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Spatial distribution of seabird biomass removal and overlap with fisheries in a large marine ecosystem

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Abstract

Globally, seabirds remove a prey biomass equivalent to commercial fishery landings, suggesting likely competition for resources that will vary spatially and seasonally. Using extensive aerial surveys combined with species-specific energetic requirements, we calculated and mapped at-sea removal of prey biomass by seabirds during the breeding and non-breeding seasons and compared this to the seasonal distribution of fishing effort. The distribution of prey biomass removal by seabirds was concentrated in coastal areas, with up to 6.39 kg/km^2/day of biomass consumed in the breeding season and up to 4.3 kg/km^2/day in the non-breeding season. Offshore, average biomass consumption ranged from 0.28–1.53 to 0.75–1.84 kg/km^2/day in the breeding and non-breeding seasons, respectively. Total prey biomass removal by seabirds across the study area (the Irish Exclusive Economic Zone covering an area of 341 183 km^2) was estimated at around 441.2 tonnes/day in the breeding season and 478 tonnes/day in the non-breeding season, highlighting the significant role that seabirds play in marine ecosystems. The fine-scale spatial distribution of prey biomass removal by seabirds was significantly correlated with the distribution of fishing effort in both inshore and offshore areas, highlighting potential competition for resources and/or attraction of seabirds to vessels for discards.

Keywords: ObSERVE; aerial survey; North Atlantic; competition; prey consumption

Introduction

Global commercial fisheries landings have been estimated at over 100 million tonnes annually since 2000 (Pauly and Zeller 2016, Cashion et al. 2018) and persist at these levels (e.g. 2019 estimates of 106 million tonnes, www.seaaroundus.org), with smaller forage fish accounting for 25%–30% of global catches (Alder et al. 2008, Alheit and Peck 2019). Trends in global fisheries suggest that in the future, more stocks are likely to become overexploited (Pauly and Zeller 2016). Given a global seabird diet dominated by squid, krill, and small schooling fish (e.g. sandeels, herring, and anchovies; Rountos et al. 2015) and an estimated requirement of between 57 and 96 million tonnes annually (Grémillet et al. 2018, Karpouzi et al. 2007), the targeting of forage fish stocks that are important components of the diet of many seabirds has the potential for impacts on populations through reduction in the abundance or density of prey below thresholds necessary for successful provisioning of offspring and survival (Sydeman et al. 2017). Models suggest negative impacts of harvesting lower trophic level species on marine mammals and seabirds (Smith et al. 2011), with overfishing of seabird food sources particularly affecting species with specialized diets, energetically expensive foraging, and those that engage in surface foraging (Furness and Tasker 2000). As a result, it has been suggested that one-third of seabird prey biomass should be preserved to meet the energetic requirements of seabird populations (Cury et al. 2011). Despite this, sustained global seabird-fisheries competition has been noted, even in the face of significant seabird population declines (Grémillet et al. 2018).

Competition between fisheries and seabirds has been studied primarily through overlaying distributions of seabirds and fishing vessels at regional scales (e.g. Karpouzi et al. 2007, Votier et al. 2010, Torres et al. 2013, Pereira et al. 2021) or through calculation of seabird biomass consumption based on the metabolic needs of seabirds (e.g. Ridgway 2010, Dehnhard et al. 2021) compared to local fisheries catches. Although overlap between fisheries and top predators such as seabirds does not imply any interaction between them (Torres et al. 2013), it is a necessary condition for interaction, including competition, to occur (Matthiopoulos et al. 2008). While such broad-scale overlap provides a general picture of potential interactions across large areas (Le Bot et al. 2018), they generally fail to highlight local hotspots in overlap, or account for the fact that fisheries, seabirds, and prey aggregations are all mobile, moving at finer spatial resolutions within broad overlap areas. Analysis of data at finer resolution will provide a more accurate estimate of potential interactions. Furthermore, it would allow for the detection of localized areas of importance for both seabirds and fisheries.

During the breeding season, seabirds are central place foragers with distribution limited by distance from the colony (Burke and Montevecchi 2009). Seabird species are most sensitive to variability in prey availability at this time, when parents also need to meet the energetic needs of chicks by provisioning them with food (e.g. Harding et al. 2007). During the non-breeding season, the central place foraging restriction as well as the need to provide for chicks is lifted, enabling seabirds to forage in areas further from colonies (Jessopp et al. 2013, 2020, Léandri-Breton et al. 2021). Many seabirds also undertake post-breeding dispersal or migrations, leading to a change in species distribution and composition. Furthermore, within both the breeding and non-breeding seasons, the distribution of prey resources is not evenly distributed and can be influenced by a range of mesoscale features associated with changes in productivity (e.g. Weimerskirch 2007). As such, the distribution of seabirds is likely to change considerably across seasons, and seabird-fisheries competition in an area should be examined in both breeding and non-breeding seasons (Sydeman et al. 2017, Ramírez et al. 2024). However, partly due to logistical challenges in assessing seabird distribution in the non-breeding season, most studies focus on the breeding season. Estimating the quantities of fish taken by seabirds requires a detailed knowledge of the numbers, energy requirements, diets, and foraging areas, including seasonal variations in these parameters (Furness 1990). Given that seabird foraging ranges can exceed hundreds of kilometers and vary across breeding and non-breeding seasons, seabirds are not evenly distributed at sea. Prey biomass consumption at sea is therefore likely to reflect this spatiotemporal variability in seabird distribution, with notable concentrations of foraging effort in discrete locations. When it comes to understanding potential competition for resources with fisheries, the distribution of fishing effort is also non-uniform (Kroodsma et al. 2018). Therefore, fine-scale information on seabird foraging effort and fishing effort in different seasons is important to account for this variability in assessing overlap.

Several methods have been used to identify areas of potential overlap between fisheries and seabirds, but all rely on knowledge of the spatial distribution of seabird density in relation to fishing effort (Torres et al. 2013, Le Bot et al. 2018). Aerial surveys are an effective method to obtain fine-scale data on distribution and abundance of seabirds at sea (Certain and Bretagnolle 2008, Buckland et al. 2012). This information can be compared to the spatial distribution of fishing effort at sea. For instance, automatic identification system (AIS) is compulsory on all vessels exceeding 300 gross tonnes and voluntary on smaller vessels and continuously reports vessel type and position. While acknowledging that AIS data are likely to underrepresent smaller fishing vessels, mostly operating in coastal waters, these can be used to monitor fishing activity, with aggregated data showing the spatial distribution and intensity of fishing effort (Kroodsma et al. 2018).

Ireland hosts 24 species of breeding seabirds, supporting over 500 000 breeding pairs (Burnell et al. 2023), and tracking studies have highlighted the importance of continental shelf waters as feeding grounds for several species (Edwards et al. 2013, Wakefield et al. 2013, Kane et al. 2020). At the same time, Irish waters support a fishing industry with average annual landings in Irish ports of 294 600 metric tonnes, valued at €355 million over the last ten years (CSO 2023). This figure increases substantially (408 364 metric tonnes) if unreported catches or catches within Irish waters but landed outside Ireland are included (www.seaaroundus.org, accessed July 2024). Most of this fishing effort is concentrated on continental shelf waters to the west of Ireland, in the Celtic Sea, and to a lesser extent in the Irish Sea and off the north coast (Gerritsen 2024). Given the importance of Irish continental shelf waters for both seabirds and fisheries, co-occurrence is likely to occur in this area. Therefore, we aimed to

1. map the spatial distribution and abundance of seabirds using aerial surveys;
2. determine spatial patterns of biomass removal by seabirds by accounting for the density and energetic needs of species;
3. determine the co-occurrence of seabird biomass removal and fisheries effort to investigate potential competition.

Methods

Data collection

Aerial surveys were conducted during the seabird breeding season (June–September 2021) and non-breeding season (November 2022 to March 2023) using a Partenavia *P*-68 fixed-wing aircraft equipped with bubble windows to afford observers an unrestricted view of the transect line below the aircraft. We used highly experienced observers with skills in seabird identification located on either side of the plane to identify and record seabirds on transect. Additional observers (either 1 or 2 depending on the flight) logged sightings called out by observers in real time (details below), with an audio recording backup reviewed after the flight to ensure that no records were missed during busy sighting periods. The additional loggers also acted as a further quality check for species identification on transect. The survey plane was flown at a speed over ground of 100 knots (185 km/h) and an altitude of 183 m in target weather conditions of Beaufort sea state ≤3 and visibility >1 km. Survey transects were designed to provide equal coverage probability for the survey area and consisted of equally spaced randomly placed zig-zag lines and parallel transects over 8 survey strata (Fig. 1). During surveys, the plane's geographic position was recorded every 2 s using an onboard GPS linked to a data logging computer running bespoke logging software: VOR in the breeding season of 2021 and an updated version, SAMMOA, in the non-breeding season of 2022–23 (SAMMOA 2022). Observers recorded information on environmental conditions, including sea state, glare, precipitation, and cloud cover, at the beginning of each transect line and upon any change in the survey conditions. All seabirds were recorded within a 200 m strip transect on either side of the plane (Certain and Bretagnolle 2008) with strip width determined using an inclinometer. While this methodology assumes that 100% of the birds are seen, this has been shown to be a reasonable assumption for aerial surveys for seabirds, including for cryptic auk species, within a survey altitude and speed range of 140–180 m and 150–200 km/h, respectively, and a strip width of 150–230 m (Certain and Bretagnolle 2008). A time- and location-stamped record of species (or species group where species-level identification was not possible) and group size was made when animals were abeam of the aircraft.

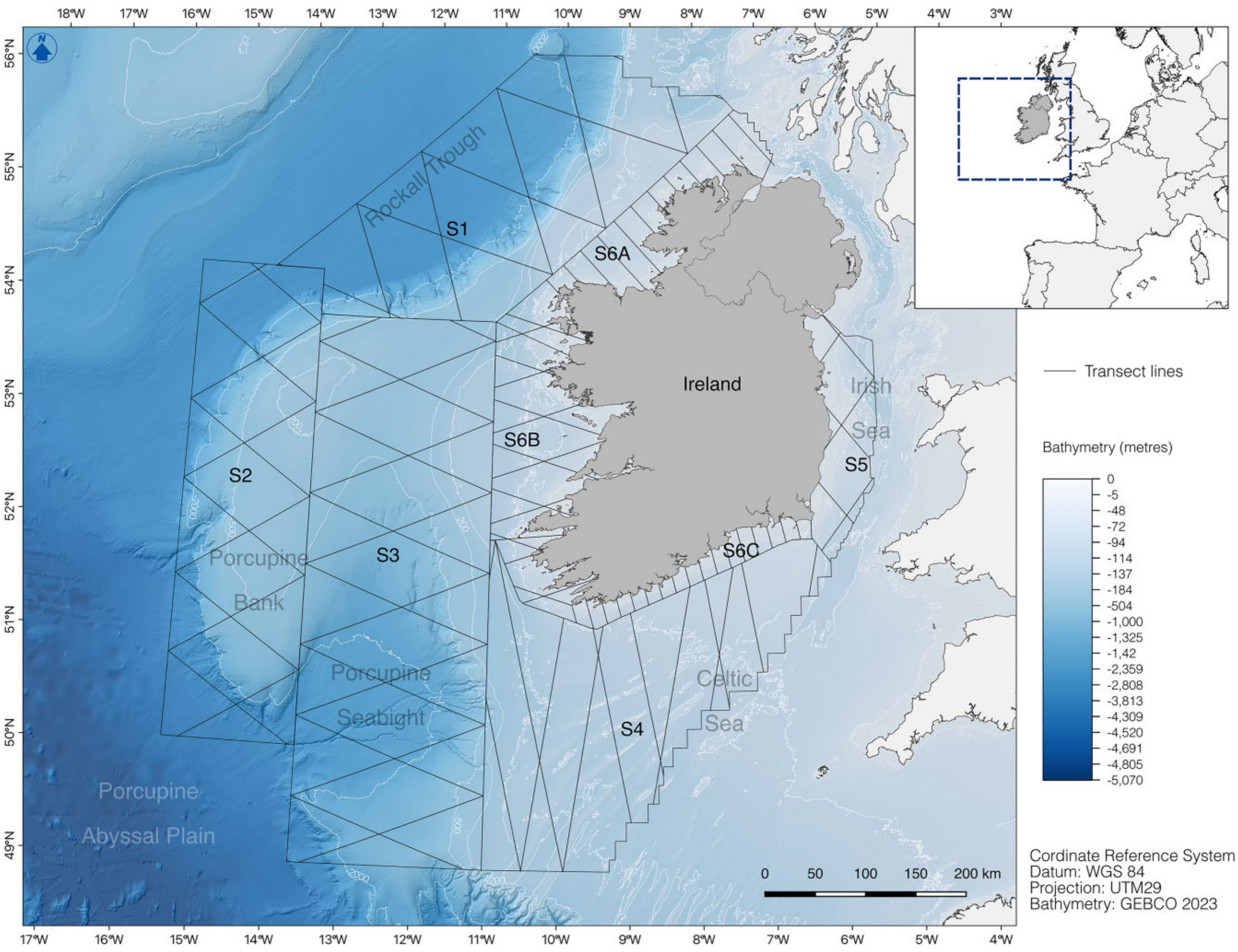

Figure 1. Map of survey area identifying broad-scale strata and transect lines flown in the breeding season 2021 and non-breeding season 2022/23.

Seabird distribution and abundance

Abundance for each species (or species group) was modelled spatially across 5 × 5 km grid squares covering the survey area using generalized additive models (GAM) with a logarithmic link function and a Tweedie error distribution using the *mgcv* package (Wood 2006) in R (R Core Team 2023). GAMs were chosen as a suitable model for density surface models (Cañadas and Hammond 2008), while the Tweedie distribution best captured the poisson-like distribution with over-dispersion in the data. The 5 × 5 km cell resolution was chosen as it was the finest consistent resolution available for environmental covariates used in modelling. Environmental variables were included in the models to account for their potential effect on the abundance of seabirds following the method of Cañadas and Hammond (2008). First, each covariate was tested individually, then a full model (with all covariates) was run to determine which variables drop in favour of others. With the results of these two steps, the significant covariates, either when used individually or from a full model, were selected. Final models were then run, using all possible combinations of the selected covariates [but running alternate models to include colinear covariates (correlation > 0.7)]. We used a backwards selection procedure, dropping terms until remaining covariates were significant. From the resulting final models containing all the potential combinations of covariates, the best model was chosen according to AIC, deviance explained, and goodness of fit. Environmental data were assigned to the centre of each 5 × 5 km grid cell, and included water depth (m), distance to the 0, 200, and 2000 m depth contours (as proxies for coastal, continental shelf, and oceanic habitats, respectively), slope and contour index (to give an index of benthic habitat and seafloor topography in the area), sea surface temperature (°C), sea bottom temperature (°C), mixed layer thickness (m), and chlorophyll-*a* concentration (mg chl/l) (as indices of marine hydrology and/or biological activity/primary productivity linked to prey availability) (Table SM1). Environmental variables related to the ocean floor topography were derived from a 15-Arc second interval grid from the General Bathymetric Chart of the Oceans (https://www.gebco.net/), whereas environmental variables related to oceanographic processes were obtained from 0.11 × 0.07 degree rasters from the COPERNICUS Marine Environment Monitoring Services (https://cds.climate.copernicus.eu/). Variable values were assigned to each 5 × 5 km cell of a grid covering the entire survey area. On-effort transects were divided into segments based on having the same environmental conditions recorded during the flight and with a mean of ~5 km to match the spatial scale of the analysis. Resulting segments ranged from 0.5 to 7.49 km. The central point of each segment was then assigned to the specific cell to which it fell, capturing the values of the environmental variables in the cell. Species abundance was modelled using the count of animals as the response variable, and the model structure was

$$\hat{N}_i = \exp\left[\ln(a_i) + \theta_0 + \sum_k f_k(z_{ik})\right],$$

where $\hat{N}_i$ is the abundance, the offset a_i is the effective search area for the ith segment (the length of the segment multiplied by twice the strip width, i.e. 0.2 km × 2), θ_0 is the intercept, f_k are the smooth functions of the explanatory covariates, and z_{ik} is the value of the kth explanatory covariate in the ith segment. Overall estimates of abundance for each species were obtained by summing across grid cells within the survey area, with 95% confidence intervals obtained using a simulation approach developed by Miller et al. (2022).

Seabird energetic requirements and biomass removal estimates

Total energetic requirement (kJ) for each species (or species group) per grid cell was estimated by multiplying the modelled seabird abundance per grid cell by species-specific energetic requirements in both the breeding and non-breeding seasons (see Table 1 for input parameters). Species-specific total energy requirement per grid cell (kJ) was calculated as

$$kJ = \sum_{i+1}^{i} (N \times \text{aFMR}) \times \frac{1}{d},$$

where N is the abundance per grid cell, aFMR is the adult daily field metabolic rate, and d is the digestion efficiency for each seabird species. Upper and lower confidence intervals of energy requirement estimates were generated using CIs around abundance and FMR estimates for the breeding and non-breeding seasons (lower 95% CI_{kJ} = lower 95%$\text{CI}_{\text{Abundance}}$ × lower 95%CI_{FMR}).

Species-specific FMR was obtained following Dunn et al. (2018) and using the Seabird FMR calculator (https://ruthedunn.shinyapps.io/seabird_fmr_calculator/). The seabird FMR calculator estimates daily field metabolic rate based on the outputs of a phylogenetically informed meta-analysis of large-scale determinants and corrects these estimates for changing energy requirements within a given latitude. Due to the large foraging ranges of many seabird species during the breeding season and wide distribution during the non-breeding season, sightings at sea cannot reliably be linked to a particular breeding colony at a specific latitude. We therefore used an average latitude of 53 degrees north, which represents the approximate middle of the study latitudinal range of the study area (49–56°N). Dunn et al. (2018) report only a small effect size of latitude, so this is unlikely to result in an error of >1% from the mean FMR value used within the latitudinal range of this study. Species-specific bird mass was sourced from BTO bird facts (https://www.bto.org/about-birds/birdfacts, accessed July 2024), and where sexual size dimorphism occurred, the mean of the two values was used, assuming a 50:50 sex ratio in the population. For the breeding season, we used FMR estimates for chick provisioning, which reflects the higher energetic cost of increased foraging to feed chicks. Virtually no FMR data are available for seabirds outside of the breeding season (Ellis and Gabrielsen 2001), so for non-breeding distributions, we applied lower FMR estimates for incubation to reflect lower daily energy expenditure during the non-breeding period (Dunn et al. 2020), as birds will not have the additional burden of provisioning chicks. Where seabirds could not be identified to species level, species group FMR was calculated according to the % contribution of each species to that group based on the most recent population census for the Republic of Ireland (Burnell et al. 2023). Where species-specific information was available on digestion efficiency, this was included, and where not available, digestion efficiency for fish-eating seabirds was assigned a mean value of 0.772, while species feeding primarily on invertebrates (e.g. storm petrel species) were assigned a mean digestive efficiency of 0.739 (Castro et al. 1989, Drent et al. 1992).

Total energy demand per cell was then converted to biomass consumed by dividing total kJ by an average prey energy density of 5.4 kJ g^{-1} taken across 78 commonly occurring seabird forage species in northeast Atlantic waters (Spitz et al. 2010), consistent with recommendations by Ridgway (2010). The biomass requirement from each species/species group was then summed across all species within each grid cell to obtain a total prey biomass removal by all seabirds within that grid cell and then summed across the entire survey area.

Because chicks being provisioned at the colony are not included in at-sea observations (breeding season only) and contribute to energetic requirements, we made a global adjustment to the total prey biomass consumption to account for this additional energetic requirement. We applied a conservative estimate of the number of chicks being provisioned based on the most recent breeding population census for Ireland coupled with data on the average number of chicks fledged per breeding pair. Daily energy requirement of chicks changes with growth from hatching to fledging, so a daily average was based on allometric equations to calculate the total kJ needed to fledge (Drent et al. 1992), divided by mean fledging duration (BTO bird facts, using the central point in ranges). Total biomass removal attributable to provisioning chicks was therefore calculated as

$$\frac{\left(\sum \left(N_c \times P \times \frac{\text{cFMR}}{2}\right) \times \frac{1}{d}\right)}{5.4},$$

where N_c is the abundance (in individuals) of the breeding population from Burnell et al. (2023), cFMR is the average chick daily field metabolic rate (divided by two considering that each chick would be provisioned by two breeding adults), P is the productivity based on average breeding success over 2000–19, obtained from the Joint Nature Conservation Council (JNCC, https://jncc.gov.uk/our-work/smp-report-1986-2019, last accessed 4 July 2024), d is the digestion efficiency, and 5.4 represents the average prey density of commonly occurring seabird prey species. We decided against applying this estimate spatially, as many breeding seabirds are more likely to forage closer to the coast while provisioning chicks, and there was no objective way of setting an appropriate distance threshold to apply to all species. Instead, we added the total chick biomass requirement to the total summed value across all grid cells.

To calculate the yearly biomass removal by seabirds, we accounted for the seasonal differences in energy requirements by multiplying breeding season daily biomass estimates by the duration of chick-rearing (fledging period in days) for each species (or the mean for seabird groups, accounting for the % contribution of each species to that group) sourced from BTO bird facts (https://www.bto.org/about-birds/birdfacts, accessed July 2024) and adding them to the non-breeding season biomass estimates multiplied by the remaining days of the

Table 1. Input parameters for estimating species-specific total energy requirement during the breeding season.

Species	Scientific name	Weight (g)[a]	Digestion efficiency[b,c]	Mean aFMR[d] Breeding (kJ) [Lower-Upper CI]	Mean aFMR[d] Winter (kJ) [Lower-Upper CI]	Chick total kJ[c]	Fledging period (days)[a]	Breeding success (2000–15)[e]	Mean cFMR[d] (kJ)
Northern gannet	*Morus bassanus*	3000	0.77[b]	4566.9 [3633–6616]	3296 [2555–4581]	118 933	90.5	0.76	1293.8
Manx shearwater	*Puffinus puffinus*	420	0.77[b]	1077.8 [560–1566]	671.4 [416–1162]	16 167	69	0.63	191.2
European storm petrel	*Hydrobates pelagicus*	27	0.74[b]	124.4 [65–246]	95 [49–185]	997	64.5	0.5	10.5
Black guillemot	*Cepphus grylle*	420	0.77[b]	912.9 [672–1187]	682.1 [487–867]	16 167	41	1.05	883.5
Atlantic puffin	*Fratercula arctica*	400	0.77[b]	904.3 [599–1280]	685.8 [421–919]	15 386	39	0.52	888.31
Common guillemot	*Uria aalge*	690	0.77[b]	1395.3 [1113–1722]	1012.7 [812–1258]	26 758	21.5	0.55	1311.8
Razorbill	*Alca torda*	710	0.77[b]	1309.5 [1020–1749]	1000.4 [737–1253]	27 546	19	0.52	1295.9
Arctic tern	*Sterna paradisaea*	110	0.80[c]	359.5 [271–473]	245.8 [198–334]	4150	22	0.22	307.2
Common tern	*Sterna hirundo*	130	0.81[c]	441.7 [303–533]	287.7 [231–382]	4917	25	0.51	355.2
Little tern	*Sternula albifrons*	56	0.77[b]	237.7 [162–346]	156.4 [120–256]	2091	19.5	0.4	202.5
Roseate tern	*Sterna dougallii*	110	0.77[2]	389.7 [265–497]	292.9 [195–354]	4150	26	0.64	379.4
Sandwich tern	*Thalasseus sandvicensis*	250	0.83[c]	584.2 [451–870]	418.4 [322–599]	9548	29	0.47	504.1
Cormorant	*Phalacrocorax carbo*	2100	0.77[b]	1534.7 [1025–2076]	1070.8 [755–1525]	82 809	50	1.89	1387.0
European shag	*Gulosus aristotelis*	1900	0.77[b]	2166.6 [1450–2741]	1507 [1049–1966]	74 810	53	1.29	1952.1
Black-legged kittiwake	*Rissa tridactyla*	410	0.76	818.1 [678–1025]	619.1 [501–742]	15 776	43.5	0.57	814.6
Great black-backed gull	*Larus marinus*	1700	0.77[b]	1717.8 [1298–2470]	1295.6 [974–1789]	66 824	52.5	0.96	1678.3
Lesser black-backed gull	*Larus fuscus*	830	0.77[b]	1119.8 [846–1546]	897.3 [618–1117]	32 277	35	0.39	1162.3
Common gull	*Larus canus*	400	0.77[b]	705.3 [536–963]	545.1 [398–709]	15 386	35	0.36	706.1
Herring gull[f]	*Larus argentatus*	1075	0.77[b]	1257.6 [1006–1825]	1056.4 [729–1307]	41 967	37	0.54	1368.3
Northern fulmar	*Fulmarus glacialis*	730	0.77[b]	1480.6 [1072–1993]	1166.4 [805–1477]	28 333	48.5	0.39	1510.9
Mediterranean gull	*Ichthyaetus melanocephalus*	320	0.77[b]	660.3 [490–870]	474.9 [357–611]	12 267	37.5	0.61	615.2

Breeding success refers to the number of chicks fledged per pair.

[a] BTO bird facts: https://www.bto.org/about-birds/birdfacts.

[b] Castro et al. (1989).

[c] Drent et al. (1992).

[d] Dunn et al. (2018).

[e] JNCC (https://jncc.gov.uk/our-work/smp-report-1986%-2019, last accessed 4 July 2024).

[f] Average weight for sexually dimorphic species assuming a 50:50 ratio of M:F.

year. Yearly biomass removal (B_y) was therefore calculated as

$$B_Y = \sum B_{\text{breeding}} \times \text{Fledging period} + B_{\text{non-breeding}} \times (365 - \text{Fledging period}),$$

where B refers to the biomass estimates in the breeding and non-breeding periods for each species or group of species.

Seabird-fisheries overlap

Fisheries data were sourced from Global Fishing Watch (www.globalfishingwatch.org), which uses satellite AIS location data to identify fishing activity based on movement patterns but largely omits smaller fishing vessels <10 m not equipped with the system. Data represent aggregated (all fishing gear) apparent fishing effort (as hours) per 0.1×0.1 degree grid cell across the study area, coinciding with the periods in which aerial surveys were carried out. Aggregated apparent fishing effort rasters were resampled using the resample function of the R package *raster* (Hijmans 2023) to ensure that they had the same resolution and extent as seabird biomass removal rasters. Fishing effort and seabird biomass removal rasters were rescaled to values between 0 and 1, and the overall spatial correlation between them in each season was tested using Dutilleul's modified *t*-test (Dutilleul 1993), which accounts for the degree of spatial autocorrelation in the data by blocking cells according to the level of autocorrelation present. In addition, a Dutilleul moving window bivariate raster correlation analysis was carried out using the *raster.modified.ttest* function of the package *spatialEco* (Evans and Murphy 2023) in R to investigate areas of high or low correlation between fisheries and seabird biomass removal. A moving window analysis is based on iterating over each pixel (in this case, each 5 km × 5 km cell) in the image with the pixels in the surrounding window, resulting in the mean value for each pixel (Hagen-Zanker 2016).

Results

Seabird distribution and abundance

Over the two survey periods, 12 674 seabird sightings, comprising 36 540 individuals and representing 17 species or species groups were recorded. The broad distribution of seabird species showed hotspots of density in the Irish Sea and southwest coasts, with clear seasonal differences in distribution and abundance for some species (Fig. SM5). The overall abundances of seabirds across the survey area totalled over 1.1 million individuals (Table 2).

Model-based estimates for the breeding season provided an abundance per grid cell for auk spp., black-backed gull spp., northern fulmar, northern gannet, herring or common gull, black-legged kittiwake, Manx shearwater, shag or cormorant, petrel spp., tern spp., and small and large gull species. Model-based estimates for the non-breeding season provided an abundance per grid cell for auk spp., black-backed gull spp., northern fulmar, northern gannet, herring or common gull, black-legged kittiwake, and petrel spp. (Table 2). In almost all cases, the environmental variables retained in models were some combination of latitude, longitude, distance to the coast, and dynamic variables such as sea surface height and sea surface temperature (Table SM2).

Table 2. Seabird sightings summary for aerial surveys in the breeding and non-breeding season.

Species	Sightings breeding season	Sightings non-breeding season	Abundance breeding season	Abundance non-breeding season
Auk spp.	1867 (5305)	1634 (6304)	311 683	343 866
Cormorant/shag	10 (12)	24 (44)	1 432	
Northern gannet	585 (1 940)	478 (1 008)	157 604	53 566
Northern fulmar	722 (1 813)	2234 (4 285)	133 585	385 235
Black-backed gull spp.	69 (79)	101 (207)	3 289	12 126
Common/herring gull	61 (123)	258 (555)	17 731	24 174
Black-headed gull	0 (0)	1 (2)		
Black-legged kittiwake	340 (393)	2739 (6 192)	32 055	394 587
Large gull spp.	56 (354)	3 (87)	17 295	
Small gull spp.	114 (152)	0 (0)	5 035	
Manx shearwater	882 (6 878)	18 (29)	385 105	
Cory's shearwater	10 (13)	11 (14)		
Great shearwater	7 (9)	0 (0)		
Shearwater spp.	3 (4)	1 (1)		
Petrel spp.	289 (531)	49 (79)	49 594	5 788
Tern spp.	73(114)	0(0)	5 579	–
Skua spp.	20 (20)	2 (2)	–	–
Wader spp.	0 (0)	13 (71)	–	–

Values in brackets are the total number of individuals corresponding to the number of sightings. Blank cells for abundance are due to too few sightings for robust estimates to be generated.

Seabird biomass removal estimates

During the 2021 breeding season, an estimated 441.2 (95% CI 319.1–614.4) tonnes of prey were removed per day by foraging seabirds across all survey strata. The additional biomass removed for chick provisioning was estimated at 46 tonnes per day during the breeding season, with the combined biomass removal (487.2 tonnes) being very similar to the 478 (95% CI 362.9–626.7) tonnes of prey removed per day across the area during the non-breeding season (Table 3). Yearly prey consumption by seabirds in Irish waters, taking into account the different duration of fledging periods for each species, was estimated at 175 214 tonnes.

In the breeding season, daily relative biomass removal was highest in the coastal strata, particularly in the Irish Sea (Stratum 5; 6.39 kg/km^2/day). The Celtic Sea had the highest removed biomass, (96.7 kg/km^2/day (95% CI 74–138), followed by waters off the west coast (73.8 kg/km^2/day (95% CI 54.7–104.5). Northern gannets, auk species, and Manx shearwaters were the species or species groups with the highest prey consumption, representing 39%, 23%, and 23% of the biomass removed by seabirds in summer, respectively (Tables SM3–SM5). In coastal strata and the Irish Sea, biomass removal was dominated by auks and Manx shearwater, whereas northern gannets consumed the highest amounts of prey in offshore strata. Interestingly, kittiwakes, despite high abundances, accounted for only 1.4% of seabird biomass removal in the breeding season.

During the non-breeding season, daily relative biomass removal was highest in the coastal strata, particularly along the south coast. Absolute biomass removal was highest along the West and South coasts, with less biomass removed in the Irish Sea (Table 3). Northern gannets, northern fulmars, auks, and black-legged kittiwakes were the species or species

Table 3. Total energy requirement, mean density of biomass removal, and estimated forage fish biomass removal assuming an energy density of 5.4 kJ/g wet weight (Spitz et al. 2010).

Stratum	Breeding season			Non-breeding season		
	Energy requirement (kJ/day × 10^6)	Biomass removal (kg/km^2/day)	Biomass removal (tonnes/day)	Energy requirement (kJ/day × 10^6)	Biomass removal (kg/km^2/day)	Biomass removal (tonnes/day)
1	202.1	0.6	37.5 (27.6–53.7)	250.93	0.75	46.5 (34.5–60.7)
2	89.7	0.28	16.6 (11.1–23.6)	276.88	0.85	51.3 (36.5–65.4)
3	398	0.73	73.8 (54.8–104.5)	552.64	1.02	102.4 (76.7–135.3)
4	521.9	1.53	96.7 (74–138)	630.35	1.84	116.8 (90.2–155.8)
5	379.1	6.39	70.3 (50.8–92.4)	187.04	3.15	34.7 (27.1–44.2)
6A	247.5	2.89	45.9 (33.4–62.7)	269.99	3.16	50 (38.7–65.1)
6B	347	3.69	64.3 (42.1–89.9)	184.44	1.96	34.2 (26.3–45.3)
6C	195.1	3.66	36.2 (25.4–50.7)	228.85	4.3	42.5 (32.9–54.9)
Total	2380.3	1.29	441.21 (319.1–614.4)	2581.12	1.4	478.4 (362.9–626.7)

Figures in brackets represent upper and lower 95% CIs. Detailed results of biomass removal per species, strata, and season are shown in Tables SM3–SM5.

groups with the highest consumption, representing 44.7%, 24%, 17%, and 12% of the biomass removed by seabirds in winter, respectively (Tables SM3–SM5). Except for strata 1, 2, and 5, in which biomass removal was dominated by northern fulmars and auks, northern gannets consumed the highest amount of prey in winter.

Areas of highest energy requirement and corresponding prey biomass removal varied spatially between seasons. Although consistently higher in coastal areas, the hotspots of biomass removal were in the northern Irish Sea in the breeding season and the central Irish Sea, Southeast, and South Coasts in the non-breeding season (Fig. SM1–SM4). Notable hotspots of prey biomass removal occurred further offshore in the southwest and northeast in winter, primarily due to the distribution of northern gannets (Figs. 2 and SM1–SM4).

Seabird-fisheries overlap

There was a significant correlation between seabird biomass removal and fishing effort in both the breeding season (ρ = 0.446, 181 d.f., $P < .001$) and the non-breeding season (ρ = 0.165, 238 d.f., $P = .011$). The Dutilleul moving window bivariate raster correlation analysis highlighted areas of both positive and negative spatial correlation between fishing effort and seabird prey biomass removal (Fig. 3). In the breeding season, areas of strong ($\rho > 0.7$) positive correlation suggesting increased interaction/competition between fisheries and seabirds occurred primarily along the continental shelf edge along the Porcupine Seabight, the Porcupine Bank, and the Celtic Sea. Areas of negative correlation were more sparsely distributed across the continental shelf. In the non-breeding season, a strong positive correlation was consistently located in the slope edge west of the Porcupine Bank, while a strong negative correlation occurred in areas of the Porcupine Bank and along the 200 m bathymetry line (Fig. SM5).

Discussion

Using extensive aerial surveys, this study provides seasonal estimates of prey consumption by an estimated 1.1 million seabirds foraging across an area of 341 183 km^2 during both the breeding and non-breeding periods. The breeding season abundance is consistent with national breeding population estimates (Burnell et al. 2023) while factoring in a portion of birds remaining at the nest, non-breeders, and breeding birds from large UK populations foraging in these waters. Based on estimates of reported and unreported catches in Irish waters of 1119 tonnes/day (www.seaaroundus.org, last accessed 4 July 2024), seabirds are removing ~43% of the biomass removed by fisheries.

Spatiotemporal variability of prey consumption by seabirds

The broad distribution of seabirds across the survey area highlighted clear hotspots of density in the Irish Sea, the offshore waters of the southwest, and coastal waters more generally. Seasonal variability in the location of biomass removal hotspots likely reflects the response of seabirds to changing environmental conditions and prey distribution, as well as changes in the composition of the seabird community during overwintering or migration in the non-breeding season. This broad distribution of seabirds was highly consistent with results of previous surveys using the same methodology (but not covering the coastal strata surveyed in this study and thus unsuitable for generating abundance and biomass removal estimates) in two summers and two winters in 2015–17 (Rogan et al. 2018), suggesting that our surveys are fairly representative of the broad distribution of seabirds in the region and not an anomalous year. The higher prey consumption in the Irish Sea during the breeding season is consistent with the location and foraging ranges of large colonies of common guillemots and razorbills around Dublin (Burnell et al. 2023), as well as large colonies and foraging ranges of Manx shearwaters in Wales (Burnell et al. 2023). While razorbills and guillemots have short foraging ranges (Thaxter et al. 2012) and are likely to remain within the western Irish Sea, Manx shearwaters from Welsh colonies regularly forage in the western Irish Sea (Dean et al. 2015) contributing to a large number of sightings. Similarly, areas of higher prey consumption occurring along the southwest coast are likely to reflect the distribution of northern gannets, which breed in two large colonies totalling ~48 000 pairs (Burnell et al. 2023) in the southwest. While the area also supports large numbers of northern fulmars, black-legged kittiwakes, Manx shearwaters, and storm-petrels (Burnell et al. 2023), the high energy requirement in

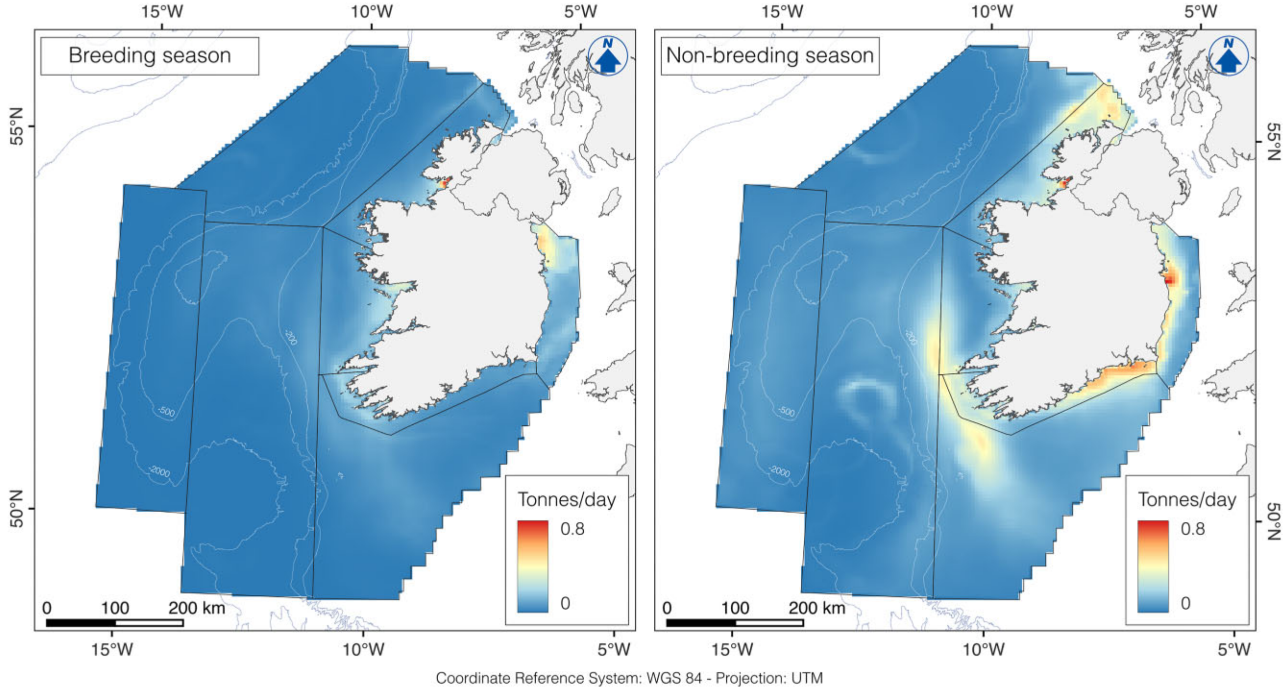

Figure 2. Spatial distribution of biomass removal per day (in tonnes in each 5 km × 5 km grid cell) by seabirds in Irish waters during the breeding season (left) and non-breeding season (right).

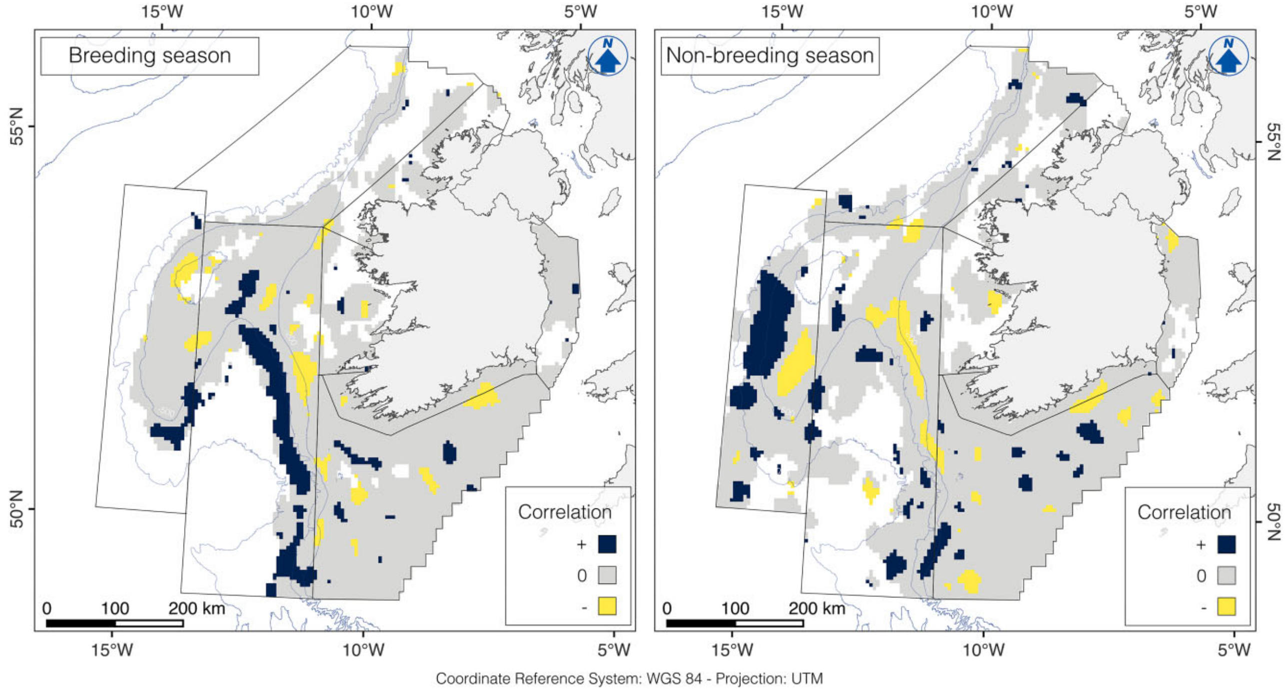

Figure 3. Areas of high positive and negative spatial correlation ($\rho > 0.7$) between prey consumption by seabirds and fishing effort. White areas indicate where zero fishing effort was recorded.

this area will be disproportionately influenced by the higher energetic needs of the large (3 kg) northern gannet. In winter, the high abundances of auk species, black-legged kittiwakes, and lower numbers of northern gannets (but due to large size and metabolic requirements having a large effect on biomass removal estimates) determined the areas of higher prey consumption in the Irish Sea, south coast, and southwest coast, respectively. High abundances of northern fulmars appear to be driving the areas of high seabird biomass removal in the waters beyond the continental slope off the west coast.

Our annual prey consumption estimates by seabirds at 175 214 tonnes, represents around 0.2% of the annual food consumption by the world's seabirds (Brooke 2004, Karpouzi et al. 2007) and equates to less than half of the biomass removed by fisheries in the EEZ. This is similar to the proportion of seabird prey consumption to fisheries landings in the wider northeast Atlantic, where estimated seabird prey consumption is 5.95 million tonnes per annum (Barrett et al. 2006) compared to 13.13 million tonnes of fisheries landings (www.seaaroundus.org, accessed July 2024). Globally, annual seabird prey consumption is estimated to be 57–90 million tonnes (Brooke 2004, Karpouzi et al. 2007, Grémillet et al. 2018) compared to 110 million tonnes removed by fisheries (www.seaaroundus.org, accessed July 2024), suggesting that in the northeast Atlantic, fisheries are removing a greater proportion of the available biomass than global averages. Overexploitation of the available fish stocks in this region may have knock-on effects in reducing breeding success in seabird populations (Cury et al. 2011) as well as immature/adult survival.

Overlap between seabirds and fisheries

When assessing overlap between seabirds and fisheries, the scale used can heavily affect results (Torres et al. 2013). There was an overall positive correlation between seabird prey biomass removal and fishing effort across the EEZ, suggesting that at the broadest scale, both seabirds and fisheries are targeting the same areas. However, the strength of this correlation was low, particularly in the non-breeding season, suggesting spatial heterogeneity. The fine spatial resolution of estimated prey removal by seabirds and moving window bivariate raster correlation analysis allows for a more refined analysis of overlap with fishing effort. Information on fishing effort was largely limited to larger vessels, which excludes inshore vessels. In Ireland, this represents 82% of the fishing fleet but only 6% of the landings (Fitzpatrick et al. 2020), so while this will underestimate fishing activity, the small contribution of these fisheries to overall fish biomass removal and the fact that these mostly target species not consumed by seabirds [composed largely of brown crab (*Cancer pagurus*), whelk (*Buccinum undatum*) and lobster (*Homarus gammarus*)], suggest the overall competition between these missing vessels and seabirds is likely to be low. Larger vessel landings for Ireland include a large component of pelagic forage fish species, including blue whiting (*Micromesistius poutassou*), whiting (*Merlangius merlangus*), herring (*Clupea harengus*), and horse mackerel (*Trachurus* spp.) (www.seaaroundus.org), all species likely to occur in the diet of seabirds. While pelagic trawlers targeting these species only account for 4% of fishing effort in the Irish EEZ, they represent more landings than any other gear type in terms of volume (Gerritsen 2024), suggesting the potential for competition, particularly within areas of high overlap.

Breeding season surveys highlighted an extensive area of positive correlation between seabird prey removal and fishing effort along the shelf edge. This area has high effort of pelagic trawls (Gerritsen 2024) and is well within the foraging range of breeding gannets, Manx shearwaters and Northern fulmars that dominated seabird sightings in the area. Both gannets and fulmars are also known to associate with fishing vessels for discards (Bicknell et al. 2013, Bodey et al. 2014, Darby et al. 2021). In the non-breeding season, we noted a strong positive correlation between seabird prey removal and fishing effort along the slope edge west of the Porcupine Bank, reflecting a high abundance of northern fulmars and longline fisheries in this area. This is consistent with associations between fulmars and fishing vessels in the North Atlantic (Løkkeberg and Robertson 2002, Fangel et al. 2017, Darby et al. 2021). Given the fact that fulmars are listed as Vulnerable in Europe and are the second-most frequently bycaught species in the northeast Atlantic, with some 22 883 birds estimated bycaught annually (Ramírez et al. 2024), our analysis identifies discrete areas where mitigation may be targeted. It should be acknowledged that despite positive spatial correlation and a likely targeting of the same prey species, fisheries and seabirds may not be taking the same component of the available biomass. Seabirds are largely limited to foraging within the top ∼50 m of the water column due to dive depth limitations, while fisheries can operate at much deeper depths and often target larger size classes. Spatial correlation may, however, suggest more indirect competition as well as utilization of fishery discards or increased bycatch risk. Conversely, the negative correlation observed in the Irish Sea highlights a lack of competition. This area supports large numbers of auks that target clupeids, sandeels and gadids (Riordan and Birkhead 2018), while the main fishery in the area targets Norway lobster (*Nephrops norvegicus*) and other demersal fish species (Gerritsen 2024). Such knowledge of both positive and negative correlations between fisheries and seabirds can aid more detailed assessment of seabird-fisheries interactions to contribute to improved conservation and management measures.

Assumptions and limitations

Our results are based on a number of assumptions that may affect interpretation of the results. First, a primary assumption of the strip-transect methodology is that 100% of the birds are seen and recorded accurately. While this is likely to be an overestimation of actual detection success, it has been shown to be a reasonable assumption for aerial surveys for seabirds within a 150–230 m strip width (Certain and Bretagnolle 2008), and the 200 m strip width has been successfully adopted in other studies investigating the density and abundance of seabirds at sea (e.g. Pettex et al. 2017). However, this assumption is likely to result in an underestimate of seabird density and biomass removal. We also accounted as much as possible for uncertainty in species identification by weighting the contribution to biomass removal by the relative proportion of species within each higher taxonomic grouping breeding in Ireland to avoid estimates being over or under-inflated due to a disproportional abundance of species with a smaller or larger FMR. Some seabird species, such as great cormorants (*Phalacrocorax carbo*) and some gulls (*Larus* spp.), also feed in freshwater, estuarine or terrestrial habitats, while we assume that biomass removal across all seabirds is from marine sources. However, together these species account for <3% of the total Irish seabird population, and so this is likely to result in only a small overestimate of marine biomass removal. Conversely, while results include the energetic requirement of chicks from Irish breeding birds, they do not account for the energetic requirement of chicks from an unknown number of birds breeding in the UK but foraging in Irish waters. The UK holds very large populations of breeding seabirds (Burnell et al. 2023), and tracking studies from UK colonies for species detected in high abundances during the breeding season surveys (Manx shearwaters, gannets and fulmars in particular) have been shown to forage well within the Irish EEZ (Edwards et al. 2013, Wakefield et al. 2013, Dean et al. 2015), suggesting that our estimate of biomass removal by breeding seabirds is underestimated. A number of parameters used in calculations were also species averages and unlikely to reflect any spatial variability in individual weight, latitude, FMR, and breeding status of observed birds. However, the potential effect on estimated biomass removal of this is likely to be quite small compared to the uncertainty surrounding the abundance estimates with their wide confidence intervals. We therefore stress the importance of considering the 95% CIs provided.

Implications for conservation

Results identify clear hotspots of prey consumption by seabirds, representing critical foraging grounds for breeding seabirds as well as migrants during the non-breeding season. Access to sufficient prey resources influences seabird population dynamics through breeding success, juvenile recruitment, and adult survival (Sydeman et al. 2017). Competition with fisheries and bycatch have also been highlighted as some of the highest impacts on seabirds (Dias et al. 2019), and this study identifies discrete areas of co-occurring prey consumption by seabirds and fishing effort. Future work on seabird species-specific biomass removal and gear/species-specific biomass removal by fisheries could provide further information on the likely impacts of different fisheries on seabirds. Furthermore, our estimates of seabird energy requirements can feed into spatially explicit ecosystem models, adding information on direct and indirect interactions between seabirds and fisheries in an ecosystem context (Le Bot et al. 2018).

Seabirds, among many other top predators, are affected by human activities at sea (Halpern et al. 2015, Dias et al. 2019). The proliferation of offshore energy generation will inevitably lead to an increase in the space allocated to offshore renewable energy (Lloret et al. 2023). Because several seabird species show avoidance of windfarms (Dierschke et al. 2016, Maxwell et al. 2022), and fishing activities are limited within their perimeter (Gill et al. 2020), the area available to both seabirds and fishing vessels will likely be reduced, potentially increasing overlap. From a management perspective, models have suggested that an adaptive biomass-limit harvest rule for forage fish may have positive outcomes for seabirds with minimal trade-offs to fisheries (Koehn et al. 2021), while empirical data from a closure of sandeel fisheries within the foraging range of breeding seabirds was associated with an increase in breeding success for kittiwakes, but not for auk species (Searle et al. 2023). Information on important foraging areas for seabirds as well as areas of high use by both seabirds and fisheries highlighted in this study provides key information to inform spatial management of activities at sea.

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Author contributions

Conceptualisation: MJ; Funding aquisition: MJ, ER, DT; Project Administration: MJ, ER, AB, OGP.; Investigation: AB, SG, OGP, ER, MJ; Data curation: OGP; Formal analysis: MJ, AC, OGP; Writing - original draft: MJ, OGP; Writing - review & editing: MJ, OGP, ER, AB, SG, AC, DT;

Supplementary data

Supplementary data is available at *ICES Journal of Marine Science* online.

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Data availability

Fisheries data underlying this article are downloadable from Global Fishing Watch (www.globalfishingwatch.org). Aerial survey data underlying this article are from Phase 2 of the ObSERVE programme under the Irish Department of Environment, Climate and Communications (DECC) and are available on request through the DECC websites: https://www.gov.ie/en/publication/12374-observe-programme/?referrer=, https://www.gov.ie/observe/.

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