



## Original Article

# Change in the North Sea ecosystem from the 1970s to the 2010s: great skua diets reflect changing forage fish, seabirds, and fisheries

Gabriella E. Church<sup>1</sup>, Robert W. Furness<sup>2</sup>, Glen Tyler<sup>3</sup>, Lucy Gilbert<sup>2</sup>, and Stephen C. Votier<sup>1\*</sup>

<sup>1</sup>Centre for Life and Environmental Sciences, School of Biosciences, Environment & Sustainability Institute, University of Exeter, Cornwall Campus, Penryn, Cornwall TR10 9EZ, UK

<sup>2</sup>College of Medical, Veterinary and Life Sciences, University of Glasgow, Glasgow G12 8QQ, UK

<sup>3</sup>Coastal and Marine Ecosystems & Use, Scottish Natural Heritage, Ground Floor, Stewart Building, Alexandra Wharf, Lerwick, Shetland ZE1 0LL, UK

\*Corresponding author: tel: +44 1326 259416; e-mail: [s.c.votier@exeter.ac.uk](mailto:s.c.votier@exeter.ac.uk).

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Understanding anthropogenic impacts are crucial to maintain marine ecosystem health. The North Sea has changed in recent decades, largely due to commercial fishing and climate change. Seabirds can act as useful indicators of these changes. By analyzing  $n = 20\,013$  pellets and  $n = 24\,993$  otoliths regurgitated by great skuas *Stercorarius skua* in northern Scotland over five decades from the 1970s to the 2010s (in 36 years 1973–2017), we reveal how the diet of this top predator has changed alongside the changing North Sea ecosystem. Sandeels *Ammodytes* spp. were the most common dietary item during the 1970s, but became virtually absent from the 1980s onward. Discarded whitefish dominated skua diets from the 1980s to the present day, despite long-term declines in North Sea discard production. However, the discarded fish eaten by great skuas has become smaller and the species composition changed. Skua pellets only rarely contained avian prey in the 1970s but this increased during the 1980s, and fluctuated between 10% and 20% from the 1990s to 2010s. There have also been changes in the avian prey in the diet—black-legged kittiwakes *Rissa tridactyla* generally being replaced by auks *Alcid* spp. and northern fulmars *Fulmarus glacialis*. The Shetland marine ecosystem has experienced steep declines in sandeel stocks and in seabirds that feed on them. Great skuas have been able to prey switch to respond to this change, supported by abundant discards, enabling them to maintain a favourable population status while other seabird species have declined.

**Keywords:** climate, diet, ecosystems, fisheries, indicators, seabirds.

## Introduction

Anthropogenic perturbations, most notably commercial fisheries and climate change, have fundamentally altered marine ecosystems (Halpern *et al.*, 2008). Fisheries have led to the degradation or loss of natural habitat, reduced species richness and abundance, altered species assemblages, and modified food webs (Jackson *et al.*, 2001; Myers and Worm, 2003; Lotze *et al.*, 2006). Anthropogenic greenhouse gas production has led to ocean acidification, rising sea temperatures, changing wind conditions, and

increasing ultraviolet light exposure (Halpern *et al.*, 2008; Hoegh-Guldberg and Bruno, 2010). These changes have led to shifts in species distributions, altered food web dynamics, and decreased ocean productivity (Hoegh-Guldberg and Bruno, 2010). Understanding the full extent of the ecological consequences of human actions is therefore a crucial aspiration in marine ecology (Halpern *et al.*, 2008; Crain *et al.*, 2009).

The North Sea has not been immune to climate and fisheries-related effects (Halpern *et al.*, 2008), leading to a suite of

profound ecological changes in recent decades (Heath, 2005; Dulvy et al., 2008). For example, the North Sea underwent a regime shift during the mid-1980s as the dominant boreal-adapted copepods were replaced by warm-temperature species; a consequence of warmer waters and altered wind regimes (Beaugrand, 2004). This led to a 70% decrease in zooplankton overall biomass since 1960 (Beaugrand, 2004), with knock-on consequences for sandeels *Ammodytes* spp.—the most important forage fish in the region—with a reduction in overall biomass and a loss in lipid content (Arnott and Ruxton, 2002; Wanless et al., 2004). This in turn has had negative consequences for upper trophic level consumers such as seabirds and marine mammals, which were previously reliant on the large biomass and high lipid content characteristics of these fish (Wanless et al., 2005; Frederiksen et al., 2006; MacLeod et al., 2007). As a consequence, seabird species previously reliant on sandeels declined to their lowest levels since systematic recording began (Cook et al., 2014; JNCC, 2013). Nevertheless, seabird species differences in their ability to find alternative foods mean effects have been uneven across taxa, leading to changes in seabird community structure (Mitchell et al., 2004). The North Sea is one of the most heavily fished areas in the world (Frid et al., 2000; Daan et al., 2005). Fish extraction has resulted in a reduction in the average size of fish (Daan et al., 2005), and there has been a switch toward smaller-bodied southern fish species as boreal fish species also shift their range northward (Perry et al., 2005). Moreover, several decades of policy change enabling discarding of undersize, unwanted, and over quota fish has led to a reduction in overall seabird species diversity, altered predator–prey dynamics and favoured some scavenging seabird species (Catchpole et al., 2005; Bicknell et al., 2013). However, changes to the way in which fisheries manage discarding in the North Sea are underway. Currently there is a phased discard ban (also called the landing obligation) as part of reform to the EU Common Fisheries Policy (CFP). The ban prohibits the discarding of quota fish, being phased-in over the period 2015–2019. Prior to the discard ban, fisheries in the North Sea generated over 13% of the total estimated global discards, despite only covering 0.2% of the global ocean area. Therefore the impact of this change in discarding is likely to be particularly profound in the North Sea (Kelleher, 2005; Diamond and Beukers-Stewart, 2011; Bicknell et al., 2013; Sarda et al., 2015). The aim of the current study is to determine how changes since the 1970s in forage fish, seabird communities and discards in the North Sea are reflected in the diet of a marine top predator, the great skua *Stercorarius skua*.

Seabirds are useful indicators of marine ecosystem changes across various spatial and temporal scales (Cairns, 1988; Piatt et al., 2007; Durant et al., 2009; Moreno et al., 2016). To quantify the influence of change on seabird populations, many studies focus on demographic rates such as survival (e.g. Sandvik et al., 2005; Votier et al., 2008b), breeding performance (e.g. Cury et al., 2011; Sherley et al., 2018), and chick condition (Sherley et al., 2018), but such parameters may be relatively insensitive to change because seabirds are long-lived and have bet-hedging life histories (Dobson and Jouventin, 2007). Moreover, for generalist consumers that are able to switch between wide varieties of different prey, a more temporally sensitive indicator of change is dietary variation. Great skuas are dietary generalists at the population level and foraging specialists at the individuals level (Votier et al., 2004b, c). They are top predators in marine food webs, feeding extensively on discards, as well as sandeels, seabirds, and

terrestrial mammals (Votier et al., 2004a,b,c). The objective of the current study is to determine how great skua diet has changed over 36 years from 1973 to 2017. To determine the nature and magnitude of changes the study specifically aims to show how skua diets represented by regurgitated pellets have changed in terms of: (1) the proportions of the main prey types (discarded fishes, sandeels, seabirds, and other prey); (2) the species composition and size of discarded fish; and (3) the type of seabirds eaten. We also provide long-term abundance estimates of discards, sandeels, and seabirds to contextualize these changes. Together this will provide insight into the changing diet of a marine predator over a period of profound changes in the North Sea ecosystem.

## Material and methods

### Study site, diet sampling and characterising the changing prey base

Data were collected from the largest great skua colony in the world, on Foula, Shetland, UK (60°08'N, 2°05'W), which supported ~2293 breeding pairs during 1998–2002 (Mitchell et al., 2004), representing ~24% of the UK (~9600 pairs) and ~14% of the global population (~16 000 pairs) of this species. Diet was sampled via analysis of regurgitated pellets of indigestible prey. These were collected from breeding territories and non-breeding club sites during June and July over 36 years between 1973 and 2017.

Prey items were identified to the lowest possible taxon, before being broken down or removed to prevent resampling. Most pellets comprised a single prey item but where more than one prey item was present, we recorded all prey items to provide a frequency of occurrence. Pellets were identified to the lowest possible taxon based on features outlined in Furness (1997) and Votier et al. (2003) (see below for more details). Sampling ensured a broadly representative coverage of the whole colony, since the prey types tend not to be evenly distributed within colonies due to individual foraging specialization (Votier et al., 2004a, b, 2007, 2008a). Breeding skuas aggressively defend their territory, and this behaviour was used to delineate territory boundaries. Pellets were located by thoroughly and systematically searching territories, however pellets tended to be concentrated at one or more sitting places (usually on a high mound within the territory, often characterized by short green grass fertilized by skua excreta), as well as around wet ditches and pools where skuas drink. In some instances repeat sampling of the same territories occurred both within (approximately every 3–7 days) and among years. Pellets were also sampled from “club sites” where groups of up to ~100 non-breeding individuals gather to roost and bathe (Klomp and Furness, 1990). We pooled data from breeding territories and club sites to increase our sample size and also because there was a strong degree of concordance between the two (Votier et al., 2008a).

### Four main prey types

In order to assess temporal trends in the main prey types (whitefish, seabirds, sandeels, and others), we collected pellets during 36 years between 1973 and 2017.

### Fish prey in the diet

During 25 years from 1975 to 2017, fish sagittal otoliths found in regurgitated pellets were retained for identification by

comparison with photographs and diagrams (with the following species identified: haddock *Melanogrammus aeglefinus*, blue whiting *Micromesistius poutassou*, Atlantic cod *Gadus morhua*, Norway pout *Trisopterus esmarkii*, deep-sea redfish *Sebastes mentella*, whiting *Merlangius merlangus*, common dab *Limanda limanda*, European flounder *Platichthys flesus*, European hake *Merluccius merluccius*, lesser argentine *Argentina sphyraena*, long rough dab *Hippoglossoides platessoides*, common ling *Molva molva*, European plaice *Pleuronectes platessa*, saithe *Pollachius virens*, black sea bream *Spondyliosoma cantharus*, sandeel *Ammodytes* sp., poor cod *Trisopterus minutus*, North Atlantic codling *Lepidion eques*, and blackspot grenadier *Coelorhynchus coelorhynchus*). Otolith lengths were measured to the nearest 0.5 mm and from these we were able to back-calculate fish length based on the equations in Furness and Hislop (1981) and Härkönen (1986).

#### Bird prey in the diet

During 17 years from 1975 to 2017, bird remains in pellets were identified on the basis of feather colour and smell, as well as the presence of any skeletal remains. Because of difficulties in differentiating among bird prey species, we allocated bird remains in pellets into one of five categories: auk (comprising Atlantic puffin *Fratercula arctica*, common guillemot *Uria aalge* and razorbill *Alca torda*), gull/tern (mostly black-legged kittiwakes *Rissa tridactyla*, but possibly some terns *Sterna* spp. and *Larus* spp.), northern fulmar (*Fulmarus glacialis*), storm-petrel (mostly European storm-petrel *Hydrobates pelagicus*), and others (great skua, European shag *Phalacrocorax aristotelis*, northern gannet *Morus bassanus*, common eider *Somateria mollissima*, unidentified bird eggs, and unidentified passerine).

#### Seabird abundance

Estimates of seabird colony sizes on Foula (1965 to 2017) were obtained from a variety of different sources (see Figure 8 for details).

#### Sandeel availability

We provide information on the Shetland sandeel stock assessment (1976 to 2006). These are annual estimates (tonnes) as on 1 July each year based on a combination of catch-based virtual population analysis (VPA) and survey data from the International Council for the Exploration of the Seas (1976–2000) and Marine Scotland Science (2001–2006).

#### Availability of discards

We obtained mean annual estimates (tonnes) of discards for haddock (1987–2016) and whiting (1990–2015) from ICES sub-area IVa in the northwestern North Sea ([www.ices.dk](http://www.ices.dk)). Long-term estimates of discards for other species of discarded fish that are also food for great skuas were not available.

### Statistical analysis

#### Decadal variation in consumption of main prey types

To examine how consumption of the four most frequently occurring prey types (whitefish, seabirds, sandeels, and others) have changed among decades we used contingency tables, with the predicted values of equal proportions of each diet type across decades. Analysis was based on counts of prey types in June/July,

combined for breeders and non-breeders, with the sample size the number of individual prey species identified. We also calculated standardized residuals (standard normal deviate  $z$ ) for each cell in the contingency tables as a measure of how much this differed from the expected value and thus how much it contributed to the final test statistic (analogous to *post-hoc* tests):

$$z = \frac{\text{observed} - \text{expected}}{\sqrt{\text{expected}}}$$

#### Decadal variation in consumption of fish from discards

To examine how consumption of the four main discarded fish species (based on sagittal otoliths these were: whiting, haddock, Norway pout, blue whiting) and others varied between decades, we used contingency tables and also calculated standardized residuals in the same way as for pellets.

#### Variation in size of fish from discards consumed

As the amount of discards change, skuas may become more of less selective and this could be reflected in the size of fish consumed. Therefore, to examine how the mean annual size of haddock and whiting eaten by skuas (estimated from otolith length) was related to respective annual discards (tonnes), including year as a random effect (to account for multiple measurements in all years), we used generalized additive models (GAMs)—one model for each species of fish. This approach was chosen because it makes no *a priori* assumptions about the response curve shape or parametric response function.

#### Decadal variation in seabird prey

Finally, we used contingency tables to examine how the five most frequently occurring seabird groups in skua pellets (auk, gull/tern, fulmar, storm-petrel, and others) varied by decade. Presence/absence in pellets was the sampling unit therefore, since more than one prey item can be found in a single pellet, the sample size is greater than the number of pellets.

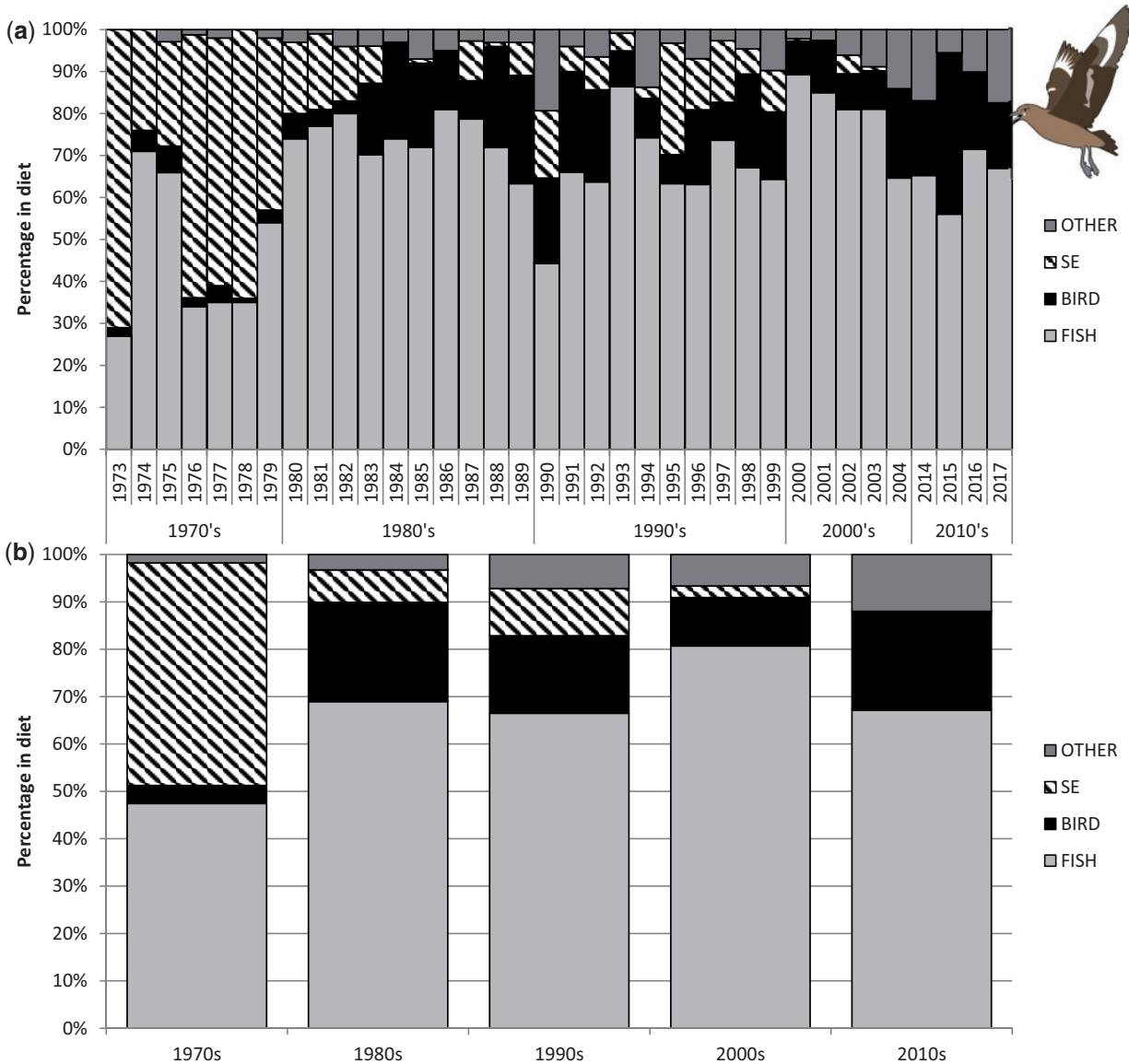
We used the R (v.3.3.0) statistical environment (R Core Team, 2016) for all of the above analysis.

## Results

### Decadal variation in consumption of four main prey types

A total of 20 013 great skua regurgitated pellets were collected during 1973–2017 ( $n = 36$  years, mean  $55.92 \pm 606.98$  year<sup>-1</sup>, range 91 to 2262 year<sup>-1</sup>). We pooled data by decade for further analysis (1970s:  $n = 7$  years, mean  $469.57 \pm 638.88$  year<sup>-1</sup>, sum 3287; 1980s:  $n = 10$  years, mean  $378.00 \pm 551$  year<sup>-1</sup>, sum 3780; 1990s  $n = 10$  years, mean  $755.6 \pm 594.19$  year<sup>-1</sup>, sum 7556; 2000s:  $n = 5$  years, mean  $954.8 \pm 757.21$  year<sup>-1</sup>, sum 4774; 2010s:  $n = 4$  years, mean  $154.00 \pm 96.65$  year<sup>-1</sup>, sum 616).

There was pronounced inter-annual variation in the proportions of the four main prey types (whitefish, sandeel, seabird, and others) (Figure 1a). Overall, the number of pellets containing each of these prey types varied significantly among decades (Figure 1b;  $\chi^2_{12} = 4458.84$ ,  $n = 20\ 014$ ,  $p < 0.001$ ). The key changes can be summarized as follows (see Table 1 for standardized residuals as a measure of the degree to which each cell differed from expected). Fish, almost exclusively whitefish obtained as discards from fishing boats, were the predominant dietary

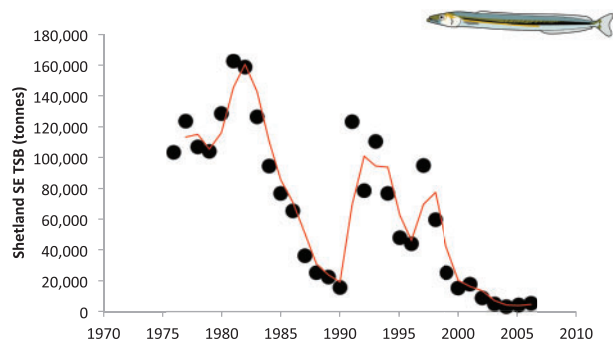


**Figure 1.** (a) Inter-annual variation in the four most frequent prey items found in regurgitated pellets of great skuas *Stercorarius skua* in 36 years (1973–2017) at Foula, Shetland, UK. (b) Inter-decadal variation in the four most frequent prey items (sample sizes are reported in the main text). SE = sandeel (*Ammodytes* spp.).

**Table 1.** Standardized residuals as a measure of the degree to which each cell differed from the expected for four main prey types (a) and five types of discarded fish (b).

	1970s	1980s	1990s	2000s	2010s
(a)					
Fish	-13.93	+1.32	-0.76	+11.36	-0.03
Bird	-95.5	+11.78	+5.91	-6.7	+4.62
Sandeel	+52.88	-10.99	-8.01	-20.62	-8.97
Other	-8.6	-6.11	+5.7	+3.01	+6.7
(b)					
Whiting	-0.17	+19.52	+3.38	-23.42	-7.31
Haddock	+4.52	-12.94	-4.88	+20.77	-4.49
Norway Pout	-1.34	-11.71	+6.34	+1.97	+3.94
Blue whiting	-5.42	-10.71	-7.58	+19.02	+18.97
Other	-3.77	+3.39	-2.61	-1.36	+10.35

item and this has remained the case throughout the decades (minimum proportion 48% in the 1970s, maximum 81% in the 2000s). Sandeels were abundant during the 1970s (found in 47% of pellets) but were scarce thereafter—this pattern is not mirrored in the Shetland sandeel total stock biomass, which declined steeply during the 1980s and 2000s, but showed a recovery during the 1990s (Figure 2). Seabird prey increased sharply from the 1970s (4%) to the 1980s (21%), but declined to 10% in the 1990s before increasing in the 2010s (21%). Other prey items (mostly terrestrial mammals such as sheep *Ovis aries* and rabbits *Oryctolagus cuniculus*, marine invertebrates such as goose barnacle *Lepas* sp. and some other fish such as mackerel *Scomber scombrus*, herring *Clupea harengus*, and garfish *Belone belone*) have remained relatively consistent over the period, representing only a small proportion of total diet items represented in pellets



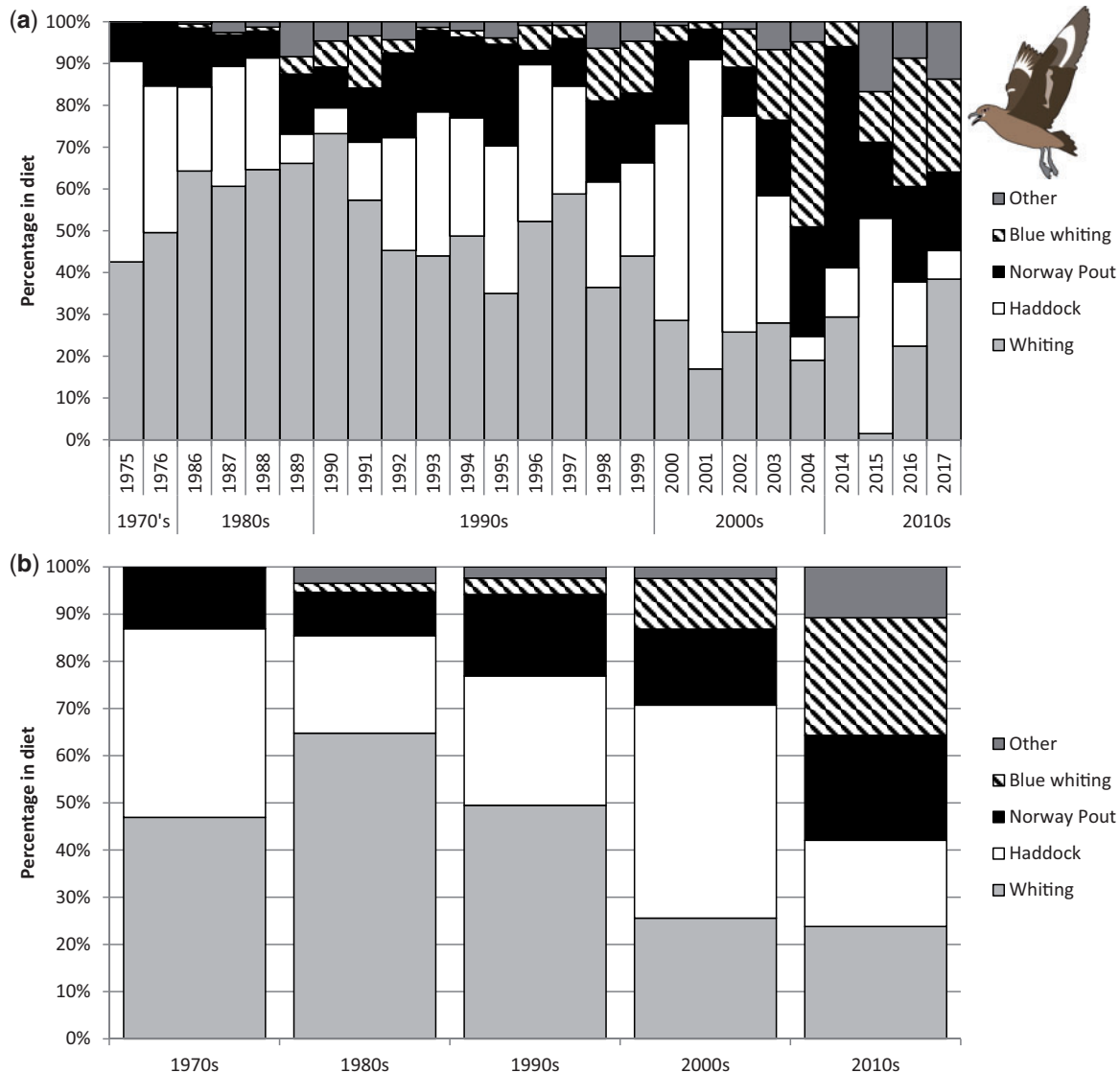
**Figure 2.** Sandeel (SE) total stock biomass (TSB—tonnes) of the Shetland stock (1976–2006). These are annual estimates as on 1 July each year based on VPA and survey data from the International Council for the Exploration of the Seas (1976–2000) and Marine Scotland Science (2001–2006) (fitted line represents 2-year running mean).

(1% in the 1970s, 3% in the 1980s, 6% in the 1990s, 5% in the 2000s, and 7% in the 2010s).

**Decadal variation in consumption of fish from discards**

A total of 24 993 sagittal otoliths were collected from skua pellets during 1975–2017 ( $n=25$  years, mean  $694.25 \pm 1066.41 \text{ year}^{-1}$ , range 17 to 4634  $\text{year}^{-1}$ ). We pooled data by decade for further analysis (1970s:  $n=2$  years, mean  $294.00 \pm 100.41 \text{ year}^{-1}$ , sum 588; 1980s:  $n=4$  years, mean  $1498.00 \pm 1483.57 \text{ year}^{-1}$ , sum 5992; 1990s:  $n=10$  years, mean  $1250.7 \pm 1428.58 \text{ year}^{-1}$ , sum 12507; 2000s  $n=5$  years, mean  $1090.4 \pm 581.96 \text{ year}^{-1}$ , sum 5452; 2010s  $n=4$  years, mean  $113.5 \pm 102.18 \text{ year}^{-1}$ , sum 454).

There was pronounced inter-annual variation (1975–2017) in the proportions of the five main species of discarded fish otoliths (haddock, whiting, Norway pout, blue whiting, and others) in skua diets (Figure 3a). The proportions of pellets containing otoliths from these five species of discarded fish varied significantly by decade ( $\chi^2_{16} = 2921.07$ ,  $n=24\ 993$ ,  $p < 0.001$ ; Figure 3b).



**Figure 3.** (a) Inter-annual variation in the five most frequent sagittal otolith types found in regurgitated pellets of great skuas in 25 years (1975–2017) at Foula, Shetland, UK. (b) Inter-decadal variation in the five most frequent otoliths (numbers refer to sample sizes for each fish category).

The key changes can be summarized as follows (see Table 1 for standardized residuals as a measure of the degree to which each cell differed from expected). The proportion of pellets containing whiting has declined from a peak of 65% in the 1980s to 24% in the 2010s; haddock has showed much variation without a clear signal, with the maximum 45% in the 2000s and minimum 18% in the 2010s; Norway pout and blue whiting have both increased over time, peaking during the 2010s; other fish, representing at least 14 species (listed in the Material and methods) have been scarce in pellets throughout, but peaking at 11% in the 2010s. These patterns are apparent in the context of overall long-term declines in the quantities of haddock and whiting discarded in the waters around Shetland (Figure 4).

**Temporal variation in size of discarded fish consumed**

A total of 9029 sagittal otoliths from skua pellets of the four main discarded fish species (haddock, whiting, blue whiting, and Norway pout) were measured during 1976–2016 ( $n=22$  years, mean  $429.9 \pm 438.64 \text{ year}^{-1}$ , range 25 to  $1792 \text{ year}^{-1}$ ).

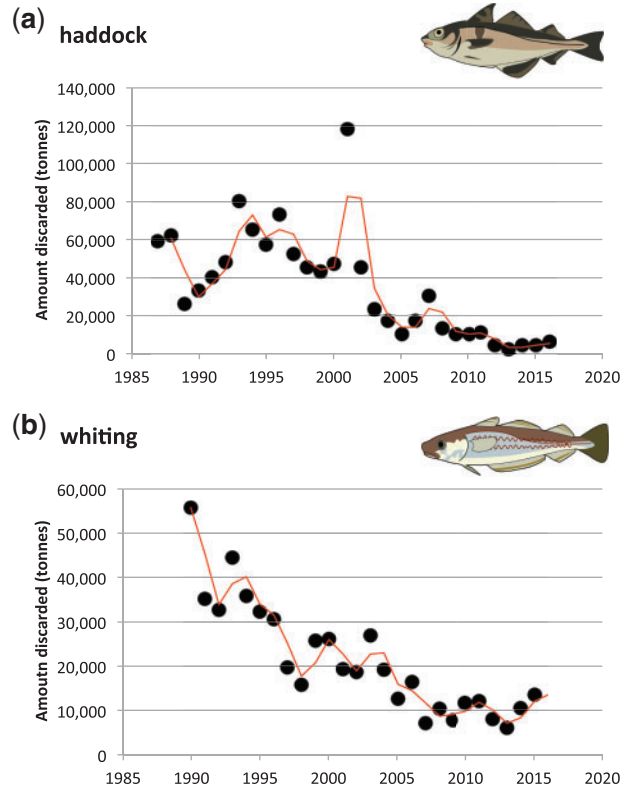
Variation in the sizes of the four main discarded fish species is shown in Figure 5a–d. The size of haddock based on regurgitated pellets was statistically significantly positively associated with haddock discard estimates (GAM:  $\text{edf}=2.482$ ,  $F=7.118$ ,  $p=0.0004$ ; Figure 6a), while whiting size was not significantly associated with discard estimates (GAM:  $\text{edf}=2.099$ ,  $F=2.313$ ,  $p=0.0959$ ; Figure 6b).

**Decadal variation in seabird consumption**

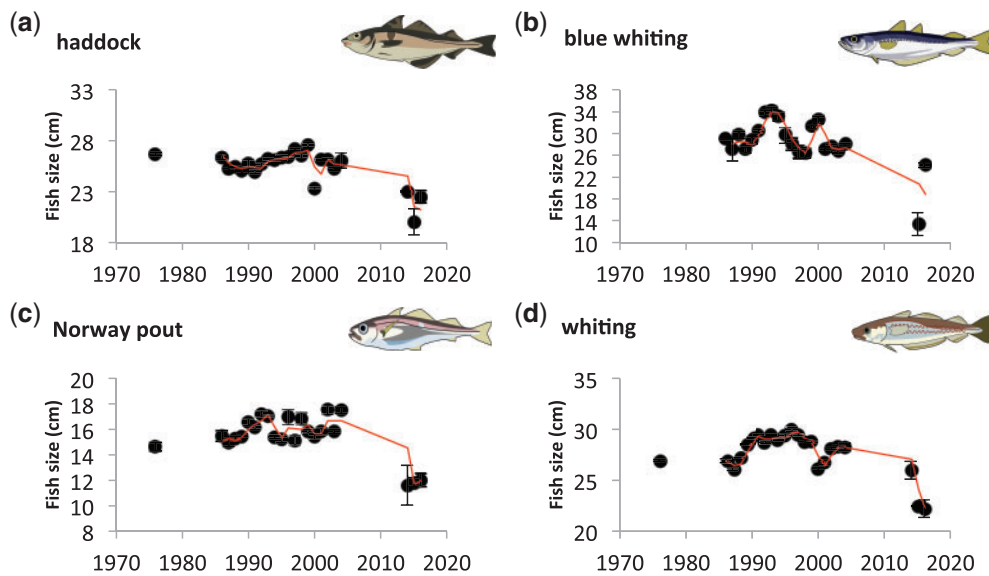
A total of 1496 skua pellets containing bird remains identified below the level of class were sampled during 1975–2017 ( $n=17$  years, mean  $88.0 \pm 97.46 \text{ year}^{-1}$ , range 7 to  $373 \text{ year}^{-1}$ ). We pooled data by decade for further analysis (1970s:  $n=2$  years, mean  $66.33 \pm 33.38 \text{ year}^{-1}$ , sum 110; 1980s:  $n=1$  year, sum 89; 1990s:  $n=5$  years, mean  $141.2 \pm 162.05 \text{ year}^{-1}$ , sum 706; 2000s:

$n=5$  years, mean  $94.8 \pm 58.86 \text{ year}^{-1}$ , sum 474; 2010s:  $n=4$  years, mean  $29.25 \pm 20.34 \text{ year}^{-1}$ , sum 117).

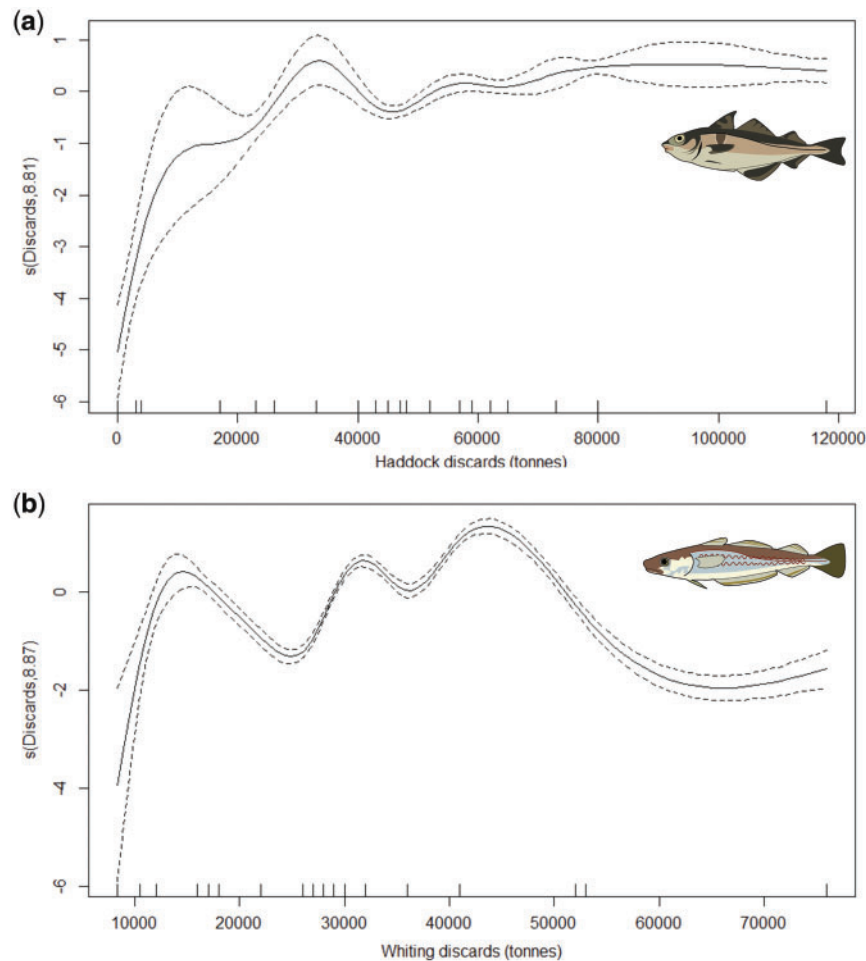
There was pronounced inter-annual variation in the proportions of the five main seabird species in great skua pellets (auks,



**Figure 4.** Inter-annual variation (1987 to 2016) in the mean (tonnes) of discarded haddock (a) and whiting (b) in ICES area IVa (NE Atlantic waters around Shetland, UK) with line representing fitted 2-year running mean.



**Figure 5.** Variation in the size of (a) haddock, (b) blue whiting, (c) Norway pout, and (d) whiting consumed ( $\pm$ SE) in the diet of great skuas (1976–2016), back-calculated from sagittal otoliths (line represents 2-year running mean). Minimum landing size of haddock is 30 cm and whiting is 27 cm.



**Figure 6.** Variation in the size of (a) haddock, (b) whiting consumed ( $\pm$ SE) in great skua pellets (back-calculated from sagittal otoliths) in relation to inter-annual variation in the mean (tonnes) of discarded haddock and whiting in ICES area IVa (NE Atlantic waters around Shetland, UK).

fulmars, gulls/terns/kittiwakes, storm-petrels, and others; Figure 7a). Overall, the number of pellets containing each of these species varied significantly by decade ( $\chi^2_{16} = 912.83$ ,  $n = 3908$ ,  $p < 0.001$ ; Figure 7b). The key changes can be summarized as follows: the incidence of gulls, terns, and kittiwakes (mostly kittiwakes) decreased sharply during the 2010s; the proportions of pellets containing fulmar were variable with larger numbers in the 1980s (although with only 1989 sampled in the 1980s) followed by a decrease in the 1990s and then a gradual increase until the 2010s; the percentage of auk pellets dropped from a peak in the 1970s but has increased each decade since; storm-petrels are scarce and consistent over time; and the incidence of “other” birds (comprising great skua, European shag, northern gannet, common eider, unidentified bird eggs, and unidentified passerine) have been relatively consistent, except for their disappearance in the 1980s.

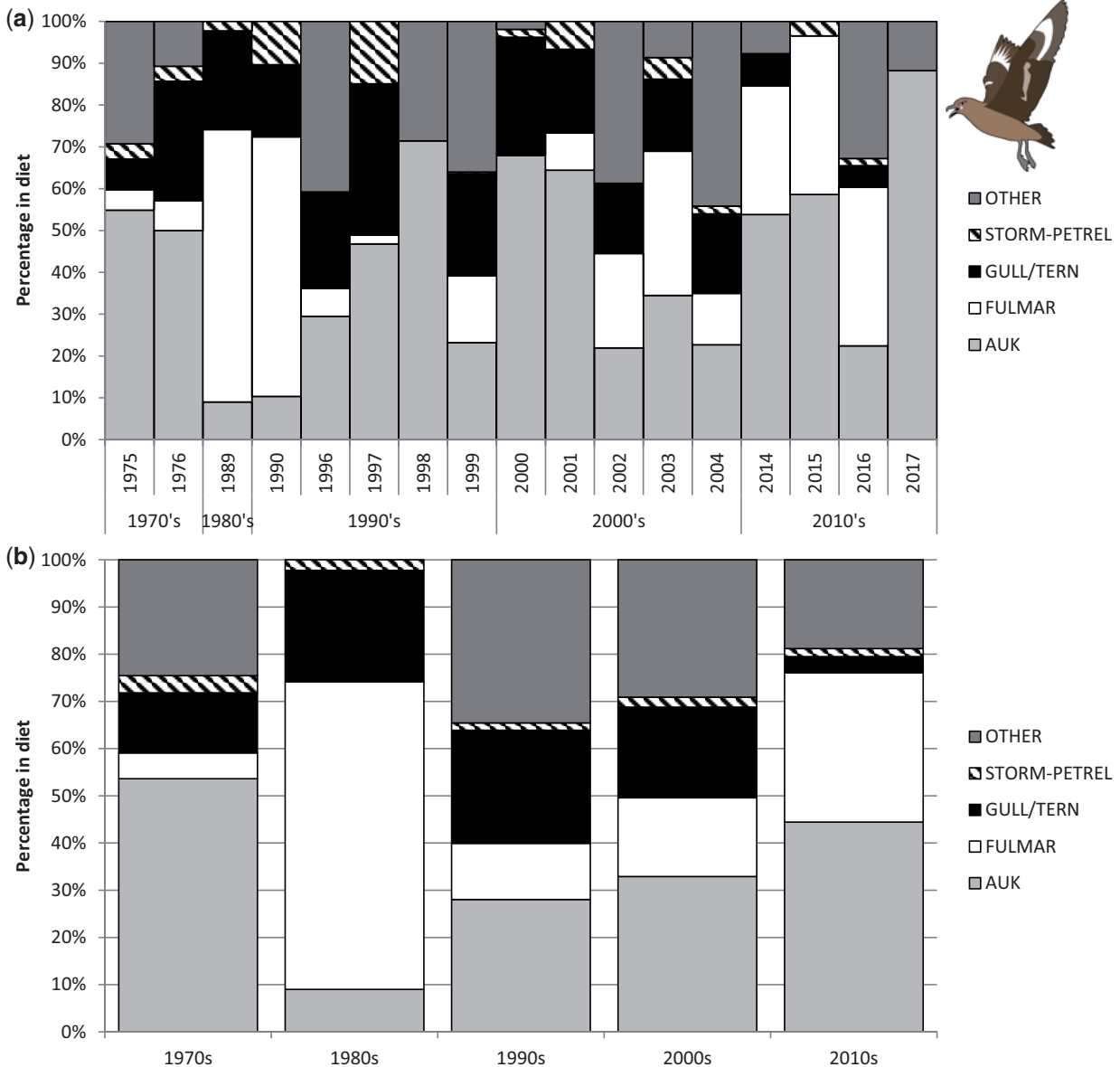
### Changing seabird community

Overall, the number of seabirds breeding on Foula has decreased greatly during 1965–2016 (Figure 8). Northern gannets are the only species to have increased (Figure 8b), although great skua numbers have remained relatively stable around 2000 pairs

(Figure 8e). Northern fulmars have declined following a peak of  $\sim 47\,000$  AOSs (apparently occupied sites; equating to pairs) in 1987, although are still the most numerous seabird breeding on the island with  $\sim 9\,000$  AOSs in 2015 (Figure 8a). Common gullmots have declined steeply following a peak of  $\sim 60\,000$  individuals in 1987, to  $\sim 13\,000$  in 2015 (Figure 8h)—they are now the second most numerous seabird on the island. Atlantic puffins (Figure 8j) are the third most abundant seabird on Foula with  $\sim 6\,000$  individuals seen in 2016, although this is in stark contrast to the  $\sim 70\,000$  in 1976. The remaining five species (European shag, Arctic skua, black-legged kittiwake, Arctic tern, and razor-bill) have all shown similar steep declines from peaks during the late 1970s and 1980s reducing to just a few hundred pairs or less at the most recent estimate.

### Discussion

Here we have shown how great skua diets have changed across five decades. Overall we can see that skua pellets are no longer dominated by sandeels as they were during the 1970s. Skuas have retained a long-term reliance on feeding on discarded fish, although both the species composition and size of fish have changed. Skuas have also fed on seabirds throughout this period, being low in the 1970s, but relatively stable thereafter; however



**Figure 7.** (a) Inter-annual variation in the five most frequent seabird prey types found in great skua regurgitated pellets (1975–2017) on Foula, Shetland, UK. (b) Inter-decadal variation in the five most frequent seabird prey types.

there has been a major shift away from species such as kittiwakes, to feed instead on fulmars and auks—probably a reflection of a changing seabird assemblage over the last five decades. We discuss the implications of these changes for seabird communities and for monitoring the impacts of marine ecosystem change below.

**Sampling protocol**

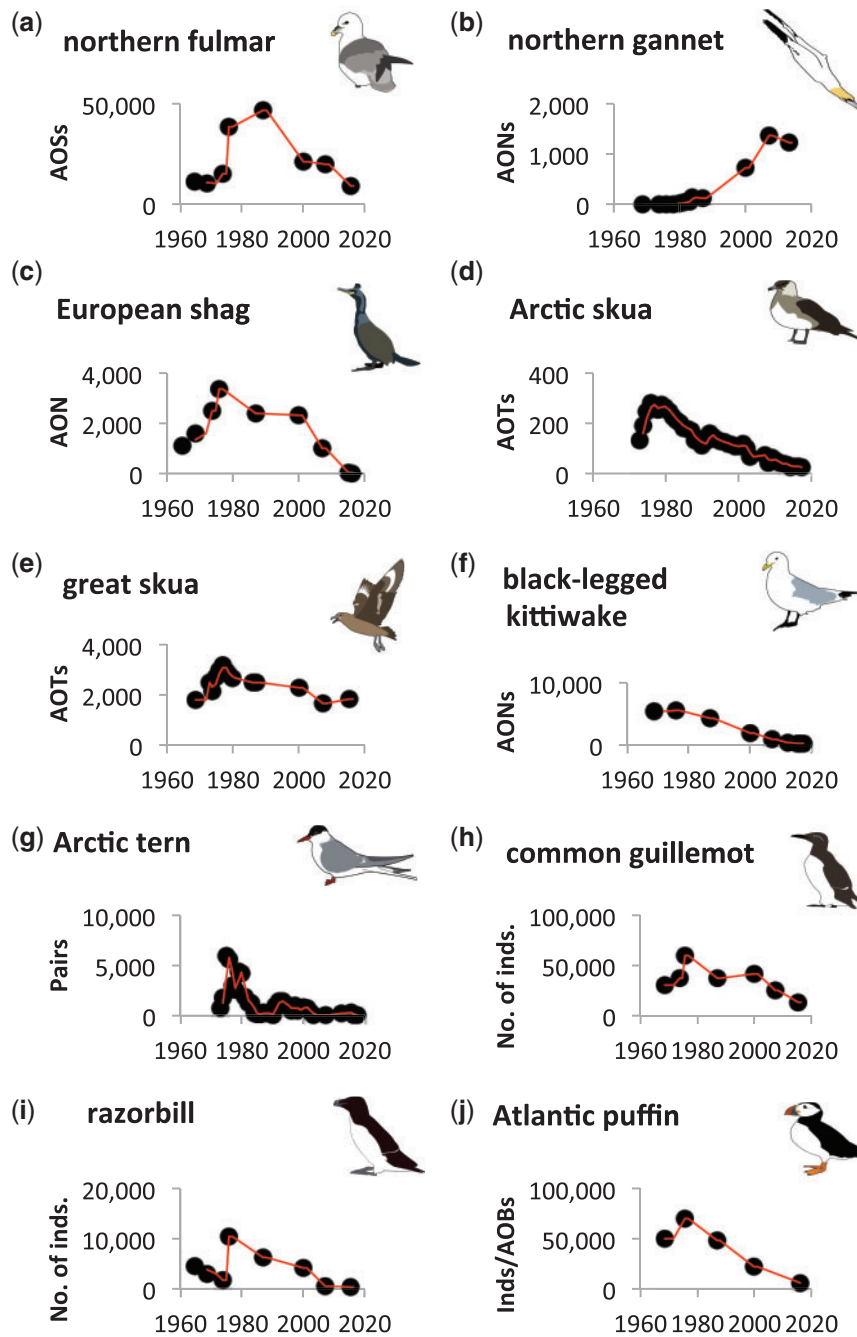
Dietary assessment techniques have a wide range of assumptions and biases, with pellets known to bias toward indigestible prey (Votier et al., 2001, 2003; Barrett et al., 2007). For this reason, our results here may under-represent soft-bodied prey. However, previous studies of great skua diets using a range of different diet sampling approaches such as the analysis of spontaneous regurgitates and observed feeds that are less likely to bias toward hard body parts, reveal similar patterns to those shown by pellet

analysis (Votier et al., 2003). Moreover, the same approach was used across all our sampling intervals allowing us to conduct this comparative study. We therefore conclude that our dietary sampling is appropriate and provides an effective way to monitor long-term changes in the diet of this marine top predator. Furthermore, we did not sample all years in all decades, and this varied depending on the type of dietary analysis conducted. Yet we still believe our study captures long-term diet variation and is important since this level of detail in diet studies is rare (see Howells et al., 2017).

**Decadal variation in consumption of main prey types**

During the 1970s, 47% of great skua pellets were composed of sandeels, but this dropped to 7% in the 1980s and at no time since has this recovered to more than a few percent (Figure 1a





**Figure 8.** Population estimates of ten species of seabird breeding on Foula, Shetland (1965–2016) (with running mean in red). Abbreviations along the abscissa: AOSs, apparently occupied sites; AONs, apparently occupied nests; AOTs, apparently occupied territories; AOBs, apparently occupied burrows. Sources: 1965—[Fabrıtus \(1969\)](#); 1969—[Cramp et al. \(1974\)](#); 1976—[Furness \(1981\)](#); 1981—[Furness \(1983\)](#); 1986—[Ewins et al. \(1986\)](#); 1987—[Furness \(1987\)](#); 2000—[Harvey et al. \(2000\)](#); 2012—[Heubeck & Mellor \(2012\)](#); 2015—[Heubeck & Mellor \(2015\)](#); 2016—[Heubeck & Mellor \(2016\)](#); 2017—[Heubeck et al. \(2017\)](#).

and b). Consistent with this, the Shetland sandeel total stock biomass declined steeply during the 1980s ([Figure 2](#)). These declines resulted in a closure of the Shetland sandeel fishery in 1990 ([Poloczanska et al., 2004](#)), although the sandeel population crash was likely also influenced by climate-induced reductions in recruitment, specifically low levels of recruitment in years with warm winters ([Frederiksen et al., 2004](#); [Poloczanska et al., 2004](#)). There was a recovery in the Shetland sandeel stock during the

mid-1990s, but thereafter it declined further. These patterns are mirrored by the incidence of sandeels in great skua diets ([Figure 1a and b](#)).

The proportion of skua pellets containing seabirds was lowest during the 1970s at 4% but increased sharply during the 1980s to 21% and remained at 10–20% for the next three decades ([Figure 1a and b](#)). Variability in the proportion of pellets containing seabirds likely reflects variation in the

availability of alternative prey, such as discards and sandeels (Votier *et al.*, 2004a), although seabird predation will also be influenced by the availability of seabirds as either carrion or prey. Overall, seabird numbers have declined steeply in Foula over the five decades of this study (Figure 8), yet in the 2010s 21% of 616 pellets contained bird remains, which indicates that there are still opportunities for great skuas to feed on other seabirds. It is not clear whether the observed changes in the usage of seabirds for prey have been driven by differences in foraging behaviour at the skua population level or because of changes in the incidence of individual skuas specializing as seabird predators (Votier *et al.*, 2004b, c).

The fish component of the diet was dominated by demersal whitefish, which occur beyond the diving range of most seabirds and are therefore either scavenged from fisheries or kleptoparasitized from other seabirds (Votier *et al.*, 2010, 2013). Great skuas are abundant, dominant scavengers at fishing vessels in Shetland waters (Hudson and Furness, 1989), so this most likely represents the former. Whitefish were by far the most numerous prey item, ranging from 48% in the 1970s to 81% in the 2000s (Figure 1a and b). This strong reliance on scavenged fish occurred against a backdrop of overall declining discard production in the North Sea following peaks during the latter part of the 1970s (Figure 3; ICES, 2002; Heath and Cook, 2015).

Other dietary items in pellets included mammals and some other mainly pelagic fishes, (i.e. herring, mackerel, and garfish). These appear to have increased slightly in the diet in recent decades, but still represent a very small proportion (maximum 6% during the 1990s). Great skuas regularly feed on rabbits and sheep, the latter as carrion (Votier *et al.*, 2004a, b, 2008a) and may obtain pelagic fishes either by catching them at sea, by kleptoparasitizing other seabirds such as gannets, or by scavenging (Bicknell *et al.*, 2013).

### Decadal variation in consumption of fish from discards

Sagittal otoliths found in pellets show that great skuas feed predominantly on four discarded fish species—haddock, whiting, blue whiting, and Norway pout (Figure 3), all of which are discarded in large quantities in Shetland waters (ICES, 2017). Whiting and haddock dominated, being replaced to a degree by other fish during the past two decades, reflecting a decline in discards of whiting and haddock (Votier *et al.*, 2004a, 2008a).

Over the period 2015–2019 there is an obligation to land all fish under quota or with a total allowable catch (De Vos *et al.*, 2016; Veiga *et al.*, 2016). Haddock and whiting were banned from discarding in 2016, but their otoliths still appeared in great skua pellets in 2016 and 2017. It is not clear whether this is because of enforcement problems (Catchpole *et al.*, 2014) or whether skuas catch these fish in another way (such as via kleptoparasitism or by taking net spillage; Votier *et al.*, 2013). More work is required to understand fully the implications of the landing obligation for skuas and other seabirds (Bicknell *et al.*, 2013; Votier *et al.*, 2010, 2013).

### Decadal variation in size of discarded fish consumed

Fish lengths calculated from sagittal otoliths indicate that great skuas eat haddock and whiting that are below the minimum landing size (Figure 5; 30 cm and 27 cm, respectively). Therefore, these fish likely represent either undersized fish discarded from catches or net slippage—rather than high grading (where fishers sort their catch in favour of the most valuable species).

Additionally, these fish are significantly larger than the estimated size at which these species migrate from pelagic waters and settle in demersal waters (Bastrikin *et al.*, 2014). This provides further evidence that these are beyond the diving range of skuas and also that they are unlikely to be kleptoparasitizing other seabirds feeding naturally on these types of Gadidae (Greenstreet *et al.*, 1999).

The size of discarded fish found in skua pellets changed relatively little during the 1970s, 1980s, 1990s, and 2000s, but all four species studied showed a steep decline in the 2010s (Figure 5). This coincides with an overall decline in the sizes of fish in the North Sea (Daan *et al.*, 2005), which may be a function of size-selective fishing, increases in small fish due to reduced levels of predation (Daan *et al.*, 2005), high grading (Planque *et al.*, 2010), and climate effects such as increasing water temperatures giving smaller body sizes a fitness advantage (Perry *et al.*, 2005; Baudron *et al.*, 2014). For skuas eating haddock, there was a significant positive association between the size of these fish and the amount of haddock discarded (Figure 6a). One possible explanation is that with more haddock discards available, skuas may be able to select larger fish.

### Decadal variation in seabird predation

Great skuas in Foula demonstrate variable preferences/opportunities in seabird prey between years, although because of variable numbers of years sampled our findings should be treated with some caution (Figure 7). Auks peaked in skua pellets at 54% in the 1970s, but dropped steeply in the 1980s and then increased steadily each decade until reaching 44% in the 2010s. Fulmar presence in pellets peaked in the 1980s at 65% but then, following a drop in the 1990s, has increased each decade to 32% in the 2010s. Gulls/terns (mostly representing kittiwakes) have shown a steady decline in percentage occurrence in pellets since peaking in the 1980s/1990s. These changes broadly mirror the status of the seabird breeding community on Foula (Figure 8). The vast majority of seabirds breeding on Foula have declined steeply over the past five decades, with European shag, Arctic skua, black-legged kittiwakes, Arctic tern, and razorbill showing trajectories toward localized extinction. It is therefore unsurprising that kittiwakes are now very scarce in skua diets, being instead replaced by the still relatively numerous (but still at historically low levels) northern fulmar and auks (Figure 8). Most of the declines in breeding seabird populations on Shetland have been attributed to changes in the availability and size of sandeel and sprat *Sprattus sprattus* stocks (Cury *et al.*, 2011; Miles *et al.*, 2015), however predation by great skuas may have also played a role, at least for some species. Great skuas are generalists and opportunists that feed facultatively on seabirds when other prey is scarce (Votier *et al.*, 2004a), or specialize as seabird predators (Votier *et al.*, 2004c), and as such may exert strong top-down pressure on prey populations. Elsewhere in Shetland and in Orkney, great skua predation pressure has been linked with declines in numbers of kittiwakes (Oro and Furness, 2002; Votier *et al.*, 2004b, 2008c) and Arctic skuas (Furness, 1977; Meek *et al.*, 2011; Perkins *et al.*, 2018). However, there is no clear evidence for similar effects of skua predation upon some other seabird species (Miles *et al.*, 2015), although we cannot completely exclude this possibility.

### Conclusion

Tracking variation in the diet of a top marine predator over five decades has reflected concomitant environmental changes in an area heavily affected by anthropogenic activity. In the case of

discarded fish, sandeels, and seabird prey, their occurrence in skua pellets appears related to their availability, suggesting that great skuas are sensitive to variation in these resources. The trends revealed in skua foraging behaviour reflect changes in fisheries management, climate change impacts on forage fish, as well as changes in the structure of seabird communities. This dietary flexibility may be part of the reason for the comparative success of great skuas over a period of decline for so many other seabird species in this region (Figure 8). Moreover, it hints at a restructuring of the assemblage from one dominated by species that feed on small shoaling to fish to one comprised mostly of large generalist species (i.e. great skuas and gannets). Therefore our findings suggest that great skuas are an effective study species for tracking environmental change when other data, such as sandeel stock size, might be unavailable.

This investigation highlights the importance of long-term diet data. Monitoring programmes typically focus on gathering demographic information, however variation in diet can reveal important aspects of changes in consumers and by inference the ecosystems they inhabit. This information is required in tandem with demographic information, as well as information on movement, to provide a more complete understanding of the incidence and implications of change in marine ecosystems.

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