

# Prey-switching to fishery discards does not compensate for poor natural foraging conditions in breeding albatross

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Fishery discards supplement food for many seabirds, but the impacts of declining discards are poorly understood. Discards may be beneficial for some populations but have negative impacts by increasing bycatch risk or because they are junk-food. The Falkland Islands support > 70% of global black-browed albatross *Thalassarche melanophris* populations, which feed on discards. However, the effect of discards on population demographics, and implications of fishery management changes, are unknown. We analysed stomach contents of black-browed albatross chicks across eight breeding seasons (2004–2020) from New Island, Falkland Islands, to assess variation in discard consumption and how this relates to foraging conditions and breeding success. Across years, 68%–98% of samples contained natural prey, whilst 23%–88% of samples contained fishery discards. Discard consumption was positively related to fishery catches of hoki *Macruronus magellanicus* and sea surface temperature anomalies SSTA (°C), and negatively related to breeding success. These results suggest a diet-switching behaviour for Falkland Islands albatrosses, whereby birds switch from preferred natural prey to suboptimal discards when environmental conditions, and hence natural feeding opportunities, are unfavourable. Crucially, this study highlights that fishery discards do not compensate for poor natural foraging conditions for breeding albatrosses in the long term.

**Keywords:** Albatross, Diet-switching, Ecosystem-based management, Fishery discards, Stomach content analysis.

## Introduction

Assessing fisheries impacts on marine predators is a key objective in sustainable marine management. Fisheries can negatively impact seabirds via incidental mortality (bycatch) in fishing gear, changes in the community structure, and because they compete for the same stocks (Votier *et al.*, 2004; Wagner and Boersma, 2011; Grémillet *et al.*, 2018). Conversely, fisheries discards—unwanted fish and processing offal—can provide a predictable and plentiful food resource for scavenging seabirds (Real *et al.*, 2018; Sherley *et al.*, 2020). Therefore, discarding has implications for marine food-webs, as well as for the ecology and demography of scavenging birds (Bicknell *et al.*, 2013).

Discards can support millions of scavenging seabirds (Sherley *et al.*, 2020) and some seabird populations have increased in areas where discards are abundant, e.g. kelp gulls *Larus dominicanus* on the Patagonian Shelf (Yorio and Caille, 2004) and great skuas *Stercorarius skua* in the North Sea (Votier *et al.*, 2004). Accordingly, global changes in catches (Branch *et al.*, 2011; FAO, 2020) and discard bans in the European Union, Norway, Chile, and New Zealand may have knock-on effects on discard-dependent species (Votier *et al.*, 2004; Bicknell *et al.*, 2013; Sherley *et al.*, 2020; but see Le Bot *et al.*,

2019). However, studies assessing this issue tend to focus on European waters (Bicknell *et al.*, 2013; Oro *et al.*, 2013; Le Bot *et al.*, 2019).

Albatrosses regularly follow fishing vessels (Phillips *et al.*, 2016) and, while much research has focussed on how this impacts seabird bycatch risk, little is known about the demographic consequences of discard provision. The black-browed albatross *Thalassarche melanophris* has a southern circumpolar distribution and frequently interacts with fisheries where it scavenges on discards and suffers high bycatch (reviewed in Phillips *et al.* (2016)). In the Falkland Islands, where over 70% of its global population breeds (Wolfaardt, 2013), discard consumption appears particularly prevalent compared to populations elsewhere (DNA-based study, McInnes *et al.*, 2017a). Indeed, discard consumption has been suggested as a contributing factor to increasing black-browed albatross populations in the Falkland Islands (Thompson and Riddy, 1995; Croxall and Gales, 1998; McInnes *et al.*, 2017a), which contrasts with general declines elsewhere in their range (Birdlife International, 2018). Nevertheless, studies testing a direct link between discard consumption and population change in the Falkland Islands are lacking.

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Black-browed albatross breeding in the Falkland Islands forage over the Patagonian Shelf throughout the year (Ponchon *et al.*, 2019). During winter, there is evidence that in the northern part of the wintering range they feed extensively on discards, according to gut contents of beached birds and victims of fishery bycatch off southern Brazil (Colabuono and Vooren, 2007) and stable isotope analysis from intentionally captured live birds that foraged near vessels off northern Argentina (Mariano-Jelicich *et al.*, 2014, 2017). However, it is unclear whether birds sampled as a result of interactions with fisheries are representative of the wider population. Breeding adults and chicks in the Falkland Islands appear to feed predominantly on natural prey (Thompson, 1992 (stomach content analysis); Granadeiro *et al.*, 2014 (stable isotope analysis); McInnes *et al.*, 2017b (DNA-based analysis)), and while some tracked individuals associate with fishing vessels at sea, they do not seem to specialise on fisheries' waste (Granadeiro *et al.*, 2014). However, discards during the breeding season may be more important in some years (McInnes *et al.*, 2017a), and more research is therefore required to develop a fuller understanding of how discard feeding varies annually in relation to natural foraging conditions and prey availability. Furthermore, none of the previous studies conducted in the Falkland Islands assess the direct influence of diet on breeding success (but see elsewhere, e.g. Le Bot *et al.*, 2019).

Due to a discard management reform in the Falkland Islands trawl fleet, whereby discards are to be stored temporarily before batch discharging (Kuepfer and Barton, 2018; Kuepfer *et al.*, 2022), an improved understanding of discard use by black-browed albatross is especially pressing. In addition, the black-browed albatross is a sentinel of the Patagonian Shelf Large Marine Ecosystem (Ventura *et al.*, 2021a), and an indicator species used by the Commission for the Conservation of Marine Living Resources (CCAMLR) Ecosystem Monitoring Program (CEMP). Therefore, dietary information will not only help to inform black-browed albatross conservation, but also promote a more complete understanding of fishery impacts in the Southern Ocean marine ecosystem, and further afield (Bestley *et al.*, 2020).

The current study uses multi-annual chick diet and breeding performance data to further our understanding of the importance of discards in supporting the Falkland Islands black-browed albatross population. Our objectives are threefold: (i) quantify chick diet and prey origin (natural vs. discards); (ii) assess inter-annual diet variability in relation to discard and natural prey availability; and (iii) determine the nature of the relationship between discard use and breeding success. In light of available information, we hypothesise that black-browed albatross prefer natural prey for chick provisioning, but that they switch to discards depending on availability and natural foraging conditions. Specifically, we would expect a diet switch to discards when natural foraging conditions are poor, and reproductive performance is stressed.

## Materials and methods

### Study area and fleet characteristics

Chick diet was sampled at New Island, Falkland Islands (51° 43'S, 61° 18'W, Figure 1a), which supports approximately 15500 breeding pairs (Wolfaardt, 2013). Breeding adults concentrate their foraging south-west of New Island over the southern Patagonian Shelf within the Falkland Islands Conservation Zones (FCZs) and the Argentine Exclu-

sive Economic Zone (EEZ) (Ventura *et al.*, 2021a; Figure 1a). The Patagonian Shelf is one of the most productive marine ecosystems in the world, supporting high biodiversity and important fisheries (Baylis *et al.*, 2021), notably demersal finfish freezer trawlers targeting predominantly Argentine hake *Merluccius hubbsi*, hoki *Macruronus magellanicus* and rock cod *Patagonotothen ramsayi* (average annual landings of finfish trawlers 2011–2020: Argentina 155230 t; Falkland Islands 70166 t; Ministerio de Agricultura, Ganadería y Pesca Argentina ([https://www.magyp.gob.ar/sitio/areas/pesca\\_maritima/desembarques](https://www.magyp.gob.ar/sitio/areas/pesca_maritima/desembarques); Falkland Islands Government, 2020; Figure 1). Finfish fisheries discard bycatch of non-commercial or undersized fish, and also dump offal (head and guts) of commercial fish at sea. Patagonian long-finned squid (*Doryteuthis gahi*, hereafter Loligo), also sometimes caught as bycatch in the finfish fishery, is not discarded. Trawling for Loligo occurs to the east of the Falkland Islands, outside the key foraging areas of New Island breeding birds, and outside our sampling period (late February–May; August–October). Finally, between February and May, the Patagonian Shelf also hosts one of the world's largest cephalopod fisheries (Arkhipkin *et al.*, 2015; Harte *et al.*, 2019), jigging for Argentine shortfin squid (*Illex argentinus*, hereafter Illex; average annual landings 2011–2020: Argentina 104166 t; Falkland Islands 114050 t—Ministerio de Agricultura, Ganadería y Pesca Argentina [https://www.magyp.gob.ar/sitio/areas/pesca\\_maritima/desembarques](https://www.magyp.gob.ar/sitio/areas/pesca_maritima/desembarques); Falkland Islands Government, 2020). Discards from these vessels are limited, as the squid is generally packed whole (Laptikhovsky *et al.*, 2006; Arkhipkin *et al.*, 2015).

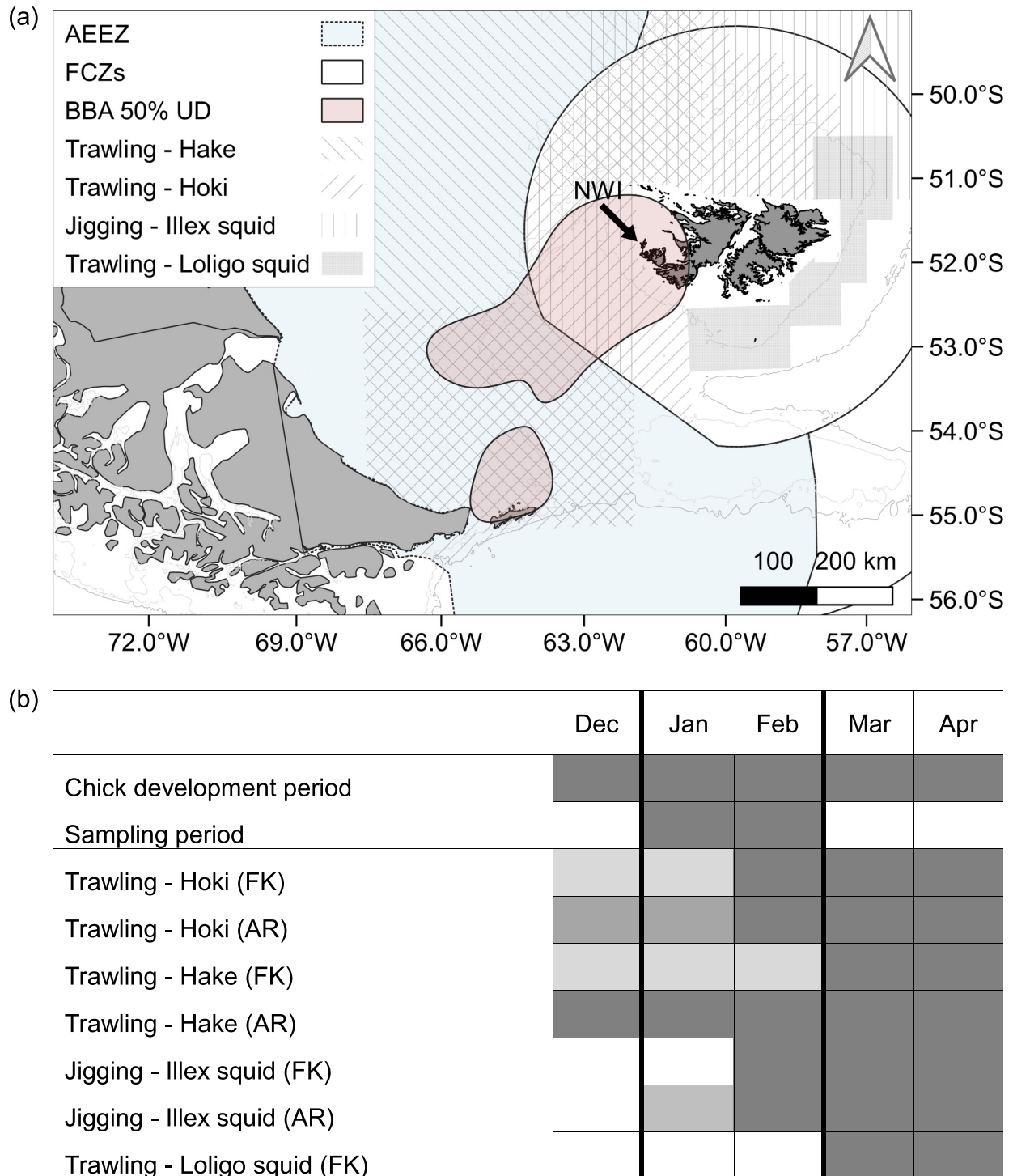
### Sampling

Diet samples were collected during mid-chick rearing (late January and February) across eight seasons between 2003/04 and 2019/20 (hereafter 2004 to 2020) via induced regurgitation. Freshly fed chicks were briefly inverted over a bucket with the stomach and throat gently massaged until the stomach felt empty or regurgitation stopped. The procedure took less than a minute and chicks were never sampled more than once. This procedure has no significant effect on survival or albatross fledging mass (Phillips, 2006). Individual diet samples were weighed whole (total mass, g), and again after draining off the stomach oils (drained mass, g).

### Diet composition

#### Prey identification and grouping

Prey items were first separated into one of six dietary categories: (i) fish, (ii) cephalopods, (iii) crustaceans, (iv) gelatinous zooplankton, (v) carrion, and (vi) non-food (internal parasites, plant matter, pebbles and plastics), and the drained mass of these groups was recorded. Fish, crustaceans and cephalopods were further identified to the highest possible resolution using reference collections (Falkland Islands Fisheries Department (FIFD) unpubl data; Xavier and Cheral, 2009) and through consultation with local specialists (B. Lee, Z. Shcherbich (FIFD)). The minimum number of individuals was determined through counts of whole animals and fresh loose hard structures (fish = bones, otoliths; cephalopods = squid gladius, beaks (with wings attached), statoliths; crustaceans = carapaces with both eyes still attached to minimise the risk of counting items originating from secondary ingestion). Otoliths and cephalopod beaks were paired based on left and right (otolith), lower and upper (beak), size,



**Figure 1.** (a): New Island (NW) in western Falkland Islands, and its proximity to the South American continent. The 50% Utilisation Distribution (UD) of breeding black-browed albatross tracked from NW (Ventura *et al.*, 2021a) overlaps with key fisheries on the Patagonian Shelf inside the Falklands Conservation Zones (FCZs) and the Argentine Exclusive Economic Zone (AEEZ). Fisheries areas inside the AEEZ are approximate and highlight only areas of key catches (adapted from Irusta *et al.*, 2016; Morsan *et al.*, 2017). The 200-m and 1000-m isobaths are shown. (b): Temporal overlap of chick development, sampling period, and fishing activities, with darker shading indicating increased relative catches. FK = Falkland Islands; AR = Argentina.

and level of erosion. Eroded and accumulated squid beaks and heavily eroded/brittle otoliths were assumed to have originated from previous meals (Furness *et al.*, 1984; Van Heezik and Seddon, 1989), and were excluded from all analyses. Fresh prey of fish or cephalopods that could not be identified to species level were only included in analyses involving the main prey groups of fish and cephalopods.

Individual prey items identified to species level were then further categorised as either fisheries discard or natural prey (Table S1). We assumed prey was natural if it met one of the following criteria: (i) the species inhabits depths (including during diel migration) accessible to black-browed albatrosses (~19 m, Guilford *et al.*, 2022) and is not caught in fisheries in the Falkland Islands or on the southern Patagonian Shelf; (ii) the species is a commercially fished benthopelagic or pelagic fish potentially accessible to black-browed albatrosses, but smaller than the minimum size caught in the Falkland Islands trawl fishery (Falkland Islands Government, 2020 and previous annual reports); (iii) the fishing period, discard policy or processing makes the species very unlikely to be available from fisheries. The latter is the case for *Illex* and *Loligo* squid, which could feasibly be obtained both as discards and as natural prey, regardless of size (Prince, 1980; Arkhipkin *et al.*, 2013, 2015). However, we believe that the majority of these squid found in stomach samples were caught naturally because: (i) discards of *Loligo* and *Illex* are negligible as they are generally packed whole (98% and 96%, respectively in Falkland Islands waters), and discarding *Loligo* in Falkland Islands waters is illegal (Laptikhovskiy *et al.*, 2006; Arkhipkin *et al.*, 2015); (ii) whilst squid can be taken directly from the trawl net (A. Kuepfer pers obs), the main *Loligo* fishery operates outside the diet sampling period (Figure 1b; Falkland Islands Government, 2020). Conversely, we assumed that prey originated from discards if at least one of the following three criteria was met: (i) large fish heads were present in the absence of the bodies; (ii) the species is a demersal fish of any size that inhabits depths beyond the dive depth of black-browed albatrosses (> 19 m, Guilford *et al.*, 2022); or (iii) the species is a commercially fished benthopelagic or pelagic fish, which, depending on its age, is potentially accessible to black-browed albatrosses, but is within the size and age class caught in the Falkland Islands demersal-trawl fishery (Falkland Islands Government, 2020 and previous annual reports). The latter corresponded specifically to hoki and southern blue whiting (*Micromesistius australis*). Size classes of these species were reconstructed from intact otoliths (maximum sagittal length (mm)) using a microscope equipped with a graticule and by applying species-specific allometric formulae (Table S2).

### Annual indices of prey availability

To estimate discard availability, we used fishery catch data from January and February of each study year from the Argentine EEZ (Sanchez *et al.*, 2012; Navarro *et al.*, 2014; Navarro, 2019; Ministerio de Agricultura, Ganadería y Pesca Argentina ([https://www.magyp.gob.ar/sitio/areas/pesca\\_maritima/desembarques/](https://www.magyp.gob.ar/sitio/areas/pesca_maritima/desembarques/)) and the FCZs (Falkland Islands Government, 2020 and previous annual reports). The amount of discard available (particularly from processing offal) was assumed to be directly proportional to catches.

Data on natural prey abundance during study years were unavailable, with the exception of just three years of *Loligo* biomass (Ramos and Winter, 2020). Therefore, we used two

remotely sensed proxies of foraging conditions: net primary production (NPP, mg/m<sup>2</sup>) and sea surface temperature anomalies (SSTA, °C). Primary production can influence prey availability to seabirds through bottom-up processes (Frederiksen *et al.*, 2006; Chassot *et al.*, 2010; Anguita and Simeone, 2015); sea surface temperature has been associated with feeding conditions and prey abundance, as it can affect primary and secondary productivity (Behrenfeld *et al.*, 2006; Barbraud *et al.*, 2012). SSTA, in particular, has previously been found to affect demographic aspects of black-browed albatross and other seabirds in the Falkland Islands (e.g. breeding success, breeding probability (Ventura *et al.*, 2021a), breeding pair divorce rates (Ventura *et al.*, 2021b); chick provisioning rates, and chick growth (Quillfeldt *et al.*, 2007, 2010)). Monthly NPP and SSTA were calculated for January and February in the core foraging area (50% UD) of breeding birds tracked between 2008 and 2019 during early breeding (October–December; Ventura *et al.*, 2021a; Figure 1). The NPP data, produced by Copernicus Marine Environment Monitoring Services were downloaded at a spatial resolution of 0.04° ([https://resources.marine.copernicus.eu/?option=com\\_csw&view=details&product\\_id=OCEANCOLOUR\\_GLO\\_CHL\\_L4\\_REP\\_OBSERVATIONS\\_009\\_082](https://resources.marine.copernicus.eu/?option=com_csw&view=details&product_id=OCEANCOLOUR_GLO_CHL_L4_REP_OBSERVATIONS_009_082)). SSTA data were downloaded from NOAA at a spatial resolution of 0.01° (<https://coastwatch.pfeg.noaa.gov/erddap/griddap/jpIMURSST41anommday.html>).

### Breeding success

Since 2003/04, 170 to 259 nests have been followed daily from egg-laying through to hatching, and subsequently weekly until chicks reached 60 days of age, at which point they are considered to have survived to fledging (Catty *et al.*, 2010). We define breeding success as the percentage of nests where egg laying occurred that contained a live chick after 60 days.

### Statistical analysis

All data analyses were conducted in R version 4.0.5 (R Core Team, 2021). Statistical significance was set at  $\alpha = 0.05$ .

### Diet composition

To assess whether the number of sampled chicks was sufficient to describe diet diversity, we randomized annual samples 100 times, and constructed species accumulation curves as a function of sample size (the number of stomach samples collected in a given year—package `vegan::accumcomp`; Oksanen *et al.*, 2019). Sample sizes were considered sufficient to describe the full diversity of the diet when the fitted cumulative prey curves reached an asymptote (Figure S1).

As samples were all collected within a specific time period (mid-chick rearing), samples from January and February were pooled. Prey were quantified using a range of metrics (Table 1), including percentage drained mass (M%), percentage frequency of occurrence (FO%), percentage numeric frequency (N%), and percentage index of relative importance (IRI%) (Barrett *et al.*, 2007), where:

M%; the percentage of total drained sample mass represented by a prey group,

FO%; the percentage of stomach samples in which a particular prey was present,

**Table 1.** Metrics used to quantify prey at different taxonomic levels. For practical reasons, it was not possible to obtain M% of individual species. Counts of individual crustaceans were not consistently collected across years. M% = percentage drained mass; FO% = percentage frequency of occurrence; N% = percentage numeric frequency; IRI% = percentage index of relative importance ( $IRI = FO\% \times (N\% + M\%)$ ).

	M%	FO%	N%	IRI%
<b>Main prey groups including...</b>				
Fish	✓	✓	✓	✓
Cephalopod	✓	✓	✓	✓
Crustacean	✓	✓		
Others	✓	✓		
<b>Species of...</b>				
Fish		✓	✓	
Cephalopod		✓	✓	
Crustacean		✓		
<b>Origin</b>				
Discard		✓		
Natural		✓		

N%; the number of individuals of a particular prey present as a percentage of all individual fish and cephalopod species counted,

$$IRI\% = (IRI / \sum IRI) \times 100, \text{ where } IRI = FO\% \times (N\% + M\%)$$

These different metrics of prey quantification provide complementary dietary information, including variability of prey abundance (FO%), frequency of prey encountered (N%), or approximate nutritional contribution (M%; IRI%) (Duffy and Jackson, 1986; Barrett *et al.*, 2007). For practical reasons, however, and because individual crustaceans were not consistently counted across years, it was not possible to obtain all metrics for all taxonomic groups and levels (Table 1). For example, it was not possible to calculate N% (and hence IRI%) for crustaceans, and M% (and hence IRI%) could not be obtained for individual prey species (and therefore prey origin), because it was impractical to separate out and identify every individual fish bone or flesh remains. Also, we did not attempt to back-calculate the original biomass of individual fish species, because, particularly with discarded fish, it is not always clear whether the chick was fed the entire fish, or just a part of it.

### Inter-annual variation in diet

Following explorative ordination techniques using non-metric multi-dimensional scaling (nMDS), and testing for equal variance in multivariate dispersion, we used a permutational multivariate analysis of variance (PERMANOVA) (package `vegan::adonis`, Oksanen *et al.*, 2019) based on the Bray-Curtis similarity index to explore inter-annual trends in diet composition of key prey groups (presence/absence of fish, cephalopods, and crustaceans), and prey origin (presence/absence of fisheries discards and natural prey). An analysis of similarity percentage (SIMPER) was employed to calculate the contribution of each prey species (%) to the diet differences observed in the PERMANOVAs (Clarke, 1993).

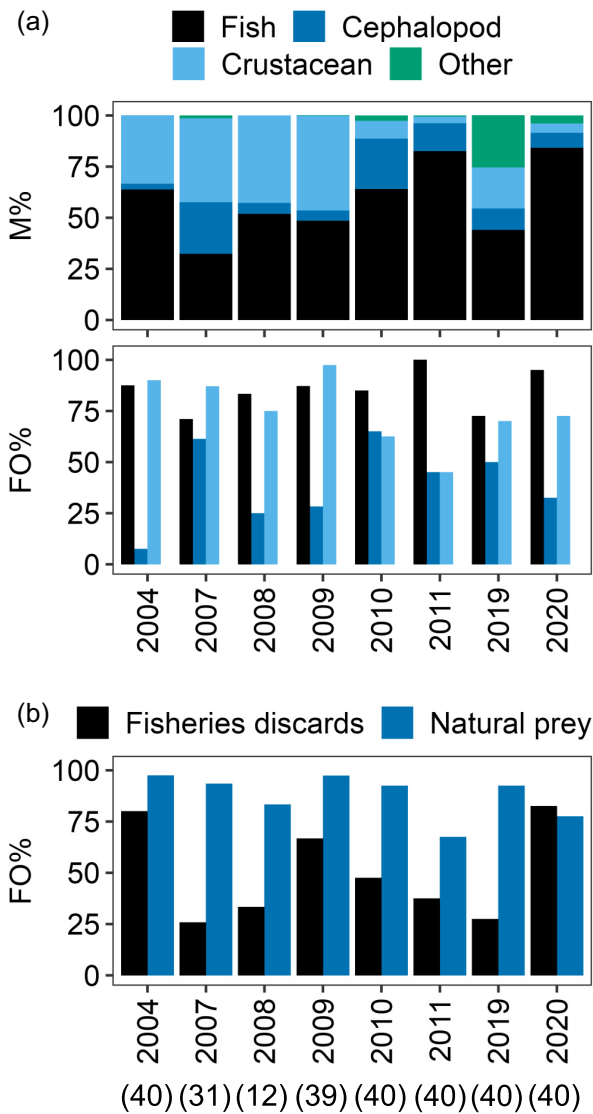
### Relationship between discard consumption and prey availability

Annual trends in discard consumption were assessed in relation to commercial fishery catches and environmental in-

dices of natural prey availability using linear regression models on logit-transformed dietary proportions. Our response variables were FO% and N% of hoki and banded whiptail (*Coelorrinchus fasciatus*, hereafter grenadier), FO% of fishery discards, and (IRI%) of fish. The latter was used due to the high percentage of fish that was categorised as discards (see results). Hoki and grenadier were used because these species represented the most numerous and frequently occurring discard species (see results). For hoki, analyses were based exclusively on specimens categorised as discards. Due to small sample sizes (and to avoid model over-parameterisation), each model was run separately with one of eight alternative explanatory variables. These were hoki catches in (i) Argentina (January), (ii) Argentina (February), (iii) Falklands (January), and (iv) Falklands (February), as well as (v) SSTA (January), (vi) SSTA (February), (vii) NPP (January), and (viii) NPP (February). The decision not to combine January and February values of catch data and of environmental data was because over 70% of samples originated from February. We would therefore assume February prey conditions to be more influential, especially in the case of catch data where no temporal lag would be expected. The decision not to combine Argentine and Falklands catches was based on the changes in commercial species distribution between Argentine and Falkland Islands waters during this period (e.g. Winter and Ramos, 2020). In exploratory analyses, we also tested various lags for environmental variables (October–December), but as there was no relationship, we restricted candidate variables to January and February. The candidate models (including a null model) for the same response variable were compared using the Akaike's Information Criterion corrected for small sample size AICc, with lower AICc indicating a better model fit. A model was deemed to have predictive power if the  $\Delta AICc$  was  $\geq 2$  compared to the null model. The significance level was adjusted using the Bonferroni correction with the alpha value of 0.05 divided by the number of models with predictive power to minimise Type 1 error. Model validation involved inspection of residuals for outliers and patterns, and goodness-of-fit was determined using the R-squared value. We did not perform similar analyses to assess trends in natural prey consumption, because we have reasons to believe that our data for this group are underestimated (see results and discussion).

### Relationship between discard consumption and breeding success

In order to assess the relationship between breeding success and discard consumption, we fitted generalised linear mixed models (GLMM) in `glmmTMB` (function `glmmTMB`, Brooks *et al.*, 2017). We used a binomial distribution (1 = chick fledged or 0 = chick failed) with a logit-link function as our response variable and fitted separate models with each of the following explanatory variables (i) FO% of hoki or grenadier, (ii) N% of hoki or grenadier, (iii) FO% of fishery discards, and (iv) IRI% of fish. All analyses of hoki again only included specimens categorised as discards. We included “year” as a random effect to account for repeat diet measures within each sampling year. This is particularly relevant as we used “year” to account for good and resource poor years, different yearly natural prey availability and discard availability. The AICc was used for model selection, with individual models assessed against the null model. Model fit was evaluated using numerous visual and numerical



**Figure 2.** Prey found in stomach samples of black-browed albatross chicks at New Island, Falkland Islands, between 2004 and 2020, quantified in (a) percentage drained mass (M%) and percentage frequency of occurrence (FO%) of key prey groups; (b) percentage frequency of occurrence (FO%) of prey origin. Sample sizes are denoted in brackets underneath sampling year.

assessments typically conducted for binary data, including inspection of residuals for normality, patterns and outliers using the DHARMA package (Hartig *et al.*, 2021), and performance of the Hosmer-Lemeshow test (Hosmer *et al.*, 2013). The R-squared values were calculated after Nakagawa and Schielzeth (2013).

## Results

### Diet composition

We extracted 2620 prey items from 282 chick regurgitates during eight seasons between 2004 and 2020 (2004, 2007–2011, 2019, 2020). Overall, 99% of prey items belonged to either fish [85% (FO); 57% (M); 83% (IRI)], crustacean [75% (FO); 26% (M)] or cephalopod [39% (FO); 12% (M); 17% (IRI)] (Figure 2a). This includes fresh prey that were identified

as one of these prey groups, but which could not be identified to any higher taxonomic resolution. Gelatinous zooplankton (jellyfish and salps) were recorded in four seasons, as well as small numbers of bivalves, gastropods and carrion (penguin feathers).

Twenty-two different taxa were identified (fish: 5 orders, 7 families, 11 species; cephalopod: 2 orders, 5 families, 5 species; crustacean: 4 orders, 6 species; Table S3). The most frequent species of crustacean were lobster krill *Munida gregaria* [67% (FO)] and *Themisto gaudichaudii* [9% (FO)], both categorised as natural prey. The most important cephalopod was Loligo [20% (FO); 18% (N)], followed by Illex [3% (FO); 2% (N)] and *Moroteuthopsis ingens* [3% (FO); 1% (N)], also all categorised as natural prey. Fish species were generally dominated by prey categorised as discards: pelagic hoki [29% (FO); 16% (N)], demersal grenadier [23% (FO); 11% (N)], and benthopelagic rock cod *Patagonotothen ramsayi*, [19% (FO); 16% (N)] (Table S3). The exception was 2019, when pelagic Fuegian sprat *Sprattus fuegensis*, categorised as natural prey, was the most frequent and abundant fish species [35% (FO); 30% (N)] (Table S3).

Across the years, naturally obtained prey were found in 88.0% of samples [annual range: 67.5–97.5% (FO)] (Figure 2b). Eighty percent of identified fish were categorised as fishery discards (but see discussion on possible underestimation of natural fish prey such as Fuegian sprat). As such, fishery discards were present in 50% of diet samples across years [annual range: 22.6–87.5% (FO); Figure 2b]. All discard species corresponded with target or bycatch species of trawl fisheries operating on the Patagonian Shelf (Table S3). Ninety percent ( $n = 204$ ) of measurable hoki and 100% ( $n = 200$ ) of grenadier were categorised as discards, making them the most abundant and frequently present discard species identified.

### Inter-annual variation in diet

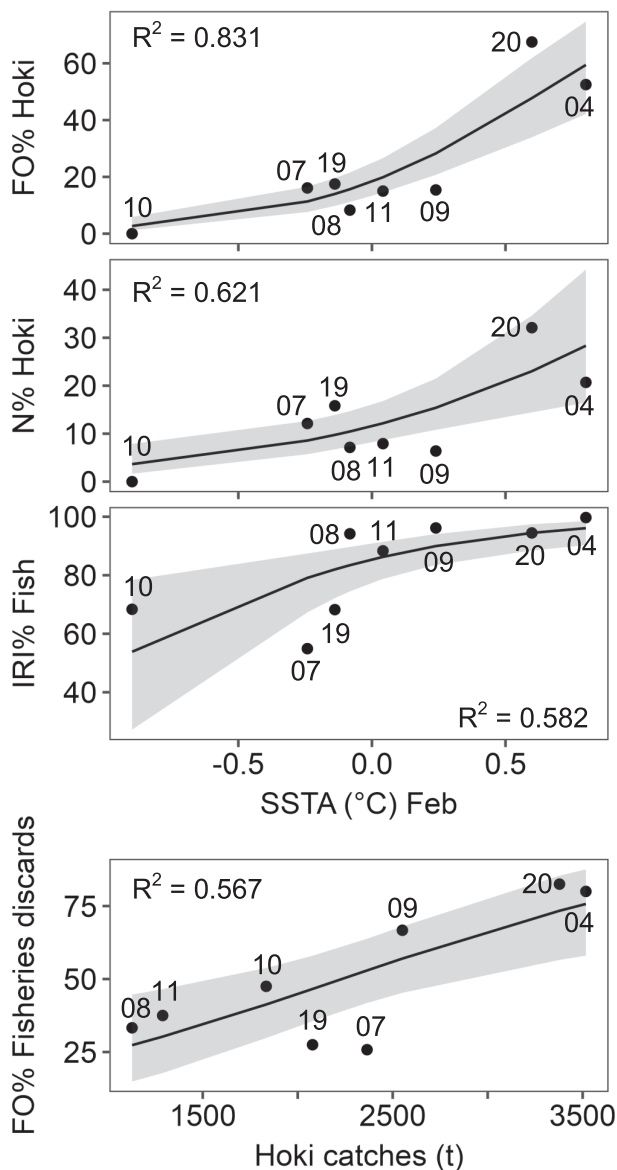
Diet composition differed among years in terms of FO% and M% of key prey groups (fish, crustaceans, cephalopods: PERMANOVA, FO%:  $R^2 = 0.205$ ,  $P = 0.01$ ; M%:  $R^2 = 0.212$ ,  $P = 0.01$ ), and FO% of prey origin (fisheries discards and natural prey, PERMANOVA,  $R^2 = 0.163$ ,  $P = 0.01$ ). The SIMPER analysis revealed that, on average, lobster krill, hoki, Loligo, rock cod, grenadier, *T. gaudichaudii* and Fuegian sprat contributed 50% to the observed inter-annual differences in diet composition (Table S4). Lobster krill and hoki were the only two species found in the diet every year, although between 2008 and 2011, rock cod was the most prevalent fish species (Table S3).

### Relationship between discard consumption and prey availability

We found a significant positive relationship between consumption of hoki (FO% and N%) and SSTA (February), as well as between consumption of fish (IRI%) and SSTA (February) (Table 2; Figure 3). The trends between grenadier consumption and fishery catches or SSTA were not significant, unless one outlier (year = 2010) was removed (Linear regression, SSTA (February) FO%:  $P = 0.005$ ; N%:  $P = 0.003$ ). Consumption of fisheries discards (FO%) was also positively influenced by February hoki catches in the Falkland Islands (Table 2; Figure 3). Based on the R-squared values, between 57 and 83% of the variability in the data was explained by the models (Table 2). Inspection of residuals found no issues of

**Table 2.** Linear model outputs and AICc values for model comparison.  $\Delta$ AICc is the difference in AICc compared to the null model. Coefficient estimates (Est.) and standard errors (Std. Err.) are on the logit scale. Hoki (F) indicates that only specimens categorised as fisheries discards were considered in the analysis. We only include models that showed higher predictive power compared to the null model ( $\Delta$ AICc  $\geq 2$ ).

Response variable	Fixed effect	Est.	Std. Err.	z-value	p-value	Adjusted R <sup>2</sup>	AICc	$\Delta$ AICc
FO% Hoki (F)	SSTA (Feb)	2.340	0.393	5.947	0.001	0.831	22.8	-9.8
N% Hoki (F)	SSTA (Feb)	1.381	0.391	3.529	0.012	0.621	22.7	-3.4
IRI% Fish	SSTA (Feb)	1.794	0.548	3.275	0.017	0.582	28.1	-2.6
FO% Fisheries	Hoki catches FI (Feb)	<0.001	<0.001	3.187	0.019	0.567	25.3	-2.3



**Figure 3.** Prey consumption  $\pm$  95% CI by black-browed albatross chicks in relation to sea surface temperature anomalies (SSTA) in February, and February commercial catches of hoki in the Falkland Islands. The raw data points are superimposed, with the year indicated (04 = 2004, etc.). We only include models that showed higher predictive power compared to the null model ( $\Delta$ AICc  $\geq 2$ ). FO% = percentage frequency of occurrence, N% = percentage numeric frequency, IRI% = percentage index of relative importance.

homogeneity, however, outliers were identified for all response variables apart from fish (IRI%). Removal of outliers increased statistical significance of results for hoki (N%) and grenadier (FO% and N%); however, we retained all data points in order to maximise our small dataset. No relationship was found between SSTA (February) and hoki catches (February), which could have confounded our results (Table S5). Further, no effect was found between diet and NPP in January or February.

### Relationship between discard consumption and breeding success

We found a significant negative relationship between black-browed albatross breeding success and consumption of hoki (FO%), grenadier (FO% and N%), and fishery discards (FO%; Table 3, Figure 4). The relationship with fish (IRI%) was significant only before the Bonferroni correction (Table 3). Inspection of residuals and individual Hosmer-Lemeshow tests found no indication that model fit was poor (all  $p > 0.05$ ) (Hosmer *et al.*, 2013).

### Discussion

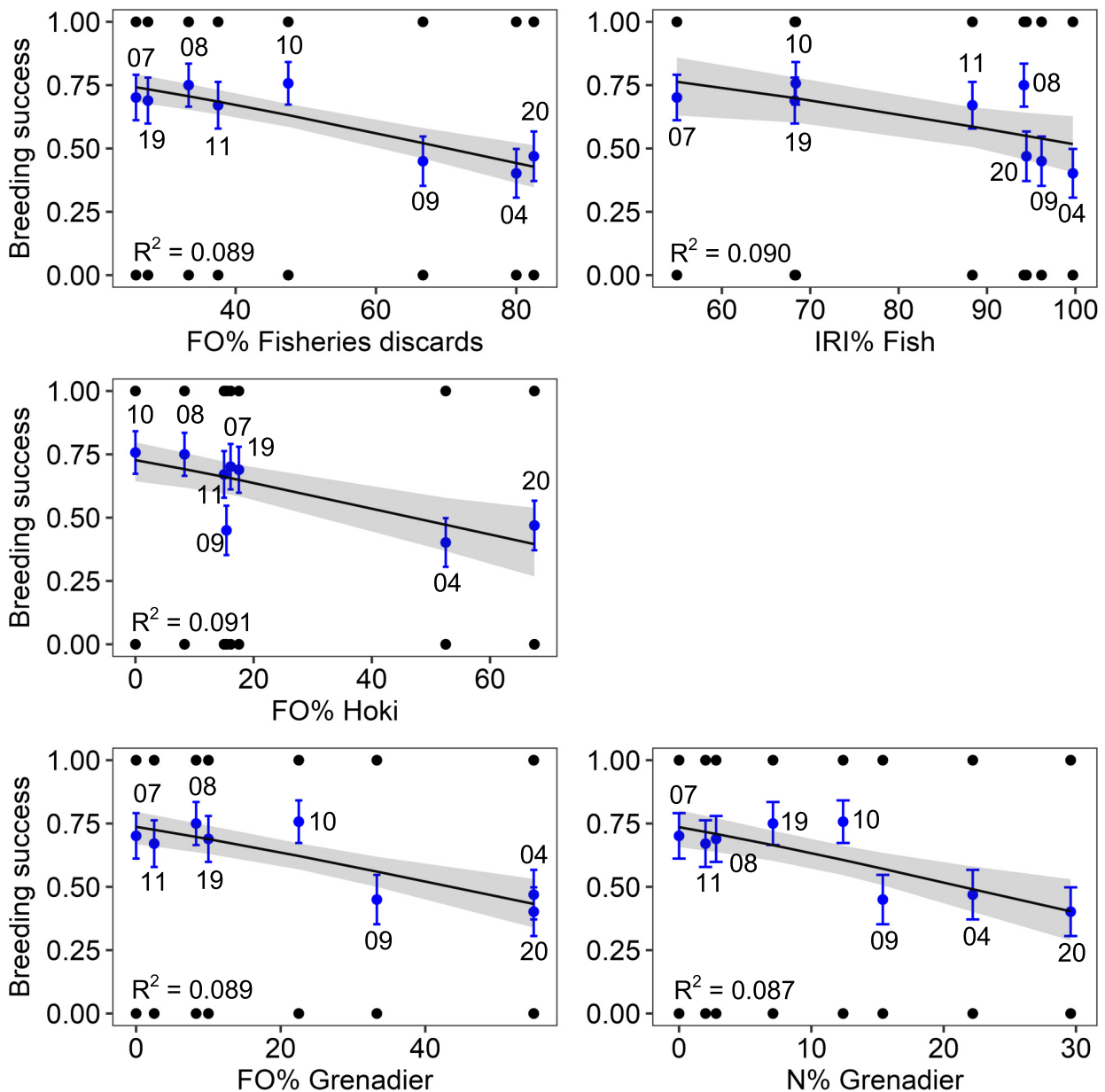
Our study represents the first long-term assessment of black-browed albatross chick diets from the world's largest population in the Falkland Islands and provides essential information on fisheries interactions for this species. We found that chicks at New Island were fed predominantly on naturally foraged crustaceans, cephalopods and fish, but also regularly received fishery discards. Moreover, the quantity of discards in the diet was positively related to fishery catches of hoki and SSTA (Figure 3), and negatively related to breeding success (Figure 4). Our findings suggest a prey-switching behaviour, whereby black-browed albatross increase discard consumption in years of poor natural foraging conditions when breeding success is reduced.

### Diet composition and trends

Throughout the eight study seasons between 2004 and 2020, fish and crustaceans dominated chick diet, while cephalopods represented the lowest proportion of these three top prey groups (Figure 2). The importance of fish, in particular, corroborates findings for black-browed albatross diets in the Falkland Islands previously (Thompson, 1992; McInnes *et al.*, 2017b) and elsewhere, including at colonies in South Georgia, (Prince, 1980; Reid *et al.*, 1996; McInnes *et al.*, 2017b; Mills *et al.*, 2020), Kerguelen (Cherel *et al.*, 2000, 2002; McInnes *et al.*, 2017b), Chile (Arata and Xavier, 2003; McInnes *et al.*, 2017b), Australia (McInnes *et al.*, 2017b) and New Zealand (McInnes *et al.*, 2017b). Compared to stomach contents examined in 1986/87 (Thompson, 1992), the occurrence of

**Table 3.** Outputs of GLMM with logit link function assessing black-browed albatross breeding success as a function of diet estimates and goodness of fit validation statistics.  $\Delta$ AICc is the difference in AICc compared to the null model. Coefficient estimates (Est.) and standard errors (Std. Err.) are on the logit scale. Hoki (F) indicates that only specimens categorised as fisheries discards were considered in the analysis. We only include models that showed higher predictive power compared to the null model ( $\Delta$ AICc  $\geq$  2).

Fixed effect	Est.	Std. Err.	z-value	p-value	Marginal R <sup>2</sup>	Conditional R <sup>2</sup>	Conditional model	
							AICc	$\Delta$ AICc
FO% Fisheries discards	-0.024	0.005	-5.24	<0.001	0.073	0.089	2473	-9.8
IRI% Fish	-0.025	0.010	-2.43	0.015	0.040	0.090	2480	-2.4
FO% Hoki (F)	-0.021	0.006	-3.40	<0.001	0.057	0.091	2477	-5.2
FO% Grenadier	-0.024	0.005	-4.41	<0.001	0.066	0.089	2475	-7.8
N% Grenadier	-0.048	0.013	-3.77	<0.001	0.058	0.087	2477	-6.1



**Figure 4.** GLMM outputs  $\pm$  95% CI assessing breeding success of black-browed albatross at New Island, Falkland Islands, against various metrics of discard consumption. The raw binary data (black dots), average annual breeding success values  $\pm$  95% CI (blue dots), and the conditional R<sup>2</sup> value are provided. The numbers indicate the year (04 = 2004, etc.). We only include models that showed higher predictive power compared to the null model ( $\Delta$ AICc  $\geq$  2). FO% = percentage frequency of occurrence, N% = percentage numeric frequency, IRI% = percentage index of relative importance.

crustaceans was higher, whilst that of fish and cephalopods has remained similar. This may reflect an expansion of pelagic swarms of lobster krill on the Patagonian Shelf (Diez *et al.*, 2016).

The species diversity of the black-browed albatross diet was lower at New Island compared to other sites such as South Georgia (Mills *et al.*, 2020) or Diego Ramirez, Chile (Arata and Xavier, 2003), which likely reflects food web differences or prey availability within the Patagonian Shelf Large Marine Ecosystem. Total species diversity, as well as diversity within certain years, was nonetheless higher than previously identified for New Island using stomach content analysis (Thompson, 1992) and DNA (McInnes *et al.*, 2017a). Key prey included species of commercial interest and of ecological importance within the Patagonian Shelf, and were generally comparable to those identified in previous dietary studies from this colony (Thompson, 1992; McInnes *et al.*, 2017a).

Across years, between 68 and 98% of samples contained natural prey, of which lobster krill, followed by *Loligo*, were the most frequent and abundant. In addition to Fuegian sprat, these species form the dominant dietary component of many marine predators breeding in the Falkland Islands, including seabirds (Baylis *et al.*, 2014; Handley *et al.*, 2017). Fuegian sprat, one of the most important pelagic fish in the southwest Atlantic (Agnew, 2002; García Alonso *et al.*, 2020), was scarce in our samples (except in 2019). However, large numbers of unidentifiable small fish lenses were found in the samples, and a previous DNA-based diet study from New Island found Fuegian sprat to be the dominant fish prey in 2013/14 and 2014/15 (McInnes *et al.*, 2017a). Stomach content analysis provides a high level of taxonomic resolution but can result in the underestimation of more fragile and easily digested species (Votier *et al.*, 2003; McInnes *et al.*, 2016) and taxa with small otoliths (Van Heezik and Seddon, 1989). It is therefore possible that we underestimated the importance of Fuegian sprat, and potentially other natural prey such as jellyfish (McInnes *et al.*, 2017b). Complementary methods such as DNA metabarcoding or stable isotope analysis could help confirm this (McInnes *et al.*, 2016). The distinct isotopic signature of pelagic Fuegian sprat to that of other key prey can help determine the importance of these fish in black-browed albatross chick diet (e.g. Granadeiro *et al.*, 2014; A. Kuepfer unpubl data). While the isotopic signature of jellyfish overlaps with that of lobster krill in our system (A. Kuepfer unpubl data), McInnes *et al.* (2017b) successfully used DNA to demonstrate high consumption of jellyfish by breeding black-browed albatrosses (though less so at New Island).

Fishery discards were present in 23 to 88% of samples across years, illustrating considerable inter-annual variation in discard consumption. Discard species were representative of target or bycatch species of trawl fisheries, with hoki and grenadier being the most consistent and abundant discard species in stomach samples. In summer, Falkland Islands hoki catches tend to be focused in deep waters to the southwest of the Falkland Islands where it is most abundant (Falkland Islands Government, 2020). The grenadier species *C. fasciatus*, not previously reported in black-browed albatross diet studies, is a frequent bycatch species in the Falkland Islands hoki fishery (Winter and Lee, 2018). Between 2008 and 2011, rock cod was the dominant fish prey in diet samples, which coincides with the rise and collapse of rock cod biomass and its importance as a commercial species in the Falkland Islands waters between 2007 and 2015. This followed the decline of

the southern blue whiting biomass and catches in this fishery (Laptikhovskiy *et al.*, 2013; Baylis *et al.*, 2021; Winter, 2021), which, too, is reflected in the chick diet in our study.

### Relationship between breeding success, discards and foraging conditions

As hypothesised, the relationship between discard consumption and breeding success in New Island black-browed albatross was negative (Figure 4). A negative relationship between discard consumption and breeding success has previously been linked to the “junk-food” hypothesis, which suggests that chick development can be adversely affected if chicks are fed on discards that are often lean compared with natural prey (e.g. Grémillet *et al.*, 2008). Lipid-poor diets can negatively affect chick development (Kitaysky *et al.*, 2006; Mullers *et al.*, 2009). Demersal fish, such as grenadier, tend to have a lower caloric content compared to pelagic prey such as Fuegian sprat (ca. 4.8 kJg<sup>-1</sup> vs. 7.2 kJg<sup>-1</sup> wet mass, respectively; Ciancio *et al.*, 2007). Hoki, however, has a lipid content comparable to that of sprat due to its fatty liver (6.51 kJg<sup>-1</sup> wet mass, Eder and Lewis, 2005), and hence not all discards consumed by New Island chicks can be considered nutritionally poor. Besides the nutritional content of prey, other interacting aspects may make discards suboptimal meals, such as prey abundance and location (e.g. Jodice *et al.*, 2006), or the risk of incidental mortality in fishing gear. Changes in foraging distribution and provisioning rates have been offered as an explanation for relationships between diet and breeding success in the closely related grey-headed albatross *T. chrysostoma* at South Georgia (Xavier *et al.*, 2013; Mills *et al.*, 2020). Such an effect would have to be assessed for Falkland Islands breeding black-browed albatrosses using GPS tracking data.

While discard consumption showed a positive relationship with February hoki catches in the Falkland Islands fishery (Figure 3), the positive influence of February SSTA on consumption of hoki (N% and FO%) and fish (IRI%) suggests that discard use may not simply be influenced by its availability, but could also be driven by underlying environmental conditions (Wren *et al.*, 2019). High sea surface temperature can in some systems negatively impact primary production, particularly in upwelling and frontal ecosystems like the Patagonian Shelf (Behrenfeld *et al.*, 2006; Barbraud *et al.*, 2012 but see elsewhere e.g. Inchausti *et al.*, 2003; Rolland *et al.*, 2008). In turn, this can result in poor feeding conditions for seabirds (reviewed in Quillfeldt and Masello, 2013; Carroll *et al.*, 2015; Furness, 2016), and negatively impacts black-browed albatross breeding success at New Island (Ventura *et al.*, 2021a, b). Moreover, and possibly more relevant given the absence in time-lag, SSTA can have a direct effect on prey availability by shifting frontal zones and preferred foraging habitats (see e.g. Wren *et al.*, 2019; Ventura *et al.*, 2021c), potentially driving birds to feed more on discards (see e.g. Votier *et al.*, 2004; Conners *et al.*, 2018). It is possible that our results could be confounded if hoki preferred warmer waters; however, the current and previous research have found no relationship between abundance and temperature in hoki (Alemany *et al.*, 2018), including the closely related *M. novaeseelandiae* (Francis *et al.*, 2006). We did not find a relationship between discard consumption and NPP, but a diet shift by black-browed albatross and grey-headed albatross in relation to primary production has been demonstrated in the South Georgia and Scotia Sea marine ecosystem (Mills *et al.*, 2020).

Our findings, though based on a limited number of years, support a diet-switching hypothesis whereby black-browed albatross increase discard consumption during years of poor natural foraging conditions, characterised by high SSTA. Such a diet switch has been recorded in the North Pacific black-footed albatross *Phoebastria nigripes* that increased discard consumption during a year of record-high SST (Conners *et al.*, 2018) and also in the Benguela system where Cape gannets *Morus capensis* increased discard consumption when natural prey were scarce (Tew Kai *et al.*, 2013; Cohen *et al.*, 2014). In light of predicted rising sea surface temperatures as a result of climate change (IPCC, 2019; Franco *et al.*, 2022), this pattern warrants particular attention in the context of conservation. The impact of environmental and fishery effects on prey availability are likely to be highly complex and system-specific, however (Inchausti *et al.*, 2003; Rolland *et al.*, 2008; Wren *et al.*, 2019). For example, Rolland *et al.* (2008) found that SSTA and trawling effort were positively correlated with breeding success of black-browed albatross on Kerguelen.

### Discard availability and population trends

It has previously been suggested that abundant discards facilitated an increase in the Falkland Islands black-browed albatross population (Croxall and Gales, 1998; McInnes *et al.*, 2017a). We confirm that albatross chicks are primarily fed natural prey (see also Granadeiro *et al.*, 2014; McInnes *et al.*, 2017a, 2017b), although discards are clearly important, particularly during periods of poor natural foraging conditions. Discards may provide a buffering effect of unknown magnitude during such years (Church *et al.*, 2018), and changes to discard availability as a consequence of discard management in the Falkland Islands trawl fleet could reduce such a buffering effect. Importantly, however, our data suggest that discards do not fully compensate for poor natural foraging conditions during the breeding season in the Falkland Islands because the breeding success in these years of increased discard consumption remained low. This is consistent with findings by Mullers *et al.* (2009) and Le Bot *et al.* (2019) who concluded that fishery discards do not provide an adequate alternative to natural food for birds during breeding. Continued monitoring of black-browed albatross diet in the Falkland Islands, along with an improved understanding of natural prey availability through systematic surveys would provide increased insight into conclusions drawn. Furthermore, additional research is required to understand the incidence and implications of discard consumption during non-breeding.

In a wider context, our study highlights the importance of diet monitoring when assessing population dynamics and effects of changing discard management (Votier *et al.*, 2004, 2008). In a period of climatic change and a drive towards an ecosystem-based approach to fisheries management, we urge marine management policy makers to practice caution when assuming that fishery discards are entirely beneficial to seabirds, and recommend improved monitoring of non-commercial, lower and mid-trophic species to enhance our understanding of the ecosystem health and variability.

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### Supplementary material

Supplementary material is available at the *ICES Journal of Marine Science* online version of this manuscript.

### Authors contributions

Conceptualization—AK, PC, SV; design and methodology—AK, FV, PC, RM, RS, SV; participating in the collection of data—AK, OA, PC, RM; analysis of the findings—AK, FV, RS, SV; drafting of the manuscript—AK, PC, RS, SV; and revision of the manuscript—all authors.

### Compliance with ethical standards

Diet samples and breeding data were collected under research licence issued by the Falkland Islands Government Environmental Department, and with approval from the University of Exeter College of Life and Environmental Sciences Penryn Research Ethics Committee.

### Data availability statement

The data underlying this article will be shared on reasonable request to the corresponding author.

### Conflict of interest

The authors have no conflicts of interest to declare.

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