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Longterm dietary shift and population decline of a pelagic seabird — A health check on the tropical Atlantic?

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Long-term dietary shift and population decline of a pelagic seabird—A health check on the tropical Atlantic?

Running head Bio-indicators and marine ecosystem function

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Abstract

In the face of accelerating ecological change to the world's oceans, seabirds are some of the best bio-indicators of marine ecosystem function. However, unravelling ecological changes that pre-date modern monitoring programmes remains challenging. Using stable isotope analysis of feathers and regurgitants collected from sooty terns (*Onychoprion fuscatus*) nesting at a major Atlantic colony, we reconstructed a long-term dietary time series from 1890 to the present day, and show that a significant dietary shift occurred during the second half of the twentieth century coinciding with an apparent population collapse of approximately 84%. After correcting for the 'Suess Effect', $\delta^{13}C$ in feathers declined by ~1.5‰ and $\delta^{15}N$ by 2‰ between the 1890s and the present day, indicating that birds changed their diets markedly over the period of population decline. Isotopic niches were equally wide before and after the population collapse but isotopic mixing models suggest that birds have grown ever more reliant on nutrient-poor squid and invertebrates as teleost fish have declined in availability. Given that sooty terns rely heavily on associations with sub-surface predators such as tuna to catch fish prey, the rapid expansion of industrialised fisheries for these species over the same period seems a plausible mechanism. Our results suggest that changes to marine ecosystems over the past 60 years have had a dramatic impact on the ecology of the most abundant seabird of tropical oceans, and highlight the potentially pervasive consequences of large predatory fish depletion on marine ecosystem function.

1 | INTRODUCTION

Since the middle of the twentieth century, intensified human use of marine resources, population growth and accelerating industrialization have contributed to a period of unprecedented change in the ecology of the world's oceans. Some estimates suggest that 90% of all large fishes in the oceans may already have been extracted (Myers & Worm, 2003) and many of the largest fisheries in the world are considered to be under threat (Pauly & Zeller, 2016). Accelerating climate change and marine pollution have also had wide-ranging effects on marine ecosystem function (Lotze, Coll, Magera, Ward-Paige, & Airoldi, 2011), with the pace and impacts of change continuing to increase (McCauley et al., 2015). It is estimated that ~1 billion people rely on fish for their daily diet as do 200 million people for their livelihoods (Béné et al., 2016). Given that oceans sustain so many people and are so biodiverse, it is imperative that we understand how marine ecosystems function, and how they are changing.

Seabirds act as sensitive bio-indicators for the direct and indirect effects of anthropogenic pressures on the marine environment through the study of their foraging behaviour, breeding performance and demographics (Furness & Monaghan, 1987). The longevity of seabirds, their regular censusing, and the sensitivity of focal species to changes in resource availability make them invaluable ‘barometers’ by which the health of the marine environment can be monitored (but see Grémillet & Charmantier, 2010). Phenology and breeding performance are known to be strongly influenced by oceanic conditions, food availability and fishing activities in both temperate (Frederiksen, Wanless, Harris, Rothery, & Wilson, 2004) and tropical (LeCorre, 2001) waters. In the latter case, many foraging seabirds associate with cetaceans and predatory fish such as tuna (*Thunnus* spp.) that drive prey to the surface where they are captured by plunge diving and surface feeding (Ballance & Pitman, 1999). Prey may be sufficiently abundant but remain unavailable to tropical seabirds without the presence of such underwater predators (Maxwell & Morgan, 2013; Veit & Harrison, 2017), particularly where foraging occurs over pelagic waters, far from upwelling areas or other physical oceanographic features that naturally result in large congregations of prey at the sea surface (Au & Pitman, 1986). Global declines of large predatory fishes since the middle of the twentieth century as a result of over-fishing, and lack of appropriate management measures (Myers, Baum, Shepherd, Powers, & Peterson, 2007; Juan-Jordá, Mosqueira, Cooper, Freire, & Dulvy, 2011), may therefore have had significant impacts on the ecology of tropical oceanic seabirds. Other drivers of global environmental change may also have impacted on seabird foraging success and demography. For example, ocean warming has been linked to changes in prey population dynamics (Howells et al., 2017), and range shifts of both forage fish and pelagic predators in temperate and tropical oceans (e.g. Perry, Low, Ellis, & Reynolds, 2005; Monllor-Hurtado, Pennino & Sanchez-Lizaso, 2017), potentially diminishing food availability to seabirds through reductions in both prey availability and accessibility (e.g. Howells et al., 2017).

Studies of contemporary seabird diets, breeding success and population dynamics have provided valuable data on threats currently facing marine ecosystems. However, changes to such ecosystems may have occurred that pre-date modern monitoring programmes. Here, we use a historical ecology approach to investigate how long-term changes to marine food webs have influenced the foraging ecology of the world's most abundant tropical seabird, the sooty tern (*Onychoprion fuscatus*) at the Atlantic's largest nesting colony on Ascension Island (Hughes, Martin, Giles, & Reynolds, 2017a). Sooty terns are long-lived (in some cases >38 years old; Schreiber et al., 2002), pan-tropically distributed (Schreiber et al., 2002), and near-obligate commensals of tuna and other sub-surface predators (Au & Pitman, 1986), making them ideal indicators of the status of tropical marine ecosystems. The species is currently regarded as of 'Least Concern' by the IUCN owing to a healthy global population of 21–25 million birds (species account retrieved from http://datazone.birdlife.org). Nevertheless, a number of sizeable populations have declined markedly (reviewed in Hughes et al., 2017a), including that at Ascension Island. Hughes et al. (2017a) compared the breeding population size of sooty terns on the island between 1950 and the present day, observing that since 1958, when there were an estimated 3.32 million birds, it declined by 84% to estimates of 350,000 individuals in 2013. This mirrors the estimated 69.7% decline in the global seabird population between 1950 and 2010 (inclusive) calculated by Paleczny, Hammill, Karpouzi and Pauly (2015) based upon data from 3,213 breeding populations of 324 seabird species. Such declines in sooty tern numbers on Ascension Island are unprecedented; earlier estimates of the population in 1877 and 1942 suggested it contained 2.43 and 2.35 million birds, respectively (Hughes et al., 2017a).

Here, we investigate whether the steep decline in the size of the breeding population of sooty terns on Ascension Island can be related to changes in their diet. Since it is impossible to observe birds' foraging behaviour directly at sea, stable isotope analysis (SIA) was used to reconstruct diets from isotopic values of contour feathers grown over many months prior to their collection from each bird. Once formed, feathers are inert metabolically and their composition therefore reflects food consumed at the time of growth (Ramos, González-Solís, Croxall, Oro, & Ruiz, 2009). To investigate how diets have changed over decadal scales, we plucked contour feathers from museum specimens of adult breeding sooty terns collected from the island between 1890 and 1972, and from fresh corpses or live birds captured on the colonies between 2006 and 2012. A similar approach has been successfully used in previous studies to reconstruct historical seabird diets (e.g. Hilton et al., 2006; Norris, Arcese, Preikshot, Bertram, & Kyser, 2007; Blight, Hobson, Kyser, & Arcese, 2015).

We studied the foraging behaviour and ecology of sooty terns by examining whether their: (i) feather isotopic values change, (ii) isotopic niches overlap, and (iii) diet composition changes either side of their population collapse. We discuss dietary reconstructions from feathers in the context of fundamental changes in marine food webs that have occurred across the same period, in particular the global declines in large predatory fish upon which sooty terns are almost wholly dependent to forage successfully. Finally, we discuss how findings may shape marine conservation initiatives in the future.

2 | MATERIALS AND METHODS

2.1 | Study area and species, and the seabird community

The study was carried out on Ascension (07°57′S, 14°24′W), a 97 km^2 volcanic island that is isolated in the tropical South Atlantic with its nearest neighbour being the island of St Helena 1,300 km to the south-east. The territory contains several Important Bird Areas (IBAs), including the sooty tern nesting grounds at the ‘Wideawake Fairs’ (IBA SH009) (site description retrieved from http://datazone.birdlife.org), and provides the only breeding location for significant numbers of sooty terns in the central, tropical Atlantic Ocean (Hughes et al., 2017a). A detailed account of the breeding biology of sooty terns on the island is provided by Ashmole (1963a). The seabird community on Ascension Island has been heavily impacted by predation by invasive species (e.g. domestic cats [*Felis silvestris catus*]; Hughes, Martin, & Reynolds, 2008; common mynas [*Acridotheres tristis*]; Hughes, Martin, & Reynolds, 2017b). Declines in the size of seabird populations were so steep that they provoked a seabird restoration project in 2002 by the Royal Society for the Protection of Birds (RSPB) that aimed to promote recovery of former large and diverse seabird populations (Pickup, 1999). It has been partially successful (Ratcliffe et al., 2010) but the sooty tern population has continued to struggle in its recovery (Figure 1), despite the eradication of feral cats (Hughes et al., 2017a).

2.2 | Feather sampling

Terns typically moult and breed mutually exclusively (Ashmole, 1963b) but only on Ascension Island do individual sooty terns breed sub-annually (Reynolds, Martin, Dawson, Wearn, & Hughes, 2014); they start their post-nuptial (basic) moult (when all feathers are replaced) when still breeding (Ashmole, 1963b). Therefore, contour feathers provide a dietary record of birds in the latter stages of breeding and on migration. Skins were located by searching museum databases (e.g. https://arctos.database.museum/, http://www.ornisnet.org/, http://www.vertnet.org/), leading to correspondence with museum curators on five continents (Table S1). In total, 187 skins were located (Table S2). SJR either travelled to museums to collect feathers or sent instructions to curators to ensure that sampled feathers were from equivalent breast areas on all specimens. Contour feathers were also obtained from dead birds that had collided with radio masts on Ascension Island and from live birds during ringing on the island (Table S2). For each sample a pair of contour feathers was collected from both the left- and right-hand sides of the breast in its mid-zone ~3 cm on either side of the keel ridge. Feathers were stored in a domestic refrigerator prior to SIA.

2.3 | Food sources for diet reconstruction

Sooty terns breeding on the island are on migration for at least six months of every sub-annual cycle (Ashmole, 1963a) and thus cannot be observed directly feeding at sea. Furthermore, no regurgitant samples were available from birds in museum collections. Schreiber et al. (2002) described their diet as containing small (teleost) fish such as halfbeaks (*Oxyporhamphus micropterus*), blue flying fishes (*Exocoetus volitans*), redlip blennies (*Ophioblennius atlanticus*), Simony's frostfishes (*Benthodesmus simonyi*) and hairtails (*Trichiurus* spp.) (Ashmole, 1963a), and squid (Teuthida). Their diet when breeding can be readily reconstructed from regurgitant samples when sooty terns are handled; their regurgitated prey is far less digested than that from other seabird species (Ashmole & Ashmole, 1967). In 2012 during ringing of breeding adults we (i.e. SJR, BJH, CPW and RCD) noted a more catholic diet in birds that rarely regurgitated fish but more often violet sea snails (*Janthina janthina*), megalops (a larval stage) of Sally Lightfoot crabs (*Grapsus grapsus*), and locusts (Acrididae spp.) (Figure S1). While regurgitant samples from breeding birds are not truly reflective of their diet during the sub-annual cycle, breeding birds travel hundreds of kilometres out to sea when foraging (Soanes, Bright, Brodin, Mukhida, & Green, 2015; Neumann, Larose, Brodin, & Feare, 2018; JB, unpubl. data), and thus likely contain similar prey to those consumed by birds between breeding seasons.

2.4 | Stable isotope analysis

We performed SIA on contour feathers for δ^{13}C (^{13}C/^{12}C) and δ^{15}N (^{15}N/^{14}N) to estimate the foraging habitat and trophic positioning of birds. Carbon is enriched by ~0.8‰ in coastal or benthic areas in relation to offshore or pelagic foraging areas whereas nitrogen is enriched at each successive trophic level by 2–5‰ (Quillfeldt, McGill, & Furness, 2005). Contour feathers retain dietary information of birds in the year of feather collection (Inger & Bearhop, 2008) with all feathers of breeding sooty terns on Ascension Island moulted sub-annually (Ashmole, 1963b). To determine δ^{13}C and δ^{15}N of each of four prey groups ($n = 15$ in each group), we used: (i) muscle of teleost fish species (false halfbeaks [*Oxyporhamphus similis*], blue flying fishes, redlip blennies and Simony's frostfishes), (ii) squid (Teuthida), (iii) marine invertebrates (Sally Lightfoot crabs and violet sea snails), and (iv) terrestrial invertebrates (locusts), from regurgitations of birds when handled and prey dropped by flying birds at the breeding colonies. Small samples (~10 g) of these prey were dried at 60°C for 48 hours in an oven (Heratherm^{TM} General Protocol Oven, Thermo Scientific, Waltham, MA, USA) and then ground into powder using a mixer mill (MM400, Retsch, Leeds, UK). Powder was rinsed five times (10 minutes per rinse) in 2:1 chloroform:methanol (Sigma-Aldrich, St. Louis, MO, USA) to extract lipids prior to SIA (Kojadinovic, Richard, Le Corre, Cosson, & Bustamante, 2008). Because lipid extraction might change the δ^{15}N values, separate samples of each of the main prey items were analysed for δ^{13}C (subjected to lipid extraction) and δ^{15}N (without lipid extraction) values (Kojadinovic et al., 2008). The C:N ratio was used to assess the effectiveness of the delipidation process. To remove surface contaminants each feather was washed three times (5 minutes per wash) in a 2:1 chloroform:methanol solution. Feather and dietary samples were then dried at 60°C for 48 hours (as above) with feathers then cut into small fragments. The carbon and nitrogen isotopic composition of samples was determined by mass spectrometry (Thermo Delta VS, ThermoFisher Scientific, Waltham, MA, USA). Replicate measurements of internal laboratory standards (acetanilide) indicated a precision of <0.2‰ for both $\delta^{13}C$ and $\delta^{15}N$.

Since the Industrial Revolution the burning of fossil fuels has a lower $\delta^{13}C$ than background carbon causing an exponentially accelerating decrease of $\delta^{13}C$ in the biosphere – the so-called 'Suess Effect' (Keeling, 1979). In addition, the increase in atmospheric CO_2, and thus aqueous CO_2, has increased phytoplankton fractionation, reducing its $\delta^{13}C$ values (Rau, Takahashi, Des Marais, Repeta, & Martin, 1992). Thus, raw $\delta^{13}C$ values of sooty tern feathers were adjusted following Hilton et al. (2006), Jaeger and Cherel (2011), and Carravieri, Cherel, Jaeger, Churlaud and Bustamante (2016).

2.5 | Data analyses

All statistical analyses were carried out in R (Version 3.01) (R Development Core Team, 2016). To test if the trend in $\delta^{13}C$ and $\delta^{15}N$ before and after the population collapse differed significantly we ran linear mixed-effect models (LMMs) (lme4 R library; Bates, Mächler, Bolker, & Walker, 2015) to control for uneven sample sizes between decades (i.e. with 'decade' included as a random effect). They tested the effect of: (i) decade (1890, 1920, 1940, 1970, 2000 and 2010), and (ii) the decade × period (1980–1940 vs. 1970–2010) interaction on the $\delta^{13}C$ and $\delta^{15}N$ values. The decade × period interaction was included to test for differences in slopes between the two time periods. We randomly selected 50 values from the 104 samples of the 1920 decade to run the models to ensure that this decade was not over-represented in terms of sample size compared to the others. All values are presented as the mean ± 1 SD unless otherwise stated. Residuals were tested for normality (Q-Q plots) and homogeneity (Cleveland dotplots) before each statistical test; they were transformed when required (Zuur, Ieno, & Elphick, 2010). All analyses were performed using an alpha threshold of .05.

The Stable Isotope Bayesian Ellipses in R (SIBER; Jackson, Inger, Parnell, & Bearhop, 2011) package was used to establish the isotopic niche width of birds, based on isotopic values of feathers before (i.e. between 1890s and 1940s) and after (i.e. between 1970s and 2010s) the population collapse. The standard ellipse area after small sample size correction (SEA_C) measure was used to compare estimated isotopic niches between the two periods. This is an ellipse that has 40% probability of containing a subsequently sampled datum regardless of sample size. We used the Bayesian estimate of the standard ellipse and its area (SEA_B) measure to test for differences between the two periods by comparing p (the proportion of ellipses) before with that after the population collapse, for 10^4 replicates (see Jackson et al., 2011 and Parnell et al., 2013 for further details). All metrics were calculated using *standard.ellipse* and *convexhull* functions from the SIBER R package.

Dietary composition of birds was estimated from isotopic values of feathers and their prey using a Bayesian multisource stable isotope mixing model (SIAR; Parnell & Jackson, 2011). The proportions of the four main dietary items (fish, squid, marine invertebrates and terrestrial invertebrates) between the two study periods (1890s–1940s and 1970s–2010s) were compared with a Chi-square test. This allowed us to assess the birds' trophic position for the periods of 1890s to 1940s and of 1970s to 2010s. Since there are no diet-blood trophic discrimination factors (TDFs) available for sooty terns, we applied mean enrichment factors generally accepted for seabirds of 1 and 3‰ to $\delta^{13}C$ and $\delta^{15}N$ values, respectively, between each prey group and feathers (Caut, Angulo, & Courchamp, 2009; Kelly, 2000). A SD of ±

1.0‰ was taken into account, considering potential differences in fractionation factors among species. To test the robustness of this approach we: (i) ran a sensitivity analysis (after Inger et al., 2006) that revealed model outputs varied by a maximum of 4% when TDFs varied by 1–2‰ for δ^{13}C and 3–5‰ for δ^{15}N values, and (ii) used the discrimination estimation (DEsiR) functions in the Stable Isotope Discrimination Estimation in R (SIDER; Healy et al., 2017) package to estimate TDF values for sooty terns. It compares isotopic values of our study species with those of others in a large database of reported TDF values and, based on phylogenetic relatedness, it uses Bayesian imputation methods to calculate the most likely TDF values. It estimated modal values of 1.1‰ and 2.8‰ for δ^{13}C and δ^{15}N, respectively, a deviation of only ~1.1% from the TDFs we chose. Therefore, it validated our approach.

3 | RESULTS

3.1 | Temporal trends in isotopic values

There were significant temporal trends in both carbon and nitrogen isotopic values of feathers across the decades from 1890 to 2010. Carbon isotopic values of feathers from the 2010s were significantly lower than those of feathers collected from birds in the 1970 and 2000 decades which, in turn, were lower than those of feathers from museum skins collected between the 1890s and 1940s (Figure 2a; Table 1). The nitrogen isotopic values of feathers from birds sampled in the field in the 2000 and 2010 decades were significantly lower than those in feathers of museum specimens collected in the 1920s and 1940s which, in turn, were lower than those from the 1890s (Figure 2b; Table 1). Moreover, the decrease in the slope of models for both carbon and nitrogen isotopic values was steeper for the 1970–2010 period of decades following the population collapse compared to the 1890–1940 period of decades preceding it, as shown by the significantly negative decade × period interaction (Table 1).

3.2 | Isotopic niche widths

The isotopic niche widths of birds reconstructed from isotopic values of feathers collected in decades before (1890s–1940s) and after (1970s–2010s) the population collapse were similar (SEA_C: before – 0.97; after – 0.88; SEA_B: *p* value = .43; see **Materials and methods** for further details). There was no overlap in these isotopic niches between these periods although the niches of birds decreased both in $\delta^{13}C$ and $\delta^{15}N$ values from the former to the latter period (Figure 3).

3.3 | Isotopic values of prey and reconstructed diets of birds across decades of sampling

The mean $\delta^{13}C$ and $\delta^{15}N$ values differed between prey categories – fish, squid, marine invertebrates and terrestrial invertebrates (Figure 4). The C:N mass ratios for fish (3.01), squid (2.87), marine (3.12) and terrestrial invertebrates (2.77) were similar indicating the delipidation treatment (**Materials and methods**) was equally as effective across all prey samples. According to dietary estimates provided by the isotopic mixing models, birds underwent a dietary shift between the decades in the 1890s–1940s period, when they fed significantly more on fish prey (mean relative contributions: fish – 0.62; squid – 0.26), and those in the 1970s–2010s period, when they fed significantly more on squid (fish – 0.26; squid – 0.57; Chi-square test: $\chi^2_3 = 28.30$, *p* value < .001) (Figure 5). Moreover, accompanying a more squid-dominated diet were marine and terrestrial invertebrates that constituted greater proportions of birds' diets in the 1970s–2010s period (marine invertebrates – 0.08; terrestrial invertebrates – 0.11) compared with the 1890s–1940s period (marine invertebrates – 0.06; terrestrial invertebrates – 0.04) (Figure 5).

4 | DISCUSSION

Significant declines were found in both the $\delta^{13}C$ and $\delta^{15}N$ values of contour feathers collected over the 120-year study period (Figure 2a and b), indicating that the diets of these sooty terns have changed over a period when breeding population size has declined markedly (Figure 1). Inferred foraging niches of sooty terns before (1890s–1940s) and after (1970s–2010s) the population collapse did not overlap, despite widths being similar (Figure 3). Isotopic mixing models indicated that this was due to a significant decrease in the proportion of teleost fish in the diet (from 0.62 pre-1950 to 0.26 post-1970) and a corresponding increase in the proportion of squid (from 0.26 to 0.57), and of marine and terrestrial invertebrates (from 0.06 and 0.04 to 0.08 and 0.11, respectively) (Figure 5).

Field observations of breeding sooty terns on Ascension Island also suggest that the proportion of fish in their diets has declined since the middle of the twentieth century, decreasing from 0.60 in 1958–1959 (Ashmole & Ashmole, 1967), to 0.50–0.60 in 1972 (Johnston, 1973) and to only 0.17 in 2004 (Hughes, 2014). In 2012 birds were predominantly feeding on squid and other low energy content foods, reflecting the struggle to locate fish prey. These observations support our SIA findings (Figure 5) and provide further evidence of a dietary shift. A similar dietary shift by breeding sooty terns was observed in the Dry Tortugas (FL, USA) 8,000 km away from Ascension Island: between 1920 and 1941 squid were absent from diets but they were a common dietary constituent between 1992 and 1994 (Colchero, 2008).

We worked with museum skins primarily because they extended the study beyond the period for which reliable field observations of sooty terns on Ascension Island were available. However, the number of years for which feathers were available for analysis (n = 11) was necessarily restricted to those when museum collectors and field ornithologists made visits to the island. Unfortunately, a lack of prey specimens in museums collected contemporaneously with these visits also results in an unavoidable temporal mismatch between dietary samples and feathers used in our SIA (a known limitation when using isotopic mixing models; Inger & Bearhop, 2008). Stable isotope analysis lends itself well to dietary reconstruction of seabirds using museum specimens (Barrett et al., 2007), but without access to historical prey too, it is difficult to know whether the isotopic prey composition remained constant over the period of study (Bond & Jones, 2010). Some caution is therefore required when interpreting our results. Although we acknowledge that temporal and spatial changes in the stable isotopic values at the base of the food webs could partly explain the changes we found in isotopic values of feathers, there is evidence to suggest that processes driving the distribution of carbon and nitrogen stable isotope values are temporally stable over relatively large spatial scales (e.g. MacKenzie, Longmore, Preece, Lucas, & Trueman, 2014).

4.1 | What has caused the dietary shift?

The middle part of the twentieth century, during which the dietary shift apparently occurred, marked the beginning of a period of major change in the world's oceans with the expansion of industrialised fishing and an acceleration of anthropogenic climate change dramatically altering marine food webs (Estes et al., 2011). Shifts in diet from predominantly fish to a greater dependence on less nutritious prey such as squid have been reported regularly in seabird species over the past 50 years, and have often been attributed to the direct depletion of forage fish by fisheries (see Kowalczyk, Chiaradia, Preston, & Reina, 2014 and references therein). In the case of sooty terns, no commercial fisheries exist for the small, pelagic species typically found in their diet. However, the rapid growth of commercial fisheries for tuna and other large-bodied, predatory species since the 1960s may have caused a similar effect on prey availability through the disruption of foraging associations on which terns depend to locate and catch fish at the surface (Au & Pitman, 1986; Veit & Harrison, 2017).

While many large predatory fish are opportunistic foragers (Cherel, Sabatié, Potier, Marsac, & Ménard, 2007), a large proportion of their diet can comprise fish species (e.g. Dragovich & Potthoff, 1972; Potier et al., 2007) with inevitably other fish species also driven to the surface as they hunt.

According to some estimates, the abundance of large pelagic fish in tropical international waters has declined by ~90% over a 50-year period (Safina, 2003), including substantial reductions in the biomass of surface-schooling tunas such as yellowfin (*Thunnus albacares*) and skipjack (*Katsuwonus pelamis*) in the Atlantic (Cullis-Suzuki & Pauly, 2010; Juan-Jordá et al., 2011). Total nominal catches of these species in the eastern tropical Atlantic (ETROP), where sooty terns from Ascension Island are known to forage extensively (SJR, unpublished data), increased 15-fold since the 1940s, when 0.10 M tonnes were landed, to the 1970s when 1.67 M tonnes were extracted. A peak of 2.04 M tonnes was landed during the 2000s (International Commission for the Conservation of Atlantic Tunas [ICCAT]; https://www.iccat.int/en/accesingdb.HTM; Figure 6a). Note that data for the 2010s were only available to 2014. With fewer sub-surface predators to associate with, terns may have had to rely more heavily on alternative modes such as feeding at night when squid rise to the top of the water column (Ashmole & Ashmole, 1967), or exploiting less mobile prey from lower trophic levels (e.g. invertebrates), as indicated by declines in $\delta^{15}N$ values of feathers (Figures 2b and 3). In addition to reducing the availability of fish prey, declining predator populations may have increased availability of alternative food items that are now more common in the diet of sooty terns (e.g. see Emslie, Polito, & Patterson, 2013). For example, global populations of cephalopods have increased dramatically in the past 60 years (Doubleday et al., 2016) with the loss of their major predators, resulting in foraging terns perhaps now encountering squid far more frequently.

The availability of fish prey to adult seabirds may also be strongly influenced by ocean warming and associated environmental change that can significantly impact their foraging success (e.g. Howells et al., 2017). In the case of sooty terns, changes in diet composition could be mediated through shifts in the range and behaviour of forage fish (Perry et al., 2005), and of the pelagic predators they associate with (e.g. Kitagawa et al., 2000; Hazen et al., 2013). Mean annual sea surface temperature anomaly (SSTa) in the waters surrounding Ascension Island increased by ~0.80ºC from the 1890s to the 2010s, with the biggest increase (by ~0.55ºC) occurring between the 1970s and the 2010s (UK Meterological Office Hadley [HadISST1]; http://www.metoffice.gov.uk/hadobs/hadisst/; Rayner et al., 2003; Figure 6b). It is possible that changes in the distribution or behaviour of forage fish and large marine predators may therefore have occurred as a result of ocean warming, particularly in the last 40 years. There appears to be a strong relationship between declining $\delta^{15}N$ isotopic values of feathers (Figure 2b) and increasing SSTa (Figure 6b) that suggests that birds are responding to changes in prey availability and accessibility in warming foraging areas through changes in diet. However, given the high mobility of sooty terns and their extensive foraging range during inter-breeding periods (Schreiber et al., 2002; SJR, unpublished data), it seems likely that they would have been able to track any regional shifts in distributions of prey or feeding associates.

Given the timescales involved, unravelling the precise causes of the observed dietary shift is likely to be challenging. Applying a similar ‘historical ecology’ approach (e.g. Wu, Liu, Fu, Xu, Li, & Li, 2017) using SIA to other species in Ascension Island’s seabird community that are less dependent on ‘facilitated foraging’ (Maxwell & Morgan, 2013) (e.g. noddies [*Anous* spp.] and tropicbirds [*Phaethon* spp.]) may help to determine the extent to which observed changes have been driven by the disruption of feeding associations as opposed to more general changes in prey availability (Gagne, Hyrenbach, Hagemann, & Van

Houtan, 2018). Nevertheless, it is apparent that a fundamental shift in the diet of sooty terns at Ascension Island has occurred over the past 60 years which most likely has its roots within anthropogenic disturbances to marine food webs over the same period.

4.2 | Can the dietary shift explain population decline?

Undoubtedly invasive species have impacted on the breeding success and demographics of sooty terns on the island (Stonehouse, 1962; Hughes et al., 2017b; Hughes, Dickey, & Reynolds, In press). Domestic cats, black rats (*Rattus rattus*) and common mynas were all introduced to Ascension Island during the eighteenth and nineteenth centuries and depredate incubating adults, chicks and eggs (cats were later eradicated in 2001–2004). However, none of these introductions was coincidental with the apparent population decline of sooty terns (Figure 1), nor is there evidence that populations of these species reached critical levels at around that time. Rats were reported as being highly abundant on the island in 1725 (Ritsema, 2006) but were rarely seen in low-lying areas in the mid-twentieth century (Ashmole, 1963a and other reports), perhaps due to the influence of cats which had been introduced in 1815 to control their numbers. Predation by cats was also a persistent threat to seabirds throughout the nineteenth century during which time many of the island's resident, ground-nesting species were eradicated from the mainland (Stonehouse, 1962). As such, invasive species do not satisfactorily explain the reported collapse in sooty tern numbers during the middle part of the twentieth century and nor is it straightforward to estimate their relative impacts.

The link between diet and breeding success has been well established in numerous seabird species (e.g. see Kowalczyk et al., 2014 and references therein), particularly with regard to the lipid/energetic content (Wanless, Harris, Redman, & Speakman, 2005). With reduced teleost fish consumption, terns have had to rely on an increasingly low quality diet of squid and invertebrates which is considerably lower in lipid and may often fail to meet energetic demands of breeding. Limited data are available on the breeding success of sooty terns prior to their population collapse but years of low productivity have occurred (Ashmole, 1963a) and years of high breeding success still occur now (Hughes, 2014). Variation in food availability and breeding success is typical in seabirds, and most of these long-lived species are able to survive recruitment gaps or occasional breeding failures linked to environmental stochasticity. However, Cury et al. (2011) identified a threshold in prey availability (corresponding to ~$^1/_3$ of maximum biomass) beyond which seabird breeding success is consistently compromised, potentially precipitating population collapses such as those experienced on Ascension Island and elsewhere.

It is noteworthy that while populations of many pelagic predators have continued to decline in recent decades (Cullis-Suzuki & Pauly, 2010) and ocean warming has continued to accelerate, this trend has not been paralleled by a sustained decline in numbers of sooty terns as might be expected if it was wholly attributable to an environmentally-mediated shift in diet. Instead, the tern population has apparently stabilised in size (Figure 1). Conservation measures on the breeding grounds such as the eradication of feral domestic cats from Ascension Island in 2002 (Ratcliffe et al., 2010) have likely promoted adult and chick survival and may have offset pressures on food availability. It is also possible that the population has reached a new, reduced carrying capacity that can be maintained within the altered marine food web. So-called ‘regime shifts’ between alternative stable states are a common feature of marine ecosystems (deYoung et al., 2008) and can be triggered by climate events and over-fishing of top predators resulting in system-wide trophic cascades (Daskalov, Grishin, Rodionov, & Mihneva, 2007; deYoung et al., 2008). Our results suggest that the historical sooty tern population decline on Ascension Island may be at least partly explained by a fundamental change in diet over the same period driven by ecosystem-wide changes affecting the tropical Atlantic (Ostrom et al., 2017).

4.3 | Implications for marine conservation

Seabirds represent key bio-indicators of marine ecosystem status (Furness & Greenwood, 1993), and sooty terns are no exception. Their steep population decline over approximately the last 30 years on Ascension Island is mirrored to a lesser extent elsewhere in their range (reviewed in Hughes et al., 2017a). These declines are indicative of a widespread and consistent pressure on the ecology of the species as evidenced in the long-term dietary shift in our dataset. Indeed, similar long-term dietary shifts have been reported in various seabirds (e.g. Hilton et al., 2006; Wiley et al., 2013), often associated with population decline (e.g. Hilton et al., 2006), suggesting that our findings are symptomatic of wider pressures impacting marine ecosystems. The close correspondence between historical shifts in the diet and population status of sooty terns, and the expansion of industrial fisheries into the areas where they forage serves to highlight further the potentially cascading impacts of predatory fish depletion for marine ecosystem function and adds further urgency to the need to secure sustainable fisheries for these species. The announcement of a large-scale marine reserve to be designated in the waters surrounding Ascension Island by 2019 may go some way to improving the status of our study population. However, given the wide distribution and considerable mobility of both sooty terns and of the species with which they associate, it is likely that ocean-scale solutions will be needed to reinstate past food webs and reverse historical declines.

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Tables

TABLE 1 Summary table of linear mixed-effect models (LMMs) explaining trends in carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) isotopic values of feathers from sooty terns sampled from decades within two periods before (1890s–1940s) and after (1970s–2010s) their population collapse on Ascension Island in the South Atlantic

	Estimate	**SE**	$F_{(5,120)}$	***p* value**
$\delta^{13}C$				
Decade	-0.43	0.13	4.19	.04
Decade × Period	-0.14	0.07	7.50	.01
$\delta^{15}N$				
Decade	-0.38	0.19	11.32	.002
Decade × Period	-0.10	0.03	6.16	.02

Figure captions

FIGURE 1 Estimated numbers (+ 95% confidence limits) of sooty terns breeding on Ascension Island in the South Atlantic from 29 censuses that took place before (three predators; filled bars) and after (two predators; open bars) the cat eradication programme. Note that spaces have been inserted between the bars on the left to highlight the irregularity of censuses. Note also that the sub-annual breeding cycle results in birds breeding twice in 1996, 2004, 2008 and 2012 when two censuses took place

FIGURE 2 Box and whisker plots showing (a) carbon ($\delta^{13}C$) and (b) nitrogen ($\delta^{15}N$) isotopic values (median, 25–75% inter-quartile range, non-outlier range and outliers) of feathers from sooty terns breeding on Ascension Island in the South Atlantic in different decades (see text for further details). The $\delta^{13}C$ values are corrected for the 'Suess Effect' following Hilton et al. (2006). Sample sizes of birds are indicated within brackets. In both plots the grey shading represents the transition between before and after the population collapse of the Ascension Island sooty tern population (Hughes et al., 2017a)

FIGURE 3 Bivariate plots of $\delta^{15}N$ against $\delta^{13}C$ demonstrating the isotopic niche areas reconstructed from SIA of feathers from sooty terns breeding on Ascension Island in the South Atlantic in decades before (1890s–1940s) and after (1970s–2010s) their population collapse (Hughes et al., 2017a). The Standard Ellipse Areas corrected for small sample size (SEA_Cs) are represented by the solid lines (see Parnell et al., 2013 for more details on these metrics of isotopic niche width based on SIA)

FIGURE 4 Stable isotope bi-plot of carbon-nitrogen (mean ± 1 SD) showing the isotopic values of the four main prey groups in the diet of sooty terns from Ascension Island in the South Atlantic: teleost fish species (false halfbeaks, blue flying fishes, redlip blennies and Simony's frostfishes), squid (Teuthida), marine invertebrates (Sally Lightfoot crabs and violet sea snails), and terrestrial invertebrates (locust species) (see Figure S1)

FIGURE 5 Estimated contributions of each of the four prey groups (teleost fish species [false halfbeaks, blue flying fishes, redlip blennies and Simony's frostfishes], squid [Teuthida], marine invertebrates [Sally Lightfoot crabs and violet sea snails], and terrestrial invertebrates [locust species]; see Figure S1) to the diet of sooty terns breeding on Ascension Island in the South Atlantic in decades (a) before (1890s–1940s) and (b) after (1970s–2010s) their population collapse (Hughes et al., 2017a). Contributions are presented by dietary proportions as calculated with SIAR (95, 75 and 50% credibility intervals) using $\delta^{13}C$ and $\delta^{15}N$ values of adult contour feathers and of their main prey

FIGURE 6 (a) Historical trends in tuna catches (in millions of tonnes [t]) in the east tropical Atlantic Ocean (see https://www.iccat.int/en/accesingdb.HTM for further details), and (b) mean (+ 1 SD) sea surface temperature anomaly (SSTa) within a 1,000 km buffer surrounding Ascension Island (data retrieved from http://www.metoffice.gov.uk/hadobs/hadisst/). In both plots the grey shading represents the transition between before and after the population collapse of the Ascension Island sooty tern population (Hughes et al., 2017a). During the collapse there was a 15-fold increase in skipjack and yellowfin tuna catches for the eastern tropical Atlantic region in the 1970s and a five-fold increase in the average SSTa until the 2010s

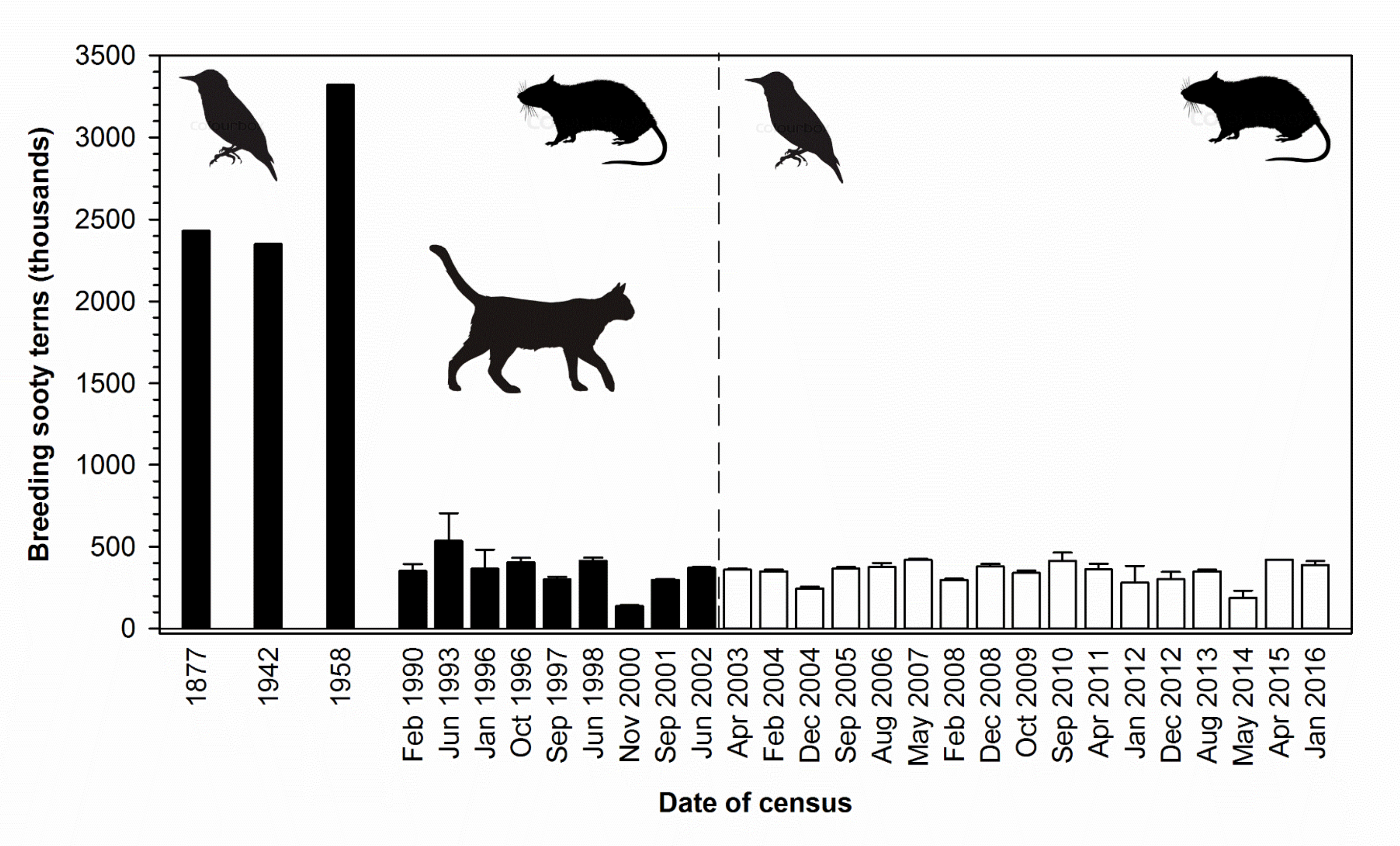

Breeding sooty terns (thousands)
3500
3000
2500
2000
1500
1000
500
0
1877
1942
1958
Feb 1990
Jun 1993
Jan 1996
Oct 1996
Sep 1997
Jun 1998
Nov 2000
Sep 2001
Jun 2002
Apr 2003
Feb 2004
Dec 2004
Sep 2005
Aug 2006
May 2007
Feb 2008
Dec 2008
Oct 2009
Sep 2010
Apr 2011
Jan 2012
Dec 2012
Aug 2013
May 2014
Apr 2015
Jan 2016
Date of census

Figure 1.

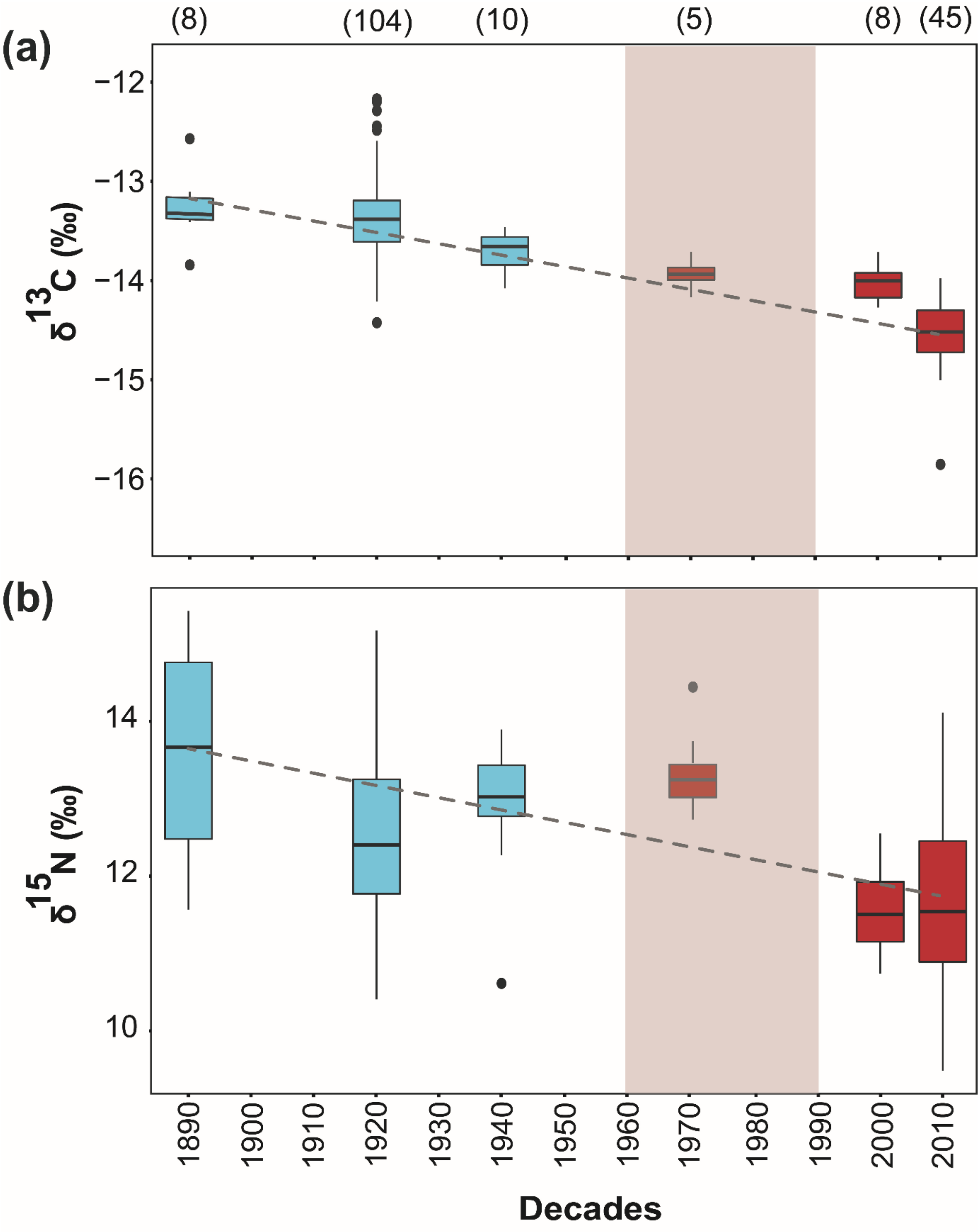
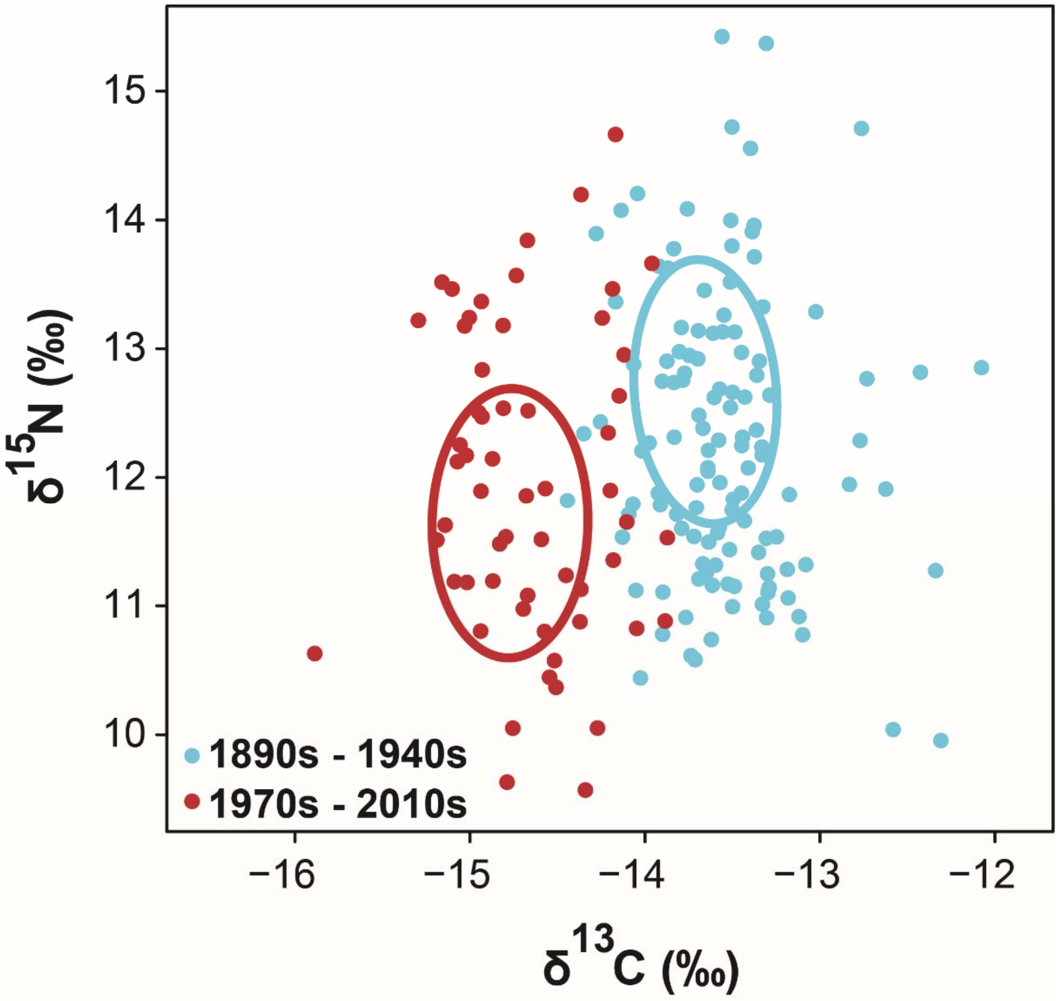
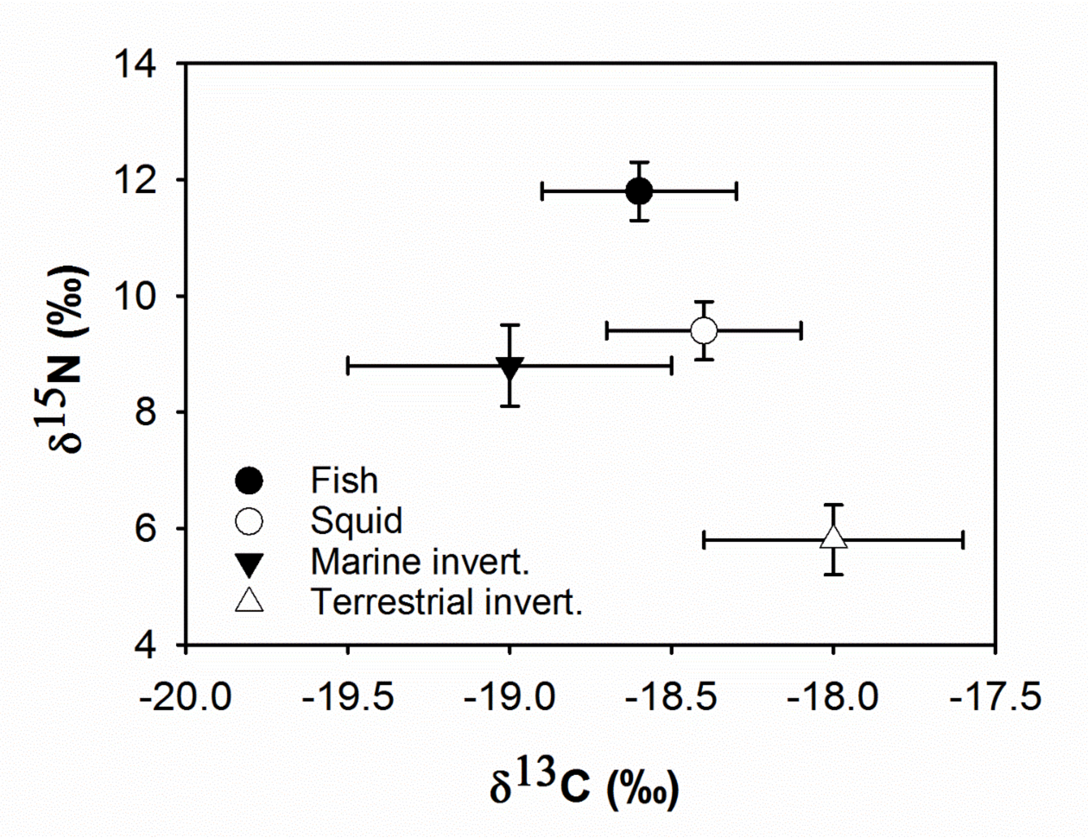

(a)
(8)
(104)
(10)
(5)
(8)
(45)
−12
−13
−14
−15
−16
δ13C (‰)
(b)
14
12
10
δ15N (‰)
1890
1900
1910
1920
1930
1940
1950
1960
1970
1980
1990
2000
2010
Decades

Figure 2.



15
14
13
12
11
10
$\delta^{15}N$ (‰)
● 1890s - 1940s
● 1970s - 2010s
−16
−15
−14
−13
−12
$\delta^{13}C$ (‰)

Figure 3.



808

809 **Figure 4.**

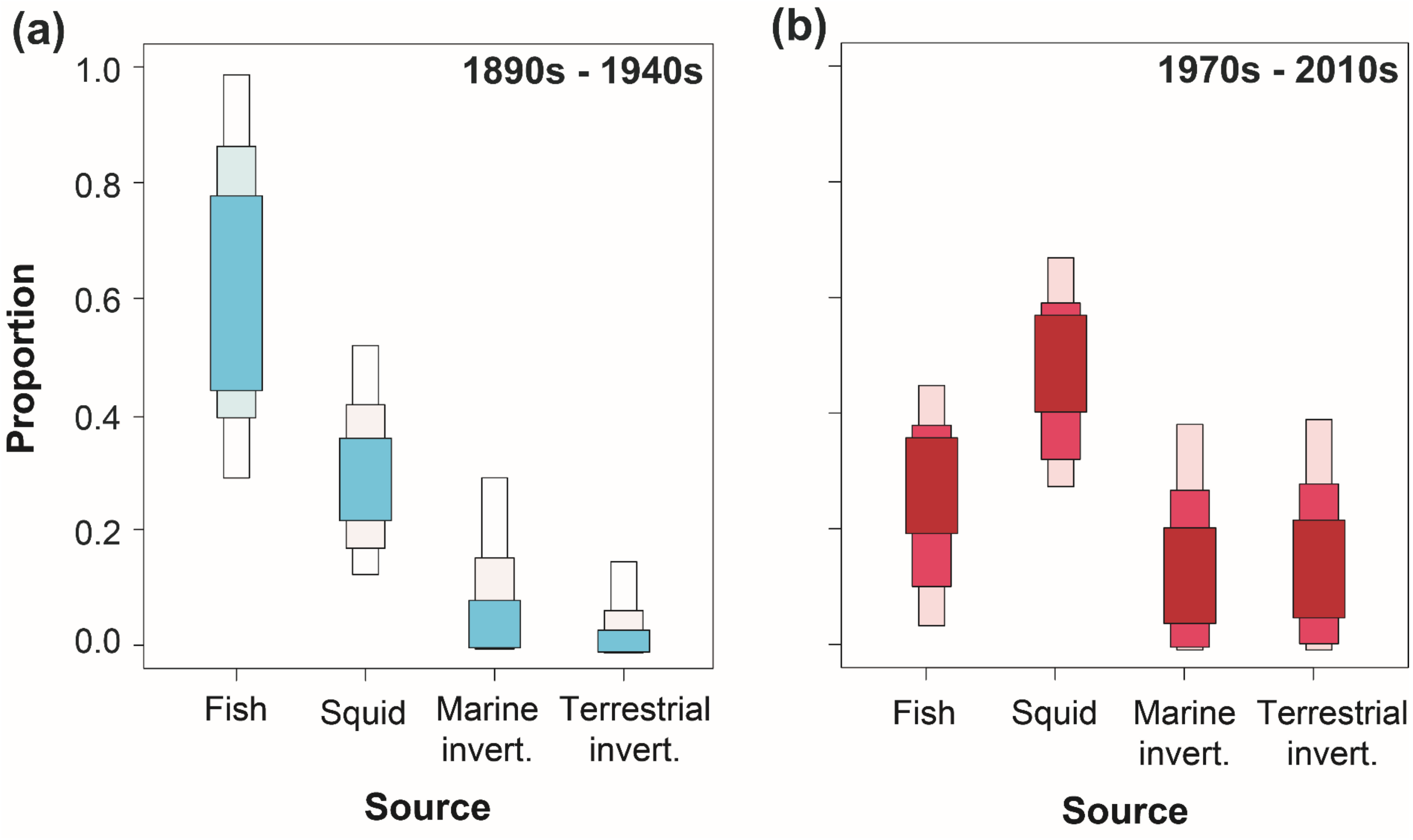

(a)
1890s - 1940s
Proportion
1.0
0.8
0.6
0.4
0.2
0.0
Fish
Squid
Marine invert.
Terrestrial invert.
Source
(b)
1970s - 2010s
Fish
Squid
Marine invert.
Terrestrial invert.
Source

Figure 5.

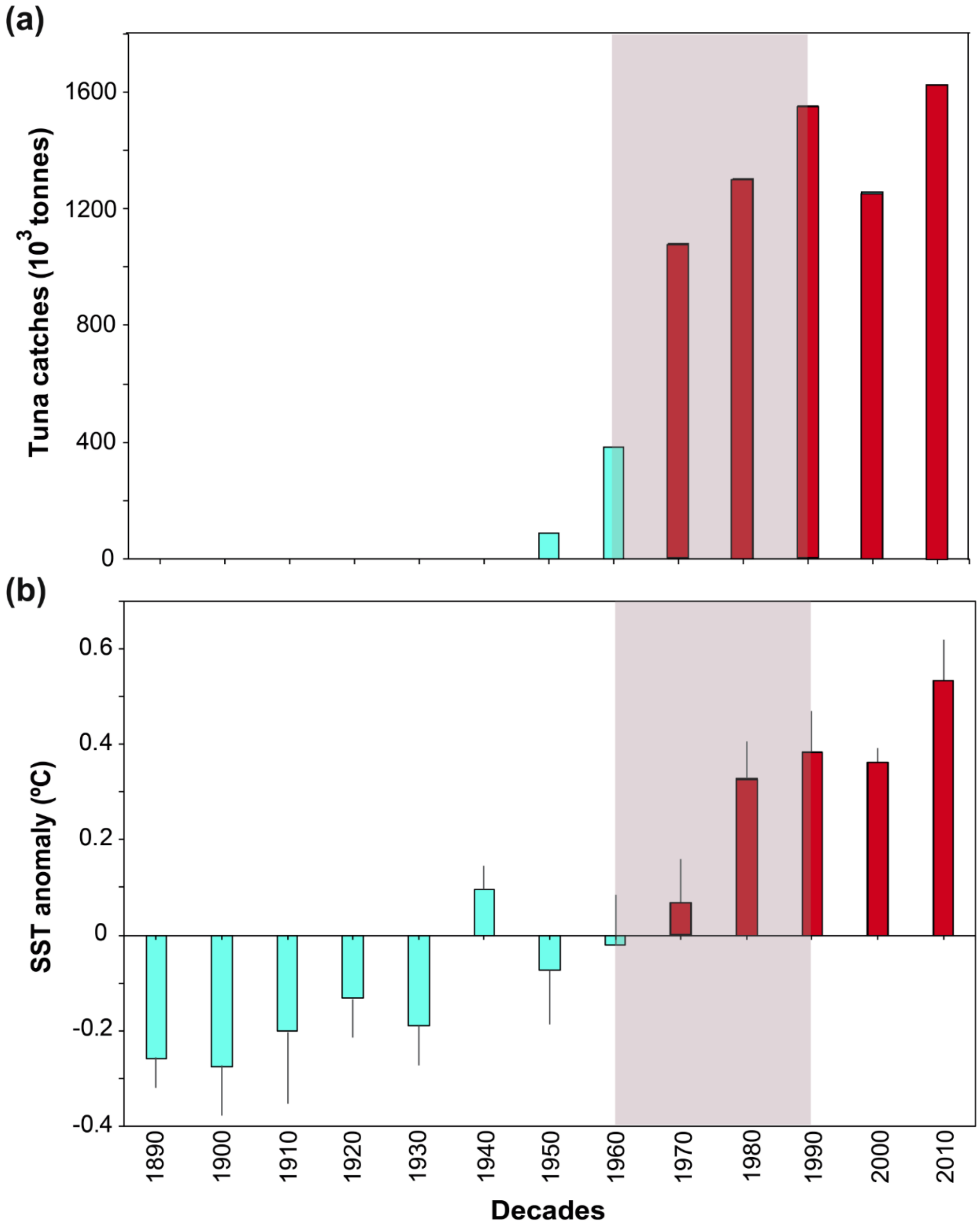

(a)
Tuna catches (10^3 tonnes)
0
400
800
1200
1600
(b)
SST anomaly (ºC)
-0.4
-0.2
0
0.2
0.4
0.6
1890
1900
1910
1920
1930
1940
1950
1960
1970
1980
1990
2000
2010
Decades

Figure 6.

Supporting information

TABLE S1 Details of museums and their curators who assisted with initial enquiries about specimens of sooty tern skins collected from Ascension Island in the South Atlantic

Name of museum	Location	Name(s) of curator(s)
American Museum of Natural History	New York, NY, USA	Mary LeCroy, Merle Okada, Paul Sweet, and Tom Trombone
Australian Museum	Sydney, NSW, Australia	Walter Boles
Bombay Natural History Society	Mumbai, India	Rahul Khot
Conner Museum	Washington State University, Pullman, WA, USA	Kelly Cassidy
Delaware Museum of Natural History	Wilmington, DE, USA	Jean Woods
Denver Museum of Nature & Science	Denver, CO, USA	Jeff Stephenson
Florida Museum of Natural History	Gainesville, FL, USA	Dave Johnston and Tom Webber
Great North Museum-Hancock Collection	Newcastle upon Tyne, UK	Dan Gordon
Fundación Miguel Lillo	Tucumán, Argentina	Ada Echevarria
Instituto Nacional de Pesquisas da Amazônia	Manaus, Brasil	Mario Cohn-Haft
Museum of Comparative Zoology	Harvard Museum, Boston, MA, USA	Alison Pirie and Jeremiah Trimble
Museum of Natural Science	Jackson, MS, USA	Nick Winstead
Museum of Natural Science	Louisiana State University, Baton Rouge, LA, USA	Steve Cardiff and James van Remsen
National Museum of Ireland-Natural History Division	Dublin, Ireland	Nigel Monaghan
National Museum of Natural History-Collection of Birds	Paris, France	Jérôme Fuchs and Marie Portas
National Museums Liverpool	Liverpool, UK	Tony Parker
National Museums Scotland	Edinburgh, UK	Bob McGowan
Natural History Museum-Bird Group	Tring, UK	Mark Adams and Robert Prys-Jones
Natural History Museum of Denmark	Copenhagen, Denmark	Jon Fjeldså
Natural History Museum of Los Angeles County	Los Angeles, CA, USA	Kimball Garrett
Natural History Museum-University of Oslo	Oslo, Norway	Jan Lifjeld
Oxford University Museum of Natural History	Oxford, UK	Malgosia Nowak-Kemp
Peabody Museum of Natural History	Yale University, New Haven, CT, USA	Rick Prum and Kristof Zyskowski
Royal Museum for Central Africa	Tervuren, Belgium	Alain Reygel

Royal Ontario Museum-Department of Natural History (Ornithology)	Toronto, ON, Canada	Allan Baker and Mark Peck
Smithsonian Institution-Division of Birds	Washington DC, USA	Christina Gebhard, Chris Milensky, and Storrs Olson
Swedish Museum of Natural History	Stockholm, Sweden	Per Ericson and Ulf Johansson
Western Australian Museum	Welshpool, WA, Australia	Ron Johnstone
Zoological Institute	Russian Academy of Sciences, St Petersburg, Russia	Vladimir Loskot

TABLE S2 Details of contour feathers of sooty terns breeding on Ascension Island in the South Atlantic between the 1890s and the 2010s. Sources: AMNH – American Museum of Natural History, New York, NY, USA; BJH – B. John Hughes; CPW – Colin P. Wearn; Flor. Mus. Nat. Hist. – Florida Museum of Natural History, Gainesville, FL, USA; Hancock – Great North Museum-Hancock Collection, Newcastle upon Tyne, UK; Mus. Nat. Sci. LSU – Museum of Natural Science, Louisiana State University, Baton Rouge, LA, USA; Nat. Mus. Liverpool – National Museums Liverpool, Liverpool, UK; Nat. Mus. Scotland – National Museums Scotland, Edinburgh, UK; NHM Tring – Natural History Museum-Bird Group, Tring, UK; NMNH Paris – National Museum of Natural History-Collection of Birds, Paris, France; Peabody – Peabody Museum of Natural History, Yale University, New Haven, CT, USA; SJR – S. James Reynolds; and Smithsonian – Smithsonian Institution-Division of Birds, Washington DC, USA

Sample number	**Source**	**Catalogue number**	**Decade of collection**
1	Hancock	B020.71	1890
2	Nat. Mus. Scotland	NMS.Z.1956.3 (3161)	1890
3	NHM Tring	2012.102.1	1890
4*	NHM Tring	1880.11.18.707	–
5	Smithsonian	USNM118379	1890
6	Smithsonian	USNM118380	1890
7	Smithsonian	USNM118381	1890
8	NHM Tring	1894.10.28.7	1890
9	NHM Tring	1899.1.4.19	1890
10*	NHM Tring	1899.1.4.20	–
11*	NMNH Paris	–	–
12*	Nat. Mus. Liverpool	–	–
13*	NHM Tring	1922.12.6.49	–
14*	NHM Tring	1922.12.6.50	–
15	Peabody	YPM44863	1920
16	Peabody	YPM44864	1920
17	Peabody	YPM44865	1920
18	Peabody	YPM44866	1920
19	Peabody	YPM44868	1920
20	Peabody	YPM44869	1920
21	Peabody	YPM44870	1920
22	Peabody	YPM44871	1920
23	Peabody	YPM44872	1920
24	Peabody	YPM44873	1920

25	Peabody	YPM44874	1920
26	Peabody	YPM44875	1920
27	Peabody	YPM44876	1920
28	Peabody	YPM44877	1920
29	Peabody	YPM44878	1920
30	Peabody	YPM44879	1920
31	Peabody	YPM44888	1920
32	Peabody	YPM44889	1920
33	Peabody	YPM44890	1920
34	Peabody	YPM44891	1920
35	Peabody	YPM44892	1920
36	Peabody	YPM44893	1920
37	Peabody	YPM44894	1920
38	Peabody	YPM44895	1920
39	Peabody	YPM44896	1920
40	Peabody	YPM44897	1920
41	Peabody	YPM44898	1920
42	Peabody	YPM44899	1920
43	Peabody	YPM44901	1920
44	Peabody	YPM44902	1920
45	Peabody	YPM44903	1920
46	Peabody	YPM44904	1920
47	Peabody	YPM44905	1920
48	Peabody	YPM44906	1920
49	Peabody	YPM44907	1920
50	Peabody	YPM44908	1920
51	Peabody	YPM44909	1920
52	Peabody	YPM44921	1920
53	Peabody	YPM44922	1920
54	Peabody	YPM44923	1920
55	Peabody	YPM44924	1920
56	Peabody	YPM44925	1920
57	Peabody	YPM44934	1920
58	Peabody	YPM44935	1920
59	Peabody	YPM44936	1920
60	Peabody	YPM44937	1920
61	Peabody	YPM44938	1920
62	Peabody	YPM44939	1920
63	Peabody	YPM44940	1920
64	Peabody	YPM44941	1920
65	Peabody	YPM44942	1920
66	Peabody	YPM44943	1920
67	Peabody	YPM44944	1920
68	Peabody	YPM44945	1920
69	Peabody	YPM44946	1920
70	Peabody	YPM44947	1920
71	Peabody	YPM44948	1920
72	Peabody	YPM44949	1920
73	Peabody	YPM44950	1920
74	Peabody	YPM44951	1920
75	Peabody	YPM44952	1920
76	Peabody	YPM44953	1920
77	Peabody	YPM44954	1920
78	Peabody	YPM44955	1920
79	Peabody	YPM44956	1920

80	Peabody	YPM44967	1920
81	Peabody	YPM44968	1920
82	Peabody	YPM44969	1920
83	Peabody	YPM44970	1920
84	Peabody	YPM44971	1920
85	Peabody	YPM44972	1920
86	Peabody	YPM44973	1920
87	Peabody	YPM44974	1920
88	Peabody	YPM44975	1920
89	Peabody	YPM44976	1920
90	Peabody	YPM44977	1920
91	Peabody	YPM44978	1920
92	Peabody	YPM44981	1920
93	Peabody	YPM44982	1920
94	Peabody	YPM44983	1920
95	Peabody	YPM44984	1920
96	Peabody	YPM44985	1920
97	AMNH	269206	1920
98	AMNH	269227	1920
99	AMNH	269226	1920
100	AMNH	269225	1920
101	AMNH	269224	1920
102	AMNH	269223	1920
103	AMNH	269222	1920
104	AMNH	269221	1920
105	AMNH	269220	1920
106	AMNH	269219	1920
107	AMNH	269218	1920
108	AMNH	269217	1920
109	AMNH	269216	1920
110	AMNH	269215	1920
111	AMNH	269214	1920
112	AMNH	269213	1920
113	AMNH	269212	1920
114	AMNH	269211	1920
115	AMNH	269210	1920
116	AMNH	269209	1920
117	AMNH	269208	1920
118	AMNH	269207	1920
119	AMNH	308427	1940
120	AMNH	308426	1940
121	AMNH	308425	1940
122	AMNH	308424	1940
123	AMNH	308423	1940
124	AMNH	308422	1940
125	AMNH	308421	1940
126	AMNH	308428	1940
127	AMNH	308429	1940
128*	Mus. Nat. Sci. LSU	LSUMZ73125	–
129	NHM Tring	1962.42.2	1940
130	Smithsonian	USNM534287	1970
131	Smithsonian	USNM534285	1970
132	Smithsonian	USNM534286	1970
133	Smithsonian	USNM534288	1970
134	Flor. Mus. Nat. Hist.	UF37533	1970

135	BJH	09Aug2006.1	2000
136	BJH	09Aug2006.2	2000
137	BJH	09Aug2006.3	2000
138	BJH	09Aug2006.4	2000
139	BJH	09Aug2006.5	2000
140	BJH	09Aug2006.6	2000
141	BJH	09Aug2006.7	2000
142	BJH	09Aug2006.8	2000
143	CPW/SJR	8Jan2012.1	2010
144	CPW/SJR	8Jan2012.2	2010
145	CPW/SJR	8Jan2012.3	2010
146	CPW/SJR	8Jan2012.4	2010
147	CPW/SJR	8Jan2012.5	2010
148	CPW/SJR	8Jan2012.6	2010
149	CPW/SJR	8Jan2012.7	2010
150	CPW/SJR	8Jan2012.8	2010
151	CPW/SJR	8Jan2012.9	2010
152	CPW/SJR	8Jan2012.10	2010
153	CPW/SJR	8Jan2012.11	2010
154	CPW/SJR	8Jan2012.12	2010
155	CPW/SJR	8Jan2012.13	2010
156	CPW/SJR	8Jan2012.14	2010
157	CPW/SJR	8Jan2012.15	2010
158	CPW/SJR	8Jan2012.16	2010
159	CPW/SJR	8Jan2012.17	2010
160	CPW/SJR	8Jan2012.18	2010
161	CPW/SJR	8Jan2012.19	2010
162	CPW/SJR	8Jan2012.20	2010
163	CPW/SJR	8Jan2012.21	2010
164	CPW/SJR	8Jan2012.22	2010
165	CPW/SJR	8Jan2012.23	2010
166	CPW/SJR	8Jan2012.24	2010
167	CPW/SJR	8Jan2012.25	2010
168	CPW/SJR	4Dec2012.21	2010
169	CPW/SJR	4Dec2012.22	2010
170	CPW/SJR	4Dec2012.23	2010
171	CPW/SJR	4Dec2012.24	2010
172	CPW/SJR	4Dec2012.25	2010
173	CPW/SJR	4Dec2012.26	2010
174	CPW/SJR	4Dec2012.27	2010
175	CPW/SJR	4Dec2012.28	2010
176	CPW/SJR	4Dec2012.29	2010
177	CPW/SJR	4Dec2012.30	2010
178	CPW/SJR	4Dec2012.31	2010
179	CPW/SJR	4Dec2012.32	2010
180	CPW/SJR	4Dec2012.33	2010
181	CPW/SJR	4Dec2012.34	2010
182	CPW/SJR	4Dec2012.35	2010
183	CPW/SJR	4Dec2012.36	2010
184	CPW/SJR	4Dec2012.37	2010
185	CPW/SJR	4Dec2012.38	2010
186	CPW/SJR	4Dec2012.39	2010
187	CPW/SJR	4Dec2012.40	2010

*Samples omitted from subsequent statistical analyses as they yielded outlying $\delta^{13}C$ and $\delta^{15}N$ values even after processing multiple replicates through stable isotope analysis (SIA)

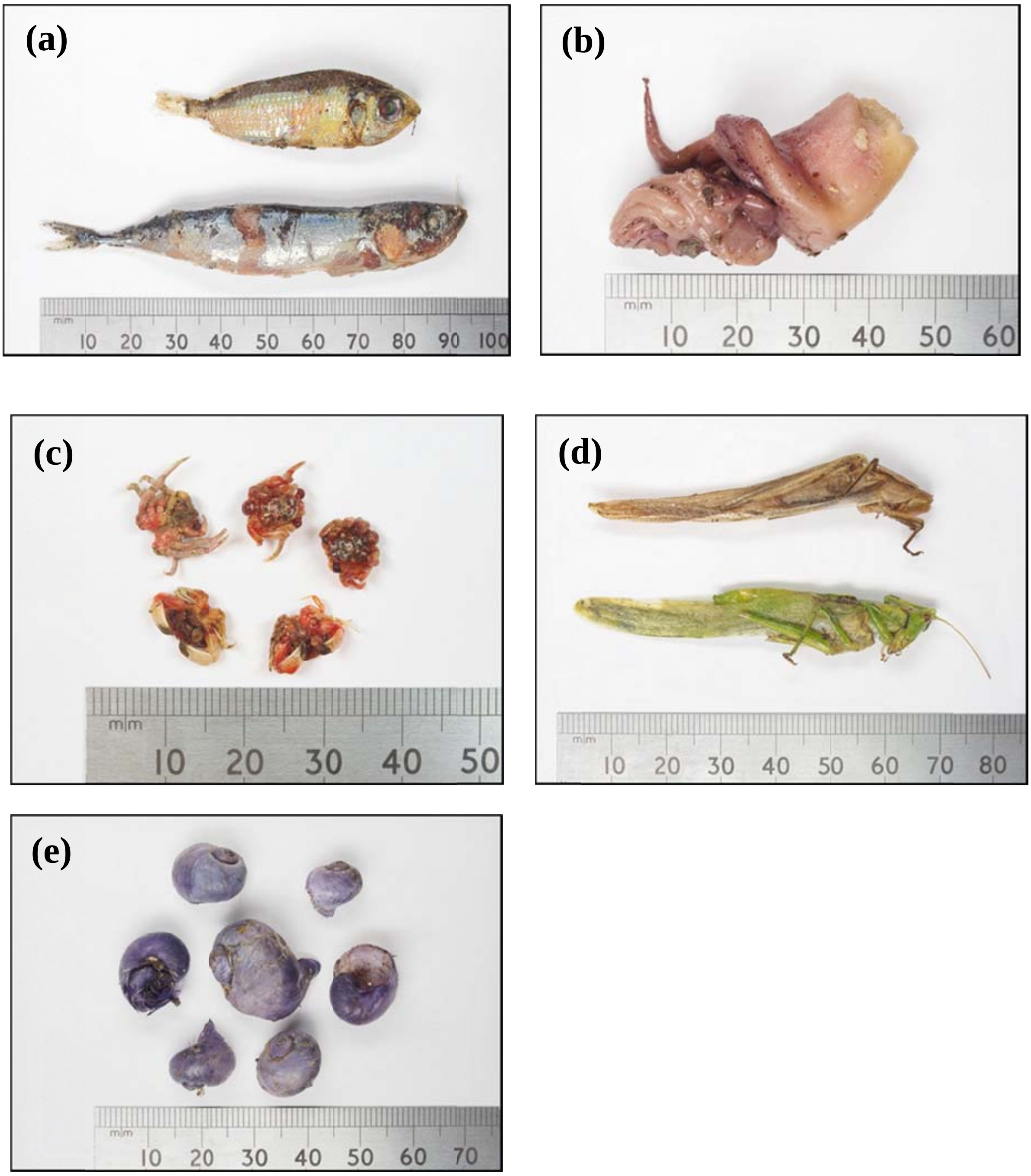


FIGURE S1 Diet items (from regurgitations) of breeding sooty terns on Ascension Island in the South Atlantic collected during ringing in December 2012. (a) Teleost fish, (b) squid (Teuthida), (c) megalops of Sally Lightfoot crabs, (d) locusts, and (e) violet sea snails. (Photos: N. Day)