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ORIGINAL ARTICLE

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Scavenger communities and fisheries waste: North Sea discards support 3 million seabirds, 2 million fewer than in 1990

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Abstract

Every year fisheries discard >10 million tonnes of fish. This provides a bounty for scavengers, yet the ecological impact of discarding is understudied. Seabirds are the best-studied discard scavengers and fisheries have shaped their movement ecology, demography and community structure. However, we know little about the number of scavenging seabirds that discards support, how this varies over time or might change as stocks and policy change. Here, we use a Bayesian bioenergetics model to estimate the number of scavenging birds potentially supported by discards in the North Sea (one of the highest discard-producing regions) in 1990, around the peak of production, and again after discard declines in 2010. We estimate that North Sea discards declined by 48% from 509,840 tonnes in 1990 to 267,549 tonnes in 2010. This waste had the potential to support 5.66 (95% credible intervals: 3.33–9.74) million seabirds in the 1990s, declining by 39% to 3.45 (1.98–5.78) million birds by 2010. Our study reveals the potential for fishery discards to support very large scavenging seabird communities but also shows how this has declined over recent decades. Discard bans, like the European Union's Landing Obligation, may reduce inflated scavenger communities, but come against a backdrop of gradual declines potentially buffering deleterious impacts. More work is required to reduce uncertainty and to generate global estimates, but our study highlights the magnitude of scavenger communities potentially supported by discards and thus the importance of understanding the wider ecological consequences of dumping fisheries waste.

KEYWORDS
discards, energetics, fisheries, food requirements, scavengers, seabirds

1 | INTRODUCTION

Understanding fishery impacts is imperative for understanding marine ecology and conservation. The global marine fishing industry currently dumps ~10 million tonnes (10%) of their annual catch (Zeller, Cashion, Palomares, & Pauly, 2018), yet discarding is probably one of the least studied component of fishery impacts. Discarding peaked at 18.9 million tonnes in 1989, but has since almost halved (Zeller et al., 2018), and changes in policy, such as discard bans in the European Union (EU Landing Obligation), Norway, Chile and New Zealand, are likely to reduce discarding further (Real et al., 2018). Although bans are desirable for stock management, they may have unforeseen knock-on effects for the mammals, seabirds, fishes and crustaceans that scavenge on discharged biomass (Bicknell, Oro, Camphuysen, & Votier, 2013; Heath, Cook, Cameron, Morris, & Speirs, 2014; Oro, Genovart, Tavecchia, Fowler, & Martínez-Abraín,

2013). However, we are unable to understand fully the impact of changing discards because of knowledge gaps about the number/biomass of scavengers supported, how this has changed over time, or might vary in the future (Heath et al., 2014; Real et al., 2018).

Seabirds are the best-studied consumers of fisheries waste (Oro et al., 2013). At least 52% of species feed on discards to some degree, and fisheries waste is the dominant dietary item in some populations (Bicknell et al., 2013; Oro et al., 2013). Discarding has shaped many aspects of seabird ecology, including their movements (Bartumeus et al., 2010; Bodey et al., 2014; Votier et al., 2010), demography (Bicknell et al., 2013; Oro et al., 2013), and community structure (Church, Furness, Tyler, Gilbert, & Votier, 2019; Votier et al., 2004). However, there is still relatively little known about the number of seabirds that discards can support, how this has changed over time and what the likely consequences of changes in discard availability may be for seabird communities. A fuller understanding of the wider ecosystem-level impact of fisheries requires that we address this knowledge gap.

The North Sea is one of the world's largest discard-producing regions (Heath & Cook, 2015; Zeller et al., 2018) and also supports an internationally important seabird assemblage (Garthe, Camphuysen, & Furness, 1996; Paleczny, Hammill, Karpouzi, & Pauly, 2015). This makes it an excellent system in which to estimate the number of scavengers that could be supported by discards. During peak production in the late 1980s and early 1990s, North Sea fisheries generated 500,000–900,000 tonnes of discards (Alverson, 1997; Camphuysen & Garthe, 1997; Tasker et al., 2000). These were estimated to support ~6 million seabirds in 1990 by Garthe et al. (1996) in one of the only studies to attempt such a calculation. However, the model used to arrive at that figure did not account for the precision of its input variables; had that uncertainty been propagated, the final estimate could have been very imprecise, with 95% confidence intervals of 2.2 and 16.3 million birds (Stratoudakis, 1999). At the time, the largest source of variation in the model came from very poor estimates of discard production (Stratoudakis, 1999). More reliable discard data for the region have recently become available which show a steep decline in the overall quantity of fish discharged over the period 1978–2011 (Heath & Cook, 2015). Moreover, catches have also shifted away from fish that are easy for seabirds to swallow (~80% roundfish) to less easily ingested fish (>50% flatfish) (Heath & Cook, 2015), and the North Sea seabird community has also changed since the 1990s (Church et al., 2019; Mitchell, Newton, Ratcliffe, & Dunn, 2004). A robust estimate—acknowledging the inevitable uncertainties and accounting for long-term changes in discarding practices—of the size and composition of the discard scavenging seabird community in the North Sea is therefore overdue.

Here, we combine data on seabird abundance, diet and energetic expenditure, together with fisheries discard rates and fish energy content into bioenergetics models to estimate the number of seabirds that could be supported by discards in the North Sea around the time of peak production in the early 1990s (hereafter the 1990 model) and following discard declines in the late 2000s (hereafter the 2010 model) (Figure 1). We implement our model in a Bayesian framework, so that we can carry over input parameter uncertainty, and present our estimates split by species and by breeding and non-breeding seasons. We also consider our work in the context of global fisheries so that a broader understanding of the size of scavenging communities might be achieved. Finally, we discuss the ecological implications of our results in light of potential changes in practise and policy around discarding—the least studied component of fisheries impacts.

2 | METHODS

We focussed on a scavenger community of eight regular discard consuming North Sea seabird species (see Table 1 for species names, Figure 2) (Garthe et al., 1996). We define “discards” as fish and invertebrates caught at sea, but subsequently discharged, and “offal” as the livers and intestines of marketable fish removed during sorting and cleaning, and subsequently thrown overboard (Garthe et al., 1996). For the purposes of our model, we assumed that both the availability of natural prey and discards were constant in space and time. We implemented our bioenergetics model in JAGS (v.4.3.0; Plummer, 2003), an open-source software for fitting Bayesian hierarchical models using Monte-Carlo Markov

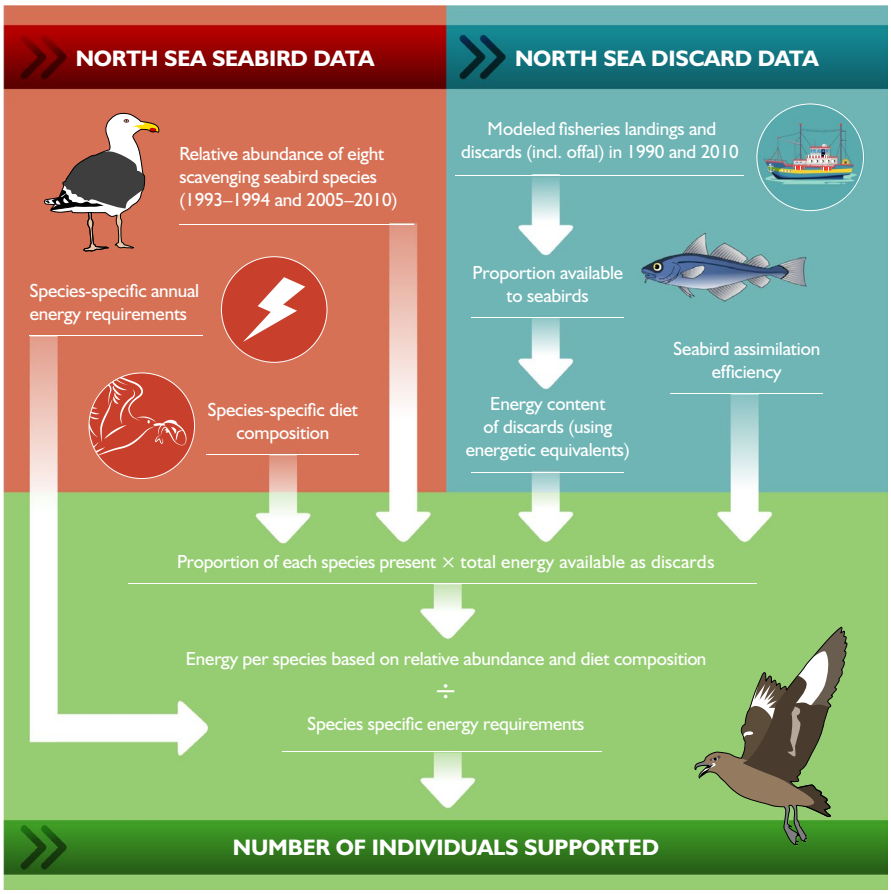

FIGURE 1 Schematic outlining the bioenergetic model used to estimate the number of seabirds in the North Sea supported by discards in 1990 and 2010

Chain (MCMC) simulation. We called JAGS via the "jagsUI" library (v. 1.4.9) for the open-source software R (v.3.2.3). Inference was based on three chains (iterations = 1,100,000 samples, burn-in = 100,000, thinning = 10). Convergence was checked visually and using Gelman–Rubin diagnostics (all $\widehat{R}$ values ≤1.01) (Brooks & Gelman, 1998). Unless specified, we present means ± 95% Bayesian credible intervals (CI).

2.1 | North Sea seabird abundance

For our 1990 model, we used published estimates of the relative abundance (proportions) of the eight seabird species (*s*) derived from the European Seabirds at Sea (ESAS) database and the International Bottom Trawl Survey (IBTS) database (Camphuysen et al., 1995; Garthe et al., 1996). We used the mean from both studies from May to June and August to September 1994 as the estimates for the breeding abundance ($M_{B,s}$) and the mean from both studies for surveys in January/February 1993 and October–November 1994 as the estimate for the non-breeding abundance ($M_{N,s}$; Table 1). For our 2010 model, we calculated mean abundances using data in the ESAS database (v.5.0). Birds were counted by strip-transect during ship-based surveys in the North Sea (Camphuysen & Garthe, 2004; Tasker, Jones, Dixon, & Blake, 1984). As coverage has been unequal over seasons and has decreased in recent years, the data from 2005 to 2010 were pooled to provide adequate coverage for ICES areas IVa, IVb and IVc and seasons, giving a total survey area of 23,266 km^2. Species-specific correction factors were applied to account for birds that may have been overlooked (Stone et al., 1995). Abundances of all eight species were calculated separately for the three areas, and separately for a breeding (May to August) and a non-breeding period (September to April). Abundances were averaged over the three areas (to give geographic regions equal representation) and converted to relative abundance proportions (Table 1).

2.2 | Seabird energy requirements

For both the 1990 and 2010 model, we calculated species-specific annual energy requirements ($R_{A,s}$) as:

$$R_{A,s} = (F_{B,s} \times P_{B,s}) + (F_{N,s} \times P_{N,s}) \quad (1)$$

where $F_{B,s}$ and $F_{N,s}$ are field metabolic rates (FMR, kJ/d) for breeding and non-breeding seabirds, respectively, and $P_{B,s}$ and $P_{N,s}$ are species-specific breeding and non-breeding periods (in days), respectively (Table 1). To estimate $F_{B,s}$ and $F_{N,s}$, we used a web-based Seabird FMR Calculator tool (https://ruthedunn.shinyapps.io/seabird_fmr_calculator) which uses a phylogenetically informed meta-analysis of seabird FMR during the breeding season (Dunn,

TABLE 1 Input data for seabird body mass, breeding and non-breeding periods, relative abundance (split by the breeding and non-breeding periods), and percentage of the diet made up of discards (discard consumption range) for the eight focal species

Species	Body mass[b] mean (g)	Breeding[b] period (d)	Non-breeding[b] period (d)	Relative abundance				Discard consumption range[a] (%)
				1990 Breeding	1990 Non-breeding	2010 Breeding	2010 Non-breeding	
Northern fulmar (*Fulmarus glacialis*, Procellariidae)	790	107	258	0.627	0.429	0.217	0.204	25–80
Northern gannet (*Morus bassanus*, Sulidae)	2,920	143	222	0.036	0.033	0.083	0.083	8–70
Great skua (*Stercorarius skua*, Stercorariidae)	1,418	103	262	0.006	0.001	0.009	0.005	30–80
Common gull (*Larus canus* Laridae)	387	89	276	0.003	0.026	0.024	0.139	10–30
Lesser black-backed gull (*Larus fuscus*, Laridae)	830	68	297	0.040	0.007	0.410	0.126	30–60
Herring gull (*Larus argentatus*, Laridae)	958	95	270	0.044	0.218	0.145	0.154	22.5–40
Great black-backed gull (*Larus marinus*, Laridae)	1,600	128	237	0.019	0.068	0.009	0.126	30–66
Black-legged kittiwake (*Rissa tridactyla*, Laridae)	400	90	275	0.225	0.218	0.102	0.164	30–50

[a]Sources for discards consumption: Camphuysen and Garthe (2000); Camphuysen and Garthe (1997); Church et al. (2019); Furness, Ensor, and Hudson (1992); Furness and Hislop (1981); Furness and Tasker (1999); Garthe and Hüppop (1994); Tasker and Furness (1996); Votier et al. (2010).

[b]Sources for body mass, and breeding and non-breeding periods: Cramp et al. (1983a); Cramp et al. (1983b); Dunning Jr (2007); Gabrielsen, Mehlum, and Nagy (1987); Hahn, Bauer, and Klaassen (2007); Phillips and Hamer (2000); Schreiber and Burger (2002); Snow and Perrins (1998) and Stephen C. Votier.

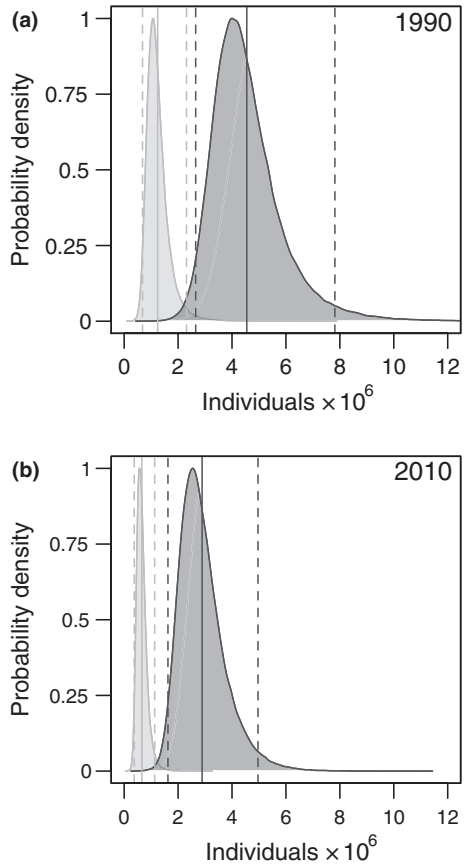

FIGURE 2 Posterior probability densities (polygons), means (solid line) and 95% CI (dashed lines) for the estimated number of seabirds consuming fishery discards in the North Sea during the breeding (light grey) and non-breeding seasons (dark grey) in (a) 1990 (b) 2010

White, & Green, 2018). The tool requires inputs of species, body mass, colony latitude and breeding phase, and outputs an estimate of daily FMR with confidence intervals for each of three breeding phases: incubation, brood and crèche (post-guard) (Dunn et al., 2018). We used species-specific mean body masses (Table 1) and assumed a colony latitude of 55°N in each case. We then used the resulting estimate ($\bar{x}$), lower (L) and upper (U) confidence intervals to estimate a standard deviation (SD) for each species (s) and in each of the three breeding phases (p) based on the central limit theorem:

$$SD_{p,s} = \frac{(U_{p,s} - \bar{x}_{p,s})/1.96 + (\bar{x}_{p,s} - L_{p,s})/1.96}{2} \quad (2)$$

We then used these values to specify informative gamma priors (Figure S1). For $F_{N,s}$, we used the estimates of FMR during incubation to specify Gamma($\alpha_{N,s}$, $\beta_{N,s}$), where $\alpha_{N,s}$ = the shape parameter ($\bar{x}^2_{p,s}/SD^2_{p,s}$), and $\beta_{N,s}$ = the rate parameter ($\bar{x}^2_{p,s}/SD^2_{p,s}$) and p = incubation. For $F_{B,s}$, we combined all three breeding phase estimates by taking 999,999 random samples (sim) from a gamma distribution (using the "rgamma" function for R), with one third generated using the shape and rate from each breeding phase. We then extracted species-specific shape ($\alpha_{B,s}$) and rate ($\beta_{B,s}$) parameters for breeding, based on the mean ($\bar{x}_{sim}$) and SD (SD_{sim}), where $\alpha_{B,s} = (\bar{x}_{sims}/SD_{sim})^2$ and $\beta_{B,s} = \bar{x}_{sims}/SD^2_{sim}$.

2.3 | Seabird diet composition

For both 1990 and 2010, we modeled the species-specific discard proportions in the diet (α_s) using 39 observations from 9 studies (ranges and sources shown in Table 1). We kept these values consistent for the two model runs because we could not find any specific diet studies for this period that reported a percentage of discards in the diet that fell outside of the range we used to capture the uncertainty in this parameter (Table 1; see Appendix S1 for details) and the one long-term diet study that collected across this period showed no evidence of a temporal trend in the proportion of great skua pellets containing discards (Church et al., 2019; Figure S2). Because there were between 3 and 8 observations for each species (Figure S3), we combined the data and used beta regression, with species as a random effect:

$$\begin{aligned} Y_j &\sim \text{Beta}(\varsigma_j, \rho_j), \\ \varsigma_j &= \mu_j \tau_{j,s}, \\ \rho_j &= (1-\mu_j)\tau_{j,s}, \\ \log(\tau_{j,s}) &\sim \text{Normal}(0, 10^{-3}), \\ \mu_j &= \theta_s X_j + b_{j,s} \end{aligned} \quad (3)$$

where Y_j are the 39 observed proportions, θ_s is the coefficient estimate for a species-specific mean proportion, $b_{j,s}$ denotes a random effect accounting for repeat observations (j) within species (s), and X_j is a vector denoting the species to which an observation belongs. For θ_s, we specified a uniform prior bounded by the minimum and maximum observation in the data set: Uniform(0.08,0.8) and used Normal(0,1/σ^2) for the hyper-prior associated with the random effect ($b_{j,s}$), where the precision was 1/ σ^2~Gamma(10^{-3},10^{-3}). Finally, the amount of its annual energy requirement that each species could obtain from discards ($D_{A,s}$) was as follows:

$$D_{\text{A,S}} = R_{\text{A,S}} \times \alpha_{\text{S}} \quad (4)$$

2.4 | Energy available from discards

To calculate the energy available as discards, we used informative gamma priors which we generated by multiplying the modeled mean (±95% CI) tonnage landed and discarded by mixed demersal fisheries in the North Sea in each of 1990 and 2010 (Heath & Cook, 2015) by energetic equivalents for each discard type (Table 2) to obtain calorific values (Figures S4and S5). To estimate the tonnage of benthic invertebrates discarded, we incorporated the published range of 4–11 kg of benthic invertebrates discarded for every kg of sole (*Solea solea*, Soleidae) landed (Bergman, Fonds, De Groot, & Van Santbrink,

TABLE 2 Input data for the mean biomass of discards thrown back into in the North Sea in 1990 and 2010 for the six discard types (Heath & Cook, 2015), the energetic equivalents used to convert the biomass into calorific values and the range of each discard type consumed by seabirds (based on the sources given). The calorific value of discards shown are the means estimated by the bioenergetics models

Discard type	Discarded mean biomass (tonnes) (95% credible intervals)		Energetic equivalent[a] (kJ/g)	Calorific value of discards (kJ × 10^6)		Range of discards consumed (proportion)[c]
	1990	2010		1990	2010	
Roundfish	120,768 (68,843–186,573)	56,819 (22,568–106,707)	4.0	483,072 (275,372–746,292)	227,274 (90,273–426,830)	0.23–0.95
Elasmobranchs	4,587 (841–11,455)	2,192 (364–5,626)	4.0	18,348 (3,363–45,819)	8,770 (1,456–22,506)	0.12–0.15
Flatfish	120,970 (61,584–199,913)	74,493 (38,533–122,342)	4.0	483,880 (246,335–799,650)	297,971 (154,130–489,370)	0.03–0.70
Offal	48,692 (39,291–59,028)	26,219 (21,287–31,660)	9.0	438,228 (353,619–531,256)	235,968 (191,587–284,936)	0.41–1.00
Other marketable species	14,445 (6,095–26,277)	13,576 (5,290–25,666)	4.0	57,781 (24,381–105,109)	54,304 (21,161–102,664)	0.36–0.84
Benthic invertebrates[b]	200,378 (107,965–304,859)	94,251 (50,585–144,249)	2.0107	402,899 (217,086–612,979)	189,510 (101,712–290,041)	0.003–0.17
Total	509,840 (284,619–788,105)	267,549 (138,627–436,251)	-	1,884,208 (1,470,494–2,348,266)	1,013,796 (767,184–1,304,664)	-

[a]Energetic equivalents following Garthe et al. (1996) and based on Cummins and Wuycheck (1971); Daan (1975); Furness et al. (1988); Hislop, Harris, and Smith (1991); Sidwell (1981)

[b]The discarded biomass of benthic invertebrates are the means estimated by the bioenergetics models because this is based on 4–11 kg of benthic invertebrates discarded for every kg of sole landed (see Methods). We used a mean of 26,694 tonnes of sole landed in 1990 and 12,561 tonnes in 2010 (Heath & Cook, 2015)

[c]Sources for proportion of discards consumed—Roundfish—(Camphuysen et al., 1995; Camphuysen & Garthe, 1997; Catchpole, Frid, & Gray, 2005; Furness, Edwards, & Oro, 2007; Garthe et al., 1996; Garthe & Hüppop, 1993, 1994; Sotillo et al., 2014; Walter & Becker, 1997); Elasmobranchs—(Garthe et al., 1996); Flatfish—(Camphuysen, 1993, 1994; Camphuysen et al., 1995; Camphuysen & Garthe, 1997; Catchpole et al., 2005; Garthe et al., 1996; Garthe & Hüppop, 1993, 1994; Sotillo et al., 2014; Walter & Becker, 1997); Offal—(Camphuysen, 1993, 1994; Camphuysen et al., 1995; Camphuysen & Garthe, 1997; Furness et al., 2007; Garthe et al., 1996; Hudson & Furness, 1989); Other marketable species—(Garthe & Hüppop, 1994); Benthic invertebrates—(Camphuysen, 1994; Camphuysen et al., 1995; Camphuysen & Garthe, 1997; Catchpole et al., 2005; Garthe et al., 1996; Walter & Becker, 1997).

1996; Camphuysen et al., 1995; Fonds, 1991; Fonds, Verboom, & Groeneveld, 1992) as a uniform prior in both models. Offal was assumed to make up 11% of roundfish landed mass, 6.5% for flatfish (Furness, Hudson, & Ensor, 1988) and 2.35% for other marketable species caught (Garthe et al., 1996). Because these values were reported without uncertainty, we assessed the sensitivity of our model to them by rerunning the 1990 model with the offal produced from roundfish (11%), flatfish (6.5%) and other marketable species (2.35%) increased and decreased by 10%, and by rerunning the 2010 model with the amount of offal discharged set to zero (see Supplementary Results in Appendix S1). We then used the resulting mean ($\bar{x}$), lower (L) and upper (U) 95% confidence intervals to estimate a standard deviation (SD) for each discard type (t) following equation 2 and used these values to specify informative gamma priors: Gamma(δ_t, ϖ_t), where δ_t = the rate parameter ($\delta_t = \bar{x}_t^2/SD_t^2$) and ϖ_t = the shape parameter ($\varpi_t = \bar{x}_t/SD_t^2$).

Seabirds do not always consume all available discards, and consumption rates vary by type (Camphuysen et al., 1995; Garthe et al., 1996). We therefore modeled the uncertainty in the proportion of the available discards that seabirds consume for each discard type (Figure S6) using 61 observed consumption rates from 12 field studies (see Table 2) for both 1990 and 2010. There were between 2 and 16 observations per discard type, so we combined the data and used beta regression, with discard type as a random effect. However, 100% of offal was eaten in one discard experiment (Garthe et al., 1996) and although 0 and 1 may be genuine outcomes, their logits are undefined (Smithson & Verkuilen, 2006). One common solution is to transform the data (Z) to a variable ($\acute{Z}$) in the open interval (0, 1) using a weighted average (Smithson & Verkuilen, 2006):

$$\acute{Z} = (Z(N-1)+k)/N \tag{5}$$

where N is the sample size and k is a constant. The choice of k is essentially arbitrary (Smithson & Verkuilen, 2006), and we used 0.5092 (the mean of Z) as that minimized the overall error between $\acute{Z}$ and Z (<7 × 10^{-17}). Thus, the type-specific consumption rates (c_t) were modeled as:

$$\begin{gathered}\acute{Z}_j \sim \text{Beta}(\varsigma_j,\rho_j),\\ \varsigma_j = \mu_j\tau_{j,t},\\ \rho_j = (1-\mu_j)\tau_{j,t},\\ \log(\tau_{j,t}) \sim \text{Normal}(0, 10^{-3}),\\ \mu_j = c_t V_j + b_{j,t}\end{gathered} \tag{6}$$

where $\acute{Z}_j$ are the 61 observed proportions transformed into the interval (0,1), c_t is the coefficient estimate for a type-specific mean proportion, $b_{j,s}$ denotes a random effect accounting for repeat observations (j) within type (t) and V_j is a vector denoting the discard type to which an observation belongs. For c_t, we specified a uniform prior: Uniform(0,1) and used Normal(0,1/σ^2) for the hyperprior associated with the random effect ($b_{j,t}$), where the precision was 1/σ^2~Gamma(10^{-3},10^{-3}).

2.5 | Energy from discards assimilated by seabirds

The amount of energy animals assimilate varies according to food type. We used 45 data points from 14 studies on 22 seabird species consuming diets of various fish and invertebrate species to model the uncertainty in assimilation efficiency for all discard types (Figure S7) using beta regression. For both 1990 and 2010, the mean assimilation efficiency (G_{mod}) was modeled as:

$$\begin{gathered}\upsilon_j \sim \text{Beta}(\xi_j,\varrho_j),\\ \xi_j = \eta_j\tau,\\ \varrho_j = (1-\eta_j)\tau,\\ \log(\tau) \sim \text{Normal}(0, 10^{-3}),\\ \eta_j = G_{mod}\end{gathered} \tag{7}$$

where υ_j are the 45 observed assimilation efficiencies and G_{mod} is the coefficient estimate for a mean assimilation efficiency, for which we specified an uninformative uniform prior: Uniform(0,1).

The available energy from invertebrates (G_I) was thus:

$$A_I = ((W_I \times E_I) \times G_{mod}) \times C_I \tag{8}$$

where C_I is the beta distribution for the proportion of invertebrate discards consumed, E_I is the gamma distribution for the energy available from invertebrate discards, G_{mod} is the beta distribution for the modeled assimilation efficiency and W_I is the uniform distribution Uniform(4,11) for the conversion factor from landings of sole. For the five other discard types (t; roundfish, flatfish, elasmobranchs, offal and other marketable species, Table 2) the available energy (G_t) was defined as:

$$G_t = (C_t \times E_t) \times G_{mod} \tag{9}$$

where C_t is the type-specific beta distribution for the proportion of discards consumed, E_t is the gamma distribution for the energy available from each discard type and G_{mod} is the beta distribution for the modeled assimilation efficiency. The total energy that can be assimilated from discards (G) was thus:

$$G = \sum_{t=1}^{5} G_t + G_I \tag{10}$$

The annual total energy available to each seabird species ($E_{A,s}$) was therefore:

$$E_{A,S} = ((G \times P_{B,S}) \times M_{B,S}) + ((G \times P_{N,S}) \times M_{N,S}) \tag{11}$$

where $L_{B,s}$ and $L_{N,s}$ are (respectively) the breeding and non-breeding season seabird abundances.

2.6 | Number of seabirds supported

The number of seabirds supported by discards in each species (T_s) was as follows:

$$T_s = E_{A,s}/D_{A,s} \tag{12}$$

TABLE 3 Estimated numbers of eight North Sea seabirds (in thousands) supported by discards in 1990 and 2010, and the estimated number of mature individuals in their European populations in 2015 (BirdLife International, 2015)

	No. of individuals supported × 10^3 (95% credible intervals) in 1990			No. of individuals supported × 10^3 (95% credible intervals) in 2010			European population 2015 (individuals × 10^3)
Species	Breeding	Non-breeding	Annual	Breeding	Non-breeding	Annual	
Northern fulmar	601.13 (264.7–1,3,274.6)	1,227.92 (598.6–2,565.2)	1,805.97 (911.3–3,713.7)	111.18 (47.9–247.5)	312.07 (148.6–655.4)	412.22 (203.1–849.7)	~7,000
Northern gannet	25.30 (9.4–63.6)	42.50 (16.7–104.6)	66.40 (26.8–162.2)	31.06 (11.3–78.9)	57.25 (22.0–142.0)	86.19 (34.0–211.8)	1,370
Great skua	4.07 (2.0–8.2)	1.25 (0.7–2.4)	5.61 (3.1–10.8)	3.18 (1.6–6.4)	4.52 (2.3–8.9)	7.75 (4.1–15.1)	~34.5
Common gull	9.05 (2.9–22.9)	337.34 (116.1–826.7)	325.29 (114.5–790.7)	43.01 (13.7–110.1)	961.06 (324.7–2,376.1)	946.55 (326.0–2,321.2)	~2,160
Lesser black-backed gull	40.68 (17.9–93.1)	32.94 (15.0–74.6)	75.54 (35.2–169.8)	224.66 (96.2–519.3)	322.50 (143.4–736.3)	553.90 (251.1–1,253.4)	~1,400
Herring gull	69.37 (27.7–164.1)	1,185.75 (504.0–2,725.7)	1,188.33 (515.0–2,710.0)	123.25 (48.2–292.3)	447.44 (186.4–1,033.5)	558.15 (236.9–1,279.0)	~2,430
Great black-backed gull	21.27 (9.4–48.8)	159.78 (74.1–360.1)	173.54 (83.3–385.8)	5.48 (2.4–12.7)	157.96 (71.5–359.4)	155.04 (72.5–348.3)	~400
Black-legged kittiwake	472.97 (201.8–1,118.4)	1,560.52 (699.9–3,642.5)	2,014.62 (911.0–4,679.8)	114.44 (47.8–273.2)	627.54 (274.1–1,467.7)	727.66 (320.9–1,696.7)	~4,410
Total	1,243.85 (680.8–2,652.8)	4,548.00 (2,652.8–7,815.7)	5,655.31 (3,329.9–9,736.6)	656.25 (373.1–1,132.3)	2,890.36 (1,624.1–4,963.4)	3,447.47 (1,980.3–5,784.0)	19,204.5

and the total number of seabirds supported by discards in the North Sea (T) was as follows:

$$T = \sum_{s=1}^{8} T_s \quad (13)$$

To provide a sense of relative scale, we compare our outputs to species-specific estimates of the number of mature individuals in their European breeding populations (Table 3). We use the European breeding populations because individuals of at least some of our focal species move into, and winter in, the North Sea from other parts of Europe during their non-breeding seasons (Fort et al., 2012; Frederiksen et al., 2012; Garthe, Hallgrimsson, Montevecchi, Fifield, & Furness, 2016).

3 | RESULTS

3.1 | North Sea discard production

We estimate that North Sea mixed demersal fisheries generated 509,840 (284,619–788,105) tonnes of discards in 1990 and this declined by 48% to 267,549 (138,627–436,251) tonnes in 2010 (Table 2). Roundfish, which are particularly important food for seabirds because they can be easily swallowed, declined by 52.9% (Table 2; from 120,768 to 56,819 tonnes). When taking account of the energetic content of different discard types, this represented 1,884 (1,471–2,348) and 1,014 (767–1,305) billion kJ of biomass discarded from North Sea mixed demersal fisheries in 1990 and 2010, respectively.

3.2 | Number of seabirds supported by North Sea discards

After accounting for assimilation efficiency and consumption rates in 1990, 720 (499–984) billion kJ were available to support an estimated 1.24 (0.68–2.65) million birds during breeding and 4.55 (2.65–7.82) million during the non-breeding season (Figure 2A). In 2010, 385 (257–548) billion kJ of discards could be used, potentially supporting 656,255 (373,084–1,132,250) birds during breeding and 2.89 (1.62–4.96) million individuals during the non-breeding season (Figure 2B). Combining the seasonal posteriors gave a total of 5.66 (3.33–9.74) million seabirds potentially supported in 1990 versus 3.45 (1.98–5.78) million individuals—or 39% fewer—able to consume fishery discards in the North Sea in 2010 (Figure 3A).

3.3 | Changes in scavenging seabird community supported by discards

The largest declines in the number of birds supported were for northern fulmars and black-legged kittiwakes, and the largest increases were in the numbers of lesser black-backed gulls and common gulls potentially feeding on discards (Figure 3B). Although the overall number has approximately halved, the annual estimate for 2010 still represents ~18% (CI: 10–30%) of these eight species' estimated European populations in 2015 (Table 3), with this percentage being highest for common gulls at ~44% (CI: 15–108%) and lowest for northern fulmars at ~6% (CI: 3–12%) (Table 3).

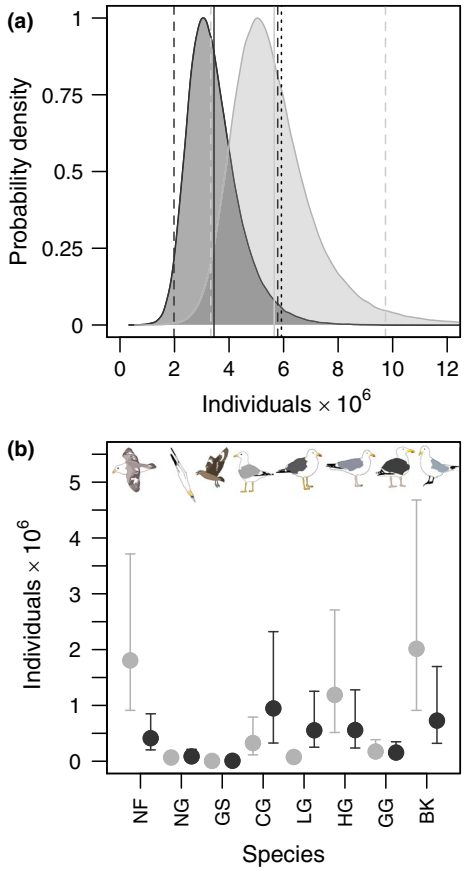

FIGURE 3 (a) Posterior probability density (polygon), mean (solid line) and 95% CI (dashed lines) for the total estimated number of seabirds consuming fishery discards in the North Sea in 1990 (light grey lines and polygon) and 2010 (dark grey lines and polygon). A previous estimate of 5.9 million individuals supported by discards in 1990 (Garthe et al., 1996) is also shown (black dotted line) and (b) Posterior means (circles) and 95% CI (whiskers) for the estimated number of individuals consuming discards in the North Sea in 1990 (light grey) and 2010 (dark grey) for the eight focal species: BK, black-legged kittiwake; CG, common gull; GG, great black-backed gull; GS, great skua; HG, herring gull; LG, lesser black-backed gull; NF, northern fulmar; NG, northern gannet

4 | DISCUSSION

In this study, we estimate the number of seabirds that could be supported by discards in the North Sea, incorporating sources of uncertainty to include credible intervals around these values. We estimate that the change in discard composition (especially the decline in easily swallowed roundfish) and the 48% fall in total discard production in the North Sea from 1990 to 2010 (Table 2) led to a reduction of ~2.2 million seabirds (39%) potentially supported by fishery waste (Figure 2). Wide credible intervals notwithstanding, the mean decline

suggests substantial changes in the size and relative composition of the seabird scavenging assemblage. Below we discuss our approach, variation among species and seasons, the ecological implications in light of changes to fishing policy and the global implications of this study.

4.1 | Estimates of discard production

Our estimates of the biomass discarded into the North Sea were based on hind-cast estimates from landed weights and length distributions from scientific trawl surveys (Heath & Cook, 2015). Catches in the scientific trawl surveys might differ substantially from commercial catches by other gear types, and there are likely to be other biases that we could not account for in our model. Nevertheless, these discard estimates appear to be robust. Our 1990s estimate of 509,840 (284,619–788,105) tonnes is in keeping with earlier estimates, which placed the total amount of fish and benthic invertebrates at between 500,000 and 900,000 tonnes in the 1980s and 1990s (Alverson, 1997; Camphuysen & Garthe, 1997; Tasker et al., 2000). Of that, ~330,000 tonnes were considered to be demersal fish in 1991 (see Heath & Cook, 2015) which compares well to our estimate for 1990 of 260,770 (137,363–424,218; Table 2) for all fish combined. Regardless, understanding how many scavengers are supported by fisheries discards will continue to depend on improved methods to estimate the biomass thrown back into the sea (Heath & Cook, 2015; Stratoudakis, 1999).

4.2 | Challenges in estimating the size of discard communities

Models of the type used here are limited by the quality and extent of data available for specific input parameters (Stratoudakis, 1999). Despite there being relatively good data on discards (Heath & Cook, 2015) and the diet and abundance of scavenging seabirds available for the North Sea, our input parameters contained considerable uncertainty. When propagated through the model, this resulted in estimates with wide credible intervals (Figure 2), highlighting the challenges of generating precise estimates of the size of the scavenger community supported by discards, as well as the value of modeling these in a Bayesian framework.

Minimizing the uncertainty when estimating scavenger numbers supported by discards requires careful collection of data on scavenger ecology and biology. For example, estimates of the proportion of discards that get consumed by seabirds predominately come from a large-scale experimental programme undertaken in the North Sea in the 1990s in which potential prey were discarded at fixed intervals in time (Camphuysen et al., 1995; Garthe et al., 1996; Garthe & Hüppop, 1998). The number of experimental results was small for some discards types (e.g. elasmobranchs), so the posterior uncertainty for this input parameter was influenced by our choice of prior to some extent (Figure S6). Also, these experiments reflected discharge rates from some gear types, such as those used in longline fisheries, but may overestimate consumption rates that occur following pulsed discharges from vessels engaged in demersal and pelagic trawling (Depestele, Rochet, Dorémus, Laffargue, & Stienen, 2016). We are not aware of any comparable, large-scale discarding experiments that have been undertaken since (presumably for logistical and financial reasons), although smaller-scale and shorter-term experiments continue (Depestele et al., 2016; Sotillo, Depestele, Courtens, Vincx, & Stienen, 2014). We recommend that such studies consider examining the influence of varying discharge rates on species-specific discard consumption.

Bioenergetics models are also sensitive to changes in diet composition and we therefore rely on accurate dietary data to parametrize models of this kind. Our data came from a range of methods, including analysis of chick regurgitates, pellets, isotopes and observations at sea, thus providing a robust estimate of seabird diet. However, there are uncertainties. For instance, there is strong intra-specific variation in discard consumption, with some individuals specializing on fisheries waste (Patrick et al., 2015; Tyson, Shamoun-Baranes, Van Loon, Camphuysen, & Hintzen, 2015; Votier, Bearhop, Ratcliffe, Phillips, & Furness, 2004; Votier et al., 2010). Moreover, the amount to which seabirds rely on discards likely changes with age (Votier, Bearhop, Fyfe, & Furness, 2008), their annual cycle (Sotillo et al., 2014) and the availability of natural prey (Votier, Furness, et al., 2004). However, there remain little data available to parameterize a link between individual behaviour and population level effects of the kind relevant to our model (Patrick et al., 2015). Therefore, we urge that monitoring programmes incorporate data on seabird diet, at-sea distribution and abundance, across the full annual cycle and all components of the population to enable an effective ongoing assessment of the effects of changing discards on seabird populations.

4.3 | Ecological implications of declining discards on seabird communities

Shrinking stocks and discard bans will reduce fisheries waste, leading to less food for scavengers. Our study was able to quantify this change in the North Sea over a period of profound change. The revised estimate of 5.66 (3.33–9.74) million seabirds potentially supported in 1990 declined to 3.45 (1.98–5.78) in 2010. Other studies have suggested that the relative biomass of scavenging seabirds and marine mammals can be maintained under scenarios where discards from fisheries are reduced gradually (Fondo, Chaloupka, Heymans, & Skilleter, 2015; Heath et al., 2014), perhaps because these groups are opportunistic and can quickly switch their diet away from fisheries waste (Tew Kai et al., 2013; Votier, Furness, et al., 2004). Abrupt changes associated with discard bans, like the EU's Landing Obligation, however, are expected to have substantial impacts on these species (Bicknell et al., 2013; Depestele et al., 2016; Fondo et al., 2015; Heath et al., 2014; Moutopoulos, Tsagarakis, & Machias, 2018). In this context, it is noteworthy that our results suggest that a 39% decline in abundance of scavenging seabirds could already have occurred alongside a relatively gradual reduction in discards (~48%) over the two decades of our study, with some species affected more than others.

The biggest declines in our model were in the numbers of northern fulmars (~1.4 million or 77%), black-legged kittiwakes (~1.3 million or 64%), herring gulls (~630,000 or 53%) and great black-backed gulls (~18,500 or 11%) supported (Table 1, Figure 2). These reductions represent significant percentages of the 2015 European population (Table 3) and of the numbers of these species thought to winter in the North Sea in the late-1980s and early-1990s; ~1.9 million northern fulmars, ~1 million black-legged kittiwakes, ~900,000 herring gulls and ~300,000 great black-backed gulls (Skov, Durinck, Leopold, & Tasker, 2007). These declines also coincide with population declines at some North Sea colonies in each of these species (BirdLife International, 2015; Camphuysen & Gronert, 2012; Church et al., 2019; Foster, Swann, & Furness, 2017). The reasons for these declines are not entirely clear, and may not necessarily be underpinned by changes in discards (Skov & Durinck, 2001), though changes in herring gull numbers at some sites have been linked to declining discards (Foster et al., 2017). Some species may have been better able to buffer the gradual reduction in discards by feeding on alternative prey, being more aggressive competitors or by dispersing to novel habitats (Bicknell et al., 2013; Votier, Furness, et al., 2004). Prey switching could help to explain the increases in numbers of northern gannets (30%) and great skuas (38%) that could be supported (Table 1, Figure 2). Both species are dominant scavengers at fishing vessels (Oro et al., 2013) whose populations have remained relatively stable or increased during 1990 to 2010 (Hayhow et al., 2017). There were also sharp increases in the number of common (191%) and lesser black-backed gulls (633%) that could be supported, with our estimates suggesting that >30% of the European population of both species are potentially using North Sea discards at some point during their annual cycle (Table 3). These large increases are likely because of changes in the distribution of these gulls (Oro et al., 2013) leading to higher relative abundance in the European Seabirds at Sea data used in our model.

Lastly, exactly how the ecological impacts of discard bans will manifest themselves remains unclear. They are likely to interact with climate-mediated declines in forage fish abundance (Church et al., 2019) and concurrent changes in policy that will reduce the accessibility of other anthropogenic subsidies, notably food waste at landfill sites (Real et al., 2017). Some scavengers will decline dramatically if they cannot find alternative prey sources (Heath et al., 2014), while other species may benefit from discard bans via reduced bycatch risk (Bicknell et al., 2013). Moreover, as the options that some species have relied on in the past disappear, trying to exploit alternative food sources could bring them into greater conflict with humans. For example, large gulls may be forced into inland breeding and feeding grounds (Bicknell et al., 2013; Osterback, Frechette, Hayes, Shaffer, & Moore, 2015) where they are considered a nuisance, and great skua are likely to switch to predating other smaller seabird species (Votier, Furness, et al., 2004), some of which are now of conservation concern (Church et al., 2019). This could ultimately lead to a conundrum for management, as has occurred in southern Africa where great white pelicans (*Pelecanus onocrotalus*, Pelecanidae) and Cape fur seals (*Arctocephalus pusillus pusillus*, Otariidae) are actively managed to stop them predating on four Endangered seabird species (David et al., 2003; Mwema, de Ponte Machado, & Ryan, 2010). Finally, despite legislation, it is unclear how Landing Obligations will be implemented or enforced, highlighting further the need to quantify accurately discard production and its potential effect on scavengers.

4.4 | Global context

While we focus on the North Sea, seabirds are attracted to feed on discards worldwide with associations reported from the southwest Atlantic (Granadeiro, Phillips, Brickle, & Catry, 2011), western Mediterranean (Oro & Ruiz, 1997), southern South America (Gonzalez-Zevallos & Yorio, 2006), Baltic Sea (Garthe & Scherp, 2003), northwest Atlantic (Montevecchi, 2002), southeast Atlantic (Crawford, Underhill, Raubenheimer, Dyer, & Martin, 1992), Canary Current (Camphuysen & van der Meer, 2005) and Australian waters (Svane, 2005). There are no global estimates of the number of seabirds that fisheries waste could support, but it is likely to be considerable given the global biomass of discards across all ocean basins. The historically high biomass of North Sea discards probably led to a particularly large scavenging community, making it inappropriate to scale our estimate up to other regions. Instead, a reliable global estimate would require not only detailed data on discards (Zeller et al., 2018) and seabird numbers (Paleczny et al., 2015), but also the composition of seabirds attending vessels and their diet. Such studies would be of particular significance given the large regional changes in discard production over time (Zeller et al., 2018).

5 | CONCLUSIONS

We estimate that North Sea discards can support ~3.45 million seabirds per annum, but this declined by 39% from close to the period of peak discard production in the 1990s, indicating a shift away from a scavenger-dominated ecosystem. These findings are important in the context of global discard declines and bans, including the EU's Landing Obligation, as this gradual reduction may lessen any deleterious impacts of an abrupt drop in discards. Nevertheless, discards still have the potential to support large numbers of scavenging seabirds in the North Sea and the general lack of empirical data on the impacts of fishery discards at an ecosystem level makes it difficult to predict the real ecological consequences of the landing obligation. Further work is needed to monitor the response of seabird scavengers to changing fishery practices where discard bans are implemented and to quantify their numbers globally, particularly if we are serious about adopting an ecosystem-level approach to fisheries management. Data on global discard rates are available (Zeller et al., 2018), but information on seabird community composition, their diet and how this varies over time are also required in order to construct robust bioenergetics models.

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DATA AVAILABILITY STATEMENT

The data used in the models are either in the Tables or appended at the end of the Supporting Information.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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