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Research Paper

Spatial and within-season variation in the diet of a declining seabird described through digital photography and citizen science

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ABSTRACT. Understanding an animal's diet is a crucial component of conservation, but diet data are often labor intensive to collect and are frequently scarce. Atlantic Puffins (*Fratercula arctica*; hereafter Puffins) are vulnerable to global extinction and have declined in some parts of their UK and Irish range. Differences in population trajectories may relate to diet, but Puffin diet data are currently only collected at a handful of colonies. We explored whether citizen science could address this data gap by inviting visitors to Puffin colonies in 2017 to submit their photographs of Puffins carrying prey. In total, 602 people submitted 1402 images from 35 colonies. We identified the species group, size, and number of prey items in each bill load. Photograph quality was excellent, with 89% of birds in images providing useable diet information. In total 11,150 prey items were counted and measured from 1198 Puffins across 27 colonies. We demonstrated a lack of bias in the sample of photos provided by citizen scientists and described how Puffin chick diet varies in prey composition, prey length, number of prey per bill load, and load biomass over large spatial scales and throughout the breeding season. The diet of Puffin chicks from regions where severe declines have occurred, most notably Shetland, were characterized by a lower prey biomass, higher numbers of fish per load, and a high proportion of small, transparent sandeels consistently through the season. By contrast, in regions where Puffin populations are thought to be increasing, load biomass was high, the number of prey per load low, and larger non-transparent sandeels were the dominant prey, which persisted right through the breeding season. Results from our study show colonies and regions where birds may be expending more effort (collecting more prey items) for lesser returns (lower load biomass) and emphasize the value of collecting diet data across large spatial scales.

Variation spatiale et intra-saisonnière du régime alimentaire d'un oiseau marin en baisse, décrite grâce à la photographie numérique et à la science citoyenne

RÉSUMÉ. La compréhension du régime alimentaire d'un animal est un élément crucial de la conservation, mais la collecte de données sur le régime demande souvent beaucoup de travail et n'est pas fréquemment effectué. Les macareux moines (*Fratercula arctica*; ci-après macareux) sont vulnérables à l'extinction mondiale et ont diminué dans certaines parties de leur aire de répartition au Royaume-Uni et en Irlande. Les différences de tendance démographique des populations peuvent être liées au régime alimentaire, mais les données sur le régime des macareux ne sont actuellement collectées que dans une poignée de colonies. Nous avons cherché à savoir si la science citoyenne pouvait combler ce manque de données en invitant les visiteurs de colonies en 2017 à soumettre leurs photographies de macareux transportant des proies. Dans l'ensemble, 602 personnes ont soumis 1402 images provenant de 35 colonies. Nous avons identifié le groupe d'espèces, la taille et le nombre de proies transportées dans chaque charge de bec. La qualité des photographies était excellente, 89 % des oiseaux sur les images ayant permis de fournir des informations sur le régime alimentaire. Au total, 11 150 proies ont été comptées et mesurées à partir de 1198 macareux provenant de 27 colonies. Nous avons démontré l'absence de biais dans l'échantillon de photos fournies par les citoyens et décrit comment le régime alimentaire des poussins varie en termes de composition de proies, de longueur de proies, du nombre de proies par charge de bec et de biomasse de proies par charge sur de grandes échelles spatiales et tout au long de la saison de nidification. Le régime alimentaire des poussins provenant de régions où des baisses marquées ont eu lieu, notamment les îles Shetland, était caractérisé par une biomasse de proies plus faible, un plus grand nombre de poissons transportés par charge et une forte proportion de petits lançons transparents tout au long de la saison de nidification. En revanche, dans les régions où l'on pense que les populations de macareux augmentent, la biomasse des charges était élevée, le nombre de proies par charge faible et les grands lançons non transparents étaient les proies dominantes, tout au long de la saison. Les résultats de notre étude font état de colonies et de régions où les oiseaux peuvent déployer plus d'efforts (collecter plus de proies) pour des retours moindres (biomasse de charge plus faible) et soulignent la valeur de la collecte de données sur le régime alimentaire à travers de grandes échelles spatiales.

Key Words: *citizen science; diet; forage fish; monitoring; predator-based diet sampling; puffin; sandeel; sand lance*

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INTRODUCTION

Understanding the composition and dynamics of animal diet is crucial for identifying limiting factors in populations of declining species (Miles et al. 2015), characterizing niche specialization (Balzani et al. 2021), tracking energy flow through foodwebs (Vander Zanden and Vadeboncoeur 2002), and planning for species conservation under future climate and land/sea-use scenarios (Sadykova et al. 2020). Seabirds are a highly threatened group (Croxall et al. 2012, BirdLife International 2018a), but the collection of seabird diet data is often challenging because many species feed below water and/or away from land (Lewison et al. 2012). The resulting paucity of diet data hinders our understanding of the causes of population declines (Becker and Beissinger 2006). Where diet data do exist, their scope is often restricted to a small number of breeding colonies, meaning that spatial variation in diet is frequently poorly characterized. This limits our understanding of how prey composition and diet could shape population processes and hinders the use of seabirds as indicators of change in other trophic levels or marine environments (Wanless et al. 2004, Thayer and Sydeman 2007, Sydeman et al. 2017, Depot et al. 2020).

Atlantic Puffins (*Fratercula arctica*; hereafter Puffins) are one species in which knowledge of diet during the breeding season is restricted to a small number of colonies (Harris and Wanless 2011). The global Puffin population is undergoing rapid population decline (BirdLife International 2018b). Declines have been linked to climate change, through reduced prey availability and subsequent breeding failure, in several parts of their global range, including the British Isles (Martin 1989, Anker-Nilssen and Lorentsen 1990, Durant et al. 2003, Mitchell et al. 2004, Harris and Wanless 2011, Kress et al. 2016, Hansen et al. 2021, Owen et al. 2023). In their UK and Irish ranges, low productivity and steep declines have been recorded in some, but not all, colonies (Eaton et al. 2015, JNCC 2016, Owen et al. 2023). The latest UK and Ireland Puffin census showed that, overall, Puffin populations have declined by around 15% since 2000, with increases in relatively few colonies (e.g., The Flannans and Lunga in Northwest Scotland, Skomer in Wales, and Coquet in Northeast England) and declines in many others (e.g., Rathlin in Northern Ireland, the Isle of May in Southeast Scotland, Sule Skerry in Orkeny, and Fair Isle and Hermaness in Shetland; Owen et al. 2023). Declines in the Northern Isles of Shetland and Orkney appear to have been particularly widespread (Miles et al. 2015, Hughes et al. 2018, Owen et al. 2018, 2023). However, the lack of spatial and temporal resolution in Puffin diet data means that it is not currently possible to understand how these different population trajectories relate to underlying variation in available prey.

At present, Puffin diet is routinely studied at only two colonies in the UK: the Isle of May, Southeast Scotland (Harris and Wanless 2011), and Fair Isle, Shetland (Miles et al. 2015). These data consist of observations of food items brought by adult Puffins to feed chicks at the colony and do not necessarily reflect the diet of the adult birds themselves (but see Fayet et al. 2021). In other parts of the Puffin's global range, breeding season diet data have been collected in Norway (Røst, Hornøya, Runde (Barrett et al. 2002), Iceland (E. Snær Hansen, *personal communication*), and the North American east coast, Gulf of Maine region (Diamond and Devlin 2003, Kress et al. 2016, Scopel et al. 2019). Although Puffin diet at studied colonies is well documented, the degree to which prey composition, prey quantity, and variation within the season can be generalized to other colonies and regions is thought to be low (Harris and Wanless 2011).

Puffin diet data are collected at a relatively small number of colonies because current methods of data collection are labor intensive and require specialist skills. Four methods have been used: (1) capturing chick-rearing adults carrying prey as they approach a burrow, so that the prey are dropped and collected for identification (e.g., Wanless et al. 2018); (2) observing prey carried by chick-rearing adults to burrows using binoculars (Barrett 2015) or photographs taken by researchers (Sanders 2008, Anker-Nilssen 2010); (3) examining the stomach contents of dead individuals (Lilliendahl and Sólmundsson 1997); and (4) using biochemical markers of diet in body tissues or feces such as stable isotopes, fatty acids, and DNA metabarcoding (Hedd et al. 2010, St. John Glew et al. 2019, Fayet et al. 2021). Collecting concurrent data at multiple colonies using any of the above methods would be logistically challenging and costly in terms of both time and money. Citizen science is one tool that can increase the scale at which ecological data are gathered (Dickinson et al. 2012, Hochachka et al. 2012). Puffins are one of the most photographed bird species in the UK and are highly visible during the breeding season, when they can easily be seen carrying prey items to chicks. Recent technological advances in smartphones and digital cameras have increased the opportunities to take and share high-quality photographs (Gaglio et al. 2017). As such, there is potential to use photographs gathered by the public to increase the spatio-temporal coverage of Puffin diet sampling.

We tested whether a citizen science approach using digital photography could be used to sample prey brought by adult Puffins to their chicks across multiple UK colonies and throughout the chick-rearing period. We addressed data quality challenges by testing for potential sources of bias. We used the data to examine spatial and temporal (within-season) variation in Puffin chick diet. We aimed to (1) test the robustness of using citizen science to collect Puffin chick diet data; (2) quantify prey type, biomass, and total prey number per load at multiple colonies around the UK; and (3) determine how diet varies across the chick-rearing period. We provided a multi-colony baseline against which to assess the impact of future environmental change on Puffin chick diet and validated an approach that could be extended temporally (collecting photographs from multiple years) to assess how diet relates to population trends over time.

METHODS

Data Collection

We invited the public to submit photographs of Puffins carrying prey from UK and Irish colonies during the breeding season of 2017, using communication materials created for the Puffarazzi project. These materials comprised: a website, including a map of all UK and Irish Puffin colony locations recorded during the last national census; technical photography guidance; a flyer for display at colonies; social media content; a press release that led to television, newspaper, and magazine coverage; and targeted communication by email to the membership of the Royal Society for the Protection of Birds (RSPB) and managers of nature reserves with breeding Puffins. Accompanying these communications

was guidance to avoid disturbance to Puffins, e.g., by avoiding burrow areas and minimizing the time spent taking photographs. We asked observers to submit any pictures of Puffins carrying prey, not just aesthetically pleasing photos.

Photo submission was via a webpage built using accessible web tools. Photos of a maximum size of 4032 x 4032 pixels and 4 MB were uploaded individually by the submitter as .jpg, .jpeg, or .png files, along with metadata. The requirement to individually upload each photograph was purposefully done to ensure metadata were correctly assigned to each photo. This prioritized data quality over data quantity because the increased time spent uploading by the submitter (approximately two minutes total per photo) may have discouraged participation in some cases. Using a standardized online form, we asked submitters to provide the following metadata: (1) location, selecting from a predetermined list of known Puffin colonies; (2) date of photograph, in standard format; (3) the time of the photograph, accurate to a few minutes if possible; and (4) the camera equipment used to take the picture, selected from a dropdown option of SLR, smartphone, compact camera, or other. Submitters also had the opportunity to provide further information in a free text box. In addition, we asked submitters to confirm they had only uploaded one photo of each individual Puffin, via a tick-box. Photo submission was open from May to September 2017, which fully encompasses the late May to mid-August period of chick-rearing by Puffins in the UK (Harris and Wanless 2011).

Image analysis

Image analysis was both managed and carried out by six of the authors (CCZ, FW, GL, OP, RH, SH). SH was first supported by researchers experienced in seabird prey identification to produce a pictorial guide detailing how to identify and measure prey in Puffin bills from photographs (available on request). SH then peer-to-peer trained all other image analysts. Each image analyst was tested to ensure accurate and consistent identification before starting on the dataset. Images and metadata were curated automatically by the visual content web tool Stackla (latterly available as Visual UGC: powered by Stackla https://www.nosto.com/products/visual-ugc/) that was embedded within the website design. This created a spreadsheet with a line for each image uploaded, containing a link to the cloud-stored image and columns with the metadata as entered by the submitter. This meant that the image analysis team could easily manage the image database and assign tasks in the spreadsheet without the need for time-consuming sharing of image files. Each photograph was analyzed independently by two analysts and SH carried out an additional moderation step if results from the first two analysts differed in any way, by looking again at the image and selecting the most accurate of the two results. Puffin bill loads from photographs taken at the same colony on the same day were visually compared (bill load, order of prey, any other distinctive characteristics in the image) to remove any duplicate images of the same bird. For each photograph, we recorded: (1) the number of prey items in different species groups; (2) the length of each prey item relative to Puffin bill depth; and (3) three separate levels of confidence in identification, count, and measurement of prey.

Number of prey items in species groups

We grouped prey species from families in which species-level identification from photographs was difficult. Atlantic herring (Clupidae: *Clupea harengus*) and sprat (Clupidae: *Sprattus sprattus*) were grouped as clupeids. Members of the cod family were grouped as gadoids, except rockling (Gadoids in the family *Lotidae*, hereafter rockling), which is a common prey and easy to identify separately. Most fish identified as rockling were likely to be three-bearded rockling (*Gaidropsarus vulgaris*) with lesser numbers of northern rockling (*Ciliata septentrionalis*), and five-bearded rockling (*C. mustela*; Harris and Hislop 1978). Sandeels could not be identified to species level, but previous studies have shown that the vast majority are likely to be lesser sandeel (*Ammodytes marinus*; Harris and Hislop 1978, Harris and Wanless 2011). Seabird diet studies often benefit from splitting sandeels into 0 group (young of the year) and 1+ (> 1 year old) age classes. We were not able to differentiate 0 group and 1+ sandeels from images, nor did we find clear bimodality in the fish lengths that could have potentially been used to separate 0 group and 1+ fish. However, we were able to identify transparency of sandeels and use this information to differentiate two sandeel categories. The first is transparent sandeels in which fish are completely or partially transparent, with dark dots visible running longitudinally. This corresponds to young fish that are either post-larval or juvenile (Reay 1970). The second is non-transparent sandeels in which fish are completely silvered, corresponding to fish that have completed metamorphosis and will be made up of both juvenile and adult fish (*A. marinus* complete the growth of silver scales within a year but do not usually mature to adults until after age 2; Reay 1970). Prey not captured by any prey type category were recorded as "other." Prey not identifiable to any category were classed as "unidentified."

Length of prey in relation to Puffin bill depth

The length of each fish was estimated by measuring from the tip of the snout to the tip of the tail (for squid the mantle length was measured). Measurements were recorded in units of maximum bill depth excluding the cere (measurement "c" in Harris 1979) to the nearest 0.5 bill depths and converted to centimeters by multiplying by 3.5 (mean bill depth of 160 male Puffins on the Isle of May = 3.64 ± 0.011 cm and 170 female Puffins = 3.41 ± 0.011 cm; Harris and Wanless 2011). A visual aid such as string or digital ruler was used to transpose bill depths onto fish. If the whole fish was not visible, observers used anatomical features of the fish to estimate how much of the fish was obscured and thus estimate the full length, e.g., the position of the pectoral or anal fins relative to head or tail, or the tapering body shape of each species. In addition, the observer could assess whether the lengths of obscured fish in a load were likely to be similar to lengths of fish of the same species that were unobscured. For example, if obscured fish had similar girths, fin sizes, and similar sized herringbone skin patterns to unobscured fish of the same species in the same load, they were considered to have a similar length (see Appendix 1 for a worked example). The sizing is therefore an estimate but likely to be at least as reliable as traditional methods of observing prey delivered to Puffin chicks using binoculars, which have previously been shown to be accurate (Rodway and Montevecchi 1996).

Level of confidence in identification, count, and measurement of prey

Four separate levels of confidence (1 = confident, 2 = fairly confident, 3 = not confident, 4 = not possible from this photo) were recorded by observers for: (1) prey type identification; (2) prey length estimation; and (3) number of prey items.

Data analysis

Estimating biomass

We estimated load biomass using the fish length-weight relationship:

$$\text{Weight (g)} = a \times \text{Total Length (cm)}^b$$

where a and b are published constants (Froese et al. 2014; available via https://www.fishbase.de; Appendix 2). Published constants relate to individual species and our data are collected at the prey group level. Therefore, for clupeids, we used the average of the constants for herring and sprat (though they were in fact identical). For gadoids, we used the average of whiting (*Merlangius merlangus*) and saithe (*Pollachius virens*) because these two species are described as common in Puffin diet, whereas cod (*Gadus morhua*) is rare (Harris and Wanless 2011). For rockling, we used the most common species previously identified in Puffin diet, which is three-bearded Rockling (Harris and Wanless 2011). We used the same length-weight relationship for both transparent and non-transparent lesser sandeels. For squid, we used the published length-weight information for *Alloteuthis subulata* (Robinson et al. 2010; Appendix 2) because examination of the photographs suggested this species was most likely. For the small number of unidentified prey (n = 48; 0.4% of prey items), we used an average of the clupeid and sandeel values. In all cases, we selected the most recent relationships calculated for sea areas closest to the UK.

Potential sources of bias in data collection and image analysis

We investigated potential bias in the species composition, number of fish in a load, and the size of prey in photographs submitted by the public. We did this using a control dataset collected on the Farne Islands, where any Puffin approaching the colony was photographed, regardless of whether it was first seen to be carrying prey (see Appendix 3 for details). We also checked whether the aspect of a photograph (whether the Puffin bill was shown from the front or the side in the photograph; hereafter aspect) affected our estimation of prey size (Appendix 3). Finally, we checked for differences in the distribution of front and side aspect photographs among colonies and consistent differences between observers in measuring fish lengths (Appendix 3).

Sample size

Samples collected by citizen scientists are likely to vary in number between Puffin colonies. We investigated how the reliability of prey composition estimates change with sample size. We resampled the mean proportion of sandeels (both transparency classes) in prey loads, with replacement, over 1000 simulations, in simulated samples from 1 to the actual number of birds sampled at each colony and plotted the resulting curves and 95% confidence intervals.

Spatial variation in Puffin chick diet

To examine how Puffin chick diet composition varied between six ecologically coherent regions (hereafter regions; West England and Wales; West Scotland and East Ireland; Orkney; Shetland; East Scotland and North East England; and East and South England), we fitted a generalized linear mixed model (GLMM) with prey abundance explained by prey type interacting with region. We used regions as defined by Cook and Robinson (2010, Table 4.1 in the manuscript) and Cook et al. (2011), which are based on covariance in trends in seabird abundance across 11 species. We chose this regional definition because we found models using these regions had a better fit than those using OSPAR regions (OSPAR 2010) and/or latitude for most prey groups. We account for the high numbers of zeros for some species groups within regions by including a term for zero-inflation within prey type by region. Because data collected closer together in the season are more likely to be similar than data collected at dates further apart, we accounted for variation between regions in the dates of photographs submitted by including a random effect term for Julian date. Because photos provided by members of the public may not cover the complete diurnal cycle and the times of photographs taken at some colonies will be constrained by the times of boat trips to islands (see Appendix 4), we included time (as cumulative minute of the day) as a random effect. Finally, we found measurement of fish length varied between observers (Appendix 3), and therefore controlled for among observer variation by including observer as a random effect. We specified a negative binomial distribution with quadratic parameterization (the variance increases quadratically with the mean). We excluded unidentified and other prey types due to low sample sizes, and only included photos with a confidence level of 1 or 2 in species identification.

To examine how the total number of fish in the load varied between regions, we fitted a GLMM with number of fish explained by region, specifying a Gaussian distribution. We included random terms for observer, Julian date, and time of day within date, and a dispersion term for region, as total variance in number of fish varied with region. We only included photos with a confidence level of 1 or 2 in the count of fish.

To examine how biomass varied between regions, we fitted a GLMM with square-root transformed biomass data explained by region and photo aspect, specifying a Gaussian distribution. We included random terms for observer, Julian date, and time of day (as cumulative minutes) within date. Aspect was included as a random effect in the biomass model because we found the aspect of the photograph (taken from the side or the front) impacted measurements of fish length (Appendix 3). We only included photos with a confidence level of 1 or 2 in all three categories of sizing, count, and species identification.

We excluded the Orkney region from all analyses due to a low sample size. We subtracted a constant 175 days from all dates to center the data prior to analysis so that the intercept was day 175 not day 0. All models were fitted using the glmmTMB package (Magnusson et al. 2017), final model formulas were chosen based on the type of response variable, and model residuals were assessed for appropriate distribution, dispersion, and outliers with the "simulateResiduals" function of the DHARMa package (Hartig 2017). Estimated marginal means (predicted values),

based on simulations taking all model uncertainties into account, were calculated using the ggpredict function (type = "sim") of the ggeffects package (Lüdecke et al. 2020). We calculated pairwise comparisons between regions, with p-values adjusted using the Tukey method for comparing a family of estimates, using the emmeans package (Lenth 2023). All analyses were undertaken in R 4.2.1 (R Core Team 2022).

Within-season variation in Puffin chick diet

To examine how dietary composition changed throughout the breeding season, we modeled the proportion of each prey category observed per load for each region independently using proportional odds cumulative link models in the R VGAM package (Yee 2010). These models are similar to ordered multinomial logistic regression models (McCullagh 1980). Models in which we included separate categories for each fish species did not converge, probably due to a lack of observations in rarer prey types. We therefore simplified our prey type categories by pooling all observations of clupeid, rockling, and gadoid as other fish. As our response variable, we used a four-level categorization of prey type (transparent sandeel, non-transparent sandeel, other fish, and other items, the latter being any prey not captured by the original prey categories) fitted as a four-column response variable. However, in some regions the "other" category was never observed, in which case we defaulted to a three-column response variable. As a predictor variable, we included day of the year fitted using a non-linear cubic spline. We anticipated differences in sample size over the chick rearing season would increase uncertainty in model estimates at time points with fewer samples. We therefore generated 95% confidence intervals around model predictions using a non-parametric bootstrapping approach.

We modeled seasonal variation in both biomass per load and the number of items per load using the R brms package (Bürkner 2017). In each case, the effect of day of the year was fitted using thin-plate regression splines (Wood 2006) with a separate spline estimated for each region. To model biomass per load, we used a Gamma error distribution with a log-link to capture the fact that (1) biomass per load is always above 0 and (2) appeared to have a long right-tail based on visual inspection of the data. To model the number of prey items per load, we used a truncated Gaussian distribution with a lower bound of one (prey loads had to contain at least one prey item). A truncated Gaussian distribution was judged to perform better than a similarly truncated Poisson or negative binomial distribution based on posterior predictive checks for each model specification (posterior predictive checks for both models are displayed in Appendix 5). We used a student's t prior for splines with 3 degrees of freedom, mu of 0 and a sigma of 1. Models were run in brms using 4 chains of 4000 iterations each with a warmup of 1000 iterations. We showed how uncertainty in model estimates changed at time points with fewer samples by plotting the 95% credible interval for these models.

RESULTS

Sampling using citizen scientists

The submission website received 13,579 views from 10,761 unique viewers between 20 May 2017 and 31 October 2017. A total of 602 citizen scientists uploaded 1402 photos from 35 sites, taken between 17 May and 15 August. Of the photographs, 92 were excluded either because they did not contain prey or because they were duplicates. Four photographs were removed because the dates were very early in the breeding season (3 and 4 May). The remaining 1306 photographs each contained between 1 and 4 Puffins carrying prey. The total number of Puffins sampled across photographs was 1346.

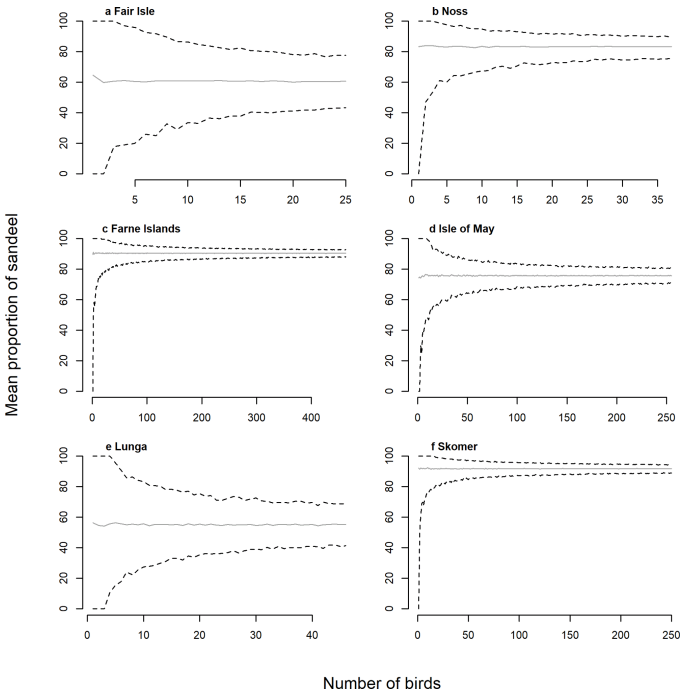
Prey identification was completed over a period of two months. A high proportion (89%) of Puffin bill loads were sufficiently clear to assign prey to species groups with a confidence score of 1 or 2, i.e., prey type confidence categories: 1 = 814 birds (61%), 2 = 384 birds (29%), 3 = 122 birds (9%), 4 = 26 birds (2%). A similarly high proportion (94%) of Puffin images were sized with confidence categories 1 or 2, i.e., prey size confidence categories: 1 = 863 birds (64%), 2 = 397 birds (30%), 3 = 56 birds (4%), 4 = 30 birds (2%). The total number of fish per load was also scored with a confidence of 1 or 2 in most (82%) cases, i.e., number of prey confidence categories: 1 = 489 birds (36%), 2 = 620 birds (46%), 3 = 188 birds (14%), 4 = 49 birds (4%). Retaining only images in which the confidence in species assignment was high (score 1 or 2) gave a final sample of 11,150 individual prey items from 1198 birds, containing information from 27 colonies (Table 1).

Resampling the data showed the width of confidence intervals around the mean proportion of sandeel decreased rapidly up to around 15 birds sampled (Fig. 1). Samples from 7 colonies contained 15 or more samples (Table 1), while 20 colonies had samples of fewer than 15 birds. Nine of the 27 colonies were sampled over fewer than 7 consecutive days. The colonies with the largest sample sizes were the Farne Islands, Isle of May, and Skomer (462, 255, and 248 Puffins sampled, respectively). Of the 9 British colonies, which held over 10,000 occupied burrows at the time of the last complete national census (Owen et al. 2023), 3 were not sampled (St Kilda, Sule Skerry, the Flannan Isles; all NW Scotland), due to their remote locations. Coverage was unequal across regions: East and South England = 468 birds, East Scotland and North East England = 280 birds, Orkney = 10 birds, Shetland = 89 birds, West England and Wales = 266 birds, West Scotland and East Ireland = 85 birds (Table 1).

Potential biases

Neither the number of fish counted in photos ($X^2 = 1.74$, $p = 0.19$) nor the mean length of fish ($X^2 = 1.01$, $p = 0.32$) were dependent on whether the photo was part of the control set or submitted by the public (see Appendix 3 for detailed results). We did not have adequate numbers of non-sandeel prey within our sample to accurately test differences in prey composition between control and public photos. However, there was no effect of data source (control or public) on the proportion of non-transparent sandeels identified in the photos ($X^2 = 0.09$, $p = 0.77$). When testing the effect of photograph aspect on length of prey, we found that prey was measured on average 0.75 cm shorter per prey item in photos taken from the side compared to from the front (n = 311 prey, $X^2 = 10.2$, CI = -0.52 - -0.15, $p < 0.01$). We therefore controlled for potential size bias due to photo aspect by including aspect as a fixed effect when modeling biomass data (because biomass is calculated from the fish length estimates). We found measurement of fish length varied between image analyst in the unmoderated test dataset ($X^2 = 1046.8$, $p < 0.0001$). We therefore controlled for inter-observer variation by including observer in data analyses. This reaffirmed the importance of retaining a moderation step in

Fig. 1. Resampled mean sandeel (transparent and non-transparent) proportion (gray line) and 95% confidence intervals (dashed lines) in the diets of Atlantic Puffins (*Fratercula arctica*) from 6 example colonies generated over 1000 simulations. Confidence intervals around the mean proportion of sandeel decrease rapidly before approximately 15 birds sampled. X axis limits are defined by the actual sample collected.



the analysis of the main dataset, which acts as a further control on variation introduced between observers (see Appendix 3 for detail on all potential bias results).

Spatial variation in Puffin chick diet

Prey composition

Sandeels were an almost ubiquitous part of Puffin chick diet, accounting for between 33% and 100% of overall diet in 26 of the 27 colonies sampled, but the proportion of transparent and non-transparent sandeels was variable between colonies (Fig. 2; Appendix 6) and regions (puffin prey composition dependent on region; z value = 5.7, $p < 0.0001$; Appendices 7 and 8). The highest occurrence of non-transparent sandeels was in West England and Wales, where they accounted for 84% of the 1161 prey items sampled. Modeled simulations predicted 7.6 (± 4.6 SE) non-transparent sandeels per load in this region. A high occurrence of non-transparent sandeels was also found in three other regions: East and South England (79% of 4353 prey sampled; 7.5 [± 5.3 SE] non-transparent sandeel per load); East Scotland and North East England (69% of 2600 prey sampled; 6.6 non-transparent sandeels [± 6.3 SE] per load); and West Scotland and East Ireland (47% of 622 prey sampled; 3.5 [± 4.0 SE] non-transparent sandeels per load; Fig. 3). Non-transparent sandeels accounted for just 5% of the total prey sampled in the Shetland region (0.7 [± 2.0 SE] non-transparent sandeels per load), with loads instead dominated by transparent sandeels. Transparent sandeels accounted for 72% of total fish sampled in Shetland (9.8 (± 7.2 SE) transparent sandeels per load), a significantly higher proportion than found in any other region (Fig. 3; Appendix 9). Transparent sandeels made up only 5% of all prey sampled in West Scotland and East Ireland (0.4 [± 1.5 SE] transparent sandeels per load), 8% in West England and Wales (0.7 [± 2.1 SE] transparent sandeels per load), 15% in East and South England (1.4 [± 3.4 SE] transparent sandeels per load), and 21% in East Scotland and North East England (2.0 [± 4.0 SE] transparent sandeels per load; Fig. 3).

Clupeids were uncommon in most regions (0–0.5 clupeids per load) except for West Scotland and East Ireland where they accounted for 28% of all prey sampled (1.9 [±2.9 SE] clupeids per load; Fig. 3). Rockling were more common in the diet of Puffins in northern colonies, accounting for 18% of total fish sampled in Shetland (2.4 rockling [± 3.0 SE] per load) and West Scotland and East Ireland (1.3 rockling [±2.9 SE] per load), but were rare elsewhere (Figs. 2, 3; Appendix 7). Gadoids were very rare in samples from English and Welsh colonies and present only in low numbers elsewhere, except at one colony, Fair Isle in Shetland, where almost one quarter of the diet was gadoids (Figs. 2, 3; Appendix 6). The only prey recorded as "other" were squid (possibly *Alloteuthis subulata*), which were recorded in five loads from the Farne Islands and one from Skomer. Pairwise comparisons of prey composition between regions are presented in Appendix 9.

Number of prey items, prey length, and biomass per load

The highest number of prey per load was found in Shetland, with 11.7 (± 5.5 SE) items of prey predicted based on model simulations. The number of prey in loads sampled in the Shetland region was significantly higher than all other regions (Fig. 4; Appendix 10), with 9.2 (± 3.4 SE) prey per load in East and South England, 8.9 (± 3.3 SE) prey per load in West England and Wales, 8.7 (± 4.9 SE) prey per load in East Scotland and North East England, and 6.9 (± 2.7) prey per load in West Scotland and East Ireland (Fig. 3). Conversely, the biomass of loads sampled from Shetland colonies was significantly lower than all other regions (Appendix 11), with 2.0 g (± 0.6 SE) predicted per load compared with 5.2 g (± 0.6 SE) in West England and Wales, 4.4 g (± 0.7 SE) in East Scotland and North East England, 4.4 g (± 0.7 SE) in East and South England, and 3.1 g (± 0.7 SE) in West Scotland and East Ireland (Fig. 3). Prey length data also highlight the difference between regions, with Shetland notable for a peak prey length of 3–4 cm compared to all other regions which peak at 5–6 cm. This is the result of an absence of non-transparent sandeels. Furthermore, larger sandeels in the 5–6 cm range still show transparency in Shetland (Fig. 5; Appendices 12 and 13).

Within-season variation in Puffin chick diet

Prey composition throughout the breeding season

The proportion of different prey groups in Puffin chick diet showed a non-linear relationship with day of the year (Appendix 5), and prey composition patterns also varied between regions. In East Scotland and North East England, we observed an increase in the proportion of non-transparent sandeel in the diet from mid-May up to a peak in mid-June before a subsequent decline (Fig. 6). A similar pattern was also observed in the East and South

Table 1. Number and date range of Atlantic Puffins (*Fratercula arctica*) and prey items sampled by citizen scientists at 27 colonies during 2017.

Region	Colony (OSPAR Area; E = East, W = West)	Abbreviation	n birds†	n prey sampled†	Sample date range†	Sampling period† (d)
Eastern and Southern England	Coquet Island (E)	CO	6	42	31 May–10 Jun	21
	Farne Islands (E)	FN	462	4297	23 May–30 Jul	69
Eastern Scotland and Northeast England	Bullers of Buchan (E)	BU	5	32	29 May–10 Jul	43
	Caithness Cliffs (E)	CA	2	14	17 Jun	1
	Craigleith (E)	CR	1	9	5 Jun	1
	Flamborough/Bempton (E)	FB	14	85	29 May–12 Aug	76
	Fowlsheugh (E)	FW	3	15	16 Jun–30 Jul	45
	Isle of May (E)	IM	255	2445	17 May–22 Jul	67
Orkney	Stroma (E)	ST	2	8	28 Jun	1
	Westray (E)	WE	8	55	26 Jun–28 Jul	33
Shetland	Fair Isle (E)	FA	25	286	18 Jun–21 Jul	34
	Fetlar (E)	FE	2	19	23 Jun	1
	Foula (E)	FO	4	36	26 Jul–2 Aug	8
	Hermaness, Unst (E)	HE	7	83	15 Jun–12 Jul	28
	Noss (E)	NO	37	514	10 Jun–15 Aug	67
	Sumburgh Head (E)	SU	14	223	19 Jun–7 Aug	50
West England and Wales	Gwylan Islands (W)	GW	4	16	31 May	1
	Mincarlo (W)	MC	2	9	30 May–14 Jun	16
	Puffin Island Anglesey (W)	PI	1	10	25 Jun	1
	Skokholm (W)	SK	11	82	27 May–14 Jul	49
	Skomer (W)	SM	248	2248	21 May–25 Jul	66
West Scotland and Ireland	Great Skellig (W)	GR	1	6	8 Jun	1
	Lunga (W)	LU	46	341	12 Jun–28 Jul	47
	Mingulay (W)	MG	1	10	8 Jun	1
	Puffin Cove (E)	PC	10	74	14 Jun–22 Jul	39
	Shiant Islands (W)	SH	24	174	14 Jun–5 Jul	22
	Staffa (W)	SF	3	17	4 Jul–9 Jul	6

†Prey type confidence category 1 and 2 only.

Fig. 2. Atlantic Puffin (*Fratercula arctica*) diet composition at 27 sites in the UK and Ireland during 2017. Proportions of prey types are the means across all birds sampled within each colony. Letter codes are colony abbreviations, given in Table 1. The size of pie charts is proportional to sample sizes, which are also given in Table 1. Please note that colonies CO, BU, CA, CR, FB, FW, ST, WE, FE, FO, HE, SU, GW, MC, PI, SK, GR, MG, PC, and SF are represented by samples from fewer than 15 birds and therefore are not necessarily representative of typical diet at that colony.

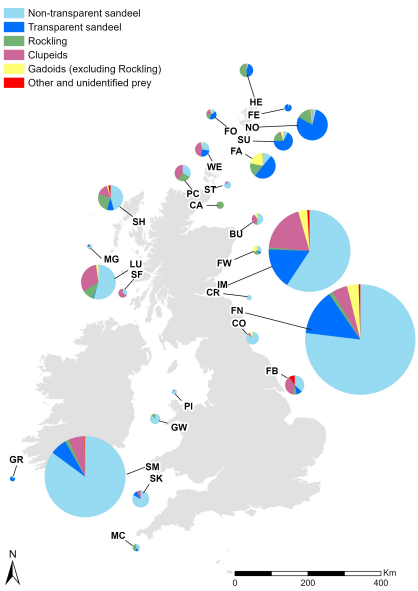


Fig. 3. Estimated marginal means (predicted values) based on simulations controlling for all model uncertainties, showing: (a) predicted count of each prey type in Atlantic Puffin (*Fratercula arctica*) fish loads by region; (b) predicted total number of fish in loads by region; and (c) predicted biomass, g, in loads by region; with 95% confidence intervals shown by dashed lines. Calculated with the ggpredict function of the ggeffects package.

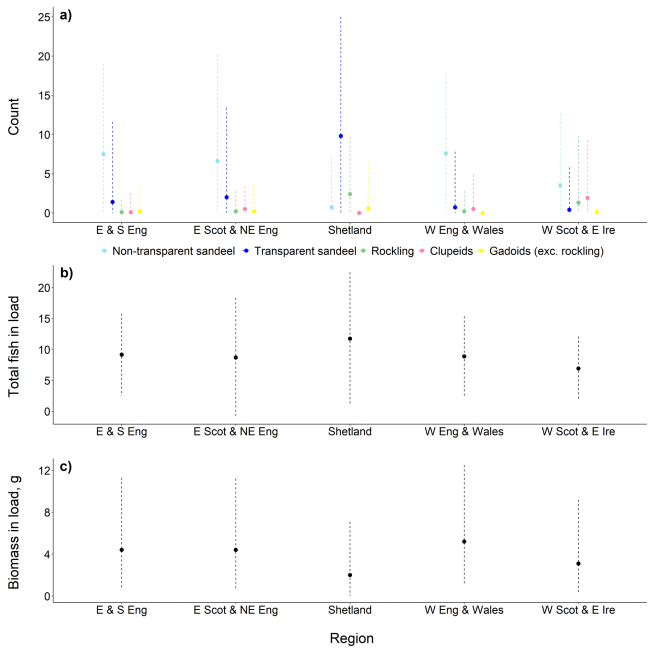
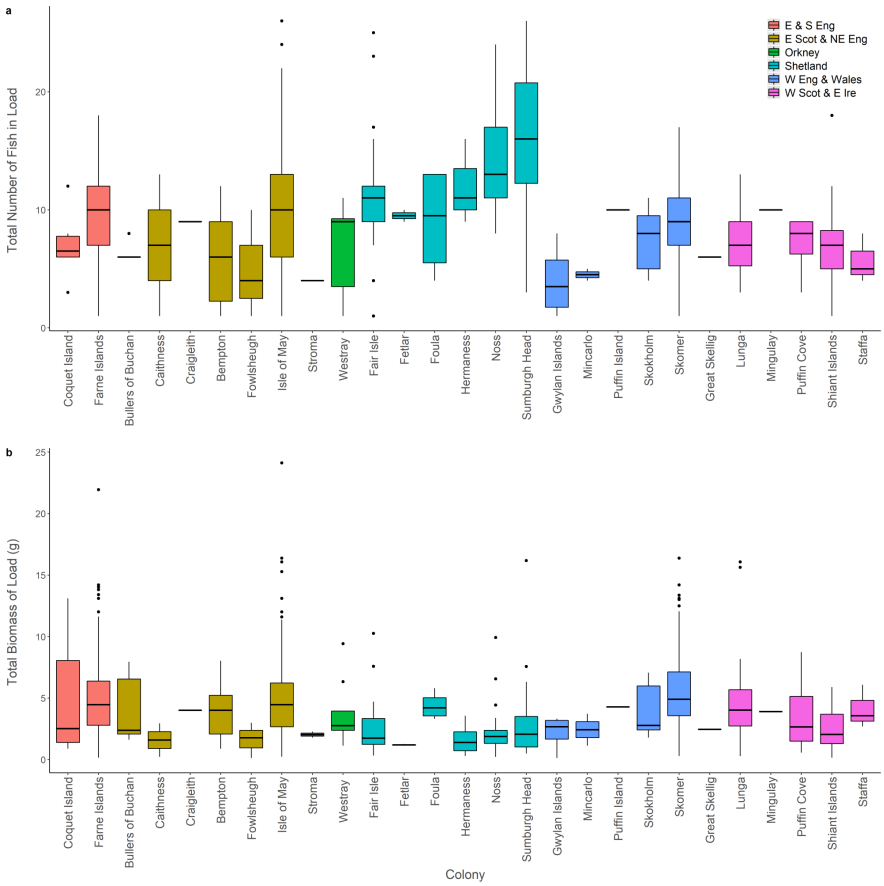


Fig. 4. Median number of fish per load (a) and biomass per load (b) in Atlantic Puffins (*Fratercula arctica*) at 27 colonies in the UK and Ireland in 2017. Number of birds sampled per colony given in Table 1.



England region except that, although the proportion of non-transparent sandeel in the diet again peaked in mid-June, it subsequently plateaued after this date. In West England and Wales, non-transparent sandeel were the dominant prey item in prey loads in late May, and the proportion of non-transparent sandeel in prey loads steadily increased from late May until late July. In West Scotland and East Ireland, non-transparent sandeel made up the highest proportion of prey per load until the end of June after which point the proportion of non-transparent sandeel dropped sharply and the proportion of other fish species in the diet rose. Based on the results reported above, these were most likely to be clupeids and rockling. In this region, the proportion of transparent sandeels remained relatively low throughout the breeding season. In the Shetland region, transparent sandeels were the dominant prey item from early June to early July. Transparent sandeels remained an important prey item in Shetland after early July but the proportion of other fish in the diet also increased after this point; these were mostly rockling and, on Fair Isle, gadoids. From early June onward the proportion of non-transparent sandeels in the diet of Puffins in Shetland remained low.

Number of prey items and biomass per load throughout the breeding season

The number of prey items per load rose in both the East and South England region and the East Scotland and North East England region during the first half of June, before declining thereafter (Fig. 7; Appendix 5). This decline was particularly marked in East Scotland and North East England, though the available sample size at later summer dates beyond 30 June was relatively limited in this region. In contrast, in the West England and Wales region the number of prey items per load steadily increased from the end of May until mid-July. We found little evidence of a seasonal trend in the number of prey items per load in both the Shetland and West Scotland and East Ireland regions.

Biomass per load rose during the period from late May to mid-June in three of the five regions: East Scotland and North East England, East and South England, and West England and Wales. Biomass continued to increase slightly throughout the season in the West England and Wales region but declined after mid- to late-June in the other two regions (Fig. 8; Appendix 5). There was a gradual increase in load biomass over the season in the Shetland region but little evidence of seasonal trends in load biomass in the West Scotland and East Ireland region.

Fig. 5. The number of observations recorded within each fish length bin across different regions for three distinct prey categories (transparent sandeel, non-transparent sandeel, and other fish). The other fish category combines data on the lengths of prey species recorded as clupeids, gadoids, or rockling. Data on these species were combined for ease of visualization. Data for the Orkney region were not included due to the low number of observations in this region. More data on fish lengths are presented in Appendices 12 and 13.

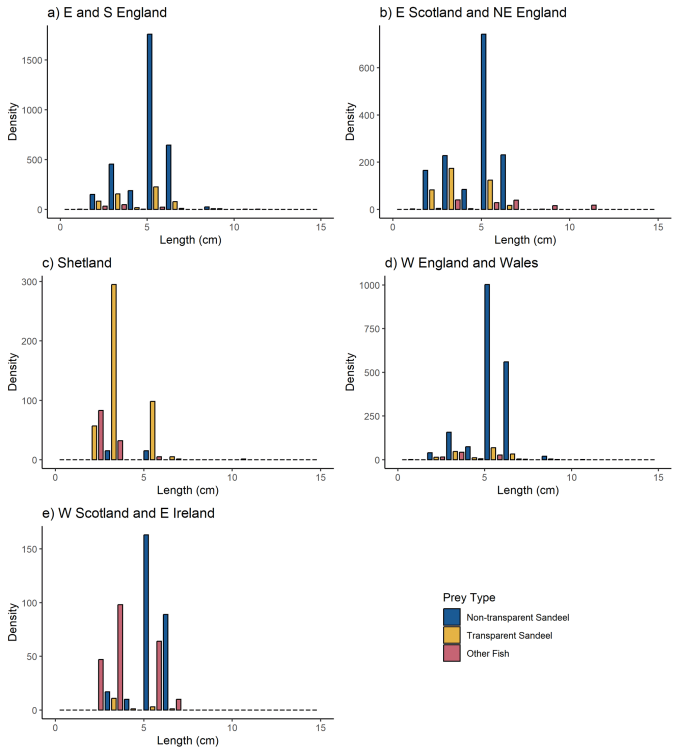
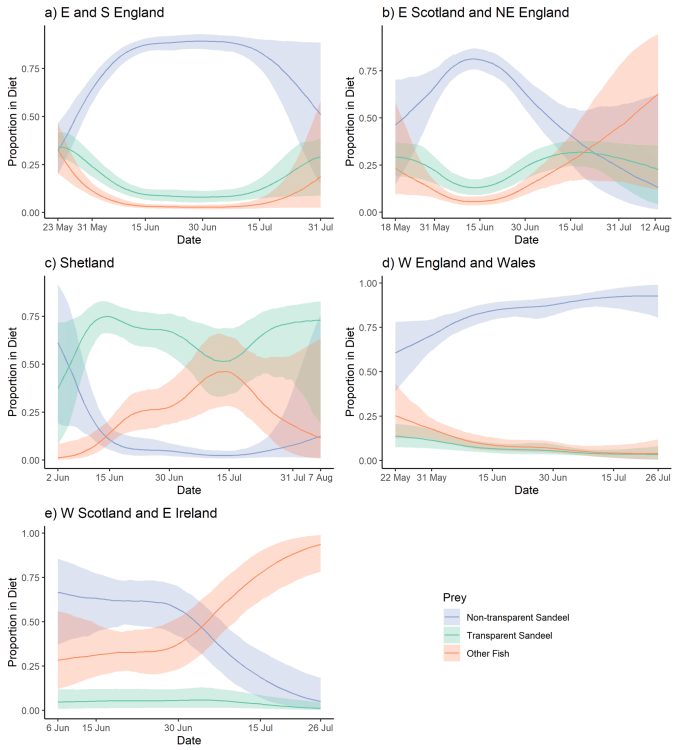


Fig. 6. The proportion of non-transparent sandeel (blue), transparent sandeel (green), and fish species (orange) in the diet of Atlantic Puffins (*Fratercula arctica*) within each region (a–e) in 2017. Solid lines represent the mean proportion of a prey item in the diet by date with corresponding 95% confidence intervals (opaque colors) estimated via boot-strap resampling. Note in some regions, we observed a fourth prey category "other items." However, prey items in this group were so rarely observed we did not include the corresponding fitted curve on the plot for the sake of clarity.



DISCUSSION

Multi-colony studies of seabird diet are rare, particularly those covering large spatial extents or multiple time periods, which limits our understanding of trophic interactions and population ecology (Barrett et al. 2007). We worked alongside citizen scientists to document variation in prey fed to Puffin chicks at multiple colonies around the UK and Ireland, greatly extending the spatial coverage of diet data for Puffins. We demonstrated a lack of bias in the sample of photos provided by citizen scientists and described large-scale and seasonal variation in Puffin chick diet composition. The result is a key conservation resource, describing important differences in diet between regions and confirming the potential for the approach to be extended to include multiple years to assess how change in diet relates to population trends over time.

Spatial and temporal variation in Puffin chick diet

The diet of Puffin chicks from regions in which severe declines have occurred, most notably Shetland (Miles et al. 2015, Owen et al. 2018, 2023), were characterized by a lower prey biomass, higher numbers of prey per load, smaller prey sizes, and a high proportion of transparent sandeels. By contrast, in Welsh colonies, where overall Puffin populations are increasing (Brown and Eagle 2018, Stubbings et al. 2018, Owen et al. 2023), load biomass was higher than other areas, the number of prey per load was relatively low, prey were larger, and non-transparent sandeels were the dominant prey throughout the breeding season. These differences are consistent with observations of a collapse in the sandeel population in Shetland (Furness 2007) and a lack of alternative prey, notably sprats, which have been largely absent from Shetland since the 1970s (Corten 1986), leading to a reduced prey base. Maturation rates of sandeels in Shetland are slower than elsewhere in the North Sea (MacDonald et al. 2019), and this may be shown in our prey length data, in which larger sandeels (5–6 cm) were still transparent in the Shetland region. Poor growth leads to slower maturation and successive years of these conditions would result in a decreased sandeel stock biomass (MacDonald et al. 2019). Our study has increased the number of sampled colonies in Shetland from one to six and has shown a continued absence of non-transparent sandeels and lack of suitable alternative prey in this region. Fayet et al. (2021) found that in declining colonies in Southern Iceland and Norway, Puffins traveled further to forage than in stable colonies in Wales and Northern

Fig. 7. The seasonal trend in biomass per load carried by Atlantic Puffins (*Fratercula arctica*) in each region (a–e) in 2017. Dark blue represents the mean biomass per load whereas the light blue envelope represents the 95% credible interval (95% CRI). The x-axis extends from the earliest observation in the region to the latest.

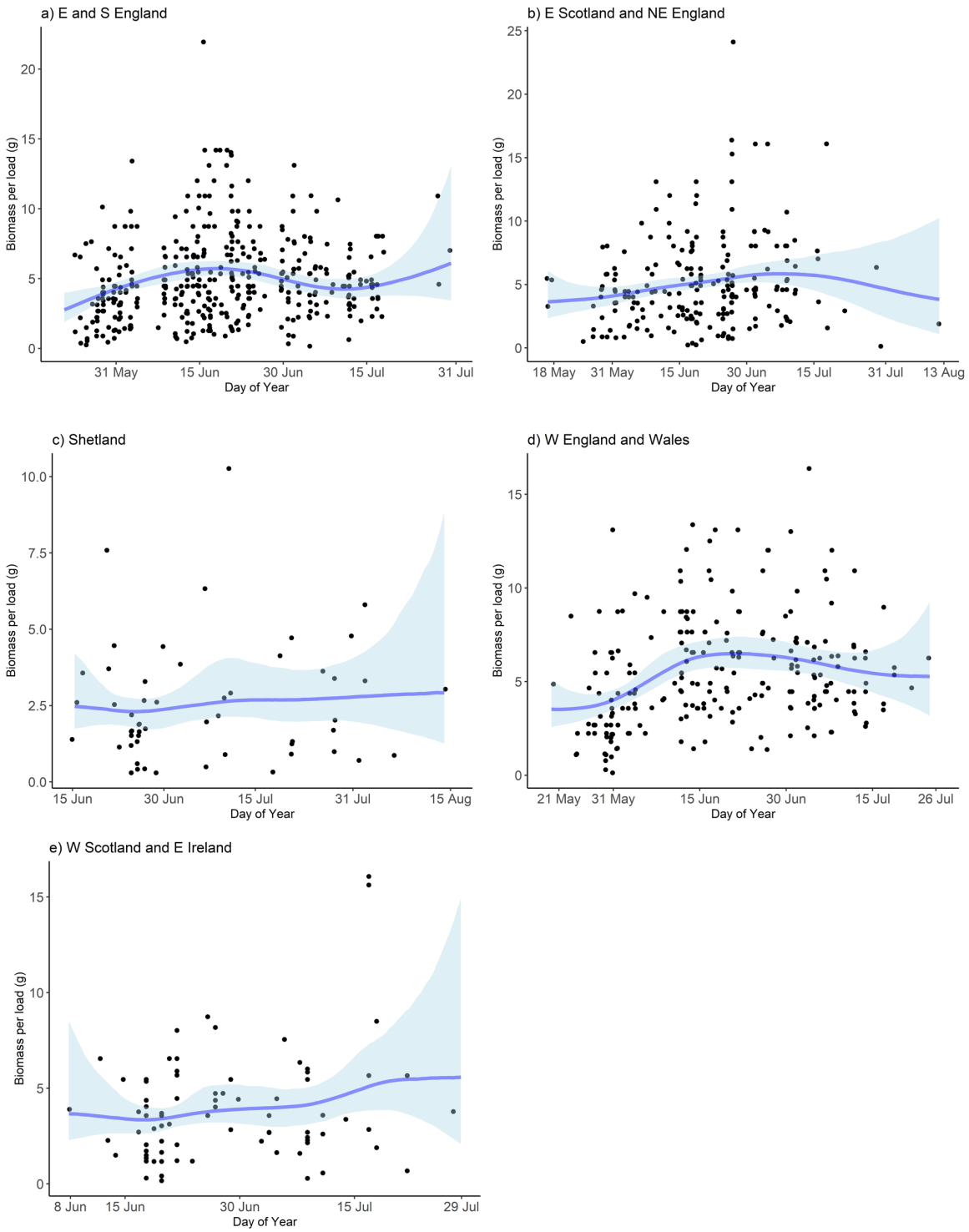
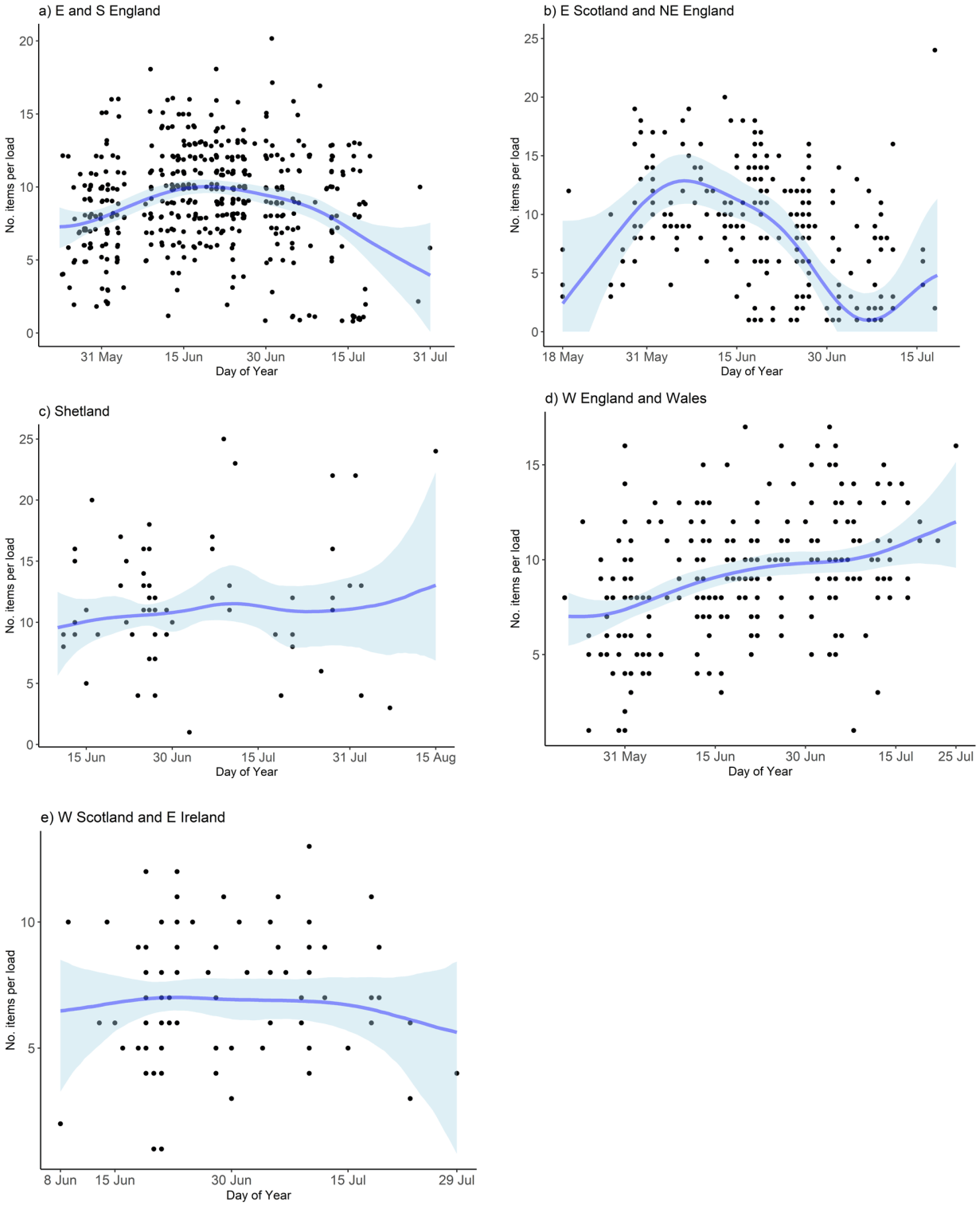


Fig. 8. The seasonal trend in the number of prey items per load carried by Atlantic Puffins (*Fratercula arctica*) in each region (a–e) in 2017. Dark blue represents the mean number of prey items per load whereas the light blue envelope represents the 95% credible interval (95% CRI). The x-axis extends from the earliest observation in the region to the latest.



Iceland. Razorbills (*Alca torda*) and Common Murres (*Uria aalge*) tracked from Fair Isle in Shetland have also been observed to travel relatively long distances compared to the same species at more southerly colonies (Wakefield et al. 2017). It seems likely that Puffins in Shetland are not only finding loads of lower biomass but are also traveling further and incurring higher flight costs than birds in other regions.

Our results are consistent with findings from the two colonies where Puffin chick diet is routinely sampled in the UK using traditional methods (examining prey from adults caught in mist-nets): the Isle of May in the East Scotland region and Fair Isle in the Shetland region. The decrease we observed in non-transparent sandeels and increase in clupeids on the Isle of May within the chick-rearing period (Appendix 14) accords with the behavior of prey in this area because non-transparent sandeels re-bury in the sand toward the latter part of the Puffin breeding season in late June (Rindorf et al. 2000). The data from mist-netting sampling from the Isle of May long-term study also showed a decrease in sandeel proportion and simultaneous increase in clupeid from late June in 2017 (M. Harris *personal communication*). The relatively high proportion of gadoids in the diet of Puffin chicks from Fair Isle in our sample (Appendix 14) is unusual across the colonies we sampled but is consistent with a mean proportion of 30.7% (± 22.8) gadoid in the diet over 27 years sampling on Fair Isle (Miles et al. 2015). The load biomass measured on Fair Isle has decreased over the same period, from around 10 g in the 1990s to around 3 g in 2013 (Miles et al. 2015), and we found a mean load biomass that was lower still in 2017 (2.6 g ± 2.2 g). A steady increase in the mean number of fish per load occurred on Fair Isle from under 5 prey per load in the 1980s to around 11 in the early 2010s, and we observed a mean of 10.0 ± 4.8 prey in 2017. Mist-netting was used in the 1970s to study diet on several UK colonies. In common with our findings, higher numbers of prey per load resulted in lower overall load weight, particularly at St. Kilda and Hermaness (Harris and Hislop 1978). The high number of sandeels in the diets of Puffins from Skomer in our sample is consistent with results from Fayet et al. (2021), who used DNA metabarcoding to identify fish species present in Puffin feces and found sandeels in 100% of samples from 6 adults and 90% of samples from 10 chicks. As with our results, they also detected herring and sprat, but in contrast to our data, found no rockling, instead identifying haddock *Melanogrammus aeglefinus* in the diet.

We described how prey composition, number, and biomass vary between regions. We also observed differences in diet between colonies in the same region, e.g., the increased occurrence of rockling and gadoids on Fair Isle that was not observed on Noss. Therefore, although we were constrained by small sample sizes at some colonies to model dietary trends at the regional level, we emphasize the value of collecting detailed colony-level diet data when possible. Puffins are central-place foragers, needing to return to the colony regularly to feed chicks during breeding. This restricts foraging ranges to areas accessible from colonies, and so variation in prey composition between colonies and regions likely reflects differing sea conditions, habitat types, and the available prey base within the foraging range of colonies. For example, Puffin diet on the east coast of North America was broadly similar across 3 colonies over 150 km apart (Scopel et al. 2019), likely reflecting the relatively constant density over large spatial scales of the major prey, herring (*Clupea harengus*; Wurtzell et al. 2016). Local resources around the UK, however, are likely to show more variation between colonies because species like sandeels, which are restricted to sandbank habitats, have a highly localized distribution (Wright et al. 2000). Segregation of foraging areas to mitigate parapatric competition from conspecifics, as observed in other species including auks (e.g., Common Murres; Wakefield et al. 2017) could also occur in Puffins and promote diet differences between neighboring colonies.

The diets of few seabird species have been recorded across many colonies in the same year. A notable exception is Common Murre diet in which volunteers collected a considerable amount of data across a large spatial extent (Anderson et al. 2014). Broadly, as with our Puffin data, Common Murre chick diets contained higher proportions of sandeel (assumed to be adults) and gadoids in the north of the UK and a greater proportion of clupeids in the south, though there were more nuanced differences between colonies reflecting the regional clustering of sandeel populations. Gadoids also occurred more frequently in the north, and particularly in Shetland, where the authors suggest the lower lipid content of gadoids accords with the low murre productivity in this region. The decrease in sandeel in Common Murre chick diet as the breeding season progressed was in common with Puffin chick diet in our study in all regions except Shetland, where numbers were always low, and West England and Wales, where sandeels continued to be used throughout the season.

Wider implications for Puffin conservation

Puffins are susceptible to changes in food availability, which is thought to be a major driver of Puffin population declines (e.g., Durant et al. 2003). Climate change is causing increased sea temperatures, changes in storminess cycles, and large shifts in zooplankton abundance and distribution (Carpenter et al. 2016, Edwards et al. 2020). Exceptionally, large offshore wind arrays are planned in the UK that are expected to change ocean stratification and primary productivity (Carpenter et al. 2016) and displace seabirds from foraging areas (Welcker and Nehls 2016). British and Irish waters are also likely to continue to support large commercial fisheries. Although advances have been made in tracking seabirds to determine where they forage (Wakefield et al. 2017, Fayet et al. 2021), complementary data on prey availability and variation in diet between colonies and regions remain scarce. Seabird diet data collected across multiple colonies around the UK are important to better understand the impacts of climate change, renewable energy developments, and fishing practices on Puffin colonies.

Our large-scale, concurrent Puffin chick diet dataset establishes a baseline for future monitoring. We also provide an image analysis method that could be used to collect images over a range of years and/or sourced from historical collections to enable changes in diet to be monitored at multiple colonies over multiple years, which would allow the impact of changes in ocean climate variables (e.g., sea surface temperature) and fisheries practices to be related to impacts on Puffin productivity. Long-term monitoring of Puffin chick diet in colonies across the global range of Puffins using methods such as the Puffarazzi would provide valuable data on changes in prey abundance and size and would document apparent collapses in prey bases, such as has been observed in Shetland. This information could be used to inform

fisheries management, for example, recommending the temporary closures of fisheries involving prey species near particular colonies. In addition, Puffins are also useful potential indicators of prey populations and oceanographic change within the foraging ranges of colonies, particularly because they have a relatively long chick-rearing period with prey visibly carried.

Our study also emphasizes the importance of species other than sandeels as prey items, with clupeids and rockling forming important parts of the diet in some regions previously not well studied. Colonies with access to a more varied prey base may prove more robust to changing marine environments and declining sandeel abundance. Puffin population declines are likely to be most severe where declines in the availability of a dominant prey species (for example, adult sandeels) are exacerbated by a lack of suitable alternative prey. This emphasizes the need for a concerted conservation management approach that integrates the needs of alternate prey species alongside those of dominant prey.

The citizen science approach

The use of citizen scientists to collect image data was effective at providing a low-cost, large-scale method for generating diet data for Puffin chicks. The costs of repeating a similar approach to gather data would include: a website (relatively low-cost); a press release (many research organizations have inbuilt capacity to support this), and staff time to share the existence of the initiative with stakeholder agencies managing relevant wildlife reserves. Further resource from trained image analysts is required to identify prey in images. There are opportunities to share ownership of this task with citizen scientists in partnership with professional scientists who can ensure data quality and provide mentorship. The use of artificial intelligence could further be used to automate the process of prey ID from images, though would require significant resource to design, train, test, use, and maintain algorithms and so may not be suitable for short-term projects and may lessen engagement opportunities (McClure et al. 2020).

A high proportion of submitted photos were suitable for analysis and were not biased in terms of either prey length or number. Scientific robustness was further enhanced by the inclusion of a moderation step in our image analysis method and by accounting for both observer variation and the effect of photo aspect (front or side) on prey measurements. The dominance of sandeels in our test dataset, matched by location and date to the control dataset, made it difficult to satisfactorily ascertain whether there was a bias toward certain prey types in photos submitted by the public. However, we expect public behavior to remain similar across colonies, meaning that biases, if present, are likely to be consistent, thus allowing for comparisons between colonies and across years. Another potential outcome of using citizen scientists to collect data is unequal spatial coverage. Most submitted photos (88%) were from just three colonies, due to convenience of location and ease of access. Sampling was unequal across regions and the Orkney region was particularly poorly sampled. It is also important to ensure appropriate temporal coverage because we, and others (Harris et al. 2022), have shown pronounced changes in diet within the breeding season, meaning that sampling at multiple time points will be more effective in characterizing diet. Citizen science offers the potential for increasing both the spatial and temporal extent of data collected. This study has shown which colonies and time periods are most likely to be under-sampled by the public. In the future, steps could be taken to further increase the coverage and evenness of sampling, for example, through actively requesting photos from specific colonies and emphasizing the value of photographs from throughout the season.

Sampling using citizen scientists and digital photography is not intended to replace the intensive sampling used at well-studied colonies, rather to complement it. Traditional sampling methods provide physical prey samples and therefore give information on prey nutritional content (Wanless et al. 2004). They also allow identification of prey to species rather than species group, although very small prey items are thought to be underestimated because they are less visible to collectors after being dropped (Rodway and Montevecchi 1996). However, using citizen scientists and photography to study Puffin diet has several important advantages. First, the welfare of Puffins is improved because no prey items are taken from Puffins and no birds are handled (though it is important to make photographers aware of guidelines to minimize disturbance). Additionally, sampling prey by catching adult Puffins at multiple colonies is either resource intensive, or in some cases, not feasible. For example, at some very small or steeply declining colonies, or colonies with low productivity in any one year, capture rates of adults can be too low to collect adequate prey samples (Anker-Nilssen 2010). Inviting participation from the public also provides an opportunity for increasing societal engagement in species conservation, attracting people from diverse backgrounds or younger age groups, which is thought to be an important requirement for biodiversity conservation (Kobori et al. 2016).

CONCLUSION

A citizen science approach was inexpensive, gained societal support, and provided a robust method of collecting a unique baseline dataset of Puffin chick diet across multiple colonies within the same year, allowing the examination of spatio-temporal variation in diet at a previously unprecedented scale. We characterized shifts in prey composition throughout the breeding season and showed where birds may be expending more effort (collecting more prey items) for lower returns (lower load biomass). Together this information will be used to better understand links between Puffin diet and productivity, with important implications for Puffin conservation.

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LITERATURE CITED

Anderson, H. B., P. G. H. Evans, J. M. Potts, M. P. Harris, and S. Wanless. 2014. The diet of Common Guillemot *Uria aalge* chicks provides evidence of changing prey communities in the North Sea. Ibis 156:23–34. https://doi.org/10.1111/ibi.12099

Anker-Nilssen, T. 2010. Key-site monitoring in Røst in 2009. SEAPOP, Trondheim, Norway. https://seapop.no/wp-content/uploads/2021/03/seapop-short-report-12-2010.pdf

Anker-Nilssen, T., and S.-H. Lorentsen. 1990. Distribution of Puffins *Fratercula arctica* feeding off Røst, northern Norway, during the breeding season, in relation to chick growth, prey and oceanographical parameters. Polar Research 8:67–76. https://doi.org/10.3402/polar.v8i1.6805

Balzani, P., S. Vizzini, F. Frizzi, A. Masoni, J.-P. Lessard, C. Bernasconi, A. Francoeur, J. Ibarra-Isassi, F. Brassard, D. Cherix, and G. Santini. 2021. Plasticity in the trophic niche of an invasive ant explains establishment success and long-term coexistence. Oikos 130:691–696. https://doi.org/10.1111/oik.08217

Barrett, R. T. 2015. Atlantic Puffin *Fratercula arctica* chick growth in relation to food load composition. Seabird 28:17–29. https://doi.org/10.61350/sbj.28.17

Barrett, R. T., T. Anker-Nilssen, G. W. Gabrielsen, and G. Chapdelaine. 2002. Food consumption by seabirds in Norwegian waters. ICES Journal of Marine Science 59:43–57. https://doi.org/10.1006/jmsc.2001.1145

Barrett, R. T., K. (C. J.) Camphuysen, T. Anker-Nilssen, J. W. Chardine, R. W. Furness, S. Garthe, O. Hüppop, M. F. Leopold, W. A. Montevecchi, and R. R. Veit. 2007. Diet studies of seabirds: a review and recommendations. ICES Journal of Marine Science 64:1675–1691. https://doi.org/10.1093/icesjms/fsm152

Becker, B. H., and S. R. Beissinger. 2006. Centennial decline in the trophic level of an endangered seabird after fisheries decline. Conservation Biology 20:470–479. https://doi.org/10.1111/j.1523-1739.2006.00379.x

BirdLife International. 2018b. *Fratercula arctica*. The IUCN Red List of Threatened Species 2018. Birdlife International, Cambridge, UK. https://dx.doi.org/10.2305/IUCN.UK.2018-2.RLTS.T22694927A132581443.en

BirdLife International. 2018a. State of the world's birds: taking the pulse of the planet. BirdLife International, Cambridge, UK. https://www.birdlife.org/papers-reports/state-of-the-worlds-birds/

Brown, R., and G. Eagle. 2018. Skokholm Seabird Report 2018. The Wildlife Trust of South and West Wales, Brecon, Wales. https://www.welshwildlife.org/sites/default/files/2022-03/Skokholm-Seabird-Report-2018.pdf

Bürkner, P.-C. 2017. brms: an R package for Bayesian multilevel models using Stan. Journal of Statistical Software 80:1–28. https://doi.org/10.18637/jss.v080.i01

Carpenter, J. R., L. Merckelbach, U. Callies, S. Clark, L. Gaslikova, and B. Baschek. 2016. Potential impacts of offshore wind farms on North Sea stratification. PLoS One 11:e0160830. https://doi.org/10.1371/journal.pone.0160830

Cook, A. S. C. P., M. Parsons, I. Mitchell, and R. A. Robinson. 2011. Reconciling policy with ecological requirements in biodiversity monitoring. Marine Ecology Progress Series 434:267–277. https://doi.org/10.3354/meps09244

Cook, A. S. C. P., and R. A. Robinson. 2010. How representative is the current monitoring of breeding seabirds in the UK? British Trust for Ornithology, Norfolk, UK. https://www.bto.org/sites/default/files/shared_documents/publications/research-reports/2010/rr573.pdf

Corten, A. 1986. On the causes of the recruitment failure of herring in the central and northern North Sea in the years 1972-1978. ICES Journal of Marine Science 42:281–294. https://doi.org/10.1093/icesjms/42.3.281

Croxall, J. P., S. H. M. Butchart, B. Lascelles, A. J. Stattersfield, B. Sullivan, A. Symes, and P. Taylor. 2012. Seabird conservation status, threats and priority actions: a global assessment. Bird Conservation International 22:1–34. https://doi.org/10.1017/S0959270912000020

Depot, K. M., L. C. Scopel, S. W. Kress, P. Shannon, A. W. Diamond, and K. H. Elliott. 2020. Atlantic Puffin diet reflects haddock and redfish abundance in the Gulf of Maine. Marine Ecology Progress Series 656:75–87. https://doi.org/10.3354/meps13537

Diamond, A., and C. Devlin. 2003. Seabirds as indicators of changes in marine ecosystems: ecological monitoring on Machias Seal Island. Environmental Monitoring and Assessment 88:153–181. https://doi.org/10.1023/A:1025560805788

Dickinson, J. L., J. Shirk, D. Bonter, R. Bonney, R. L. Crain, J. Martin, T. Phillips, and K. Purcell. 2012. The current state of citizen science as a tool for ecological research and public engagement. Frontiers in Ecology and the Environment 10:291–297. https://doi.org/10.1890/110236

Durant, J. M., T. Anker-Nilssen, and N. C. Stenseth. 2003. Trophic interactions under climate fluctuations: the Atlantic Puffin as an example. Proceedings of the Royal Society of London. Series B: Biological Sciences 270:1461–1466. https://doi.org/10.1098/rspb.2003.2397

Eaton, M., N. J. Aebischer, A. F. Brown, R. Hearn, L. Lock, A. J. Musgrove, D. Noble, D. A. Stroud, and R. D. Gregory. 2015. Birds of conservation concern 4: the population status of birds in the UK, Channel Islands and Isle of Man. British Birds 108:708–746.

Edwards, M., A. Atkinson, E. Bresnan, P. Helaouet, A. McQuatters-Gollup, C. Ostle, S. Pitois, and C. Widdicombe. 2020. Plankton, jellyfish and climate in the North-East Atlantic. MCCIP Science Review 2020:322–353. https://doi.org/10.14465/2020.arc15.plk

Fayet, A. L., G. V. Clucas, T. Anker-Nilssen, M. Syposz, and E. S. Hansen. 2021. Local prey shortages drive foraging costs and breeding success in a declining seabird, the Atlantic Puffin. Journal of Animal Ecology 90:1152–1164. https://doi.org/10.1111/1365-2656.13442

Froese, R., J. T. Thorson, and R. B. Reyes, Jr. 2014. A Bayesian approach for estimating length-weight relationships in fishes. Journal of Applied Ichthyology 30:78–85. https://doi.org/10.1111/jai.12299

Furness, R. W. 2007. Responses of seabirds to depletion of food fish stocks. Journal of Ornithology 148:247–252. https://doi.org/10.1007/s10336-007-0152-2

Gaglio, D., T. R. Cook, M. Connan, P. G. Ryan, and R. B. Sherley. 2017. Dietary studies in birds: testing a non-invasive method using digital photography in seabirds. Methods in Ecology and Evolution 8:214–222. https://doi.org/10.1111/2041-210X.12643

Hansen, E. S., H. Sandvik, K. E. Erikstad, N. G. Yoccoz, T. Anker-Nilssen, J. Bader, S. Descamps, K. Hodges, M. d. S. Mesquita, T. K. Reiertsen, and Ø. Varpe. 2021. Centennial relationships between ocean temperature and Atlantic Puffin production reveal shifting decennial trends. Global Change Biology. 27:3753–3764 https://doi.org/10.1111/gcb.15665

Harris, M. P. 1979. Measurements and weights of British Puffins. Bird Study 26:179–186. https://doi.org/10.1080/00063657909476636

Harris, M. P., S. D. Albon, M. A. Newell, C. Gunn, F. Daunt, and S. Wanless. 2022. Long-term within-season changes in the diet of Common Guillemot (*Uria aalge*) chicks at a North Sea colony: implications for dietary monitoring. Ibis 164:1243–1251 https://doi.org/10.1111/ibi.13063

Harris, M. P., and J. R. G. Hislop. 1978. The food of young puffins *Fratercula arctica*. Journal of Zoology 185:213–236. https://doi.org/10.1111/j.1469-7998.1978.tb03323.x

Harris, M. P., and S. Wanless. 2011. The puffin. Bloomsbury, London, UK.

Hartig, F. 2017. DHARMa: residual diagnostics for hierarchical (multi-level/mixed) regression models. R Foundation for Statistical Computing, Vienna, Austria. https://cran.r-project.org/web/packages/DHARMa/index.html

Hedd, A., D. A. Fifield, C. M. Burke, W. A. Montevecchi, L. M. Tranquilla, P. M. Regular, A. D. Buren, and G. J. Robertson. 2010. Seasonal shift in the foraging niche of Atlantic Puffins *Fratercula arctica* revealed by stable isotope ($\delta^{15}N$ and $\delta^{13}C$) analyses. Aquatic Biology 9:13–22. https://doi.org/10.3354/ab00225

Hochachka, W. M., D. Fink, R. A. Hutchinson, D. Sheldon, W.-K. Wong, and S. Kelling. 2012. Data-intensive science applied to broad-scale citizen science. Trends in Ecology and Evolution 27:130–137. https://doi.org/10.1016/j.tree.2011.11.006

Hughes, R. D., F. Le Bouard, G. Bradbury, and E. Owen. 2018. A census of the Atlantic Puffins *Fratercula arctica* breeding on Orkney in 2016. Seabird 31:56–63. https://doi.org/10.61350/sbj.31.56

Joint Nature Conservation Committee (JNCC). 2016. Seabird population trends and causes of change: 1986-2015 report. Joint Nature Conservation Committee, Peterborough, UK.

JNCC. 2019. Seabird Monitoring Program.

Kobori, H., J. L. Dickinson, I. Washitani, R. Sakurai, T. Amano, N. Komatsu, W. Kitamura, S. Takagawa, K. Koyama, T. Ogawara, and A. J. Miller-Rushing. 2016. Citizen science: a new approach to advance ecology, education, and conservation. Ecological Research 31:1–19. https://doi.org/10.1007/s11284-015-1314-y

Kress, S. W., P. Shannon, and C. O'Neal. 2016. Recent changes in the diet and survival of Atlantic Puffin chicks in the face of climate change and commercial fishing in midcoast Maine, USA. Facets 1:27–43. https://doi.org/10.1139/facets-2015-0009

Lenth, R. V. 2023. emmeans: estimated marginal means, aka least-squares means. R package version 1.8.4-1. R Foundation for Statistical Computing, Vienna, Austria. https://CRAN.R-project.org/package=emmeans

Lewison, R., D. Oro, B. Godley, L. Underhill, S. Bearhop, R. P. Wilson, D. Ainley, J. M. Arcos, P. D. Boersma, P. G. Borboroglu, T. Boulinier, M. Frederiksen, M. Genovart, J. González-Solís, J. A. Green, D. Grémillet, K. C. Hamer, G. M. Hilton, K. D. Hyrenbach, A. Martínez-Abraín, W. A. Montevecchi, R. A. Phillips, P. G. Ryan, P. Sagar, W. J. Sydeman, S. Wanless, Y. Watanuki, H. Weimerskirch, and P. Yorio. 2012. Research priorities for seabirds: improving conservation and management in the 21st century. Endangered Species Research 17:93–121. https://doi.org/10.3354/esr00419

Lilliendahl, K., and J. Sólmundsson. 1997. An estimate of summer food consumption of six seabird species in Iceland. ICES Journal of Marine Science 54:624–630. https://doi.org/10.1006/jmsc.1997.0240

Lüdecke, D., F. Aust, S. Crawley, and M. Ben-Shachar. 2020. ggeffects: create tidy data frames of marginal effects for 'ggplot'; from model outputs. R Foundation for Statistical Computing, Vienna, Austria. https://cran.r-project.org/web/packages/ggeffects/index.html

MacDonald, A., D. C. Speirs, S. P. R. Greenstreet, P. Boulcott, and M. R. Heath. 2019. Trends in sandeel growth and abundance off the east coast of Scotland. Frontiers in Marine Science 6:201. https://doi.org/10.3389/fmars.2019.00201

Magnusson, A., H. Skaug, A. Nielsen, C. Berg, K. Kristensen, M. Maechler, K. van Bentham, B. Bolker, and M. Brooks. 2017. Package 'glmmTMB'. R Package v.0.2.0. R Foundation for Statistical Computing, Vienna, Austria. http://cran.nexr.com/web/packages/glmmTMB/glmmTMB.pdf

Martin, A. 1989. The diet of Atlantic Puffin *Fratercula arctica* and Northern Gannet *Sula bassana* chicks at a Shetland colony during a period of changing prey availability. Bird Study 36:170–180. https://doi.org/10.1080/00063658909477022

McClure, E. C., M. Sievers, C. J. Brown, C. A. Buelow, E. M. Ditria, M. A. Hayes, R. M. Pearson, V. J. D. Tulloch, R. K. F. Unsworth, and R. M. Connolly. 2020. Artificial intelligence meets citizen science to supercharge ecological monitoring. Patterns 1:100109. https://doi.org/10.1016/j.patter.2020.100109

McCullagh, P. 1980. Regression models for ordinal data. Journal of the Royal Statistical Society: Series B (Methodological) 42:109–127. https://doi.org/10.1111/j.2517-6161.1980.tb01109.x

Miles, W. T., R. Mavor, N. J. Riddiford, P. V. Harvey, R. Riddington, D. N. Shaw, D. Parnaby, and J. M. Reid. 2015. Decline in an Atlantic Puffin population: evaluation of magnitude and mechanisms. PLoS One 10:e0131527. https://doi.org/10.1371/journal.pone.0131527

Mitchell, P. I., S. F. Newton, N. Ratcliffe, and T. E. Dunn. 2004. Seabird populations of Britain and Ireland: results of the seabird 2000 census (1998–2002). T. and A. D. Poyser, London, UK.

OSPAR. 2010. Quality status report. OSPAR Commisison, London, UK.

Owen, E., O. Prince, C. Cachia-Zammit, R. Cartwright, T. Coledale, S. Elliott, S. Haddon, G. Longmoor, J. Swale, F. West, and R. Hughes. 2018. Counts of Puffins in Shetland suggest an apparent decline in numbers. Scottish Birds 38:223–231. Owen, E., A. Steinfurth, and R. Hughes. 2023. Atlantic Puffin. In D. Burnell, A. J. Perkins, S. F. Newton, M. Bolton, T. D. Tierney, and T. E. Dunn, editors. 2023. Seabirds count: a census of breeding seabirds in Britian and Ireland (2015-2021). Lynx Nature Books, Barcelona, Spain.

R Core Team. 2022. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. http://www.R-project.org

Reay, P. J. 1970. Synopsis of biological data on North Atlantic sandeels of the genus Ammodytes (*A. tobianus*, *A. dubius*, *A. americanus* and *A. marinus*). Food and Agriculture Organization of the United Nations, Rome, Italy. https://www.fao.org/3/a8703e/a8703e.pdf

Rindorf, A., S. Wanless, and M. P. Harris. 2000. Effects of changes in sandeel availability on the reproductive output of seabirds. Marine Ecology Progress Series 202:241–252. https://doi.org/10.3354/meps202241

Robinson, L., S. P. R. Greenstreet, H. Reiss, R. Callaway, J. Craeymeersch, I. de Boois, S. Degraer, S. Ehrich, H. M. Fraser, A. Goffin, I Kröncke, L. L. Jorgenson, M. R. Roberson, and J. Lancaster. 2010. Length-weight relationships of 216 North Sea benthic invertebrates and fish. Marine Biological Association of the United Kingdom. Journal of the Marine Biological Association of the United Kingdom 90:95. https://doi.org/10.1017/S0025315409991408

Rodway, M. S., and W. A. Montevecchi. 1996. Sampling methods for assessing the diets of Atlantic Puffin chicks. Marine Ecology Progress Series 144:41–55. https://doi.org/10.3354/meps144041

Sadykova, D., B. E. Scott, M. De Dominicis, S. L. Wakelin, J. Wolf, and A. Sadykov. 2020. Ecological costs of climate change on marine predator-prey population distributions by 2050. Ecology and Evolution 10:1069–1086. https://doi.org/10.1002/ece3.5973

Sanders, J. 2008. Fish brought to young Atlantic Puffins *Fratercula arctica* on Burhou, Channel Islands. Seabird 21:105–107. https://doi.org/10.61350/sbj.21.105

Scopel, L., A. Diamond, S. Kress, and P. Shannon. 2019. Varied breeding responses of seabirds to a regime shift in prey base in the Gulf of Maine. Marine Ecology Progress Series 626:177–196. https://doi.org/10.3354/meps13048

St. John Glew, K., S. Wanless, M. P. Harris, F. Daunt, K. E. Erikstad, H. Strøm, J. R. Speakman, B. Kürten, and C. N. Trueman. 2019. Sympatric Atlantic Puffins and Razorbills show contrasting responses to adverse marine conditions during winter foraging within the North Sea. Movement Ecology 7:33. https://doi.org/10.1186/s40462-019-0174-4

Stubbings, E. M., B. I. Büche, J. A. Riordan, B. Baker, and M. J. Wood. 2018. Seabird monitoring on Skomer Island in 2018. JNCC report. Joint Nature Conservation Committee, Peterborough, UK.

Sydeman, W. J., J. F. Piatt, S. A. Thompson, M. García-Reyes, S. A. Hatch, M. L. Arimitsu, L. Slater, J. C. Williams, N. A. Rojek, S. G. Zador, and H. M. Renner. 2017. Puffins reveal contrasting relationships between forage fish and ocean climate in the North Pacific. Fisheries Oceanography 26:379–395. https://doi.org/10.1111/fog.12204

Thayer, J. A., and W. J. Sydeman. 2007. Spatio-temporal variability in prey harvest and reproductive ecology of a piscivorous seabird, *Cerorhinca monocerata*, in an upwelling system. Marine Ecology Progress Series 329:253–265. https://doi.org/10.3354/meps329253

Vander Zanden, M. J., and Y. Vadeboncoeur. 2002. Fishes as integrators of benthic and pelagic food webs in lakes. Ecology 83:2152–2161. https://doi.org/10.1890/0012-9658(2002)083[2152:FAIOBA]2.0.CO;2

Wakefield, E. D., E. Owen, J. Baer, M. J. Carroll, F. Daunt, S. G. Dodd, J. A. Green, T. Guilford, R. A. Mavor, P. I. Miller, M. A. Newell, S. F. Newton, G. S. Robertson, A. Shoji, L. M. Soanes, S. C. Votier, S. Wanless, and M. Bolton. 2017. Breeding density, fine-scale tracking and large-scale modeling reveal the regional distribution of four seabird species. Ecological Applications 27:2074–2091. https://doi.org/10.1002/eap.1591

Wanless, S., M. P. Harris, M. A. Newell, J. R. Speakman, and F. Daunt. 2018. Community-wide decline in the occurrence of lesser sandeels *Ammodytes marinus* in seabird chick diets at a North Sea colony. Marine Ecology Progress Series 600:193–206. https://doi.org/10.3354/meps12679

Wanless, S., P. J. Wright, M. P. Harris, and D. A. Elston. 2004. Evidence for decrease in size of lesser sandeels *Ammodytes marinus* in a North Sea aggregation over a 30-yr period. Marine Ecology Progress Series 279:237–246. https://doi.org/10.3354/meps279237

Welcker, J., and G. Nehls. 2016. Displacement of seabirds by an offshore wind farm in the North Sea. Marine Ecology Progress Series 554:173–182. https://doi.org/10.3354/meps11812

Wood, S. N. 2006. Generalized additive models: an introduction with R. Chapman and Hall/CRC, Boca Raton, Florida, USA.

Wright, P. J., H. Jensen, and I. Tuck. 2000. The influence of sediment type on the distribution of the lesser sandeel, *Ammodytes marinus*. Journal of Sea Research 44:243–256. https://doi.org/10.1016/S1385-1101(00)00050-2

Wurtzell, K. V., A. Baukus, C. J. Brown, J. M. Jech, A. J. Pershing, and G. D. Sherwood. 2016. Industry-based acoustic survey of

Atlantic herring distribution and spawning dynamics in coastal Maine waters. Fisheries Research 178:71–81. https://doi.org/10.1016/j.fishres.2015.11.011

Yee, T. W. 2010. The VGAM package for categorical data analysis. Journal of Statistical Software 32:1–34. https://doi.org/10.18637/jss.v032.i10

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Appendix 1: Worked example of a typical process of size estimation in photographs where both ends of the fish are not visible

1) The observer assesses which prey species are present in the photo by zooming in and inspecting each prey item and comparing it to a set of example images for each species type.

In Figure A1.1, the observer recorded transparent sandeel (an example transparent sandeel is marked with a pink dot) and rockling (an example rockling is marked with a yellow dot).

Figure A1.1. Example photo of a puffin carrying prey to illustrate the image analysis process. A and B show the limits used to measure the maximum bill depth (Harris, 1979). Photo credit: Michael von Herrath.

2) Observer records the number of prey of each species type.

In Figure A1.1, the observer recorded 15 transparent sandeels and 10 rockling.

3) Observer measures each fish in multiples of bill depth (distance between A and B*), rounding to the nearest 0.5 bill depths. Where both ends of the fish are not visible, the observer estimates the likely position of the hidden head/tail using anatomical information on the visible part of the fish as described in the methods.

In Figure A1.1, all rockling appear to be similar in size to each other as they have similar sized herringbone body markings and body depth. None of the rockling are visible in their entirety so the observer looks for information on the visible portion of the fish to estimate how much of the fish is hidden. No fins are visible in rockling but the observer checks the taper of body depth and uses this to decide that nearly the whole body length is visible except for the head and a small part of the body, which is grasped in the bill. The observer decided to record all rockling as 0.5 x bill depth. All transparent sandeels also appear to be similar sizes, with e.g., similar eyeball sizes, tail fin lengths, body depth and similar sized dot patterns along body. The observer records all transparent sandeel as 1 x bill depth.

4) Observer records the level of confidence in the assessment for the number, species and lengths of prey.

In Figure A1.1, the observer scored a high degree of confidence in prey type identification (level 1), and the prey length estimation and number of prey items fairly confident (level 2).

*After learning from the analysis process used in this paper we changed our measure for future image analysis and now recommend using the upper mandible depth, because this is slightly easier to use since it is usually unobscured by the bill load.

Appendix 2: Length-Weight conversion constants used to estimate prey biomass.

Table A2.1. Length-weight conversion constants used to estimate prey biomass.

Species Group	**a**	**b**
Clupeids	0.00562	3.09
Rockling	0.00479	3.08
Sandeels	0.00275	3.11
Gadoids	0.00646	3.06
Unidentified	0.00410	3.10
Squid*	-3.10600	2.15

*The length-weight formula for calculating squid biomass:

$$\text{Log}_{10}(\text{Weight}) = a + (b * \log_{10}(\text{Mantel length in mm}))$$

Appendix 3: Investigating potential sources of bias in Puffarazzi data collection and image analysis

METHODS

Potential sources of bias in image collection

Photographs sampled from the public may be biased towards puffins carrying more fish, bigger fish, or fish of a certain species. This could occur either because these puffins are more visible, or because the resultant photographs are thought to be more attractive. To investigate this, we compared a control set of photographs collected over two weeks in June 2019 on the Farne Islands with photos submitted by the public for the same colony and period. The control set was photographed by an experienced seabird reserve manager who photographed any puffin approaching the colony, regardless of whether the puffin was first seen to be carrying food. Resulting photographs were filtered for those with puffins carrying food, giving a total of 3471 photos over 14 days. The public submitted 214 photos for the same colony and period. We sub-sampled the control dataset, selecting 10% of photos at random for each of the 14 days, except where this resulted in a lower sample size than that of the public, whereby we increased the number of control photos to match. This resulted in a final sample size of 358 control photos and 214 photos from the public. Each photo was assigned a unique photo ID. Image analysis was both managed and carried out by 19 of the authors (CCZ, FW, GL, OP, RH, SH, AB, JB, WB, TB, FD, AE, AF, KF, JH, KH, EK, SS, HS). We evaluated differences in the number of prey items and total length of prey items per load between control photos and those submitted by the public using linear mixed effects models. Response variables were the total number of prey items recorded in each photo (one observation per photo), and individual fish lengths recorded in each photo (multiple observations per photo). Photo ID nested within date were included as random effects in both models, and data source (control vs. public) as a fixed effect. Visual inspection of residual plots of both count and size models showed no obvious deviations from heteroscedasticity. The count data was not obviously skewed, and a linear model was found to be a better fit than using a Poisson distribution. We compared prey composition in photos taken by the public vs. control with a Fisher's exact test, to account for small sample sizes of some prey groups. We also ran a binomial generalized linear mixed effects model to check for the effect of data source on the proportion of sandeel prey in photographs compared to non-sandeel prey. Data source was included as a fixed effect, and photo ID as a random effect. Date was removed as a random effect as it did not account for any variation. Small sample sizes of other prey groups precluded running more species-specific models.

Potential sources of bias in image analysis

The length of fish measured from a photo taken from the side aspect may be underestimated compared to fish measured from a photo taken from the front aspect, owing to a possible foreshortening effect of objects oriented so that they project towards a lens and/or the increased difficulty in measuring prey size when not all of the prey item is visible. To investigate this, we used 17 different pairs of photos of the same fish load carried by the same puffin, one image taken from the side, and one image taken from the front. The pairs of photographs were sourced from the personal collections of authors and contacts, along with five pairs that were sourced from BirdGuides.com. Each photograph was allocated for image

analysis by 11 different observers, interspersed with images submitted by the public for the main dataset, so that each image was analysed independently. Each observer analysed both photos from the pair. Data from one pair of photos from one observer was removed from the final dataset after the observer identified that the bird and fish load were the same (thus removing the independence of analysis). Images were analysed in the same way as for the main dataset. However, the results from these paired images could not be put through the usual moderation step (where a third, expert observer checks results of the same image from two different observers and retains the most accurate). We evaluated differences in the length of prey items between photos taken from the side and photos taken from the front using a linear mixed effects model. The response variable was the individual fish lengths recorded in each photo (multiple observations per photo). Aspect (side or front) was included as a fixed effect, and photo ID nested within image pair as random effects. Observer was also included as a random effect, fitted with a random slope term to allow for a heterogeneous effect of aspect on sizing of fish between observers. Visual inspection of residual plots of models showed no obvious deviations from heteroscedasticity.

We also checked for differences in the distribution of front and side aspect photographs among colonies in the main dataset. Pictures were classified as front aspect where both ends of a prey item were visible in >50% of fish in the bill, otherwise they were classified as side aspect. We ran a binomial GLM, and plotted the predicted proportions of front and side aspect pictures and 95% CI for each colony.

Consistent differences between observers in measuring fish lengths could also bias results. We used the same dataset described above to test the effect of observer on fish length, using a linear mixed effects model. The response variable was the individual fish lengths recorded in each photo (multiple observations per photo). Observer and aspect were included as fixed effects, with an interaction term, and photo ID nested within image pair as random effects. Visual inspection of residual plots of models showed no obvious deviations from heteroscedasticity.

RESULTS

Potential sources of bias in image collection

After removing photos with a confidence level of 3 or 4 in the relevant category, 474 photos (297 control and 177 public) could be used to assess the impact of data source (public or control) on the total number of fish carried by puffins, and 577 photos (336 control and 201 public) on size of fish. Neither the number of fish counted in photos ($X^2 = 1.74$, $p = 0.19$) nor the mean length of fish ($X^2 = 1.01$, $p = 0.32$) was dependent on whether the photo was part of the control set or submitted by the public. A Fishers' exact test showed there to be a significant effect of data source (public or control) on the composition of prey in photos. However, pairwise comparisons showed this to be solely due to the presence of 8 clupeids in control photos compared to 0 clupeids in photos submitted by the public, out of a total 5564 fish. We may not have adequate sample sizes of non-sandeel prey to accurately test differences in prey composition between control and public photos: out of the 5564 prey items identified across both photo types, 5422 were non-transparent sandeels (97.4%). Of the remaining prey groups, across both photograph types, 1.4% were rockling (80 fish), 0.5% were gadoids (27 fish), 0.2% were transparent sandeels (13 fish), 0.1% were clupeids (8 fish)

and 0.3% were unidentified (14 fish). However, there was no effect of data source on the proportion of sandeels identified in the photos ($X^2 = 0.09$, $p = 0.77$).

Potential sources of bias in image analysis

When testing the effect of photograph aspect (whether a bird was photographed from the side or front) on length of prey, we found that prey was measured on average 0.75 cm shorter per prey item in photos from the side aspect compared to from the front (n = 311 prey, $X^2 = 10.2$, CI = -0.52 - -0.15, $p < 0.01$). The relationship between photo aspect and length of fish varied with observer (rather than being a constant effect across all photos). Including data with lower confidence gave a larger sample size but did not change the result (n = 372, $X^2 = 11.8$, CI = -0.52 - -0.16, $p < 0.001$; prey measured 0.78cm shorter). Side aspect images were the most common in all colonies. However, there was a higher proportion of photos taken from the front at Lunga (37.5%; CI [25.8%, 50.8%]) and Skomer (31.3%; CI [26.0%, 37.0%]) compared to the Isle of May (14.1%; CI 10.6%, 18.6%]) and the Farne Islands (19.7%; CI [16.4%, 23.4%]; Fig. S8). Therefore, prey sizes in the Farnes or the Isle of May could be underestimated relative to those at to Lunga and Skomer. Small sample sizes at most other colonies precluded statistical comparison. We controlled for potential size bias due to photo aspect by including aspect as a fixed effect in models using the fish length data (analyses of biomass).

We found measurement of fish length varied between observers ($X^2 = 1046.8$, $p < 0.0001$). We therefore controlled for among observer variation by including observer as a random effect in data analyses.

However, it is important to note that we were only able to test the difference between the two extremes of aspect and underestimation of prey length is likely to be less in photos taken from an intermediate aspect, as in these cases the observer is usually able to see at least part of some fish on both sides of the bill to aid size estimation (rather than one side only in photos taken fully from the side). Our test also precluded the use of a moderation step which is always included in the analysis of the main study dataset. This would have discarded the least accurate result between two separate observers. We may therefore have overestimated the effect of photo aspect in the moderated, main study dataset, but still recommend accounting for both aspect and observer variation in similar projects.

Appendix 4: Time-of-day distribution of photos of puffin bill loads submitted by citizen scientists for six example puffin colonies

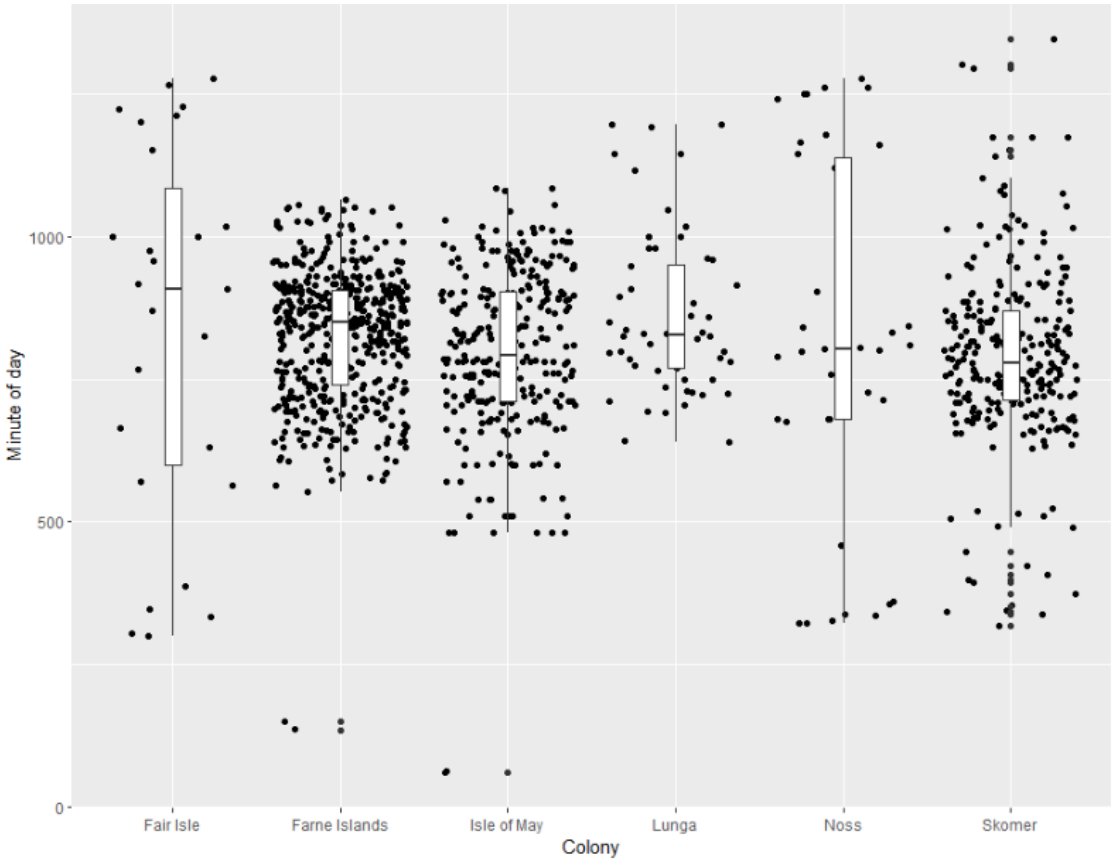


Figure A4.1. The time of day (shown by cumulative minute) that photographs were taken which were submitted by citizen scientists for six example puffin colonies. Most records are restricted to part of the diurnal cycle.

Appendix 5: Results tables for models of seasonal variation in puffin diet and posterior predictive checks for Bayesian models of seasonal variation in biomass and prey number

Results from VGAM models of proportion of prey types per load for each region in 2017. Smoother df reports degrees of freedom for each smoother along with associated χ^2 and *p*-values.

Region	**Intercept**	**Smooth Terms**	**Shape**	**N**
E and S England	1.58 (1.52 – 1.64)	1.31 (0.40 – 2.99)	2.70 (2.36 – 3.08)	400
E Scotland and NE England	1.62 (1.53 – 1.72)	0.80 (0.05 – 2.56)	2.18 (1.80 – 2.58)	217
Shetland	0.92 (0.72 – 1.13)	1.27 (0.03 – 4.60)	1.81 (1.23 – 2.52)	55
W England and Wales	1.69 (1.62 – 1.77)	1.52 (0.45 – 3.53)	3.51 (2.89 – 4.17)	224
W Scotland and E Ireland	1.36 (1.20 – 1.52)	1.63 (0.04 – 5.10)	1.99 (1.45 – 2.63)	78

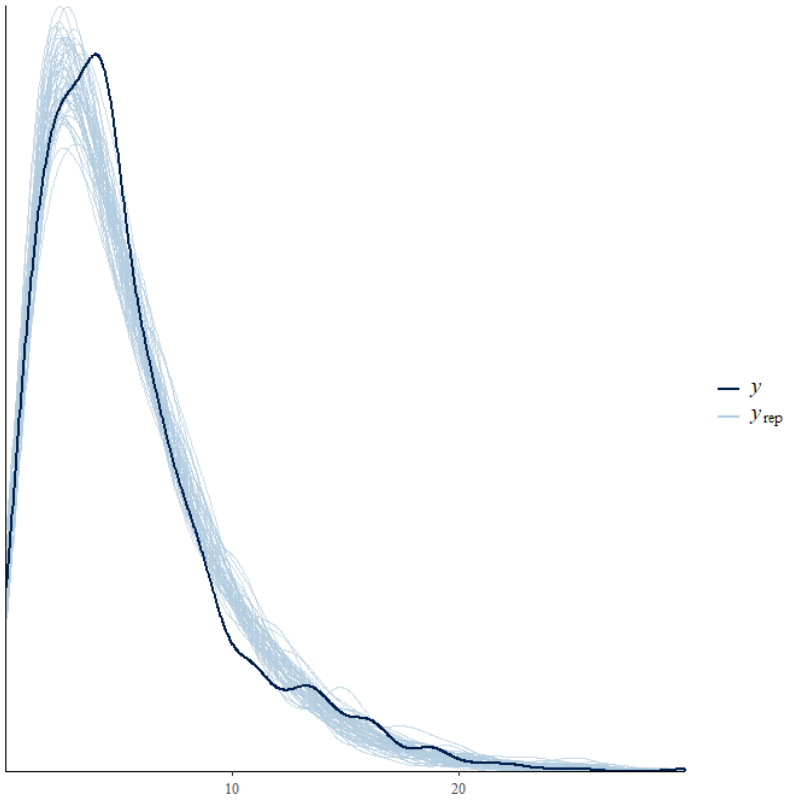
Biomass per load throughout the breeding season in 2017 in each region. Data modelled using a Gamma distribution with a separate shape term for each region. Coefficients for smooth term express the degree of 'wiggliness' in non-linear smoother.

Region	**Smoother df**	χ^2	***p*-values**	**N**
E and S England	2.9	512	< 0.001	492
E Scotland and NE England	3	319	< 0.001	269
Shetland	3.1	171	< 0.001	96
W England and Wales	2.8	27	< 0.001	287
W Scotland and E Ireland	3.1	115	< 0.001	86

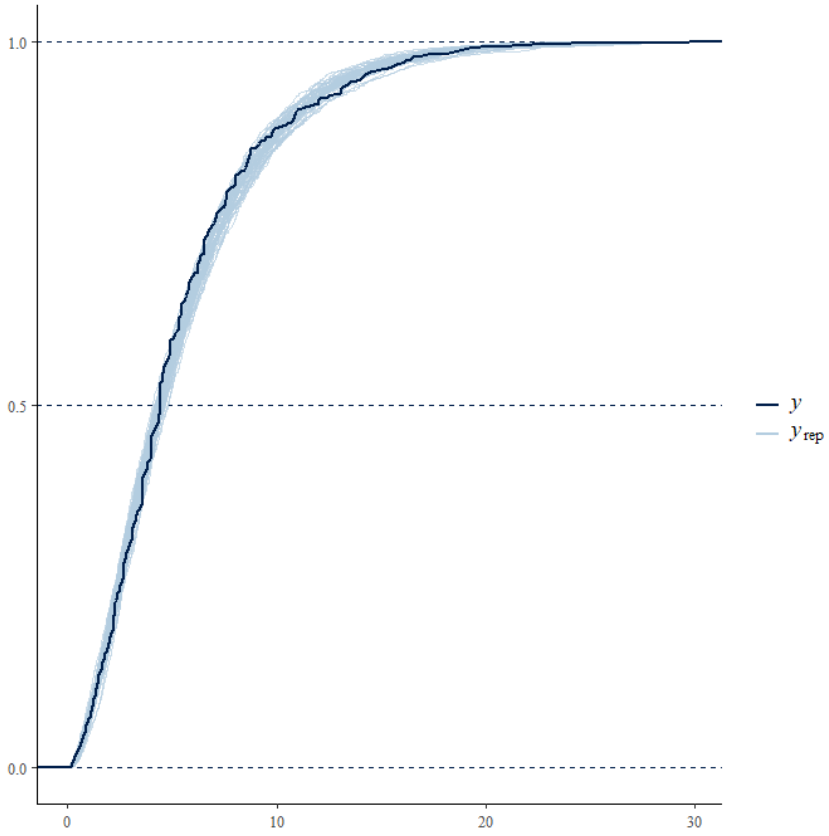
Number of prey items per load throughout the breeding season in 2017 in each region. Data modelled using a truncated Gaussian distribution with a separate sigma term for each region. Coefficients for smooth term express the degree of 'wiggliness' in non-linear smoother.

Region	Intercept	Smooth Terms	Sigma	N
E and S England	8.93 (8.62 – 9.22)	6.39 (2.43 – 13.85)	3.38 (3.16 – 3.61)	472
E Scotland and NE England	7.26 (6.12 – 8.14)	20.2 (6.78 – 45.86)	5.50 (4.88 – 6.24)	251
Shetland	12.35 (11.10 – 13.46)	7.56 (0.21 – 36.31)	5.34 (4.49 – 6.36)	64
W England and Wales	8.71 (8.33 – 9.05)	7.31 (0.98 – 16.79)	3.17 (2.93 – 3.44)	275
W Scotland and E Ireland	6.82 (6.06 – 7.45)	3.52 (0.10 – 12.43)	2.99 (2.52 – 3.63)	97

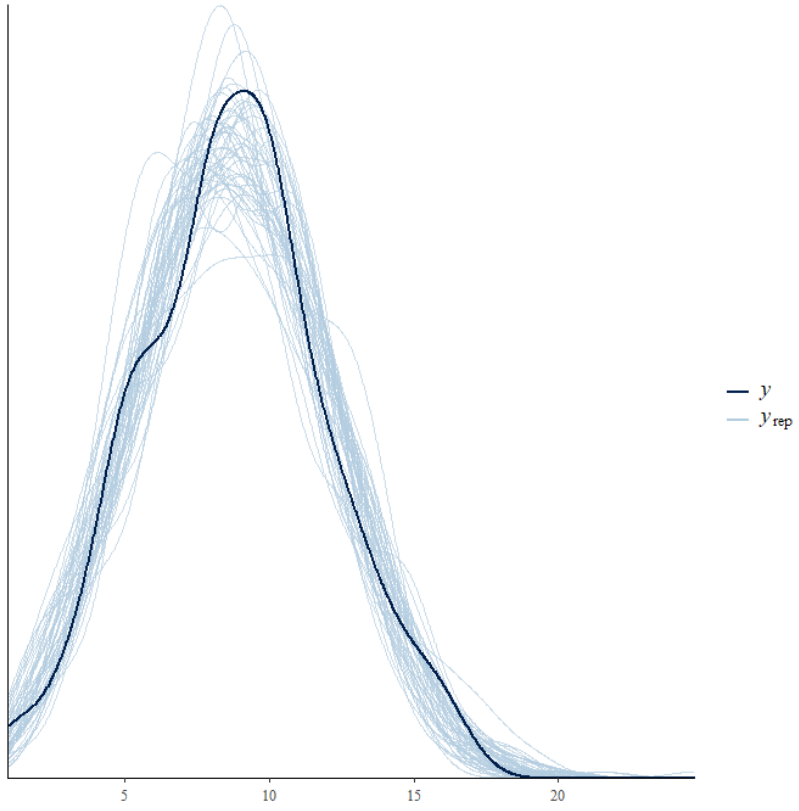
Posterior predictive checks of model fit for models of biomass per load. Raw data (y) is displayed as a dark blue line overlaid with 100 simulations (y_{rep}) from the fitted model in light blue.



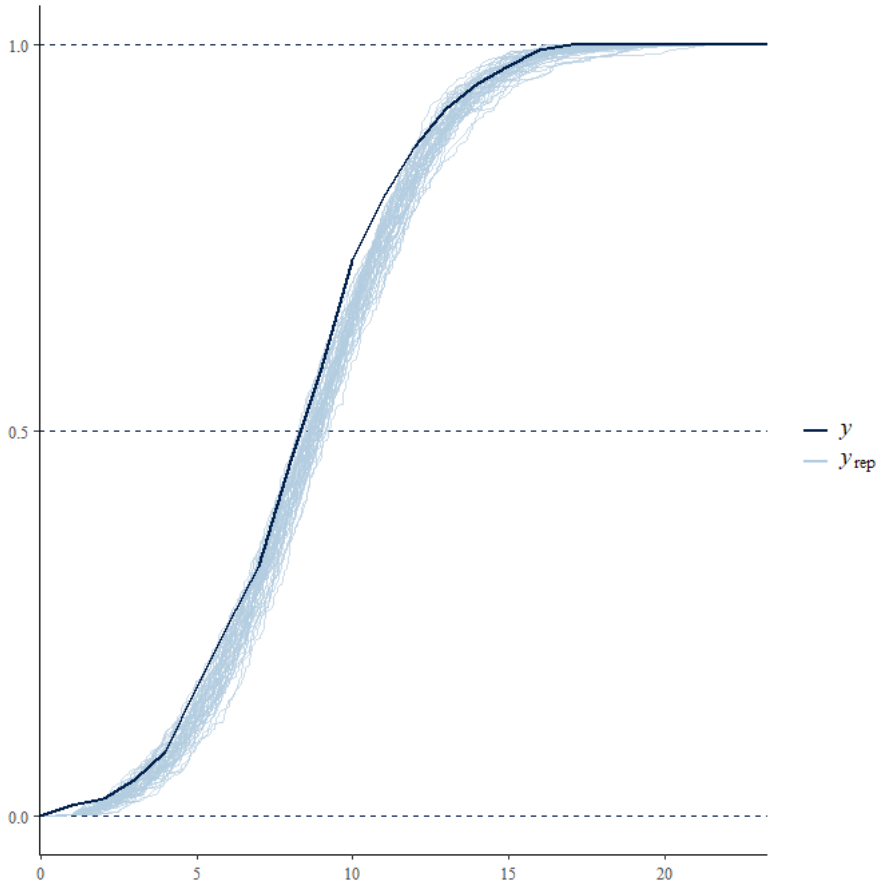
Empirical cumulative distribution function (ecdf) plot for models of biomass per load. Raw data (y) is displayed as a dark blue line overlaid with 100 simulations (y_{rep}) from the fitted model in light blue.



Posterior predictive checks of model fit for models of number of prey items per load. Raw data (y) is displayed as a dark blue line overlaid with 100 simulations (y_{rep}) from the fitted model in light blue.



Empirical cumulative distribution function (ecdf) plot for models of number of prey items per load. Raw data (y) is displayed as a dark blue line overlaid with 100 simulations (y_{rep}) from the fitted model in light blue.



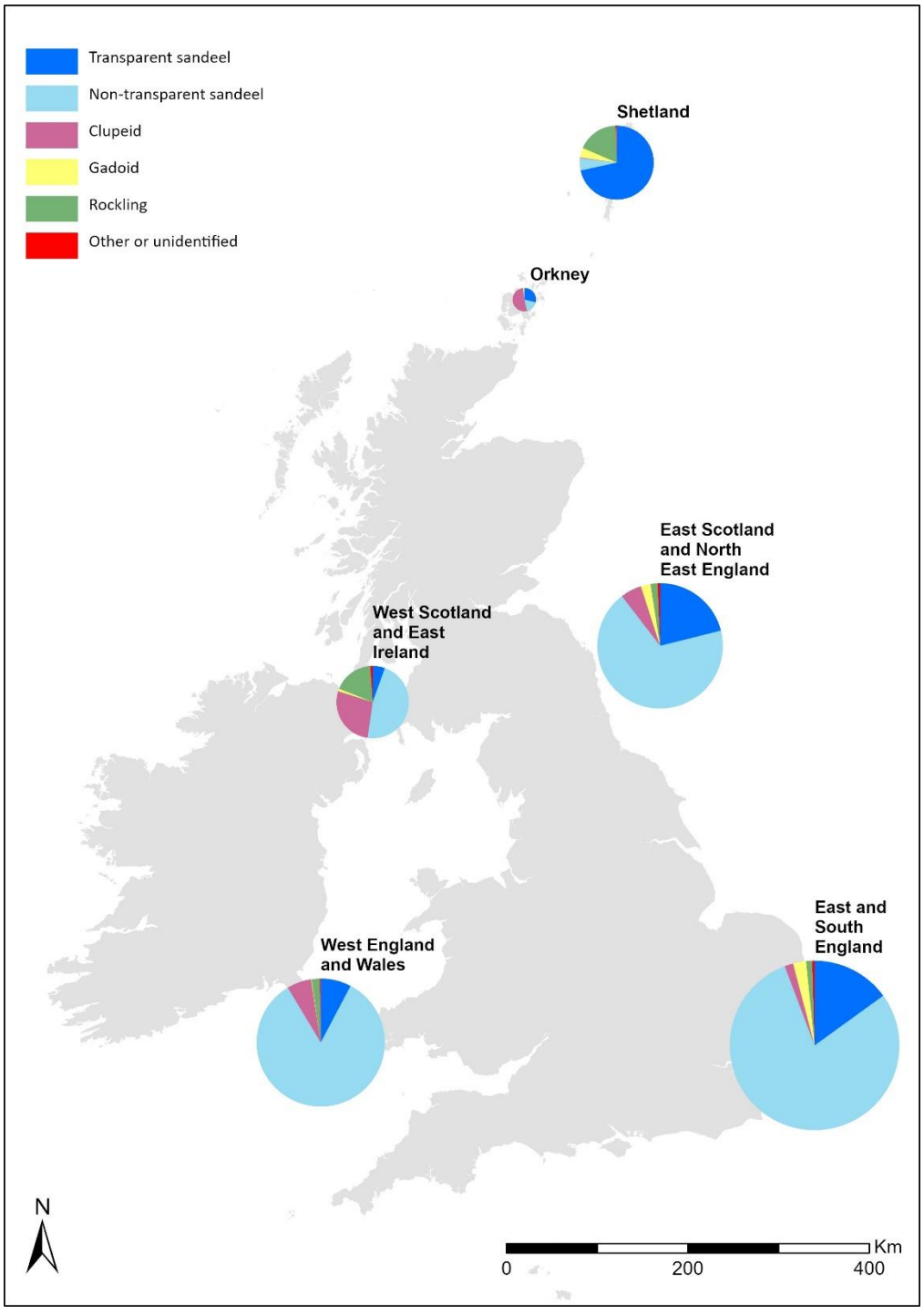
Appendix 6: Abundance and proportion of prey types in bill loads at 27 puffin colonies in the UK and Ireland

Table A6.1. Mean proportion and abundance, and standard deviation (SD), of prey types at 27 Puffin colonies in the UK and Ireland.

			Non-transparent sandeel				Transparent sandeel				Clupeids				Gadoids (excl. Rockling)				Rockling				Other			
Region	Colony	N photos	Mean prop.	SD	Mean abundance	SD	Mean prop.	SD	Mean abundance	SD	Mean prop.	SD	Mean abundance	SD	Mean prop.	SD	Mean abundance	SD	Mean prop.	SD	Mean abundance	SD	Mean prop.	SD	Mean abundance	SD
E & S Eng	Coquet Island	6	0.86	0.22	6.2	3.54	0	0	0	0	0.06	0.14	0.3	0.82	0.08	0.2	0.5	1.22	0	0	0	0	0	0	0	0
	Farne Islands	460	0.77	0.39	7.4	4.43	0.13	0.31	1.4	3.46	0.05	0.2	0.2	0.87	0.03	0.15	0.2	0.99	0.01	0.08	0.1	0.69	0	0.03	0	0.13
E Scot & NE Eng	Bempton	14	0.37	0.46	3.1	4.03	0.1	0.28	0.9	2.48	0.38	0.47	1.5	2.5	0	0	0	0	0.06	0.15	0.5	1.29	0	0	0	0
	Bullers of Buchan	5	0.5	0.47	3	2.83	0	0	0	0	0.35	0.49	2.4	3.29	0.1	0.15	0.6	0.89	0.05	0.11	0.4	0.89	0	0	0	0
	Caithness Cliffs	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	7	8.49	0	0	0	0
	Craigleith	1	1	na	9	na	0	na	0	na	0	na	0	na	0	na	0	na	0	na	0	na	0	na	0	na
	Fowlsheugh	3	0.33	0.58	0.3	0.58	0.08	0.14	0.3	0.58	0	0	0	0	0.33	0.58	3.3	5.77	0.25	0.43	1	1.73	0	0	0	0
	Isle of May	231	0.59	0.45	6.7	5.76	0.16	0.33	2.1	4.45	0.19	0.38	0.4	0.94	0.04	0.16	0.2	0.88	0.01	0.06	0.1	0.55	0	0	0	0
Orkney	Stroma	1	0.88	0.18	3.5	0.71	0	0	0	0	0.13	0.18	0.5	0.71	0	0	0	0	0	0	0	0	0	0	0	0
	Westray	8	0.28	0.45	0.5	0.76	0.25	0.46	2.3	4.17	0.44	0.5	4	5.04	0.03	0.09	0.1	0.35	0	0	0	0	0	0	0	0
Shetland	Fair Isle	25	0.11	0.31	0.8	2.63	0.49	0.46	7	7.48	0	0	0	0	0.21	0.41	1.6	3.17	0.18	0.33	2	3.66	0	0	0	0
	Fetlar	2	0.06	0.08	0.5	0.71	0.94	0.08	9	1.41	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	Foula	4	0.16	0.19	1.5	2.38	0.4	0.49	5.3	6.4	0.19	0.38	0.8	1.5	0.04	0.08	0.3	0.5	0.21	0.42	1.3	2.5	0	0	0	0
	Hermaness, Unst	7	0.05	0.13	0.4	1.13	0.43	0.45	5	5.54	0	0	0	0	0	0	0	0	0.52	0.42	6.3	5.71	0	0	0	0
	Noss	37	0.04	0.18	0.4	1.76	0.79	0.27	11.3	5.42	0	0	0	0	0.01	0.07	0.1	0.67	0.15	0.21	1.9	2.55	0	0	0	0
	Sumburgh Head	14	0.08	0.23	1.2	3.72	0.67	0.38	11.6	8.08	0.02	0.09	0.1	0.27	0.05	0.18	0.1	0.53	0.18	0.26	2.9	4.31	0	0	0	0
W Eng & Wales	Gwylan Islands	4	0.87	0.19	3.3	2.63	0	0	0	0	0	0	0	0	0	0	0	0	0.13	0.19	0.8	0.96	0	0	0	0
	Mincarlo	2	0.38	0.53	1.5	2.12	0.13	0.18	0.5	0.71	0	0	0	0	0	0	0	0	0.5	0.71	2.5	3.54	0	0	0	0
	Puffin Island	1	0.9	na	9	na	0	na	0	na	0.1	na	1	na	0	na	0	na	0	na	0	na	0	na	0	na
	Skokholm	11	0.83	0.38	6.3	3.69	0.09	0.3	0.5	1.51	0.08	0.27	0.7	2.41	0	0	0	0	0	0	0	0	0	0	0	0
	Skomer	248	0.85	0.3	7.6	3.73	0.07	0.21	0.7	2.28	0.06	0.19	0.6	1.61	0	0.01	0	0.14	0.02	0.11	0.2	1.3	0	0	0	0.06
W Scot & E Ire	Great Skellig	1	0.17	na	1	na	0.83	na	5	na	0	na	0	na	0	na	0	na	0	na	0	na	0	na	0	na
	Lunga	46	0.54	0.47	3.9	3.44	0.01	0.05	0	0.29	0.32	0.42	2.3	3.08	0.02	0.15	0.1	0.74	0.11	0.29	1.1	2.77	0	0	0	0
	Mingulay	1	0.8	na	8	na	0.1	na	1	na	0	na	0	na	0	na	0	na	0	na	0	na	0	na	0	na
	Puffin Cove	10	0.33	0.45	2.8	3.71	0	0	0	0	0.4	0.49	3.1	3.87	0	0	0	0	0.27	0.44	1.5	2.55	0	0	0	0
	Shiant Islands	24	0.46	0.51	2.8	3.83	0.09	0.23	1.1	3.72	0.15	0.33	1.1	2.54	0.02	0.1	0.1	0.41	0.25	0.4	1.9	3.12	0	0	0	0
	Staffa	3	0.33	0.58	2.7	4.62	0	0	0	0	0.67	0.58	3	2.65	0	0	0	0	0	0	0	0	0	0	0	0

Appendix 7: Puffin diet composition at six regions in the UK and Ireland during 2017

Figure A7.1. Puffin diet composition at six regions in the UK and Ireland during 2017. Proportions of prey types are the means across all birds sampled within each region. The size of pie charts is proportional to the number of birds sampled in that region (East and South England n=466 birds, East Scotland and North East England n=255, Orkney n=9, Shetland n=89, West England and Wales n=266. West Scotland and East Ireland). Note that the sample size from Orkney is small and therefore may be unrepresentative of diet had we achieved a larger sample size.



Appendix 8: Model output table for generalised linear mixed model (GLMM) showing regional variation in Puffin chick diet

Table A8.1. Model output table for GLMM describing regional variation in Puffin chick diet. Prey abundance count data is explained by prey type interacting with region. Total fish in load and biomass are both explained by region. 95% confidence intervals shown in brackets.

	Abundance	**Total fish in load**	**sqrt(Total biomass)**
Predictors	*Incidence Rate Ratios*	*Estimates*	*Estimates*
(Intercept)	4.57 *** (3.24 – 6.45)	11.76 *** (10.23 – 13.28)	1.61 *** (1.39 – 1.82)
Shetland	*Reference*	*Reference*	*Reference*
E & S Eng	1.94 *** (1.38 – 2.72)	-2.61 *** (-4.05 – -1.17)	0.68 *** (0.50 – 0.87)
E Scot & NE Eng	2.18 *** (1.55 – 3.08)	-3.08 *** (-4.62 – -1.55)	0.68 *** (0.49 – 0.88)
W Eng & Wales	1.78 *** (1.26 – 2.51)	-2.89 *** (-4.36 – -1.42)	0.82 *** (0.63 – 1.02)
W Scot & E Ire	1.32 (0.91 – 1.91)	-4.84 *** (-6.35 – -3.34)	0.34 ** (0.11 – 0.56)
clupeids	0.29 (0.07 – 1.30)		
gadoids	0.95 (0.56 – 1.59)		
transparent sandeel	2.66 *** (1.83 – 3.86)		
rockling	0.98 (0.66 – 1.46)		
E & S Eng:clupeids	0.89 (0.20 – 4.04)		
E & S Eng:gadoids	0.33 *** (0.19 – 0.59)		
E & S Eng:transparent sandeel	0.30 *** (0.21 – 0.44)		
E & S Eng:rockling	0.27 *** (0.16 – 0.47)		
E Scot & NE Eng:clupeids	0.48 (0.11 – 2.13)		
E Scot & NE Eng:gadoids	0.32 *** (0.17 – 0.58)		

E Scot & NE Eng:transparent sandeel	0.29 *** (0.20 – 0.43)		
E Scot & NE Eng:rockling	0.26 *** (0.15 – 0.46)		
W Eng & Wales:clupeids	1.13 (0.25 – 5.04)		
W Eng & Wales:gadoids	0.10 * (0.01 – 0.81)		
W Eng & Wales:transparent sandeel	0.25 *** (0.16 – 0.37)		
W Eng & Wales:rockling	0.65 (0.37 – 1.13)		
W Scot & E Ire:clupeids	2.59 (0.58 – 11.55)		
W Scot & E Ire:gadoids	0.58 (0.19 – 1.77)		
W Scot & E Ire:transparent sandeel	0.27 *** (0.15 – 0.48)		
W Scot & E Ire:rockling	0.97 (0.60 – 1.58)		
Both sides of fish viewable in photo	*Reference*	*Reference*	*Reference*
Both sides of fish NOT viewable in photo			-0.24 *** (-0.33 – -0.14)
Random Effects			
σ^2	0.86	NA	0.35
τ_{00}	0.00 $_{date}$	1.78 $_{date:minutes}$	0.04 $_{date:minutes}$
	0.00 $_{minutes}$	0.00 $_{minutes}$	0.00 $_{minutes}$
	0.01 $_{:sizing\_by}$	0.51 $_{sizing\_by}$	0.01 $_{sizing\_by}$
	0.00 $_{sizing\_by}$	0.48 $_{date}$	0.02 $_{date}$
N	76 $_{date}$	76 $_{date}$	76 $_{date}$
	450 $_{minutes}$	434 $_{minutes}$	427 $_{minutes}$
	5	6 $_{sizing\_by}$	6 $_{sizing\_by}$
	6 $_{sizing\_by}$		
Observations	5945	1103	1056
Marginal R^2 / Conditional R^2	0.342 / NA	NA	0.124 / NA

** p<0.05 ** p<0.01 *** p<0.001*

Appendix 9: Pairwise comparisons of prey composition between regions

Table A9.1. Pairwise comparisons of prey composition between regions. P values adjusted using Tukey method for comparing a family of 25 estimates, with tests performed on the log scale. Comparisons produced using emmeans package (Length et al. 2023).

Contrast	Prey type	ratio	SE	df	null	t ratio	*p*
Shetland / EandSEng	Non-transparent sandeel	0.515	0.089	5900	1	-3.834	0.001
Shetland / EScotandNEEng	Non-transparent sandeel	0.458	0.081	5900	1	-4.438	0.000
Shetland / WEngandWales	Non-transparent sandeel	0.562	0.098	5900	1	-3.308	0.008
Shetland / WScotandEIre	Non-transparent sandeel	0.759	0.143	5900	1	-1.458	0.590
EandSEng / EScotandNEEng	Non-transparent sandeel	0.890	0.040	5900	1	-2.592	0.072
EandSEng / WEngandWales	Non-transparent sandeel	1.090	0.045	5900	1	2.077	0.230
EandSEng / WScotandEIre	Non-transparent sandeel	1.474	0.126	5900	1	4.537	0.000
EScotandNEEng / WEngandWales	Non-transparent sandeel	1.226	0.061	5900	1	4.113	0.000
EScotandNEEng / WScotandEIre	Non-transparent sandeel	1.657	0.149	5900	1	5.603	0.000
WEngandWales / WScotandEIre	Non-transparent sandeel	1.351	0.119	5900	1	3.421	0.006
Shetland / EandSEng	Clupeids	0.577	0.432	5900	1	-0.734	0.948
Shetland / EScotandNEEng	Clupeids	0.960	0.713	5900	1	-0.055	1.000
Shetland / WEngandWales	Clupeids	0.496	0.368	5900	1	-0.945	0.879
Shetland / WScotandEIre	Clupeids	0.293	0.217	5900	1	-1.659	0.460
EandSEng / EScotandNEEng	Clupeids	1.665	0.338	5900	1	2.508	0.089
EandSEng / WEngandWales	Clupeids	0.861	0.170	5900	1	-0.758	0.943
EandSEng / WScotandEIre	Clupeids	0.509	0.097	5900	1	-3.533	0.004
EScotandNEEng / WEngandWales	Clupeids	0.517	0.085	5900	1	-4.016	0.001
EScotandNEEng / WScotandEIre	Clupeids	0.306	0.049	5900	1	-7.356	0.000
WEngandWales / WScotandEIre	Clupeids	0.591	0.091	5900	1	-3.424	0.006
Shetland / EandSEng	Gadoids	1.549	0.363	5900	1	1.867	0.335
Shetland / EScotandNEEng	Gadoids	1.450	0.370	5900	1	1.458	0.590
Shetland / WEngandWales	Gadoids	5.384	5.544	5900	1	1.635	0.475

Shetland / WScotandEIre	Gadoids	1.318	0.711	5900	1	0.512	0.986
EandSEng / EScotandNEEng	Gadoids	0.936	0.198	5900	1	-0.314	0.998
EandSEng / WEngandWales	Gadoids	3.475	3.534	5900	1	1.225	0.737
EandSEng / WScotandEIre	Gadoids	0.851	0.439	5900	1	-0.314	0.998
EScotandNEEng / WEngandWales	Gadoids	3.713	3.802	5900	1	1.281	0.703
EScotandNEEng / WScotandEIre	Gadoids	0.909	0.481	5900	1	-0.181	1.000
WEngandWales / WScotandEIre	Gadoids	0.245	0.275	5900	1	-1.252	0.720
Shetland / EandSEng	Transparent sandeel	1.705	0.139	5900	1	6.527	0.000
Shetland / EScotandNEEng	Transparent sandeel	1.556	0.136	5900	1	5.059	0.000
Shetland / WEngandWales	Transparent sandeel	2.274	0.271	5900	1	6.898	0.000
Shetland / WScotandEIre	Transparent sandeel	2.834	0.669	5900	1	4.410	0.000
EandSEng / EScotandNEEng	Transparent sandeel	0.913	0.076	5900	1	-1.088	0.813
EandSEng / WEngandWales	Transparent sandeel	1.334	0.154	5900	1	2.501	0.090
EandSEng / WScotandEIre	Transparent sandeel	1.662	0.393	5900	1	2.150	0.199
EScotandNEEng / WEngandWales	Transparent sandeel	1.461	0.172	5900	1	3.214	0.012
EScotandNEEng / WScotandEIre	Transparent sandeel	1.821	0.433	5900	1	2.518	0.087
WEngandWales / WScotandEIre	Transparent sandeel	1.246	0.313	5900	1	0.877	0.905
Shetland / EandSEng	Rockling	1.897	0.405	5900	1	3.001	0.023
Shetland / EScotandNEEng	Rockling	1.750	0.388	5900	1	2.522	0.086
Shetland / WEngandWales	Rockling	0.862	0.192	5900	1	-0.665	0.964
Shetland / WScotandEIre	Rockling	0.782	0.126	5900	1	-1.526	0.546
EandSEng / EScotandNEEng	Rockling	0.923	0.253	5900	1	-0.294	0.998
EandSEng / WEngandWales	Rockling	0.455	0.125	5900	1	-2.869	0.034
EandSEng / WScotandEIre	Rockling	0.412	0.096	5900	1	-3.800	0.001
EScotandNEEng / WEngandWales	Rockling	0.493	0.136	5900	1	-2.572	0.076
EScotandNEEng / WScotandEIre	Rockling	0.447	0.107	5900	1	-3.368	0.007
WEngandWales / WScotandEIre	Rockling	0.907	0.218	5900	1	-0.408	0.994

Appendix 10: Pairwise comparisons of the total number in fish in sampled loads between regions

Table A10.1. Pairwise comparisons of the total number in fish in sampled loads between regions. *p* values adjusted using Tukey method for comparing a family of 5 estimates. Comparisons produced using emmeans package (Length et al. 2023).

Contrast	Estimate	SE	df	t ratio	p value
Shetland - EandSEng	2.60	0.73	1091	3.53	0.004
Shetland - EScotandNEEng	3.09	0.78	1091	3.95	0.001
Shetland - WEngandWales	2.89	0.75	1091	3.86	0.001
Shetland - WScotandEIre	4.84	0.77	1091	6.30	0.000
EandSEng - EScotandNEEng	0.49	0.36	1091	1.36	0.652
EandSEng - WEngandWales	0.29	0.26	1091	1.12	0.794
EandSEng - WScotandEIre	2.24	0.34	1091	6.61	0.000
EScotandNEEng - WEngandWales	-0.20	0.38	1091	-0.52	0.985
EScotandNEEng - WScotandEIre	1.75	0.43	1091	4.08	0.000
WEngandWales - WScotandEIre	1.95	0.36	1091	5.35	0.000

Appendix 11: Pairwise comparisons of the total biomass in sampled loads between regions

Table A11.1. Pairwise comparisons of the total biomass in sampled loads between regions. *p* values adjusted using Tukey method for comparing a family of 5 estimates, with results averaged across photo aspects. Contrasts are still on the sqrt scale. Comparisons produced using emmeans package (Length et al. 2023).

Contrast	Estimate	SE	df	t ratio	p value
Shetland - EandSEng	-0.68	0.10	1046	-7.12	2.06E-11
Shetland - EScotandNEEng	-0.68	0.10	1046	-6.85	1.27E-10
Shetland - WEngandWales	-0.82	0.10	1046	-8.22	5.07E-13
Shetland - WScotandEIre	-0.34	0.12	1046	-2.92	2.92E-02
EandSEng - EScotandNEEng	0.00	0.05	1046	-0.03	1.00E+00
EandSEng - WEngandWales	-0.14	0.05	1046	-2.76	4.61E-02
EandSEng - WScotandEIre	0.34	0.08	1046	4.20	2.80E-04
EScotandNEEng - WEngandWales	-0.14	0.06	1046	-2.29	1.47E-01
EScotandNEEng - WScotandEIre	0.34	0.09	1046	4.02	5.96E-04
WEngandWales - WScotandEIre	0.49	0.09	1046	5.62	2.49E-07

Appendix 12: Summary statistics for recorded fish lengths in each colony

Table A12.1. Summary statistics for recorded fish lengths in each colony. Fish lengths were recorded from submitted photographs in units of maximum bill depth excluding the cere to the nearest 0.5 bill depths and converted to centimetres by multiplying by 3.5 (see main text). Sample size (*n*) per prey category denotes the number of individuals in each category for which length was estimated.

Region	Colony	Prey Category	*Length (cm)*						
			Min	25% quartile	Mean	Median	75% quartile	Max	*n*
East Scotland and Northeast England	Coquet Island	Non-transparent Sandeel	3.50	3.50	5.31	7.00	7.00	7.00	29
	Farne Islands	Transparent Sandeel	0.87	3.50	4.51	5.25	5.25	8.75	567
		Non-transparent Sandeel	1.75	5.25	5.17	5.25	5.25	10.50	3196
		Clupeids	3.50	5.25	6.09	5.25	7.00	10.50	48
		Gadoids	1.75	1.75	2.99	3.50	3.350	5.25	48
		Rockling	1.75	1.75	2.56	1.75	3.50	3.50	28
	Bempton	Transparent Sandeel	5.25	5.25	5.25	5.25	5.25	5.25	12
		Non-transparent Sandeel	1.75	3.50	4.80	5.25	5.25	7.00	43
		Clupeids	3.50	5.25	6.06	7.00	7.00	10.50	13
		Rockling	1.75	1.75	1.75	1.75	1.75	1.75	3
	Bullers of Buchan	Non-transparent Sandeel	5.25	6.12	6.54	7.00	7.00	7.00	15
		Clupeids	3.50	3.50	3.50	3.50	3.50	3.50	6
		Rockling	3.50	3.50	3.50	3.50	3.50	3.50	2
	Caithness	Rockling	3.50	3.50	3.50	3.50	3.50	3.50	14
	Fowlsheugh	Transparent Sandeel	7.00	7.00	7.00	7.00	7.00	7.00	1
		Non-transparent Sandeel	3.50	3.50	3.50	3.50	3.50	3.50	1
	Isle of May	Transparent Sandeel	0.70	3.50	3.77	3.50	5.25	7.00	389
		Non-transparent Sandeel	1.75	3.50	4.79	5.25	5.25	8.75	1393
		Clupeids	3.50	3.50	7.70	7.00	8.75	10.50	78
		Gadoids	3.50	3.50	4.80	5.25	5.25	7.00	27
		Rockling	1.75	2.19	2.63	2.63	3.06	3.50	2
Shetland	Fair Isle	Transparent Sandeel	1.75	1.75	4.28	5.25	5.25	7.00	99
		Non-transparent Sandeel	3.50	3.50	4.30	3.50	3.50	10.50	11
		Gadoids	1.75	1.75	2.80	2.62	3.50	5.25	20

		Rockling	1.75	1.75	2.66	3.50	3.50	3.50	23
	Fetlar	Transparent Sandeel	3.50	3.50	3.50	3.50	3.50	3.50	8
		Non-transparent Sandeel	3.50	3.50	3.50	3.50	3.50	3.50	1
	Foula	Transparent Sandeel	3.50	3.50	4.92	5.25	5.25	7.00	21
		Non-transparent Sandeel	3.50	3.50	4.38	4.38	5.25	5.25	6
		Clupeids	5.25	5.25	5.25	5.25	5.25	5.25	3
		Gadoids	7.00	7.00	7.00	7.00	7.00	7.00	1
		Rockling	3.50	3.50	3.50	3.50	3.50	3.50	5
	Hermaness	Transparent Sandeel	1.75	3.50	3.38	3.50	3.50	3.50	14
		Rockling	1.75	1.75	1.82	1.75	1.75	3.50	25
	Noss	Transparent Sandeel	1.75	3.50	3.49	3.50	3.50	7.00	199
		Non-transparent Sandeel	3.50	5.25	5.09	5.25	5.25	5.25	10
		Rockling	1.75	1.75	1.75	1.75	1.75	1.75	23
	Sumburgh Head	Transparent Sandeel	1.75	1.75	3.38	3.50	3.50	5.25	114
		Non-transparent Sandeel	3.50	4.38	4.67	5.25	5.25	5.25	3
		Clupeids	3.50	3.50	3.50	3.50	3.50	3.50	1
		Gadoids	3.50	3.50	3.50	3.50	3.50	3.50	2
		Rockling	1.75	1.75	2.14	1.75	1.75	3.50	18
West England and Wales	Gwylan Islands	Non-transparent Sandeel	3.50	5.25	5.43	5.25	5.25	7.00	10
	Mincarlo	Transparent Sandeel	5.25	5.25	5.25	5.25	5.25	5.25	1
		Non-transparent Sandeel	7.00	7.00	7.00	7.00	7.00	7.00	3
		Rockling	3.50	3.50	3.50	3.50	3.50	3.50	5
	Puffin Island	Non-transparent Sandeel	5.25	5.25	5.25	5.25	5.25	5.25	9
	Skokholm	Transparent Sandeel	5.25	5.25	5.25	5.25	5.25	5.25	5
		Non-transparent Sandeel	3,50	5.25	5.48	5.25	7.00	7.00	65
	Skomer	Transparent Sandeel	1.75	3.50	4.83	5.25	5.25	8.75	170
		Non-transparent Sandeel	0.87	5.25	5.56	5.25	7.00	10.50	1770
		Clupeids	3.50	3.50	4.49	4.38	5.25	8.75	63
		Gadoids	7.00	7.00	7.00	7.00	7.00	7.00	2
		Rockling	1.75	1.75	2.48	1.75	3.50	5.25	24

West Scotland and East Ireland	Great Skellig	Transparent Sandeel	3.50	3.50	4.73	4.38	5.25	7.00	5
		Non-transparent Sandeel	4.38	4.38	4.38	4.38	4.38	4.38	1
	Lunga	Transparent Sandeel	5.25	5.25	5.25	5.25	5.25	5.25	2
		Non-transparent Sandeel	3.50	5.25	5.83	5.25	7.00	7.00	175
		Clupeids	1.75	3.50	4.60	5.25	5.25	7.00	83
		Rockling	1.75	1.75	2.82	3.50	3.50	3.50	49
	Mingulay	Transparent Sandeel	3.50	3.50	3.50	3.50	3.50	3.50	1
		Non-transparent Sandeel	5.25	5.25	5.25	5.25	5.25	5.25	9
	Puffin Cove	Non-transparent Sandeel	3.50	3.50	5.16	5.25	7.00	7.00	20
		Clupeids	3.50	3.50	4.72	5.25	5.25	5.25	23
		Rockling	1.75	1.75	2.33	1.75	3.50	3.50	9
	Shiant Islands	Transparent Sandeel	3.50	3.50	3.50	3.50	3.50	3.50	67
		Non-transparent Sandeel	3.50	5.25	5.48	5.25	5.25	7.00	8
		Clupeids	3.50	3.50	3.69	3.50	3.50	5.25	27
		Gadoids	5.25	5.25	5.25	5.25	5.25	5.25	2
		Rockling	1.75	1.75	2.42	1.75	3.50	3.50	21
	Staffa	Non-transparent Sandeel	5.25	5.25	5.25	5.25	5.25	5.25	8
		Clupeids	3.50	3.50	4.20	3.50	5.25	5.25	5
Orkney	Westray	Transparent Sandeel	3.50	3.50	3.50	3.50	3.50	3.50	9
		Non-transparent Sandeel	3.50	4.81	7.87	7.00	10.00	14.00	4
		Clupeids	3.50	4.81	4.81	5.25	5.25	5.25	30

Appendix 13: Summary statistics for recorded fish lengths in each region

Table A13.1. Summary statistics for recorded fish lengths in each region. Fish lengths were recorded from submitted photographs in units of maximum bill depth excluding the cere to the nearest 0.5 bill depths and converted to centimetres by multiplying by 3.5 (see main text). Sample size (*n*) per prey category denotes the number of individuals in each category for which length was estimated.

Region	Prey Category	*Length (cm)*						
		Min	25% quartile	Mean	Median	75% quartile	Max	*n*
East and Southeast England	Transparent Sandeel	0.87	3.50	4.51	5.25	5.25	8.75	567
	Non-transparent Sandeel	1.75	5.25	5.17	5.25	5.25	10.50	3225
	Clupeids	3.50	5.25	6.09	5.25	7.00	10.50	48
	Gadoids	1.75	1.75	2.99	3.50	3.50	5.25	48
	Rockling	1.75	1.75	2.56	1.75	3.50	3.50	28
East Scotland and Northeast England	Transparent Sandeel	0.70	3.50	3.82	3.50	5.25	7.00	402
	Non-transparent Sandeel	1.75	3.50	4.81	5.25	5.25	8.75	1452
	Clupeids	3.50	5.25	7.22	7.00	8.75	10.50	97
	Gadoids	3.50	3.50	4.80	5.25	5.25	7.00	27
	Rockling	1.75	3.50	3.17	3.50	3.50	3.50	21
Shetland	Transparent Sandeel	1.75	3.50	3.70	3.50	3.50	7.00	455
	Non-transparent Sandeel	3.50	3.50	4.57	5.25	5.25	10.50	31
	Clupeids	3.50	4.81	4.81	5.25	5.25	5.25	4
	Gadoids	1.75	1.75	3.04	3.50	3.50	7.00	22
	Rockling	1.75	1.75	2.16	1.75	1.75	3.50	94
West England and Wales	Transparent Sandeel	1.75	3.50	4.85	5.25	5.25	8.75	176
	Non-transparent Sandeel	0.87	5.25	5.56	5.25	7.00	10.50	1857
	Clupeids	3.50	3.50	4.49	4.38	5.25	8.75	63
	Gadoids	7.00	7.00	7.00	7.00	7.00	7.00	2
	Rockling	1.75	1.75	2.65	1.75	3.50	5.25	29
West Scotland and East Ireland	Transparent Sandeel	3.50	3.50	4.10	3.50	4.60	7.00	16
	Non-transparent Sandeel	3.50	5.25	5.66	5.25	7.00	7.00	279
	Clupeids	1.75	3.50	4.43	5.25	5.25	7.00	138
	Gadoids	5.25	5.25	5.25	5.25	5.25	5.25	2
	Rockling	1.75	1.75	2.66	3.50	3.50	3.50	79
Orkney	Transparent Sandeel	3.50	3.50	3.50	3.50	3.50	3.50	9
	Non-transparent Sandeel	3.50	4.81	7.87	7.00	10.00	14.00	4
	Clupeids	3.50	4.81	4.81	5.25	5.25	5.25	30

Appendix 14: Change in the raw frequencies of prey observations by week in six example Puffin colonies in 2017

Figure A14.1. Change in the raw frequencies of prey observations by week in six example Puffin colonies in 2017. n = total number of prey observed.