



# Inter-colony and inter-annual variation in discard use by albatross chicks revealed using isotopes and regurgitates

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## Abstract

Effective marine ecosystem monitoring is critical for sustainable management. Monitoring seabird diets can convey important information on ecosystem health and seabird–fishery interactions. The diet of breeding black-browed albatross (*Thalassarche melanophris*) has previously been assessed using stomach content analysis (SCA) or stable isotope analysis (SIA), but not both methods together. Combining dietary sampling approaches reduces biases associated with using single methods. This study combines SCA and SIA to study the diet of black-browed albatross chicks, with a specific focus on fishery discard consumption, at two Falkland Islands colonies (New Island 51°43'S, 61°18'W and Steeple Jason Island 51°01'S, 61°13'W) during two consecutive breeding seasons (2019 and 2020). SCA provided high taxonomic resolution of short-term diet and priors for stable isotope mixing models, with multiple measures of dietary items (e.g. numeric frequency N%, frequency of occurrence FO%). By contrast, SIA of down feathers provided a single and more integrated dietary signal from throughout chick development. Although the two methods disagreed on the dominant prey group (SCA—crustacean; SIA—pelagic fish), the complementary information suggested a chick diet dominated by natural prey (SCA: 74%–93% [FO], 44%–98% [N]; SIA: minimum 87%–95% contribution). Nonetheless, SCA revealed that a high proportion of breeding adults do take discards. We detected consistent colony-specific diets in relation to prey species, but not in relation to higher discard use. Overall, discard consumption was highest in 2020, the year characterised by the poorest foraging conditions. Our results have implications for fisheries management and future dietary studies assessing discard use.

**Keywords** Fishery discards · Seabird diet · Stomach content analysis · Stable isotope analysis · *Thalassarche melanophris*

## Introduction

In an era of rapid marine ecosystem change, monitoring is critical for the sustainable management of our oceans. Top predators, such as seabirds, are often regarded as useful

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indicators of marine ecosystem health (Velarde et al. 2019; Bestley et al. 2020), but indices require careful consideration (Durant et al. 2009). For example, changes in seabird demography, distribution, or breeding biology can reflect environmental change (e.g. Votier et al. 2005; Cury et al. 2011; Sydeman et al. 2021), or impacts of anthropogenic activities such as fishing (e.g. Einoder 2009; Pardo et al. 2017; Sherley et al. 2017). However, seabird populations and distributions alter relatively slowly with time (Nevoux et al. 2010) and non-breeders may buffer the effects of environmental or anthropogenic change (Votier et al. 2008a), making it challenging to detect such impacts (e.g. Sherley et al. 2018). By contrast, dietary variation may be a more sensitive indicator of change.

Seabird diets reflect an individual's foraging behaviour, including prey preference, foraging distribution and dietary flexibility (e.g. Gaglio et al. 2018; Church et al. 2019), and indicate the quantity, quality and accessibility of prey at the species and population level (Buren et al. 2012; Velarde et al. 2019). In addition, seabird diets may provide information on fishery interactions, including variation in discard use (Votier et al. 2004, 2008b), or bycatch risk (Einoder 2009; Phillips et al. 2016). Methods to accurately study seabird diets can therefore form an integral part of monitoring strategies and ecosystem-based approaches to fisheries management, such as in the Commission for the Conservation of Marine Living Resources (CCAMLR) Ecosystem Monitoring Programme (CEMP) (also see e.g. Scopel et al. 2019).

A range of morphological and biochemical methods exist for assessing diet, and each provide different information and biases (Votier et al. 2003; Barrett et al. 2007). Stomach content analysis (SCA) and stable isotope analysis (SIA) are common approaches for assessing seabird diet (Duffy and Jackson 1986; Barrett et al. 2007; McInnes et al. 2016). SCA provides high taxonomic resolution, but this tends to reflect short time scales (days to weeks), and can underestimate soft-bodied prey (Votier et al. 2003; Inger and Bearhop 2008; McInnes et al. 2017b). Conversely, SIA typically provides dietary information integrated over longer time scales during tissue growth (weeks to months; Inger and Bearhop 2008; Phillips et al. 2014). However, stable isotope mixing models, which are used to quantify prey source contribution to a diet mixture, rely on prior knowledge of diet and are only informative if key prey differ in their isotopic composition (Inger and Bearhop 2008; Phillips et al. 2014). Combining morphological and biochemical analyses can address the pitfalls of individual methods (Karnovsky et al. 2012; Bonin et al. 2020), and a complementary approach is therefore recommended when using seabird diet for monitoring (Bot et al. 2018; Ceia et al. 2022).

The black-browed albatross *Thalassarche melanophris* (hereafter BBA) is the world's most abundant species of

albatross, and its diet has been well-studied (see McInnes et al. 2017a). It is used as a bio-indicator in the CEMP, as well as a sentinel of the Patagonian Shelf Large Marine Ecosystem (Ventura et al. 2021). The population breeding in the Falkland Islands is of particular interest, because it is the world's largest (> 70% of breeding populations), and, in contrast to several other populations, is increasing in size (BirdLife International 2018).

BBA breeding in the Falkland Islands forage over the Patagonian Shelf, where large numbers scavenge at fishing vessels for discards, consequently falling victim to bycatch (Granadeiro et al. 2011, 2014; Kuepfer et al. 2022a, b). Dietary studies, however, suggest that they predominantly consume natural prey (Thompson 1992; Kuepfer et al. 2022a (SCA); Granadeiro et al. 2014 (SIA); McInnes et al. 2017a (DNA)), although discards appear important when natural foraging conditions are unfavourable (Kuepfer et al. 2022a). Discard consumption also varies amongst colonies, with larger colonies thought to consume more discards (Thompson 1992; McInnes et al. 2017a). However, the previous diet studies all applied different individual methods (SCA: Thompson 1992; Kuepfer et al. 2022a; DNA: McInnes et al. 2017a, b; SIA: Granadeiro et al. 2014), and (apart from McInnes et al. 2017a) focussed on either individual years or individual colonies. It is therefore difficult to distinguish methodological biases from temporal and spatial variation in diets when comparing results. At a time when discard management in the Falkland Islands is changing (through the introduction of batch discarding by trawlers; Kuepfer and Barton 2018; Kuepfer et al. 2022b), and the climate warming across BBAs' range (Franco et al. 2022), it is important to gain a more comprehensive dietary understanding for this globally significant population.

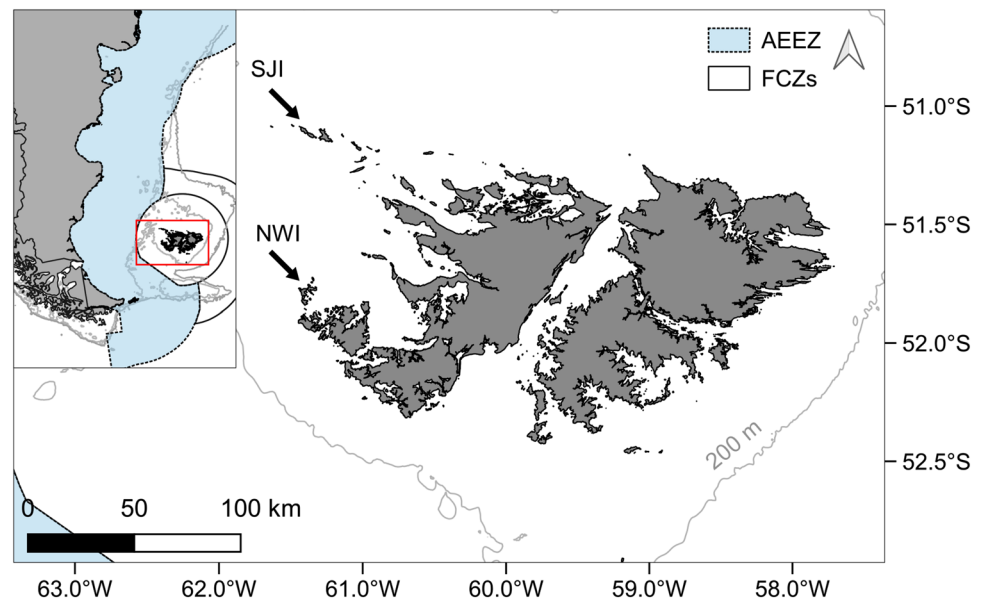
Here, we use SCA and SIA to study BBA chick diet at two Falkland Islands colonies from two consecutive breeding seasons. Specifically, we (1) quantify diet, (2) assess the importance of discards and natural prey and (3) determine how diet varies between colonies and years. Considering previous findings, we hypothesise that (1) natural prey will dominate across years and colonies but that (2) discard consumption will be higher at the larger colony.

## Materials and methods

### Study area and fleet characteristics

Fieldwork took place in the austral summer of 2018/2019 and 2019/2020 (hereafter 2019 and 2020) during mid-chick rearing (~6–12 weeks of age) at New Island (NWI, 51°43'S, 61°18'W) and Steeple Jason Island (SJI, 51°01'S, 61°13'W), located in the west and north-west of the Falkland Islands

**Fig. 1** Location of New Island (NWI) and Steeple Jason Island (SJI) in the Falkland Islands on the Patagonian Shelf, east of the South American continent. The 200-m and 1000-m depth contours are shown as grey lines. AEEZ Argentine Exclusive Economic Zone, FCZs Falklands Conservation Zones



(Fig. 1). NWI and SJI, respectively, support approximately 16,000 and 210,000 breeding pairs of BBA (Crofts 2020).

Chick-rearing adults from NWI and SJI concentrate their foraging on the southern Patagonian Shelf, although they generally segregate by colony whilst at sea (NWI: south-west/west; SJI: north-west/north; Catry et al. 2013). The area is extensively fished, predominantly by bottom trawlers for finfish and jiggers for Argentine shortfin squid (*Illex argentinus*, hereafter *Illex*) (Seco Pon et al. 2015; Falkland Islands Government 2021). There is also some longlining (2–4 vessels within the Falklands Conservation Zones (FCZs) and the Argentine Exclusive Economic Zone (AEEZ) combined at <math>40^{\circ}</math> S latitude; Seco Pon et al. 2015; Falkland Islands Government 2021). Discards of demersal and benthopelagic fish are available to seabirds from bottom-trawl vessels throughout the year, including during chick rearing (Fig. S1). Squid discards are limited, as *Illex* and Patagonian long-finned squid (*Doryteuthis gahi*, hereafter Loligo) are generally packed whole, and discarding of the latter is prohibited in Falkland Islands waters (Laptikhovskiy et al. 2006; Arkhipkin et al. 2015).

## Sampling

### Stomach content analysis

Stomach contents were collected from chicks using induced regurgitation (after Phillips 2006) during late January through to mid-February at NWI, and in mid-March at SJI (NWI 2019: 29 January–17 February; NWI 2020: 25 January–23 February; SJI 2019 and 2020: 12–16 March). For logistical reasons, it was not possible to sample both colonies simultaneously. Only freshly fed chicks were

sampled, and each chick was only sampled once. To obtain a measurement of meal size and stomach oil content, individual stomach samples were weighed whole (total mass, g), and again after stomach oils had been drained (wet mass, g).

Prey were first separated into key prey groups (fish, cephalopod, crustacean, jellyfish and carrion), and subsequently identified to the lowest possible taxonomic level using reference collections (Falkland Islands Fisheries Department (FIFD), unpubl. data; Xavier and Cherel 2009) and with assistance from specialists (B. Lee, Z. Shcherbich). Minimum number of individuals (MNI) was determined through assemblage of whole animals and fresh loose hard structures. MNI for carrion (penguin feathers) and jellyfish within individual samples was always 1, as it was impossible to determine whether parts originated from a single or multiple individuals. Eroded or brittle structures were excluded from all analyses, as these were assumed to have originated from previous meals.

Prey that were identified to species level were further categorised as fishery discards or natural prey based on numerous criteria relating to natural accessibility of prey to albatrosses, fishing and discard practices, and reconstructed prey size (see Kuepfer et al. 2022a for further details; Table S1). Large fish heads in the absence of the bodies were categorised as discards because at-sea catch processing generally involves heading and gutting of fish (see Kuepfer et al. 2022a). For species where reconstructed size was used to assist with classification (hoki *Macruronus magellanicus* and southern blue whiting *Micromesistius australis*), maximum sagittal length (mm) was measured from intact otoliths (one from each otolith pair as well as unpaired otoliths) using a binocular microscope equipped with a graticule to

**Table 1** Metrics used to quantify prey at different taxonomic levels

	M%	N%	FO%	IRI%
<b>Main prey groups</b>				
Fish	✓	✓	✓	✓
Cephalopod	✓	✓	✓	✓
Crustacean	✓	✓	✓	✓
Carrion (penguin feathers)	✓	✓	✓	✓
Jellyfish	✓	✓	✓	✓
<b>Individual species of...</b>				
Fish		✓	✓	
Cephalopod		✓	✓	
Crustacean		✓	✓	
<b>Origin</b>				
Discards		✓	✓	
Natural prey		✓	✓	

M% percentage drained mass, FO% percentage frequency of occurrence, N% percentage numeric frequency, IRI% percentage index of relative importance

reconstruct the original size of the prey from allometric formulae (Table S2). Finally, prey were quantified using four different metrics (see below, Table 1).

### Stable isotope analysis

Multiple down feathers from across the body were collected from a random sample of 55–73 chicks at NWI (mid-February, chick age 62 days Catry et al. 2011; Ventura et al. 2021) and at SJI (mid-March, chick age approximately  $84 \pm 7$  days). At this age, given the large increase in body surface area since hatching, the stable isotope composition of down feathers is no longer expected to reflect egg nutrients. Rather, they provide dietary information from the first 2 months of chick development and are therefore directly comparable between NWI and SJI, despite the discrepancy in sampling months.

To characterise stable isotopes of potential prey, we sampled muscle tissue of specimens collected during the FIFD ground-fish surveys in February 2019 and 2020. Sampling focussed south, west and north of the FCZs, where GPS tracked BBA breeding on NWI and SJI forage during chick rearing (Granadeiro et al. 2011; Ventura et al. 2021). Prey species were chosen based on available knowledge of BBA diet in the Falkland Islands (McInnes et al. 2017a, b; Kuepfer et al. 2022a; current study), and included demersal, pelagic and benthopelagic species of fish, cephalopods, crustaceans and jellyfish.

Prey muscle and albatross chick feathers were processed following Meier et al. (2017). To avoid biases in analyses of  $\delta^{13}\text{C}$  related to the presence of lipids in muscle samples (see e.g. Bearhop et al. 2002; Post et al. 2007), *a-priori* lipid

extraction was conducted on lipid-rich samples, defined as species with a C:N > 3.5 (Post et al. 2007). The effervescent test (after e.g. Carabel et al. 2006) confirmed the absence of carbonates from all crustacean samples. Samples were weighed into tin capsules (approx. 0.7 mg) and analysed for  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values by continuous-flow isotope ratio mass spectrometry at the National Environmental Isotope Facility Stable Isotope Ecology Laboratory, East Kilbride. Samples were analysed using a Elementar vario Pyrocube elemental analyser (2013), coupled with a Thermo Fisher Delta XP Plus Isotope Ratio Mass Spectrometer (IRMS). Ratios were corrected for instrument drift and linearity using interspersed samples of internal laboratory standards (gelatine, glycine and alanine mixtures) with known stable isotope values (for details see Jones et al. 2020). Stable isotope ratios were expressed in  $\delta$  notation in parts per thousand (‰) relative to Vienna Pee Dee Belemnite ( $\delta^{13}\text{C}$ ) or air ( $\delta^{15}\text{N}$ ). Precision of the measurements was 0.09‰ for  $\delta^{13}\text{C}$  and 0.17‰ for  $\delta^{15}\text{N}$ , based on the standard deviation of the most common lab standard used (gelatine).

### Statistical analysis

All statistical analyses were conducted in R version 4.0.0 (R Core Team 2021). The significance value of frequentist statistical tests was set at  $\alpha = 0.05$ , unless stated otherwise.

### Stomach content analysis

To assess whether the number of stomach content samples obtained from chicks was sufficient to describe dietary species diversity, samples from individual colony/year combinations were randomised 100 times, and an accumulation curve was constructed as a function of sample size (package `vegan::accumcomp`, Oksanen et al. 2019). Sample sizes would be considered sufficient to describe the full diversity of the diet if the fitted cumulative prey curves reached an asymptote.

Prey were subsequently described using a range of metrics, after Barrett et al. (2007), and following the method of Kuepfer et al. (2022a) (Table 1). First, key prey groups (fish, crustacean, cephalopod, jellyfish and carrion) were quantified as a percentage index of relative importance (IRI%) as:

$$IRI\% = \left( IRI_p / \sum_{i=1}^n IRI_{p,i} \right) \times 100, \quad (1)$$

$$IRI_p = FO\% \times (N\% + M\%)$$

where FO% is the percentage of stomach samples (*i*) in which a particular prey type (*p*) was present; N% is the number of individuals of a particular prey type present

expressed as a percentage of the total prey number at that taxonomic level and M% is the percentage of the total drained sample mass represented by a particular prey type.

Next, individual prey species and categories constructed from identified species (i.e. fish subgroups and prey origin [discards and natural]) were quantified by FO% and N%. We did not obtain M% (and hence IRI%) at these levels, because it was impractical to separate out, and identify, every individual fish bone or loose flesh to obtain species-specific mass (see also Kuepfer et al. 2022a).

Different methods of prey quantification provide complementary dietary information: M% informs on meal size and can indicate approximate nutritional contribution of similar prey; FO% indicates the variability of prey abundance, and N% measures the frequency of prey encounter (Duffy and Jackson 1986; Barrett et al. 2007). The IRI% is considered the most comprehensive approach, as it integrates information from numerous metrics, thereby reducing biases associated with any one measure (Duffy and Jackson 1986; Liao et al. 2001; Mills et al. 2020). The absence of IRI% of prey origin (as explained above) is therefore unfortunate; however, given that crustaceans and cephalopods were categorised as natural prey, and most fish as discards (Table S1), the IRI% of key prey groups can serve as a proxy for prey origin.

Wilcoxon rank sum tests were used to assess (1) differences in meal size, and (2) differences in prey species composition between years and colonies. Year or colony were used as our explanatory variables in individual tests, whilst our dependent variables were either (1) the different meal fractions (total/ liquid/drained); (2) counts or presence/absence of prey species from either discards or natural prey. To minimise Type 1 errors, the significance level was adjusted using the Bonferroni correction to  $\alpha=0.025$ . As stomach content samples were not collected simultaneously at the two colonies, inter-colony comparison warrants some caution due to possible seasonal effects (see Discussion).

### Stable isotope analysis

To compare isotopic values ( $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ ) of chicks between colonies, we conducted multivariate analysis of variance (MANOVA) with *post hoc* ANOVAs, and compared isotopic niche using SIBER (Stable Isotope Bayesian Ellipses in R; Jackson et al. 2011). We did not compare niche space between years due to insufficient certainty around the isotopic baseline for the two years, which makes it difficult to discern potential differences resulting from baseline shifts or diet shifts.

To assess the percentage contribution of different prey, a series of Bayesian mixing models with a multiplicative error structure of residual  $\times$  process error and uninformative Dirichlet priors were applied using the MixSIAR package

(Stock and Semmens 2016). Individual mixing models were run for each colony/year combination (NWI 2019, SJI 2019, NWI 2020, and SJI 2020). Mixing model convergence was assessed using the Gelman–Rubin and Geweke’s diagnostics (Stock and Semmens 2016).

Uncertainty in SIA can be related to isotopic similarity amongst prey types (Phillips and Gregg 2001; Phillips et al. 2014). Further, the discriminatory power of mixing models rapidly deteriorates when more than six prey sources are included, so aggregating isotopically and biologically similar sources is recommended (Phillips et al. 2014). We therefore tested the isotopic differences between prey species using MANOVAs, and based on ecological and isotopic similarities, aggregated them into four a-priori groups: (1) pelagic fish; (2) demersal fish; (3) benthopelagic fish + squid; (4) crustacean + jellyfish.

The decision to include or exclude a particular species as a prey source was informed by our colony/year-specific SCA results (see below, Table 2)—only prey species that comprised  $> 10\%$  (FO) of the stomach contents in any colony/year were included, as the exclusion of uncommon prey tends to improve mixing model accuracy (Phillips et al. 2014). In all models, we further included potentially important prey which may easily be missed or underestimated in SCA due to soft body parts (i.e. jellyfish and Fuegian sprat (*Sprattus fuegensis*); McInnes et al. 2017a, b). Where the isotopic values of individual species did not differ significantly between years (MANOVAs), species were pooled from both years to increase sample size (Table S4, Fig. S2). In the absence of stable isotope values for a particular prey species in one year, we used the values available from the other year (Table S4).

Diet-tissue trophic discrimination factors (TDFs) have not been published for Procellariidae, and we therefore used values estimated using Stable Isotope Discrimination Estimation in R (SIDER, Healy et al. 2018): Feathers:  $\delta^{15}\text{N}$   $4.09 \pm 1.19$ ,  $\delta^{13}\text{C}$   $2.21 \pm 1.25$ . SIDER is designed to predict TDFs of consumers based on their ecology and phylogenetic relatedness (Healy et al. 2018), and the values determined by SIDER therefore provide for the most up-to-date and biologically justified models (also see e.g. Swan et al. 2020).

## Results

### Stomach content analysis

Stomach contents were collected from 143 chicks across the 2 years and colonies (NWI 2019 & 2020:  $n=40$ ; SJI 2019:  $n=32$ ; SJI 2020:  $n=31$ ). Meals were significantly heavier in 2020 at NWI due to the higher liquid portion (Mann–Whitney  $U$  tests; Total:  $W=392$ ,  $P=0.004$ ; Liquid:  $W=325$ ,  $P=0.001$ ; Drained:  $W=770$ ,  $P=0.924$ ; Fig. 2).

**Table 2** Prey species found in regurgitate samples from black-browed albatross chicks at New Island (NWI) and Steeple Jason Island (SJI) in 2019 and 2020

Species	FO%				N%			
	NWI		SJI		NWI		SJI	
	2019	2020	2019	2020	2019	2020	2019	2020
<b>Fish</b>								
<b>Demersal Fish</b>								
Banded whiptail grenadier <i>Coelorinchus fasciatus</i> §	10.0	55.0		6.5		(19.6)		
Common hake <i>Merluccius hubbsi</i> ‡			37.5	29.0			(11.0)	(20.1)
Dwarf codling <i>Notophycis marginata</i> §		20.0						
Red cod <i>Salilota australis</i> ‡			12.5					
Kingclip <i>Genypterus blacodes</i> ‡				6.5				
<b>Benthopelagic Fish</b>								
Hoki <i>Macruronus magellanicus</i> ‡^	32.5	70.0	34.4	22.6	(13.2)	(28.9)	(10.2)	(9.1)
Southern blue whiting <i>Micromesistius australis</i> ‡^		10.0						
Butterfish <i>Stromateus brasiliensis</i> §		5.0		9.7				
<b>Pelagic Fish</b>								
Feebian sprat <i>Sprattus fuegensis</i> ^	35.0	17.5		12.9	(29.7)	(9.0)		(10.8)
<b>Unidentified Fish</b>								
Fish spp.	5.0	7.5						
<b>Crustacean</b>								
Lobster krill <i>Munida gregaria</i> ^	65.0	60.0	84.4	64.5	66.3	22.7	80.9	97.2
<i>Themisto gaudichaudii</i> ^	5.0	7.5	6.2	12.9			(17.0)	(10.2)
Amphipod sp.		17.5				(6.0)		
<b>Cephalopods</b>								
Argentine shortfin squid ( <i>Illex</i> ) <i>Illex argentinus</i> ‡^	10.0	5.0	59.4	38.7			(25.0)	(20.4)
Patagonian short-finned squid (Loligo) <i>Doryteuthis gahi</i> ‡^	40.0	25.0	28.1	19.4	(41.2)	(16.4)	(24.1)	(8.6)
Squid spp.	5.0	5.0						
Octopus spp.				9.7				
<b>Jellyfish</b>								
<i>Medusa</i> spp.^		5.0		22.6				
<b>Carrion</b>								
Spheniscidae spp.^		5.0		12.9				

Only species which occurred at minimum 5% frequency of occurrence (FO%) or numeric frequency (N%) in any given year/colony are presented. Values in brackets represent N% as calculated excluding crustaceans from the total prey count, as very high counts of crustaceans resulted in negligible N% of other species

‡Fishery target species available as discards

§Bycatch species available as discards

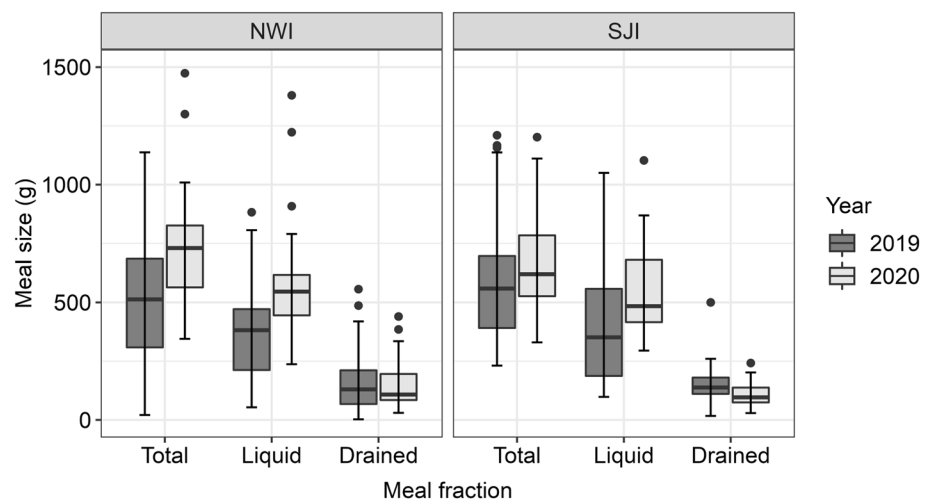
^Prey naturally accessible to black-browed albatross during at least part of their life history

At SJI, although the total meal size did not vary between years, liquids were significantly heavier (before Bonferroni correction), and drained samples significantly lighter in 2020 (Mann–Whitney *U* tests; Total:  $W=290$ ,  $P=0.138$ ; Liquid:  $W=234$ ,  $P=0.036$ ; Drained:  $W=534$ ,  $P=0.019$ ; Fig. 2).

We extracted 9092 prey items from 143 drained regurgitates. The three dominant prey categories were crustacean, fish and cephalopods (Fig. 3a). Jellyfish and carrion

(penguin species) were only found in 2020, but their relative importance remained negligible at both colonies (Fig. 3a, Table S3). Crustaceans had the highest relative importance across colonies/years (IRI% = 49–67%), except at NWI 2019, where fish dominated with 80% (IRI). At both colonies, the IRI% of fish was approximately double in 2020 compared to in 2019 (Fig. 3a). Cephalopods, dominated by squid, consistently showed smaller

**Fig. 2** Meal sizes (g) as sampled through regurgitation from black-browed albatross chicks at New Island (NWI) and Steeple Jason Island (SJI) in 2019 and 2020. The box shows the interquartile range, with the thick horizontal line representing the median. The whiskers represent the 95% percentiles



IRI% than fish and crustaceans across colonies and years (IRI% = 4–15%, Fig. 3a).

The asymptotes of species accumulation curves were not fully reached; however, the flattening of the species accumulation curves provides confidence that the most important identifiable prey had been captured (Fig. 4). Species richness was higher at SJI than at NWI in 2019, but higher at NWI than SJI in 2020, and was considerably higher in 2020 than in 2019 at both colonies (Fig. 4).

The composition of dominant species differed between colonies but was broadly consistent across years (Table 2). The most frequent and most numerous species encountered at both colonies was lobster krill (*Munida gregaria*) (Table 2). Individual lobster krill consisted exclusively of adults at NWI, whereas at SJI, both adults and juveniles were present at a ratio of approximately 2:5 in 2019 and 1:50 in 2020. In terms of cephalopods, *Loligo* squid was the most numerous and abundant species at NWI, whilst *Illex* squid dominated at SJI (Table 2). In terms of fish, demersal common hake (*Merluccius hubbsi*) was the most frequent and numerous fish species at SJI in both years, followed by benthopelagic hoki (Fig. 3b; Table 2). At NWI, pelagic Fuegian sprat dominated in 2019, whilst hoki dominated in 2020 (Fig. 3b; Table 2). Ninety-nine percent ( $n = 134$ ) of all measurable hoki, and one hundred percent of measurable southern blue whiting ( $n = 6$ ) fell within the size classes caught in the Falkland Islands fishery in 2019 and 2020 during comparable months, and we therefore classified all hoki and southern blue whiting as discards.

Prey origin varied between years at NWI, but not at SJI. Discard consumption at NWI was significantly higher in 2020 compared to in 2019 (Wilcoxon rank sum test; FO%:  $W = 360$ ,  $P < 0.001$ ; N%:  $W = 257$ ,  $P < 0.001$ ), whilst natural prey declined in terms of N% (Wilcoxon rank sum test; N%:  $W = 1143$ ,  $P < 0.001$ ; Fig. 3c). Discards also varied between colonies, being significantly higher at SJI in 2019 (Wilcoxon

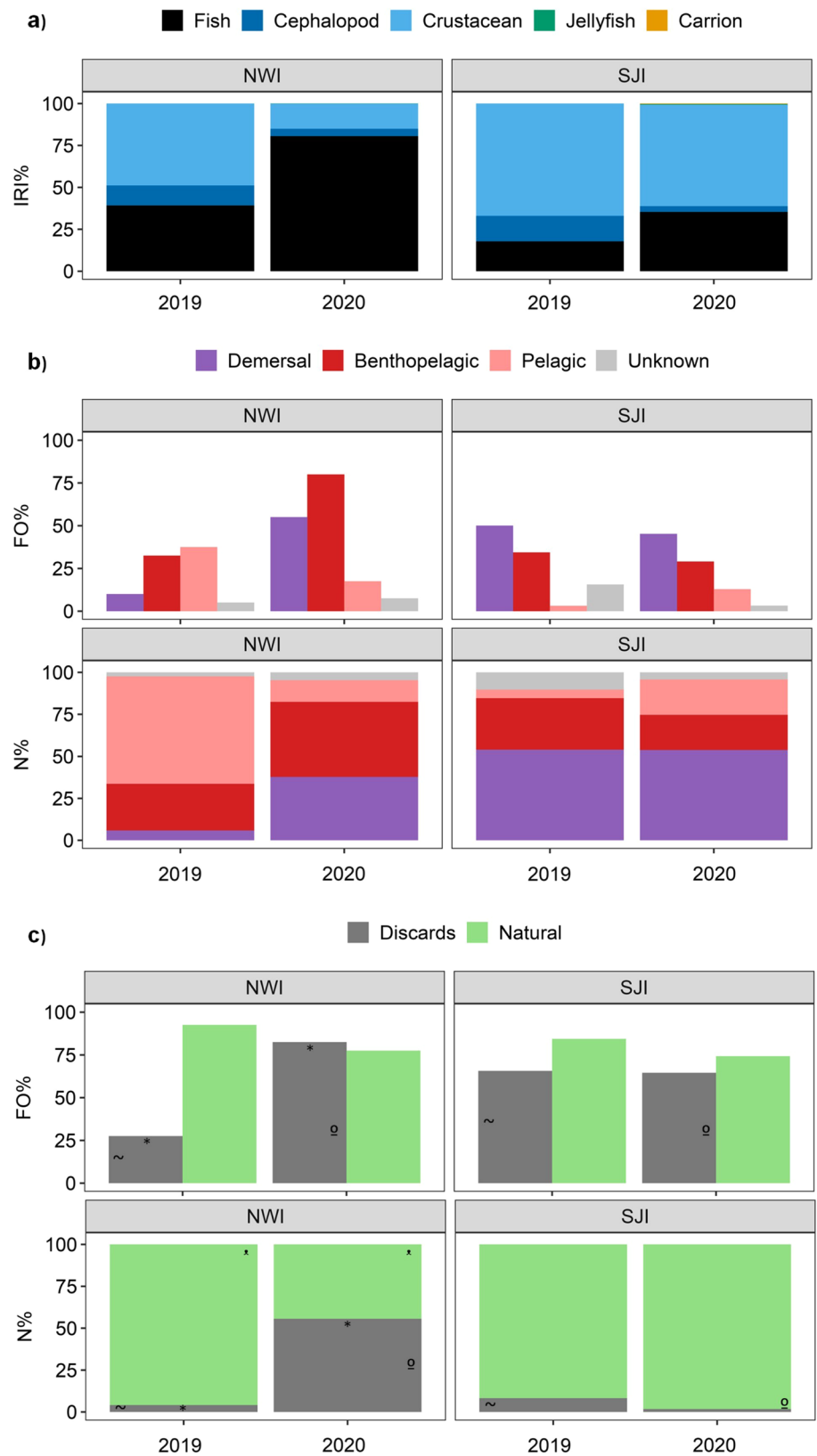
rank sum test; FO%:  $W = 366$ ,  $P < 0.001$ ; N%:  $W = 66$ ,  $P < 0.001$ ) but higher at NWI in 2020 (Wilcoxon rank sum test; FO%:  $W = 772$ ,  $P = 0.024$ ; N%:  $W = 825$ ,  $P = 0.016$ ; Fig. 3c). Natural prey consumption did not differ between colonies regardless of year (Fig. 3c).

### Stable isotope analysis

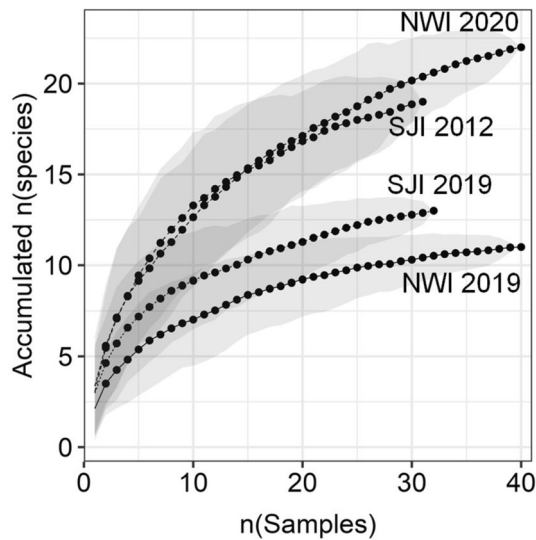
Based on chick down feathers (Table 3), we found a significant difference in the isotopic niche of chicks from NWI and SJI in 2020, but not in 2019 (MANOVA; 2019: Pillai's Trace = 0.016,  $F(1, 137) = 1.087$ ,  $P = 0.340$ ; 2020: Pillai's Trace = 0.125,  $F(1, 108) = 7.675$ ,  $P < 0.001$ ; Fig. 5), with, respectively, 88% and 75% point-estimate of overlap based on the maximum likelihood SEAc (standard ellipse area corrected for small sample size). *Post hoc* ANOVAs showed that the difference was due to significantly higher  $\delta^{15}\text{N}$  at SJI in 2020 ( $\delta^{15}\text{N}$ :  $P < 0.001$ ;  $\delta^{13}\text{C}$ :  $P = 0.049$ ). As the difference of 0.29‰ in  $\delta^{15}\text{N}$  is relatively close to the limit of the machine reading precision of 0.17‰, some caution is warranted for interpretation. The ratio of C/N in down feathers was significantly lower in 2019 compared to in 2020 at both colonies (Mann–Whitney  $U$  tests;  $W = 1700$ ,  $P < 0.001$ ), but no difference was found between colonies (Mann–Whitney  $U$  tests;  $W = 7493$ ,  $P = 0.656$ ).

Mixing models estimated pelagic fish as the largest contributor to chick diet across both colonies and years (mean = 69–79%; Fig. 6, Fig. 7). Crustacean + jellyfish were the second most important diet source: 14–19% across years and colonies (Fig. 7). Demersal fish, as well as benthopelagic fish + squid, were estimated to contribute relatively little to the diet (Fig. 7; Table S5), although note that for SJI 2020, the model struggled to discern between the groups of benthopelagic fish + squid and crustacean + jellyfish (Fig. 6). By summing the percentage estimates of prey groups that are categorised as entirely natural prey (pelagic fish; crustacean + jellyfish), we found that natural prey was the dominant

**Fig. 3** Black-browed albatross chick diet based on regurgitation from New Island (NWI) and Steeple Jason Island (SJI) in 2019 and 2020, quantified as **a** percentage index of relative importance (IRI%) of main prey groups; **b** percentage frequency of occurrence (FO%) and percentage numeric frequency (N%) of fish subgroups; and **c** percentage frequency of occurrence (FO%) and percentage numeric frequency (N%) of discards and natural prey. Note that the negligible IRI% of jellyfish and carrion renders these practically invisible on the plot. The various symbols indicate which groups are significantly different from one another within each metric







**Fig. 4** Accumulation curves with 95% confidence intervals (shaded area) of prey species extracted from black-browed albatross chick regurgitate samples collected at New Island (NWI) and Steeple Jason Island (SJI) in 2019 and 2020

diet for all colony/year combinations (mean minimum estimate 91.4–94.6%, excluding squid). Although the differences were relatively small, consumption of fishery discards was higher in 2020 than in 2019 at both colonies, and was higher at SJI than at NWI in both years (Table 4).

### Discussion

A complementary approach to diet analyses can help minimise methodological bias, and therefore enable more robust inference (Bot et al. 2018). Using SCA and SIA to assess inter-colony and inter-annual variation in BBA diet, we found that chicks were primarily fed natural prey during mid-chick rearing, although dominant prey sources and species identified varied between methods and colonies. Whilst discards contributed less to the diet than natural prey regardless of sampling method, SCA provided higher discard use estimates compared with SIA. Our results have implications for fisheries management and future dietary studies assessing discard use.

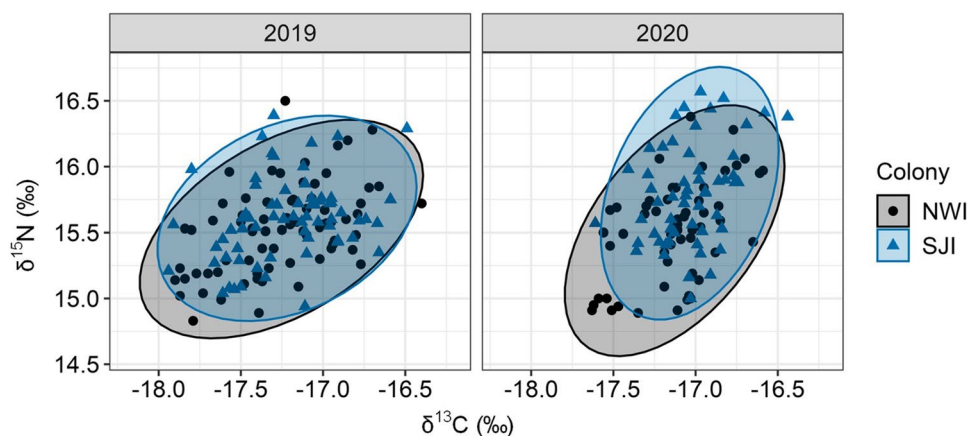
### Diet composition

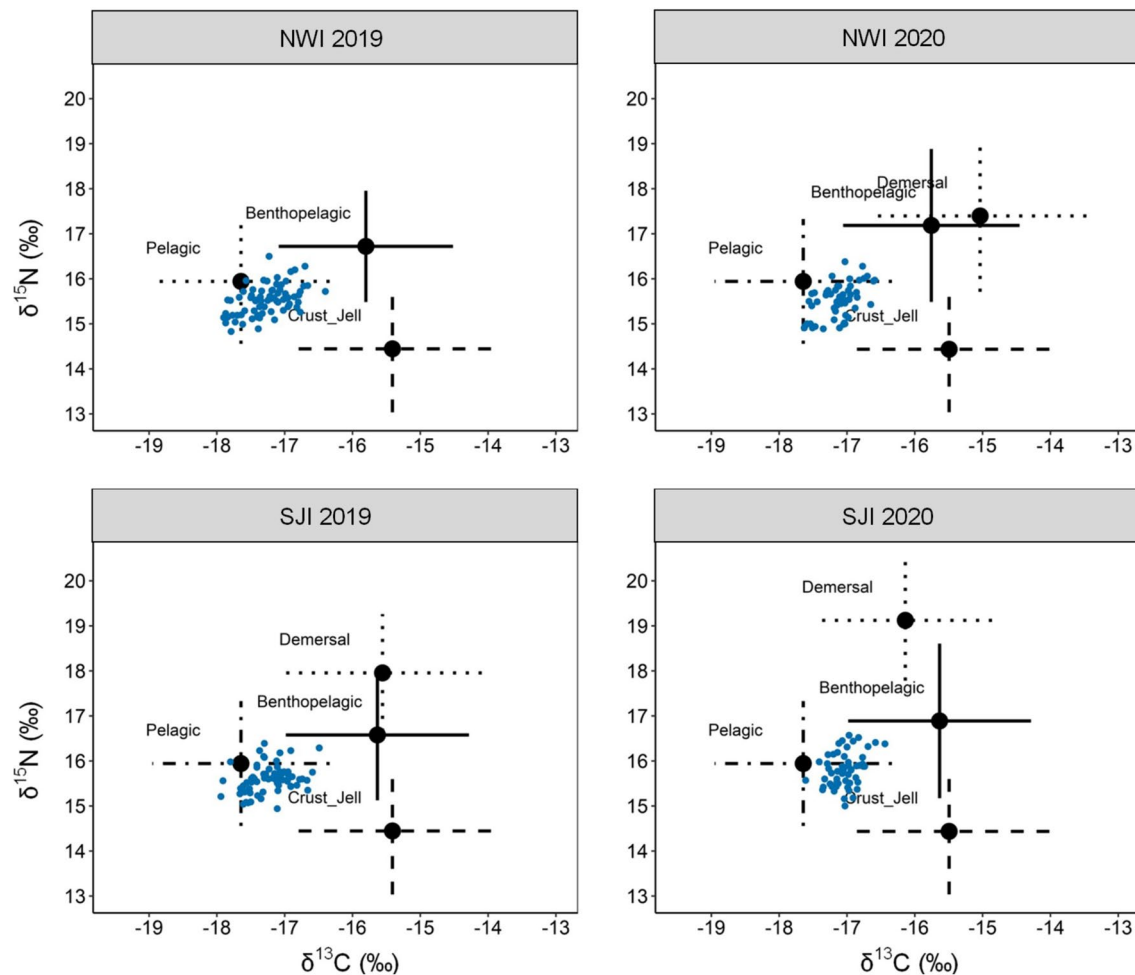
Based on SCA, crustaceans, demersal fish and benthopelagic fish were the dominant prey, whilst SIA suggested that pelagic fish were most important. These results are consistent with SIA studies during early chick rearing at NWI in 2011 (Granadeiro et al. 2014), and DNA metabarcoding of adults and chicks at NWI and SJI in 2014 and 2015 (McInnes et al. 2017a, b). Both SCA and SIA indicate that cephalopods play a relatively minor role in chick diet, as found previously at these colonies (Granadeiro et al. 2014 (SIA); McInnes et al. 2017b (DNA); Kuepfer et al. 2022a (SCA)), as well as at other BBA colonies (McInnes et al. 2017b).

**Table 3** Isotopic values (mean ± sd) of black-browed albatross chick down feathers from New Island (NWI) and Steeple Jason Island (SJI) in 2019 and 2020

Year	Colony	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$	C/N	N (samples)
2019	NWI	-17.25 ± 0.34	15.53 ± 0.33	3.16 ± 0.03	73
2019	SJI	-17.22 ± 0.31	15.61 ± 0.31	3.16 ± 0.02	66
2020	NWI	-17.13 ± 0.27	15.51 ± 0.38	3.67 ± 0.16	55
2020	SJI	-17.04 ± 0.22	15.80 ± 0.38	3.63 ± 0.29	55

**Fig. 5** Isotopic niche of black-browed albatross chicks from New Island (NWI) and Steeple Jason Island (SJI) based on down feathers in 2019 and 2020 showing SIBER ellipses containing 95% of the data





**Fig. 6** Isotopic values of black-browed albatross chick feathers (blue dots) from New Island (NWI) and Steeple Jason Island (SJI) in relation to four prey groups (pelagic fish, demersal fish, benthopelagic

prey (fish + squid), crustacean + jellyfish (Crust\_Jell)). Chick feather values are presented after correction for diet-tissue isotopic discrimination

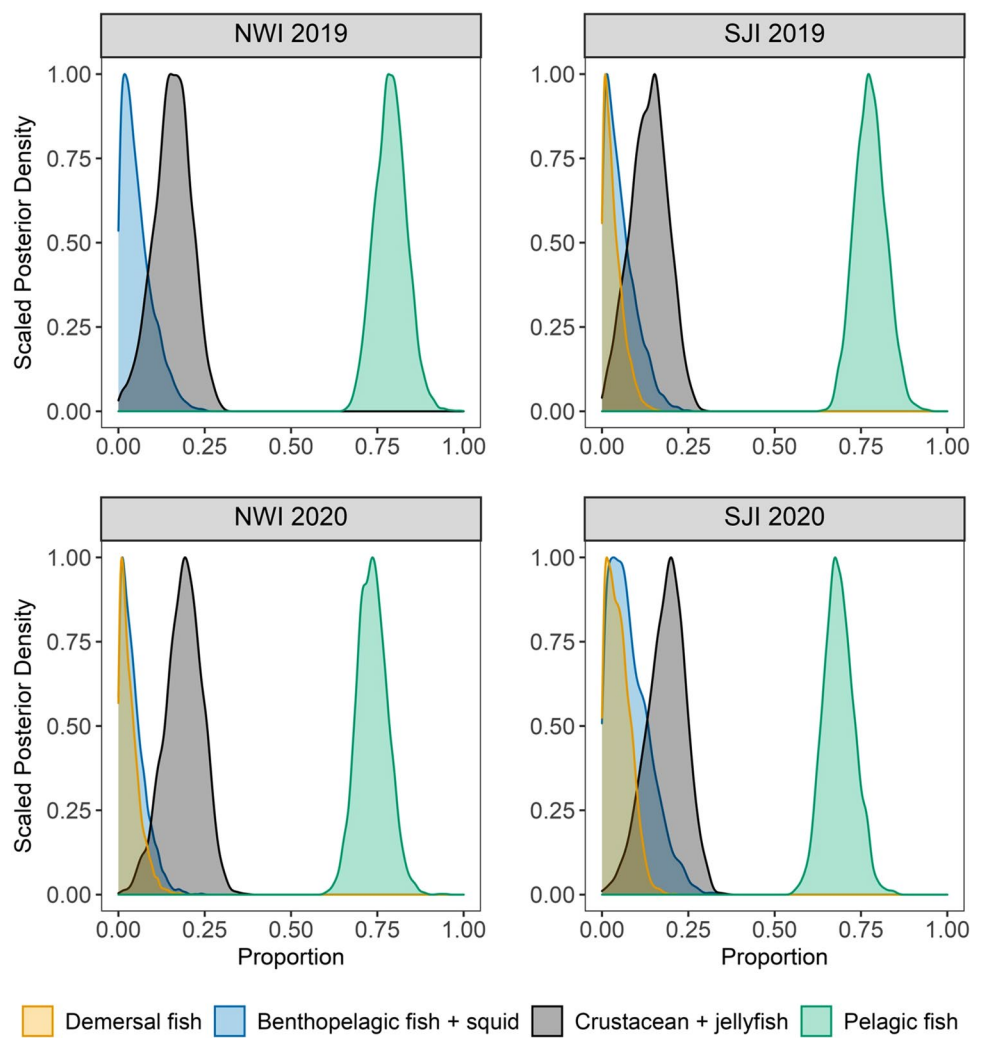
Jellyfish were scarce in SCA but stable isotope mixing models suggest that jellyfish are more common than this (on average 14–19% across colonies/years). Nevertheless, this should be treated with caution given their isotopic similarity to crustaceans. However, previous work using DNA metabarcoding suggests that they are much more prevalent than crustaceans (SJI: up to 80% FO, 50% relative abundance (RA); NWI: up to 20% FO, 8% RA; McInnes et al. 2017b), further highlighting the importance of combining techniques.

SCA identified Fuegian sprat as the dominant pelagic fish, whilst, historically, southern blue whiting was more common in the diet of BBA (Thompson 1992). Increased Fuegian sprat consumption was also found in 2014 and 2015 (McInnes et al. 2017a) and likely reflects a shift in the ecosystem following the collapse of the southern blue whiting stock in 2004–2007 (Laptikhovskiy et al. 2013). Unlike southern blue whiting, Fuegian sprat is not targeted

by fisheries within the foraging range of NWI and SJI breeding albatross, and discards of this species are rare and patchy (Falkland Islands Government 2021).

Despite the close proximity of NWI and SJI (~75 km), SCA revealed inter-colony diet differences, which appear to be stable over time (Thompson 1992; McInnes et al. 2017a). In particular, the dominant fish and squid were hoki and Loligo at NWI, but common hake and *Illex* at SJI. We cannot entirely exclude an influence of differences in timing between colony visits (NWI: January/February; SJI: March); for example, whilst hoki catches in 2019 and 2020 peaked in January and February, hake catches peaked in March (Ramos and Winter 2019, 2020; Winter and Ramos 2020). However, Thompson (1992) also found increased hake (and *Illex*) at SJI when sampled in January, compared to at NWI sampled in February/March. Our results may therefore also reflect differences in prey availability at colony-specific foraging sites (see Granadeiro

**Fig. 7** Posterior density estimates from MixSIAR models for the contribution of prey sources to the diet of black-browed albatross chicks for 2019 and 2020 at New Island (NWI) and Steeple Jason Island (SJI)



**Table 4** Percentage contribution of discards and natural prey as estimated from stomach content analysis (SCA) and stable isotope analysis (SIA)

	Discards		Natural prey	
	SCA (FO%; N%)	SIA (% contribution)	SCA (FO%; N%)	SIA (% contribution)
NWI 2019	27.5%; 4.2%	0.0–5.3%	92.5%; 95.8%	94.6–99.9%
SJI 2019	65.6%; 8.3%	3.3–8.6%	84.4%; 91.7%	91.4–96.7%
NWI 2020	82.5%; 55.7%	3.4–7.7%	77.5%; 44.3%	92.4–96.7%
SJI 2020	64.5%; 1.8%	4.6–13.2%	74.2%; 98.2%	86.7–95.3%

Estimates from SIA for discards are the summed mean values of [demersal prey]–[demersal + (squid + benthopelagic prey)]; for natural prey, this represents the summed mean values for [pelagic fish + (crustacean + jellyfish)]—[pelagic fish + (crustacean + jellyfish) + (benthopelagic fish + squid)], as shown in Table S5

et al. 2011). Indeed, hoki is most abundant in the south-west of the FCZ where NWI birds forage, whereas hake is the dominant catch in the north-west, where SJI birds feed (Catry et al. 2013; Ramos and Winter 2019; Winter and Ramos 2020; Ventura et al. 2021).

Finally, there were differences in trophic niche between colonies. The  $\delta^{15}\text{N}$  values were higher at SJI, although this

was only apparent in 2020. This result is suggestive of relatively increased consumption of higher trophic prey (e.g. hake or grenadier).

## Relevance of fishery discards

As predicted, albatross chicks were overall fed primarily natural prey; nonetheless, chicks regularly received discards (based on FO%; Table 4). Previous studies have shown limited fishery interactions during early BBA chick rearing (December–early January; Granadeiro et al. 2014)—a period of low fishing effort in Falkland Islands and Argentine waters (see also McInnes et al. 2017a). Some studies suggest discard consumption is more frequent during later chick rearing (from February, McInnes et al. 2017a). Our study supports the high proportion of birds taking discards, but found natural prey to generally remain the main prey source.

Previous multi-colony research suggests higher discard consumption at SJI compared to NWI (Thompson 1992; McInnes et al. 2017a). However, based on SCA, we found that whilst discard consumption was higher at SJI in 2019, the reverse was the case in 2020. Stable isotope mixing model results, which are temporally more comparable, were inconclusive in this regard, because the models cannot distinguish between benthopelagic squid (natural prey) and benthopelagic fish (discards). However, excluding the confounding prey source, discards were higher at SJI, particularly in 2020, which agrees with the increased trophic niche discussed above.

Discard consumption was higher in 2020, although the extent of this varied between methods. Breeding BBA from the Falkland Islands appear to increase discard consumption during periods of poor natural foraging conditions (Kuepfer et al. 2022a). Indeed, the present study provides some indication of potentially increased nutritional stress in 2020: Prey diversity was higher in 2020, which could result from birds compensating for the scarcity of preferred prey by targeting alternative species (Quillfeldt et al. 2010; van Donk et al. 2017). Significantly higher C/N ratios in 2020 could suggest prey being of inferior protein quality (Robbins et al. 2005). Further, meals contained more stomach oil in 2020, which could

be an effect of prolonged foraging trips (supported also by GPS tracking from P. Catry, unpubl. data; also see Warham et al. 1976; Chaurand and Weimerskirch 1994; Connan et al. 2005). The season 2020 also saw reduced chick weight at NWI (on average  $-7.3\%$ ), and reduced breeding success at both NWI ( $-22\%$ ) and SJI ( $-25\%$ ) (P. Catry, unpubl. data; Crofts and Stanworth 2021; Kuepfer et al. 2022a). Combined, these indicators support the argument of increased discard consumption during periods of increased nutritional stress in Falkland Islands BBA.

## SCA and SIA—a critical evaluation

Our key objectives were to quantify diet (particularly in the context of fisheries), and test for inter-annual and colony-specific differences. Combining SCA with SIA provided us with complementary information and helped with interpretation of results in several aspects (Table 5).

In contrast to SIA, SCA supplied high taxonomic and morphological details, including information on prey size (age class) and visual confirmation of processed waste from fisheries. This assisted with categorisation and quantification of prey as discards or natural prey. It also enabled us to distinguish between isotopically similar (but from a management perspective, very different) prey (here squid vs benthopelagic fish; crustacean vs jellyfish—although see below). This can be important to complement SIA; if our main prey source was found to be benthopelagic prey, SCA could have helped us determine whether this was dominated by discards (benthopelagic fish) or natural prey (squid). In our case, this confounding prey source only contributed a small amount to the overall diet source of BBA chicks, and therefore bears little influence on the overall result regarding the dominant prey origin.

SCA was also important for selecting mixing model inputs, although our results emphasise that using informative priors from conventional methods in stable isotope mixing

**Table 5** Advantages and caveats of stomach content analysis (SCA) and stable isotope analysis (SIA) for assessing seabird diet and discard use

Advantages	SCA	SIA	Caveats
High taxonomic resolution	✓		
Information on meal size	✓		
Information on prey size/age class	✓		
Visual cues of processing waste	✓		
Distinguish isotopically similar prey	✓		Only necessary in ecosystems where key prey are isotopically similar
Informs stable isotope mixing models	✓		Information is biased by differential digestion rate
Provides a single, integrated dietary signal		✓	
Larger temporal window		✓	Different tissues provide different temporal windows (see e.g., Inger and Bearhop 2008; Phillips et al. 2014)
Independent of digestion rate		✓	

models can transfer methodological biases leading to erroneous results (Swan et al. 2020). For example, compared to SCA, SIA suggests the importance of pelagic fish, but more moderate contribution from crustaceans. This difference may reflect differential digestion of prey. Whilst fragile prey like sprat or jellyfish are more easily digested, and hence likely underestimated in SCA, the opposite is true for large or rigid organisms like demersal fish or crustaceans.

We note that differences between methods may in parts also be related to short-term differences in the temporal window they represent, particularly for SJI where down growth and stomach content sampling did not overlap (see also e.g. McCluskey et al. 2021). However, this does not appear to be the case at NWI, where pelagic prey also dominated in both years based on SIA of plasma (reflective of the diet from the previous few days (Phillips et al. 2014)) collected in February 2019 and 2020 (A. Kuepfer unpubl. data).

A further potential issue of using SCA in the absence of a complementary method is the large number of ways this type of diet information can be quantified (e.g. FO%, N%, IRI%). These each have their own biases (see Barrett et al. 2007) and care must be taken when selecting a suitable metric to use based on the study objectives. In our case, a multitude of SCA metrics allowed us to draw more comprehensive conclusions in relation to discard consumption, and also gain insight into the proportion of breeders that interact with vessels (although see e.g. Granadeiro et al. 2011; 2014). Meanwhile, SIA provided a sense check for prey source quantification by providing a single, integrated signal representing multiple meals.

Finally, our SCA was subject to confounding temporal effects due to non-simultaneous sampling. Previous SCA and DNA studies at these colonies suffered from the same limitation (Thompson 1992; McInnes et al. 2017a). The complementary use of feather SIA in the present study assisted with inter-colony comparison due to its more long-term dietary signal. This aspect also makes SIA a suitable candidate for studying diet during the non-breeding period (see e.g. Bugoni et al. 2010; Mariano-Jelicich et al. 2013; Granadeiro et al. 2014), although care must be taken to obtain a meaningful prey field in time and space (Quillfeldt et al. 2015).

## Seabird diet in the context of fisheries management

Our dietary results highlight important aspects in terms of fisheries management. First, natural prey are important for BBA chicks, underlining the importance of understanding pelagic fish distribution and abundance in the Falkland Islands (Kuepfer et al. 2022a) and elsewhere (Barrett et al. 2007; Boldt et al. 2022). Second, whilst discards do not

contribute substantially to chick diets, a high proportion of adults deliver discards to their young, thus incurring a risk of bycatch. Therefore, we echo previous authors that any management actions aiming to reduce discard availability, and therefore bycatch risk (e.g. batch discharging as currently implemented in the Falkland Islands trawl fleet), will be of conservation benefit (e.g. Granadeiro et al. 2011, 2014; Kuepfer et al. 2022b).

Going forward, seabird diet provides a helpful fishery and ecosystem monitoring tool but requires appropriate methodological consideration. Given climatic changes and continued fishery presence across the Patagonian Shelf (and elsewhere), we recommend the use of stable isotopes to capture broader time scales, but in combination with SCA to allow continued prey species identification in a potentially changing ecosystem. We also recommend multiple SCA metrics be considered (N%, FO%, M%, IRI%), as these can provide complementary information on important prey and the extent of seabird–fishery interaction.

**Supplementary Information** The online version contains supplementary material available at <https://doi.org/10.1007/s00227-023-04191-7>.

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**Author contributions** AK, PC, SCV and SB contributed to the study conception, design and methodology; material preparation and data collection was undertaken by AK with support from PC, PB and AA; data processing was performed by AK, OB and JN; data analysis was conducted by AK with support from SCV, SB, RBS, JN, PC and OB. The first draft of the manuscript was written by AK, and all authors commented on the manuscript. Resources for this project were provided by PB, AA, SCV and JN; Supervision: SCV, RBS, SB, PC, PB and AA.

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**Data availability** The dataset analysed during the current study is available from the corresponding author on reasonable request.

## Declarations

**Conflict of interest** The authors have no competing interests to declare that are relevant to the content of this article.

**Ethical approval** Diet samples were collected under research licence issued by the Falkland Islands Government Environmental Department (R29/2017) and with approval from the University of Exeter College of Life and Environmental Sciences Penryn Research Ethics Committee.

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