Methods

We adopt the model of Rice[18] where permeability is a strongly decreasing function of effective normal stress, $k = f(\bar{\sigma}_n)$. Specifically, $k = k_0 \exp(-\bar{\sigma}_n/\sigma^*)$, where k_0 is the permeability at zero effective stress, and σ^* is a constant with lower values of σ^* corresponding to highly cracked rocks. Using this form for the permeability, we solve the diffusion equation with a spatially variable permeability[28]:

$$\frac{\partial P}{\partial t} = \frac{1}{\phi(\beta_{\mathrm{f}} + \beta_{\phi})}\left[\nabla \frac{k_0 \exp\left(-\frac{\bar{\sigma}_n}{\sigma^*}\right)}{\eta} \nabla P + \dot{\Gamma}(P, T)\right] \tag{1}$$

where P is the fluid pressure above hydrostatic, β_{f} and β_{ϕ} are the fluid and pore (crack) compressibility, and $\dot{\Gamma}$ is a source term. The source term is assumed to be zero here, but is included in equation (1) to show that the pressure dependence of the dehydration (or de-carbonization) kinetics could provide an additional direct fluid source from coseismic fluid pressure reductions[29]. The effective normal stress used in equation (1) and acting on fault planes is calculated as[30]:

$$\bar{\sigma}_n = \frac{\sigma_1 + \sigma_3 - 2P_{\mathrm{f}}}{2} + \frac{\sigma_1 - \sigma_3}{2}\cos 2\theta \tag{2}$$

where σ_1 and σ_3 are the maximum and minimum principal stress, P_{f} is the total fluid pressure (for example, $P + \rho_{\mathrm{w}} g z$), θ is the dip angle, ρ_{w} is the density of water, g is the acceleration of gravity, and z is the depth. We take $\theta = 40°$ (determined from the earthquake focal mechanisms), σ_1 as the weight of the overburden (for example, $\rho_{\mathrm{r}} g z$), where ρ_{r} is the rock density, and we assume $\sigma_3 = 0.7\sigma_1$ to reflect this extension tectonic environment.

We solve equation (1) with an implicit finite difference scheme, using the simplified model geometry and initial conditions shown at the top of Fig. 3. A no-flow boundary condition is imposed on all boundaries except the upper surface, where a constant head (for example, hydrostatic pore pressure) boundary condition is imposed. We use crack compressibility $\beta_{\phi} = 10^{-8}\,\mathrm{MPa}^{-1}$, fluid compressibility $\beta_{\mathrm{f}} = 10^{-10}\,\mathrm{MPa}^{-1}$, and a temperature-dependent viscosity for water (assuming a temperature gradient of $25\,°\mathrm{C\,km}^{-1}$). We assume that the flow properties of supercritical CO_2 (the phase of CO_2 at the source depth) are the same as for water because CO_2 at this P–T condition is ten times more compressible than water, but it is of the same order less viscous, resulting in similar flow properties. Note that the model can be made much more complicated by considering two-phase flow, dual porosity, anisotropic permeability, and other complexities. However, we find this simple model sufficient to show a very strong correlation between the calculated pressure field and the precise locations of aftershock hypocentres.

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Correspondence and requests for materials should be addressed to S.A.M. (steve.miller@erdw.ethz.ch).

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Changes in fisheries discard rates and seabird communities

Stephen C. Votier[1], **Robert W. Furness**[1], **Stuart Bearhop**[1,2], **Jonathan E. Crane**[1], **Richard W. G. Caldow**[3], **Paulo Catry**[4], **Kenny Ensor**[1], **Keith C. Hamer**[5], **Anne V. Hudson**[1], **Ellen Kalmbach**[6], **Nicholas I. Klomp**[7], **Simone Pfeiffer**[1,8], **Richard A. Phillips**[9], **Isabel Prieto**[1] **& David R. Thompson**[10]

[1] *Institute of Biomedical and Life Sciences, University of Glasgow, Glasgow G12 8QQ, UK*
[2] *School of Biology and Biochemistry, Queens University, Belfast, Medical Biology Centre, 97 Lisburn Road, Belfast BT9 7BL, UK*
[3] *Centre for Ecology and Hydrology, Winfrith Technology Centre, Winfrith Newburgh, Dorchester, Dorset DT2 8ZD, UK*
[4] *Unidade de Investigação em Eco-Etologia, ISPA, Rua Jardim do Tabaco 44, Lisboa, Portugal*
[5] *Faculty of Biological Sciences, University of Leeds, Leeds LS2 9JT, UK*
[6] *Department of Animal Ecology, University of Groningen, Kerklaan 30, 9751NN Haren, The Netherlands*
[7] *Johnstone Centre, School of Environmental and Information Sciences, Charles Sturt University, PO Box 789, Albury, New South Wales 2640, Australia*
[8] *Institute of Ecology, Dornburger Strasse 159, University of Jena, 07743 Jena, Germany*
[9] *British Antarctic Survey, High Cross, Madingley Road, Cambridge CB3 0ET, UK*
[10] *National Institute of Water and Atmospheric Research Ltd, PO Box 14-901, Kilbirnie, Wellington, New Zealand*

It is clear that discards from commercial fisheries are a key food resource for many seabird species around the world[1–8]. But predicting the response of seabird communities to changes in discard rates is problematic and requires historical data to elucidate the confounding effects of other, more 'natural' ecological processes. In the North Sea, declining stocks, changes in technical measures, changes in population structure[9] and the establishment of a recovery programme for cod (*Gadus morhua*[10]) will alter the amount of fish discarded. This region also supports internationally important populations of seabirds[11], some of which feed extensively, but facultatively, on discards, in particular on undersized haddock (*Melanogrammus aeglefinus*)

and whiting (*Merlangius merlangus*)[1–3]. Here we use long-term data sets from the northern North Sea to show that there is a direct link between discard availability and discard use by a generalist predator and scavenger—the great skua (*Stercorarius skua*). Reduced rates of discarding, particularly when coupled with reduced availability of small shoaling pelagic fish such as sandeel (*Ammodytes marinus*), result in an increase in predation by great skuas on other birds. This switching of prey by a facultative scavenger presents a potentially serious threat to some seabird communities.

Current fishery practices produce vast quantities of waste in the form of offal and the discarding of an estimated 25–30 million tonnes of undersized fish worldwide each year[12]. There is also evidence that populations of scavenging seabirds have increased considerably where discards are plentiful[1–2,11]. It is likely that declines in discard availability (from the closure of fisheries or changes in management policy) will affect seabird communities both directly and indirectly. Scavenging species are affected directly in terms of foraging ecology[7], breeding biology[8] and overwinter condition[13]. But only a few seabird species in each community feed on fishery discards, and these tend to be large seabirds that can compete effectively at fishing boats for this resource[3].

Indirect effects include increased depredation of smaller seabirds by scavengers facing a shortfall in their energy budgets[14]. Such effects may be confounded by the fact that scavengers can also feed on alternative prey such as small, shoaling, lipid-rich species, for example, sandeels and capelin (*Mallotus villosus*)[14–16], that may themselves fluctuate in abundance in association with the biomass of predatory fish and hence catch-per-unit effort and discard rates. Long-term data have enabled us to examine the effect of changes in discard rates, and discard use by seabirds—a natural experiment—on seabird communities as a whole.

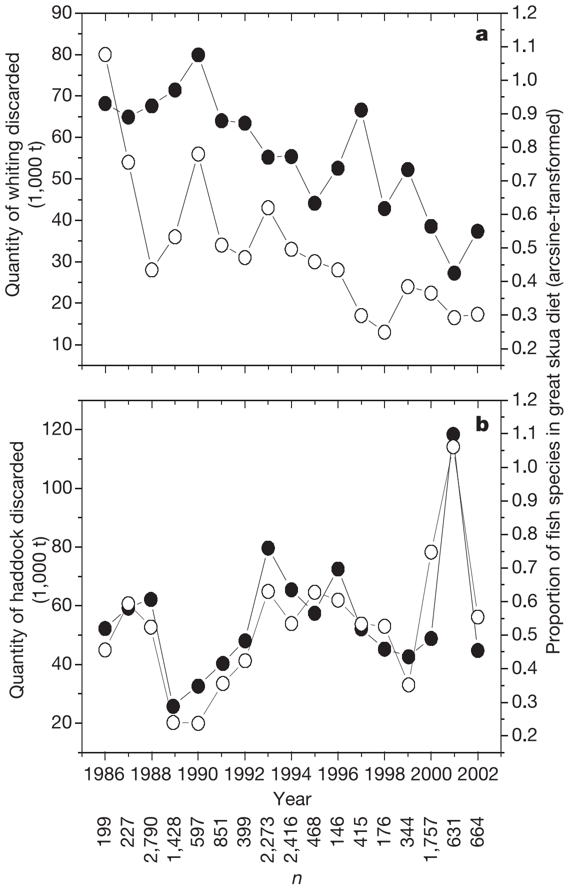

Figure 1 Composition of the diet of great skuas tracks the quantity of fishery discards. There are significant correlations between ICES estimates of discards (filled circles) and the (arcsine-transformed) percentage of these fish in the diet of great skuas (open circles) for both whiting (**a**) and haddock (**b**) for the period 1986–2002. The sample number of otoliths for each year is indicated (*n*).

The North Sea supports many important fisheries, including a large fishery operating mainly in the north that targets white fish (cod, haddock, whiting and saithe (*Pollachius virens*)) and generates substantial quantities of waste[1]. Over the past 40 yr, there have been large declines in stocks of these fish in the North Sea[9], during which time *per capita* mortality due to fishing has tended to increase. Although there have been large variations in discard rates from year to year depending on highly variable levels of recruitment (ref. 4 and see Methods), in general the volume of fish discarded has fallen less rapidly than the stocks[9]. The northern North Sea also supports large breeding populations of scavenging seabirds including northern fulmar (*Fulmarus glacialis*), northern gannet (*Morus bassanus*), great skua, lesser black-backed gull (*Larus fuscus*), herring gull (*Larus argentatus*) and great black-backed gull (*Larus marinus*)[11] and, although it is highly desirable to recover depleted gadoid stocks through reductions in fishery quotas or fishery closures[10], an unavoidable consequence of such action will be an unprecedented reduction in food supply for scavenging seabirds.

The great skua is a top predator in marine food webs, feeding extensively on discards, as well as on sandeels and seabirds[15,16], which makes it an ideal species with which to evaluate the complex relationship between fisheries and seabird community structure. Great skuas experienced rapid population growth in the past century[11]; this growth is almost certainly due to protection from persecution and is also related to increases in discard availability. Although this species is the subject of an intensive long-term study at the largest colony in the world (Foula, Shetland, UK; 60° 08′ N, 02° 05′ W), many standard breeding biology and population-level parameters do not readily lend themselves to analysing the importance of discard availability.

Drawing conclusions from changes in breeding numbers may be confounded because great skuas are long-lived with very stable populations from year to year, and changes in the recruitment of nonbreeders buffer the effects of environmental change[17]. In addition, because of the long delay between fledging and maturity, changes in breeding numbers are likely to lag behind changes in

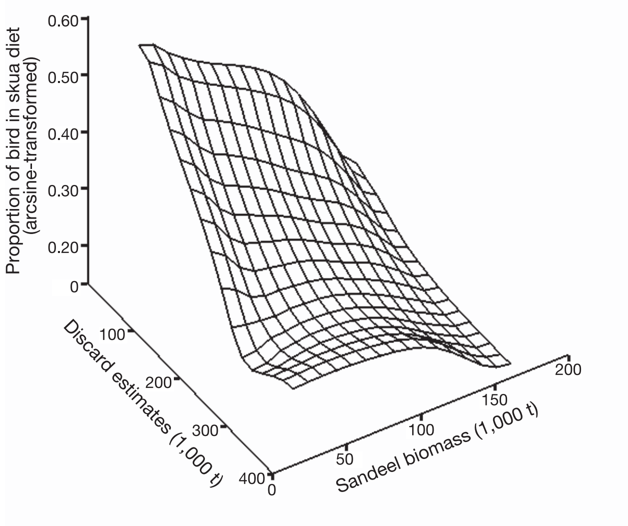

Figure 2 Declining discard and sandeel availability results in an increase in seabird predation. The relationship between the percentage of bird prey in the diet (arcsine-transformed) and both discard and sandeel availability is shown for the period 1974–1994. The relationship has been fitted by using T4253H smoothing in SPSS Advanced Statistics (Version 10.0, Chicago).

discard rates[2]. Changes in breeding frequency and success may also occur as a consequence of other unquantified environmental factors in both the breeding and the wintering season, or may be counterbalanced by prey-switching[18]. But by studying the diet choice of this generalist predator over a long period of time, we can test directly the importance of discards and the use of other prey in relation to discard availability.

To investigate the use of discarded white fish species, we compared the proportion of discards in the diet of great skuas with International Council for the Exploration of the Sea (ICES) estimates of quantities of fish discarded during 1986–2002 (see Methods). These data show that there are highly significant positive correlations between discard estimates and the importance of both whiting (arcsine square-root-transformed data: correlation coefficient, $r = 0.62$, degrees of freedom, d.f. $= 15$, $P = 0.008$; Fig. 1a) and haddock (arcsine square-root-transformed data: $r = 0.78$, d.f. $= 16$, $P < 0.0001$; Fig. 1b) in the diet of great skuas.

We analysed the relationship between the (arcsine square-root-transformed) percentage of bird prey consumed by great skuas and the abundance of both of their other main food resources, white fish discards and sandeels, to test whether changes in these two principal resources influence prey-switching to other seabirds (see Methods). We found a significant, negative, additive effect of the availability of discarded white fish (Fig. 2; Wald statistic $= 6.29$, d.f. $= 1$, $P = 0.01$) and the biomass of Shetland sandeel stock (Fig. 2; Wald statistic $= 19.43$, d.f. $= 1$, $P = 0.001$) on the proportion of bird in the diet of great skuas.

Estimates of discarded whiting and haddock varied considerably during 1986–2002 (Fig. 1). Discard rates are influenced by various complex and interactive factors, including stock size, recruitment, net mesh size, gear selectivity, legal minimum landing size, behaviour of fishermen and overall fishing intensity[4]. Therefore, the relationship between discard availability and discard use by great skuas is unlikely to be driven by unmeasured environmental factors and provides, to our knowledge, the most compelling evidence of a direct causal relationship between fishery discards and use by a top marine predator.

The declines in discard availability have coincided with long-term declines in the biomass of sandeel spawning stock, for which the lowest observed values were recorded in 2000 (ref. 9). It would seem that this has exacerbated the prey-switching tendency of great skuas and hence their likely impact on other seabird populations. Although one of the longer-term consequences of low sandeel abundance and an absence of discards may be a marked reduction in great skua breeding performance and population size, their ability to switch prey may buffer them from these consequences for some time. With relatively stable populations[11] and low levels of deferred breeding[19], variation in the percentage of bird prey in great skua diets will almost certainly reflect changes in predation rates on other seabirds.

There is evidence from elsewhere in Shetland that great skua predation reduced one large population of black-legged kittiwakes (*Rissa tridactyla*) by 54–85% between 1981 and 1995 (ref. 20), and negatively affected adult survival of black-legged kittiwakes on Foula[21]. Bioenergetics models indicate that a slight increase in the percentage of bird in the diet results in large numbers of other seabirds being consumed by great skuas. For example, a 5% increase in bird in the great skua diet at Foula is equivalent to the consumption of an additional 1,000 northern fulmars or 2,000 black-legged kittiwakes (Box 1). Although it is extremely difficult to quantify this impact on prey populations, this may reflect a substantial component of annual mortality (Box 1). We may there-

Box 1

Bio-energetics modelling to quantify seabird predation by great skuas

By using published values of energetic requirements of great skuas, as well as population estimates, it is possible to calculate the approximate amount of food needed to support the adult great skua population on Foula. With these data, we can explore a hypothetical model in which bird prey in the diet increases by 5%. We use published estimates of the calorific content of bird meat to calculate the mass of bird required to meet this requirement. Finally, by dividing this total by the body mass values of specific prey species, we can estimate the number of birds that would need to be eaten, if this model were true. We present population estimates of adult seabird prey (breeding numbers from published surveys in 2000 (ref. 27) and estimates of nonbreeders calculated by using published life-history parameters of each species for productivity, annual survival and age of first breeding) to provide a context for this theoretical predation rate.

It has been calculated[16] that adult great skuas require 2,480 kJ per bird per day for maintenance and activity (field metabolic rate). In the first 15 d of July (the period of diet sampling in this study), around 5,000 adult great skuas are present on Foula (breeders and nonbreeders combined)[17,27], giving an energetic requirement for this period of 1.86×10^8 kJ (that is, $15 \times 2{,}480 \times 5{,}000$). If we assume a 5% increase in birds in the diet, this would represent 9.3×10^6 kJ, which, for calorific values of 10.9 kJ g^{-1} for whole birds, would be equivalent to 853.2 kg of birds. If this energetic demand were met by consuming fully grown seabirds of a single species, the estimates shown in Box 1 Table 1 would apply.

We cannot, however, easily quantify the demographic groups that are affected by great skuas, which has implications for assessing the impact on population levels. For species such as fulmars and puffins that fledge chicks late in the summer, predation by great skuas is almost completely on adults. For kittiwakes and guillemots, predation is on adults and fledglings, and in some colonies on chicks. Observations of prey remains indicate that predation of adult birds predominates in April to mid-July, whereas predation of fledglings forms a larger part of the diet in late July. Predation of adult seabirds will affect populations of long-lived species more rapidly than will predation of eggs and chicks[28]; however, it is rarely possible to distinguish between pellets containing feathers from adult and those containing feathers from young birds. The effect of killing only an additional few per cent of the adult population of seabirds can be profound, given the high survival rates and low recruitment characteristic of these species, and can change a low rate of population growth into a population decline[28].

Box 1 Table 1 **Estimates of single species needed to support a 5% increase in seabird consumption by great skuas**

Species	Adult population estimate	Body mass (kg)*	Number of birds consumed†	Adult population consumed (%)
Northern fulmar	64,800	0.8	1,067	1.6
Black-legged kittiwake	6,400	0.41	2,094	32.8
Common guillemot	54,000	0.86	992	1.8
Atlantic puffin	55,000	0.4	2,133	3.9

*Data from ref. 29.
†Equivalent to 853.2 kg of bird prey/body mass.

fore predict that other seabirds such as northern fulmar, European storm-petrel (*Hydrobates pelagicus*), Leach's storm-petrel (*Oceanodroma leucorhoa*), common guillemot (*Uria aalge*) and Atlantic puffin (*Fratercula arctica*), which are already killed in large numbers by great skuas[16], might experience marked population declines before the skuas do themselves, because the skuas are able to switch from feeding on discards or sandeels.

Current numbers of seabirds may be artificially maintained in the northwestern North Sea owing to depleted stocks of piscivorous fish, which reduces competition for small schooling fish, and to the provision of discards and offal by fisheries[22]. In some areas, however, rates of predation on seabirds by great skuas have already reached levels that seem to be unsustainable[18,20]. It is unlikely that this predator simply has a beneficial role in maintaining healthy populations by removing sick or weak individuals.

Although it would not be appropriate to maintain current rates of discarding for the sake of seabirds, further drastic cuts in white fish catches in the North Sea will exacerbate the problem of great skua predation in the short term and may lead to marked reductions in seabird populations. It is clear, however, that sandeel abundance, in addition to white fish discard rates, influences prey-switching in this top marine predator (Fig. 2). Thus, measures to conserve stocks of sandeels should be maintained and perhaps given even greater priority to avert the scenario suggested here that is likely to occur if the discarding of white fish were to cease. In the longer term it is unclear whether the North Sea seabird community will return to a more 'natural' former state, or whether the effects of diet switching and predation will cause it to lurch to a completely different composition. ☐

Methods

Annual variations in discard availability

Data on the quantities of white fish discarded in the northwestern North Sea are provided by ICES[9,23]. Since 1960, there have been several step changes in technical measures such as net mesh size, minimum landing size and single-species quotas. These have interacted with changes in the behaviour of fishermen (such as the amount of selective upgrading by discarding marketable fish), resulting in discard rates of whiting falling faster than catches of this fish[9,23]. The proportion (by mass) of whiting caught in the North Sea that is discarded has decreased significantly in the past 40 yr ($r = -0.54$, d.f. = 40, $P < 0.05$); by contrast, the proportion of haddock discarded has not changed[9,23]. Despite the changes in the discard rate of whiting, the annual catch (tonnes) explains 91.5% of the variance in whiting discarded annually from 1960 to 2001; the relationship is best described by an exponential relationship: discard mass $= 11.783e^{0.0114(\text{catch mass})}$. For haddock, the annual catch (tonnes) explains 61% of the variance in the quantity of haddock discarded annually from 1960 to 2001; the relationship is best described by a linear regression: discard mass $= 0.3538(\text{catch mass}) + 10.95$.

Diet composition

Indigestible material regurgitated as pellets provides a reliable assessment of diet composition in great skuas[24]. Pellets were collected annually from club sites of nonbreeding birds on Foula, Shetland, in the first half of July (the peak period of the breeding season of skuas) during 1974–2002. Pellets of breeders were collected in only 6 yr; however, the proportion of bird in the pellets from nonbreeders' club sites correlates with that in the pellets from breeders' territories sampled in the same years (arcsine square-root-transformed $r = 0.83$, d.f. = 5, $P = 0.02$). Each pellet was identified to the lowest possible taxon and removed to prevent recounting. Any fish otoliths were stored dry before being measured and were identified by a guidebook[25].

To investigate the importance of discarded white fish species in skua diets, we applied linear regression to compare the proportion of haddock and whiting otoliths in skua diets (arcsine square-root-transformed) and ICES discard estimates of these two species. Haddock and whiting are demersal species, living at depths where great skuas, and other species that the skuas may kleptoparasitise such as northern gannet, are unable to catch them. In addition, the size of fish in the diet of great skuas (calculated from the length of otoliths[25]) is predominantly just below the commercial size limit (haddock: mean 27.6 cm, range 21.1–36.9 cm, $n = 4{,}739$; whiting: mean 30.1 cm, range 18.5–40.2 cm, $n = 8{,}032$), indicating that these are discards[26].

Using residual maximum likelihood models, we constructed a mixed model with (arcsine square-root-transformed) percentage of bird pellets (total number of pellets: 1974, $n = 100$; 1975, $n = 558$; 1976, $n = 483$; 1977, $n = 100$; 1978, $n = 100$; 1979, $n = 100$; 1980, $n = 100$; 1981, $n = 100$; 1982, $n = 100$; 1983, $n = 305$; 1984, $n = 100$; 1985, $n = 100$; 1986, $n = 200$; 1987, $n = 98$; 1988, $n = 598$; 1989, $n = 796$; 1990, $n = 187$; 1991, $n = 100$; 1992, $n = 694$; 1993, $n = 117$; 1994, $n = 199$) in the diet as the response variable, and tonnes of sandeels in the Shetland stock using virtual population analysis (VPA) from 1974 to 1994 (ref. 9; the period for which these data are available) and tonnes of haddock and whiting (combined) discarded in the northwestern North Sea (ICES subarea IV) as predictor covariates. All interactions were nonsignificant and were therefore removed from the model (Table 1).

To correct for problems of temporal autocorrelation and independence of data points, we entered covariates of all independent variables into the model for values at year$_{(n+1)}$/year$_n$. None of these terms was significant in the final model.

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Correspondence and requests for materials should be addressed to S.C.V. (s.votier@bio.gla.ac.uk) or R.W.F. (r.furness@bio.gla.ac.uk).