Follow-up studies on seabird distribution and concentration areas in the Dutch North Sea

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Sovon-rapport 2025/30

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Inhoud

1. Introduction 6
  1.1 Background 6
  1.2 Question 6
  1.3 Expert team 7

2. Seabird concentration areas and their consistency in time 8
  Samenvatting 8
  Abstract 8
  2.1 Aim of this study 8
  2.2 Methods 9
    2.2.1 Collection and spatial modelling of historical seabird distribution data 9
    2.2.2. From density maps to concentration areas 10
  2.3 Results 12
    2.3.1 Results by species 12
  2.4 Discussion and conclusion 18
  Supplement 1 20
  Supplement 2 21

3. Distribution of Common Guillemots on the Dutch Continental Shelf in summer: moulting and chick-rearing areas 24
  Samenvatting 24
  Abstract 24
  3.1 Introduction 24
  3.2 Methods 25
    3.2.1 Ship-based surveys 25
    3.2.2 Aerial surveys 25
    3.2.3 Statistical analysis 26
  3.3 Results 26
    3.3.1 Abundance 26
    3.3.2 Moult 27
    3.3.3 Chicks 28
    3.3.4 Large-scale distribution: aerial surveys 29
  3.4 Discussion and conclusion 30
  3.5 Acknowledgements 31
  Supplement 32

4. Distribution of Common Guillemots in late summer in the Dutch North sea: the effect of wind on clustering 34
  Samenvatting 34
  Abstract 34
  4.1 Introduction 34
  4.2 Methods 35
    4.2.1 Aerial surveys 35
    4.2.2 Wind data 36
    4.2.3 Distance analysis 36
    4.2.4 Statistical analysis 36
  4.3 Results 36
    4.3.1 Effect of wind on guillemot distribution 39
  4.4 Discussion 41

5. Co-occurrence of Black-legged Kittiwakes and alcids in the Dutch North Sea: dependency on feeding associations as a driver of seabird distribution 42
Samenvatting 42
Abstract 42
5.1 Introduction 43
5.2 Methods 43
5.2.1 Small-scale species foraging associations: ship-based surveys 43
5.2.2 Large-scale affinity of species distributions: aerial surveys 44
5.3 Results 45
5.3.1 Small-scale species foraging associations: ship-based surveys 45
5.3.2 Large-scale affinity of species distributions: aerial surveys 48
5.4 Discussion and conclusion 49
Supplement 51

6. Drivers of seabird distribution: a discussion and potential future directions 52
Samenvatting 52
Abstract 52
6.1 Introduction 52
6.2 Methods 53
6.3 Results & discussion 54
6.3.1 Discussion of van Donk *et al* (2024) 54
6.3.2 Potential additional covariates and adjustments to the models 55
6.4 Conclusions 56

7. Conclusions 57
7.1 Seabird concentration areas and their consistency in time 57
7.2 Moult and chick distribution in Common Guillemots and the effect of wind 57
7.3 MSFAs as drivers of seabird distributions 57
7.4 Drivers of seabird distribution: discussion of van Donk *et al.* (2024) 57
7.5 Overall conclusion 58

Literature 59

1. Introduction

1.1 Background

In spring 2024, the report *Geactualiseerd landelijk overzicht van vogelsoorten met concentraties van (inter)nationaal belang* (Vogel *et al* 2024[1]) was published. That report described the main concentration areas of bird species regularly occurring in the Netherlands, including species that mainly make use of the North Sea, based on a newly developed approach to collate, weigh and visualise data on bird distribution and abundance. It showed that within the northern part of the North Sea, there is a large concentration area ('NCP-North area') that regularly harbours above-average abundances of various seabird species (including Razorbill, Common Guillemot and Great Black-backed Gull). These insights may affect agreements under the Noordzeeakkoord (NZA), of which agreement 4.34 states that it will be examined whether certain existing areas, designated under the EU Habitats Directive, also qualify under the Birds Directive and, if so, these will be designated as Birds Directive areas. Three areas are partially within the mentioned concentration area: Doggersbank, Centrale Oestergronden and Klaverbank (Dogger Bank, Central Oystergrounds and Cleaver Bank).

The Birds Directive states that the most important areas for birds must be designated as Special Protection Areas based on scientific, ornithological information. The three Habitats Directive areas were initially designed based on an evaluation of the ecological value in which other features than birds, including diversity of benthic invertebrates and general habitat features, were also considered, and do not coincide very well with the most relevant areas for seabirds (Vogel *et al.* 2024). The NCP-North area indicates the region where seabirds often occur in higher densities than elsewhere in recent years, but it is not clear to what degree the presence and abundance of the species is stable in space and time. The question to what extent this is the case is highly relevant for the long-term effectiveness of a conservation policy focusing on designating protected areas where seabirds are safeguarded from detrimental human activities. How sure can one be that designated areas that cover important parts of the current seabird distribution will still do after say three or four decades? The answer to this question is highly relevant also to general spatial planning issues and the execution of activities while taking into account nature values.

The Ministry of Landbouw, Visserij, Voedselzekerheid en Natuur (LVVN) has asked Sovon Vogelonderzoek Nederland (Sovon) and Waardenburg Ecology (Waardenburg) to do additional research on the distribution of seabirds in the Dutch sector of the North Sea, with the main aim to quantify and deepen our understanding of the stability of seabird distributions. This report addresses this main topic based on several sub-questions.

1.2 Question

The main question addressed in this study is: Are there bird concentration areas within the Dutch North Sea area that are consistently used over long periods of time, and if so, where are these areas and how can they be ornithologically substantiated and delineated?

For effective protection of areas with fixed geographical boundaries where birds of international importance are concentrated, it is important to know whether these areas are also consistently used in the long term. In a first chapter, we focus on the observed distributions during aerial surveys, comparing historic (1991-2013) with current (2014-2022) distributions:

- Seabird concentration areas and their consistency in time;

However, to understand why the distribution of some species may be more consistent in time than others, we need to understand the drivers of seabird distributions. Studying the factors that drive these distributions is however complex, and an impossible task to complete in a single study. Therefore, several sub-studies have been formulated that target specific phenomena associated with seabird distributions in the Dutch sector of the North Sea, with the following titles:

- Distribution of Common Guillemots on the Dutch Continental Shelf in summer: moulting and chick-rearing areas;
- Distribution of Common Guillemots in late summer in the Dutch North sea: the effect of wind on clustering
- Co-occurrence of Black-legged Kittiwakes and alcids in the Dutch North Sea: dependency on feeding associations as a driver of seabird distribution;
- Drivers of seabird distribution: a discussion and potential future directions.

These sub-studies are described in the following chapters, followed by an abstract and a final conclusion addressing the main question. These chapters include an extensive Dutch summary.

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[1] Translated title: Updated overview of bird species with internationally important concentrations in the Netherlands

1.3 Expert team

Within the project, a small group of outside experts, not part of the project team, was asked to critically read and discuss early chapters of the report and discuss the approach taken to compare historical and recent bird distributions, to ensure that the methods and results were understandable, correct and suggest adjustments where necessary. The expert team was made up of people with knowledge of different disciplines, to ensure a broader perspective, and consisted of Martin Poot (Wageningen Marine Research), Floor Heinis (Heinis Advies) and Karen Brandenburg (CBS). We would like to thank all three experts for their time, effort, constructive feedback, and good ideas.

2. Seabird concentration areas and their consistency in time

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Samenvatting

In dit hoofdstuk is onderzocht of zeevogels zich door de jaren heen concentreren in dezelfde gebieden op de Noordzee, wat een voorwaarde is voor een effectieve bescherming door middel van het aanwijzen van beschermde mariene gebieden. Om na te gaan of concentratiegebieden stabiel zijn op de schaal van decennia pasten we de aanpak waarmee Vogel *et al.* (2024) concentratiegebieden afbakenden op basis van recente gegevens (2014–2022) toe op oudere vliegtuigtellingen van zeevogels op de Noordzee (1999–2013) en vergeleken de resultaten. Tellingen vanuit vliegtuigen langs transecten op de Noordzee werden ruimtelijk gemodelleerd tot vlakdekkende dichtheidskaarten per vogelsoort. Op basis hiervan werd per seizoen (jaar) de survey geselecteerd met de grootste aantallen per soort, en de deelgebieden bepaald met de hoogste dichtheden. Deelgebieden die in minstens 25% van de seizoenen behoorden tot de vijf gebieden met de grootste aantallen vogels werden gedefinieerd als concentratiegebieden. De ligging hiervan werd vergeleken met de recente concentratiegebieden met behulp van een statistische maat voor overlap (α MLE).

Voor de meeste onderzochte soorten was de overlap tussen de historische en recente concentratiegebieden significant groter dan verwacht bij afwezigheid van een associatie, wat wijst op een zekere mate van ruimtelijke stabiliteit. De overlap was aanzienlijk groter bij kustgebonden dan bij pelagische vogelsoorten, wat begrijpelijk is omdat de eerste consistent slechts de kustnabije delen van het NCP gebruiken. Hoewel ook bij de pelagische zeevogels een significante overlap werd gevonden was de *mate* hiervan niet al te groot, wat aangeeft dat de temporele stabiliteit in concentratiegebieden tussen de twee beschouwde periodes vrij beperkt is. Dit strookt ook met de aanzienlijke variatie in de ligging van gebieden met de hoogste dichtheden die er was tussen jaren binnen de beschouwde periodes.

Hoewel er dus wel enige temporele consistentie is in de gebieden waar zeevogels zich concentreren op de Noordzee, is er ook een grote variatie tussen jaren in hun verspreiding. Dit maakt het lastig om binnen vaste beschermde gebieden een groot deel van de op de Noordzee aanwezige vogelpopulaties effectief te beschermen. Daarom wordt aanbevolen om het beleid voor zeevogelbescherming niet alleen te richten op gebiedsbescherming, maar ook op maatregelen die druk op zeevogels verminderen in het gehele zeegebied.

Abstract

In this chapter we investigated whether seabirds tend to consistently concentrate in the same areas of the North Sea over the years—an important condition for effective designation of marine protected areas for seabirds. To assess whether concentration areas are stable over a decadal timescale, we applied the method used by Vogel *et al.* (2024) to delineate concentration areas based on recent data (2014–2022) to older aerial seabird surveys from the Dutch North Sea (1999–2013) and compared the results. For most of the species examined, the overlap between historical and recent concentration areas was significantly greater than expected in the absence of any association, indicating some degree of spatial stability. It was considerably greater for coastal than for pelagic species. Although a significant overlap was also found for most pelagic seabirds, its extent was relatively limited, indicating that temporal stability in concentration areas between the two periods was rather restricted. This corresponds with the considerable variation in the locations of high-density areas between years within the periods studied. The large temporal variation in seabird distribution renders it difficult to effectively protect a large proportion of the populations within fixed sea areas.

2.1 Aim of this study

As a first approach to answering the main research question about the stability of seabird distribution in relation to the designation of protected areas, we investigated whether the approach to identifying bird concentration areas at sea developed in Vogel *et al.* (2024) would give the same general results when applying it not to field data from the recent period used by Vogel *et al.*, but to similar data from an earlier period dating back a few decades. The idea behind this exercise is that (only) if the main concentration areas of seabirds have not changed much in the past few decades, we may gain some confidence that they will still be in more or less the same places a few decades into the future. The seabird distribution data used in Vogel *et al.* (2024) for the Dutch North Sea area stems from counts made from airplanes along at-sea transects conducted within the MWTL monitoring program, which has been running from 1991 onwards. However, there have been changes in the spatial distribution and cover of the transects flown and in the method of sampling (distance sampling vs. strip transects, o.a. Arts 2013). These differences must be kept in mind, but nevertheless the general methodology of data collection was deemed sufficiently similar to allow a comparison between the periods 1999-2013 and 2014-2022.

2.2 Methods

2.2.1 Collection and spatial modelling of historical seabird distribution data

Data and methods
The aerial survey data of the North Sea within the MWTL program contains records from August 1991 to June 2014 and includes all bird and marine mammal species observed during the surveys. Survey effort varied throughout the study period, mainly due to changing survey designs and the omission of certain transects in some surveys. In August 1999, a survey design was implemented that since remained in use until June 2014. This design covered the coastal zone with two transects parallel to the coast and covered the offshore area with several transects running parallel to the boundary of the Dutch Continental Shelf (see Figure 2.1). Six bimonthly surveys were conducted in August-September, October-November, December-January, February-March, April-May and June-July, with surveys generally starting from the 20th of the first month.

For this study, only survey data from August 1999 onward were used to determine seabird distributions, as the survey design has remained consistent since then and provided reasonably good coverage of the Dutch sector of the North Sea. For the data from 1999 onward, the completeness of the surveys was assessed and surveys with limited coverage due to missing transects were excluded. In this period, generally six surveys were completed in each year (season).

For modelling seabird densities, the original data were aggregated per 10×10 km grid cell to create a robust and generic framework that produces realistic results for all species. The counted birds as well as the surveyed area per species per survey were summed within each grid cell. This spatial resolution is courser than used for the models underlying the analysis in Vogel *et al.* (2024), described in Van Bemmelen *et al.* 2023, and was used to reduce the effects of very high counts in relatively small areas, which led to models predicting extreme values, in particular at the edges of the Dutch Continental Shelf.

The spatial pattern of bird density was modelled separately for each species and survey where at least 20 individuals of the species were observed, using the same statistical methods as used to study concentration areas of surveys from 2014 onward (van Bemmelen *et al.* 2023). Bird densities were modelled using the R package sdmTMB (Anderson *et al.* 2022), where 'sdm' stands for species distribution model and 'TMB' for Template Model Builder. sdmTMB uses Stochastic Partial Differential Equations (SPDEs) for spatial correlation, using functionalities from INLA (Lindgren *et al.* 2011, Lindgren & Rue 2015).

The models included an intercept and a spatial field (an SPDE). The SPDE was fitted using a so-called 'mesh', a network of nodes and edges between sample locations, that is used to account for the distance between observations in estimating spatial dependence. The resolution of the mesh balances precision and computational efficiency. Various mesh resolutions were tested in this study, with a resolution of 25 ultimately providing the best results, producing realistic modelled densities that reflect observed large-scale patterns well.

In sdmTMB, models were fitted under the assumption that the response variable, bird density per 10×10 km grid cell (n/km^2), followed a Tweedie distribution. The Tweedie distribution is capable of accommodating both low and high values. If a model with a Tweedie distribution failed to converge, a Poisson-based model was used instead, with the counted number of birds as the response, and the log of the surveyed area included as an offset. Densities were predicted on a 5×5 km grid covering the entire Dutch sector of the North Sea, to allow direct comparison to the post-2014 bird density studies.

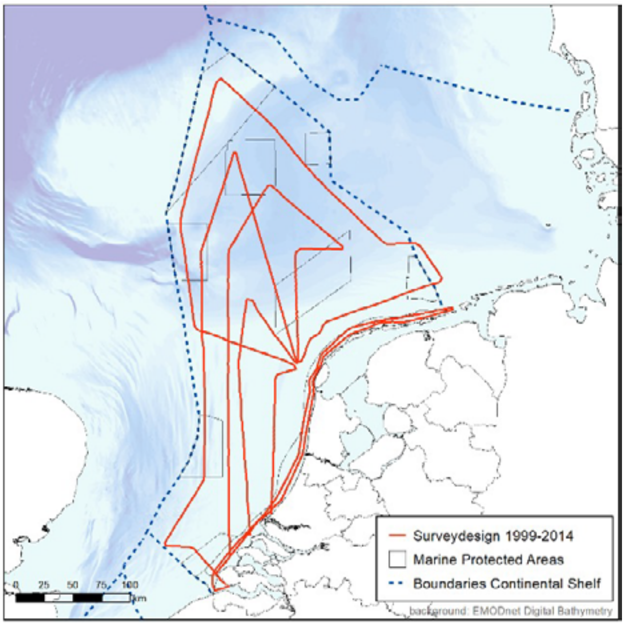


Figure 2.1: Survey design of the MWTL aerial surveys from August 1999 to June 2014

Despite using aggregated 10×10 km input data and the most optimal mesh resolution of 25, some model results still produced unrealistically high densities. These extreme values, mainly occurring at the edges of the Dutch continental shelf, were a result of the survey design providing poor coverage up to the edges of the Dutch continental shelf (because the transect lines ran parallel to these edges at some distance). To address this, extreme values were truncated at the highest observed density within a survey.

2.2.2. From density maps to concentration areas

Based on the bird densities in 5×5 km grid cells predicted by the models developed in Section 2.2.1, we identified the areas of greatest importance for individual species, as well as for all seabird species combined, following the structured selection process proposed by Vogel *et al.* (2024). This methodology follows a stepwise approach to ensure that the most significant areas are systematically identified for each species. The process involves the selection of the times (surveys) of maximum abundance within seasons, the identification of high-abundance areas, and the assessment of long-term patterns of species concentration. Finally, we evaluated how well these historically important areas overlap with current important areas identified by Vogel *et al.* (2024) using the aerial survey data from 2014-2022. The steps are described below and in Fig. 2.2):

1. We started by determining the timing of maximum abundance within seasons (hereafter referred as the seasonal maximum) for each species. Seasons run from July in the focal year (with the first survey of a season usually occurring in August) to June of the following year.
2. Next, we identified which geographic areas host the highest concentrations of individuals. For this we selected and clustered grid cells until they collectively accounted for 40% of the total (modelled) abundance in that season (the 40% quantile or ‘Q40’). This resulted in a series of clusters (‘patches’) of adjacent grid cells together making up the Q40.
3. Among the Q40 patches identified in step 2, we selected the five most important areas (Top5) per season, based on the total bird abundance within them. We did not apply a threshold of 1% of the total flyway population being present in a patch as included by Vogel *et al.* (2024) in this step, as this would have brought up the question whether to use the current 1% threshold or that valid at the time of the counts, and as some species generally occur in low densities or are spread across many small patches, making a strict percentage-based cutoff unpracticable. Furthermore, modelled densities generally result in lower abundances than those based on Distance Sampling, raising the question which method should be preferred. By standardising the selection to the Top5, we also ensured that each season contributed a comparable number of best patches, preventing that some seasons have more influence on the final result than others due to between-year variations in population density or survey conditions.
4. Once the Top5 areas were identified for each season, they were ‘stacked’ across multiple seasons, resulting in a map where each grid cell is assigned a value based on the number of seasons it was classified as part of one of the Top5 patches. For example, an area with a value of 4 indicates that its cells were selected as a Top5 area in four seasons.
5. We then defined the ‘concentration areas’ for each species as those patches that fell within the Top5 in at least 25% of the seasons for which modelled distribution data were available. This step was included to ensure that only the most consistently used, and therefore ecologically important, areas are retained. Vogel *et al.* (2024) used a threshold of at least two seasons for this criterium, but their dataset spanned eight seasons, whereas the current sets spanned between 3 and 15 years depending on the species. By using the same proportional threshold (2/8=25%), we ensured that patches had a similar (*a priori*) probability to be included in the final ‘concentration area’ in both periods.
6. Finally, we evaluated how well these historic areas overlap with the current species concentration areas determined by Vogel *et al.* (2024). For this we used the α MLE method (Maximum Likelihood Estimate of Log Odds Ratio) as proposed by Mainali *et al.* (2022) and implemented in the R-package CooccurrenceAffinity version 1.0 (Mainali & Slud 2025). In contrast with other approaches to assessing co-occurrence, such as Jaccard or Simpson, the α approach is insensitive to the prevalence of the species (i.e., how common or rare the species is in the North Sea). Positive values of α denote positive associations of concentration areas in the past and in the present (i.e., the number of cells that fall within the concentration area either in both time periods or in none is greater than the number expected if the distribution of concentration area cells were totally independent in the two periods, i.e. the two areas show more overlap than expected ‘at random’), and indicate some degree of spatial stability in time. Negative values of α mean that concentration areas in the two time periods overlap less than expected ‘at random’, indicating a significant shift in time. To make the historic and current concentration areas directly comparable, we recalculated the latter based on the annual Top5 patches without

considering the 1%-of-flyway-population criterium included by Vogel *et al.* (2024; patches meet the 1% criterium *or* fall within the Top5). The current concentration areas therefore may differ slightly from those presented in Vogel *et al.* (2024).

We used the R-packages terra version 1.8-21 (Hijmans, 2024) for spatial raster analyses, sf version 1.0-19 (Pebesma, 2018) for spatial vector manipulations, tidyverse version 2.0.0 (Wickham *et al.*, 2019) for data manipulations, and tmap version 4.0 (Tennekes, 2018) for making the maps. All analyses were run in R-version 4.4.2 (R Core Team, 2024).

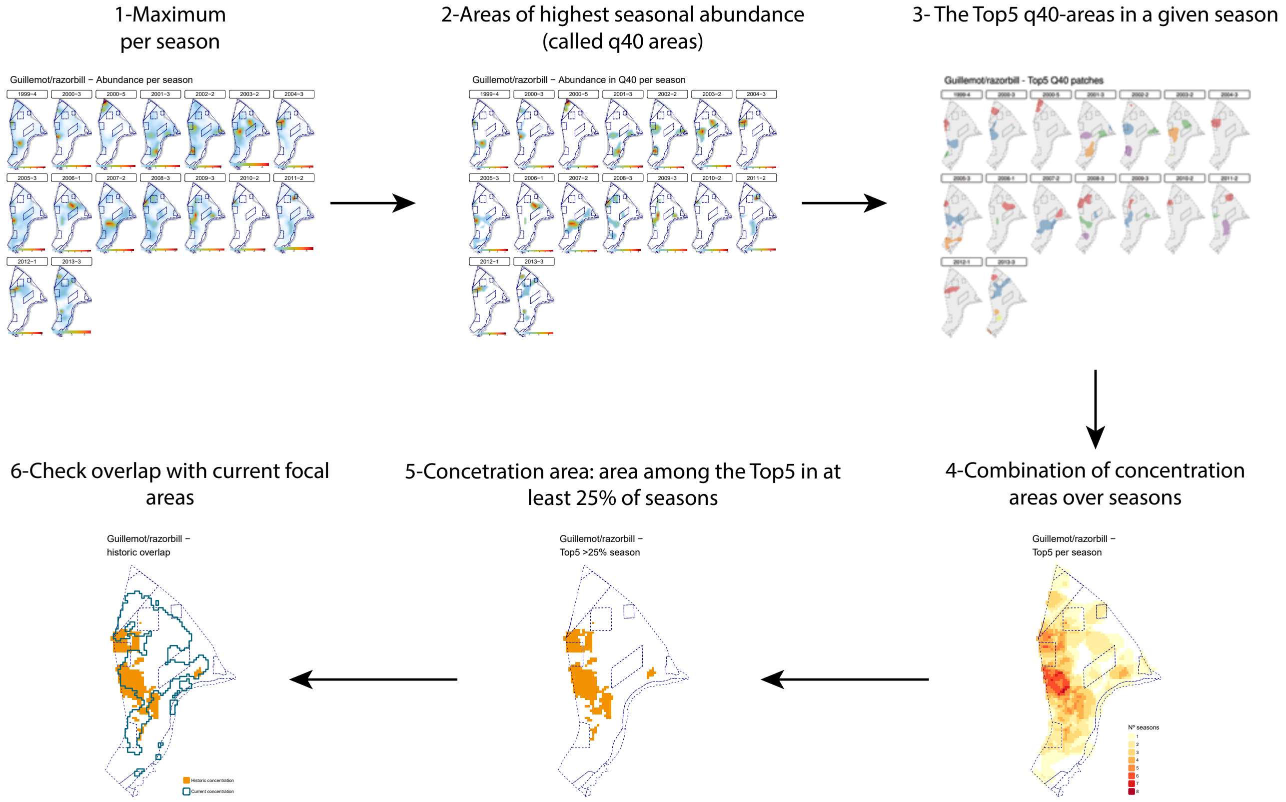


Figure 2.2. Steps in the identification of 'concentration areas' for seabird species in the Dutch North Sea based on the modelled density maps for each survey. Steps are explained more fully in the main text (§ 2.2.2).

2.3 Results

2.3.1 Results by species

Northern Fulmar (Fulmarus glacialis – Noordse Stormvogel)
Here we use the example of Northern Fulmar to describe the methodology and results per step in more detail.

Fig. 2.3 illustrates the results of step 1 of the analysis procedure: the modelled distributions (using the procedure described in paragraph 2.2.1) for the survey with the maxim number of Fulmars in each of 15 seasons. Note that seasons differ in when (during which survey) maximum abundance occurred. For example, numbers peaked in August-September in 1999-2003, January-February in 2004-2005 and in June-July in 2006. This figure illustrates how different the distribution can be across surveys and seasons, and hence the importance of using data from multiple years to identify areas where seabirds concentrate (i.e. occur in above-average numbers) regularly.

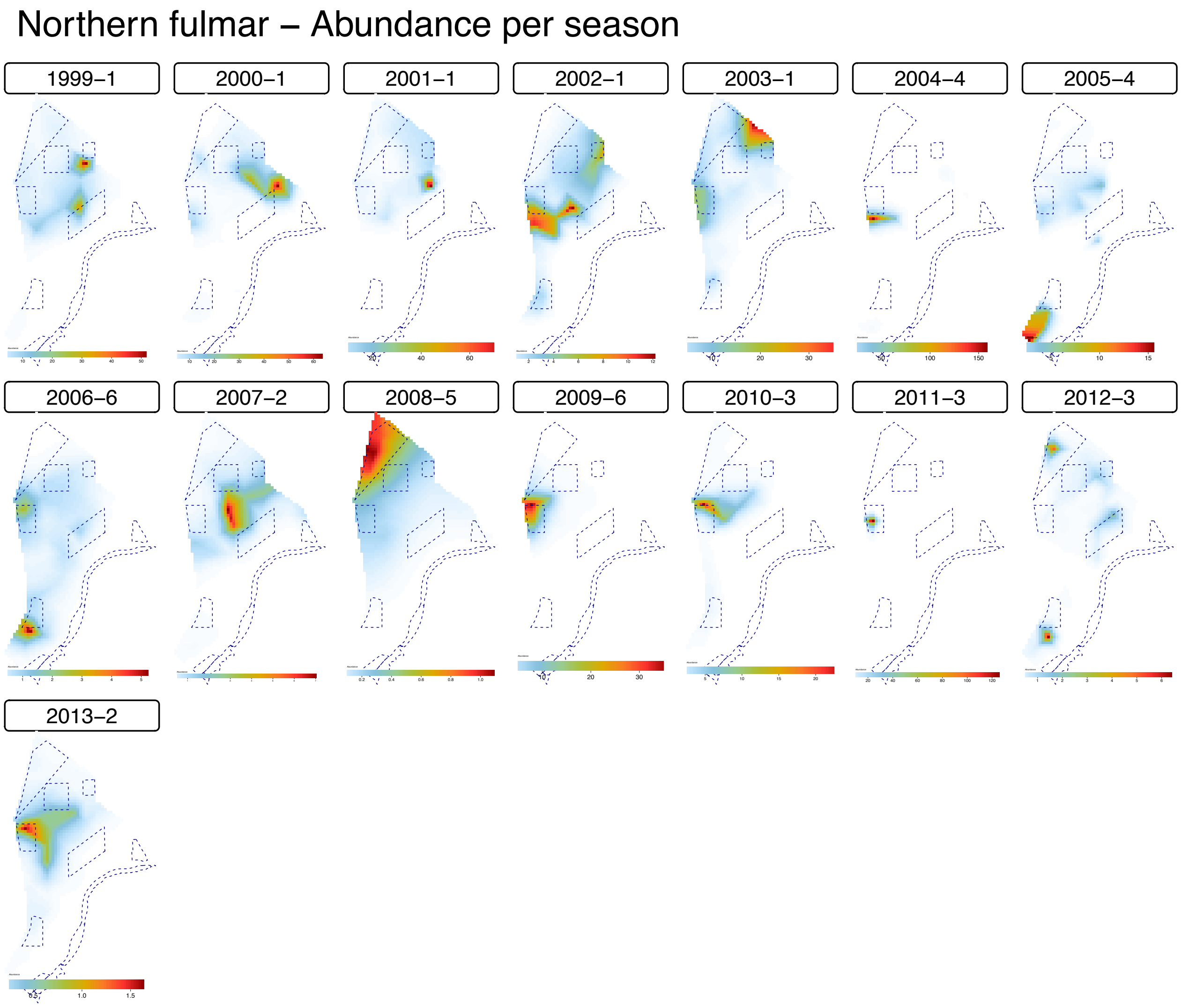


Figure 2.3. Modelled (relative) distribution of Norther Fulmars in the Dutch part of the North Sea for the surveys containing the highest (modelled) number of individuals in each season (figures behind the years indicate survey numbers, not months; survey numbers refer to the six bimonthly periods, starting in August). Boundaries of the Dutch Continental Shelf and of several (candidate) Habitat- and Bird Directive areas within it are indicated.

Fig. 2.4 then illustrates the annual locations of the Top5 patches, the five Q40-patches containing the highest numbers of Fulmars, for each year. Stacked across years, these patches amalgamate into Fig. 2.5, showing which cells lay within the Top5 patches in 1, 2, 3, etc. seasons. That no cells fell within the Top5 patches in more than 5 out of a total of 15 seasons with enough data is a further illustration of the large variability in the at-sea distribution of Northern Fulmars. With 15 seasons of data, the application of the 25% threshold means that those cells that fall within Top5 patches in at least four years (0.25*15=3.75, rounded to 4) are considered part of the 'historic concentration area'. In fig. 2.6, these are shown in orange, together with the 'current concentration area' based on the more recent data used by Vogel *et al.* (2024). From this (step 5) result, the amount of overlap between the two periods was quantified using the α MLE metric of association (step 6). For Northern Fulmar this metric has the value 1.16, with a confidence interval [0.69-1.64] that does not overlap 0 (p-value <0.001), so we conclude that the current and historic concentration areas show a significant degree of similarity, and hence consistency in time.

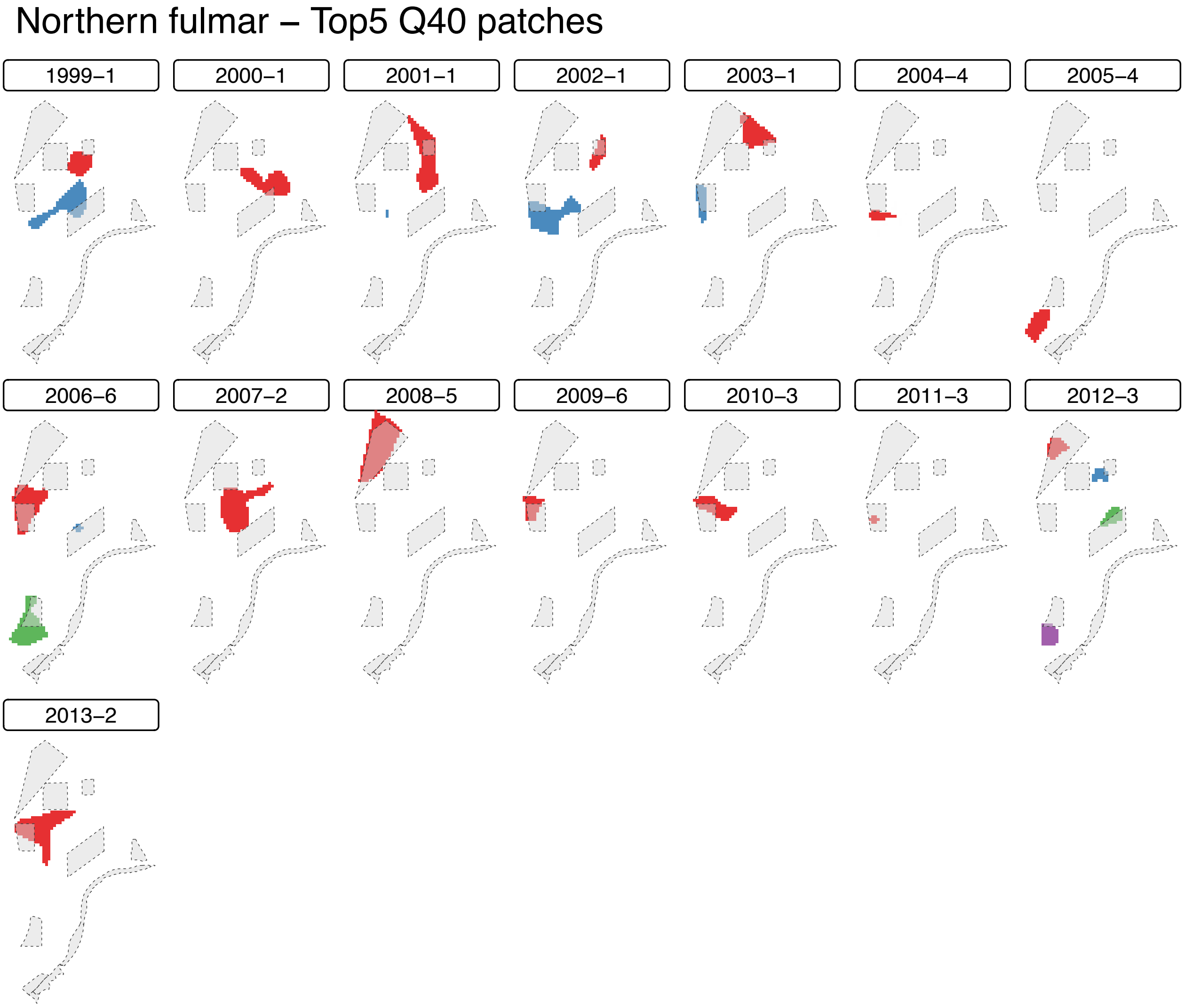


Figure 2.4. Top5 patches (Q40 patches including the highest numbers of individuals) for Northern Fulmar in each season (result of step 3 in §2.2.2).

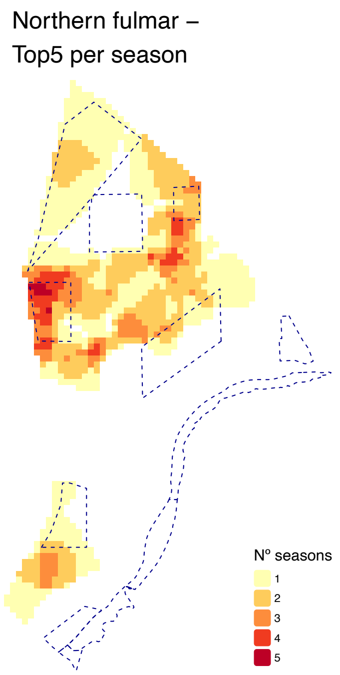


Figure 2.5. Areas in the Dutch North Sea that fall in the Top5 patches for Northern Fulmar in various numbers of seasons (step 4 in §2.2.2). Darker colours denote areas that more often harbour concentrations of Fulmars.

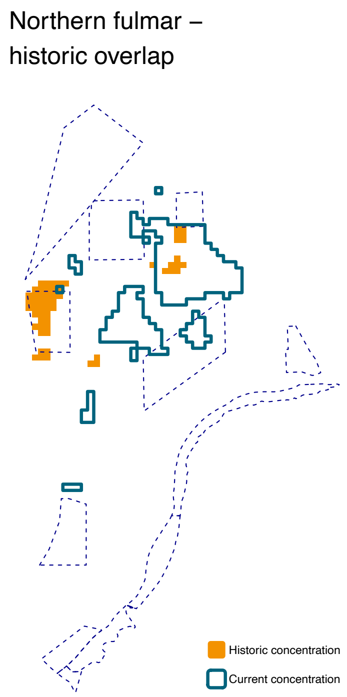


Figure 2.6. Areas in the Dutch North Sea that fall in the Top5 patches for Northern Fulmar in at least 25% of seasons with data available (i.e. 4 years in case of the Fulmar; 'historic concentration area') shown together with areas falling in the Top5 in at least 2 out of 8 seasons in the period considered by Vogel et al. 2024 ('current concentration area'). From this result (step 5 in §2.2.2), the 'a MLE' metric of association, quantifying the amount of overlap between the two periods, was calculated. Note that the current concentration areas are based on the annual Top5 patches without considering the 1%-of-flyway-population criterium and therefore is directly comparable with the historic area, but may differ slightly from the current concentration area presented in Vogel et al. (2024). Boundaries of the Dutch Continental Shelf and of several (candidate) Habitat- and Bird Directive areas within it are indicated in the map.

To some extent, the choice of the threshold number of years that a cell must fall within the Top5 Q40 patches to be included in the 'concentration area' is a subjective one. Of course, the higher this threshold is set, the fewer cells in the North Sea will meet it, and the smaller the resulting concentration areas becomes. Fig. 2.7 shows this relationship for the Northern Fulmar and illustrates that the choice of this threshold has a large effect on the resulting surface area. When comparing among species, the 'steepness' of this relationship will depend on the amount of temporal variation in the species' distribution: if a species concentrates in the same patches time after time, requiring an extra year will not cause many cells to drop out of the concentration area, and the curve will be rather flat.

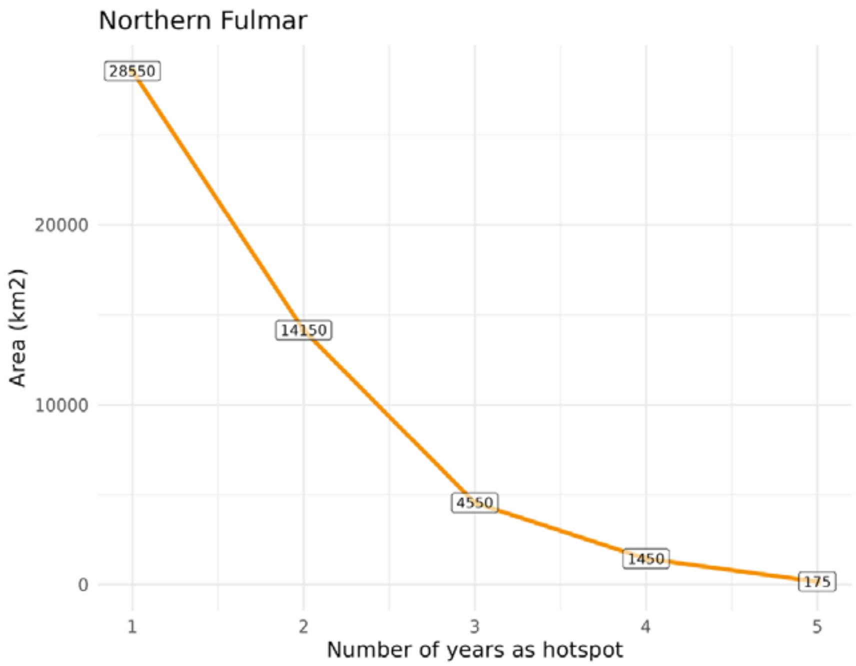


Figure 2.7. Resulting total surface of the 'concentration area' of Northern Fulmar in the Dutch North Sea in relation to the required number of years that a cell should fall withing the Top5 patches to qualify for inclusion.

Results for other species

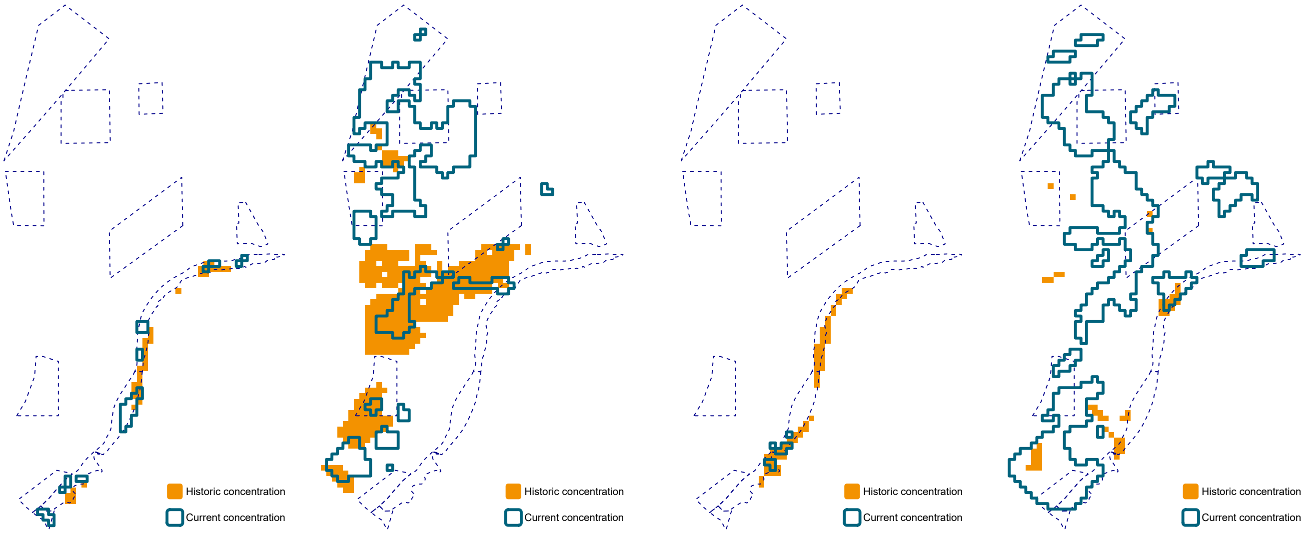
Figure 2.8 presents and compares the historic and current concentration areas for each species.

Red−throated diver − historic overlap

Northern gannet − historic overlap

Great cormorant − historic overlap

Black−legged kittiwake − historic overlap

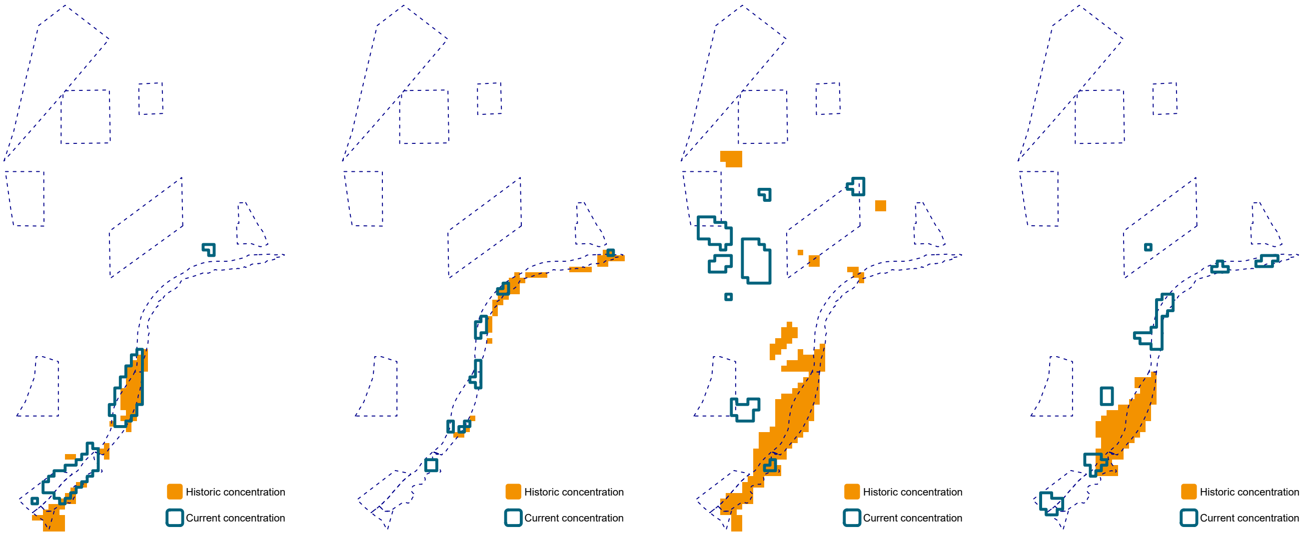


Little gull − historic overlap

Common gull − historic overlap

Great black−backed gull − historic overlap

Lesser black−backed gull − historic overlap



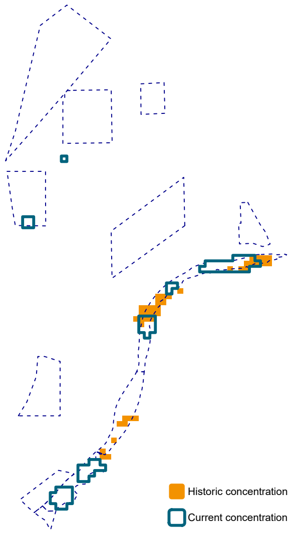
Herring gull − historic overlap

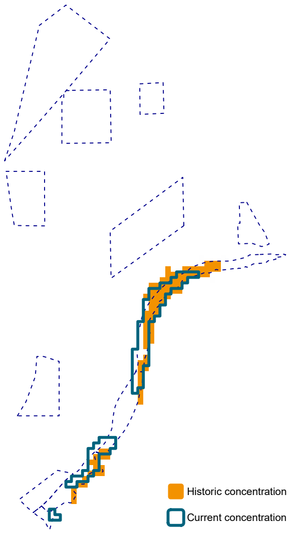
Black−headed gull − historic overlap

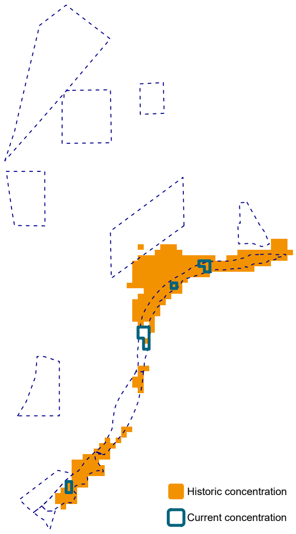
Sandwich tern − historic overlap

Common/arctic tern − historic overlap

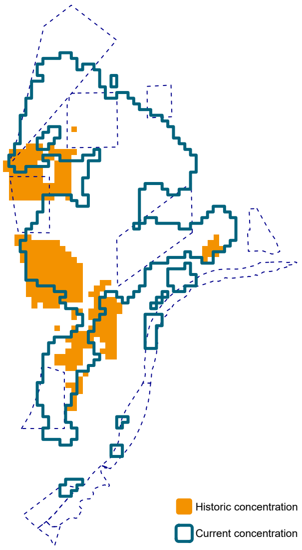
Figure 2.8. Historic and current concentration areas by species.



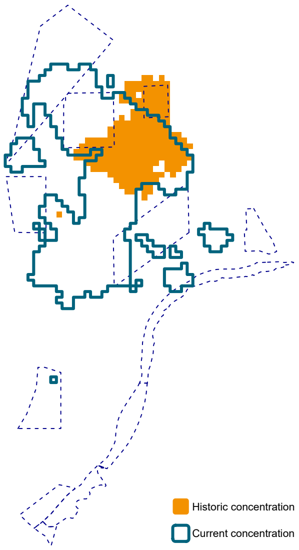




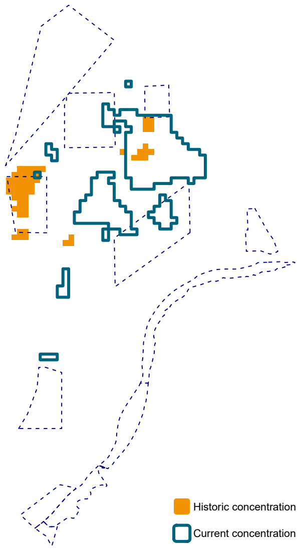
Guillemot/razorbill –
historic overlap



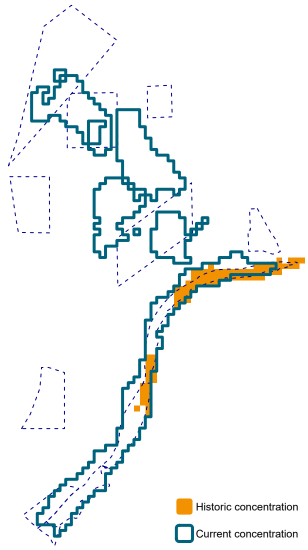
Common guillemot –
historic overlap



Northern fulmar –
historic overlap



Seabirds –
historic overlap



Seabird excl. Seaducks –
historic overlap

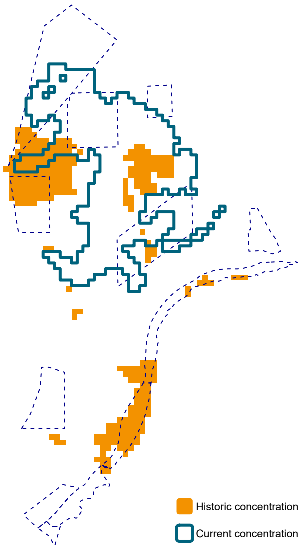


Figure 2.8. (continued)

2.4 Discussion and conclusion

Figure 2.9 summarises the result obtained per species by showing the estimated values of α MLE, the metric for overlap of the historic and current concentration areas. In virtually all species, α MLE is positive and its confidence interval does not include the value 0 (which denotes no deviation from a 'random' amount of overlap), indicating a 'significant' amount of temporal stability in the concentration areas. Only in the Lesser and Great Black-backed Gulls does α MLE not deviate significantly from 0, suggesting no or a weak association between historic and current distributions. However, values of α show considerable variation between species. There is a clear pattern that species largely confined in their distribution to the coastal zones of the North Sea have higher α MLE values than 'pelagic' seabirds with a predominantly offshore distribution. This is understandable since the 'coastal' species are consistently rare or absent in the offshore areas and present mainly in the coastal strip, which by its small area also offers less space for their distribution to vary over time. This space is much larger offshore, and in addition several species that are usually more numerous in offshore areas also venture into the coastal zone in significant numbers from time to time. Although also in these pelagic species (Norther Fulmar, Northern Gannet, Black-legged Kittiwake and Common Guillemot/Razorbill) the α MLE values were positive and differed significantly from 0, they are still fairly small. Although there is no formal interpretation scale denoting what levels of the α MLE metric indicate a 'weak' or a 'strong' affinity (the possible range of α MLE increases as the number of habitat cells considered increases), these fairly small values indicate that the *degree* of temporal stability in concentration areas between the two periods considered is rather limited. Also, in several species the historic concentration areas seem smaller in their extent than the current ones. Thus, strong α MLE may represent cases when a large part of the historic (smaller) distribution overlaps with the current (larger) distribution, but not the other way around.

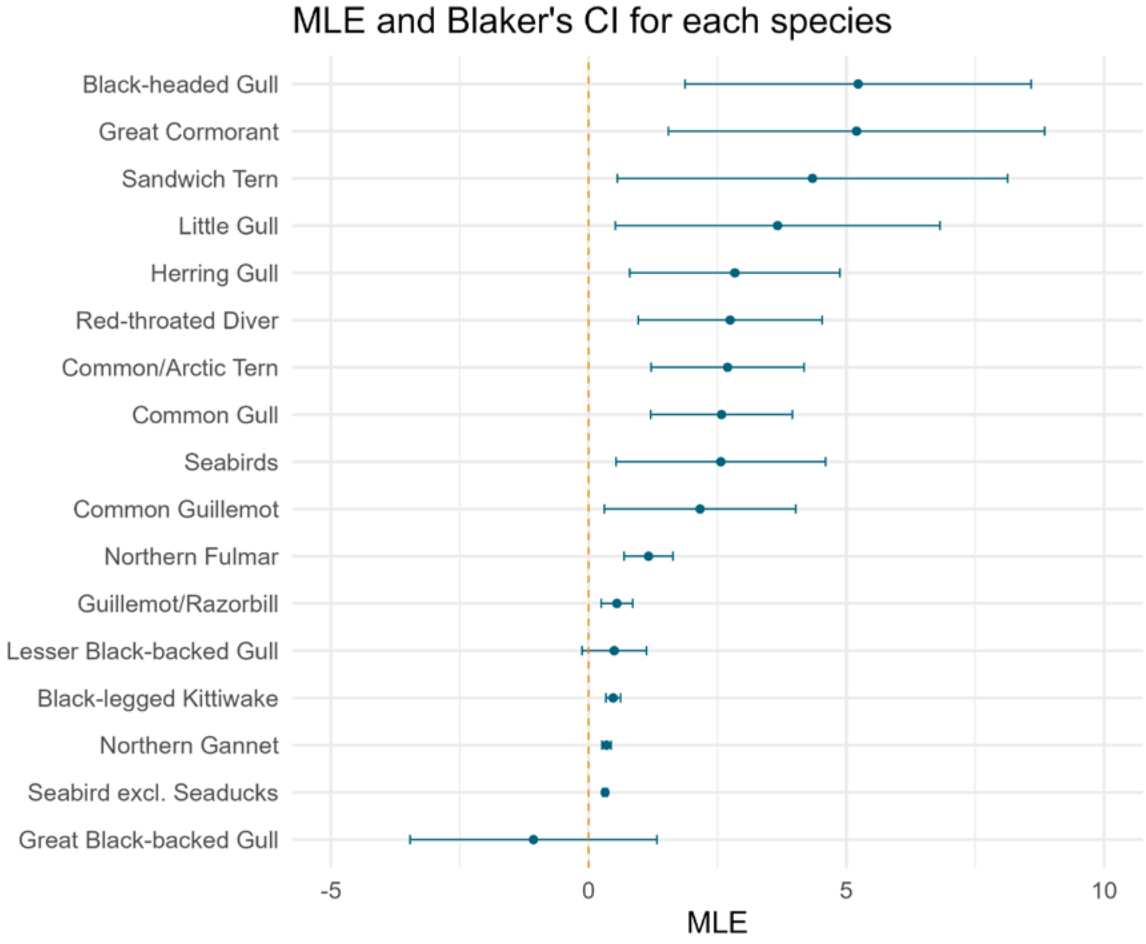
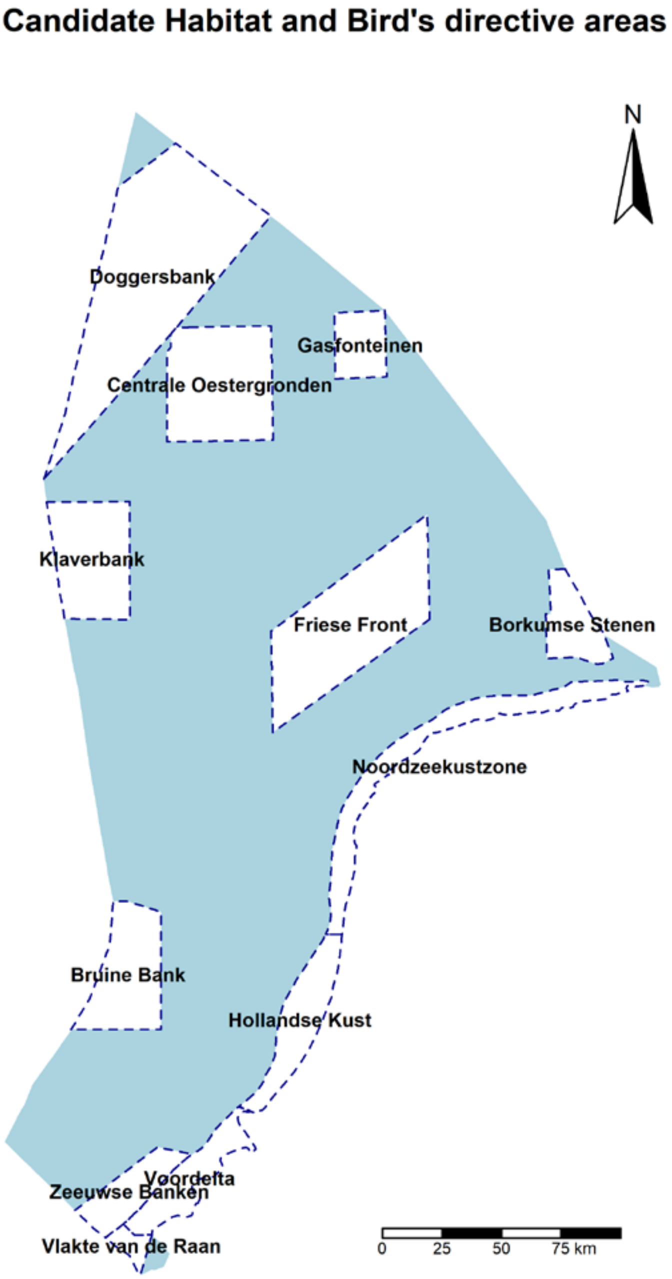


Figure 2.9. Species estimates of α MLE, the metric for overlap of the historic and current concentration areas, with confidence intervals according to Blaker's method. Positive values denote that historic and current concentration areas show more similarity in their location (i.e. overlap more) than would be expected if they were independent (in which case α=0); and negative values indicate that the distributions in the two periods tend to 'avoid' each other, i.e. overlap less than expected at random.

There is some consistency in the results on two timescales present in the current analysis. Variation in the distribution of pelagic seabirds was large already on the short term, between years within each of the study periods. This means that one needs to identify a large 'concentration area' in order to include the main distribution of seabirds within them in all or the majority of the years (e.g. Fig. 2.7). And on the larger timescale of decades, the location of time-amalgamated 'periodic concentration areas' still tends to show rather pronounced differences, even though they are by no means totally independent or different.

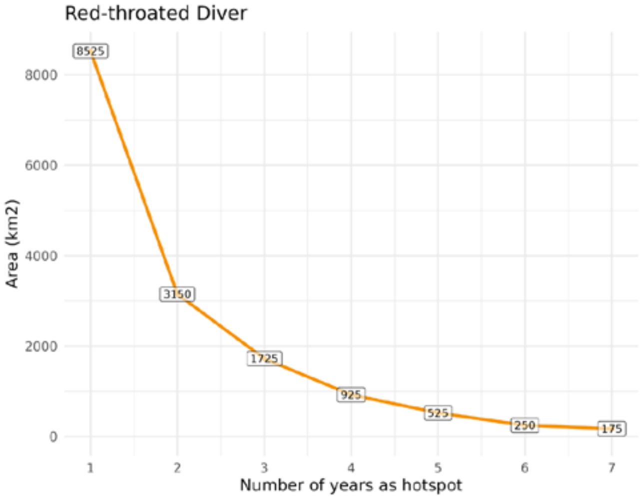
In terms of policies for management and conservation of seabirds, this would mean that it will be difficult to effectively and consistently protect a large proportion of the seabird populations of our part of the North Sea by designating limited parts of it as 'protected areas' where detrimental activities are banned, unless the protective measures are so effective in enhancing local resources for birds that they change the dynamics of the birds' distribution, to result in much more stable and predictable hotspots within their boundaries. The likelihood that such an effect can be achieved within limited marine areas is not very high, given that fish stocks that constitute the main prey base for seabirds in these areas can freely move in and out and often engage in seasonal or age-related migrations. It seems therefore wise to focus seabird conservation policy not only on protecting areas, but also on measures on a North Sea-wide scale (or even beyond) that alleviate specific pressures and bottlenecks that have been identified. Examples of such approaches are the explicit inclusion of the food requirements of seabirds in determining fisheries quota (e.g. Cury *et al.* 2011), the application of measures to reduce bycatch of seabirds (e.g. EU 2012), and measures reducing predation in seabird colonies where this reaches problematic levels.

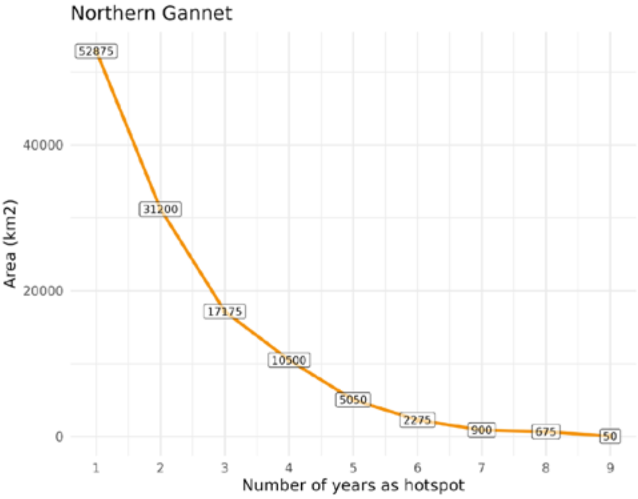
Supplement 1

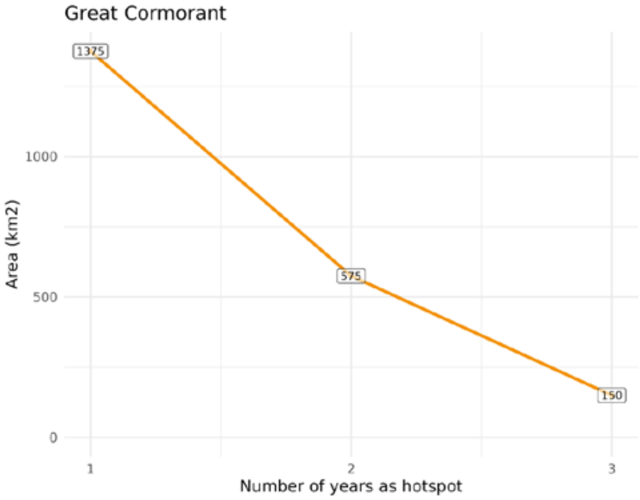


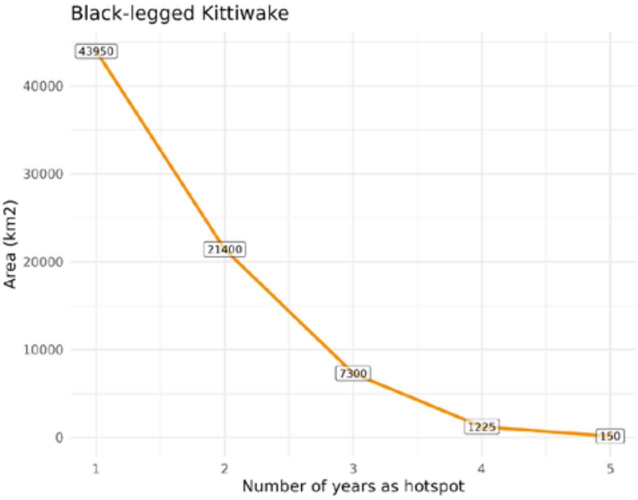
Map showing the established and candidate habitat and bird's directive protected areas in the Dutch North Sea.

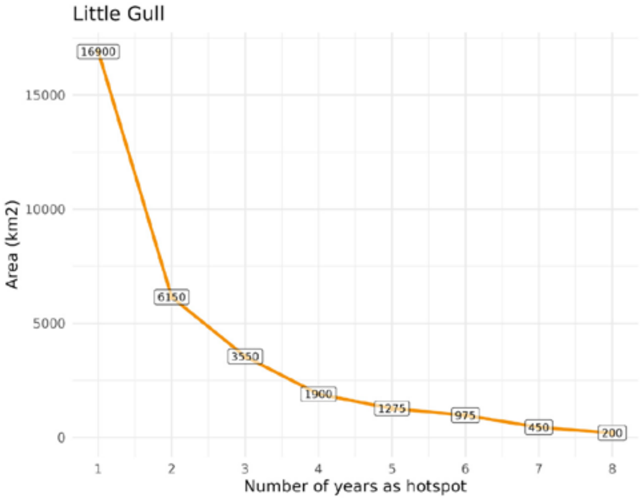
Supplement 2

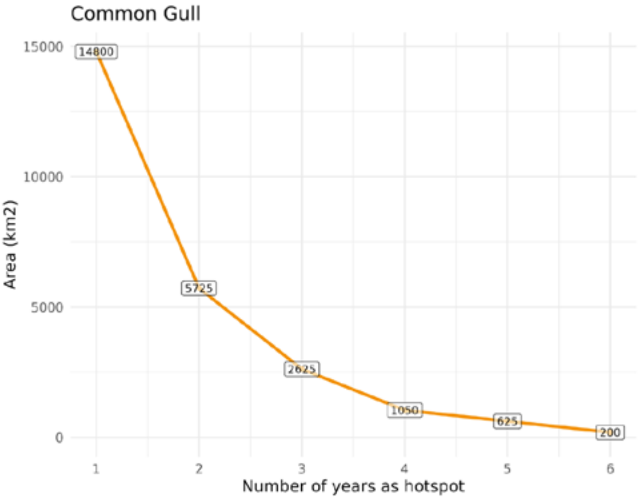


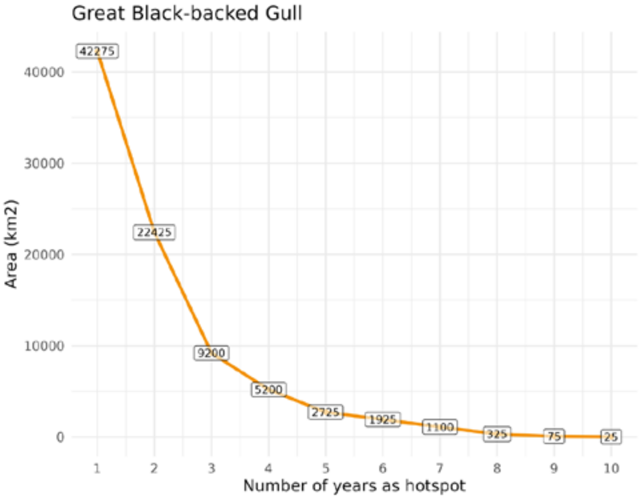


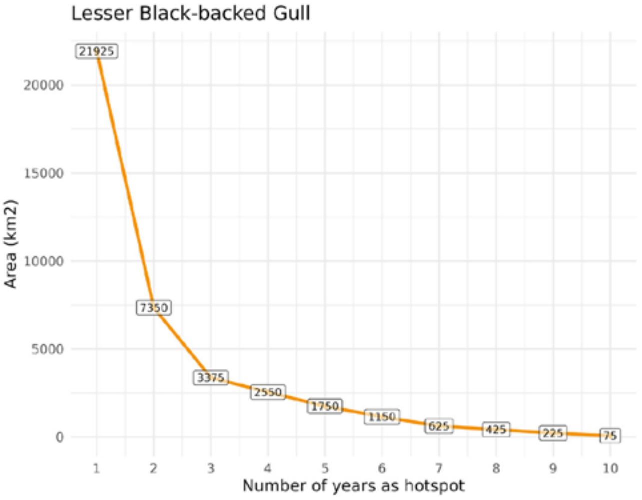


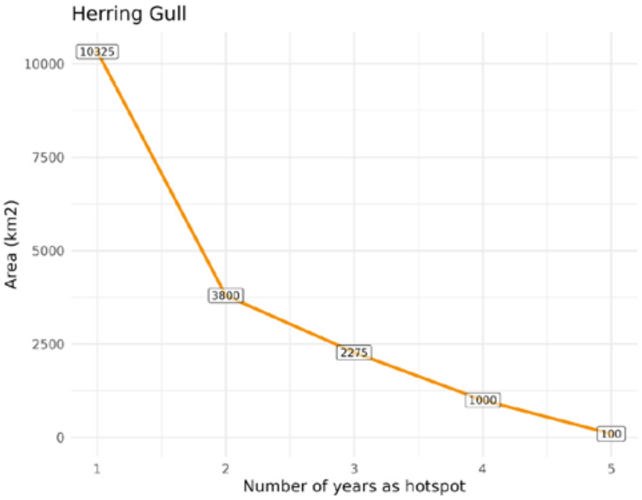


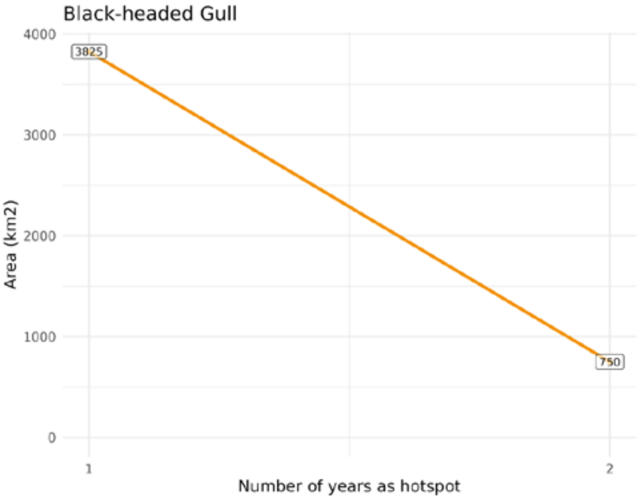


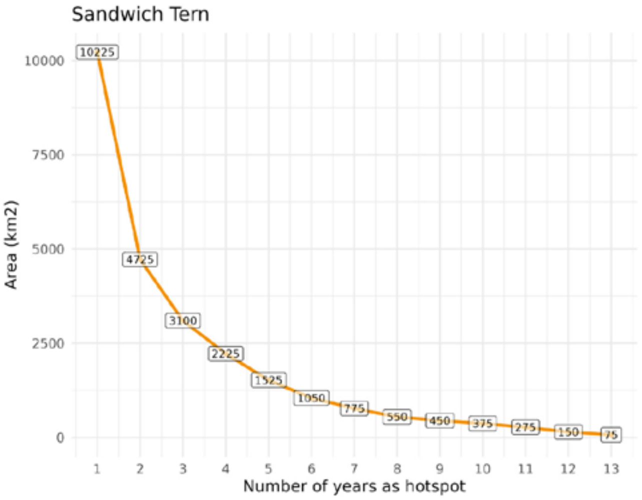


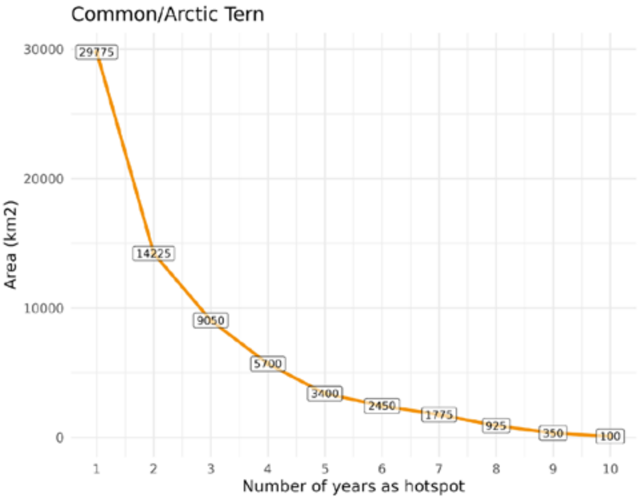

Great Black-backed Gull
Area (km2)
Number of years as hotspot
0
10000
20000
30000
40000
1
2
3
4
5
6
7
8
9
10
42275
22425
9200
5200
2725
1925
1100
325
75
25

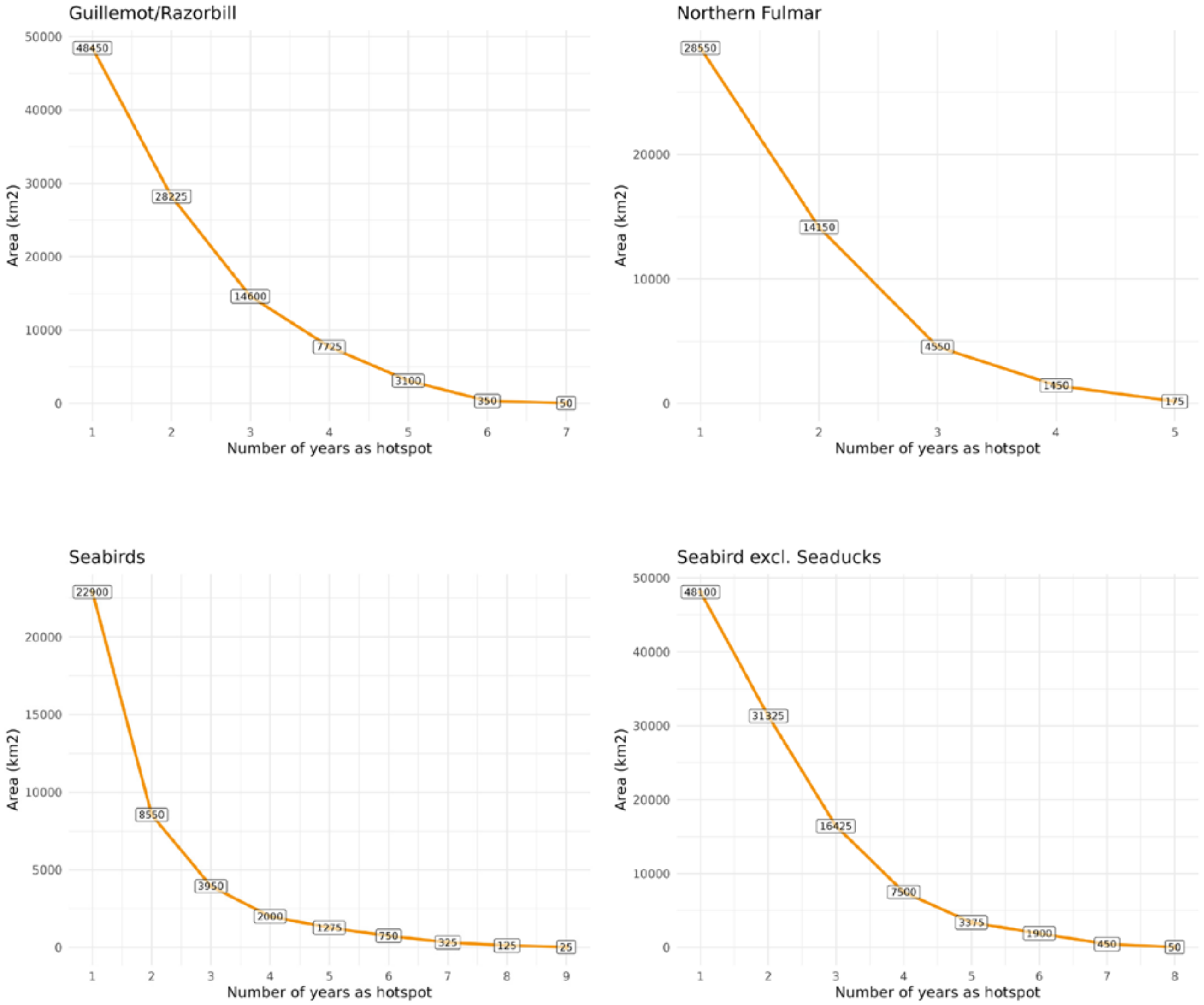

Lesser Black-backed Gull
Area (km2)
Number of years as hotspot
0
5000
10000
15000
20000
1
2
3
4
5
6
7
8
9
10
21925
7350
3375
2550
1750
1150
625
425
225
75


Herring Gull
Area (km2)
Number of years as hotspot
0
2500
5000
7500
10000
1
2
3
4
5
10325
3800
2275
1000
100


Black-headed Gull
Area (km2)
Number of years as hotspot
0
1000
2000
3000
4000
1
2
3825
750


Sandwich Tern
Area (km2)
Number of years as hotspot
0
2500
5000
7500
10000
1
2
3
4
5
6
7
8
9
10
11
12
13
10225
4725
3100
2225
1525
1050
775
550
450
375
275
150
75


Common/Arctic Tern
Area (km2)
Number of years as hotspot
0
10000
20000
30000
1
2
3
4
5
6
7
8
9
10
29775
14225
9050
5700
3400
2450
1775
925
350
100


Guillemot/Razorbill
Area (km2)
50000
40000
30000
20000
10000
0
48450
28225
14600
7725
3100
350
50
1
2
3
4
5
6
7
Number of years as hotspot
Northern Fulmar
Area (km2)
20000
10000
0
28550
14150
4550
1450
175
1
2
3
4
5
Number of years as hotspot
Seabirds
Area (km2)
20000
15000
10000
5000
0
22900
8550
3950
2000
1275
750
325
125
25
1
2
3
4
5
6
7
8
9
Number of years as hotspot
Seabird excl. Seaducks
Area (km2)
50000
40000
30000
20000
10000
0
48100
31325
16425
7500
3375
1900
450
50
1
2
3
4
5
6
7
8
Number of years as hotspot

3. Distribution of Common Guillemots on the Dutch Continental Shelf in summer: moulting and chick-rearing areas

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Samenvatting

Beschermingsdoelen van mobiele soorten kunnen alleen behaald worden als de soort tijdens alle fasen van hun jaarcyclus voldoende bescherming genieten. Bescherming zou zich met name moeten richten op perioden waarin de soort kwetsbaar is. Een voorbeeld van zo'n periode voor Zeekoeten is de zomer, waarin ze hun vliegveren ruien en waarin ze kuikens grootbrengen op zee. Zeekoetkuikens springen al op jonge leeftijd – wanneer hun lichaam nog maar ongeveer een kwart van die van volwassen vogels is – van de broedkliffen en zwemmen dan met hun vaders de zee op. Zeekoeten kunnen dan tijdelijk niet vliegen en kunnen vermoedelijk daardoor minder goed reageren op bedreigingen of slechte voedselsituaties dan in andere perioden wanneer ze door middel van vliegen sneller grotere afstanden kunnen afleggen.

In deze studie lieten we met behulp van waarnemingen vanaf schepen eerst zien dat met name in augustus Zeekoeten op de Nederlandse Noordzee ruien en kuikens hebben. Vervolgens lieten we met behulp van tellingen vanuit vliegtuigen in 2014-2023 zien hoe Zeekoeten zich over de Nederlandse Noordzee verspreiden in augustus. Die verspreiding blijft meestal beperkt tot het diepere, noordelijke deel van de Nederlandse Noordzee. Door de tellingen te ordenen naar datum, probeerden we erachter te komen hoe Zeekoeten door de Nederlandse Noordzee bewegen. Echter, deze gegevens zijn daar niet optimaal voor; daarvoor zouden meerdere tellingen achter elkaar uitgevoerd moeten worden binnen een jaar, óf zouden individuele Zeekoeten gevolgd moeten worden met behulp van zenders.

De vraag is of er gebieden binnen de Nederlandse Noordzee zijn waar proportioneel meer kuikens verblijven dan elders. Tijdens vliegtuigtellingen worden kuikens (waarschijnlijk) vaak niet als zodanig herkend, maar dat is bij scheepstellingen geen probleem. Daarom voorspelden we het aantal kuikens tijdens vliegtuigtellingen met een model gevoed met waarnemingen vanaf schepen, waarin we groepsgrootte relateerden aan het aantal kuikens in een groep. Een groepsgrootte van twee bleek de grootste kans te hebben een vader-kuiken-paar te betreffen. Ruimtelijke modellering van deze voorspellingen gaf geen aanwijzingen voor gebieden met meer kuikens dan elders. Met andere woorden, in gebieden waar Zeekoeten aanwezig zijn in augustus, zullen ook kuikens aanwezig zijn. De verspreiding van Zeekeoten in augustus beperkte zich grotendeels tot het gebied ten noorden van de 30 m dieptelijn. Binnen dit gebied kwamen hogere dichtheden met name voor tussen de Centrale Oestergronden en het Friese Front.

Abstract

Conservation goals for mobile animals such as seabirds can only be achieved if populations experience adequate protection during their entire annual cycle. Identifying areas where they spent parts of their annual cycle when they are particularly vulnerable should be priority. In case of seabirds, the period in which they perform their annual moult is an example of such vulnerability. Here, we studied where and when Common Guillemots in the Dutch sector of the North Sea perform post-breeding moult and escort their chicks – a time when they are unable to fly and may therefore be particularly vulnerable. Using ship-based seabird survey data, we show that both moult and the presence of chicks mainly occur in August. During this time, flocks of two birds often concerned father-chick pairs. Using flock size as a proxy for the presence of chicks, we used aerial seabird survey data to look for areas of higher occurrence of chicks. However, the proportion of flocks of two birds (opposed to flocks of other sizes) did not show particular spatial variation, suggesting that chicks can occur anywhere where guillemots occur. Overall, the distribution of guillemots in August was restricted to the area north of the 30 m isobath. Within this area, higher average densities occurred between the Central Oystergrounds and the Frisian Front.

3.1 Introduction

The delineation of marine areas of high seabird conservation value is mostly based on the presence and abundance of species. However, the vulnerability of species, and therefore the added value of protected areas, may vary throughout their annual cycle. For example, safeguarding reproduction requires protective measures during the breeding season and within the foraging range from colonies.

For Common Guillemots *Uria aalge* (hereafter: guillemots), besides breeding, the post-breeding and moulting periods represent times in which they are potentially particularly vulnerable to suboptimal conditions. Guillemot chicks 'fledge' from their breeding cliffs when only about a quarter of the adult body size (Merkel & Strøm 2023). Then, fathers escort their chicks to offshore areas (Camphuysen 2002, Merkel & Strøm 2023), where they avoid the high costs of commuting flights between feeding area and the colony (Elliott *et al.* 2013, Elliott & Gaston 2014) and reduce predation risk (Camphuysen 2002). Moreover, adults moult their flight feathers and become flightless for about three to four weeks. The period of moulting and before chicks become independent are thought to last 1-2 months (Varoujean *et al.* 1979, Elliott & Gaston 2014). Moulting and/or chick-rearing guillemots must therefore travel solely by swimming, which may hamper fast responses to suboptimal weather or foraging conditions, making them particularly vulnerable during this period (Davoren *et al.* 2002).

On the Dutch Continental Shelf (DCS), guillemots occur year-round, with lowest numbers in (late) spring (Camphuysen & Leopold 1994, Bemmelen *et al.* 2023). When numbers increase again in summer, their distribution remains limited to the northern part of the DCS, with the 30 m isobath as the approximate southern border. In autumn, they venture into the southern parts of the DCS. However, the spatio-temporal distribution of guillemots on the DCS is imperfectly known. Inferences of their distribution were based on uneven coverage of the DCS during earlier ship-based (from the 1980s) and aerial seabird surveys (from the late 1980s) and are potentially biased to areas with higher survey effort. From 2014 onward, seabirds have been surveyed along a set of pre-defined aerial survey transects with an even coverage of the DCS, now offering the opportunity to study the spatio-temporal distribution of guillemots in more detail and with much less spatial bias.

Here, we first show that body moult and father-chick pairs mostly occur during summer. Using a model of chick presence as a function of flock size, based on ship-based seabird survey data, we predict the occurrence of chicks in observations recorded during aerial seabird surveys in August, which covered the entire DCS. Subsequently, we estimate density surface maps of all guillemots in August, indicating where moulting birds are most likely to be found, and of potential chicks, indicating areas where father-chick pairs predominantly occur.

3.2 Methods

3.2.1 Ship-based surveys

Ship-based survey data were obtained from the European Seabirds At-Sea database, stored at https://www.ices.dk/data/data-portals/Pages/European-Seabirds-at-sea.aspx (accessed 16 May 2023). Only data collected at the Dutch Continental Shelf were selected, which covers the period of 1991 to 2022. During ship-based surveys, details of age and plumage are noted. Observateions on primary moult are recorded as "X" = in active moult and "Y" = no active primary moult. Plumage is recorded as "B" = breeding plumage, "W" = wintering plumage or "T" = transient plumage between wintering or breeding plumage, or vice versa, and refers to the plumage of the head and upper breast. Common Guillemots have an entirely dark brown breast and head in breeding plumage, and white breast, throat and ear-patch in non-breeding plumage. The plumage column is also used to record age of chicks: either as "P" = pullus, "A1" = immature auks, at most half of adult size, "A2" = immature auks, over half of adult size, or "A3" = immature auks, about same size as adult. In addition, the column 'lifestage' also includes information on age, with 1 referring to birds in their first calender-year and "I" as 'immatures'. In principle, the term 'immatures' can refer to any individual that is not yet adult. Common Guillemots start breeding at an age of 4 years, so any bird aged 0-3 years can be regarded as an immature. However, under field conditions, guillemots can usually only be reliably aged if the bird 1) shows begging behaviour towards its (apparent) father and/or 2) is substantially smaller and/or with darker coloured upperparts than an accompanying adult. Hence, we regard 'immatures' as referring to chicks. As detecting chicks or moult may be more difficult at greater distance from the observer, we also included the distance band in our analyses. Distance bands were defined as follows: A = 0-50 m, B = 50-100 m, C = 100-200 m, D = 200-300 m, E = >300 m from the transect line.

3.2.2 Aerial surveys

For details of the aerial surveys, see Bemmelen *et al.* (2023). In short, aerial seabird surveys were carried out in August, November, January, February, April and June 2014-2023. Birds were counted along pre-defined transects running perpendicular to the coast and covering the Dutch sector of the North Sea. One complete survey, was usually carried out in 5-7 days (maximum 10 days), and, including non-flying days, covered a period of 5 - 41 days (median = 19 days).

3.2.3 Statistical analysis

Abundance estimates
Per survey, the abundance of guillemots was estimated using distance sampling techniques (Buckland *et al.* 1993, 2001, 2004). See Bemmelen *et al.* (2023) for further details. To investigate whether abundance varied as a function of survey dates, we checked whether northern transects (EEZ 12-19 and the Frisian Front survey lines) were surveyed earlier than most surveys and whether median survey date of northern transects correlated with total abundance.

Moult and chicks
Using ship-based survey data from July and August, when chicks were most abundant, we assessed per sighting of guillemots whether any chicks were involved. We fitted three binomial GLMMs with the number of chicks in a flock (‘successes’) and the flock size (‘number of trials’) as the response variable, and with different sets of explanatory variables; 1) flock size, as factor levels, capped at 10 individuals, 2) distance band, and 3) the interaction of flock size and distance band. The fit of the three models was compared based on the expected log pointwise predictive density (ELPD) of these models using Pareto smoothed importance sampling in Leave-One-Out cross validation (PSIS-LOO-CV), as implemented in the loo package in R (Vehtari *et al.* 2024). The model with highest ELPD was selected to predict the probability that flocks encountered during aerial surveys included chicks.

Using the parameter estimates of the above model, we then predicted the number of chicks in each observed flock in the aerial survey data. We used the parameter estimates for the closest ship-based distance band, where detection of chicks was highest. We summed these predictions for each 5-km transect segment per survey. The summed predictions were then spatially modeled in a tweedy Generalized Linear Mixed Model (GLMM), using the package sdmTMB (Anderson *et al.* 2024), with a spatial random field and random intercepts per survey.

Considering that flocks of two birds had the highest probability of containing a chick, we also modeled the relative occurrence of pairs in an intercept-only binomial GLMM in sdmTMB, with the number of pairs as ‘successes’ and the number of flocks of other sizes as ‘failures’, a random spatial field and random intercepts per survey.

Spatiotemporal distribution
Per survey, we modelled the densities of guillemots recorded during aerial surveys in a Tweedy GLMM with a spatial random field and a random intercept per survey, using the package sdmTMB (Anderson *et al.* 2024).

We investigated potential west-east or north-south seasonal movements by plotting modeled densities against longitude or latitude per survey, ordering surveys according to the median survey date of northern transects.

3.3 Results

3.3.1 Abundance

In general, the abundance of Common Guillemots on the DCS peaks in August and is lowest in April and June (figure 1A). The numbers have increased since the start of the data series in 2014, with a step from abundances of around 200,000 individuals in 2014-2017 to around 450,000 individuals in 2018-2023 (figure 1B). Although the northern transects were surveyed in early

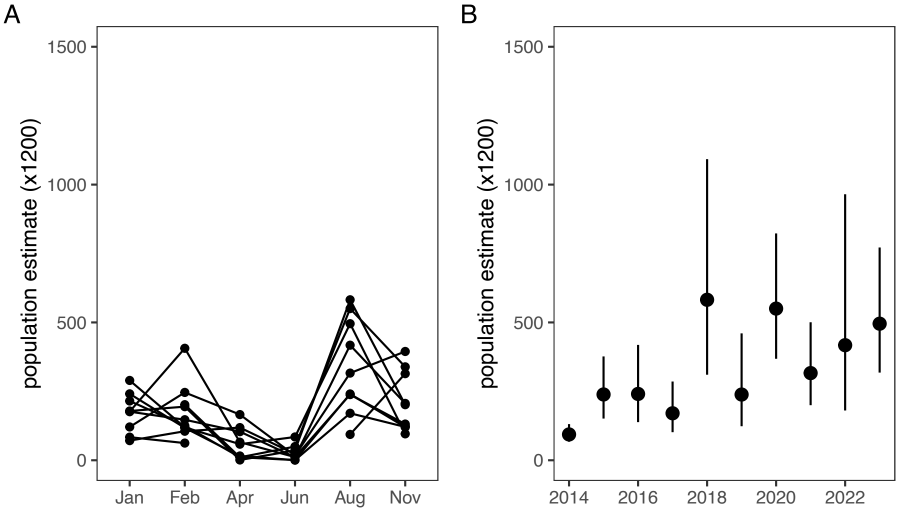

Figure 1: A. Seasonal abundance and B. annual abundance estimates for August of Common Guillemots on the DCS. Numbers peak in August and increased over the past 10 years. As is usual in count data, the uncertainty increases with abundance.

August (i.e. earlier than most surveys) in 2017, 2020 and 2021 (supplement figure 9), this did not necessarily result in lower abundance estimates (supplement figure 10). For southern transects, the surveys were carried out entirely in the second half of August (supplement figure 9).

3.3.2 Moult

The presence of primary moult was only rarely noted during ship-based surveys (n = 150 individuals) and the same applies to its absence (n = 378 individuals), relative to the total number of observed guillemots (n = 71.254 individuals – chicks excluded). Hence, although these data can indicate the occurrence of primary moult, they are too scarce to robustly calculate or estimate the spatial frequency or primary moult. In addition, the records of birds in active primary moult in some months (e.g. January) are – in light of what is known about the timing of primary moult – unlikely to be correct and may stem from confusion about the used codes or may refer to body moult instead of primary moult. Individuals showing active primary moult were noted in all months between June and November, but primarily in July-August (figure 2A), while the relative frequency peaked in August (figure 2B).

Body moult status of the head and breast was noted much more often than primary moult (n = 53.674, out of a total of 71.254 individuals). Birds in transient plumage were noted in all months, but made up a much larger share of birds scored for plumage in August, with 49% (n = 1654 individuals). Indeed, there is a substantial shift from birds mostly in breeding plumage in July to birds mostly in wintering plumage in September (figure 3). Moult to breeding plumage already takes place in mid-winter, indicated by a step-change from December to January. Another such change occurs from April-May (figure 3). These step-changes are very

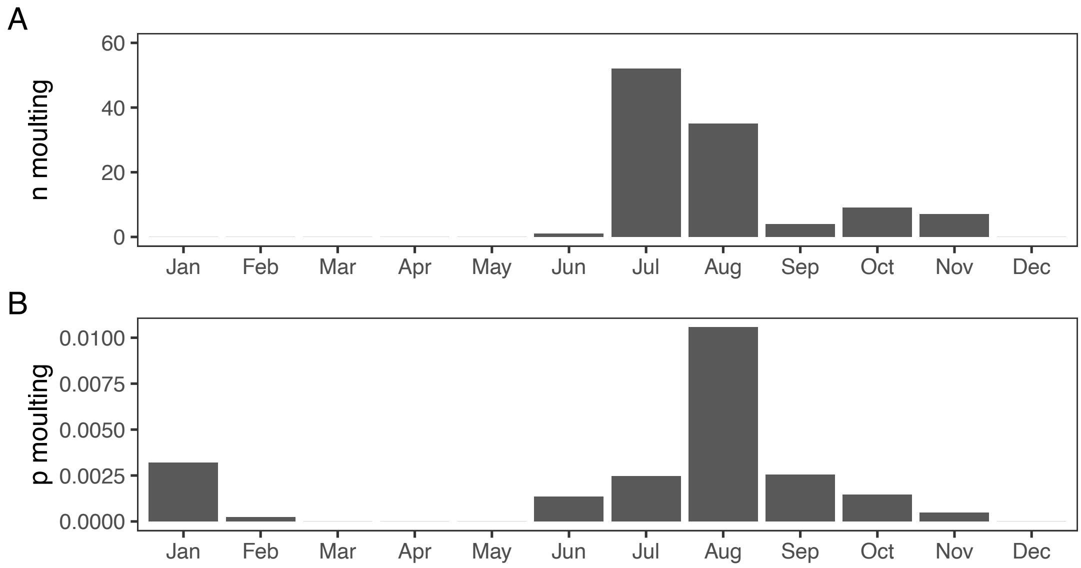

Figure 2: A. Absolute frequency of occurrences of primary moult and B. relative frequency relative to all sightings of Common Guillemots on the Dutch Continental Shelf.

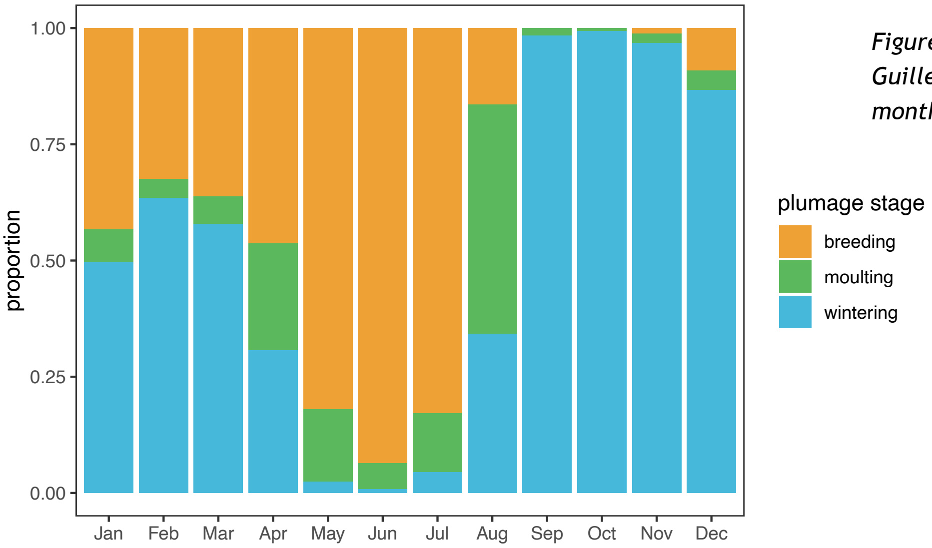

Figure 3: Proportion of Common Guillemots per plumage stage, per month.

likely age-related: adults of southern breeding populations already return to the (vicinity of) breeding ledges in mid-winter, whereas later moulting immatures do not or much later. Adults of arctic populations return to breeding ledges in February, thus well before the second step-change in April-May (Nettleship *et al.* 1985).

3.3.3 Chicks

Chicks were mostly noted in June-August, peaking in August (figure 4).

Among models of chick presence as a function of flock size and distance band, the model with both covariates but no interaction performed best (table 1). In particular flocks of two birds were most likely to contain chicks (representing a father with its chick). Single birds were unlikely to be chicks. Flocks larger than two were increasingly unlikely to contain chicks, although even numbers had slightly higher probabilities than nearby uneven numbers (figure 5A). Chicks were more likely to be detected close to the ship (figure 5B).

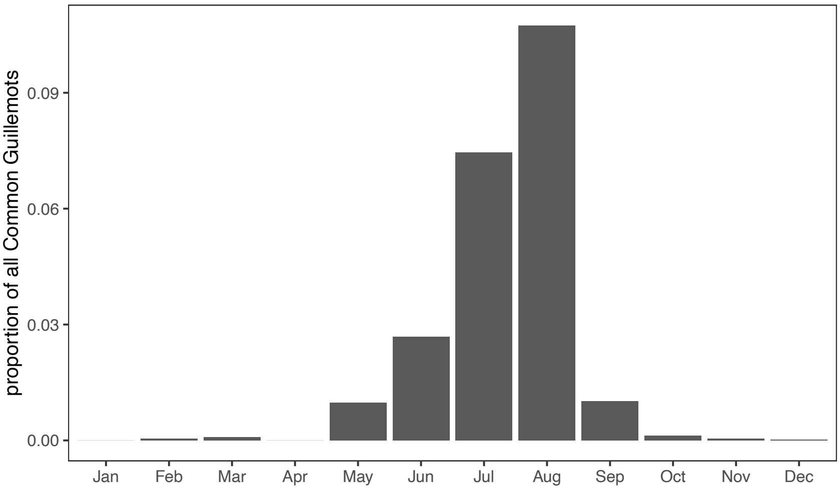

Figure 4: Proportion of Common Guillemots recorded as chicks of varying ages, per month.

model	Δelpd	SE diff
~ f_flock_size + dist_band	0.00	0.00
~ f_flock_size	-13.61	5.70
~ f_flock_size * dist_band	-21.78	8.86

Table 1: Comparison of models of the probability of the presence of chicks in Common Guillemot flocks.

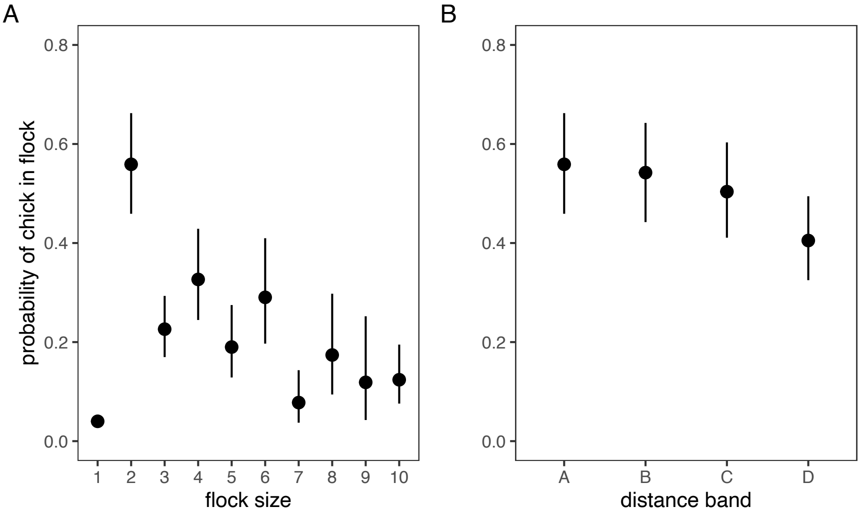

Figure 5: Conditional effects of a model with A. flock size (conditioned on distance band A) and B. distance band as covariate effects on the probability of the presence of chicks in a flock (conditioned on a flock size of 2 individuals). Distance bands are: A = 0-50 m, B = 50-100 m, C = 100-200 m, D = 200-300 m. Error bars are 95% credible intervals.

3.3.4 Large-scale distribution: aerial surveys

The distribution of guillemots in August varied between years, although the birds were generally limited in distribution to the northern half of the DCS (figure 6). In years with most northern transects surveyed early in August (2017, 2020 and 2021; supplement figure 9), birds were not distributed more to the west than in other years (figure 7). Particularly high concentrations were observed in 2015 and in 2018-2022 in an area between the Frisian Front and the Central Oystergrounds. Remarkably, guillemots were already observed well south of the 30m isobath in August 2020 and 2021.

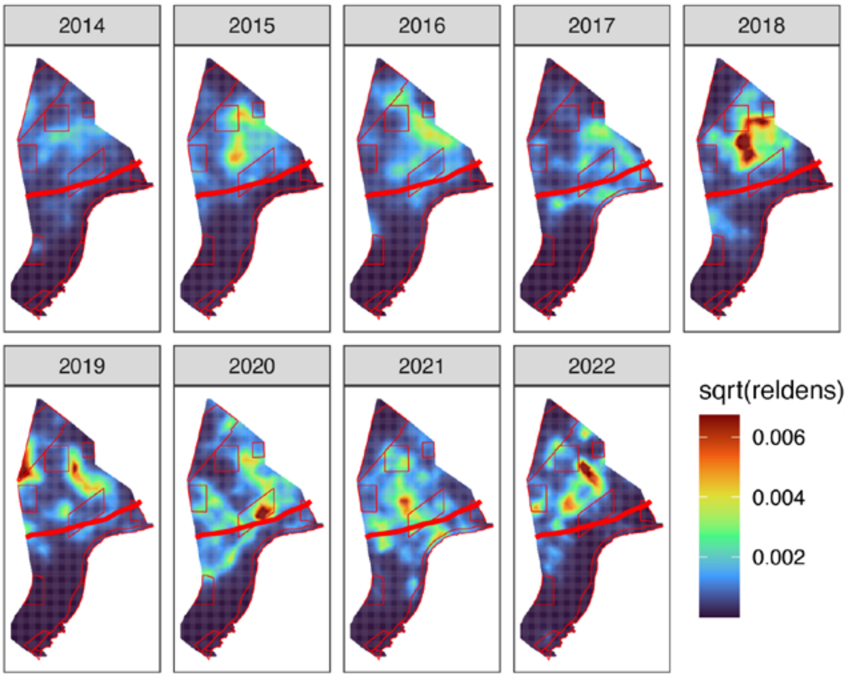

Figure 6: Survey-level maps of distribution of guillemots in August 2018-2023. The maps shows square-root transformed relative densities that have been capped at 100 birds/km2 to allow details in lower densities to be visible. Areas of conservation concern are bordered red. The thick red line is the (smoothed) 30m isobath.

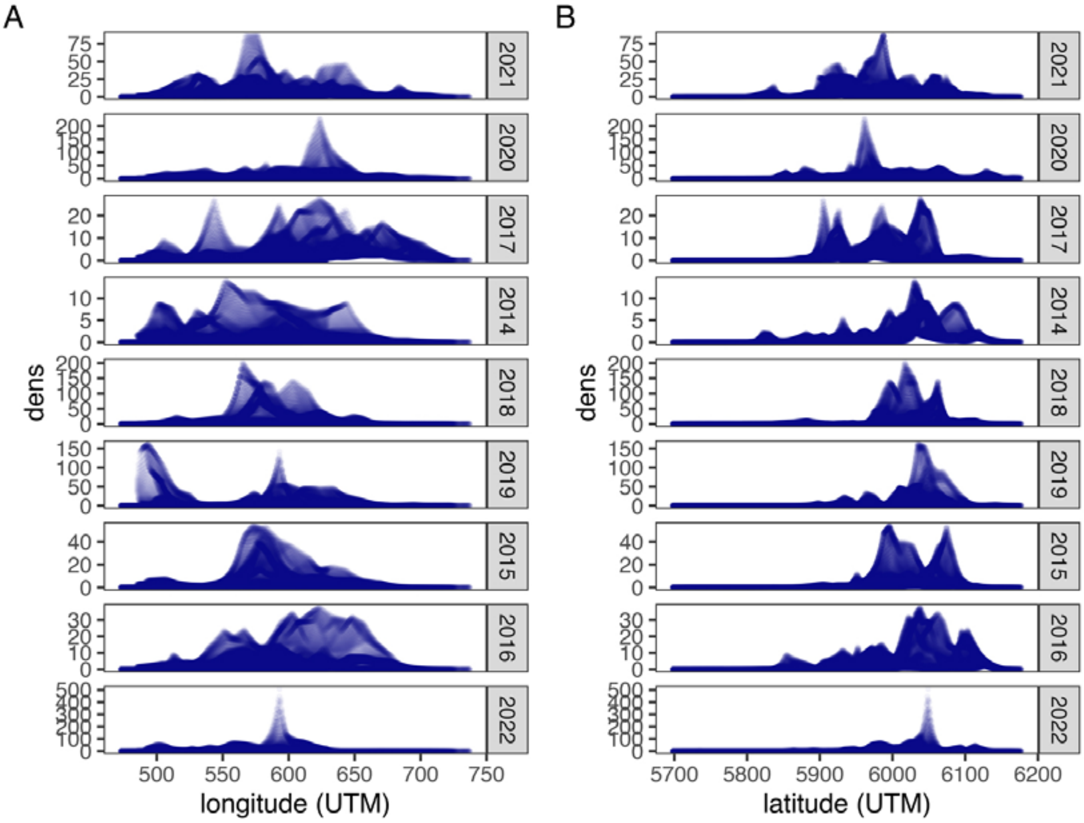

Figure 7: Modeled densities along A. longitude and B. latitude per survey. Years are ordered according to the median date at which northern transect were surveyed, with earlier surveys at the top.

The average distribution across years of guillemots in August shows higher densities between the Central Oystergrounds and the Frisian Front (figure 8A). This area is also highlighted when predicting the abundance of chicks based on flock size (figure 8B). Indeed, flocks of two birds, which have the highest probability of concerning father-chick pairs, were not particularly common relative to other flock sizes in any area (figure 8C).

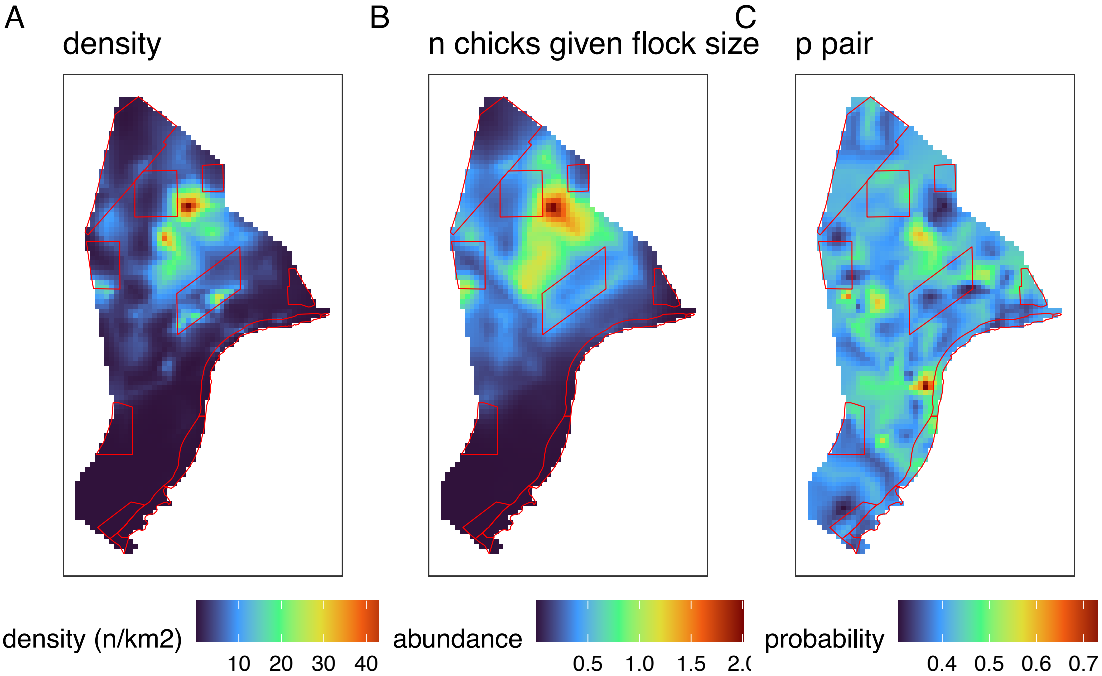

Figure 8: A. Average distribution (left) and uncertainty therein (right) of guillemots in August across 2014-2023. B. Distribution of the predicted abundance of chicks, based on flock sizes. C. Distribution of the probability of flocks of two relative to other flock sizes.

3.4 Discussion and conclusion

Common Guillemots moulted body feathers mainly in August and were chaperoning chicks mainly in July-August. Flock size was a useful predictor of whether a flock included chicks, with flocks of two birds having the highest probability of including a chick, based on observations close to the survey ship, where detection of chicks was highest. However, group size did not show substantial spatial variation, and therefore, no areas with higher probabilities of the presence of chicks were identified. Rather, our results suggest that areas with higher densities of guillemots in August will also hold more father-chick pairs.

Studying moult in seabirds is hampered by the difficulty of following individual birds at sea over prolonged periods. Hence, our knowledge of moult of guillemots is mostly based on studies of museum skins and beached birds, and is far from complete. We used moult in body feathers (the head and neck) as a proxy for the entire post-breeding moult, including the moult of primary feathers. However, the moult of different feather tracts does not run completely synchronous. The moult starts with the body feathers. Then, all primary feathers are shed in quick succession within 1-3 days. Only when the primary feathers are half-grown, after about two weeks, the moult of the secondaries and tail feathers starts (Cramp & Simmons 1983). Hence, the entire moulting period of an individual bird will take longer than the *ca.* four weeks in which the birds are flightless. On a local/regional population scale, the moulting period is even longer due to (unknown) individual variation. And finally, on the scale of the biogeographic population, the post-breeding moulting period is even longer as birds breeding further north start their moult later (it is unknown whether they moult at the same speed as southern birds) (Cramp & Simmons 1983). Hence, it is important to note that the period in which moulting guillemots occur in Dutch waters is probably longer than what is shown by moult of the head and neck feathers. It therefore likely not only encompasses August, but also late July and early September, if not longer. The same applies to the presence of fathers accompanying chicks: it is assumed that it can take up to two months before chicks become independent (Varoujean *et al.* 1979, Elliott & Gaston 2014).

The distribution of guillemots during aerial seabird surveys in August showed much variation between years. This distribution could not be convincingly linked to the timing of the surveys. Hence, no firm conclusions can be drawn as to how guillemots move through the (northern parts of) the Dutch sector of the North Sea. Performing a series of additional aerial surveys starting earlier in the season (July) and ending later in the season (September) within a single year, may shed light on this, as would extending the analysis to the entire North Sea instead of DCS only. Definitive information on movements can be obtained by tracking individual birds, which would require tag attachment methods suitable for diving birds and a tracking method with high spatial (error ideally < 1 km) and temporal (> 1 position per day) accuracy. For such a study to have a high chance of sampling birds that actually use the Dutch North Sea, birds need to be captured not in the colony (which would be easier) but ideally at sea, which is logistically and methodologically challenging but perhaps not impossible (O'Connor 2008, Heinänen *et al.* 2020, Camphuysen & Lieshout 2024).

Despite the variation between years in the distribution of guillemots in August, the area between the Central Oystergrounds and the Frisian Front held on average higher densities than elsewhere, which is reflected in the annual maps of most years (figure 6). However, the exact location of higher densities varied substantially between years within this large area.

In summary, during August, when guillemots escort their chicks into Dutch waters, no specific areas could be identified that were likely to host particularly high relative densities (proportions) of chicks. Rather, chicks likely occur anywhere where (moulting) guillemots occur in August; thus generally north of the 30m isobath. The area between the Central Oystergrounds and the Frisian Front held on average the highest densities of guillemots.

3.5 Acknowledgements

Thanks to all who helped in gathering the ESAS and MWTL survey data.

Supplement

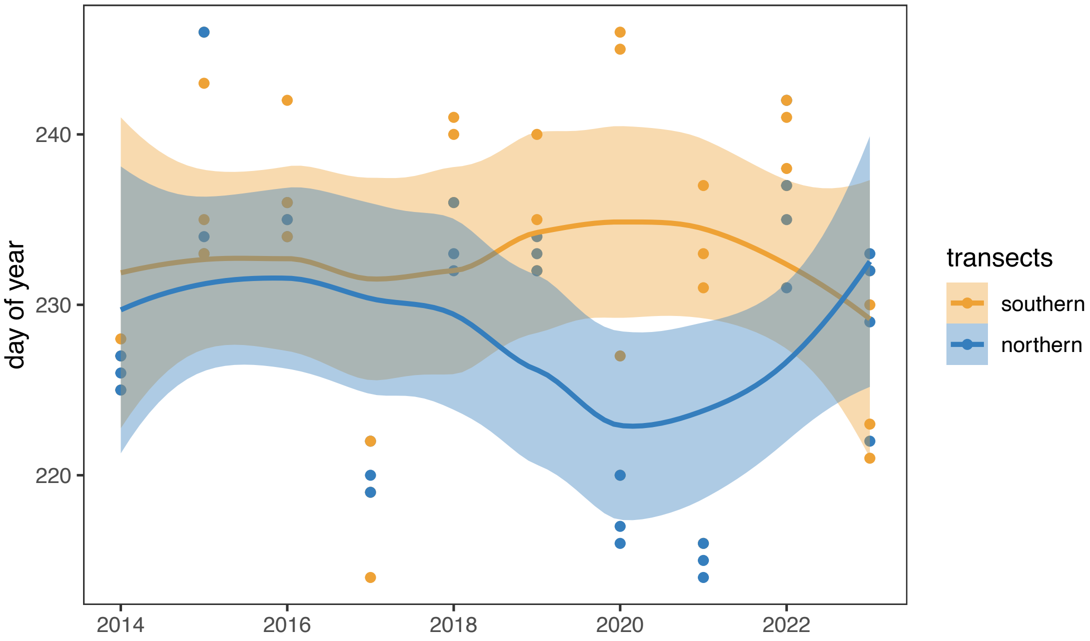

Figure 9: Dates per year show not temporal pattern for southern transects, but in some years (2017, 2020, 2021), northern transects were surveyed substantially earlier.

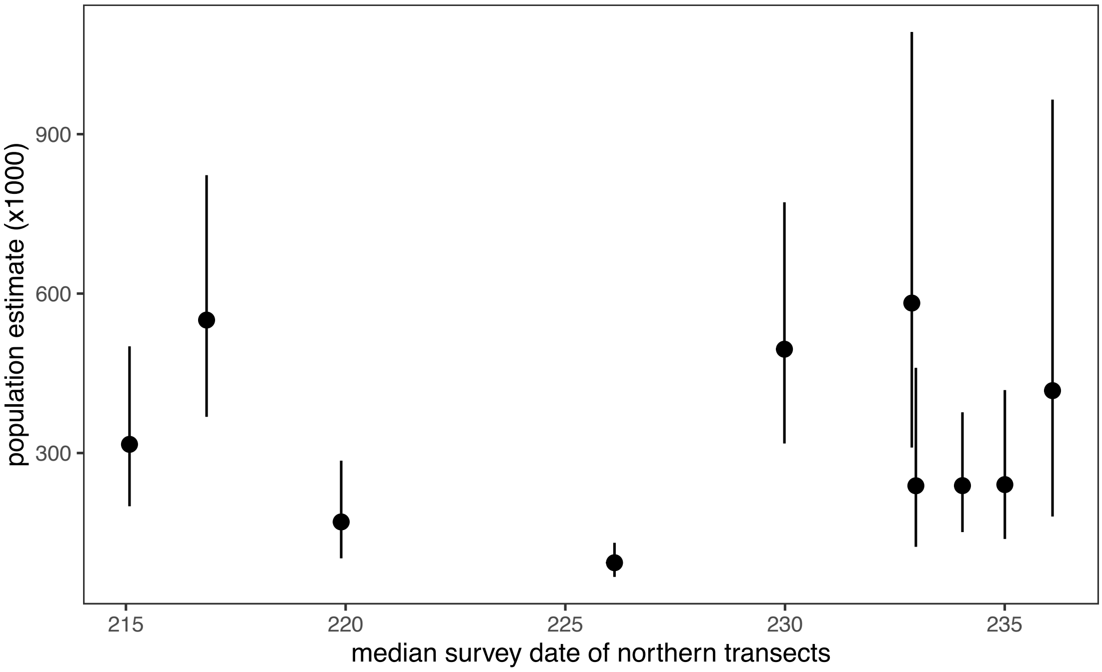

Figure 10: Population estimates as a function of median survey date of northern transects.

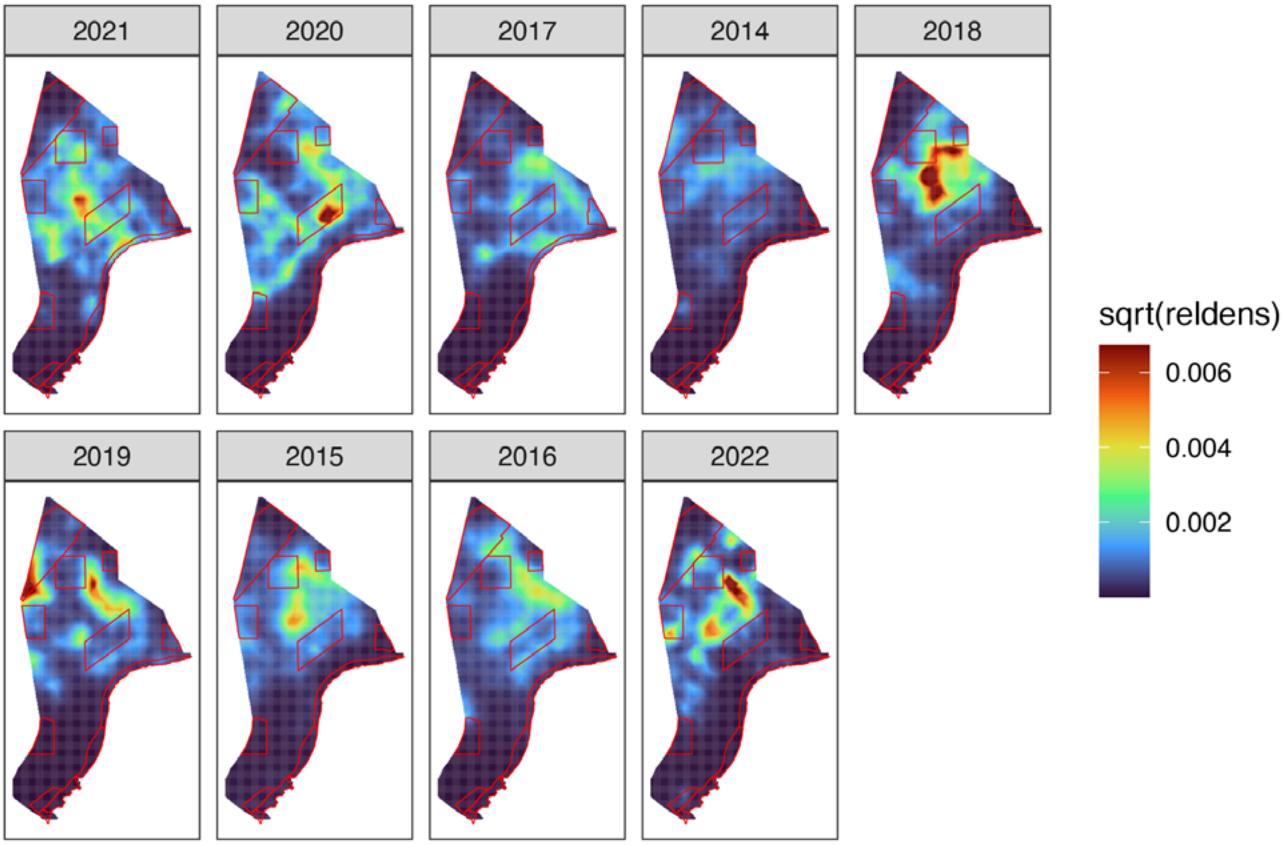

Figure 11: Same maps as in figure 7, ordered according to the median date of surveying the northern transects.

4. Distribution of Common Guillemots in late summer in the Dutch North sea: the effect of wind on clustering

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Samenvatting

Bij de ontdekking dat Zeekoeten in hoge dichtheden kunnen voorkomen op het Friese Front werd ook al duidelijk dat dit niet altijd het geval was. In sommige jaren bevonden concentraties zich elders, of waren de dichtheden meer uitgesmeerd. Gedacht werd dat dit mogelijk samenhield met wind: bij meer wind zou er een minder scherpe frontsituatie ontstaan. Met behulp van vliegtuigtellingen in augustus in 24 jaren hebben we deze hypothese onderzocht. Zowel de afstand van de locatie waar de hoogste dichtheden werden gezien, als de mate waarin deze dichtheden gepiekt of in ‘hotspots’ voorkwamen, liet geen duidelijke relatie zien met de gemiddelde windsnelheid op een centraal punt op de Noordzee, en het aantal uren met windsnelheden van 6 Bft of hoger, in de voorgaande week of twee weken. Hoewel in de meeste jaren substantiële aantallen Zeekoeten zich bevonden in het Natura 2000-gebied het Friese Front, concentreerden zich vaak nóg meer vogels ten noorden daarvan, tussen het Friese Front en de Centrale Oestergronden, een gebied dat gekenmerkt wordt door diep water en een hoog slibgehalte van de bodem. Toekomstig onderzoek om de verspreiding van Zeekoeten te begrijpen zou zich moeten richten op andere mogelijk sturende factoren. Ons begrip van hoe Zeekoeten de Nederlandse Noordzee gebruiken zou ook baat hebben bij zenderstudies, waarmee bijvoorbeeld het effect van stroming nauwkeurig onderzocht kan worden, alsook de snelheid van zwemmende Zeekoeten en hoe lang ze in een gebied blijven.

Abstract

Soon after the discovery that Common Guillemots can occur at very high densities at the Frisian Front in the Dutch sector of the North Sea, it became clear that this was not always the case. In some years, guillemots occurred much less concentrated or concentrations peaked at different spots. Wind in the period preceding the seabird surveys were hypothesized to dilute the front and thereby the guillemots. Here, we aim to test this hypothesis, using 24 years of aerial surveys in August. We related location and the peakedness of guillemot densities to the average wind and the number of hours with wind speeds at or above 6 bft over the last 7 or 14 days prior to surveys, but did not find support for relationships between these. In fact, higher concentrations of guillemots at the Frisian Front occurred in only a few of the years, with densities peaking usually further north, between the Frisian Front and the Central Oystergrounds. The annual variability of guillemots in the Dutch sector of the North Sea is substantial; future studies should focus on other, dynamic variables to explain the distribution of guillemots. Our understanding of the movements of guillemots in the Dutch North Sea would benefit from tracking studies, which can inform on the effect of currents as well as show how long guillemots stay in an area.

4.1 Introduction

Seabird distribution is often stable at larger scales but variable at smaller scales (Weimerskirch 2007). Understanding seabird distributions is important to delineate areas of high conservation value. Therefore, considerable effort has been spent in trying to understand the drivers of seabird distribution at varying spatial scales, with varying success. Mapping and understanding seabird distributions is challenging (but see e.g. Poot *et al.* 2004). Gathering distributional seabird data at relevant scales is often logistically complex and expensive. Distributions are likely to be primarily driven by food availability, but the non-breeding and/or adult diets of many seabirds are understudied and may be opportunistic. Finally, data on spatial-temporal distribution of prey abundance is usually lacking, again due to logistic difficulties, but also because many prey species are not commercially important and therefore receive scant attention in fishery research. To overcome the lack of direct measurements of prey availability for seabirds, proxies are often used in modeling seabird distributions. Such proxies often concern remotely sensed data, such as sea surface temperature and chlorophyll-a, which is often available at large scales and at regular temporal intervals. However, the link between seabird distribution and these proxies is often weak, potentially because of the small temporal time scales at which these factors may determine prey availability, and the predictive power of species distribution models for seabirds is therefore often low. For example, in a recent project on seabird distribution on the Dutch sector of the North Sea, spatial correlation terms in species distribution models explained a much larger part of the variation than the fixed effects (Donk *et al.* 2024).

With the aim of improving our understanding of seabird distributions, a potential next step would be to select specific, recurring patterns in seabird distributions and test specific hypotheses as to under which conditions these would occur. This may involve complex interactions between explanatory variables – something that is often not included in species distribution models of seabirds for various reasons, such as to avoid overfitting, to avoid overly complex models that are hard to interpret, or for computational reasons.

In this study, we aim to increase our understanding of a specific and annual phenomenon observed in the Dutch sector of the North Sea: the aggregation of large numbers of Common Guillemots *Uria aalge* (hereafter 'guillemots') in (late) summer in and around an area often referred to as the Frisian Front. Guillemots share a remarkable breeding strategy with other members of the Alcini subfamily in that chicks leave the colony at a young age while still being flightless and at a quarter of adult body mass (Merkel & Strøm 2023). At sea, they are usually accompanied by their father and swim actively to areas further offshore (Merkel & Strøm 2023), where predation pressure is likely less (Camphuysen 2002). At the same time, and thus in the same areas (Merkel & Strøm 2023), adults commence their complete post-breeding moult. As the species shows (near-)simultaneous moult of all flight feathers, the birds are temporarily flightless (Cramp & Simmons 1983) and thus depend entirely on swimming for travelling to and staying in profitable foraging areas. The period of moulting and before chicks become independent are thought to last 1-2 months (Varoujean *et al.* 1979, Elliott & Gaston 2014). Given the energetic demands of chick-rearing and moulting and the complete dependence on swimming for locomotion, guillemots that are moulting and/or chick-rearing are particularly vulnerable to disturbances or poor foraging conditions, as they are unable to fly and therefore unable to cover large distances efficiently to find areas with better conditions. Hence, a better understanding of their distribution and subsequent assignment of marine protected areas is important for the conservation of this species.

In the Dutch sector of the North Sea, guillemots are one of the most abundant seabirds from late summer to early spring. Guillemots arrive in Dutch waters during the summer, many of which are males joined by their chicks. In late summer, guillemots generally occur in largest numbers north of the 30m isobath. Part of this area is assigned as a Natura2000 area and called the Frisian Front because of the high numbers of guillemots (Lindeboom *et al.* 2005). The same name is also used for a 'bottom front', an area with higher silt concentrations in bottom sediments as well as a tidal front between well-mixed southern waters and summer-stratified deeper waters (Baars *et al.* 1991). Here, we use the name Frisian Front for the bottom front, unless otherwise stated. This high silt concentration results from deposition of dissolved sediment following a slowdown of the water currents at greater depths compared to areas to the south (Baars *et al.* 1991). In summer, tidal movements cause resuspension of nutrients from bottom sediments, which subsequently lead to increased primary productivity in higher water layers. Presumably, the increased primary productivity then feeds into higher trophic levels, which eventually attract piscivorous taxa, including seabirds such as guillemots (Leopold 1991).

However, the extent and location of the area of higher productivity may change depending on several factors. Sedimentation processes in winter and spring may show annual changes that may carry-over to the primary productivity in summer (Baars *et al.* 1991). High winds may lead to resuspension (in addition the resuspension caused by the movement of the tidal movements) and the dilution of nutrients and plankton. The effect of wind on the distribution of primary productivity could subsequently affect fish and seabird distributions. Thus, the area with high primary productivity is expected to be broad after periods with strong winds, and narrower after weak winds; guillemot distributions are expected to reflect this, with more peaked densities around the front after periods with weak winds.

Here, we first assess the summer distribution of guillemots on the Dutch continental shelf, using aerial survey data collected over more a period of 24 years. Subsequently, we study whether wind affects the degree to which guillemots show a narrow or, conversely, a broad distribution around the 30-40 m isobaths during late summer.

4.2 Methods

4.2.1 Aerial surveys

Aerial surveys were carried out over the North Sea during 1991-2024. During 1991-2014, surveys were carried out using a twin-engine Partenavia 68 flying at a height of 500 ft (*c.* 150 m asl) (Arts 2013). Birds were counted in a strip of about 100 m wide. The methodology has seen a substantial revision in 2014. From then, the survey design was intensified, with 19 transect lines running northwest-southeast, thus more or less perpendicular to the coast. In addition, flight height was decreased to 250 ft (*c.* 75 m asl), bubble windows were installed to allow viewing underneath the plane, and the distance sampling technique was introduced to account for imperfect detection of birds further from the transect line (Buckland *et al.* 1993). Data up to and including august 2022 were used. Surveys were carried out in August, November, January, February, April and June. For this study, the data from the August surveys were selected. No data was available for one year: 2013. For more details regarding the method, see Bemmelen *et al.* (2023).

Before the decrease of flying height in 2014, Common Guillemots and Razorbills *Alca torda* could not be identified to species level. Based on data from ship-based surveys, when alcids can be accurately identified to species level, Razorbills are exceedingly rare in August in Dutch waters. Therefore, we assume that large alcids seen during the August surveys concern Common Guillemots.

4.2.2 Wind data

Wind data was obtained from the NCEP/NCAR `reanalysis2` project (Kalnay *et al.* 2018) and downloaded using the RNCEP package in R (Kemp *et al.* 2012) for a pressure of 1000 hPa, which corresponds approximately to surface level. The data was downloaded for a central location in the Dutch sector of the North Sea, at 4°E 54°N. Data was downloaded for hourly intervals from 14 days ahead of each survey date to each survey date. This data comes as two vectors, in west-east and north-south direction, from which wind speed (in m s^{-1}) and wind direction (in degrees) were calculated. Then, wind speeds were summarized per observation day as follows: 1) the mean wind speed over the previous 7 days, 2) the mean wind speed over the previous 14 days, 3) the number of hours with wind speeds over 6 bft in the previous 7 days and 4) the number of hours with wind speeds over 6 bft in the previous 14 days.

4.2.3 Distance analysis

Up to 2014, it was assumed that all birds within a certain distance from the transect line were detected. In this case, the strip was set at *ca.* 100m wide. Its exact width was observer-specific and depended on the observers' length and the position of the eyes relative to the aircrafts' windows. However, detection rates often decline with distance from the transect line. To correct for this imperfect detection, distance sampling was introduced since 2014. Each sighting was assigned to a distance band, which allowed to estimate detection curves using the `mrds` package in R (Laake *et al.* 2024).

4.2.4 Statistical analysis

To show the spatial-temporal distribution of guillemots on the Dutch continental shelf, we selected all surveys in August and modelled the distribution using the `sdmTMB` package (Anderson *et al.* 2022). To show annual variation in distribution, we fitted models with a spatial random field (SPDE) for each survey. To show the average distribution, single models were fitted to the data from 1991-2013 and the data from 2014-2022.

In addition, raw counts and the effectively surveyed area (number of sides of the plane counted x transect length x effective strip width) were aggregated to a grid of hexagon cells with a diameter of 20 km. This was used as a basis for analysing the effect of wind on guillemot distribution. The 30 m isobath was simplified to a smooth line running across the width of the DSC. Then, the distance from the 30 m isobath to the center of each grid cell was calculated. Finally, the distribution of guillemots was summarized at the level of surveys as 1) the distance from the 30 m isobath where densities peaked and 2) the 90% quantile of the densities per grid cell, as a measure of peakedness and 3) the Getis-Ord statistic, as a measure of the occurrence of 'hotspots' – clustered areas with higher than average densities. These values were then plotted against the four measures of wind conditions outlined above and modeled as simple gaussian GLMs.

All analyses were performed in R version 4.4.2 (R Core Team 2023).

4.3 Results

The annual distributions of guillemots in August are shown for 1991-2013 in figure 1 and for 2014-2022 in figure 2.

In only a few years, the distribution of guillemots extends southwards to the 30 m isobath. In only 2007, 2020 and 2021, the distribution of guillemots peaks within the Frisian Front Natura 2000 area and thus at the sediment front. Other years with elevated distributions of guillemots close to the 30 m isobath, but west of the sediment front/N2000 area, are 2005 and 2010. In other years, elevated densities occurred farther north; often between the Frisian Front N2000 area and the Central Oystergrounds - for both 1991-2013 and 2014-2022 (figure 3).

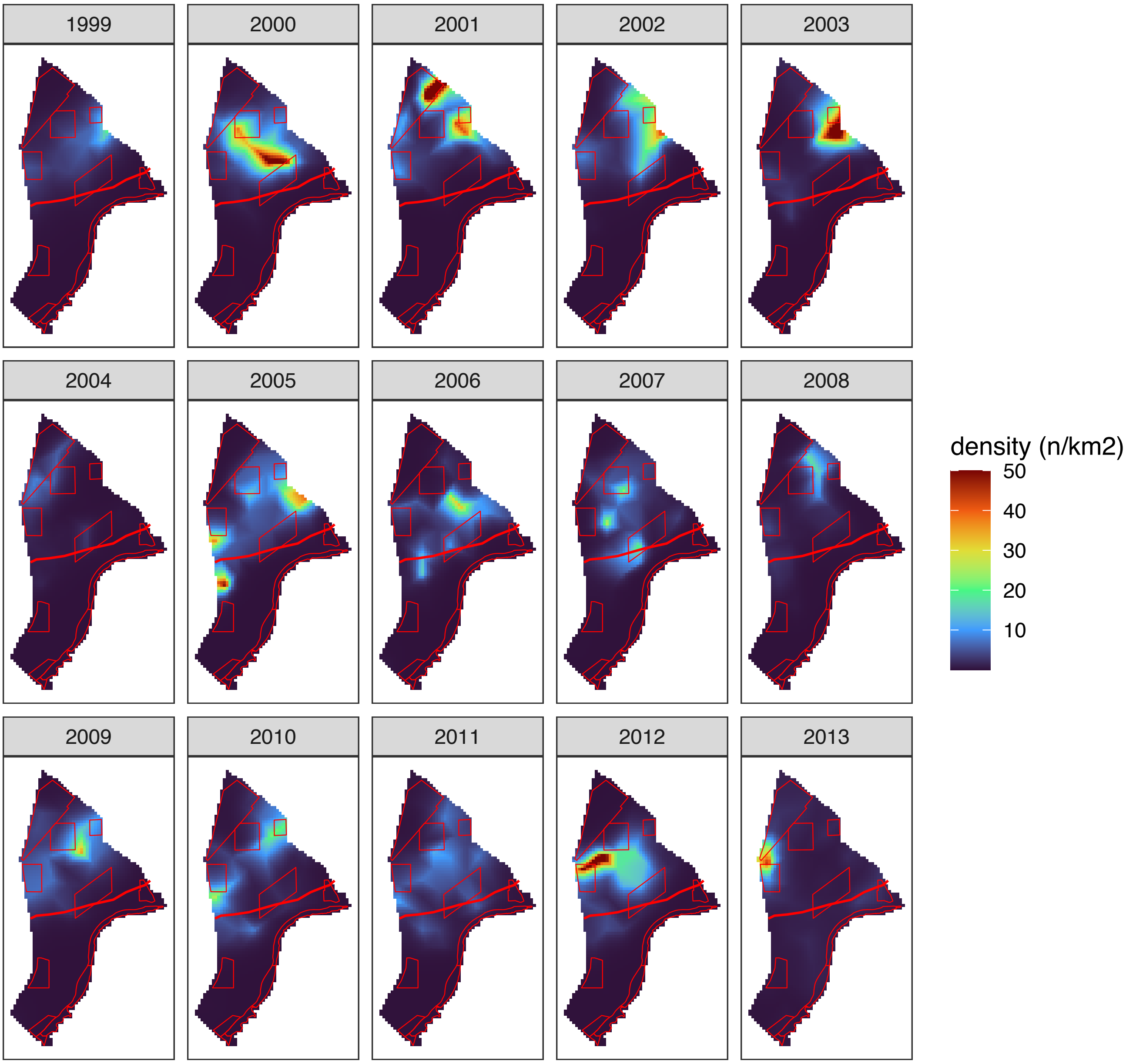


Figure 1: Predicted densities per year for August surveys in 1999-2013. The thick red line running from west to east is the simplified 30 m isobath. Red outlined polygons show Natura 2000 areas or other areas of ecological value.

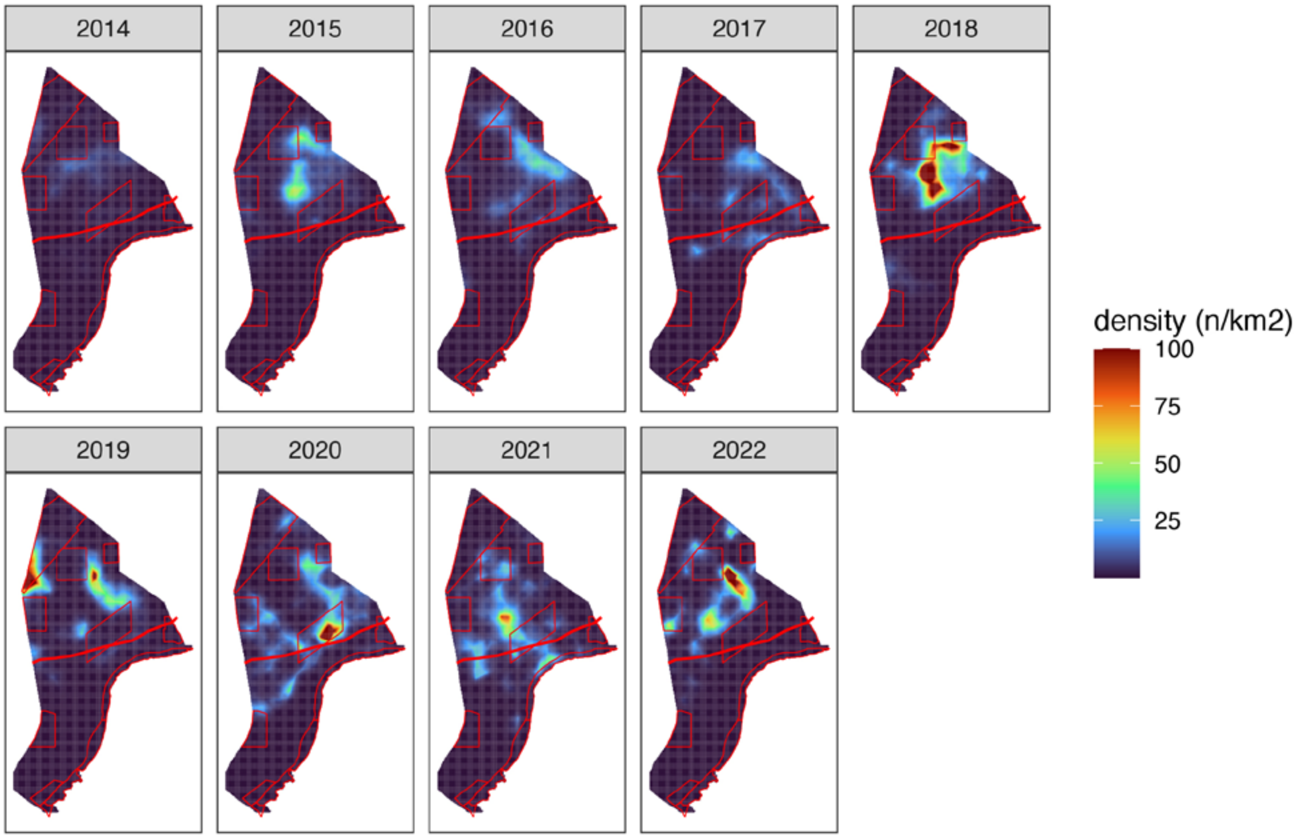
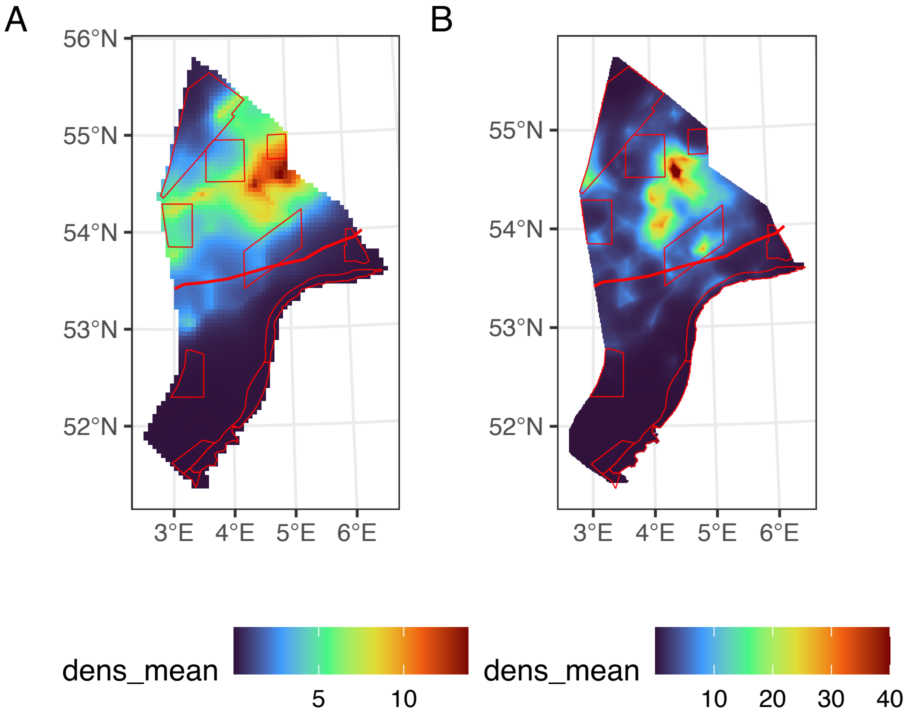


Figure 2: Predicted densities per year for August surveys in 2014-2022. The thick red line running from west to east is the simplified 30 m isobath. Red outlined polygons show N2000 areas or other areas of ecological value.



re 3: Mean densities of Common
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014-2022. The thick red line run-
from west to east is the sim-
ed 30 m isobath. Red outlined
gons show N2000 areas or other
s of ecological value. Note the
erent bird density scales of the
figures! In B., densities are
ed at 40 birds/km2 to allow
er visibility of the patterns.

4.3.1 Effect of wind on guillemot distribution

No relationship was found between the mean wind speed over the previous 7 or 14 days and the distance from the 30 m isobath where guillemot densities peaked. The same applied to the number of hours with wind speeds above 6 bft (figure 4, table 1).

No relationship was found between the mean wind speed over the previous 7 or 14 days and the 90% quantile of guillemot densities. The same applied to the number of hours with wind speeds above 6 bft (figure 5, table 1).

No relationship was found between the mean wind speed over the previous 7 or 14 days and the Getis-Ord statistic of guillemot densities. The same applied to the number of hours with wind speeds above 6 bft (figure 5, table 1).

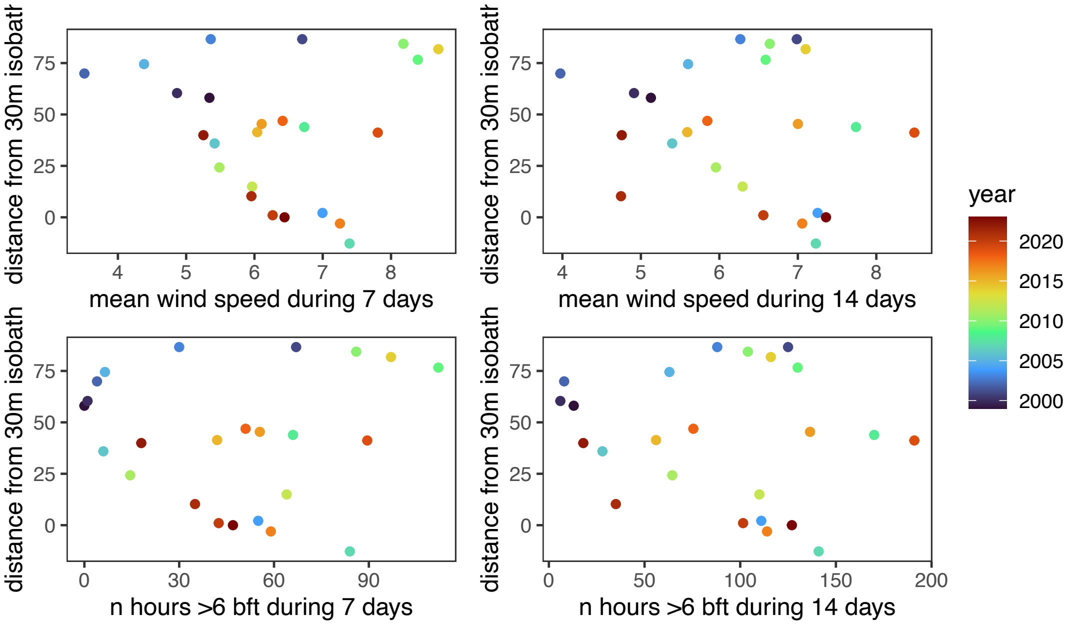

Figure 4: The distance to the 30 m isobath where guillemot densities peaked versus the mean wind speed over the 7 days (left) or 14 days (right) prior to the survey (upper panels) or the number of hours that winds exceeded 6 bft over the last 7 days (left) or 14 days (right) (lower panels). Negative distances from the 30 m isobath indicate positions south of the 30 m isobath. One dot represents one August survey.

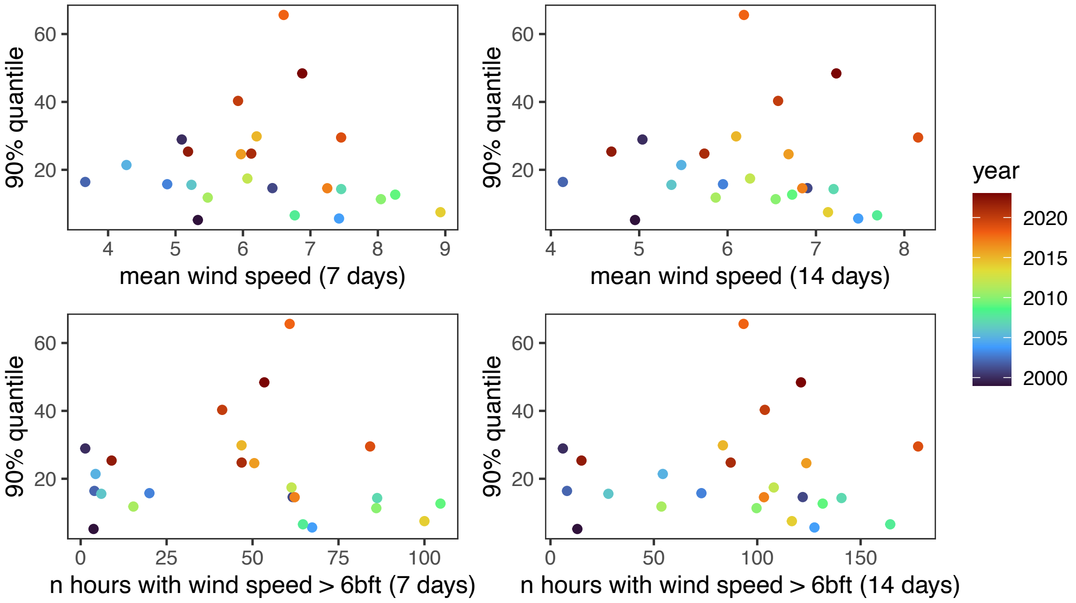

Figure 5: The 90% quantile (as a measure of spread of values) of the density of guillemots per 20 km hexagon grid cell as a function of mean wind speed (upper panels) or the number of hours with wind speeds above 6 bft (lower panels) over the previous 7 days (left panels) or 14 days (right panels). One dot represents the mean for an August survey.

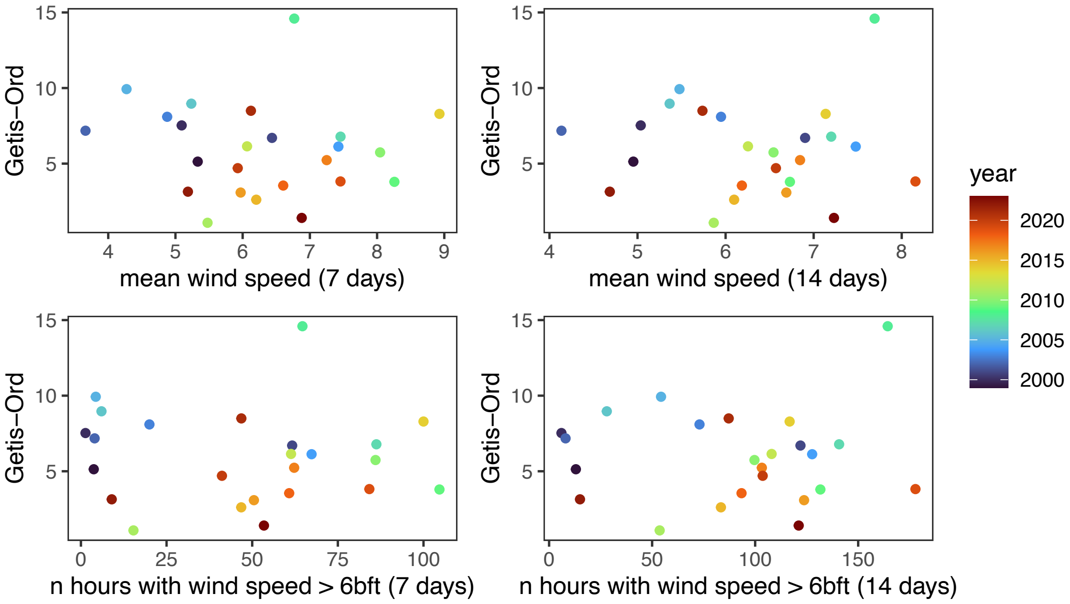

Figure 6: Getis-Ord statistics for August surveys as a function of mean wind speed (upper panels) or the number of hours with wind speeds above 6 bft (lower panels) over the previous 7 days (left panels) or 14 days (right panels). One dot represents the mean for an August survey.

response	wind	Estimate	l-95% CI	u-95% CI
distance max dens	mean 7d	-1.39	-11.80	9.64
distance max dens	mean 14d	-5.91	-18.83	7.04
distance max dens	sum 7d	0.01	-0.42	0.42
distance max dens	sum 14d	-0.09	-0.36	0.18
90% quantile	mean 7d	-0.40	-2.40	1.59
90% quantile	mean 14d	-0.12	-2.74	2.51
90% quantile	sum 7d	-0.01	-0.09	0.07
90% quantile	sum 14d	0.00	-0.05	0.06
Getis-Ord	mean 7d	-0.26	-1.28	0.78
Getis-Ord	mean 14d	0.00	-1.33	1.35
Getis-Ord	sum 7d	-0.01	-0.05	0.04
Getis-Ord	sum 14d	0.00	-0.03	0.03

Table 1: Slope estimates of the relationships between wind and 1) the distance from the 30m isobath where highest guillemot densities occurred, 2) the 90% quantile and 3) Getis-Ord statistic as shown in the figures above. Zero was within the 95% Credible Intervals of all slopes and can therefore not be excluded.

4.4 Discussion

The distribution of Common Guillemots on the Dutch continental shelf has been analysed in several earlier studies (e.g., Leopold 1991, Camphuysen & Leopold 1994, Poot *et al.* 2010, Bemmelen *et al.* 2013). Based on ship-based surveys in 1987-1990, Leopold (1991) described the elevated abundances of seabirds and marine mammals at the Frisian Front, compared to transects north and south of it. Since then, a few ship-based surveys specifically targeted the Frisian Front Natura 2000 area at different times of the year (Bemmelen *et al.* 2013, Baptist *et al.* 2019, Geelhoed *et al.* 2019, Poot *et al.* 2024) and with no additional survey effort in surrounding waters. Aerial surveys were started in the late 1980s and continue until present. Until 2014, however, these MWTL survey transects had a rather poor coverage of the Frisian Front area (Poot *et al.* 2010). Hence, only since the current MWTL aerial survey program has started in 2014, seabird distribution data has been collected at the scale of the entire North Sea, with good coverage of the Frisian Front as well as the surrounding areas.

The aerial survey data from before 2013 already shows that higher densities of guillemots at the Frisian Front do occasionally occur in August (see also Poot *et al.* 2010). The aerial surveys since 2014 confirm this with greater accuracy: only in a few years, peak densities occurred at or close to the Frisian Front (bottom front). In most years, however, the core of the distribution was positioned more to the north, in between the Frisian Front Natura 2000 area and the Central Oystergrounds, an area characterized by deep water and high slib content. These findings thus contrast with a strongly peaked occurrence of guillemots at the front, as described by Leopold (1991) and Poot *et al.* 2024. However, Leopold (1991) already recognized the annual fluctuations in where and how concentrated guillemots occurred. The years in 1987-1990 with strongly peaked occurrence, as well the few years for which aerial survey data indicates this, may have been exceptional, or conditions have changed since then.
In any case, the absence of a regular occurrence of high densities of guillemots in August at the Frisian Front sediment front likely explains why we were unable to find relationships between wind variables and the location and peakedness of elevated concentrations of guillemots relative to the 30 m isobath.

In 2014-2023, Guillemot abundance usually peaked at the Dutch continental shelf in August - instead of autumn as has been reported in previous studies (Camphuysen & Leopold 1994). Part of the decline in numbers from August to November may be explained by mortality (e.g. of chicks that have recently become independent), but it seems more likely that many guillemots leave Dutch waters in September.

In the absence of tracking data, it will remain an open question how guillemots move through Dutch waters and how movement may explain the observed spatial patterns. For example, to what degree are they transported by currents? At what speeds do they travel, how long do individuals stay within a certain area and what does that mean for the cumulative number of individuals using a specific area? Answers to these questions will have important implications for how they (can) respond to disturbances such as offshore wind farms.

Here, we studied wind effects within time frames of one or two weeks. Possibly, wind conditions across shorter time frames may influence guillemot patterns. This could be studied in future projects. Ideally, this analysis would have included data on prey fish distribution as well as to what degree these fish are available to the guillemots. For example, turbidity may affect the efficiency with which guillemots can catch fish. Additional potential drivers of the distribution of guillemots are discussed in chapter 6 in this report.

5. Co-occurrence of Black-legged Kittiwakes and alcids in the Dutch North Sea: dependency on feeding associations as a driver of seabird distribution

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Samenvatting

Zeevogels die niet diep kunnen duiken zijn voor hun voedselvoorziening afhankelijk van processen die voedsel in de bovenste waterlagen brengen. Een belangrijk voorbeeld daarvan zijn diepduikende zeevogels of zeezoogdieren, die pelagische vis opdrijven naar het wateroppervlak, waar deze vervolgens beschikbaar komen voor zeevogels die niet diep kunnen duiken. Zulke associaties tussen soorten kunnen belangrijk zijn voor de verspreiding en abundantie van zeevogels die aan het wateroppervlak eten zoeken, maar dat is nog maar weinig onderzocht.

In deze studie hebben we een zeer algemene associatie tussen soorten onderzocht: die tussen de aan het wateroppervlak foeragerende Drieteenmeeuwen *Rissa tridactly* en de twee diepduikende alk-achtigen, de Alk *Alca torda* en de Zeekoet *Uria aalge*. Met behulp van waarnemingen vanaf schepen laten we zien dat Drieteenmeeuwen een sterke voorkeur hebben voor Alken boven Zeekoeten. Dat is te begrijpen door het verschil in winterdieet: Alken eten meer vis die hoog in de waterkolom voorkomt, terwijl Zeekoeten daarnaast ook veel vissen eten die dicht bij de bodem leven. Andersom kan de mate waarin de twee alk-achtigen bezocht worden door Drieteenmeeuwen ook inzicht geven in hun dieet. We laten zien dat de mate van associatie het hoogste is in februari-april: blijkbaar eten zowel Alken als Zeekoeten dan meer pelagische vis.

Vervolgens gebruikten we vliegtuigtellingen om te onderzoeken in hoeverre de verspreiding van Drieteenmeeuwen overlap laat zien met Alken en Zeekoeten. De verspreiding van Drieteenmeeuwen bleek meer overlap te laten zien met beide alk-achtigen dan verwacht zou worden wanneer ze zich onafhankelijk van elkaar zouden verspreiding over de Nederlandse Noordzee. In februari en april was de gelijkenis met de verspreiding van Alk nét iets sterker dan met die van Zeekoet. Deze bevindingen suggereren dat gebieden die belangrijk zijn voor de ene soort, ook belangrijk zullen zijn voor de andere soort (in ieder geval binnen deze drie soorten). Het beschermen van een gebied kan dus voor meerdere soorten belangrijk zijn.

Abstract

Surface-feeding seabirds often rely for foraging on marine predators that drive prey to the surface, such as other seabird species, predatory fish or marine mammals. As the resulting multispecies feeding associations (MSFAs) mostly involve pelagic fish prey species, their relative frequency can signal the importance of pelagic fish in the diet of MSFAs producers. Morever, whether MSFAs are also driving distributions of surface-feeding species has been little studied. Here, we study feeding associations of Black-legged Kittiwakes *Rissa tridactyla* with foraging Common Guillemots *Uria aalge* and/or Razorbills *Alca torda* in the Dutch sector of the North Sea, using data from ship-based and aerial seabird surveys. Using ship-based survey data, we first show that although kittiwakes associate with both alcid species, especially with larger alcid flock sizes, they strongly prefer razorbills. Alcids were especially likely to be joined by kittiwakes in spring. These findings are in line with diet studies reporting a greater reliance on pelagic prey in razorbills than in guillemots, suggesting that this difference can be generalized across the non-breeding period, and that both alcids increase their reliance on pelagic prey in spring. The overall daily percentage of kittiwakes associating with alcids was on average 10%, but this increased substantially when more razorbills or fewer kittiwakes were present. Next, we used aerial survey data to study the overlap in distributions at large scales. We found that kittiwakes were more likely to be present along 5-km transect segments when alcids were present, and that this affinity of kittiwakes with alcids was stronger in February and April compared to other survey months, and slightly stronger with razorbills than guillemots. The spatial affinity between kittiwakes and the two alcids indicates that assignment of marine protected areas for a single species is likely to be beneficial to other species as well.

5.1 Introduction

In the marine environment, foraging opportunities for predators, such as seabirds, may be short-lived and/or occur at low densities, requiring specialized behaviour to find and exploit them. Surface-feeding seabirds that are unable to dive deeper than about ~1 m rely on processes that bring prey, that would otherwise be unavailable to them, to the surface. Such processes can be anthropogenic, for instance by fisheries discarding, or natural, for example by ceteceans and pursuit-diving seabirds. In the latter case, deep-diving predators that drive prey to the surface make these available to a range of other marine species. Occasions when several seabirds and/or cetaceans jointly exploit a foraging resource, with each species fulfilling a specific role, have been referred to as a multi-species feeding associations (MSFAs) (Camphuysen and Webb 1999).

In the North Sea, particularly common examples of MSFAs are formed when surface-feeding Black-legged Kittiwakes *Rissa tridactyla* (hereafter: kittiwakes) associate with foraging Common Guillemots *Uria aalge* (hereafter 'guillemot') and/or Razorbills *Alca torda* (hereafter 'razorbill') (Camphuysen & Webb 1999). These two closely related alcid species forage by pursuit-diving and usually act as initiators or producers in MSFAs by driving prey up to the surface, where it becomes available for kittiwakes. Kittiwakes are often the first to discover the feeding opportunity created by the alcids, and profit by catching prey by dipping or shallow plunging (two out of eleven seabird feeding modes, as described first by by Ashmole (1971) and later modified by Ainley (1977) and Ainley *et al.* (1984)). Kittiwakes often act as 'catalysts' of (these) MSFAs, attracting other seabird species seeking to further exploit the prey resource (Camphuysen and Webb 1999).

Pursuit-diving predators, the 'producers' of MSFAs, may try to drive fish towards either the sea bottom or the water surface, thereby excluding one direction prey can escape to. While demersal fish are thus expected to be hunted towards the bottom, pelagic fish will be driven towards the water surface, where it becomes available to surface-feeding predators. Indeed, predominantly small pelagic fish species, as opposed to demersal fish species, are involved as prey in MSFAs (Camphuysen and Webb 1999). We propose that therefore, MSFAs can be used to signal the diet of the producers of MSFAs (Gostischa *et al.* 2021), which would be particularly useful during the non-breeding period, when unbiased diet data for pelagic seabirds is usually difficult to obtain. For guillemots and razorbills, several studies have reported on species-specific diet in parts of the North Sea (Blake *et al.* 1985, Lilliendahl 2009), but few comparative diet studies have been carried out in the southern North Sea. These studies showed a clear difference in the non-breeding diet of the two alcids, with razorbills almost exclusively foraging on pelagic fish of small sizes and guillemots on larger fish of a broader spectrum of species, including gadoids (Blake 1984, Ouwehand *et al.* 2004, Depooter 2010).

The dependence of seabirds on (drivers of) MSFAs in shaping their diet and distribution, are poorly studied, as it requires a multitude of data of small-scale at-sea behaviour and large-scale distribution. If surface-feeding seabirds rely heavily on specific MSFAs for foraging, the frequency and distribution of species that act as drivers of MSFAs, and their diet, will ultimately determine the diet and distribution of the surface-feeding species. Species interactions are also important to consider when identifying species and areas of high conservation value (Veit and Harrison 2017). In our case, conservation of areas important to alcids may benefit kittiwakes as well – depending on the degree of dependence of kittiwakes on alcids. To assess whether this would be the case, it is important to quantify to what extent the distribution of kittiwakes and the two alcid species are linked, and which areas are therefore or primary concern for the species involved.

Here, we studied the occurrence of MSFAs of kittiwakes joining guillemots and/or razorbills in the Dutch sector of the North Sea, a non-breeding dispersal area, at considerable distance from the nearest breeding colonies of guillemots and razorbills. Considering the difference in diet in the non-breeding season between the two alcids, and that alcids feeding demersally are unlikely to bring fish to surface, we expect kittiwakes to associate more often with razorbills than with guillemots. We also study whether kittiwakes associate more often with alcids during specific times of the year - which could indicate temporal shifts in diet of the alcids. Finally, we ask whether the tendency to associate with the two alcid species is reflected in the distribution of kittiwakes. For the study of small-scale feeding associations, we used observations collected during ship-based surveys. To study large-scale co-occurrence of kittiwakes and the two alcid species, we used aerial seabird surveys that cover the Dutch sector of the North Sea within usually 5-7 days.

5.2 Methods

5.2.1 Small-scale species foraging associations: ship-based surveys

To study the small-scale behaviour of kittiwakes associating with guillemot and razorbills we used data from ship-based surveys of seabirds, stored in the European Seabirds At-Sea database (ESAS), carried out in the

Dutch sector of the North Sea between 1997 and 2021 using standardized protocols for strip-transect counts (Tasker *et al.* 1987) and for behavioural classification (Camphuysen and Garthe 2004). Given the much lower speed of ships compared to aircrafts, ship-based surveys allow much more time to observe and accurately note behaviour.

We selected all sightings of (flocks of) guillemots and razorbills, including mixed flocks, and recorded the group size, and whether and how many kittiwakes associated with that bird or flock. We also checked whether and what other species were associated with that bird or flock; we removed the small number of occasions where also marine mammals were involved, considering that in these cases, the mammals could be the drivers of prey instead of the alcids.

We first studied the preference of kittiwakes to associate with razorbills versus guillemots, where we regarded the process of kittiwakes associating with alcids as a bernoulli process, where kittiwakes may be observed associating (coded as 1) or not (coded as 0) depending on alcid species (guillemot, razorbill, or mixed), alcid flock size and kittiwake flock size. We hypothesize that the association of kittiwakes with alcids signals that the alcids were feeding on pelagic but not demersal fish, and that assocations therefore may reflect alcid diet. To study whether association rate and therefore presumably diet varies seasonally, we also included season in the models as a four-level factor (sample size was too low for razorbill and mixed flocks to allow monthly estimates), where the time-frame November to January are considered as winter; February to April as spring, May to July as summer and August to October as autumn. We then built a Bayesian Generalized Linear Mixed-effect Model (GLMM) with these fixed effects: alcid species, the log of alcid flock size, the log of kittiwake flock size, season and the interactions between alcid species and the log of alcid flock size and between season and species. Random intercepts were included for each combination of ship and date.

To study what proportion of the observed kittiwakes associated with alcids, we summed, per ship and date, the number of kittiwake flocks associating with alcids, the observed number of razorbills, guillemots and kittiwakes flocks, the proportion of guillemot flocks in the total number of alcid flocks identified to species level (where values < 0.5 thus indicate more razorbill flocks than guillemot flocks). We then modeled the number of kittiwake flocks associating with alcids ('successes') and the number of kittiwake flocks ('trials') as a function of the Log_{10} of the number of kittiwake flocks, Log_{10} of the number of alcid flocks, the proportion of guillemots and the interaction between number of alcid flocks and the proportion of guillemots. The reason for using a binomial instead of a bernoulli model as in the analysis of preference, is the difference at which we evaluate covariates: at observation-levels in the model of preference but at a daily level in the model of daily association rates.

All above models were fit using the brms package, version 2.22.0 (Bürkner 2017). The brms packages provides an interface with Stan (Team 2024). Default uninformative priors were used. Convergence of model fits were assessed based on visual inspection of the chains and whether R-hat values of were less than 1.05 (Vehtari *et al.* 2019). Posterior distributions from fitted models were obtained using the brmsmargins package, version 0.2.0 (Wiley and Hedeker 2022). Fit of models of association rates were compared based on the expected log pointwise predictive density (ELPD) using Pareto smoothed importance sampling in Leave-One-Out cross validation (PSIS-LOO-CV), as implemented in the loo package in R (Vehtari *et al.* 2024).

5.2.2 Large-scale affinity of species distributions: aerial surveys

Aerial surveys for seabirds were carried out over the Dutch North Sea since the late 1980s. From this data series, the years 2014-2023 were selected because the lower flight height of these surveys compared to earlier surveys allowed distinguishing guillemots and razorbills. Surveys were carried out using a twin-engine Partenavia with bubble windows to allow observation underneath the plane, flying at a height of 250 feet (~75 m asl) along pre-defined transects. One complete survey, was usually carried out in 5-7 days (maximum 10 days), and, including non-flying days, covered a period of 5 - 41 days (median = 19 days). For more details regarding the method, see Bemmelen *et al.* (2023).
The affinity of kittiwakes to co-occur with either guillemots or razorbills was calculated using the recently proposed method of calculating α MLE; the maximum likelihood estimate of log odds ratio (Mainali *et al.* 2022). Contrary to often used alternative indices of co-occurrence, such as Jaccard, Sørensen-Dice, and Simpson, the α MLE is insensitive to species prevalence. The sensitivity of the former indices to prevalence stems from the observation that the probability of co-occurrence increases with prevalence and can lead to bias or even incorrect interpretation of the true species affinities. Hence, α MLE should better reflect the affinity of species to co-occur at sites. We first assessed the absence/presence of each species along each 5-km transect segment of each survey. Subsequently, to exclude surveys where one or both species were very scarce or absent, we calculated α MLE for each survey where each species was detected along at least 10 segments (which excluded all surveys in June), using

the CooccurrenceAffinity package (version 1.0) in R (Mainali *et al.* 2022). An α MLE of 0 indicates that the co-occurrence of the species does not differ from the null model, the situation with no association between the species; negative values indicate a negative affinity and positive values indicate positive affinity. Finally, survey-level estimates of α MLE were compared between species and survey months in a GLMM with $alpha$ as response variable, species, survey month and the interaction between species and survey month as fixed effects, and random intercepts for surveys. As there was only a single survey in August, this month was not included in the GLMM.

All analyses were performed in R version 4.4.2 (R Core Team 2023).

5.3 Results

5.3.1 Small-scale species foraging associations: ship-based surveys

The distribution of ship-based data shows a strong temporal pattern, with fewer data collected during the 1990s, increasing data collection during the 2000s, with a peak in annual effort around 2011-2012. This distribution of data collection can be attributed to a small number of projects with repeated survey designs, in particular: the monitoring in and around the Prinses Amalia windfarm and Offshore Windfarm Egmond aan Zee in 2005-2012 (Leopold *et al.* 2012), surveys in the Brown Ridge area in 2009-2012 (Bemmelen *et al.* 2012) and 2016-2017, the ‘Shortlist Masterplan Wind’ surveys in 2010-2011 (Bemmelen *et al.* 2011) and a series of surveys at the Frisian Front with varying survey designs in 2005-2006, 2009, 2012 and 2016-2018 (Bemmelen *et al.* 2013, Geelhoed *et al.* 2019).

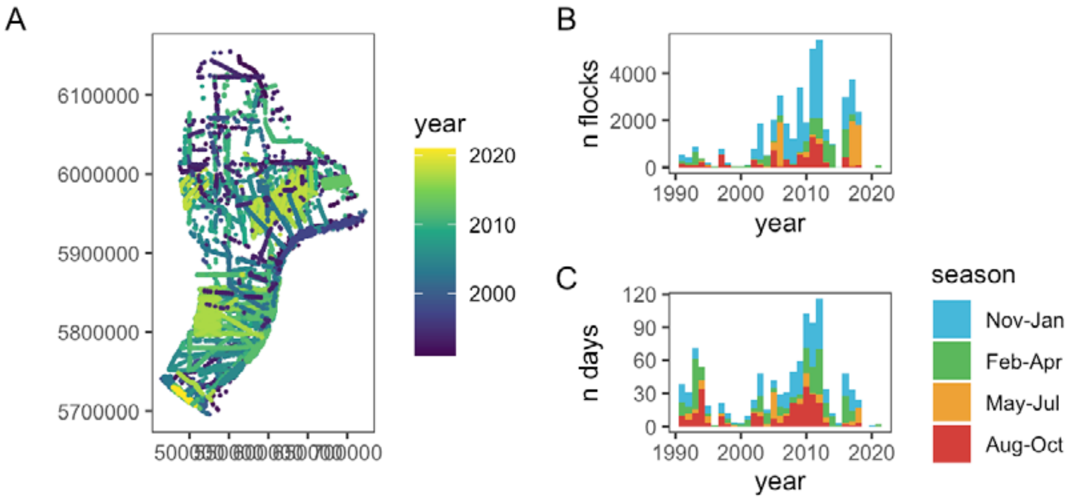

Figure 1: A. Spatial distribution of samples from the ship-based surveys collected in 1991-2021 and used to study fine-scale assocations between kittiwakes and alcids. B. Annual number of flocks of alcids and kittiwakes. C. Annual number of survey days with alcids and kitiwakes.

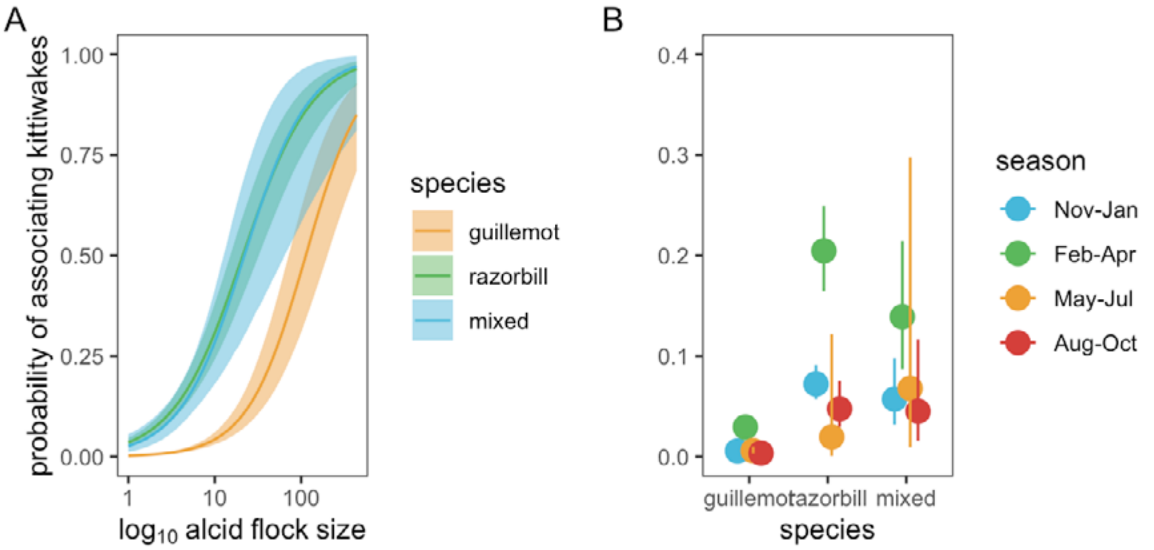

Figure 2: A. The probability of alcids flocks to be joined by kittiwakes increases with alcid group size, but rises much faster with flock size in razorbills and mixed flocks compared to guillemot flocks. Raw data is shown as the proportion of associations per flock size, where flocks larger than 15 were rounded to the nearest 10. Flocks larger than about 100 birds always had associating kittiwakes, but such large flocks were only rarely observed. B. The probability of having associating kittiwakes was larger in spring for both alcid species as well as mixed flocks, conditioned on a flock size of two, but this effect was stronger in razorbills. Errorbars are 95% credible intervals.

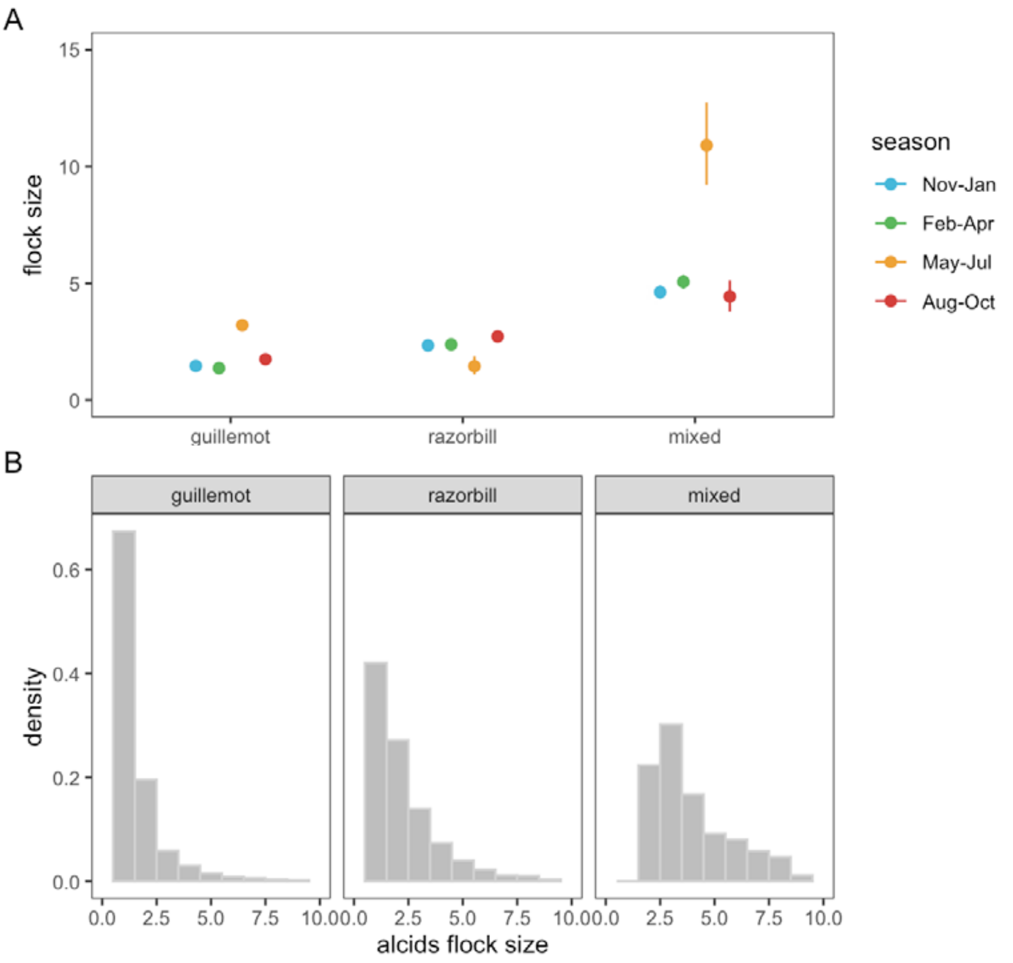

Figure 3: A. Posterior distributions of flock size per species or mixed flocks per season. B. Histograms (densities) of flock size for the two species as well as mixed flocks. The x-axes have been right-truncated to allow better visibility of details at smaller flock sizes. Maximum flock size was 440 individuals for guillemots, 44 for razorbills, and 64 for mixed flocks. Note that by definition, flock sizes of 1 are impossible for mixed flocks.

In total, 40316 alcid flocks were recorded, of which 1315 sightings concerned associations with kittiwakes. Of these associations, 381 (29% of the associations, 1% of the guillemot flocks) were with guillemots, 817 (62% and 16%) with razorbills and 117 (9% and 27%) with alcids mixed flocks. Mixed alcid flocks consisted mostly of more razorbills than guillemots (78%, n = 429); in 27% of the flocks, the number of razorbills and guillemots was equal.

For both single species and mixed flocks, larger alcid flocks were more likely to be joined by kittiwakes, with the probability approaching 1 at the largest flock sizes. This relationship was similar between razorbills and mixed flocks and much steeper than for guillemot flocks (figure 2A). Both alcid species were more often joined by kittiwakes during spring compared to the other seasons, but this effect was stronger for razorbills than for guillemots (figure 2B). Although mean flock sizes were similar between the two alcid species (figure 3A), the frequency of single birds was higher among guillemots than among razorbills and mixed flocks were most frequently composed of three individuals (figure 3B).

On most days, a minority of kittiwake sightings included associations with alcids. Overall, on 59% of the days (n = 818 d), kittiwakes did not show any assocation with alcids, despite alcids being present. However, this can partly be explained by (very) low numbers of kittiwakes: on 89% of the days with no associations, less than 20 kittiwake flocks were noted (n = 486 d). Given the low number of kittiwake flocks observed on these days, their 'weight' in the model statistics is also low. On days with associations, on average 25% of the flocks of kittiwakes associated with alcids (n = 332 d).

The model of daily association rates indicates that, again, kittiwakes were much more likely to associate with razorbills rather than guillemots, as shown by the strong negative effect of the proportion of guillemots in the total of identified alcids on the association rates (figure 4A, B). In addition, kittiwakes were more likely to associate with alcids when there were more alcids (figure 4A), but less likely to associate with alcids when there were more kittiwakes (figure 4B).

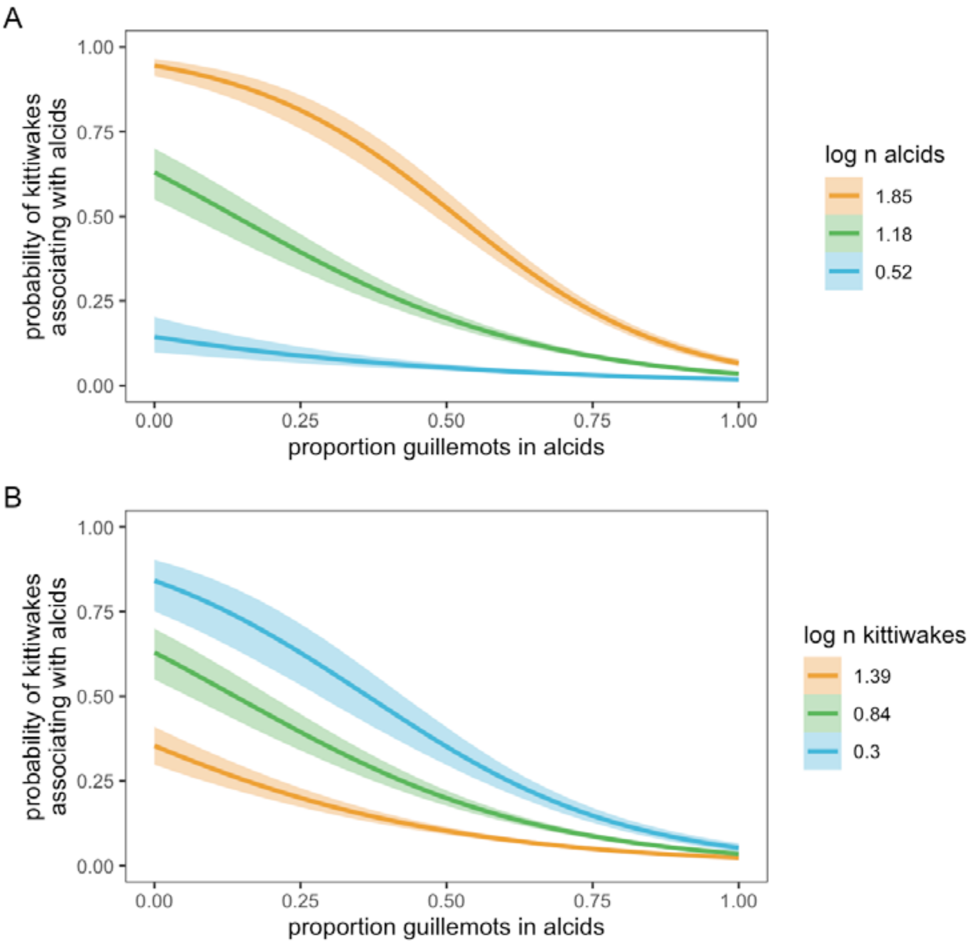

Figure 4: Daily probability of kittiwakes associating with alcids (y-axis) as a function of the abundance (colours) and ratio between the two alcid species (x-axis), where values < 0.5 incidate more razorbills than guillemots and > 0.5 more guillemots than razorbills. Relationships are shown for three abundances of alcids (A) and kittiwakes (B; on the Log_{10} scale); lines show the conditional effects with 95% credible intervals.

5.3.2 Large-scale affinity of species distributions: aerial surveys

Kittiwakes showed marginally higher affinity with razorbills than with guillemots ($\beta_{razorbill}$ = 0.923 [0.798 - 1.046]; $\beta_{razorbill}$ = 1 [0.936 - 1.185]; p = 0.048) (figure 5). In addition, there was a marked seasonal pattern in affinity, with higher values for both species in February and April compared to November and January (figure 5).

The spatial distribution of the occurrence of kittiwakes shows a clear seasonal pattern, with highest probabilities in southern areas in January and February, concentrations of higher probabilities around the Brown Ridge and Cleaver Bank in April, between the Frisian Front and the Cleaver Bank in June and August, and highest probabilities of occurrence in the northern half of the Dutch Continental Shelf in November. However, co-occurrence of kittiwakes with guillemots or razorbills did not clearly show areas where co-occurrence was recorded more often, except perhaps for areas where kittiwakes were recorded more often (figure 6).

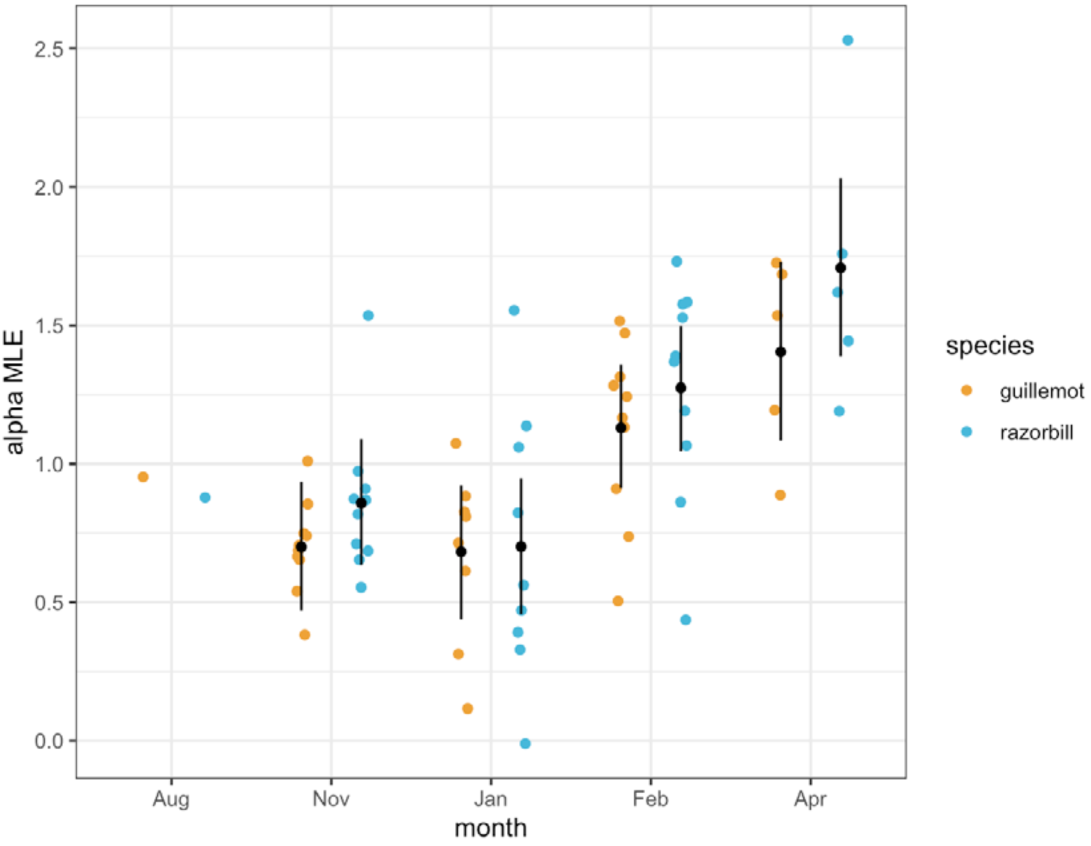

Figure 5: Affinity (α MLE) between distributions of kittiwakes and guillemots or razorbills per survey, shown per survey month. The affinity of the distribution of kittiwakes with those of the two alcids was similar between the two alcid species, always positive, and higher in February and April compared to November and January.

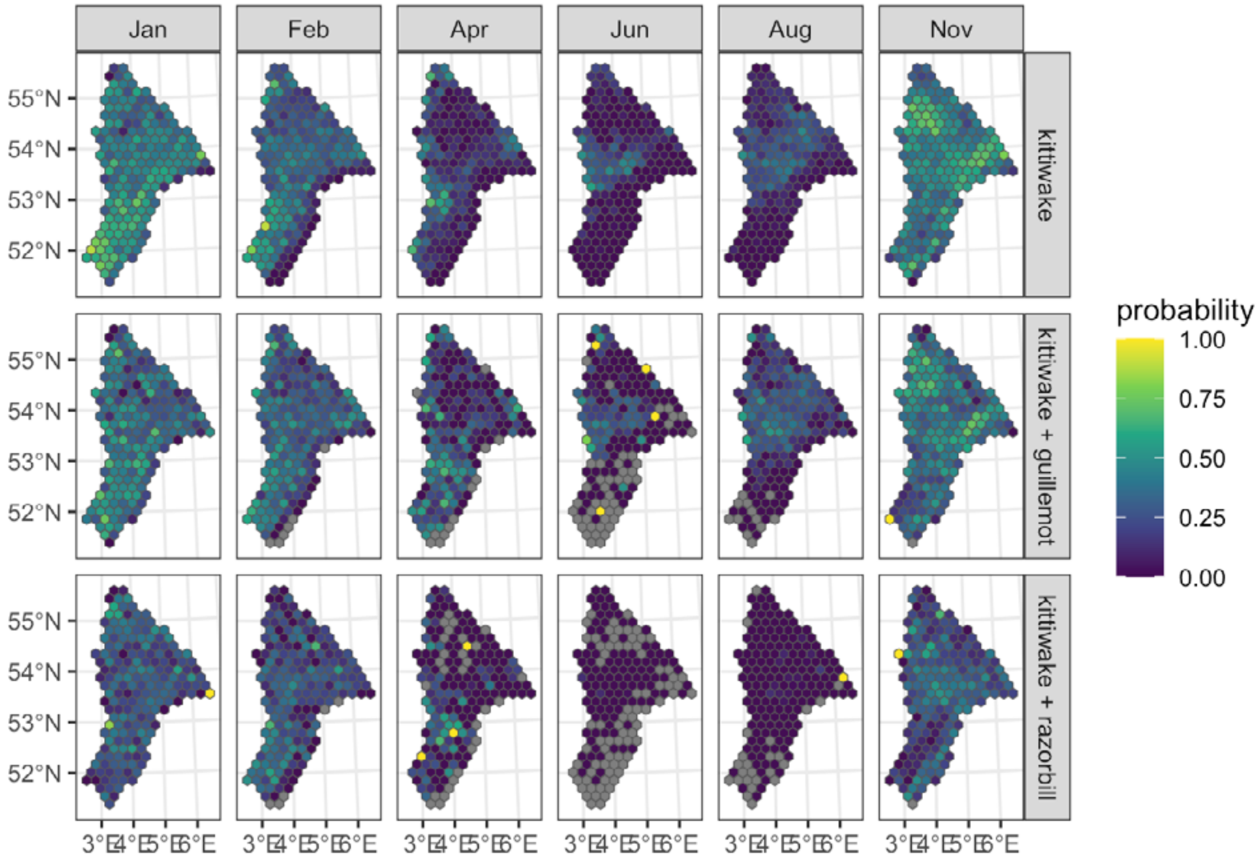

Figure 6: For each survey month, the occurrence rate (proportion of all surveys within each grid cell) of kittiwakes (upper row), guillemot (second row), co-occurrence of kittiwakes with guillemots (center row), razorbills (fourth row) or co-occurrence of kittiwakes with razorbills (lower row), based on aerial surveys between August 2014 and June 2024. Cells with no sightings of kittiwakes and/or alcids but with survey data are shown in grey. Cells with survey data in less than 5 surveys were excluded. Note that occurrence rate does not necessarily reflect abundance, and that Razorbills are rare in Dutch waters in June and August. Also, note that the spatial distribution of co-occurrence is driven by the abundance and distribution of each species, and that in several survey-months, guillemots are substantially more abundant and widespread than razorbills.

5.4 Discussion and conclusion

Our study shows a clear preference of searching or foraging kittiwakes to associate with razorbills rather than guillemots, and a slightly stronger spatial overlap in distribution with razorbill than with guillemots in the Dutch sector of the North Sea. Both at small and large scales and for both alcid species, the link between kittiwakes and alcids is stronger in spring compared to the other seasons. These results suggest that 1) razorbills rely more on pelagic versus demersal fish species than guillemots, 2) this reliance is higher in February-April for both alcids and 3) kittiwake distribution may be linked to those of both alcids and/or their prey. Despite guillemots being much more numerous than razorbills, also in absolute terms associations of kittiwakes with razorbills outnumbered those with guillemots.

That razorbills determine the attractiveness of mixed flocks is indicated by the observation that mixed alcid flocks have a similar probability of being joined by kittiwakes to flocks of razorbills only. We suggest that the general preference for razorbills over guillemots reflects the difference in diet of the two alcids, with razorbills feeding (almost) exclusively on pelagic fish but guillemots partly relying on demersal fish. This difference in diet has been documented for the Dutch sector of the North Sea in January-February 2003, when razorbills fed exclusively on pelagic fish, mainly clupeids and sandeel, whereas the diet of guillemots also included gadoids and other demersal fish (Ouwehand *et al.* 2004). Similar findings were obtained from stranded birds in Belgium (Depooter 2010). Our results suggest that, in the Dutch North Sea, the difference in diet between the two alcids can be generalized across the non-breeding period. However, there may be exceptions to this, particularly when opportunities for guillemots to forage on pelagic fish arise. For example, Leopold and Overmaat (2023) sampled bycaught guillemots in the Dutch coastal zone in January 2017, and found that stomach contents contained 90% Sprat *Sprattus sprattus* and 10% demersal fish species.

We found that the kittiwakes were more likely to occur along 5-km transect segments when alcids were present, with a slightly higher affinity with the distribution of razorbills than with the distribution of guillemots. Of course, these results do not necessarily mean that MSFAs drive kittiwake distribution; it may also be a joint consequence of prey availability. Unfortunately, there is no data available on the spatio-temporal distribution of the most important prey species, precluding analyses of the links between distribution of prey, alcids and kittiwakes. In addition, kittiwake distribution will be driven by other factors than just razorbill distribution, as is indicated by the fact that kittiwakes occur in the Dutch North Sea in substantial numbers throughout the year, while razorbills are (virtually) absent during the late spring and summer (May - August) (Bemmelen *et al.* 2023).

We hypothesized that associations of kittiwakes with alcids signal foraging on pelagic fish, and that these associations can therefore be used to map temporal and spatial patterns in the ratio between pelagic and demersal fish species in alcid diet. We found support for seasonal variation at both small and large scales, with higher association rates in spring compared to other seasons for both alcids and a concomitant higher spatial affinity of kittiwake distribution with that of razorbills and guillemots in February and April compared to November en January. This suggests that in the Dutch sector of the North Sea, both alcids forage more often on pelagic fish in spring compared to other seasons. Indeed, stomach contents of guillemots stranded on Belgian beaches contained more sandeel (the predominant prey of razorbills) in January and March compared to November and December (Depooter 2010). Alternatively or in addition to a diet switch, this may also reflect changes in behaviour of prey fish and alcid diving behaviour. If pelagic prey fish shift to shallower depths in spring, requiring alcids to dive less deep, foraging opportunities for kittiwakes are likely to occur more often. Indeed, guilemots generally dive longer and deeper than razorbills and diving depth shows seasonal variation between July and January, especially in the former species (Thaxter *et al.* 2010, Dunn *et al.* 2019), and diving behaviour has been linked to prey type in the closely related Brünnichs Guillemot *Uria lomvia* (Elliott *et al.* 2008).

In this study, we focused on the Dutch sector of the North Sea. While the methods used will be transferable to any area where kittiwakes and alcids occur (or similar feeding associations), our results may not be applicable to the behaviour of kittiwake and the two alcids in other areas for several reasons. First, diets of the two alcids may differ depending on habitat (Lilliendahl 2009). For example, studies in the northwestern North Sea, east of Scotland, indicate no strong difference in association rates of kittiwakes between the two alcids. Indeed, diet studies show that guillemots in this area and time of year forage predominantly on pelagic fish, as do razorbills (Blake 1984, Blake *et al.* 1985). Second, the abundance and occurrence of species that can act as drivers of MSFAs may differ from our study area. For example, cetaceans were regularly observed as drivers of MSFAs east of Scotland (Camphuysen and Webb 1999), but are, with the exception of Harbour Porpoise *Phocoena phocoena*, generally rare in Dutch waters (Camphuysen and Leopold 1994, Bemmelen *et al.* 2023).

Our study demonstrates the application of foraging association rates of surface-feeding seabirds with pursuit diving species as signals of potential diet, in particular the degree to which species forage on pelagic versus demersal fish. Using standardized ship-based surveys, this approach could be extended to other areas to study the (non-breeding) diet of seabirds elsewhere. In addition, the spatial affinity between kittiwakes and the two alcids indicates that assignment of marine protected areas for a single species is likely to be beneficial to other species as well.

Supplement

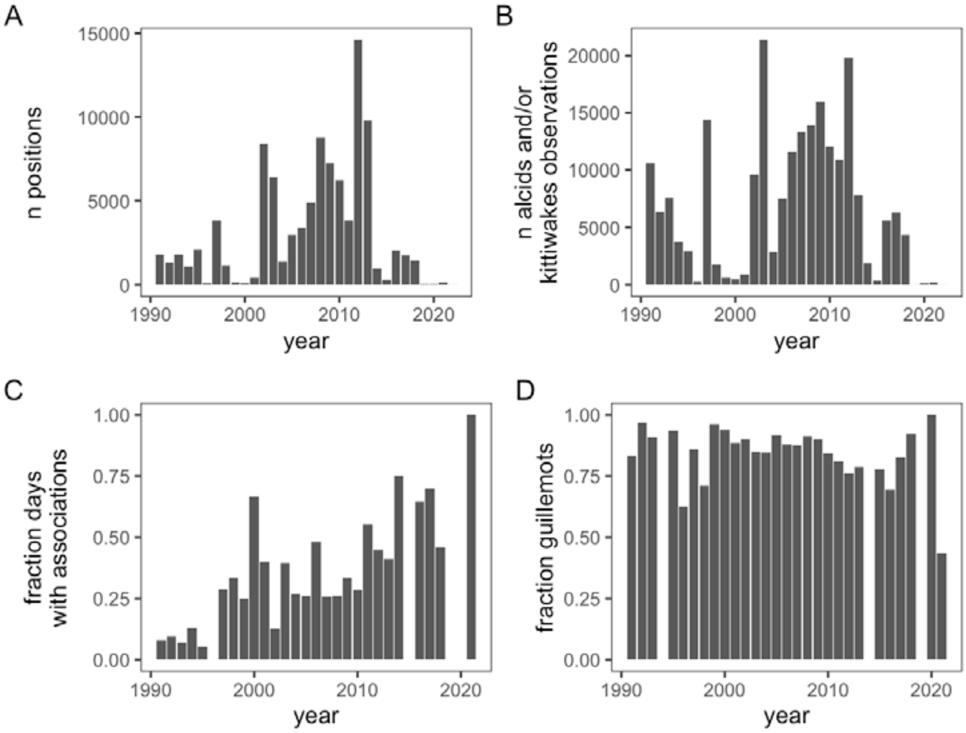

Figure 7: Ship-based survey sample sizes per year collected in the Dutch sector of the North Sea. A. The number of positions logged. B. The number of alcid and kittiwake observations. C. The fraction of days when assocations between kittiwakes and alcids were noted. D. The mean daily fraction of guillemot flocks in the total number of identified alcid flocks. Thus, values < 0.5 indicate more razorbill than guillemot flocks and vice versa.

6. Drivers of seabird distribution: a discussion and potential future directions

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Samenvatting

Het relatieve belang van statische factoren (zoals waterdiepte) en dynamische factoren (zoals wind) in het sturen van verspreidingen van zeevogels is van belang bij het aanwijzen van belangrijke vogelgebieden. Immers, indien statische factoren belangrijker zijn dan dynamische, is het waarschijnlijker dat bepaalde locaties ook in de toekomst consistent hoge dichtheden vogels zullen herbergen. Kennis over het belang van verschillende factoren kan verkregen worden door het modelleren van gegevens van zeevogelverspreidingen. Hier bespreken wij de modelresultaten van van Donk *et al* (2024), het meest recente voorbeeld van zo'n studie. Waterdiepte was geen onderdeel van de modelselectie (en werd dus in alle modellen behouden). Waterdiepte verklaart waarschijnlijk veel verspreidingspatronen op de grote schaal, zoals of een soort voornamelijk dicht bij de kust of juist *offshore* voorkomt. Zandpercentage was voor veel soorten een vrij belangrijke factor, maar opvallend zijn de sterke verschillen tussen soorten in welke maanden zandpercentage belangrijk leek te zijn. We doen verschillende suggesties voor het uitbreiden van de bestaande modellen en voor toekomstig onderzoek. Zo zou de vraag in het huidige project, in hoeverre statische en dynamische factoren de verspreiding van zeevogels sturen, een wat andere opzet van de modellen vereisen. De huidige modellen zouden kunnen worden uitgebreid met variabelen die andere aspecten in de gegevens benadrukken. Bijvoorbeeld, behalve de temperatuur kan ook de gradiënt in temperatuur van belang zijn als dit een frontsituatie aangeeft. Tot slot zou de verspreiding van zeevogels ook onderzocht kunnen worden vanuit het perspectief van individuen, door zendergegevens te koppelen aan omgevingsvariabelen. In de modellen van van Donk *et al* (2024) bleken de meegenomen variabelen maar een klein deel van de variatie in vogeldichtheden verklaren. Het begrijpen van de grote seizoenale en jaarlijkse variatie in de verspreiding van zeevogels zal dus uitdagend blijven.

Abstract

Spatial modeling of the distribution of seabirds is important for marine spatial planning and to further our understanding of the drivers of seabird distributions. In 2024, the study by van Donk *et al.* (2024) provided density maps for the Dutch sector of the North Sea based on statistical models with several environmental covariates for a set of seabirds: Northern Gannet, European Herring Gull, Lesser Black-backed Gull, Great Black-backed Gull, Black-legged Kittiwake, Razorbill, Common Guillemot and Sandwich Tern. Here, we discuss the results presented by van Donk *et al* (2024), aiming to 1) summarize and discuss their model results and 2) to identify potential additional covariates, or combinations of covariates, that may improve our understanding of seabird distributions in the Dutch North Sea.

6.1 Introduction

Mapping the distribution of seabirds is important for marine spatial planning: the identification of areas of high conservation values and areas of overlap with human activities. Many studies have attempted to summarize seabird distribution in the (Dutch) North Sea [e.g.; Stone *et al.* (1995); Camphuysen & Leopold (1994); Waggitt *et al.* (2019)]. Most of the earlier studies were based on pioneering surveys of seabirds from vessels and calculated average densities of seabirds per grid cell. This approach may give an indication of distributions but does not inform on drivers of large-scale seabird distributions.

Density maps can also be generated by spatial modeling, offering the potential to further our understanding of the drivers of seabird distribution by including covariates. Studying the relative importance of static versus dynamic environmental covariates and seabird distributions may also shed light on the consistency of seabird distributions in space and time - and thus what future changes in seabird distributions may be expected. For example, when static variables (e.g. water depth) are much more important than dynamic variables (e.g. sea surface temperature), seabird distribution can be expected to be more consistent over time than when dynamic variables are the main drivers of seabird distributions. Knowledge on the consistency of seabird distributions over time is important for marine spatial planning, including the assignment of marine protected areas, where decisions may have consequences over multiple decades.

Model-based large-scale density maps including environmental covariates, that were based on at-sea survey data, have been developed for the North Sea in two earlier studies. In 2019, Waggitt *et al.* (2019) produced a series of seabird and cetacean maps for the North-East Atlantic, including the North Sea, based on ship-based and aerial survey data as stored in the European Seabirds At Sea (ESAS) database. In 2024, van Donk *et al* (2024) provided density maps for the Dutch sector of the North Sea for a set of seabirds, as part of the *Wind op zee ecologisch programma* (Wozep). The methods and maps by van Donk *et al* (2024) were developed to be used in the *Kader Ecologie en Cumulatie* (KEC) project, which assessed the cumulative impacts of offshore wind farm developments on the North Sea. Both Waggitt *et al.* (2019) and van Donk *et al* (2024) included environmental covariates in their models. Considering that the estimated effects of covariates may differ between spatial scales and the availability of habitats (e.g., steep continental shelf edges do not occur in the Dutch sector of the North Sea), we focus here mainly on the results by van Donk *et al* (2024).

The species considered by Donk *et al.* (2024) were Northern Gannet, European Herring Gull, Lesser Black-backed Gull, Great Black-backed Gull, Black-legged Kittiwake, Razorbill, Common Guillemot and Sandwich Tern. The Great Skua *Stercorarius skua* was initially also considered, but the small number of sightings did not allow robust spatial modeling. Per study species, the report by Donk *et al.* (2024) provides a short overview of the results; a table showing which covariates were retained in the final models, conditional plots of the effect of water depth, and the resulting density maps. The main aims of the project were to provide accurate predictions of seabird densities per bimonthly period, including uncertainty estimates. Although explaining ecological causes of habitat preferences was also listed as an aim, the complexities of data preparation, model development and running the models made a huge effort, leaving no room for an in-depth discussion of the model results. This was no problem within the context of the KEC framework, as the main aim was producing the density maps. However, it is worth scrutinizing the results by Donk *et al.* (2024), as a better understanding of the model results may provide feedback for further improvement of the models and the resulting seabird density maps.

The range of covariates considered by Donk *et al.* (2024) was limited in the first place by what environmental data was available for the greater North Sea. Prey abundance and availability is obviously extremely important, but is usually (including here) not available at the appropriate time and spatial scales. As proxies of habitat and/or prey availability, water depth, sea surface temperature (SST), Chlorophyll-A, and sand percentage were considered. In addition, fishing vessel activity was included for species that are known to feed on fishery discards. The distance to (large) breeding colonies was included for the period April-September, and the presence of shipping lanes was included considering that these may be avoided by some seabird species. Per species, only covariates were included in the models that were expected (based on literature and/or expert judgement) to have an effect on the species' distribution.

Here, we discuss the results presented by Donk *et al.* (2024) in the light of the research question of this report, aiming to 1) summarize and understand their model results and 2) to suggest potential additional covariates, or combinations of covariates, that may improve future modeling attempts and our understanding of seabird distributions. We will not discuss the statistical methods used to estimate seabird distribution.

6.2 Methods

Here, we give a short summary of the methods employed by Donk *et al.* (2024). For further details, we refer to the report by Donk *et al.* (2024).

Seabirds were surveyed following standardized protocols along transect lines. Data were obtained from the European Seabirds at Sea (ESAS) database. Aerial surveys from the Dutch Continental Shelf were selected. To correct for reduced detection of (flocks of) birds at greater distance from the transect line, the *distance sampling* technique was used (Buckland *et al.* 1993). This allows to correct the observed density by either adjusting the number of birds, or the surveyed area (becoming the 'effective surveyed area'). Data were aggregated per 1 minute (aerial) or 5 minute (ship-based) transect segments.

Densities were then modelled in Generalized Linear/Additive Mixed Models (GLMMs/GAMMs), including spatial-temporal effects estimated using a stochastic partial differential equation (SPDE) (Lindgren *et al.* 2011) and a range of covariates. Models were fit using the `sdmTMB` package (Anderson *et al.* 2022). Subsequently, model selection was performed based on cross-validation.

6.3 Results & discussion

6.3.1 Discussion of van Donk *et al* (2024)

The main aim of van Donk *et al* (2024) was to develop (a method for) improved maps of North Sea seabirds for the KEC project. A second aim was to study covariate effects on the distribution and abundance of seabirds. An overview of covariates included in the statistical models of van Donk *et al.* (2024), and which were eventually selected in the 'best' model, is shown in table 1. Van Donk *et al.* (2024) succinctly discussed the model results per species, mainly focusing on summarising which covariates were retained. In addition, several statistical aspects were already highlighted in the discussion by van Donk *et al.* (2024) and will not or only shortly be repeated here. Rather, we attempt a more holistic discussion of the modeling results by evaluating how often covariates were retained overall as well as per species, and whether these showed seasonal patterns consistent across species.

It is important to realize at the outset of a discussion on the effects of covariates, that the random spatial-temporal field explained much more of the variation than the fixed effects in almost all models, as was already put forward by van Donk *et al.* (2024). In other words, there was substantial variation in counts of seabirds in space and time that could not be explained by the covariates (the fixed effects), while the covariates themselves explained only a small part of the observed densities. This indicates that there are important drivers of seabird distribution that were not included in the models. There may be several potential reasons for such omissions, such as incomplete knowledge, unavailability of data, or inappropriate scales of the covariate data.

The approach by van Donk *et al.* (2024) was to only include variables for which an expectation existed based on literature; either hypothesized or with empirical support. However, comparing the overall effects of covariates across species, as we attempt here, would be easier if all variables were included in all models.

Water depth was not part of the model selection procedure and was therefore included in all models. Water depth likely captures an important part of the large-scale habitat selection of species, for example whether they occur primarily nearshore (e.g. Herring Gull) or offshore (e.g. Black-legged Kittiwake). Van Donk *et al.* (2024) showed that the conditional effect of water depth varied seasonally within species, reflecting shifting spatial distributions.

Within species, the selection of variables in the final model differs per bimonthly period. There is not a single species in which the same set of variables is selected for each bimonthly period. As the considered variables are rough proxies of prey distribution, the seasonality of whether they are included may suggest seasonal changes in diet, the link between prey and the covariates, or both.

Sand percentage, which correlates with occurrence of sandeel (Holland *et al.* 2005, Kooij *et al.* 2008, Tien *et al.* 2017), was an important covariate in at least one to three models per species where it was considered - but never all models of a species. The set of seasons in which sand percentage was retained in the final model differed between species. Part of this will be driven by the seasonal occurrence of the seabird species; if a species is not present in a certain period, it is less likely that a relationship with sand percentage will be found. However, bimonthly periods for which sand percentage was retained did also differ between species with similar seasonal patterns. For example, for Lesser Black-backed Gull and Sandwich Tern, both migratory species that are largely absent from the North Sea in winter, sand was important during only two out of four seasonal models; and these two differed between the species. Also for species that occur primarily in winter, there seems to be little overlap in which seasons sand percentage was an important covariate. This is surprising, because sandeel form an important part of the diet of many seabirds, and their seasonal occurrence can be expected to be reflected in models across species.

Sea surface temperature and **chlorophyll-a** were important covariates in most models of Northern Gannet, Common Guillemot, Black-legged Kittiwake, Lesser Black-backed Gull and Herring Gull, but less so in models of Razorbill, Great Black-backed Gull and Sandwich Tern. In some species, the two covariates seem to alternate between models: in some models SST was retained, whether in others chlorophyll-a was retained, but rarely both. This suggests some collinearity between the two variables.

Distance to the breeding colony was only included as a covariable to be considered for a subset of species (Common Guillemot, Razorbill, Black-legged Kittiwake and Great Black-backed Gull), and only during the breeding season. For species breeding in the Netherlands, distance to (larger) breeding colonies was strongly correlated to distance to the coast and water depth, and therefore not included. For those models where it was included, only in a single model of Common Guillemot, the variable was retained. This seems surprising, but is likely explained by the use of only Dutch survey data, where all these species do not occur as breeding birds, or only in (very) small numbers, and hence these distances were fairly large almost everywhere.

Distance to shipping lanes was included in only the models of the two alcids, and was retained in only the December-January model of Common Guillemot, suggesting a very limited effect overall of shipping lanes. However, it should be noted that survey transects usually run perpendicular to the direction of shipping lanes. Hence, the amount of survey effort within shipping lanes is fairly small. In addition, it would be worthwhile to include shipping lane as a binary variable (in/out), considering that the effect of ships may reach not further than the order of hundreds of meters. Finally, shipping activities are not limited to shipping lanes. Movements of fishing vessels, for example, occur primarily outside shipping lanes. These were not considered in models of Common Guillemots and Razorbills, but may represent substantial disturbances in some areas.

Fishery activity was included in models of all four gull species, and was retained in 3-5 of the 6 models in each species. Indeed, all species have been recorded to feed on discards from fishery vessels (Camphuysen *et al.* 1995), but the species are of course also able to forage independently and occur in areas with no or little fishery activity (Baptist *et al.* 2019). It is unclear why fishery activity was not considered in the models of Northern Gannet; a species that is well known to be attracted to fishing vessels. In addition, as already mentioned above, fishing activity may also be a disturbance, for example to alcids or divers (Schwemmer *et al.* 2011). Hence, it may be interesting to also include this factor in models for these species.

6.3.2 Potential additional covariates and adjustments to the models

It should be noted that the set of covariates initially considered by van Donk *et al.* (2024) was based on a literature study and already rather extensive. Several of the initially considered covariates could not be included in the models. Variables that were excluded were salinity, wind, the occurrence of other seabird species, offshore platforms, offshore wind farms and currents. An important reason for not including certain covaraties was collinearity, for example between distance to the coast and water depth. In addition, the effect of some variables may be small-scale, or was not captured well by the data. For example, little or no survey data was available for the areas within offshore wind farms. For some variables, such as the occurrence of other seabirds or cetaceans, there is a mismatch between what would be included in the model (ideally, in this case: raw observational data of seabirds or cetaceans) and what would be used for predictions (in this case: the modeled average densities of seabirds or cetaceans). After all, predictions require gridded data across the Dutch North Sea. Similarly, the presence of active fishing vessels can have a huge effect on observed densities, but fishing activity is usually only available as fishing intensities averaged over a much longer time frame than the observations.

In the study of temporal consistency of seabird distribution, an important issue is the relative roles of static versus dynamic environmental variables in driving seabird distributions. Ideally, for this approach, a fair number of both static and dynamic variables should be included in the models. In the models by van Donk *et al* (2024), only a fairly small number of both types of variables were included – which is understandable from the perspective of collinearity. To avoid such statistical issues, a potential solution would be to compare a larger number of simpler models, each with only one environmental covariate, and then compare the model fits as a measure of each variables importance in shaping seabird distributions.

In van Donk et al (2024), no variables were considered that integrate information across the water column. Moreover, no variables were considered that directly represent transitions between water masses. For example, spatial *changes* in SST may indicate the position of a front, but the SST itself does not indicate

Table 1: Summary of the results of van Donk et al (2024). Numbers indicate the number of seasonal models where the covariate was retained in the final model; the column 'n seasons' indicates the number of seasonal models. Empty cells mean that the covariate was not considered for the species.

species	water depth	sand percentage	sea surface temperature	Chlorophyll -a	distance to breeding colony	distance to shipping lane	fisheries activity	period	n seasons
Northern Gannet	6	3	5	5				5-year	6
Common Guillemot	6	1	3	4	1	1		1-year	6
Razorbill	4	3	1	1		0		1-year	4
Black-legged Kittiwake	6	3	6	5	0		5	5-year	6
Great Black-backed Gull	6		3	3	0		4	5-year	6
Lesser Black-backed Gull	6	2	6	5			3	5-year	6
Herring Gull	6		5	5			4	5-year	6
Sandwich Tern	4	2	3	2				5-year	4

the proximity to a front. For example, whether waters are mixed or stratified, or whether a location is on the divide between mixed and stratified waters (see point 4 below), can be important determinants of the occurrence of seabirds (Schneider 1990, Begg & Reid 1997, Scales *et al.* 2014).
No weather-related variables were included. Ocean-scale distribution patterns of seabirds are clearly affected by large wind patterns - but primarily migration corridors between productive areas where seabirds stage for extended periods (Felicı´simo *et al.* 2008). Wind patterns can also shape seabird distributions at smaller scales (Mateos & Arroyo 2011), but this has never been studied in detail in the North Sea. Furthermore, wind may affect the distribution in other ways, such as has been tested elsewhere in this report, for the Frisian Front and the distribution of Common Guillemots.

Surface-feeding seabirds depend on processes that bring prey (close) to the water surface, such as pursuit-diving alcids or cetaceans that drive prey fish to the upper one meter of the water column. A typical example has been discussed elsewhere in this report: surface-feeding Black-legged Kittiwakes that associate with foraging Razorbills and – to a lesser extent – with Common Guillemots. This specific example is suitable for inclusion in the models of Black-legged Kittiwake (i.e. the observed number of Razorbills and Common Guillemots per transect segment), however, prediction is less straightforward as this would require gridded, interpolated, data, which are likely to comprise lower alcid densities than the observed densities.

Finally, a point of attention may be the time period over which counts were grouped in the models and over which densities were predicted. The idea behind including time periods in the model was to capture long-term changes in distribution. For most species, average maps were produced for 5-year periods; for Common Guillemot and Razorbill, annual maps were produced. Given the large temporal variability of seabird distributions, longer time periods may be more appropriate as these will be less influenced by extreme values.

Alternative to large-scale ship-based and aerial surveys, drivers of seabird distributions can also be studied using tracking data from individual birds. Tracking data has the advantage that it is continuous in time and space and that it explicitly captures behaviour and habitat selection at fine temporal and spatial scales. A challenge in using tracking to estimate seabird distribution, is how to scale up area use from the individual to population level. Seabirds are restricted in their movements during the breeding period by the need to regularly return to the nest, requiring tagging at multiple colonies to be able to scale up from individual tracking data, via colony-level area use, to population-level distribution.

6.4 Conclusions

An important result of van Donk *et al* (2024) is that the environmental covariates included explained only a small part of the variation in seabird densities in the Dutch North Sea. We identified and suggested multiple potential pathways to further our knowledge of the drivers of seabird distributions. In light of the substantial variation observed in seabird densities over space and time in the Dutch North Sea and in absence of strong effects of static environmental variables, predicting (future) seabird distributions will remain challenging. However, the expansion of studies on forage fish distribution in the MONS program (Couperus *et al.* 2024) provides a promising avenue for future research to understand seabird distributions but will not change the notion that seabird distributions are generally variable.

In the context of marine protected areas, the high variability in seabird distributions mean that birds will regularly reside in areas outside these areas – unless the protected areas are very large. Therefore, conservation should also address threats to seabirds on a (much) larger scale. For example, regulation of fisheries on forage fish important for many seabirds, such as sandeel, may be more effective ways to support seabird populations (Cury *et al.* 2011).

7. Conclusions

7.1 Seabird concentration areas and their consistency in time

From historic aerial survey data, we reconstructed ‘concentration areas’ for seabirds on the Dutch North Sea using the same approach as for the concentration areas identified by Vogel *et al.* (2024) on the basis of recent data. In all species considered except the Lesser and Great Black-backed Gulls, the values of α MLE, the metric for overlap of the historic and current concentration areas, was positive and differed significantly from 0, the value expected at a ‘random’ amount of overlap. Hence, there is a ‘significant’ amount of temporal stability in the concentration areas. Species largely confined in their distribution to the coastal zones of the North Sea showed more overlap in concentration areas in the two periods than ‘pelagic’ seabirds with a predominantly offshore distribution (Northern Fulmar, Northern Gannet, Black-legged Kittiwake and Common Guillemot/Razorbill). Although the α MLE were significantly positive in these species as well, their values were rather small, indicating that the *degree* of temporal stability in concentration areas between the two periods was rather limited.

Within each period, the distribution of pelagic seabirds across the Dutch North Sea showed large temporal variation, meaning that one would need to identify a large ‘concentration area’ in order to include the main distribution hotspots of a seabird species within them in all or even the majority of the years. In terms of policy for management and conservation of seabirds, these results indicate that it will be difficult to effectively and consistently protect a large proportion of the seabird populations in our part of the North Sea by designating limited parts of it as ‘protected areas’ where detrimental activities are banned. It is therefore advisable to focus seabird conservation policy not only on protected areas, but also on measures alleviating on a North Sea-wide scale specific pressures and bottlenecks for seabirds that have been identified.

7.2 Moult and chick distribution in Common Guillemots and the effect of wind

The summer period, in particular August, is the main time for Common Guillemots to moult and raise chicks in the Dutch sector of the North Sea. In this period, they are mainly restricted to the northern, deeper waters north of the 30 m isobath. An area between the Natura 2000 Frisian Front and Central Oystergrounds holds on average the highest densities. We failed to find evidence for areas that hold particularly high proportions of chicks. Thus, in August, the entire distribution (at least in the Dutch sector of the North Sea) of Common Guillemots is apparently used by father-chick pairs.

The Frisian Front area can hold substantial numbers of Common Guillemots in August, but highest densities occurred here in only a subset of the years. The distribution in August as observed during aerial surveys varied substantially between years, perhaps also as a function of the timing of the surveys. Wind in the week(s) preceding the surveys appeared to have little or no effect on where and how concentrated guillemots occurred. How guillemots move through the Dutch sector of the North Sea in this period remains unclear and would require a series of surveys within a year, or GPS-tagging of individual guillemots.

7.3 MSFAs as drivers of seabird distributions

Our study demonstrates the associations between a surface-feeding seabird, the Black-legged Kittiwake, and two pursuit-diving alcids, the Razorbill and the Common Guillemot, at both small and large scales. Kittiwakes associated with both alcid species, but strongly preferred Razorbills, especially in February-April. The practical implication of the presented results for assignment of protected areas is that areas assigned for one species will likely also benefit other species and that the distribution of some species may not only be dependent on food abundance, but also on processes that make this food available. In addition, the study also shows how interactions between other seabirds (or marine mammals) can be studied. There are several other regularly observed feeding associations, such as Northern Gannets *Morus bassanus* and large gulls *Larus* associating with Harbour Porpoises *Phocoena phocoena*, other cetaceans, or predatory fish.

7.4 Drivers of seabird distribution: discussion of van Donk *et al.* (2024)

We discussed the most recent effort to model seabird densities to estimate seabird distribution in the Dutch part of the North Sea and increase our understanding of the effects of environmental conditions on seabird distributions: the study by van Donk *et al.* (2024). An important outcome of that study was that the environmental covariates included in the models explained only a small part of the observed variation, leaving much of the spatial variation unexplained. A main limitation of the study by van Donk *et al.* (2024), as well as earlier studies, is the lack of appropriate data on prey distributions, necessitating the use of (rough) proxies.

We provided some suggestions for future studies, either by extending the models of van Donk *et al.* (2024) or using other approaches. For example, models could be extended with interactions or variables derived from existing variables, such as the 'slope' in sea surface temperature or the stratification/ mixing of the water column. Future studies could also focus more on the relative contribution of (temporally and spatially) static versus dynamic variables. Finally, an alternative approach to the study of drivers of seabird distribution is to use GPS-tracking data and relate movements at the individual scale to environmental covariates. Given the substantial variation observed in seabird densities over space and time in the Dutch North Sea and in absence of strong effects of static environmental variables, predicting (future) seabird distributions will remain challenging.

7.5 Overall conclusion

The main question addressed in this study is: Do bird concentration areas exist within the Dutch North Sea area that are consistently used over long periods of time, where are these areas and how can they be ornithologically substantiated and delineated? In this report, the question is approached in several ways in different sub-studies, the main conclusions of which are summarised in the previous paragraphs.

A general, recurrent pattern emerging from these is that is quite difficult to identify areas at sea that consistently hold a large proportion of the populations of seabirds present in the Dutch North Sea, and hence where a significant proportion of these populations can be facilitated by local conservation measures. The main reason for this is the large temporal variation (between years as shown in this analysis, but also within years) in their at-sea distribution, particularly in pelagic seabirds. Coastal species are more predictably distributed, but mainly when viewed at the scale of the entire Dutch North Sea; within the coastal zone their distributions also show more variation. Over the longer timescale of a few decades, the 'concentration areas' identified as those areas where high densities of a species occur most frequently did show some consistency over time, but the degree of this spatial consistency was rather limited in the pelagic seabirds.

A similar phenomenon was seen when looking into one species at a specific period of the year in which it might be particularly susceptible to environmental pressures. We were unable to identify regions where adult Common Guillemots accompanying flightless chicks (and themselves flightless due to wing feather moult) are proportionally more abundant than guillemots in general, making it hard to pinpoint sea areas where measures could be directed specifically at this segment of the population.

Our understanding of the causes of the large variability of seabird distributions is still very limited. Variable distribution of prey species (mostly small to medium pelagic fish) very likely is an important driver, but is in itself equally poorly understood and even more coarsely described than the birds' distributions. In addition, prey must not only be present but also accessible to the seabirds, and this may depend on even more dynamic factors like the (weather-affected) occurrence of fronts and stratification, and the presence and activity of other predator species that drive fish to the surface or make them otherwise available, as in the case of the association between Kittiwakes and alcids described in this report.

In the context of marine protected areas, this means that in order to 'cover' a significant part of the population of a species in the majority of years, a quite substantial part of the sea area would have to be designated. This applies already when considering single species. When the objective is to protect several different species, the spatial requirement becomes even larger (although this is to some extent counteracted by overlap in distributions brought about by feeding associations such as in the Kittiwake). It seems therefore wise to focus seabird conservation policy not only on protecting areas, but also on measures applied on a North Sea-wide scale (or even beyond) that alleviate specific known pressures and bottlenecks.

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