.1)	16.6 ± 0.8 (15.3 -17.5)	5.5 ± 0.2
Brazilian codling <i>Urophycis brasiliensis</i>	11	-15.6 ± 0.5 (-16.2 -14.8)	16.5 ± 0.7 (15.3 -17.7)	5.5 ± 0.2
Wreckfish <i>Polyprion americanus</i>	1	-15.7	17.7	5.9
Red porgy <i>Pagrus pagrus</i>	1	-15.9	15.5	5.2
Pink cusk-eel <i>Genypterus brasiliensis</i>	1	-16.1	14.7	5.0
Bluewing searobin <i>Prionotus punctatus</i>	9	-15.0 ± 0.5 (-15.9 -14.1)	16.9 ± 0.7 (15.8 -17.6)	5.6 ± 0.2
Catfish (Ariidae)	9	-15.4 ± 0.5 (-16.1 -14.7)	17.0 ± 0.9 (15.4 -18.2)	5.6 ± 0.3

preserved in Merck® absolute ethanol. Storage of tissues for stable isotope analysis in ethanol is a common procedure in ecological studies and regarded to be a reliable method (Hobson et al., 1997; Arrington and Winemiller, 2002). Furthermore, we used the same brand for storage of all seabird blood and prey muscle samples, to avoid differences in the carbon isotopic composition of different brands and ensure consistency among samples, after Bugoni et al. (2008b).

2.3. Age determination

Pictures of bill and general plumage were taken from albatrosses and giant petrels and wing, tail and contour moult used to identify first year juveniles from older birds (e.g. Bugoni and Furness, 2009).

Wandering (*Diomedea exulans*) and Tristan (*D. dabbenena*) albatrosses are virtually identical in plumage (Onley and Scofield, 2007), so we used the discriminant function in Cuthbert et al. (2003) to assign species before and after sexing birds.

2.4. Molecular sexing

Blood sub-samples were used for sexing birds after DNA extraction and PCR amplification of CHD genes using primers 2550F (Fridolfsson and Ellegren, 1999) and 2757R (R. Griffiths, unpublished). DNA extraction negative controls were included for every 23 samples. Positive and negative controls were included for each PCR reaction and 1/3 of all DNA extractions were repeated to confirm gender assignment. Furthermore, we used samples of previously sexed birds as controls: one male Atlantic yellow-nosed albatross (*Thalassarche chlororhynchos*) killed in fisheries and sex determined by necropsy, and four ringed wandering albatrosses which were of known sex from observations at the breeding colony (A. Wood and R.A. Phillips, British Antarctic Survey, *in litt.*).

2.5. Sample analysis

The excess of ethanol in samples was removed and all blood samples were freeze-dried, ground and homogenised. Samples of 0.6 to 0.7 mg of blood were placed in tin capsules (4x6 mm) and analysed by continuous-flow isotope ratio mass spectrometry (CF-IRMS) using a Costech Elemental Analyser (Costech ECS 4010, Milan, Italy) coupled to a Thermo Finnigan Delta Plus XP Mass Spectrometer (Thermo Finnigan, Bremen, Germany). Stable isotope ratios were expressed in δ notation as parts per thousand (‰) deviation from the international standards Pee Dee Belemnite limestone (carbon) and atmospheric air (nitrogen). Three laboratory standards were analysed for every 10 unknown samples in each analytical sequence, allowing instrument drift to be corrected. Groups of samples (e.g. by species or season) were randomised in the analytical sequence according to individuals to minimize drift with time (Jardine and Cunjak, 2005). Because lipids are depleted in ^{13}C in relation to the whole tissues, we extracted them for carbon isotope analysis and used a non-extracted subsample for nitrogen determination (Sotiropoulos et al., 2004). Lipids were extracted from prey samples using the Soxhlet extraction technique with petroleum-ether as solvent (Schlechtriem et al., 2003), prey samples were then dried in an oven, and subsequently ground, homogenized and encapsulated in the same way as blood samples. Based on internal standards (tryptophan), the analytical precision (± 1 SD) was estimated as $\pm 0.18\text{‰}$ and $\pm 0.17\text{‰}$ for $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$, respectively.

2.6. Data analysis

A Generalized Linear Model (GLM) was used to investigate the effects of different factors on the variation in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values. Factors used as explanatory variables for the model were species, with 14 levels (Table 1), sex (2 levels - male, female), season (3 levels -

summer, autumn, winter) and age (2 levels - juveniles and >1 year-old). Because the distributions of residuals of stable isotope values were not normal, values of $\delta^{15}\text{N}$ were log transformed, and $\delta^{13}\text{C}$ values were $\log[n \times (-1)]$ transformed to account for negative values.

A simple model for trophic level (TL) of each seabird species (Forero et al., 2004) was calculated as:

$$\text{TL}_{\text{bird}} = \lambda + \left[\delta^{15}\text{N}_{\text{bird}} - \left(\delta^{15}\text{N}_{\text{flying fish}} + \Delta_n \right) \right] / \Delta_n$$

where λ is the TL of flying fish (*Cypselurus* sp.), assumed to be 3.0 (Kitchell et al., 2002), $\delta^{15}\text{N}_{\text{flying fish}}$ is the mean nitrogen isotopic ratio of flying fish sampled off Brazil (8.5‰, Table 1), and Δ_n is the nitrogen isotopic enrichment factor between fish muscle and seabird blood (3.2‰, averaged from values in Hobson and Clark, 1993; Bearhop et al., 2002; Cherel et al., 2005). Flying fish are common throughout the year at the shelf break and offshore waters where seabirds were sampled, and are prey of several upper level predators, thus it is a good baseline by integrating spatially and temporally the isotopic variations of upper trophic levels.

For non-avian components of the community Forero et al. (2004) modified the parameter of isotopic fractionation (3.3‰, Rau et al., 1992) to account for whole body or muscle (vs. blood), to be typical of temperate food-webs in the southern hemisphere. However, the $\delta^{15}\text{N}$ isotopic fractionation we used in the model (3.2‰) is close to the 3.3‰ reported by Rau et al. (1992) and to the 3.4‰ for more complex food-webs with several TLs (reviewed by Post, 2002), thus we used the same parameters for calculations of TLs of seabirds and non-avian components of the community.

In order to identify multiple sources of C and N in the whole blood of seabirds we used linear mixing models using the software IsoSource version 1.3.1 (Phillips and Gregg, 2003). Stable isotope values in seabird blood were corrected for trophic enrichment factors of 3.2‰ for $\delta^{15}\text{N}$ by as above, and 1.1‰ for $\delta^{13}\text{C}$ from Bearhop et al. (2002). Two models were tested: one with three potential sources, with mean values for small pelagics, large pelagics and demersal prey (Table 1, Fig. 2); a second model with more realistic prey which had been identified as important in the first model, i.e. flying fish, blue shark, plus Antarctic krill *Euphausia superba* ($\delta^{15}\text{N}$ 5.4‰, $\delta^{13}\text{C}$ -25.4‰; Cherel, 2008). Krill was included despite being a dietary source external to the area, because the first model indicated that there was a source for the isotopic mixture not included in the model. On consideration, some of the birds sampled would be recently arrived migrants from southern latitudes and breeding birds foraging in the area (such as the wandering albatross), isotope values from these birds would be influenced by external dietary sources.

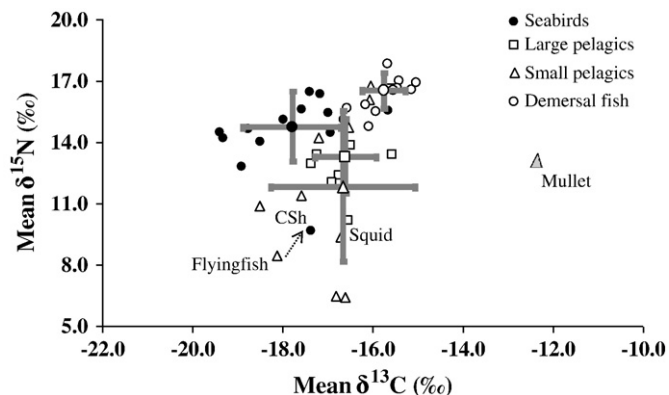


Fig. 2. Mean stable carbon and nitrogen ratios of seabird species sampled at sea off southern Brazil and their potential food sources. Arrows indicate potential fractionation from natural prey to Cory's shearwater. SD bars of each species omitted for clarity, but in grey are presented mean isotopic values (± 1 SD) of 'seabirds', 'large pelagics', 'small pelagics/bait' and 'demersal fish' categories.

In order to determine if the seabird community was structured according to body mass of bird species, we tested the correlation between body mass obtained from mean values of males and females from Brooke (2004) and TL (Spearman rank correlation). To determine differences in TL according to feeding techniques we summarize the typical technique of each species (from Harper et al., 1985; Brooke, 2004), and recorded, throughout the sampling period, the feeding behaviour of birds behind longliners and size of discards swallowed by each species (Table 2).

Temporal variations in carbon and nitrogen isotope values were tested for particular species according to season (Mann-Whitney test), or expressing days after 1 January for Pearson linear correlation. The $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of seabirds and in prey tissues were simultaneously compared by multivariate analysis of variance (MANOVA) with Wilk's lambda statistic. When significant differences were found, Tukey HSD test was used for *post hoc* comparisons between pairs. Normality and homoscedasticity, assumptions for GLM and MANOVA tests, were checked before running statistical analysis. Values are presented as mean \pm one standard deviation.

3. Results

3.1. Feeding behaviour of seabirds

In total 244 birds representing 14 species (Table 1) were sampled. Species captured ranged from 35 g storm-petrels feeding by patterning-dipping, medium-sized diving shearwaters (*Puffinus* spp.), to surface seizing greater albatrosses *Diomedea* spp. (Table 2). The preferred shark liver is usually discarded whole, but quickly fragmented by birds pecking this soft tissue. Shearwaters and less frequently *Procellaria* petrels and *Thalassarche* albatrosses, dive for discards, but feed at the surface when competition is low. Greater albatrosses and giant petrels feed exclusively at the surface, with the latter fragmenting discards by pecking the liver, while the former swallows large chunks. Even species with a soft bill such as Cape petrel (*Daption capense*) are able to remove pieces of shark liver or compete for small fragments. Wilson's storm-petrels (*Oceanites oceanicus*) wander among flocks, feeding on tiny fragments. Flocks of Cory's (*Calonectris diomedea*) and Cape Verde (*Calonectris edwardsii*) shearwaters were frequently observed during summer and autumn roosting nearby and feeding on flying fish and squids when prey were driven to the surface by tuna, but do not attend vessels for discards.

3.2. Isotopic signature in blood of seabirds

Mean carbon isotope values in blood of the 14 seabird species varied from -19.4‰ in Cape petrel to -15.6‰ in sooty shearwater (*Puffinus griseus*) (Table 1), with broad overlap in isotope values among species (Figs. 3 and 4). Despite this overlap there was significant effect of species on the combined carbon and nitrogen values (MANOVA, Wilk's lambda = 0.068, $F_{78, 812} = 29.4$, $P < 0.0001$). Characteristic low carbon values were found in some individuals from species that breed in Antarctic and sub-Antarctic regions, such as the first Cape petrel attending the vessel (and sampled) in mid April, which had $\delta^{13}\text{C} = -23.2\text{‰}$ and another specimen sampled in August with $\delta^{13}\text{C} = -23.5\text{‰}$ (Fig. 4). Other species with some individuals presenting distinct low carbon values were wandering albatrosses, white-chinned petrels (*Procellaria aequinoctialis*) and Wilson's storm-petrels. $\delta^{13}\text{C}$ values in blood of the white-chinned petrel formed two distinct groups of individuals, corresponding to birds sampled during autumn and during winter (values less than -19‰ and higher than -19‰, respectively (Fig. 4) (Mann-Whitney test $W = 371.5$, $P < 0.007$). Difference in $\delta^{15}\text{N}$ values of these two seasonal groups was marginally non-significant (Mann-Whitney $W = 350.0$, $P = 0.082$).). The temporal change in diet towards higher TLs was also evident in the correlation between calendar day after 1 January vs. nitrogen isotope values (Pearson correlation $r = 0.53$, $df = 28$, $P = 0.002$), and for carbon ($r = 0.81$, $df = 28$, $P < 0.0001$). Similar correlations were also found for black-browed albatross (*Thalassarche melanophris*) for carbon ($r = 0.52$, $df = 31$, $P = 0.002$), but not for nitrogen ($r = 0.19$, $df = 31$, $P = 0.31$). Correlation for the Atlantic yellow-nosed albatross was not significant for either carbon or nitrogen ($r = -0.1$ and 0.01 , both $df = 31$, $P = 0.57$ and $P = 0.98$, respectively). For the spectacled petrel (*Procellaria conspicillata*), correlations were significant, but negative for both carbon ($r = -0.34$, $df = 0.03$, $P = 0.03$) and nitrogen ($r = -0.72$, $df = 36$, $P < 0.0001$).

Nitrogen values in seabird blood were more variable than carbon values, and again with considerable overlap for most species (Figs. 3 and 4), despite a significant effect of species (MANOVA and GLM, see below). Some of the largest ranges for $\delta^{15}\text{N}$ values were observed for species sampled more extensively (Fig. 4). Mean $\delta^{15}\text{N}$ values for species ranged from 9.6‰ in Cory's shearwaters to 16.4‰ in southern giant petrels (*Macronectes giganteus*) (Table 1). Black-browed, Atlantic yellow-nosed and Tristan albatrosses also had high mean values. Cory's shearwater, the only species that did not attend fishing vessels for discards, had lower nitrogen values in comparison with all other species (Tukey's test, all paired comparisons $P < 0.04$,

Table 2
Body size, trophic level, feeding method and partitioning of discards from longline fisheries by Procellariiformes in the Southwestern Atlantic Ocean. NA – not applicable. * From Harper et al. (1985) and Brooke (2004).

Species	Body mass (g)*	Trophic level	Feeding behaviour*	Attending longliners for discards	Feeding location/method	Size of discarded pieces ingested
Atlantic yellow-nosed albatross	2199	5.2	surface-seizing; shallow plunging	Yes	surface; diving; kleptoparasitism	large
Black-browed albatross	3444	5.4	surface-seizing; shallow plunging	Yes	surface; diving; kleptoparasitism	large
Cape petrel	464	4.9	surface-seizing; shallow plunging; filtering	Yes	surface	small
Cory's shearwater	840	3.4	surface-seizing; pursuit plunging; pursuit-diving	No	NA	NA
Great shearwater	834	4.9	surface-seizing; pursuit plunging; pursuit-diving	Yes	diving	small
Northern giant petrel	4313	4.9	Scavenger; surface-seizing	Yes	surface; kleptoparasitism	small
Southern giant petrel	4440	5.5	Scavenger; surface-seizing	Yes	surface; kleptoparasitism	small
Southern fulmar	879	4.7	surface-seizing	Yes	surface	small
Spectacled petrel	1191	5.1	surface diving; surface seizing	Yes	diving; kleptoparasitism	medium
Sooty shearwater	803	5.2	pursuit-diving	Yes	diving	medium
Tristan albatross	7050	5.2	surface-seizing	Yes	surface; kleptoparasitism	medium
Wandering albatross	8730	4.8	surface-seizing	Yes	surface; kleptoparasitism	large
White-chinned petrel	1335	5.1	surface diving; surface seizing	Yes	diving; kleptoparasitism	medium
Wilson's storm-petrel	35	4.3	dipping-pattering	Yes	dipping; pattering	small

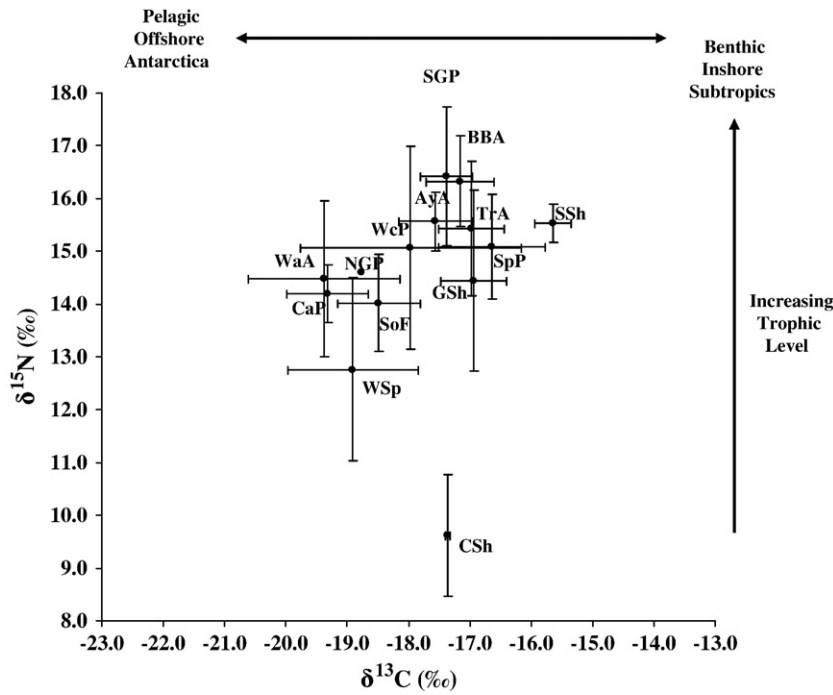


Fig. 3. Mean \pm 1 SD of stable carbon and nitrogen ratios in whole blood of albatross, petrel and shearwater species sampled at sea off southern Brazil. Species codes: CSh – Cory’s shearwater; GSh – great shearwater; SSh – sooty shearwater; WSp – Wilson’s storm-petrel; WcP – white-chinned petrel; SpP – spectacled petrel; SGP – southern giant petrel; NGP – northern giant petrel; CaP – Cape petrel; SoF – southern fulmar; BBA – black-browed albatross; AYA – Atlantic yellow-nosed albatross; WaA – wandering albatross; TrA – Tristan albatross.

Figs. 2 and 4). Species with some individuals displaying unusually low $\delta^{15}\text{N}$ were Cape petrel (these birds also had low carbon values), Wilson’s storm-petrel, white-chinned petrel, and great shearwater (*Puffinus gravis*). Comparison of closely related species showed they

did not differ in $\delta^{15}\text{N}$ (Tukey HSD test) and consequently in TLs (white-chinned vs. spectacled petrels; Tristan vs. wandering albatrosses; black-browed vs. Atlantic yellow-nosed albatrosses).

The GLM explained a significant proportion of the variation in $\delta^{13}\text{C}$ values, with three significant factors: species explained 51.9% ($F_{13, 227} = 15.0, P < 0.001$), followed by season and age, which despite being statistically significant, explained only 7.3% and 1% of the variation, respectively (season: $F_{2, 227} = 18.1, P < 0.001$; age: $F_{1, 227} = 5.3, P = 0.02$). Sex was not a significant factor in the model ($F_{1, 227} = 0.04, P = 0.84$). After simplifying this full model by removing non-significant factors (i.e. sex) the new model explained the same amount of variation in the dataset (60%) with all factors significant at $P < 0.05$. For $\delta^{15}\text{N}$, the model had a weaker performance explaining only 37.2% of the variation, again mainly due to species (32.8%, $F_{13, 227} = 9.2, P < 0.001$), followed by season ($F_{2, 227} = 5.6, P = 0.004$). The remaining factors were not significant (age: $F_{1, 227} = 3.2, P = 0.08$; sex: $F_{1, 227} = 0.07, P = 0.79$). A refined model for $\delta^{15}\text{N}$ without age and sex also explained only 37% of the variation, with remaining factors (species and season) significant at $P < 0.05$. Given these results, data for both sex and age classes were pooled for subsequent analysis.

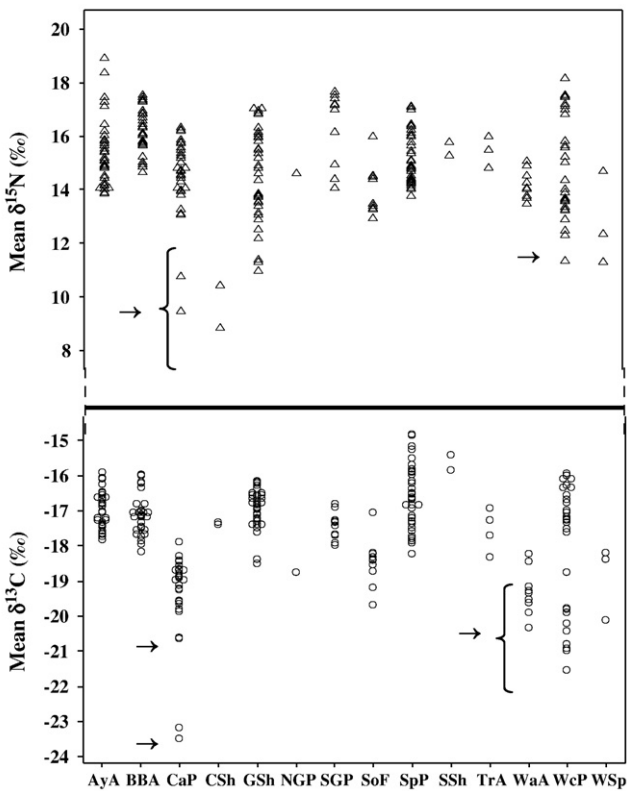


Fig. 4. Plot of individual values of $\delta^{15}\text{N}$ (above) and $\delta^{13}\text{C}$ (below) of 244 seabirds sampled off Brazil. Arrows indicate individuals with signatures from Antarctic prey (carbon) and lower trophic levels (nitrogen) suspected to be southern migrants. Species codes as in Fig. 3.

3.3. Isotope values of seabird food sources

Mean $\delta^{13}\text{C}$ values of potential food resources, represented by tissues from large pelagic predators, varied from -17.4‰ to -15.6‰ in blue and mako (*Isurus oxyrinchus*) sharks, respectively, with tuna values in between (Table 1). Carbon isotope values of small pelagic fishes and squid, including species used as bait in the pelagic longline fishery (sardines, mackerel and squid), mostly varied from -18.5‰ in the chub mackerel (*Scomber japonicus*) to -16.0‰ in cutlassfish (*Trichiurus lepturus*) (Table 1). However, this category also included mullet (*Mugil* sp.) with the lowest $\delta^{13}\text{C}$ value of -12.4‰, a characteristic coastal signature. Similar ranges of $\delta^{13}\text{C}$ values were found for demersal fish, from -16.6‰ in king weakfish (*Macrodon ancylodon*) to -15.0‰ in bluewing searobin (*Prionotus punctatus*). Categories of prey (large pelagic fish, small pelagics, demersal fish)

and seabirds differed in combined $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ isotopic signatures (MANOVA, Wilk's lambda = 0.42, $F_{6, 76} = 6.9$, $P < 0.0001$). However, One-way ANOVA with *post hoc* Tukey HSD test demonstrated the limited ability of $\delta^{13}\text{C}$ to discriminate among prey categories, only differing between seabird and demersal fish.

The range of $\delta^{15}\text{N}$ values in prey was considerably larger than $\delta^{13}\text{C}$. Nitrogen isotope ratios in large pelagic predators ranged from 10.2 to 13.9‰ in small bigeye tuna (*Thunnus obesus*) and yellowfin tuna (*Thunnus albacares*), respectively (Table 1). Large bigeye tuna showed higher isotopic values (12.0‰) than small tuna. The small pelagic species ranged considerably in isotopic values, from 6.4‰ in filefish (*Aluterus monoceros*) to 16.8‰ in cutlassfish. Demersal fish had higher and less variable $\delta^{15}\text{N}$ values, with all averages between 15 and 17‰. Seabird tissues had $\delta^{15}\text{N}$ values differing significantly from small pelagic species, but not from other prey categories. Small pelagics and demersal fish also differed in $\delta^{15}\text{N}$ values (Fig. 2).

3.4. Source partitioning as determined by IsoSource mixing models

The 3-source mixing model with small pelagics, large pelagics and demersal fish could only be run with large minimum tolerance of 2‰ and increment values of 2‰. All sources included zero in the possible solution, with wide range of feasible contributions, from 0–98% for the 1–99 percentile ranges (Fig. 5A). More importantly, seabirds were outside the mixing polygon, indicating that no solution was possible and that there was another source not included in the model.

The second model with flying fish, blue shark and krill as sources was run with 1‰ increment and 0.2‰ tolerance, as suggested by Phillips and Gregg (2003), and resulted in 50 feasible solutions. The 1–99 percentile range was small and the mean seabird isotopic value fitted inside the polygon (Fig. 5B). This model confirmed the importance of discards from longline fishery as the primary source

(blue shark 71 to 81%), a small, but consistent proportion of krill (15–20%), and flying fish comprising only 0–14% in the isotope values of seabird blood. Additional models, not shown, confirmed the negligible contribution of demersal fish to the mixture, and models without krill overestimated the importance of flying fish/pelagic prey, but with wide distribution of feasible contributions and no possible solution for these models.

3.5. Trophic structure of the seabird community

Trophic levels, as determined for each species, showed broad overlap for most of the seabird species in this study (Table 1 and Fig. 6). Cory's shearwater was an outlier, with a lower TL (mean 3.4) in comparison with all other species, which varied from 4.3 in the Wilson's storm-petrel to 5.5 in the southern giant petrel. All seabird species regularly attending fishing vessels had high TLs, including small species such as Cape petrel and southern fulmar (*Fulmarus glacialisoides*). The food web was not size structured (body mass vs. TL; Spearman rank correlation $r_s = 0.43$, $P = 0.13$, $n = 14$ species; for species with sample sizes > 9 , $r_s = 0.44$, $P = 0.24$, $n = 9$), or structured according to feeding techniques typical of the species, or the way species scavenge for discards behind longline vessels (Table 2). Partitioning of discards was observed to be in accordance to the size of discards and size of bird species, aggressiveness and diving ability (Table 2).

TL of demersal fish species was on average higher than TLs of seabirds, with some species at the same TL as seabirds (Table 1; Figs. 2 and 6). Large pelagic predators were one TL lower than seabirds (except Cory's shearwater, Fig. 6), followed by small pelagics. TL of components of the 'small pelagics' category was heterogeneous, with species differing by up to 3.5 TLs. Benthopelagic species arbitrarily assigned to this group such as cutlassfish, rough scad (*Trachurus*

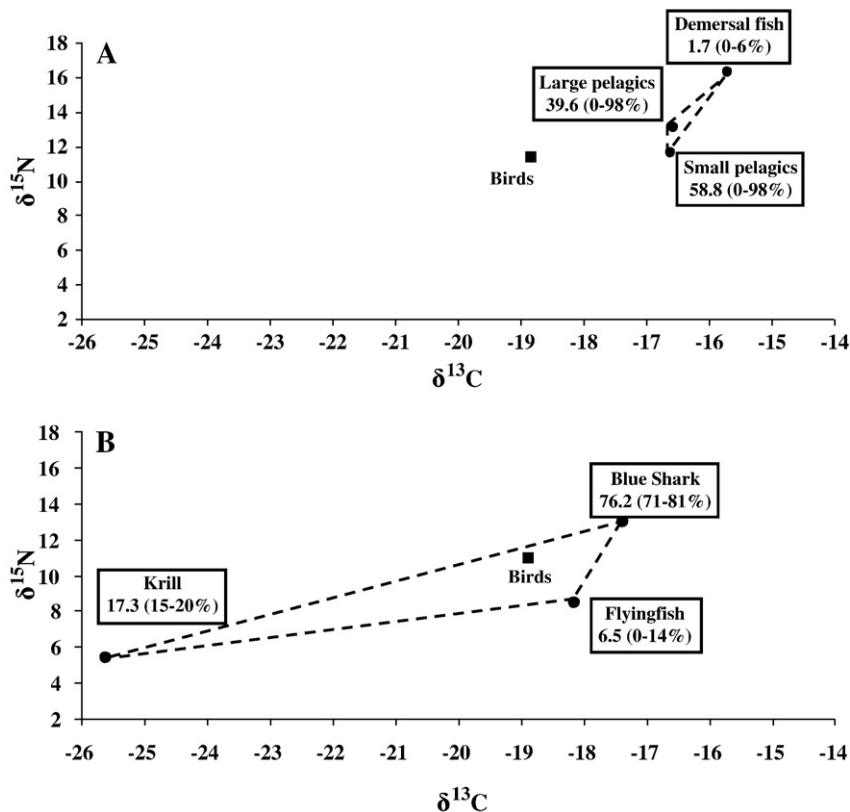


Fig. 5. Mixing polygons for $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ signatures in whole blood of albatrosses and petrels at sea off Brazil. A. linear mixing model with 'large pelagics', 'small pelagics/bait' and 'demersal fish' categories. B. linear mixing model with flying fish *Cypselurus* sp., blue shark *Prionace glauca* and krill *Euphausia superba* as sources for the isotopic mixture. Values shown in the boxes are mean % and 1–99 percentile ranges for these contributions.

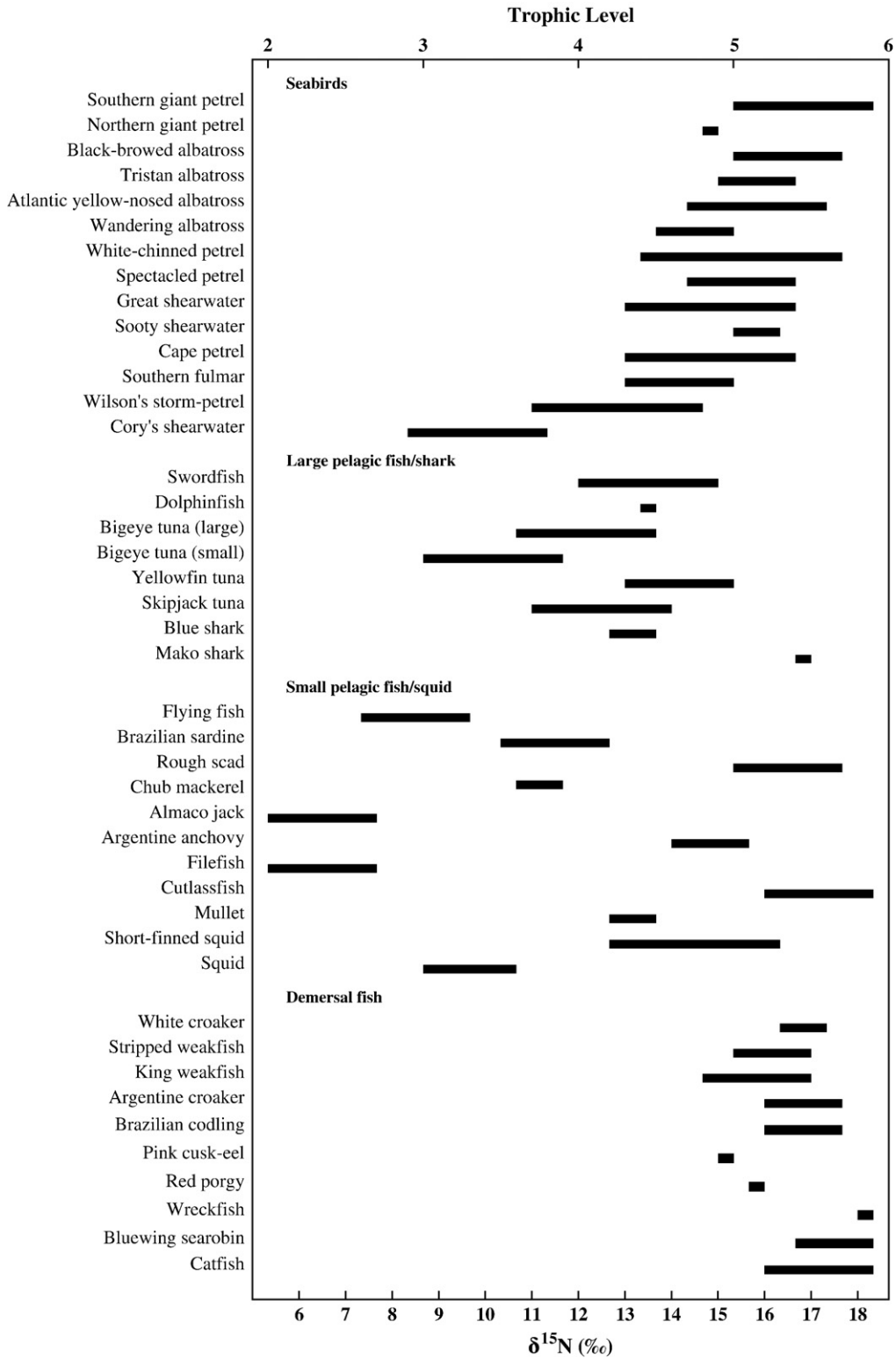


Fig. 6. Trophic levels and $\delta^{15}\text{N}$ (‰) values \pm 1 SD of albatrosses, petrels and shearwaters sampled at sea off southern Brazil and their potential food sources. Scientific names are given in Table 1.

lathami) and short-finned squid (*Illex argentinus*) used as bait, ranked high. Somewhat unexpectedly, Argentine anchovy had a mean TL of 4.9, while both squid groups (*Illex* used as bait vs. *Illex/Ommastrephes bartrami* captured by fishermen from the longline vessels, simultaneously with seabird samplings) differed by 1.5 TLs.

4. Discussion

Antarctic and sub-Antarctic seabirds, sampled in SW Atlantic Ocean after the breeding period, still had in their blood, components of their prey during breeding, which has low carbon isotope values

typical of high latitudes (Quillfeldt et al., 2005; Cherel et al., 2006; Cherel, 2008). Procellariiformes wintering off Brazil appeared to have undergone a marked shift in the isotopic values of carbon and nitrogen in their blood, in comparison to the values determined from the breeding grounds. The isotope ratios we obtained from seabird tissues are on average higher than those of large pelagic predators and lower than demersal fish. Our stable isotope data and the mixing models suggest that waste from the pelagic longline fishery is the main food source for all seabird species, except for Cory's shearwater, the only species that did not attend these fishing vessels and which exhibits correspondingly lower nitrogen isotope values, 3–4‰ lower than in other seabirds. Cory's shearwater was only observed feeding on small pelagic prey. The dependence of the majority of these bird species on the same food resource is postulated to be the primary cause of the unstructured food web resulting in considerable overlap in TLs between species and individuals. This implies inter and intra specific competition for an abundant food resource, rather than clearly defined ecological niches for each seabird species. The linear mixing model confirms that up to 80% of the carbon and nitrogen isotope composition on whole blood from 13 seabird species is from discards from the tuna-shark pelagic longline fisheries off Brazil.

Epipelagic communities are naturally less diverse than demersal and coastal communities, thus some degree of dietary overlap in seabirds, and reduced trophic niche segregation between pelagic seabirds can be anticipated. Even so, due to inter specific variation in body masses and feeding techniques, we would expect some degree of niche partitioning, with storm-petrel and Cape petrel feeding on small planktonic prey, diving birds and small albatrosses feeding on small pelagic prey, and large albatrosses scavenging natural food sources. Such structuring was not observed. We interpret this as resulting from the occurrence of artificially abundant food source, access to which is not limited to size or feeding technique, in this case taking the form of fisheries discards, especially livers, from large predatory sharks and tunas.

4.1. Methodological considerations

Seabird species sampled in this study are representative of the community of pelagic seabirds in the SW Atlantic Ocean as determined by census (Neves et al., 2006; Bugoni et al., 2008a). Because only birds attending vessels were sampled, there is a possibility of sampling bias towards individuals that specialized in feeding on discards, with those making very limited use of discards not represented. However, observations of banded birds and those with diagnostic external marks, suggests that individual birds only remain for short periods attending the same vessel. Also, due to the ability of albatrosses and petrels to cover vast distances in short periods, we are confident that the sampling is representative of the community in the area, as birds frequently moved between fishing vessels (Bugoni et al., 2009). These species are known to cover vast areas of ocean, and therefore have potential access to a wide range of natural prey sources and even discards from other fisheries.

To our knowledge, this is the first study to document the diet of a wintering seabird community by directly sampling blood at sea and combining the carbon and nitrogen isotope data from winter and breeding season blood with contemporaneous feeding observations. Conventional methods for dietary studies, like gut content analyses, are known to be biased by the more rapid digestion of soft-bodied prey and retention of hard prey fragments (Barrett et al., 2007). As with gelatinous prey which were regarded as minor prey (see Cherel and Klages, 1997 for a review of food items of albatrosses), but later recognized as being more frequently ingested (e.g. Catry et al., 2004). Viscera of large predatory fish and shark liver, in particular, are digested rapidly and are therefore generally undetected in studies using traditional methods. Even stomach content analysis of birds killed by longline fisheries in the SW Atlantic Ocean failed to report

these items (Colabuono and Vooren, 2007). We have shown both by direct observation, carbon and nitrogen stable isotope analysis in blood and from mixing models, that shark liver and remains of other large pelagic fish are the main food source of albatrosses and petrels during the wintering period in southern Brazil. Shark livers discarded in other fisheries around the world are also expected to provide food for albatrosses, petrels and shearwaters, except in fisheries where only shark finning occurs such as in Pacific Ocean waters (Gilman et al., 2008).

Linear mixing models such as the IsoSource used here (Phillips and Gregg, 2003) and Bayesian mixing models (Parnell et al., 2010) are valuable tools for the identification of food sources, particularly in complex systems like the SW Atlantic Ocean in this study. However, as we have shown in our first model (Fig. 5A), by not including the key Antarctic krill component (which was derived from outside the study area) the model overestimated the importance of flying fish, and ultimately indicated no solution possible from given data. As highlighted in previous studies (e.g. Cherel, 2008; Flaherty and Ben-David, 2010; Votier et al., 2010), the geographic range in baseline isotopic values, the habitat heterogeneity, the turnover of tissues, and especially *a priori* knowledge on the ecology of species, should be considered when modelling or interpreting results from mixing models. In our system, the role of longline fishery discards on the diet of particular seabird species, as well as the role of discards from demersal and coastal fisheries, deserves further investigation.

4.2. Wintering vs. breeding diet as revealed by stable isotopes

The carbon and nitrogen stable isotope values in SW Atlantic seabirds are on average higher than in tissues of the same species from breeding grounds in Patagonia, Antarctica and Sub-Antarctic areas (Hodum and Hobson, 2000; Forero et al., 2004; Quillfeldt et al., 2005; Cherel et al., 2006). Higher carbon isotope values would be predicted for seabirds sampled from these lower latitude areas (Quillfeldt et al., 2005; Cherel and Hobson, 2007) and also for nitrogen isotope values, indicating higher trophic levels (e.g. Hobson et al., 1994; Forero et al., 2004). More interesting, however, is the marked change in diet reflected by nitrogen and carbon isotope values and the increase in TL that occurred in most species between breeding and wintering periods, except in the case of Cory's shearwater, the only species which breeds in tropical or sub-tropical North Atlantic Ocean. During the breeding season, Cory's shearwater feeds on similar epipelagic and epimesopelagic prey and has similar $\delta^{15}\text{N}$ values in blood to those found in the wintering area (range 10–13‰, Navarro et al., 2007). The carbon and nitrogen isotope values in blood of wandering albatrosses, sampled in our area when still rearing chicks in South Georgia as determined by tarsal rings (Bugoni et al., 2008c), reflected the diet from a breeding season with foraging occurring in southern areas as well as in the SW Atlantic Ocean. The breeding season component of the diet accounts, in the mixing model, for 15–20% of the dietary isotope signature in the seabird community as a whole. Migrants from southern latitudes such as Cape petrel, Wilson's storm-petrel and white-chinned petrel, also occasionally showed isotopic signatures typical of Antarctic latitudes when sampled early in autumn (Fig. 4). It is evident that more negative $\delta^{13}\text{C}$ values carried from southern breeding grounds are influencing the mean and standard deviation of isotopic values, as also shown in the mixing model. The inshore-offshore signature detected in tissues of seabirds in other communities (e.g. Hobson, 1993; Cherel et al., 2006) and in tissues of mullets and other fishes here, was not found in albatrosses and petrels, which show typically offshore signatures.

4.3. Seabird food sources and trophic overlap

Some seabird communities are known to rely mainly on a single or a few food resources and so have overlapping TLs, for example krill

(*Euphausia* spp.) in the Antarctic and sub-Antarctic (Croxall and Prince, 1987; Hodum and Hobson, 2000), anchovies (*Engraulis ringens*) in the Humboldt Current system (Duffy, 1983), capelin (*Mallotus villosus*) in Newfoundland–Labrador (Carscadden et al., 2002). Forero et al. (2004) found a broad overlap in TL among 14 breeding seabirds in Patagonia, with 13 species within 0.7 TLs, this was interpreted as seabird species using mainly a single prey, the Argentine anchovy. Similarly, in our study, with the exception of Cory's shearwater, all other species rely predominantly on pelagic longline fishery waste during the wintering period, thus showing similar C and N isotope values and high trophic status.

The Subtropical Convergence Area in the SW Atlantic Ocean is a heterogeneous environment where a range of potential natural prey are present and expected to provide 'natural' food for seabirds with a diverse range of feeding strategies and body sizes. Furthermore, a range of fisheries operate over the adjacent continental shelf, the largest fleets trawling for shrimp and sciaenid fish and demersal gillnetting for sciaenid fish. The trawl fishery is potentially a major source of discards for seabirds, comprising undersized and non-commercial fish (Haimovici, 1998). Demersal fish had $\delta^{15}\text{N}$ values higher than seabirds (Figs. 2 and 6) and were demonstrated by the mixing model not to be important in the diet of birds sampled. Surprisingly however, direct observation indicates that albatrosses and petrels attend these vessels for discards, and thus further studies on the importance of discards from other fisheries in the diet of birds are necessary. However, a coastal isotope signature such as that obtained from mullet (*Mugil* sp.) shown in Fig. 2 and Garcia et al. (2007), was not evident in seabird blood. In contrast to other seabird communities where overlap among species is driven by the availability of a few natural food resources, the overlap among the diverse community of seabirds, and the unstructured food web we report, appears to result from anthropogenic activity, i.e. fishery discards, and results in a monotonous diet shared among species, ages and sexes.

Communities of vertebrates are expected, in general, to be size-structured, particularly in relation to their feeding behaviour. For example, Al-Habsi et al. (2008) found that a demersal fish community sampled by trawling was size-structured in terms of TL. However, Jennings et al. (2008) found that the heaviest predators rarely fed at the highest trophic level, as we also found here. The community of seabirds attending a fishing vessel for discards is frequently diverse, but large seabirds that can compete effectively at fishing boats for this resource are favoured (e.g. Hudson and Furness, 1988; Votier et al., 2004; current study). Nevertheless, discards from the Brazilian pelagic longline fishery have been demonstrated in this study to be a 'democratic' food source for seabirds with different foraging abilities, supporting birds across the entire size range, from storm-petrels to large albatrosses.

4.4. Costs and benefits of attending longline vessels: species-specific outcomes

Events occurring during the wintering periods are known to shape population dynamics of birds (Marra et al., 1998; Cherel et al., 2006; Robb et al., 2008). Whereas pelagic longline fisheries cause negative impacts on the aquatic community by removing top predator fish (Kitchell et al., 2002; Heithaus et al., 2008), the effects on seabirds are variable. Albatrosses and petrels greatly benefit from pelagic longline discards, where the preferred shark liver is a lipid-rich and convenient food source. However, the cost of this behaviour is that birds can be drowned when feeding on baited hooks (Bugoni et al., 2008a). Globally, sixty-one seabird species (mostly albatrosses and petrels) are known to be caught on longlines (Brothers et al., 1999), and this is considered to be the main cause of steep declines in 19 out of 21 albatross species currently listed as threatened globally (IUCN, 2008). Smaller species (e.g. the Cape petrel, southern fulmar, Wilson's storm-

petrel) are not able to swallow the large baited hooks used in this fishery. Overall, the negative impacts of longline fishery on the ecosystem and on the larger albatrosses and petrels appear to be greater than the benefits that this supplementary food provides for some abundant and widespread species.

Acknowledgements

We gratefully acknowledge the captain C. Oliveira and crew of the fishing vessel "Ana Amaral I" and "Akira V" for logistic support onboard the vessel. A. Gomes Jr, J.P. Castello for helping during sampling potential prey, K. Griffiths for sexing birds, T. Vaske Jr and R.A. Santos for identifying prey. We also thank the critical revision of Dr. R. Phillips and two anonymous referees, which greatly improved the manuscript. Sample analysis was funded by the Natural Environment Research Council (NERC-UK, Grant Number EK81-07/05). L.B. received a CAPES Scholarship. This study was carried out according to permits from Brazilian and Scottish Governments. [ST]

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