Foraging areas of coastal and offshore seabirds in the Dutch North Sea

An analysis of survey and tracking data

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Preface

The North Sea is one of the most heavily used seas in the world, and considerable conflict exists between nature, energy and food supply (in particular fisheries). Now and in the coming decades, the North Sea will undergo extensive changes stemming from a massive expansion in energy transition, as well as changes to fisheries and mariculture and nature conservation. Other climate-related changes and pressures (e.g. temperature increase, changing wind patterns, acidification), as well as policy-related changes e.g. sand extraction and terrestrial nutrient management can also be expected. Within the North Sea ecosystem, coastal and offshore seabirds (along with marine mammals and large predatory fish) fulfil the role of apex predators. These species represent higher trophic levels and are potentially extremely vulnerable to changes in the abundance and availability of lower trophic level organisms, such as phytoplankton via zooplankton, as well as (small) pelagic fish, which form the staple food source for most coastal and offshore seabirds.

Such huge changes to the North Sea's ecosystem will inevitably impact coastal and offshore seabirds, hence the MONS (Monitoring, Onderzoek, Natuurversterking, Soortenbescherming) program was established in 2021 by the North Sea Agreement (*Noordzeeoverleg*-NZO). MONS is a research and implementation program created by the North Sea Agreement and is co-financed by the ministries of Infrastructure & Water Management (I&W), Economic Affairs & Climate Policy (EZK), and Agriculture, Nature and Food Quality (LVVN).

The current project is commissioned by Rijkswaterstaat, Water, Verkeer en Leefomgeving (RWS WVL) and is part of a coherent set of MONS bird research projects and serves as preparation for future field studies that will contribute to answering the main questions listed below. The MONS program includes three desk studies on seabirds. These desk studies serve as preparatory studies for the field studies.

The project team at Waardenburg Ecology include Tom van der Have (project lead), Ruben Fijn, Job de Jong, Hannah Madden and Rob van Bemmelen.

The project was guided by Ricardo van Dijk and Henri Zomer (RWS WVL. Lelystad)

Mark Collier provided comments on previous versions of this manuscript.

The authors thank everyone who has contributed to this report.

Summary

Background

The MONS research programme was initiated by the North Sea Agreement and aims to guide policy decisions relating to the transitions in energy, food supply and nature in the Dutch North Sea. The programme includes studies of coastal and offshore seabird species that are sensitive to the impacts of these transitions. This project contributes to answering key questions in the MONS-research programme about the consequences of the energy and food transition on seabirds, the distribution of seabirds, and the environmental factors that determine seabird distribution in the North Sea. The overall project includes three work packages (WPs) on seabird ecology: distribution (WP2), diet (WP3) and population studies (WP4), and a final work package with an overview of knowledge gaps and recommendations for a research plan, including field studies (WP5).

Aims and research questions

The aim of Work Package 2 (ID 60) is to review existing knowledge on the foraging areas of 12 selected seabird species in the (Dutch) North Sea; these areas are crucial for the survival of individual seabirds and conservation of the target seabird populations. The main research topics for WP2 are:

(1) What are the most important resting and **foraging areas** in the (southern) North Sea for the focus species of three functional species groups?
(2) What are the **knowledge gaps** with respect to the **environmental factors** which determine these foraging areas?
(3) **Recommendations** are provided for follow-up studies (ship-based, aircraft, digital aerial surveys) of the selected seabird species, their prey and core foraging areas in the Dutch North Sea.

Selected seabird species

Twelve seabird species were selected; these selections were made based on their abundance in the (Dutch part of the) North Sea, importance of the North Sea for international populations of those species, inclusion of both wintering and breeding birds, dependence on offshore vs. coastal food sources, and diversity in feeding strategies and functional groups. These species included red-throated diver, northern fulmar, northern gannet, black-legged kittiwake, great black-backed gull, European herring gull, lesser black-backed gull, Sandwich tern, common tern, common guillemot, razorbill, common scoter.

Survey and tracking data

To date, the number of environmental factors used in the analysis of **survey data** of seabirds to construct distribution maps is very limited. Therefore, this report begins with a literature review of studies with **tracking data** (based on GPS-transmitters and

geolocators) of the target species in the North Sea area. Although a substantial number of covariates were included in these studies to explain seabird distribution, very few studies included the actual abundance of forage fish, an important prey for the majority of the selected seabird species.

Seabird distribution in the North Sea with survey data

Density distribution maps of the selected species were generated with ESAS/MWTL-data and 11 different covariates, including abiotic factors (mainly proxies for food availability), distance to nearest breeding site, distribution of other species, and factors such as disturbance (e.g. wind farms) or attraction (fishing vessels) . The results show substantial variation in observed seabird densities over space and time, and an absence of strong effects of static environmental variables. Two to four covariates were retained in the final models, depending on species and season, and only a small proportion of the variation in seabird densities in the Dutch North Sea could be explained by the available environmental factors. Possible causes for the low explanatory power of the covariates, such as unavailability of data and incomplete knowledge (e.g. abundance and availability of forage fish) are discussed.

Distribution of foraging seabirds

The occurrence of actively foraging seabirds was studied using ten years' of aerial surveys on the Dutch part of the North Sea based on a statistical model to estimate foraging probability. Since 2014, the behaviour of seabirds and their association (if any) with marine mammals has been recorded according to standardised protocols. The estimated fraction of actively foraging birds ranged from very small (<1%; in common guillemot and razorbill) to 22% in northern fulmar and 58% in common/Arctic tern.

Knowledge gaps and recommendations

Tracking and survey studies

Although tracking and survey studies have contributed significantly to our understanding of seabird distribution in the North Sea, a range of knowledge gaps have been identified with respect to this study's research questions. Most utilised data on environmental factors in the tracking and survey studies include proxies for fish abundance and availability, such as abiotic factors (e.g. water depth, sea surface temperature, stratification, wave activity, wind, tides, fronts), biotic factors (e.g. chlorophyll-a, diet, prey length), and human activity (wind farms, fishing activity).

An important knowledge gap in both survey and tracking studies is the direct relationship between seabird distribution and density and the availability of forage fish. Other environmental factors that influence food availability and potentially seabird distribution are ocean currents, temperature anomalies (e.g. heatwaves, nutrient upwelling, turbidity, moon phase, prey species behaviour, multiple species foraging associations, and shipping lanes. Knowledge gaps specifically for survey studies are the time periods between the current six arial surveys, breeding site fidelity, interactions with other seabirds and cetaceans, and the distribution of seabirds outside the Dutch continental shelf.

Availability of forage fish

The distribution of forage fish (herring, sprat and sandeel) and their importance for coastal and offshore seabirds is briefly reviewed. These forage fish species occur throughout the North Sea, including the Dutch part. The majority of the 12 selected seabird species in this study depend on these forage fish species, especially in the breeding season, for survival and reproduction. Understanding the factors that affect coastal and seabird foraging therefore requires insight into the availability of forage fish for breeding and visiting bird populations in the (southern) North Sea. Although forage fish species are monitored in relation to international stock management, the availability of forage fish stocks for seabirds is an important knowledge gap. More detailed spatial and temporal monitoring of these stocks with respect to year-round availability to seabirds is required to understand their foraging distribution and the influence of various environmental factors and human activities. The recommended follow-up studies will help provide additional data necessary for effective seabird conservation.

Nederlandse samenvatting

Achtergrond

Het MONS onderzoeksprogramma is geïnitieerd door het Noordzee Akkoord en heeft als doel om richtlijnen op te stellen voor de beleidsbeslissingen die verband houden met de transities in energieproductie, voedselwinning en natuur in de Nederlandse Noordzee. Het MONS-programma omvat onder andere studies van kust- en offshore zeevogels die gevoelig zijn voor de impact van deze transities. Dit onderzoeksrapport levert een bijdrage aan het beantwoorden van een aantal sleutelvragen in het MONS-programma over de gevolgen van de energie- en voedseltransitie voor zeevogels, de verspreiding en de omgevingsfactoren die de verspreiding van zeevogels in de Noordzee verklaren. Het totale project omvat vijf werkpakketten (WP's), waarvan drie gaan over de ecologie van zeevogels: verspreiding (WP2), dieet (WP3) en populatiestudies (WP4). Het laatste werkpakket geeft een overzicht van de kennishiaten en aanbevelingen voor vervolgstudies, waaronder veldonderzoek (WP5).

Doel en onderzoeksvragen

Het doel van werkpakket 2 (ID 60) is om een overzicht te geven van de bestaande kennis over de foerageergebieden van 12 geselecteerde zeevogelsoorten in de Nederlandse Noordzee. Deze gebieden zijn cruciaal voor de overleving van individuele zeevogels en de bescherming van de populaties van de geselecteerde soorten zeevogels. De belangrijkste onderzoekonderwerpen voor WP2:

(1) Wat zijn de belangrijkste foerageer- en rustgebieden in de zuidelijke Noordzee voor de doelsoorten van drie functionele groepen?
(2) Wat zijn de kennishiaten met betrekking tot de omgevingsfactoren die deze foerageergebieden bepalen?
(3) Wat zijn de belangrijkste aanbevelingen voor aanvullend onderzoek aan en monitoring van (met schepen, vliegtuigen, digital aerial surveys) de geselecteerde zeevogelsoorten, hun prooien en foerageergebieden?

Geselecteerde zeevogelsoorten

Twaalf soorten zeevogels zijn geselecteerd, waarbij de selectie is gebaseerd op hun abundantie in (het Nederlandse deel van) de Noordzee, het belang voor de internationale populaties van de deze zeevogels, inclusief overwinterende en broedvogels, afhankelijkheid van voedselbronnen offshore versus kustgebieden, diversiteit in voedselstrategieën en functionele groepen. De geselecteerde soorten zijn: roodkeelduiker, noordse stormvogel, jan-van-gent, drieteenmeeuw, grote mantelmeeuw, zilvermeeuw, kleine mantelmeeuw, grote stern, visdief, zeekoet, alk en zwarte zee-eend.

Tellingen en tracking data

Het aantal omgevingsfactoren dat tot op heden is gebruikt in de analyse van survey data van zeevogels is heel beperkt. Om deze reden begint dit rapport met een literatuur review van studies met tracking data (gebaseerd op GPS-zenders en geolocators) van de geselecteerde zeevogelsoorten in het Noordzeegebied. Hoewel in deze studies een substantieel aantal co-variabelen werd meegenomen om de verspreiding van zeevogels te verklaren, hebben slechts een klein aantal onderzoeken de actuele abundantie van prooivis gebruikt, terwijl dit een belangrijke prooi is van het merendeel van de geselecteerde zeevogelsoorten.

Zeevogelverspreiding in de Noordzee met tellingen

In dit rapport zijn verspreidingskaarten met dichtheden van de geselecteerde soorten opgenomen die zijn samengesteld met ESAS/MWTL – data en 11 co-variabelen, waaronder abiotische factoren (voornamelijk proxies/indicatoren voor voedselbeschikbaarheid), afstand tot de dichtstbijzijnde broedkolonie, verspreiding van andere zeevogelsoorten, en factoren zoals verstoringsbronnen (e.g. windparken) of aantrekking (vissersschepen). De resultaten laten een grote spatiële en temporele variatie zien in de waargenomen dichtheden zeevogels en de afwezigheid van sterke effecten van statische omgevingsfactoren. Twee tot vier co-variabelen bleven opgenomen in de finale modellen afhankelijk van soort en seizoen en slechts een kleine fractie van de variatie in de zeevogeldichtheden kon verklaard worden met de omgevingsfactoren. Mogelijke oorzaken van deze lage verklarende werking van de beschikbare co-variabelen zijn het ontbreken van data over relevante omgevingsfactoren en incomplete informatie over abundantie en beschikbaarheid van prooivis.

Verspreiding van foeragerende zeevogels

Het voorkomen van actief foeragerende zeevogels werd onderzocht met vliegtuig tellingen over een periode tien jaar in de Nederlandse Noordzee met een statistisch model om de foerageerwaarschijnlijkheid te schatten. Sinds 2014 is het gedrag van zeevogels en hun associatie (indien aanwezig) met mariene zoogdieren genoteerd volgens standaardprotocollen. De range van de geschatte fractie van foeragerende vogels wat groot: van zeer klein (<1%); in zeekoet en alk tot 22% in noordse stormvogel en 58% in visdief/noordse stern.

Kennishiaten en aanbevelingen

Tellingen en tracking studies

Hoewel tellingen en tracking studies een belangrijke bijdrage hebben geleverd aan het begrijpen van de verspreiding van zeevogels in de Noordzee, werden een aantal kennishiaten vastgesteld met betrekking tot de onderzoeksvragen in deze studie. De meeste omgevingsfactoren die in de analyses van tellingen en tracking studies gebruikt worden betreffen proxies/indicatoren voor de abundantie en beschikbaarheid van prooivis, zoals abiotische factoren (e.g. waterdiepte, zeewatertemperatuur [SST], stratificatie, golfwerking, wind, getij, frontsystemen), biotische factoren (e.g. chlorofyl-a, dieet, prooigrootte) en menselijke activiteiten (windparken, visserijactiviteiten).

Een belangrijk kennishiaat in de analyses van tellingen en tracking data is de directe relatie tussen zeevogelverspreiding en de dichtheden en beschikbaarheid van prooivis. Andere omgevingsfactoren die invloed hebben op de voedselbeschikbaarheid en potentiële zeevogelverspreiding zijn oceaanstromingen, temperatuur anomalieën (e.g. hittegolven), nutriënten upwelling, turbiditeit, maanfase, prooisoort gedrag, *multiple species foraging associations* (MFSA's) and scheepvaartroutes. Kennishiaten specifiek voor studies met tellingen zijn de tijdsperioden tussen de huidige zes vliegtuigtellingen per jaar, plaats-trouw aan broedkolonies, interacties met andere zeevogelsoorten en Cetacea, en de verspreiding van zeevogels buiten het Nederlandse deel van de Noordzee.

Beschikbaarheid van prooivis

De verspreiding van prooivissoorten (haring, sprot, zandspieringsoorten) en het belang daarvan voor het foerageren van zeevogels in kust- en offshore gebieden wordt kort besproken. Deze prooivissoorten komen voor in de gehele Noordzee, inclusief het Nederlandse deel. Om de factoren te begrijpen die het foerageren van zeevogels in kust- en offshore gebieden bepalen is daarom een inzicht vereist in de beschikbaarheid van prooivis voor broedende en pleisterende zeevogels in de (zuidelijke) Noordzee. Hoewel prooivissoorten gemonitord worden voor het beheer van de bestanden, is de beschikbaarheid voor zeevogels een belangrijk kennishiaat. Een meer gedetailleerde spatiële en temporele monitoring van deze bestanden met betrekking tot de jaarrond beschikbaarheid voor zeevogels is vereist om de verspreiding van foeragerende zeevogels en de invloed van relevante omgevingsfactoren beter te begrijpen. De voorgestelde vervolgstudies zullen bijdragen om de benodigde data leveren voor een effectieve zeevogelbescherming.

Contents

1 Introduction

1.1 Background

The MONS (Monitoring, Onderzoek, Natuurversterking, Soortenbescherming) program was established in 2021 by the North Sea Agreement (*Noordzeeoverleg*-NZO). MONS is a research and implementation program created by the North Sea Agreement and is co-financed by the ministries of Infrastructure & Water Management (I&W), Economic Affairs & Climate Policy (EZK), and Agriculture, Nature and Food Quality (LVVN). The current project is part of a coherent set of MONS bird research projects and serves as preparation for future field studies that will contribute to answering the main questions listed below.

The MONS program includes three desk studies on seabirds. These desk studies serve as preparatory studies for the field studies. This specification concerns the development of the research questions for these desk studies (WP1), followed by the desk studies (WP2-4), and finally, a preview of follow-up field research (WP5).

Now and in the coming decades, the North Sea will undergo extensive changes stemming from a massive expansion in energy transition, as well as changes with regard to fisheries, mariculture and nature conservation. Other climate-related changes and stressors can also be expected (e.g. temperature increase, changing wind patterns, acidification), as well as policy-related changes e.g. sand extraction and terrestrial nutrient management. Within the North Sea ecosystem, coastal and offshore seabirds (along with marine mammals and large predatory fish) fulfil the role of apex predators. These species represent higher trophic levels and are potentially extremely sensitive to changes in the abundance and availability of lower trophic level organisms, such as phytoplankton via zooplankton, as well as (small) pelagic fish, which form the staple food source for most coastal and offshore seabirds (Burthe *et al.* 2012).

1.2 MONS coastal and offshore seabirds research

1.2.1 Overall research questions and aims

Such huge changes to the North Sea's ecosystem will inevitably impact coastal and offshore seabirds, which is why the aforementioned North Sea Agreement (NZA) was created. NZA have stated: "In the NZO, agreements are made about an integrated and systematic monitoring program by the government, to measure the health and development of coastal and seabird populations".

This project contributes to answering the following key questions as formulated in the MONS research program:

1. What are the consequences of the energy and food transition on the carrying capacity, expressed in environmental factors and food conditions, for functional groups of coastal and seabirds (and marine mammals) in the North Sea?
2. What are the most important areas for birds at sea (open sea and coastal waters across the international, southern North Sea), how do those areas function, and to what extent are they vulnerable (i.e. what are the most important resting and foraging areas)?
3. What are the factors (food availability, food accessibility, staging, connectivity to areas with other functions, etc.) that determine this importance, and how vulnerable are these factors to the energy and food transition?

The research questions per work package are further elaborated below.

1.2.2 Reports

The overall research project includes an overall report with three separate reports as an annex. The MONS program contains an extensive list of products, whereby each product has a unique ID number. The products delivered will meet the requirements stated in the offer (Appendix A: Request specification, under article 3.1). The products that will be delivered per work package within this assignment are:

1. Plan of Approach (work package (WP) 1)
2. **ID 60 - Desk study foraging areas coastal and seabirds (work package 2)**
3. ID 62 - Desk study food ecology sea and coastal birds (work package 3)
4. ID 64 - Desk study population studies gulls and terns (work package 4)
5. Research advice, final report and data delivery (work package 5)

Every work package is linked to the above-mentioned key questions. In work package 2 the focus is on foraging areas of coastal and offshore seabirds, in WP3 on the diet of coastal and offshore seabirds and in WP4, the focus will be on population studies of gulls and terns. In WP5 the knowledge gaps are summarised and follow-up studies are recommended.

1.3 WP2 Aims and research questions

The aim of WP2 - ID 60 is to review existing knowledge on the foraging areas of 12 selected seabird species in the (Dutch) North Sea; these areas are crucial for the survival of individual seabirds and conservation of the target seabird populations.

The main research questions for ID60 are:

(4) What are the **most important resting and foraging areas** in the (southern) North Sea for the target species of three functional species groups?
(5) Concurrently, we aim to identify **knowledge gaps** which environmental factors determine these foraging areas and, therefore,

(6) Provide **recommendations for additional research** or survey work (ships, aircraft, digital aerial surveys) of the focal seabird species, their prey and core foraging areas within the MONS project.

1.4 Approach

To date, the number of covariates included in distribution maps based on survey data is limited. Therefore, we first carried out a literature review of **tracking studies** of the target species in the North Sea area to present an overview of the covariates used to analyse habitat choice. In addition, we present distribution maps based on the **survey data**.

1.4.1 Tracking data

GPS and geolocator data can provide ample new information about the location of seabird foraging areas. It is not possible to incorporate tracking data into distribution models constructed using survey data, since the two data sources are difficult to combine. However, tracking data can be used to identify areas where birds actively forage (instead of just passing through), allowing habitat models to be created specifically for foraging areas. In this study, we provide (1) an **overview** of all existing tracking studies of the target species, with an indication of core foraging areas, and (2) an overview of the currently known **driving factors** of habitat choice (covariates, e.g. biotic/abiotic proxies for prey abundance and availability). Furthermore, after approval from the data owners, we will (3) perform **exploratory analyses** of existing data on lesser black-backed gulls, great black-backed gulls and common terns, to determine key foraging areas. In addition, knowledge gaps will be identified, and research themes recommended and prioritized.

Results

- Chapter 3: Overview of existing and future tracking data
    - Breeding season (GPS)
    - Non-breeding season (Geolocator)
    - Spatial and temporal resolution - GPS/Geolocator
- Chapter 3: Review of driving factors (covariates)
- Chapter 3: Exploratory analysis of existing data on Dutch breeding birds with an important sea-going component
    - lesser black-backed gull
    - great black-backed gull
    - black-legged kittiwake
    - Sandwich tern
    - common tern
- Chapter 6: Identification of knowledge gaps
    - For which species or areas are no tracking data available?
    - What do/don't we know about variability between species, colonies, years?
- Chapter 6: Options for filling knowledge gaps
    - Available research techniques for distribution, prey choice and food availability
    - Species and locations where research is practically feasible
    - Prioritisation of research themes

1.4.2 Survey data

In the original project proposal, RWS requested spatial distribution modelling of seabird counting data from the European Seabirds at Sea (ESAS) database. In addition, RWS asked for an interpretation of the results about (1) **where and when** the target seabird species forage, and (2) which **environmental factors** influence their habitat choice and spatial distribution. Recently, several projects were executed, or are currently underway, to do exactly what is mentioned under (1). The most recent published study includes maps based on MWTL aerial seabird surveys since 1999 (van Donk *et al.*, 2024). Unfortunately, adding ESAS data will yield little to no new distribution information. These data are outdated and highly fragmented in time and space, making it impossible to use them to create full-coverage density maps for the entire Dutch Continental Shelf (DCS).

What will yield new knowledge from the ESAS database (and also MWTL data) is to specifically select for observations of foraging birds and multi-species feeding associations (MSFAs), such as kittiwake and razorbill flocks combined. We therefore have included the analysis of observations of foraging birds and MSFAs in this study.

Additional new insights will be gained from analysing the MWTL counts from before 2014. This will provide information about the extent to which concentration areas are sustainable in the long term. However, this is already part of an existing assignment from LVVN to WE and Sovon, and we will include the results of that project in this desk study.

In addition, the research requested under (2), namely which environmental factors determine the spatial and temporal distribution of seabirds, will provide additional information closely linked to WP3, which includes a feeding ecology analysis. Furthermore, knowledge gaps will be identified, and research themes recommended and prioritised.

Results

- Chapter 4: Maps with spatial and temporal distribution of seabirds from various programmes:
    - MWTL database before 2014 (from a separate assignment for LVVN)
    - MWTL database after 2014 (Van Donk *et al.*, (2024), and expansion through separate LVVN assignment)
- Chapter 5: Overview of observations of actively foraging birds from:
    - ESAS database
    - MWTL database before 2014
    - MWTL database after 2014
- Chapter 6: Identification of knowledge gaps
    - For the target species, what do we know about core foraging areas, and what is not known?
    - What do we know about environmental variability?

    - Which environmental factors, including prey species abundance and availability, determine the spatial and temporal distribution of seabirds?
    - Can we identify proxies (indicators) for the distribution and availability of prey species that can be implemented in habitat maps?
- Chapter 6: Filling knowledge gaps – recommendations for research including field research.
    - Available research techniques for distribution, prey choice and food availability
    - Species and locations where research is practically feasible
    - Prioritisation of research themes.

2 Materials and methods

2.1 List of selected species

The twelve seabird species selected for this project are presented in Table 2.1. Motivation for the choice of these species is outlined in WP1.

Table 2.1 Conservation status of 15 seabird species, including the 12 species selected for this report (bold), with species name, conservation status in the Netherlands, OSPAR indicators for population abundance and breeding productivity, IUCN status, and vulnerability for HPAI. This list was prepared by H. Schekkerman (SOVON; see WP4)

	NL: Conservation status					KRM/OSPAR		IUCN-status		
Species (English, *Dutch*)	Season[1]	SvI[2]	Red List[3]	trend 1980[4]	trend 12 yr[5]	D1C2[6]	D1C3[7]	Europe[8]	EU 289	HPAI[10]
Red-throated Diver *Roodkeelduiker*	nb	G		~	=	.	.	LC	LC	-
Northern Fulmar *Noordse Stormvogel*	br	.		.	.	0.61	(EN)	VU	EN	-
	nb	MO		--	-					
Common scoter *Zwarte zee-eend*	nb	ZO		=	-			LC	LC	-
Northern Gannet *Jan-van-gent*	br	.		.	.	2.76	(LC)	LC	LC	††
	nb	G		+	=					
Great Skua *Grote Jager*	nb	G		=	=	0.89	(EN)	LC	LC	††
Black-legged Kittiwake *Drieteenmeeuw*	br	G	GV	+	~	0.36	(EN)	VU	EN	†
	nb	G	.	+	=					
Great Black-backed gull *Grote Mantelmeeuw*	br	G		++	+	0.57	(EN)	LC	NT	†/††
	nb	ZO		-	=					
European Herring Gull *Zilvermeeuw*	br	ZO		-	-	0.61	(CR)	NT	VU	†
	nb	MO		=	=	0.68	.			
Lesser Black-backed Gull *Kleine Mantelmeeuw*	br	G		+	-	1.29	(EN)	LC	LC	†
	nb	G		+	++					

Little Gull	br	ZO	EB	--	~	.	.	LC	LC	-
Dwergmeeuw	nb	G	.	=	=					
Sandwich Tern	br	ZO	KW	+	-	1.02	(LC)	LC	LC	††
Grote Stern	nb	G	.	+	+					
Common Tern	br	ZO	GV	-	-	0.52	(CR)	LC	LC	†
Visdief	nb	ZO	.	+	++					
Common Guillemot *Zeekoet*	nb	G		+	+	0.96	(LC)	LC	LC	†
Razorbill *Alk*	nb	G		?	?	1.41	(LC)	NT	NT	-

1 Season: season to which Dutch conservation status (SvI, below) refers: br=breeding, nb=non-breeding.

2 SvI: formal conservation status (Staat van Instandhouding SvI) in NL: G = favourabe, MO = unfavourable, ZO = quite unfavourable (SOVON-nl).

3 Red List: species is on the list of threatened and vulnerable breeding birds in NL: EB severely threatened, BE threatened, KW vulnerable, GV sensitive (Ministerie LNV, 2004)

4 Trend 1980: numerical trend in NL since 1980 (SOVON-nl)

5 Trend 12 yr: numerical trend in NL over most recent 12-year period. (SOVON.nl)

6 D1C2: KRM/OSPAR indicator for population abundance of seabirds in the Greater North Sea: favourable (green) if ≥0.7 of ≥0.8, otherwise unfavourable.

7 D1C3: KRM/OSPAR) indicator for seabird breeding productivity: expressed as the IUCN status category in which the population would hypothetically fall if the current level of breeding productivity were maintained for three bird generations.

8 Europe: IUCN-status category fort he European population: LC least concern, NT near-threatened, VU vulnerable, EN endangered, CR critically endangered. (IUCNredlist.com)

9 EU 28: IUCN-status category for the population in the 28 EU member states.

10 HPAI: mortality by Highly Pathogenic Avian Influenza in 2022-2023: - no exceptional mortality in W-Europe, † above-average mortality with limited impact on population, †† exceptional mortality that may lead to downgrading of SvI or IUCN status.

2.2 Literature review

We collected the information provided in this review via an extensive **literature search** for both published (scientific articles and grey literature) and unpublished studies. Sources were derived from Google Scholar, ResearchGate, Waardenburg Ecology's internal library and own data/reports, Movebank, and general internet searches (e.g. Seabird Group). Key search words included SEABIRD + FORAGING + GPS and/or GEOLOCATOR + NORTH SEA, with additional searches under the target species' scientific names together with covariates such as SST, PREY, HABITAT, NAO, and so on. We selected studies based on relevance (species, maps showing tracks/foraging over the (southern) North Sea, and explanatory variables, if included).

2.3 Tracking data

Currently there are two types of tracking studies: (1) geolocator and (2) GPS tracking. These provide low- and high-resolution data respectively of an animal's movements in space and time, and are further described below.

2.3.1 Geolocators

Geolocators (GLS) are small devices that use changes in light intensity over time to estimate latitude and longitude, and record light levels at frequent intervals, often every few minutes, to generate location estimates. These estimates are usually coarse and may have location errors of up to ±185 km (Phillips *et al.* 2004). They are often deployed on birds to study their movements outside the breeding season, providing information about where individuals migrate to.

2.3.2 GPS loggers

Global positioning system (GPS) loggers are small devices that can track the movement of animals by recording their location at set intervals. These loggers typically rely on satellite GPS systems to provide accurate geospatial data. The resolution of a GPS logger refers to the frequency at which it records location data - higher resolution means more frequent recordings, giving a finer level of detail in the bird's movements. While GPS loggers can be limited by battery capacity and amount of light to charge devices, settings can be changed remotely to ensure optimal battery life and year-round data collection (i.e. more frequent points during summer and fewer during winter). For seabird tracking, GPS loggers can be used to study migration patterns, foraging behaviour, and habitat use.

GPS tracking data of breeding adult seabirds are stored in a number of different online databases such as:

BirdLife's seabird tracking database	(https://www.seabirdtracking.org/),
SEATRACK	(https://seatrack.net/),
Movebank	(https://www.movebank.org/cms/movebank-main),
SEAPOP	(https://seapop.no/en/), and
RSPB's FAME & STAR databases	(https://marine.gov.scot/information/fame-star-seabird-kittiwakes-guillemots-razorbills-and-shags-tracking-projects).

The animal tracking database Movebank is a free online platform designed for managing, sharing, analysing and archiving spatial data. Within Movebank, GPS location and movement data (e.g. timestamp, latitude, longitude, speed etc) from a tracking study can be linked to various environmental variables (covariates) from its Environmenta Data Automated Track Annotation system, which lets users automatically annotate each GPS point in their dataset with environmental variables from global remote-sensing and modelled datasets. By incorporating such data in models, researchers can determine what influence these have on an individual's spatial behaviour. These variables include, but are not limited to:

- Annual temperature and temperature variance

- Sea surface temperature (SST)
- Chlorophyll-a concentrations
- Sea depth
- Fronts
- Distance from land
- Regional temperature
- Seabed roughness.

Other factors that influence coastal and seabird behaviour include forage fish abundance, discard abundance (linked to fisheries), breeding colony index (status, size or productivity of a colony), and breeding cycle.

2.4 Survey data

The survey data used in this study are from two monitoring programmes, European Seabirds at Sea (ESAS) and the 'Monitoring Waterstaatskundige Toestand des Lands' (MWTL).

2.4.1 ESAS

The European Seabirds At Sea (ESAS) database (https://esas.ices.dk) includes mostly ship-based counts of seabirds in the greater North Sea. This dataset is managed and updated by the Brussels 'Instituut voor Natuur- en Bosonderzoek' (INBO) and includes offshore monitoring data on seabirds and marine mammals. This international database mostly contains data from the North Sea, but parts of the Northeastern Atlantic Ocean are included as well. The 'Seabirds At Sea' project, was initiated in 1979 following the discovery of major oil potential in the North Sea and an urgent need to gain more knowledge on the occurrence and distribution of seabirds in their offshore habitats. This led to the execution of large-scale ship-based surveys across the North Sea using a standardised data collection method and a first European-wide data assembly in 1991. ESAS data are collected during aerial or ship-based surveys at sea and using a methodology that allows to estimate georeferenced seabird densities. The ESAS database is collated from surveys with a wide variety of objectives (See European Seabirds At Sea (ESAS), ICES, Copenhagen, Denmark). In most (standard) surveys, all species encountered were counted. However, some surveys targeted specific species or groups of species.

2.4.2 MWTL

The 'Monitoring Waterstaatskundige Toestand des Lands' (MWTL) dataset includes data from aerial surveys covering the Dutch section of the North Sea. It contains records from August 1991 to June 2014 and includes all bird and marine mammal species observed during the surveys. The MWTL dataset is managed by Waardenburg Ecology. For more detailed information on how data are gathered for the ESAS and MWTL datasets, we refer to previous studies (e.g. Camphuysen *et al*., 2004; Fijn *et al*., 2020; van Roomen *et al*., 2013). Compared to the ESAS-dataset, the MWTL dataset is more consistent, as surveys were conducted over six months of the year following a standardised approach.

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 DCS. Six bimonthly surveys were conducted in August-September, October-November, December-January, February-March, April-May and June-July, with surveys starting preferably from the 20th of the first month. This method and the survey design were adjusted in 2014. Following this change, the lower flying height allowed identification to species level of almost all species groups, including common guillemot and razorbill. In addition, the more extensive survey transects design resulted in a more even spread of survey effort across the DCS compared to the survey design before 2014.

Counts from 1991 onwards were only selected when they had a valid geographical position (latitude and longitude) and a non-zero sampled surface area. Each count was assigned to a bimonthly period: December- January, February-March, April-May, June-July, August-September and October-November.

2.5 Fishery data

2.5.1 Global Fishing Watch

The following information is copied from the website Global Fishing Watch (GFW; https://globalfishingwatch.org/dataset-and-code-fishing-effort/). The main dataset is apparent fishing effort based on positions generated by the automatic identification system (AIS) on every vessel. Currently, the Global Fishing Watch database receives over 110 million AIS messages each day. This database, the technology and algorithms used to improve our ability to monitor global commercial fishing are continually updated. This entire dataset, dating back to 2012, can be explored on maps, through public APIs and R package, or downloaded via the data download portal. Using cloud computing, machine learning and public vessel registry information, Global Fishing Watch analyses tens of millions of AIS positions each day to map global apparent fishing effort. The production of these maps involves two key steps: (1) identification of fishing vessels in the AIS data; (2) detection of fishing activity.

AIS data

The AIS data are processed as follows. AIS is a GPS-like device that large ships, and fishing vessels over 15 m, must use to broadcast their position to avoid collisions. Each year, hundreds of thousands of AIS devices broadcast vessel location along with other information on vessel identity, course and speed. Ground stations and satellites pick up this information, meaning a ship’s movements can be followed even in the most remote parts of the ocean. AIS data are received daily from AIS providers. These data are first run through a series of algorithms designed to filter out corrupt or incomplete records and assign additional information to each AIS message, such as the distance from shore, depth and time since the vessel's previous AIS position. At this point, the AIS data are ready to be used by our machine learning models.

Detecting apparent fishing activity

GFW uses two convolutional neural networks (CNN) – a form of machine learning model – to help classify fishing vessels and predict when they are fishing. These models are referred to as, our "vessel characterisation" and "fishing detection" models, respectively. The details of both CNN models are described in detail in the supplementary materials of Kroodsma *et al*., 2018. To map fishing activity, fishing vessels in the AIS data are identified. This is accomplished by combining the comprehensive database of vessel registry information with the output of the vessel characterisation model – predicting features like gear type and size – and using the best available information for each vessel. Next, it is estimated where and when each vessel is fishing based on its movement patterns. Over a thousand vessel tracks are labelled manually to train the fishing detection model to learn what fishing movements look like. This model predicts a score for every AIS position in our database to distinguish fishing positions from non-fishing positions. When the fishing detection model scores an AIS position as a fishing position, the time associated with that AIS position is considered apparent fishing activity.

2.5.2 EMODnet

The following text is copied from https://emodnet.ec.europa.eu/en/human-activities - fisheries, fishing intensity.

The datasets on fishing intensity in the EU waters by sea basin are created every year by the International Council for the Exploration of the Sea (ICES) since 2020. Data are collected and harmonized according to the EMOdnet Human Activities dataset schema. The EMODnet dataset is updated yearly, as soon as new data from ICES Fishing Overviews are released, and is available for viewing and download on the EMODnet web portal (Human Activities, https://emodnet.ec.europa.eu/en/human-activities).

Spatial distribution

Where and when available, the fisheries overview fishing intensity data concern: i) the spatial distribution of average annual fishing effort (mW fishing hours) by ecoregion (Azores, Bay of Biscay and the Iberian Coast, Baltic Sea, Barents Sea, Celtic Seas, Faroes, **Greater North Sea**, Icelandic Waters, Norwegian Sea and Oceanic Northeast Atlantic) and by gear type (Beam trawls, Bottom otter trawls, Bottom seines, Dredges, Pelagic trawls and seines, Static gears).

Fishing effort

Fishing effort data are only shown for vessels >12 m having vessel monitoring systems (VMS); ii) the average annual subsurface (top) and surface (bottom) mobile bottom contacting fishing gear (i.e. bottom otter trawls, bottom seines, dredges, beam trawls) disturbance by ecoregion in the Bay of Biscay and the Iberian Coast, Baltic Sea, Barents

Sea, Celtic Seas, Faroes, **Greater North Sea**, Icelandic Waters, Norwegian Sea and Oceanic Northeast Atlantic, expressed as average swept-area ratios (SAR). Due to data confidentiality issues, VMS/logbook data are anonymized and aggregated in a 0.05×0.05-degree grid prior to submission to ICES, using the C-squares geocode system (polygons). The last data loaded into the database, from the ICES 2024 Fishing Overview update or revision (where available), report the 2019-2022 averages. Historical data area also included in the database, starting from the 2020 fishing overview, and reporting the 2015-2018, 2017-2020, 2018-2021, and 2019-2020 averages.

3 Overview of seabird distributions in the Dutch North Sea with tracking data

3.1 Introduction

3.1.1 Importance of the North Sea for coastal and offshore seabirds

The North Sea is a shallow shelf sea and important resting and foraging habitat for coastal and offshore seabirds during the breeding and non-breeding seasons. These seabirds forage in a wide range of marine habitats on small fish and a variety of other prey items. Seabirds such as northern gannets, black-legged kittiwakes, northern fulmars and terns forage offshore at or near the surface, northern gannets can plunge dive to 25 m or more, whereas cormorants and shags are nearshore foragers, either pursuing their prey in the water column near the surface or searching for epibenthic prey in or on the seafloor (Camphuysen & Leopold 1994). During foraging intra- and interspecific interactions can occur, such as interference competition and facilitation (Camphuysen & Webb 1999).

Functional groups
Coastal and offshore seabirds can be categorised into functional groups based on their different foraging strategies and prey preferences. For example, surface feeders such as black-legged kittiwake, tern spp. and northern fulmar feed on invertebrates such as squid, and fish such as sprat, sandeel and herring (Hunt & Furness 1996). Pursuit divers such as the common guillemot, razorbill, northern gannet, great cormorant and red-throated diver forage at medium to deep depths for fish such as herring, mackerel, sandeel and cod (Hunt & Furness 1996). Herring gulls and lesser black-backed gulls are opportunistic generalists, foraging in a variety of habitats for fish, invertebrates, mollusks, discards and anthropogenic waste (Noordhuis & Spaans 1992). Benthos-feeders such as the common scoter, great coromorant and European shag dive to catch bottom-dwelling fish near the seabed or close to rocky shores (Watanuki *et al.* 2008; Fijn *et al.* 2022b). Finally, the great skua and great black-backed gull are top predators that prey on other bird species, but also scavenge or steal food, both inland and offshore. These birds feed on fish, invertebrates, discards and anthropogenic waste, hunting independently or following other seabird species to steal food (Hunt & Furness 1996; Church *et al.* 2019).

Climate change
Marine birds in the North Sea have a complex relationship with climate, being indirectly affected by changes in food availability. Coastal and offshore seabirds depend on prey species that may each respond differently to environmental changes. For example, a favourable temperature for seabirds and their main prey could be unfavourable for the prey's own food resources, reducing prey abundance and ultimately leading to negative consequences for the seabirds that rely on them (Durant *et al.* 2004). Oceanographic

factors like water temperature, salinity, and large-scale climatic events such as the North Atlantic Oscillation (NAO), further complicate this relationship (Table 3.1). These processes influence the production, distribution and abundance of the organisms marine birds feed on. Therefore, climate-driven changes in the North Sea can impact the availability of prey for seabirds, making their foraging success highly sensitive to environmental shifts (Durant *et al.* 2004).

Table 3.1 Relationships between climate variability and some of the target species in the North Atlantic (Durant et al. 2004). SST = sea surface temperature; NAO = North Atlantic oscillation.

Species	Climate variable(s)	Population parameter(s)	Observed effect	Ref
Black-legged kittiwake	SST, salinity	Sea distribution	+/none	1
Black-legged kittiwake	SST	Hatching, fledging, breeding success	+	1
Common guillemot	SST, salinity	Sea distribution	+	1, 2
Common guillemot	Stormy conditions	Foraging cost	+	3
Common guillemot	SST	Hatching, fledging, breeding success	none	4
Common tern	Salinity	Sea distribution	-	2
Great black-backed gull	SST	Hatching, fledg~~e~~ing, breeding success		4
Herring gull	Salinity	Sea distribution	-	2
Herring gull	SST	Hatching, fledging, breeding success	+	4
Northern fulmar	SST, salinity	Sea distribution	+	1, 2
Northern fulmar	Wind speed	Field metabolic rate	-	5
Northern fulmar	NAO, air temperature	Hatching, fledging success	+/-	6
Northern gannet	SST	Breeding density	+	7
Razorbill	SST	Sea distribution	+	1

References 1: (Begg & Reid 1997), 2: (Garthe 1997), 3: (Finney et al. 1999), 4: (Regehr & Rodway 1999), 5: (Furness & Bryant 1996), 6: (Thompson & Ollason 2001), 7: (Montevecchi & Myers 1997).

3.1.2 Research questions: foraging areas of target species

In this section we present an overview of known foraging areas of the target species, and whether these areas differ between season and/or breeding status.

Research questions:

- What are the main foraging areas in the North Sea of the target seabird species (if known) based on tracking data?
- Which abiotic and/or biotic factors may explain and/or predict the importance of these areas?
- Which abiotic and/or biotic factors predict the presence and availability of prey species and forage fish in particular?

3.2 Geolocator data

An overview of available geolocator tracking studies from the **non-breeding period** on the target species relevant to the (southern) North Sea, is provided in Table 3.2.

Table 3.2 Overview of geolocator studies on the target species from the non-breeding period relevant to the (southern) North Sea, with location, time period, spatial resolution, explanatory factors (covariates) and reference. To date, no GLS studies exist for great cormorant, little gull, European herring gull, great skua. SST = sea surface temperature; NAO = North Atlantic oscillation; POC = particulate organic carbon; chl a = chlorophyll a.

Species	Location	Year	Spatial resolution	Explanatory variables	Authors
Black-legged kittiwake	Various colonies	2008 - 2010	2 locations per day	-	(Frederiksen *et al.* 2012)
Black-legged kittiwake	NE Atlantic breeding colonies	2009	2 locations per day	-	(Bogdanova *et al.* 2017)
Black-legged kittiwake	UK	2012 - 2018	2 locations per day	-	(Swindells 2020)
Common guillemot	UK	2005 & 2006	2 locations per day	SST (logger derived)	(Dunn *et al.* 2020)
Common guillemot	UK	2018-2021	Light intensity at 60 s intervals; 2 fixes/day	-	(Bennett *et al.* 2024)
Common guillemot, Atlantic puffin & razorbill	UK	2014	light intensity at 60 s intervals; recorded the maximum value in each 10 min interval; 2 fixes/day	Stable isotopes	(Glew *et al.* 2018)
Common guillemot & razorbill	UK	2018	Light intensity at 60 s intervals; 2 fixes/day	-	(Buckingham *et al.* 2022)

Common guillemot & Arctic Brunnich's guillemot	Various colonies	2007-2017	2 locations per day	SST, sea surface height, air temperature, distribution of sea ice, bathymetry	(Merkel *et al.* 2021b)
Common guillemot & Arctic Brunnich's guillemot	Various colonies	2007-2017	2 locations per day	SST, sea surface height, air temperature, distribution of sea ice, bathymetry	(Merkel *et al.* 2021a)
Common scoter	Iceland	2009-2022	2 locations per day	Date variables, stopover use/duration, clutch size, nest success, distance from wintering area to breeding site	(Aðalsteinsson *et al.* 2025)
Common tern	Germany	2009-2010	2 locations per day	Date variables	(Becker *et al.* 2016)
Common tern	Germany	2019	2 locations per day	-	(Piro & Schmitz Ornés 2022)
Common tern	Germany	2016 - 2019	2 locations per day	-	(Kürten *et al.* 2022)
Common tern (& black tern)	Sweden	2009 - 2015	2 locations per day	-	(Alerstam *et al.* 2024)
Great black-backed gull	Finnmark	2012 - 2015		N. Atlantic oscillation, Atlantic water inflow, land temp, SST, mean sea level pressure	(Layton-Matthews *et al.* 2024)
Northern fulmar	Various colonies	2007 - 2018	light every 3 s, and recorded the maximum value in each 5 or 10 min interval ; 2 fixes/day	fisheries	(Dupuis *et al.* 2021)
Northern fulmar, black-legged kittiwake, common guillemot, thick-billed murre/Brunnich's guillemot, little auk and Atlantic puffin	Various colonies	2006 - 2019	2 locations per day	SST, primary production, sea surface level, depth, slope	(Fauchald *et al.* 2021)
Northern gannet	Germany	2016	30 s / 2 fixes/day	-	(Garthe *et al.* 2024)
Northern gannet	UK & Ireland	2009-2012 or 2018	2 locations per day	stable isotope; SST, POC, chl a	(Atkins *et al.* 2023)
Northern gannet	UK	2002 & 2003	light intensity at 30 s intervals; 2 fixes/day	-	(Kubetzki *et al.* 2009)
Northern gannet	UK	2018 - 2020	2 locations per day	-	(Pollock *et al.* 2021)
Northern gannet	UK	2009 - 2011	light intensity at 60 s intervals; recorded the maximum value in each 10 min interval; 2 fixes/day	-	(Deakin *et al.* 2019)
Northern gannet	Various colonies	2002-2004; 2008-2010	2 locations per day	-	(Fort *et al.* 2012)
Razorbill	Norway	2018	2 locations per day	-	(Hestem 2019)
Red-throated diver	Various colonies	2007 - 2012; 2018 - 2019	2 locations per day	Stable isotope	(Duckworth *et al.* 2022)

Table 3.3 *Environmental factors listed in the geolocator studies in Table 3.2 used as covariates to explain the distribution in the North Sea of the focal seabird species, with biotic/abiotic, unit of measure, covariate type, representing prey type, prey availability or used as proxy. SST = sea surface temperature; NAO = North Atlantic oscillation; POC = particulate organic carbon; chl a = chlorophyll a.*

Environmental factor	biotic/ abiotic	unit	Factor type	Prey type	Prey avai-lability	Proxy
Sea surface height	abiotic	m	Depth			?
Slope	abiotic	degrees	Sea floor			?
Stable isotopes	abiotic	δ	Biological/chemical	?		
Bathymetry	abiotic	m	Depth			1
Depth	abiotic	m	Depth			1
Fisheries	biotic	-	Fisheries		1	
Distribution of sea ice	abiotic	km^2	Geography		1	
Atlantic water inflow	abiotic	-	Hydrodynamics			1
Chl-a	biotic	mg/l	Primary production			1
POC	biotic	-	Primary production			1
Primary production	biotic	-	Primary production			1
Air temperature	abiotic	ºC	Temperature			1
Land temperature	abiotic	ºC	Temperature		1	
SST	abiotic	ºC	Temperature			1
SST (logger derived)	abiotic	ºC	Temperature			1
Mean sea level pressure	abiotic	Bar	Weather		1	
N. Atlantic oscillation	abiotic	-	Weather		1	

In total, ten different covariate types were included in the 25 studies analysed (Table 3.3). In most studies the environmental covariates were used as a proxy for prey type and/or prey availability and only five studies included covariates for prey availability, such as fishery activity, distribution of sea ice, and weather (mean sea level pressure, temperature). No studies of seabird distribution with geolocators using direct estimates of prey type and abundance are yet available.

Below we present selected highlights (based on species and relevance of study to the North Sea) from some of the studies mentioned in Table 3.2, which are presented per species:

3.2.1 Black-legged kittiwake

Frederiksen *et al.* (2012) used geolocators to study the winter distribution of black-legged kittiwakes from various breeding colonies in the north Atlantic. While migration costs for kittiwakes are low, little is known about their winter diet, making it difficult to pinpoint the precise factors that influence kittiwake distribution. Kittiwakes primarily feed on surface prey but may also dive for fish and large zooplankton. Their diet likely depends on mesozooplankton, especially calanoid copepods which are abundant in near-surface waters. In the 2009/10 winter, approximately 15% of the tagged birds wintered in the North Sea and around the British Isles (Figure 3.1), however this may not fully represent all breeding areas. Distribution patterns may also differ between years, possibly due to changes in weather patterns or prey availability (Frederiksen *et al.* 2012).

While no environmental covariates were tested against the data, individual conditions such as breeding success influenced kittiwake movements. Birds from colonies with poor breeding success migrated earlier and farther across the Atlantic, with males and females possibly exhibiting different migratory behaviours (Frederiksen *et al.* 2012). While this study provides a general sense of kittiwake wintering areas, future research should explore how different age classes and environmental conditions influence winter distribution, as the movements of pre-breeders may differ significantly from those of adults.

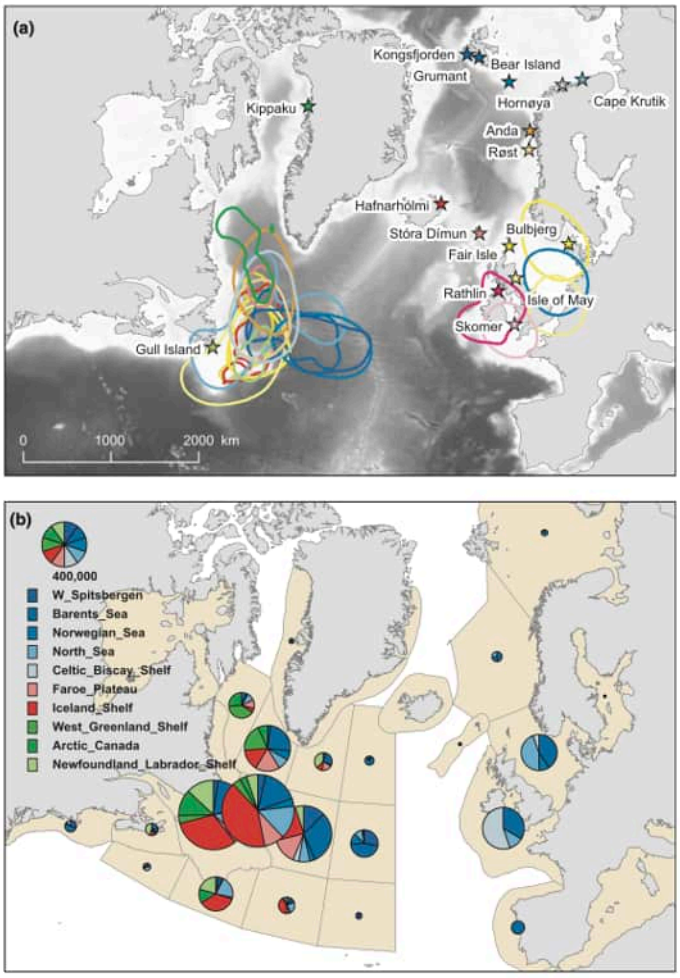


Figure 3.1 *Areas used by wintering adult kittiwakes in the North Atlantic. (a) shows 50% kernel contours for each colony in December 2009. Study colonies are also shown, with the same colour scheme used for kernel contours and colonies. Kernels were not calculated for colonies represented by < 5 birds. (b) shows the estimated number of adult kittiwakes wintering in each large marine ecosystem (LME) and offshore block, indicated by symbol size, and their distribution by breeding origin (LME), indicated by colour shading as shown. Map projection: equidistant conic. Bathymetry according to ETOPO1 (Amante & Eakins, 2009). LMEs shown as defined by UNEP and downloaded from http://www.lme.noaa.gov/ (Frederiksen et al. 2012).*

Bogdanova *et al.* (2017) deployed geolocators on black-legged kittiwakes from various Atlantic colonies to study their winter movements. Many individuals from south western colonies migrated to the North Sea (or Denmark Strait), known to be highly productive in late summer (Paramor *et al.* 2009). However, no covariate data were included in the study to expand on this. Swindells (2020) tracked 15 kittiwakes from the UK to examine their core winter ranges; two birds remained in the North Sea throughout the wintering period

Figure *3.2).*

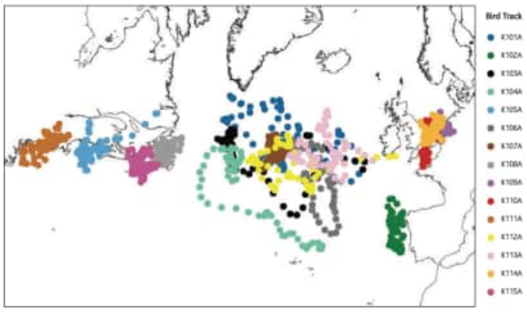


Figure 3.2 *All December positions for the primary GLS track for 15 black-legged kittiwakes tracked from the UK (Swindells 2020).*

3.2.2 Common guillemot

Dunn *et al.* (2020) deployed gelocators on 13 common guillemots breeding in the UK to investigate year-round energy expenditure. During the breeding season, daily energy expenditure (DEE) was higher due to thermoregulatory needs and increased flight activity. DEE patterns also reflected variations in SST; the moult period occurred when SST were high (Dunn *et al.* 2020). Also during moult, guillemots foraged in productive areas, possibly to support feather renewal and fat accumulation. After moult, DEE gradually increased through winter, peaking in April before the breeding season (Dunn *et al.* 2020). The DEE estimates align with those from guillemot populations elsewhere (Fort *et al.* 2013; Burke & Montevecchi 2018).

Guillemot dive activity was also influenced by stormy weather and the need to attain optimal body condition. Nocturnal diving became a strategy during winter, likely due to prey availability, with guillemots adapting their foraging behaviour to improve energy intake (Dunn *et al.* 2020). This study highlights the energetic challenges of winter and the adaptive behaviours that allow individuals to manage their energy budgets.

After the breeding season, guillemots migrated to and remained within the North Sea (Figure 3.3). From January, despite moving closer to the breeding colony, guillemots still foraged in the central part of the northern North Sea (Dunn *et al.* 2020). This shows that the North Sea provides sufficient foraging and environmental conditions to support guillemots year-round, which was also demonstrated by a later study (Bennett *et al.* 2024).

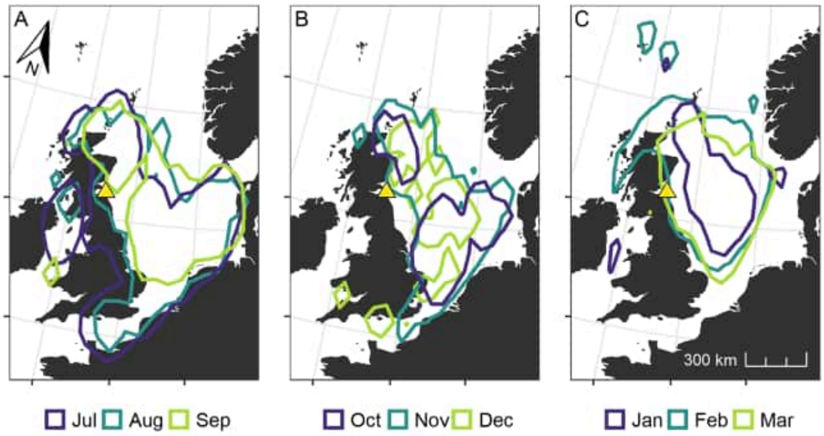


Figure 3.3 *Core areas utilised by common guillemots from the Isle of May outside the breeding season. Core use areas (50% kernel density contours) of 13 common guillemots from the Isle of May (yellow triangle) according to month and period of the non-breeding season (Dunn et al. 2020).*

St. John Glew *et al.* (2018) deployed geolocators on common guillemots, puffins and razorbills from Scotland, and upon retrieval collected feather samples from each bird to assign individuals to possible foraging areas. Guillemots most likely foraged in the southern North Sea during post-breeding secondary feather growth and pre-breeding neck feather growth. In all species and feather types, the isotope-based assignment areas overlapped geolocator estimates of likely location during the moulting period (Figure 3.4); (St. John Glew *et al.* 2018).

The authors also found that guillemots had a flexible and adaptive winter diet, while puffins and razorbills exhibited more uniform patterns (St. John Glew *et al.* 2018). Guillemots fed at a higher trophic level than razorbills, with puffins shifting from a specialised diet in summer to a lower-trophic diet in winter. Such trophic level segregation may reduce inter-specific competition outside the breeding season (St. John Glew *et al.* 2018).

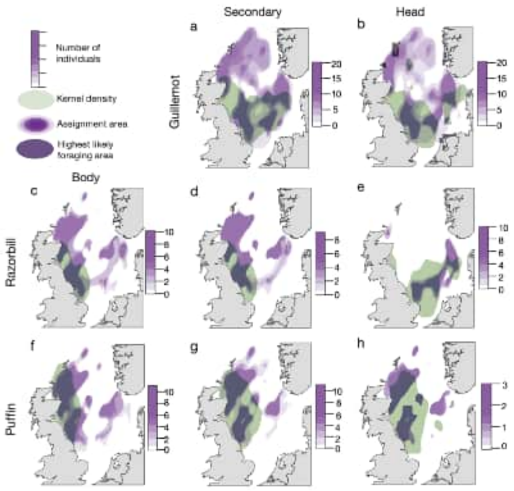


Figure 3.4 *Population isoscape assignment areas and corresponding kernal density areas for the months when moulting of each feather type for each species (guillemot, razorbill, puffin) is known to occur (St. John Glew et al. 2018).*

Buckingham *et al.* (2022) deployed geolocators on guillemots and razorbills breeding at various colonies in the UK to examine core colony distributions during post-breeding moult and mid-winter. Guillemots had a broad distribution across Scottish coastal waters, the North Sea, Norwegian Sea, and Barents Sea, while razorbills mostly stayed in Scottish waters. In mid-winter, guillemots were mostly coastal, while razorbills concentrated in the central North Sea (Buckingham *et al.* 2022).

Razorbills exhibited higher levels of aggregation, with all populations overlapping in a single area during post-breeding moult and mid-winter, unlike guillemots whose populations were more dispersed (Figure 3.5). Such differences can be attributed to variations in prey preference and winter colony attendance (Buckingham *et al.* 2022). Guillemots also had more variable foraging and diet (Ouwehand & Leopold 2004; St. John Glew *et al.* 2018), with some populations attending breeding sites from October, likely driven by local prey availability despite the higher energetic costs. In contrast, razorbills did not attend breeding colonies during the non-breeding season and instead aggregated based on prey location, suggesting a more inflexible diet (Buckingham *et al.* 2022). This behaviour is similar to patterns seen in other seabirds, such as black-legged kittiwakes (Frederiksen *et al.* 2007).

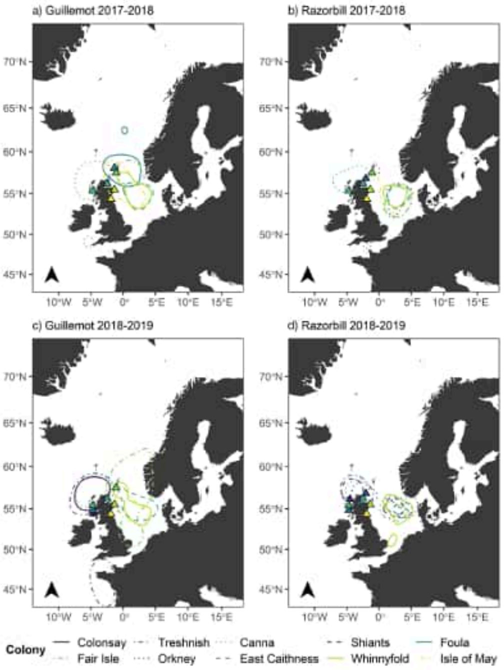


Figure 3.5 *Core colony distributions (50% kernel density contour outlines) of common guillemots and razorbills during mid-winter (6 December − 5 January). Colony locations are depicted by triangles, with colours matching the distributions (Buckingham et al. 2022).*

Merkel *et al.* (2021a) used ecologically relevant oceanographic parameters to quantify environmental niches occupied by common guillemot (and Brunnich's guillemot) during the non-breeding period based on geolocator data. The authors determined that individual movement and site fidelity (IMSF) was explained by site familiarity rather than habitat specialisation and specific environmental conditions, with the exception of depth during spring (Merkel *et al.* 2021b).

The authors identified a consistent pattern of IMSF in guillemots during the non-breeding period, persisting across multiple years (Figure 3.6). IMSF at the mesoscale was strongly supported, however there was evidence of temporal variation, particularly during late winter (Merkel *et al.* 2021b). IMSF is advantageous for guillemots since exploring new sites has energetic costs, however individuals can adjust their behaviour if conditions at a known site become unfavourable (Merkel *et al.* 2021b).

The authors concluded that site familiarity may become a less viable strategy as marine environments change due to climate change and other anthropogenic impacts. Guillemots may struggle to adjust their migration strategies to cope with rapid environmental shifts, especially given high energetic costs and reliance on experience and memory to guide migration (Merkel *et al.* 2021b). This could have significant implications for their ability to cope with habitat loss and changing ecological conditions in the North Sea.

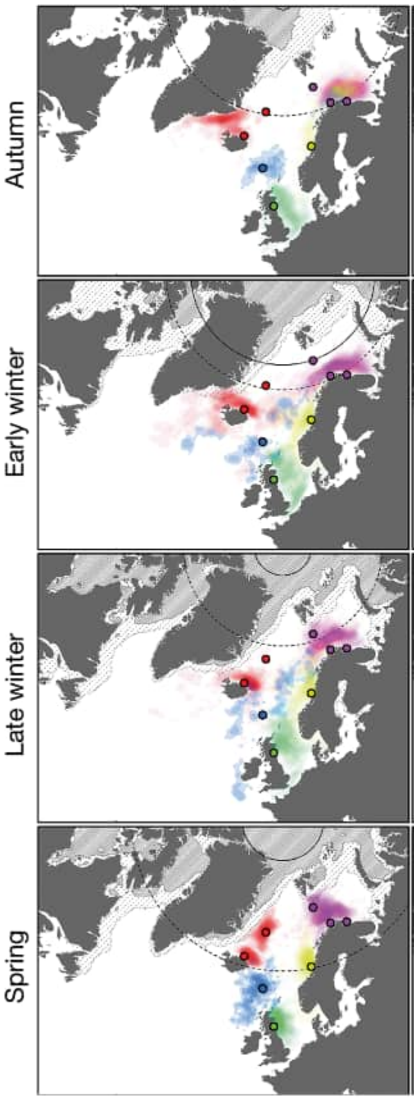


Figure 3.6 Seasonal distributions for common guillemots during autumn, early winter, late winter and spring. Kernel utilisation distributions (UD) show seasonal space use by breeding population as composite of individual UDs scaled to their respective population sample size. High colour intensity indicates use by several populations. Dots: colony locations; dashed and solid large circles: areas where location estimation was affected by or impossible due to polar night or midnight sun, respectively; grey stippled and hatched areas: 15 and 90% ten year seasonal median sea ice concentration, respectively. Colours correspond to spatiotemporal clusters identified by network analysis (Merkel et al. 2021a).

3.2.3 Common scoter

A geolocator study on 30 common scoters breeding in Iceland found females wintering further from their nest site did not exhibit reduced breeding success compared to those that wintered closer. Although foraging was not the main focus of this research, this suggests that birds wintering further south may benefit from a better winter energy balance, enabling them to commence their spring migration earlier and offset longer travel distances (Aðalsteinsson *et al.* 2025). Individual variation played a bigger role in migration and timing of breeding than the environmental covariates tested. Variation in timing decreased at each migration phase, reaching its lowest during breeding, suggesting a progressive fine-tuning of migration and breeding to align with local conditions. Distance to overwintering grounds had a limited effect on the timing of breeding or success (Aðalsteinsson *et al.* 2025). The authors recommend studying a larger number of post-breeding individuals with better tracking technology to understand the long-term patterns and effects of climate change on common scoters.

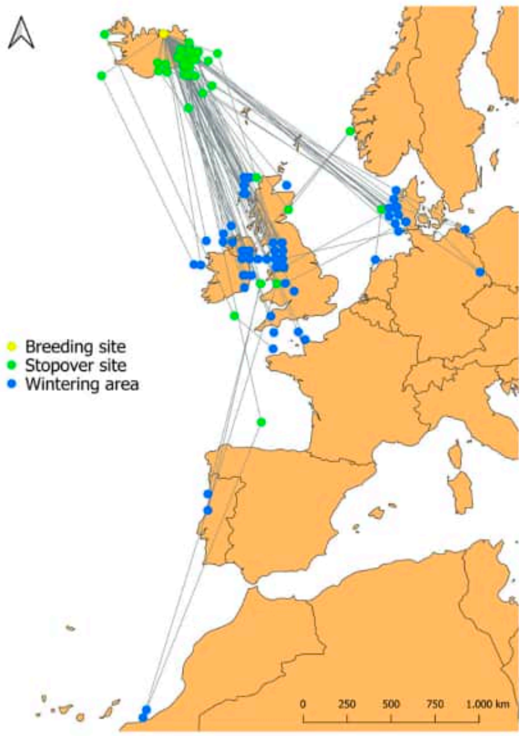
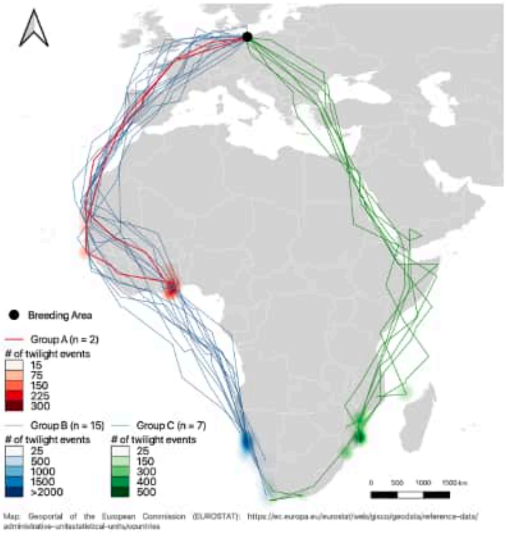


Figure 3.7 Map linking the identified wintering areas, spring stopover sites and breeding sites, for all geolocation tracks analysed from female common scoter caught in Iceland (yellow dot; 67 tracks from 30 females). The location estimates for the wintering areas and stopover sites are shown as the median latitude and median longitude of all the twilights identified as parts of these stationary periods. Owing to the inherent inaccuracies of light-level geolocation analyses, the location estimates shown here might vary considerably from the true location of the birds, and this is especially true for the stopover sites. Location estimates far out on sea or far inland are likely to be biased and should be somewhere closer to the shore (Aðalsteinsson et al. 2025).

3.2.4 Common tern

Piro & Ornés (2022) deployed geolocators on 40 common terns from Germany to track their migration routes and wintering areas. Eight birds followed the East Atlantic Flyway, travelling through and stopping at the North Sea (Figure 3.8). A separate German geolocator study tracked the migratory movements of 64 common terns, all of which travelled through the North Sea (Figure 3.9) (Kürten *et al.* 2022). A study from Sweden on six common terns found a similar flight and stopover pattern (Alerstam *et al.* 2024). While no covariate data were included in these studies, the North Sea is thought to be an important stopover site for common terns, even if it is occupied for a short period of time (Kürten *et al.* 2022; Piro & Schmitz Ornés 2022).



Map: Geoportal of the European Commission (EUROSTAT): https://ec.europa.eu/eurostat/web/gisco/geodata/reference-data/administrative-units-statistical-units/countries

Figure 3.8 Migration routes and winteringareas of common terns from Germany tracked with geolocators (Piro & Schmitz Ornés 2022).

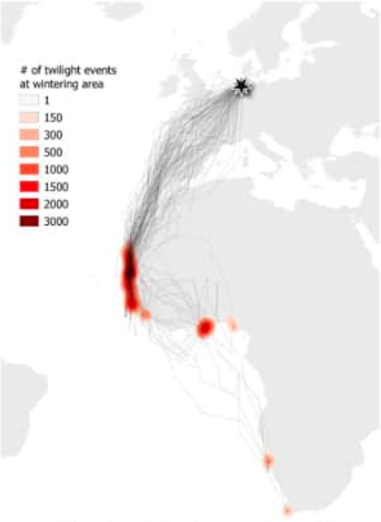


Figure 3.9 Migration routes and wintering areas of 64 common terns tracked with geolocators (Kürten et al. 2022).

3.2.5 Great black-backed gull

Layton-Matthews *et al.* (2024) tracked year-round movements of non-breeding great black-backed gulls from a colony in northern Norway. Based on geolocation data, individuals foraged close to the colony during spring (Figure 3.10). After breeding they travelled to the North Sea, where most individuals remained throughout winter (Layton-Matthews *et al.* 2024). The authors also found evidence of warmer SST increasing gull survival rates, however there was no significant temporal trend in late-winter SST over the study period (Layton-Matthews *et al.* 2024). Changes in SST from 2002 to 2017 may have driven a temporary increase in prey resources (e.g. swimming crabs), but the consequences of future increases in SST for great black-backed gulls are unknown.

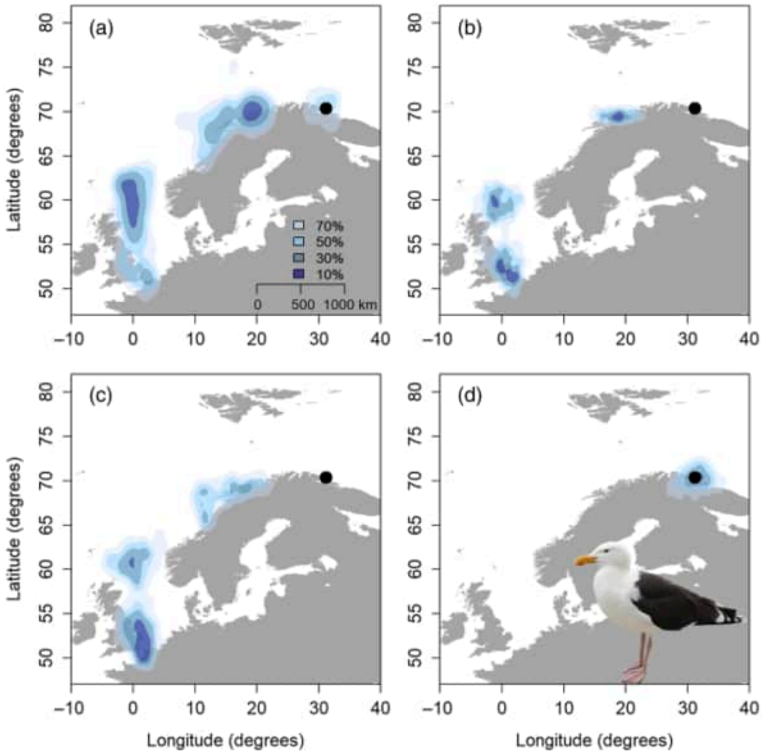


Figure 3.10 *Year-round non-breeding areas of adult great black--backed gulls from Norway based on positions from individuals with geolocators from 2012–2015 for autumn [September–October (a)], early winter [November–December (b)], late winter [January–February (c)] and spring [April (d)] seasons (Layton-Matthews et al. 2024).*

3.2.6 Northern fulmar

Fauchald *et al.* (2021) deployed geolocators on northern fulmar, black-legged kittiwake, common guillemot, Brünnich's guillemot, little auk and Atlantic puffin to create year-round species distribution models. SST, sea surface level, primary production, depth, slope, distance to coast and day length were included as explanatory variables (Fauchald *et al.* 2021). However, many of these were highly correlated (e.g. SST, day length and sea surface height). Multicollinearity is an issue when projecting future seabird distributions, especially in relation to climate change as SST varies annually. The authors stressed that the models developed were useful for assessing seabird habitat use within the time and space covered by the study but should not be relied upon for predicting future distributions, especially in a warmer climate (Fauchald *et al.* 2021). The study was also limited by gaps in the data, such as not including juvenile birds or colonies from certain regions (Fauchald *et al.* 2021).

The North Sea was shown to support high combined densities of these species across all seasons, extrapolated to 23.5 million individuals (Figure 3.11). Birds from colonies close to each other (<500 km) tended to use the same habitats, while for distant colonies (>1,000 km) the non-breeding habitats were population-specific, and in many cases did not overlap (Fauchald *et al.* 2021).

The authors also highlighted the importance of understanding colony-specific habitats, as different colonies may use distinct non-breeding areas. This has implications for mapping biodiversity hotspots, since tracking data from a few colonies may overlook areas that are critical for different populations. Therefore, careful interpretation of hotspot data and validation of tracking data is essential to ensure comprehensive marine spatial planning and effective conservation strategies (Fauchald *et al.* 2021).

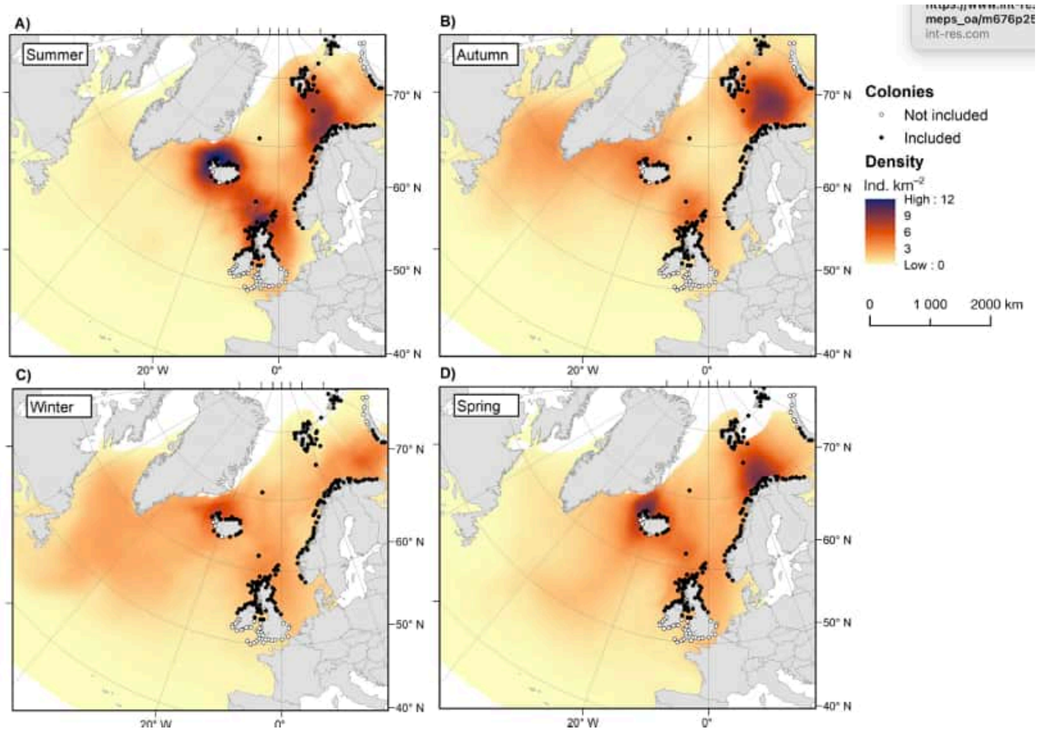


Figure 3.11 *Summed distribution of Northern fulmar, black-legged kittiwake, common guillemot, Brünnich's guillemot, little auk and Atlantic puffin in A) summer (May-July) breeding period, B) autumn (August-October) migration period, C) winter (November-January) wintering period and D) spring (February-April) migration period. Black circles: colonies included in density estimates; white circles. Colour scale shows the density of birds predicted by the species distribution models on a linear scale from 0-12 birds km^{-2} (Fauchald et al. 2021).*

3.2.7 Northern gannet

Atkins *et al.* (2023) performed stable isotope analysis and deployed geolocators on northern gannets in the UK (Ireland) to identify their overwintering areas. December monthly average or winter seasonal average SST, particulate organic carbon, chlorophyll-a and bathymetry were included as environmental variables (Atkins *et al.* 2023). Only SST had a significant effect on carbon and nitrogen isotope values (Figure 3.12), suggesting that temperature-driven changes in carbon and nitrogen dynamics are altering isotope ratios in the system. This could be due to shifts in primary production, nutrient availability, or food web structure. Of 74 tracked birds, six (8.1%) wintered in the North Sea (Atkins *et al.* 2023).

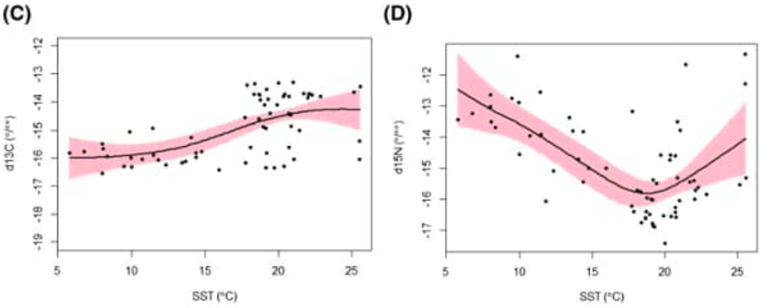


Figure 3.12 Generalised additive model (GAM) results showing significant non-linear relationships between (C), δ13C and sea surface temperature (SST) C; (D), δ15N and SST. The solid line is the model estimated mean, and the pink polygon represents the model standard error (Atkins et al. 2023).

Kubetzki *et al.* (2009) deployed geolocators on 41 chick-rearing gannets in Scotland to study their migratory movements in the non-breeding season. Three birds remained in the North Sea/English Channel, but most travelled further south (Figure 3.13). The authors recommend further studies to determine the reasons for staying in the North Sea versus migrating to West Africa.

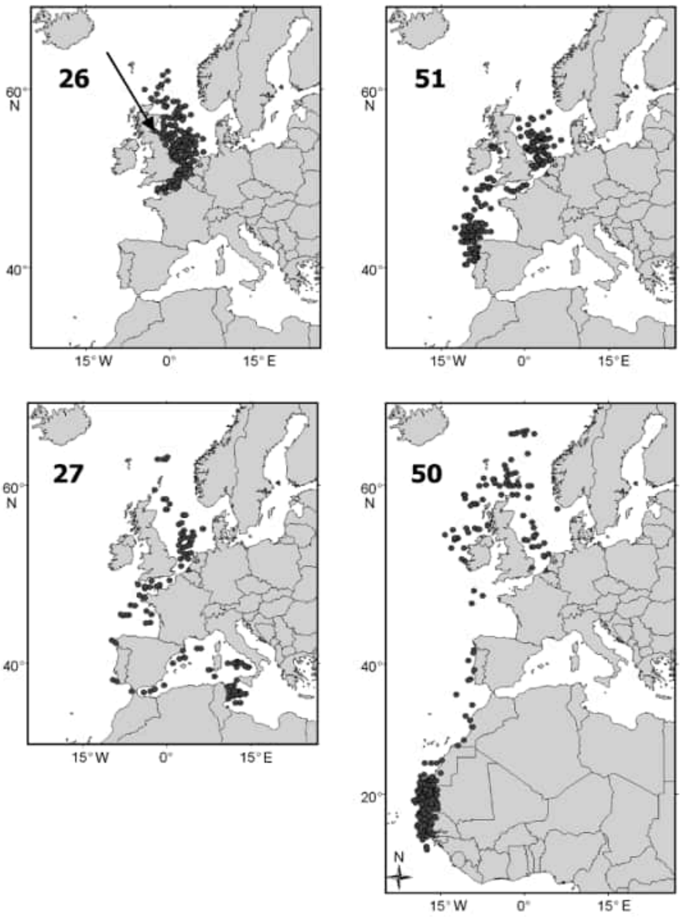


Figure 3.13 *Movements of individual northern gannets (Birds 26, 27, 50, 51) equipped with geolocators on Bass Rock (indicated by arrow in top left panel), Scotland. Each dot represents 1 of 2 daily positions roughly between October and March (Kubetzki et al. 2009).*

Similarly, Garthe *et al.* (2024) deployed geolocators on 12 northern gannets breeding in Germany to determine their winter locations. Of the 12 individuals tracked, five stayed in the North Sea (Garthe *et al.* 2024). Pollock *et al.* (2021) tracked adult and juvenile gannets from Scotland to assess their movements in relation to offshore wind farms (OWF) in the southern North Sea (Figure 3.14). The authors found that juveniles tended to migrate closer to the shore through the southern North Sea, whereas adults briefly travelled northwards to Norwegian waters in early autumn, before taking the most direct route south (Pollock *et al.* 2021).

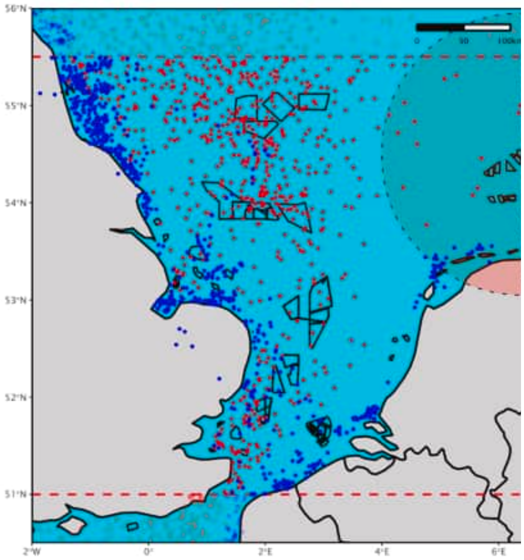


Figure 3.14 *Location estimates of adult (red dots) and juvenile (blue dots) northern gannets during autumn migration through the southern North Sea in 2018-2019. Black polygons represent operational or planned offshore wind farm areas (Pollock et al. 2021)*

3.2.8 Razorbill

Hestem (2019) investigated the spatial distribution and activity patterns of 18 razorbills from Norway during the non-breeding season of 2018-2019. One group of razorbills inhabited an area ranging from the eastern part of the North Sea to the beginning of the western part of the Baltic Sea, most having their core wintering home ranges east of the Danish Skagen peninsula (Figure 3.15). No environmental variable data were included in this study.

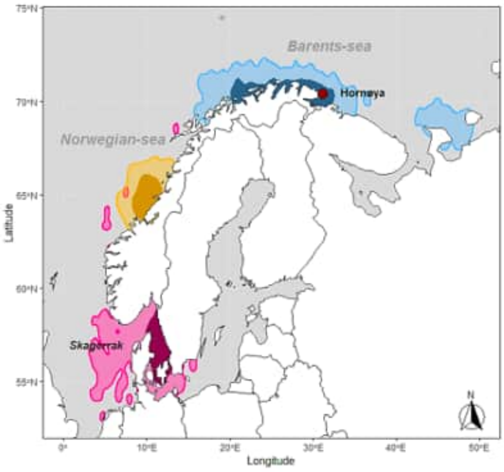


Figure 3.15 *Geographic distributions of razorbills during the wintering period displayed as 95 & 50% kernel density contours (main & core home ranges). Blue: Birds wintering in the Barents-sea region (resident). Brown: Migratory birds wintering in the Norwegian Sea. Red: Migratory birds wintering in the Skagerrak region (Hestem 2019).*

3.2.9 Red-throated diver

Duckworth *et al.* (2022) deployed geolocators on red-throated divers breeding in Finland, Iceland and Scotland. Birds from Finland migrated to the western Baltic in early winter, and southern North Sea by late winter (Figure 3.16). The authors stress the difficulties of using GLS tags on the species and strongly recommended against their use. Nevertheless, the location estimates from this study provide a good indication of the areas used during the non-breeding season, and hence migration strategy of red-throated divers (Duckworth *et al.* 2022).

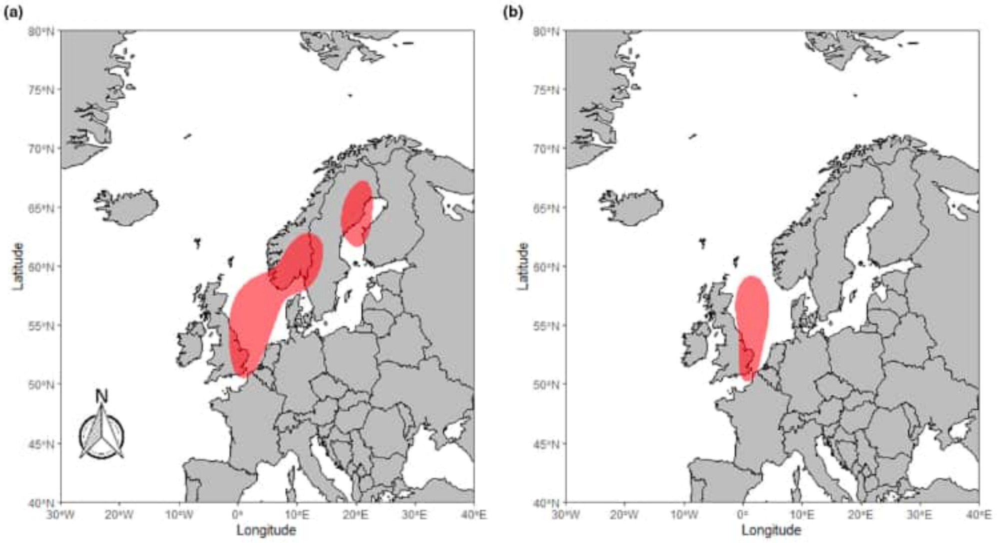


Figure 3.16 *50% kernel density distribution of red-throated divers sampled in Finland during early (a) and late (b) winter from 2017-2021 (Duckworth et al. 2022).*

3.3 GPS data

Numerous GPS tracking studies (51 in total) on coastal and offshore seabirds during the **breeding season** have been published from the UK, Ireland and western Europe (Table 3.4). Distribution and foraging behaviour during the breeding (as well as non-breeding) season can be modelled using predictive environmental variables based on high-resolution GPS data.

*Table 3.4 Overview of 51 relevant GPS studies published on the target species in the (southern) North Sea with location, time period, spatial resolution, covariates and authors. *study involved PTT satellite tags.*

Species	Location	Year	Spatial resolution	Explanatory variables	Authors
Black-legged kittiwake	UK	2010 - 2012	15-sec intervals	-	(Redfern & Bevan 2014)
Black-legged kittiwake	UK	2011 - 2012	100-sec intervals	Nighttime SST, bathymetry and chlorophyll-a; prey type	(Robertson *et al.* 2014)
Black-legged kittiwake	UK	2021	10-min intervals (10 sec in geofence)	Bathymetry, slope, gravel, sand-mud ratio, SST, ocean front, tidal height	(O'Hanlon *et al.* 2024)
Black-legged kittiwake	UK & Ireland	2010 - 2017	100-sec intervals	Bathymetry, tidal stratification, SST, ocean front strength, distance to nearest ocean front, ocean front persistence, environmental heterogeneity	(Trevail *et al.* 2021)
Common guillemot	Germany	2016 & 2017	10-min intervals	Bathymetry, slope. Mention of prey species but not studied (German N.Sea)	(Peschko *et al.* 2020)
Common scoter*	The Netherlands	2017-2019	0.7 – 9.7 locations per day	Time of day, fish density (fresh mass m^{-2})	(Camphuysen & van Lieshout 2024)
Common tern	Germany	2019	5-min intervals	Tides, sediment type, distance to coast, distance to colony, time of day	(Militão *et al.* 2023)
Common tern	The Netherlands	2021-2022	40-min intervals from 4am – 11pm	Habitat type, prey species	(Manche *et al.* 2023)
Common tern	The Netherlands	2022	40-min intervals		(van der Zwan-Krijn & Loonstra 2023)
European shag, black-legged kittiwake, common murre, razorbill	UK & Ireland	2010 - 2014	100-sec intervals	Bathymetry, slope, distance to coast, gravel, sand-mud ratio, potential energy anomaly, proportion of time water column was stratified, SST, thermal front gradient density, NPP	(Wakefield *et al.* 2017)
Great black-backed gull	Norway	2024	3-min intervals	SST, salinity, chlorophyll-a, bathymetry	(Madden *et al.* in review)
Great black-backed gull	Germany	2016	5-min intervals	Tides	(Bormann *et al.* 2019)

Great cormorant	The Netherlands	2012	2-4 min intervals (day)/1 fix (night)	Bathymetry, salinity, wave height, surface current speed, wind speed, air temperature	(Fijn *et al.* 2022b)
Herring gull	Belgium	2013 - 2017	1-10 min intervals	Habitat types as a proxy for possible prey	(van den Bosch *et al.* 2019)
Herring gull	The Netherlands	2013 - 2016	5-10 min intervals	Habitat types as a proxy for possible prey	(Van Donk *et al.* 2019)
Herring gull	The Netherlands	2013 - 2015	5-10 min intervals	Habitat types as a proxy for possible prey	(Van Donk *et al.* 2020)
Lesser black-backed gull	Germany	2008 - 2013	2, 3 & 5-min intervals	-	(Corman *et al.* 2016)
Lesser black-backed gull	The Netherlands	2019 & 2020	3-sec intervals in geofence	-	(van Erp *et al.* 2023)
Lesser black-backed gull	The Netherlands	2008 - 2011	5-20 min intervals	Prey samples collected	(Camphuysen *et al.* 2015)
Lesser black-backed gull	Germany	2013	5-min intervals	-	(Corman & Garthe 2014)
Lesser black-backed gull	Germany	2010	3-min intervals	Pellets & stable isotope, habitat selection, fishing vessels	(Garthe *et al.* 2016)
Lesser black-backed gull	The Netherlands	2008 - 2022	30 sec – 60-min intervals	-?	(Kentie *et al.* 2024)
Lesser black-backed gull	The Netherlands	2008 – 2014	60-min intervals	Pellets/regurgitates collected. Habitat types as a proxy for possible prey	(Camphuysen *et al.* 2023)
Lesser black-backed gull	The Netherlands & Belgium	2015 - 2017	3-min intervals	-	(Kavelaars *et al.* 2020)
Lesser black-backed gull	Belgium	2013 - 2017	10-3600 sec intervals	-	(Vanermen *et al.* 2020)
Lesser black-backed gull	The Netherlands	2017 & 2018	10-min intervals (3 sec in geofence)	-	(Sage & Shamoun-Baranes 2022)
Lesser black-backed gull	The Netherlands	2008 - 2013	5 & 20-min intervals	-	(Shamoun-Baranes *et al.* 2017)
Lesser black-backed gull	Germany	2008 & 2009	2-min intervals	-	(Sommerfeld *et al.* 2016)
Lesser black-backed gull	Belgium	2013 - 2018	1-30 min intervals	-	(Sotillo *et al.* 2019)
Lesser black-backed gull	The Netherlands	2008 - 2012	5-20 min intervals	Habitat types as a proxy for fishery associations	(Tyson *et al.* 2015)
Lesser black-backed gull	The Netherlands	2013 - 2017	3-min intervals	Habitat types as a proxy for possible prey	(Baert *et al.* 2018)
Lesser black-backed gull & herring gull	The Netherlands	2007	4-18 fixes per day	Habitat types as a proxy for possible prey	(Ens *et al.* 2008)
Lesser black-backed gull & herring gull	The Netherlands	2008	Not stated	Pellets/regurgitates collected. Focus on fisheries/discards	(Camphuysen *et al.* 2008)

Lesser black-backed gull & herring gull	The Netherlands & Belgium	2013 - 2015	450-s intervals	-	(Stienen *et al.* 2016)
Lesser black-backed gull & northern gannet	Germany	2008 – 2013; 2014	3 & 5-min intervals	Pellets and stable istopes	(Corman 2015)
Northern fulmar	UK	2009 - 2019	3-min intervals	Sishing effort, SST, stratification, chlorophyll-a, seabed roughness	(Darby *et al.* 2021)
Northern gannet	UK	1998, 2002, 2003	3 & 30-min intervals	Regurgitates collected	(Hamer *et al.* 2007)
Northern gannet	Germany	2014	Not stated	-	(Garthe *et al.* 2017a)
Northern gannet	Germany	2015	3-5 min intervals	distance to colony, depth, distance to land	(Garthe *et al.* 2017b)
Northern gannet	UK & Ireland	2011	2-min intervals	-	(Bennison *et al.* 2018)
Northern gannet	UK	2010 - 2012	2-min intervals	-	(Cleasby *et al.* 2015)
Northern gannet	UK	2015	2-min intervals	FLSE values as a proxy for SST and chlorophyll-a	(Grecian *et al.* 2018)
Northern gannet (juvenile)	UK	2018 & 2019	60-min intervals	-	(Lane *et al.* 2021)
Razorbill, European shag, black-legged kittiwake, common guillemot	UK	2010 - 2014	Not stated	-	(Cleasby *et al.* 2020)
Red-throated diver*	Germany	2014-2018		Salinity, bathymetry and chlorophyll-a	(Kleinschmidt et al. 2019, Burger et al. 2019, Heinänen et al 2019, Dorsch et al. 2020)
Sandwich tern	The Netherlands	2012 – 2013; 2017	5 & 10-min intervals	?	(Fijn *et al.* 2024)
Sandwich tern	The Netherlands	2012 - 2015	5-min intervals	?	(Fijn *et al.* 2017)
Sandwich tern	The Netherlands	2009 - 2013	5 & 15-min intervals	-	(Fijn *et al.* 2014)
Sandwich tern	The Netherlands	2012 & 2013	5 & 15-min intervals	?	(Fijn & Poot 2014)
Sandwich tern	The Netherlands	2012 – 2015; 2017	5-min intervals	Sediment and sand eels	(Fijn *et al.* 2022a)
Sandwich tern	UK	2016 - 2019	5 & 10-min intervals	Mention of sand eel nursery grounds and sediment	(Thaxter *et al.* 2024)
Sandwich tern	UK & the Netherlands	2013 - 2019	5-15 min intervals	Sediment type, bathymetry, temperature, wind speed, cloud, salinity, water temperature	(van Bemmelen *et al.* 2022)
Sandwich tern	UK & the Netherlands	2016 - 2021	5 & 10-min intervals	Sediment type, bathymetry	(van Bemmelen *et al.* 2024)
Sandwich tern	UK	2006 & 2007	60-sec intervals	Salinity, water temperature, sediment	(Baxter *et al.* 2011)

In total, 12 different covariate types were included in the 51 studies analysed (*Table 3.5*). In most studies the environmental covariates were used as proxy for prey type and/or prey availability, and only 15 studies included covariates for prey availability. Seven studies of seabird distribution with geolocators used direct estimates of prey type and abundance.

Table 3.5 *Environmental factors listed in the GPS studies in Table 3.4 and used as covariates to explain the distribution in the North Sea of the focal seabird species, with biotic/abiotic, unit of measure, covariate type, representing prey type, prey availability or used as proxy.*

Nr	Environmental factors	Abiotic/biotic	Unit	Environmental factor type	Prey type	Prey availability	Proxy
	bathymetry	abiotic	m	Depth			?
	distance to coast	abiotic	km	Geography		1	
	distance to colony	abiotic	km	Geography			1
	distance to nearest ocean front	abiotic	km	Hydrodynamics			1
	ocean front	abiotic		Hydrodynamics		1	
	ocean front persistence	abiotic		Hydrodynamics		1	
	ocean front strength	abiotic		Hydrodynamics		1	
	surface current speed	abiotic	m/s	Hydrodynamics		1	
	tidal height	abiotic	m	Hydrodynamics		1	
	tidal stratification	abiotic		Hydrodynamics		1	
	Tides	abiotic		Hydrodynamics		1	
	wave height	abiotic	m	Hydrodynamics		1	
	salinity	abiotic	PSU	Salinity			1
	gravel	abiotic	n/a	Seafloor			1
	sand-mud ratio	abiotic	n/a	Seafloor			1
	seabed roughness	abiotic	n/a	Seafloor			1
	sediment (mean grain size)	abiotic	µm	Seafloor			1
	Sediment type	abiotic	n/a	Seafloor			1
	slope	abiotic	Angle	Seafloor			1
	air temperature	abiotic	ºC	Temperature			1
	FLSE values as a proxy for SST and	abiotic	ºC	Temperature			1
	proportion of time water column was stratified	abiotic		Temperature			1
	SST	abiotic	ºC	Temperature			1

SST thermal front gradient density NPP	abiotic	ºC	Temperature			1
SST Nighttime	abiotic	ºC	Temperature			1
stratification	abiotic	n/a	Temperature			1
stratification - potential energy anomaly (PEA)	abiotic	J/m3	Temperature		1	
water temperature	abiotic	ºC	Temperature		1	1
time of day	abiotic	time	Time of day		1	
cloud cover	abiotic	%	Weather		1	
wind speed	abiotic	m/s	Weather			1
Fishing effort	biotic		Fishery		1	
fishing vessels	biotic		Fishery			1
Focus on fisheries/discards	biotic		Fishery		1	
environmental heterogeneity	biotic		Habitat			1
habitat selection	biotic		Habitat			1
Habitat types as a proxy for fishery associations	biotic		Habitat			1
Habitat types as a proxy for possible prey	biotic		Habitat			1
Pellets and stable istopes	biotic		Prey types	1		
Pellets/regurgitates collected.	biotic		Prey types	1		
Prey samples collected	biotic		Prey types	1		
prey species but not studied (German N.Sea)	biotic		Prey types	1		
prey type	biotic		Prey types	1		
Regurgitates collected	biotic		Prey types	1		
sand eel nursery grounds and sediment	biotic		Prey types	1		
sediments and sandeels	abiotic	µm	Prey types			1
chlorophyll-a	biotic	g/l	Primary production			1
Net primary production (NPP)	biotic	gC/m/day	Primary production			1

3.3.1 Black-legged kittiwake

Redfern & Bevan (2014) deployed GPS loggers on black-legged kittiwakes from the UK. Tagged birds had large but variable foraging ranges, utilising coastal waters but also travelling large distances to offshore foraging areas. Most foraging locations were outside an area of deep water (−80 to −100 m), suggesting that surface fish are absent or at lower densities in these areas (Redfern & Bevan 2014).

Robertson *et al.* (2014) combined GPS tracking (on adults) with regurgitate sampling from adults and chicks at a UK breeding colony. The majority (94.1%) of regurgitates contained sandeel (*Ammodytes* spp.); the remainder contained sprat (*Sprattus sprattus*) vertebrae (Robertson *et al.* 2014). The authors also incoporated environmental variables to study the influence of oceanographic features on foraging areas. SST and chlorophyll-a concentration influenced foraging of incubating adults in 2012, however environmental conditions were inconsistent between years (Robertson *et al.* 2014). Nevertheless, areas of high chlorophyll-a concentration are known to result in high aggregations of sandeel, and lower SST is correlated with sandeel growth and recruitment (Arnott & Ruxton 2002; Frederiksen *et al.* 2004; Frederiksen *et al.* 2011). In the North Sea, sandeel primarily feed on *Calanus* spp., whose abundance and distribution are also influenced by oceanographic factors (Mackas *et al.* 2001). Feeding preferences and habitat choices differ across various sandeel age groups, whereby different age classes may utilise distinct foraging areas. The kittiwakes tagged in this study fed on sandeel from various age classes during different stages of breeding, suggesting that age-related differences in habitat preferences (such as sediment type) may account for variations in the environmental factors associated with kittiwake foraging locations during incubation and chick-rearing (Robertson *et al.* 2014).

Wakefield *et al.* (2017) deployed GPS loggers on black-legged kittiwakes from Britain and Ireland to model habitat use as a function of habitat availability (Figure 3.17). Kittiwake foraging behaviour was influenced by seabed morphology and water column properties. Key factors included water stratification, SST and slope, which influence prey availability by enhancing nutrient production or facilitating prey to the surface (Scott *et al.* 2010; Embling *et al.* 2012; Cox *et al.* 2013; Carroll *et al.* 2015). In areas with low seabed slope, kittiwakes avoided steep bathymetric relief, but this preference reversed in areas with high mean slope (Wakefield *et al.* 2017). Similarly, they avoided stratified waters in areas with low stratification but preferred areas with frequent stratification (Wakefield *et al.* 2017).

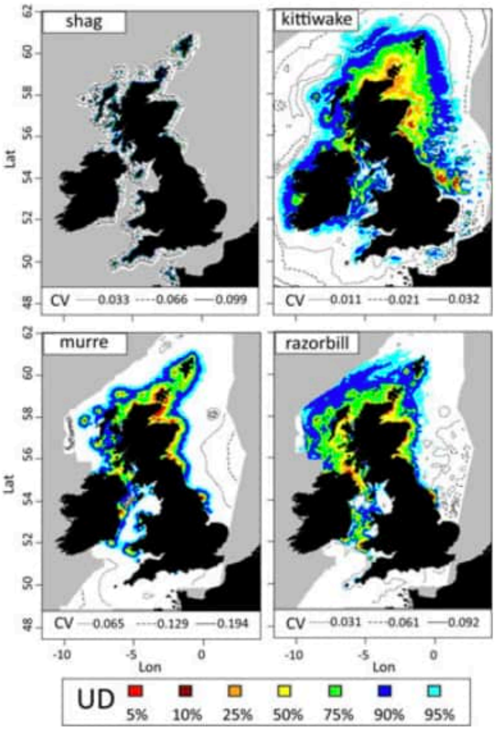


Figure 3.17 Percentage at-sea utilization distribution (UD) of seabirds breeding within Britain and Ireland during late incubation/early chick-rearing estimated as functions of colony distance, coast geometry, intra-specific competition and habitat. Warmer colours indicate higher usage. Isopleths indicate relative coefficient of variation (CV) of the estimated probability density (grey = no environmental data). Source: (Wakefield et al. 2017).

O’Hanlon *et al.* (2024) deployed GPS loggers on 20 kittiwakes from the UK to determine the influence of covariates on foraging behaviour and habitat selection. Distribution was weakly linked to environmental factors often used as proxies for prey availability, however population-level habitat selection was inconsistent. Instead, the authors observed significant individual variation in habitat preferences, making it difficult to identify important foraging areas and suggesting vulnerability to local stressors (O’Hanlon *et al.* 2024). Kittiwakes typically foraged close to the colony and showed a preference for deeper waters (Figure 3.18), although this was influenced by local bathymetry: individuals from colonies surrounded by shallow water foraged in shallower areas, while those surrounded by deeper waters foraged in deeper areas (O’Hanlon *et al.* 2024).

There was uncertainty about the role of front density on foraging, as individual responses to fronts were variable. While strong fronts are generally associated with high prey availability, kittiwakes may avoid these areas due to competition with larger predators, opting instead for weaker fronts; competition with other seabird colonies may also contribute to this variation (O’Hanlon *et al.* 2024). Additionally, the response to SST and thermal stratification varied among individuals. Kittiwakes generally preferred mixed waters and cooler SST, which are linked to higher productivity, but preferences for SST also varied by colony, suggesting local differences in prey ecology (O’Hanlon *et al.* 2024).

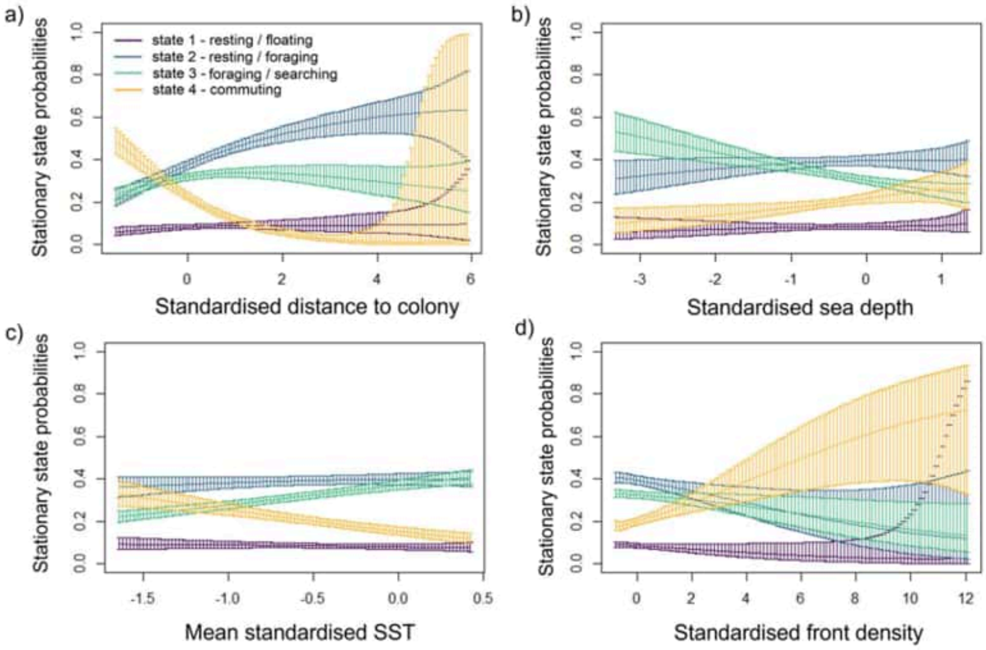


Figure 3.18 *Stationary state probabilities of 20 tracked kittiwakes, with 95% confidence intervals, showing the probability of being in each state for a) distance to colony, b) sea depth, c) sea surface temperature, and d) front density. All environmental covariates were standardised (O’Hanlon et al. 2024).*

Similarly, Trevail *et al.* (2021) equipped kittiwakes from the UK and Ireland with GPS loggers to better understand habitat selection during breeding. The authors found that kittiwakes foraged close to the colony, and that habitat selection varied based on environmental factors. On average, they preferred areas with shallower water, weaker stratification, cooler SST, and weaker or more distant fronts with lower persistence (Figure 3.19). Habitat preferences also varied between individuals and colonies (Trevail *et al.* 2021). Habitat selection was repeatable across all environmental variables, with species-level repeatability ranging from 0.13 (bathymetry) to 0.21 (SST). The degree of individual specialisation was higher in colonies with more diverse environments, particularly in relation to front strength, distance, and persistence. There was no clear trend linking individual repeatability in habitat selection to colony size, suggesting that individual specialisation is influenced more by environmental heterogeneity than by conspecific density (Trevail *et al.* 2021).

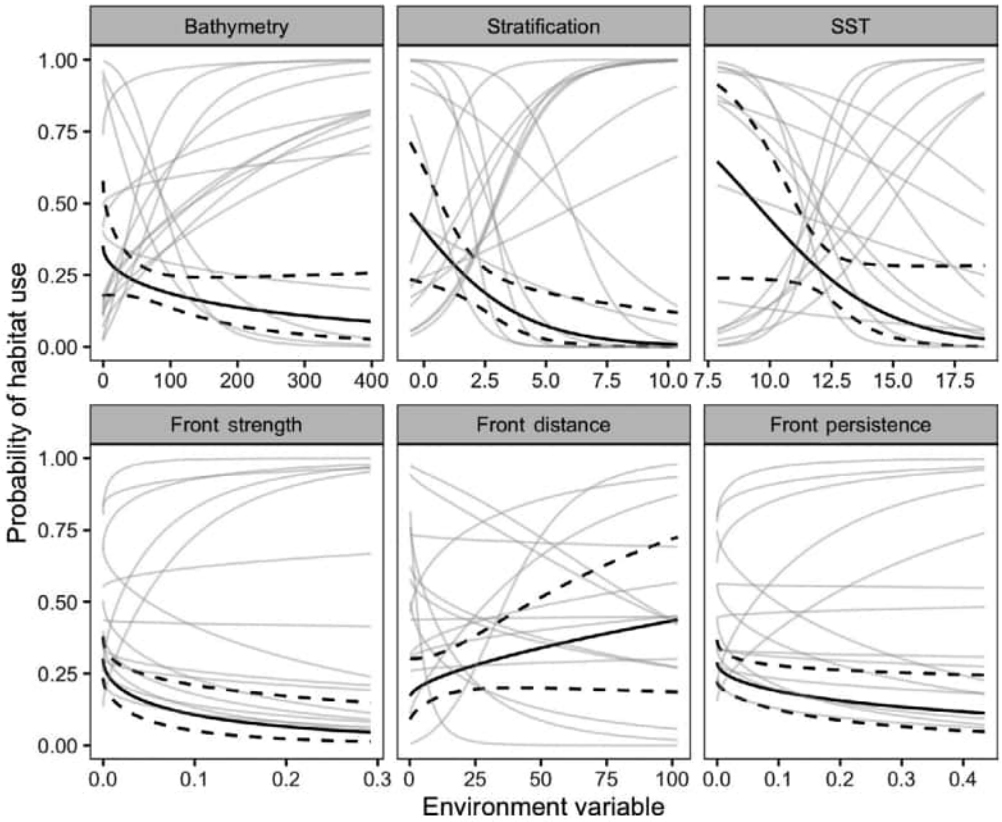


Figure 3.19 *Probability of habitat selection by kittiwakes while foraging given the: bathymetry (m), potential tidal stratification, SST, front strength, front distance and front persistence. Selection curves are shown at the species level (solid black lines ± SE; dashed lines) and from each colony (grey lines) (Trevail et al. 2021).*

Van Bemmelen *et al.* (2025) deployed GPS loggers on nine kittiwakes breeding on an offshore platform in the Dutch North Sea, and compared movements between estimated breeding stages. The authors found that kittiwakes made relatively short foraging trips in all directions during early chick-rearing (Figure 3.20). Outside early chick-rearing, kittiwake foraging trips were longer and unevenly distributed, suggesting they targeted specific feeding areas (van Bemmelen *et al.* 2025). Kittiwakes may adjust their foraging behaviour based on environmental conditions; in years with poor conditions their foraging ranges may expand, but they can adjust the time spent foraging within the same range (Schlener *et al.* 2024). This study took place in a highly productive zone between shallow mixed waters and deeper, summer-stratified waters of the central North Sea. The area is abundant with pelagic prey such as sprat (*Sprattus sprattus*), however no diet samples were collected for this study.

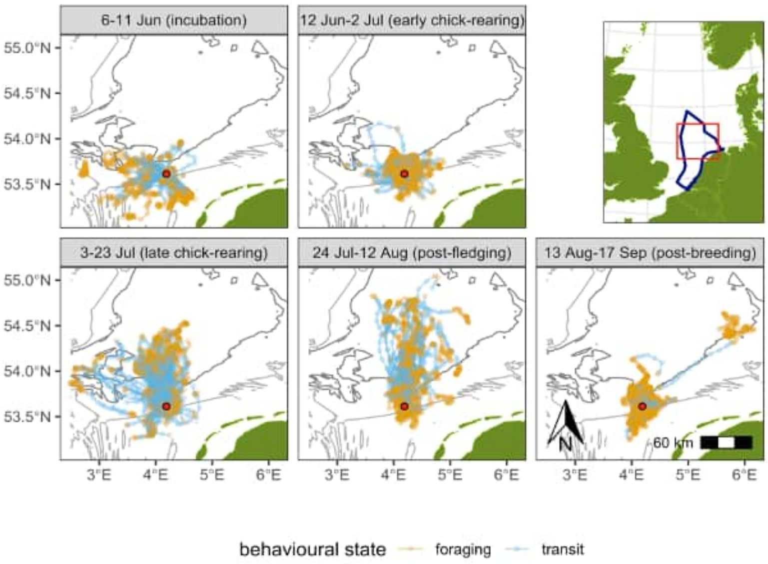


Figure 3.20 *Distribution of positions of nine black-legged kittiwakes tracked from an offshore platform in the North Sea (red dot) per assumed breeding stage. Tracks are annotated with two behavioural states. Grey lines show the -30 m (dark grey) and -40 m (light grey) isobaths. Red rectangle (inset map) shows the area within the North Sea shown in the subplots (van Bemmelen et al. 2025).*

3.3.2 Common guillemot

Peschko *et al.* (2020) deployed GPS loggers on 13 common guillemots breeding on Helgoland (Germany) to examine the impact of offshore wind farms (OWFs) on foraging behaviour. The authors revealed that guillemots largely avoided OWFs north of their breeding colony, with avoidance increasing when turbine blades were rotating (Peschko *et al.* 2020). Displacement by OWFs could increase guillemot foraging trip distance and energy expenditure, affecting individual condition and thus reproductive success. Strong avoidance of OWFs near the breeding colony, combined with a small foraging range (Figure 3.21), suggests that available foraging habitat in the North Sea was significantly reduced, forcing guillemots to compensate for lost habitat (Peschko *et al.* 2020).

Studies on prey species showed that their abundance near OWFs is generally unaffected or even positively influenced, implying that avoidance is not due to a lack of food. Furthermore, the occasional use of areas near OWFs for resting and diving suggests a "reef effect" (Lindeboom *et al.* 2011; Leopold *et al.* 2012; Vanermen *et al.* 2015), whereby increased fish diversity and abundance could attract guillemots to forage near them. However, foraging efforts were primarily concentrated in the western part of the study area, revealing that guillemots did not rely on these areas. An increase in sandeel abundance suggests that the impact of OWFs on prey availability is complex and may not fully explain guillemot behaviour (Peschko *et al.* 2020).

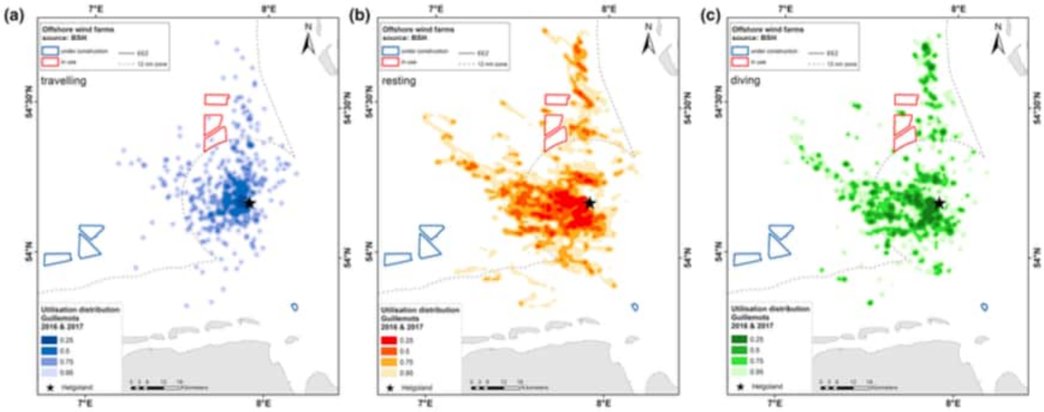


Figure 3.21 *Kernel densities of a) travelling, b) resting and c) diving positions of common guillemots tagged in 2016 and 2017. Positions visualised as percentiles: dark colour = 25% percentile, light colour = 95% percentile. OWFs on the left of a, b and c were in use in 2017 (Peschko et al. 2020).*

3.3.3 Common scoter

A recent study from the Netherlands using platform transmitter terminal (Argos PTT) and internal GPS tags on 23 common scoters provided spatial data on tracked individuals from 7 – 22 months (Camphuysen & van Lieshout 2024). The authors found that scoters exhibited flexibility in foraging and roosting locations, regularly visiting food resource areas beyond their main roosting place. Some individuals travelled substantial distances (e.g. to the UK and Denmark) to these alternative foraging sites, and others foraged further offshore at night, a behaviour that had previously not been documented (Camphuysen & van Lieshout 2024). Nevertheless, the most frequently used area was the coastal zone north of the Wadden Islands, with birds foraging on benthic shellfish banks for small bivalves and invertebrates (Figure 3.22). Most tracked birds showed a foraging preference for shallower waters, but some dove up to ±20 m.

The authors highlighted that disturbance, especially from sand dredging and/or transport, is a significant factor that can reduce usable foraging time, particularly in deeper marine habitats with stronger currents where foraging is more energetically costly (Camphuysen & van Lieshout 2024). Changes in benthic prey are critical for the scoter, with shellfish banks being influenced by broader ecosystem changes. Shifts in sediment and benthic fauna can indirectly affect scoter prey availability. The spatial data collected revealted that scoters monitor alternative food areas, possibly moving considerable distances in local prey becomes scare. This suggests that benthic prey dynamics are relevant for predicting scoter movements (Camphuysen & van Lieshout 2024).

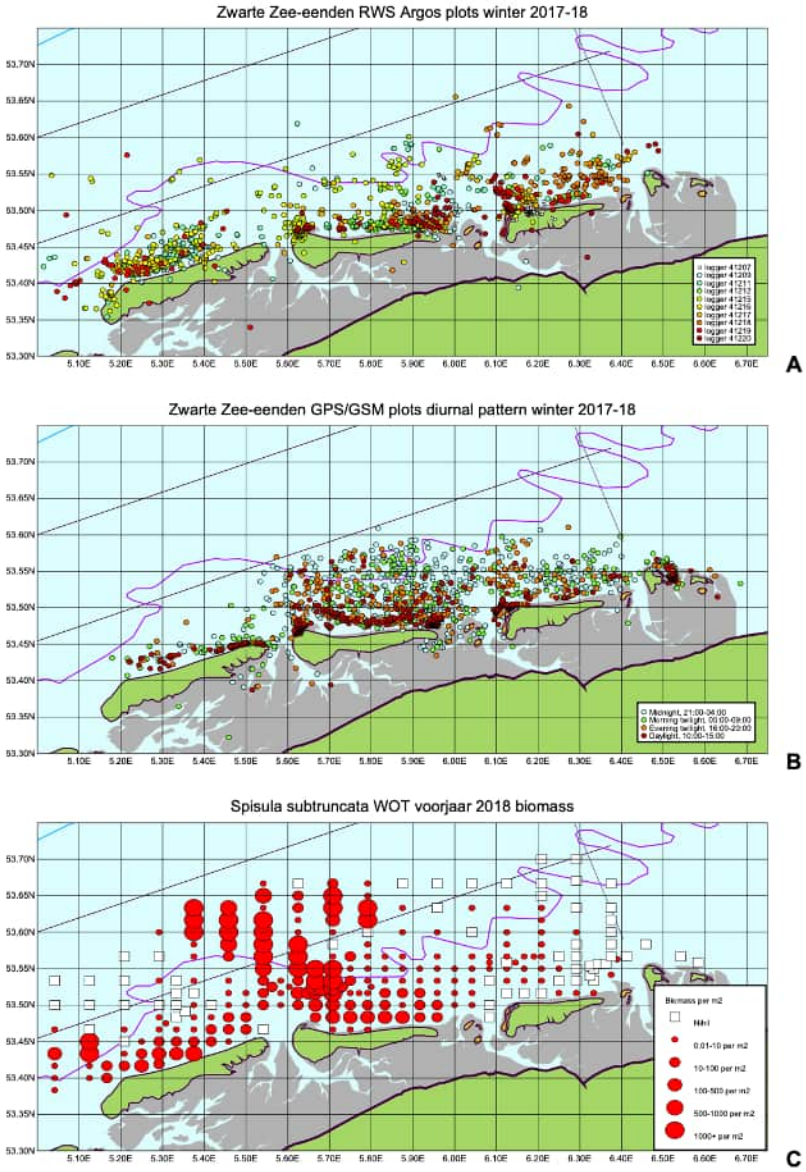


Figure 3.22 *Distribution of Common Scoters north of the West Frisian islands in relation to the distribution of a key shellfish resource:* ***A*** *Argos PTT data (colours represent individual birds),* ***B*** *GSM/GPS data (colours represent time of day), and* ***C*** *Spisula subtruncata (WOT survey with additional stations, spring 2018). (Camphuysen & van Lieshout 2024)*

3.3.4 Common tern

Militão *et al.* (2023) tracked common terns from Germany to examine which factors influence foraging behaviour during incubation. Birds foraged just after sunrise and before sunset, possibly in response to a temporal variation in prey distribution (Burrows *et al.* 1994; Cardinale *et al.* 2003). Common terns foraged primarily in shallow (<5 m depth) and coastal waters (<2 km from coast), mostly in areas with sand or silt subtidal sediment <20 km from the colony, predominantly at low tide (Militão *et al.* 2023).

The higher number of foraging positions in fine sand and silt habitats was initially thought to be linked to the habitat preferences of the terns' prey (Atlantic herring and sandeel). However, these species prefer areas with lower silt content (Reid & Maravelias 2001; Holland *et al.* 2005). This discrepancy could be due to several factors, including the relatively coarse spatial resolution (100 m) of the sediment data, and simplification of the Wadden Sea's complex habitats into three sediment types by the authors. Furthermore, changes in sediment distribution leading up to GPS deployment could have influenced foraging patterns (Militão *et al.* 2023).

Studying the diet of common terns during incubation is challenging because they typically swallow their prey at sea. However, during chick-rearing, one study found that although both males and females brought prey of similar size and nutritional value, males tended to provide more Atlantic herring and fish larvae, whereas females supplied more shrimp, insects, and smelt (*Osmerus eperlanus*) (Cansse *et al.* 2024).

A GPS study on 12 common terns in the Netherlands identified key foraging hotspots, with individuals often making short to medium-distance (20-30 km per trip) foraging flights from their breeding colony. Birds breeding on Broedeiland Stern exhibited similar foraging trip distances but flexibility in site choice depending on prey availability (Manche *et al.* 2023). Tracked terns foraged during the day in coastal gullies, shallow bays and estuarine areas where prey are abundant (Figure 3.23). The authors posit that birds may be attracted to areas such as Eemshaven harbour where prey may be concentrated due to water temperature or current (Manche *et al.* 2023). Based on camera data, diet primarily comprised small fish such as sandeel, sprat, smelt and stickleback, usually 5-10 cm in length and small enough to be carried to chicks. Diet composition can shift based on local prey availability and seasonal fish abundance.

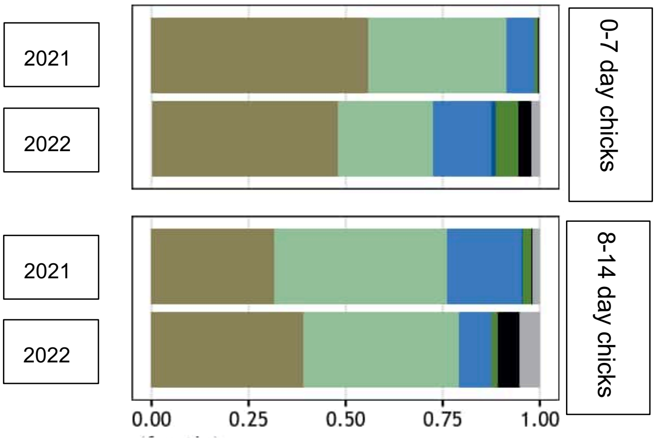


Figure 3.23 Habitat use of common terns during different stages of the breeding season in 2021 and 2022. Brown = colony; light green = Eems-Dollard; light blue = Wadden Sea; dark blue = North Sea; dark green = inland; black = Eems water outlet; grey = Eemshaven (Manche et al. 2023).

Another study on 18 chick-rearing common terns in the Netherlands found that roof-nesting birds made daily foraging trips away from their urban breeding sites (van der Zwan-Krijn & Loonstra 2023). The foraging trip distances of the tracked birds varied but were generally within a home range around the colony that allowed them to return frequently to feed their chicks. Terns favoured shallow coastal zones and tidal gullies due to the abundance of small fish, but also made use of man-made or modified bodies of water (Figure 3.24). The authors revealed that common terns exploit multiple foraging sites, with variation between individuals reflecting flexibility in habitat use likely in response to prey availability (van der Zwan-Krijn & Loonstra 2023). Some foraging hotspots correlated with areas of minimal disturbance and rich prey presence i.e. estuaries and sheltered bays. This dual use of urban nesting and natural feeding habitats demonstrates the adaptability of common terns while still relying on nearby healthy aquatic ecosystems.

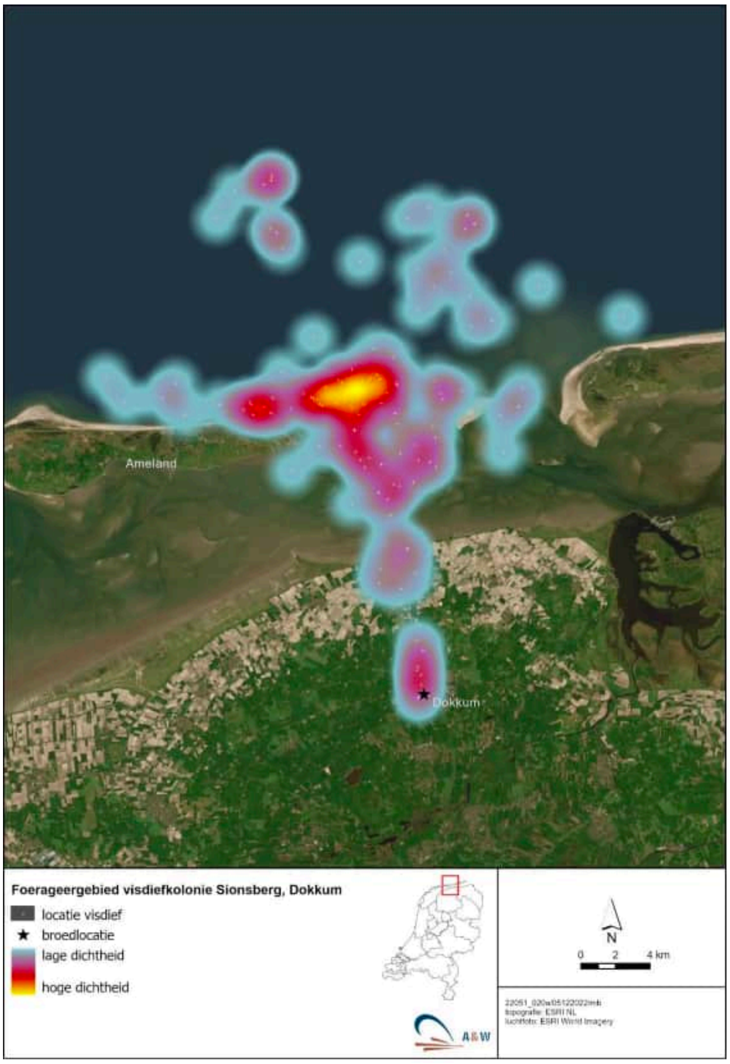


Figure 3.24 *Spatial distribution of the common tern colony at Sionsberg Dokkum (Netherlands). White crosses represent one GPS point per common tern. The heat map displays where a relatively large number of GPS points converge (yellow = high density; grey = low density). These locations were visited relatively more frequently than other areas where the birds were recorded. Black star = breeding colony. Data from May-June 2022, the chick-rearing period (van der Zwan-Krijn & Loonstra 2023).*

3.3.5 Great black-backed gull

Borrmann *et al.* (2019) deployed GPS loggers on seven great black-backed gulls from Foehr island (Germany) to examine core foraging areas and habitat use during the breeding season. Birds foraged close to the colony primarily in intertidal areas, suggesting high prey availability in the Wadden Sea area (Borrmann *et al.* 2019).

Madden *et al.* (in review) tracked 25 great black-backed gulls from Norway to examine their year-round movements, both during breeding and non-breeding. The authors identified a productive marine area where the gulls foraged during chick-rearing, possibly also in association with fishing activity (Madden *et al.* in review). Post breeding, most individuals travelled south/south west where they overwintered offshore and in coastal areas in the Netherlands, Belgium, southeast England and France. Figure 3.25 shows that great black-backed gulls foraged widely over the North Sea and English Channel (red dots) outside the breeding season, almost entirely offshore or in coastal areas.

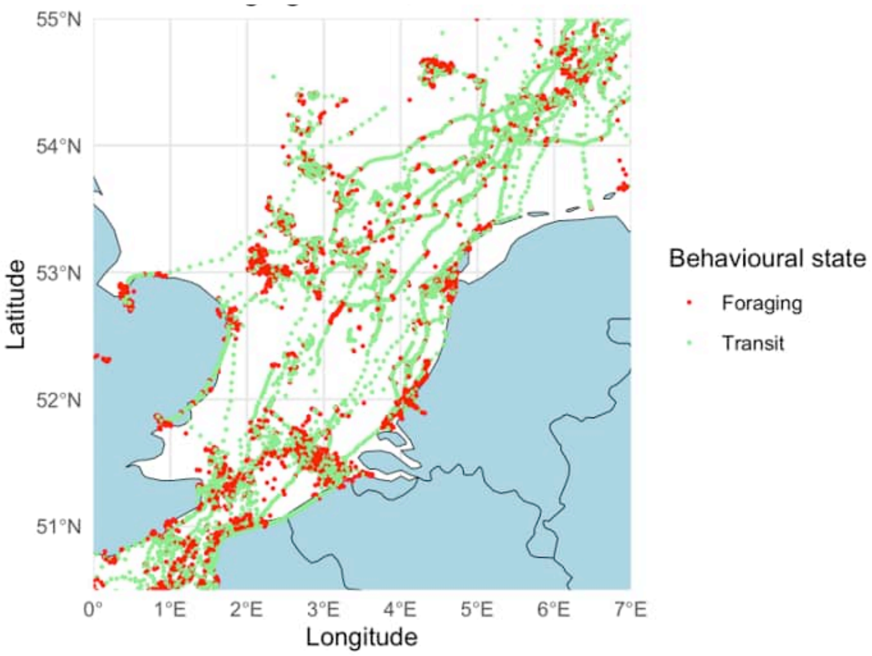


Figure 3.25 Foraging locations (red dots) of great black-backed gulls from a nest site in Norway outside the breeding season (July 2024 – February 2025). Green dots represent transit locations. Madden et al./Ecowende unpublished data.

3.3.6 Great cormorant

Fijn *et al.* (2022b) tracked great cormorants from the Netherlands to examine their at-sea distribution and the environmental factors that influence foraging. In this study, cormorants targeted various foraging habitats, ranging from shallow coastal waters to deeper areas <27 km from their colony. Three main habitat types were identified for foraging: (1) open sea or coastal sites with sandy seabeds, (2) nearshore areas, likely with rocky or hard substrates, and (3) inland freshwater bodies such as lakes and canals in agricultural regions. Of the trips recorded, 53% foraged in soft-substrate sites, 33% in hard-substrate sites, and 14% in inland freshwater sites (Fijn *et al.* 2022c).

Cormorants had a strong preference for shallow waters, with the majority foraging in waters less <20 m deep, and others in waters <10 m deep, in search of bottom-dwelling fish. Of two foraging areas identified, the northern area was shallower, had lower salinity, and higher wave activity compared to the western hotspot, though birds spent more time foraging in the latter area (Figure 3.26). Abiotic conditions at inland locations were notably different from those at saltwater foraging hotspots (Fijn *et al.* 2022c).

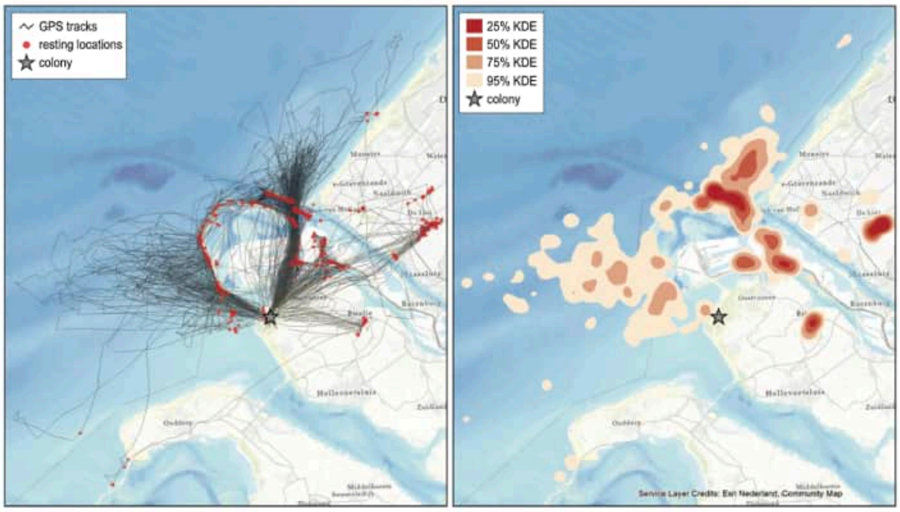


Figure 3.26 *Trips and resting locations (left) and kernel density estimates (right) calculated for foraging locations of great cormorants based on GPS data from 2012. Red dots = resting during foraging trips (Fijn et al. 2022c).*

3.3.7 European herring gull

Van den Bosch *et al.* (2019) deployed GPS loggers on herring gulls from two colonies in Belgium to determine variation in habitat and foraging specialisation. Higher consistency in foraging habitat use was linked to smaller foraging areas and shorter travel distances. However, individuals used areas spanning several square kilometers and frequently shifted between foraging sites, often daily (van den Bosch *et al.* 2019). Individuals appeared to alter their foraging movements between incubation and chick rearing. Both sexes travelled shorter distances and foraged closer to the colony during incubation. Multiple daily foraging trips to feed chicks resulted in longer distances travelled, possibly the result of dwindling resources near the colony (van den Bosch *et al.* 2019). The authors highlighted complex trade-offs between the availability, predictability and energetic value of prey, and the effort required to forage (van den Bosch *et al.* 2019).

A comparative study on 31 herring gulls from the Netherlands by van Donk *et al.* (2019) found that at-sea foraging was energetically costlier than in other habitats, mainly due to the additional time spent in flight (Van Donk *et al.* 2019). Over the past decades, resource availability for herring gulls has decreased, with stricter bycatch legislation and fewer fishing fleets in the North Sea. As discards decrease, foraging will require more time and energy for herring gulls, leading to higher competition for resources (Van Donk *et al.* 2019). A second tracking study from the Netherlands by van Donk *et al.* (2020) did not reveal foraging site fidelity, however some variation was observed between individuals (Figure 3.27). Birds with high site fidelity may miss out on unexpected food sources, like mass mortality events of razor clams (*Ensis directus*) that occasionally wash ashore, making the species more vulnerable to environmental changes (Van Donk *et al.* 2020).

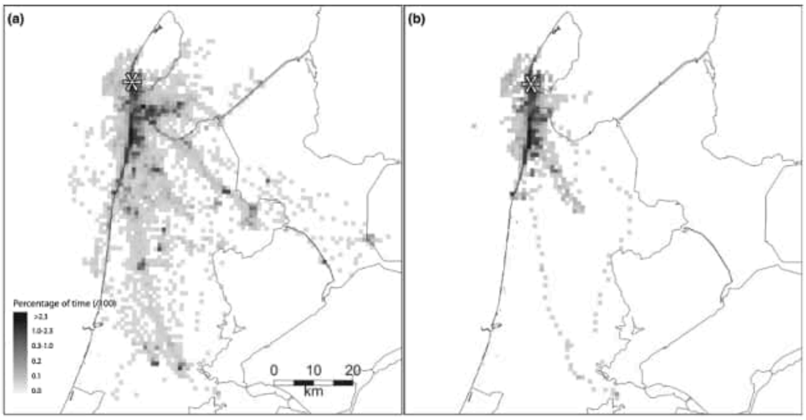


Figure 3.27 *Distribution of all GPS locations of incubating herring gulls tagged on Texel, the Netherlands. (a) all GPS locations of tracked gulls and a nest with eggs for at least 5 days and (b) distribution of individuals that favoured breakwaters over other foraging habitat (Van Donk et al. 2020).*

3.3.8 Lesser black-backed gull

Of all the target species identified for this review, the lesser black-backed gull is the most widely studied. Corman *et al.* (2016) tracked 79 incubating lesser black-backed gulls from six colonies in Germany to study whether their foraging behaviour differed between colonies, and whether these could be related to foraging habitats. They also collected pellets and performed stable isotope analysis to determine dietary diversity.

Foraging patterns varied significantly across the colonies studied. Gulls from larger colonies made longer trips, travelling greater distances than those from smaller colonies (Figure 3.28). Active foraging occurred further from colonies as colony size increased (Corman *et al.* 2016). Gulls foraged more on land than at sea, especially those from larger colonies located closer to the mainland. Daytime foraging occurred closer to colonies, while nighttime foraging occurred further away. Overall, trips were longer at night and occurred more over land than during the day. Gulls had a varied diet, consisting of terrestrial prey, including earthworms, insects, mammals) and marine prey such as discarded and natural fish and swimming crabs (Figure 3.29;.

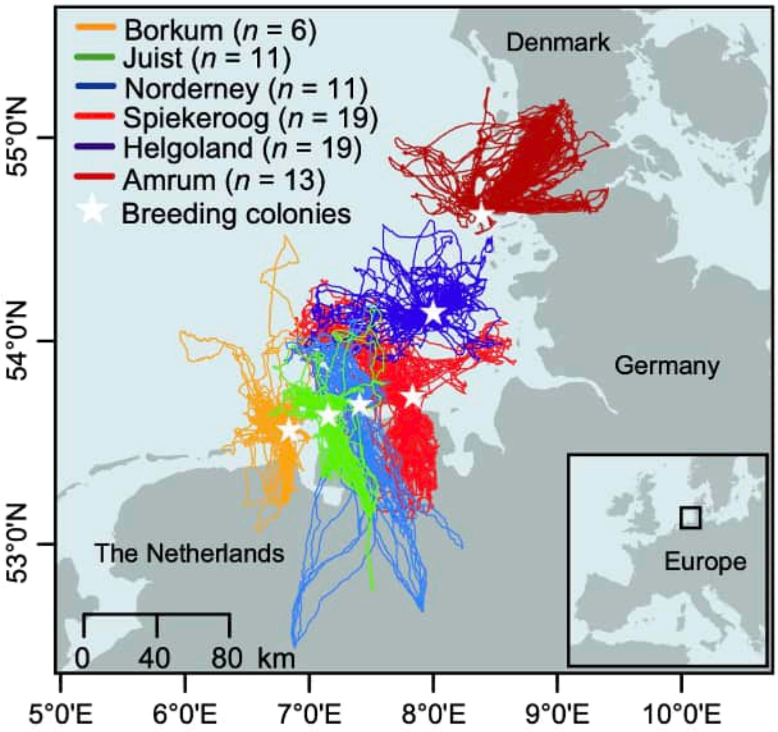


Figure 3.28 *Foraging trips of all tracked lesser black-backed gulls in the southern North Sea. Different colours represent different breeding colonies (Corman et al. 2016).*

GPS data, together with stable isotope analysis, from 82 incubating lesser black-backed gulls at five island breeding colonies in the southern North Sea found distinct differences in the foraging behaviour and diet between male and females (Figure 3.29; (Corman 2015). Males tended to forage in larger areas compared to females, and individual foraging site specialisation was evident, with minimal overlap between sexes. Furthermore, males' foraging areas decreased with increasing body mass, while females' increased. Males had a broader isotopic niche and consumed a wider range of prey than females, including more marine-based food (Discarded and natural fish, swimming crabs; Figure 3.29) (Corman 2015).

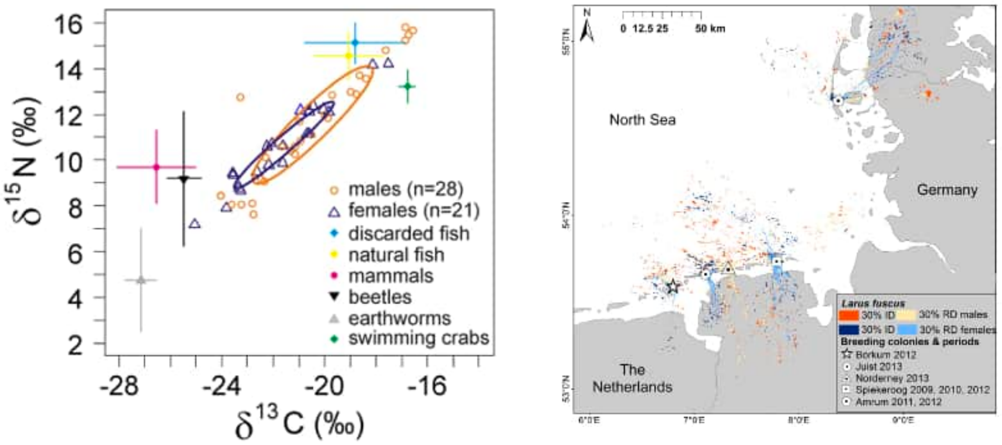


Figure 3.29 *(Left) Isotopic niche width based on stable isotope signatures (δ13C and δ15N) in red blood cells, and isotopic signatures (mean ± SD) of the six main food sources in male (orange circles) and female (blue triangles) lesser black-backed gulls from different breeding colonies on the southern North Sea coast during incubation periods from 2009 to 2013 (Corman 2015).*

(Right) Foraging habitat use in male (orange) and female (blue) lesser black-backed gulls in the southern North Sea. 30% intensity distribution (ID, intense colours) and 30% recursion distribution (RD, light colours) for both sexes (Corman 2015).

Camphuysen *et al.* (2015) collected regurgitates and pellets at the nest site, and deployed GPS loggers on 34 incubating lesser black-backed gulls from the Netherlands to examine foraging areas and habitat use. Foraging areas were primarily located to the southwest, south, southeast, and east of the colony, encompassing both marine and terrestrial habitats. The proportion of time spent in these areas varied widely among individuals, with some birds foraging almost exclusively on land and others at sea (Camphuysen *et al.* 2015). Habitat use also differed between sexes and breeding status. During breeding, males spent the majority of their time at sea (North Sea), while females divided their time between marine and terrestrial habitats (Figure 3.30). Breeding females spent about half their time foraging in the Wadden Sea, with some variation between incubation and chick-rearing. Females that failed to breed spent more time in terrestrial habitats and less in the Wadden Sea and North Sea. Similarly, failed male breeders reduced their time in the North Sea and increased their use of terrestrial habitats (Camphuysen *et al.* 2015).

Diet was dominated by marine species, with primary prey including demersal North Sea fish, pelagic Nereid worms (e.g. *Nereis longissima*) and crustaceans (e.g. *Liocarcinus holsatus*). A significant proportion of fish was likely obtained by scavenging discards behind beam trawlers (Camphuysen *et al.* 2015). Prey from intertidal zones was rare, comprising just 2% of samples, and included a few crustaceans, polychaetes, and bivalves. Despite the substantial time spent in the Wadden Sea, therefore, marine prey from the North Sea play a much larger role in the gulls' diet (Camphuysen *et al.* 2015).

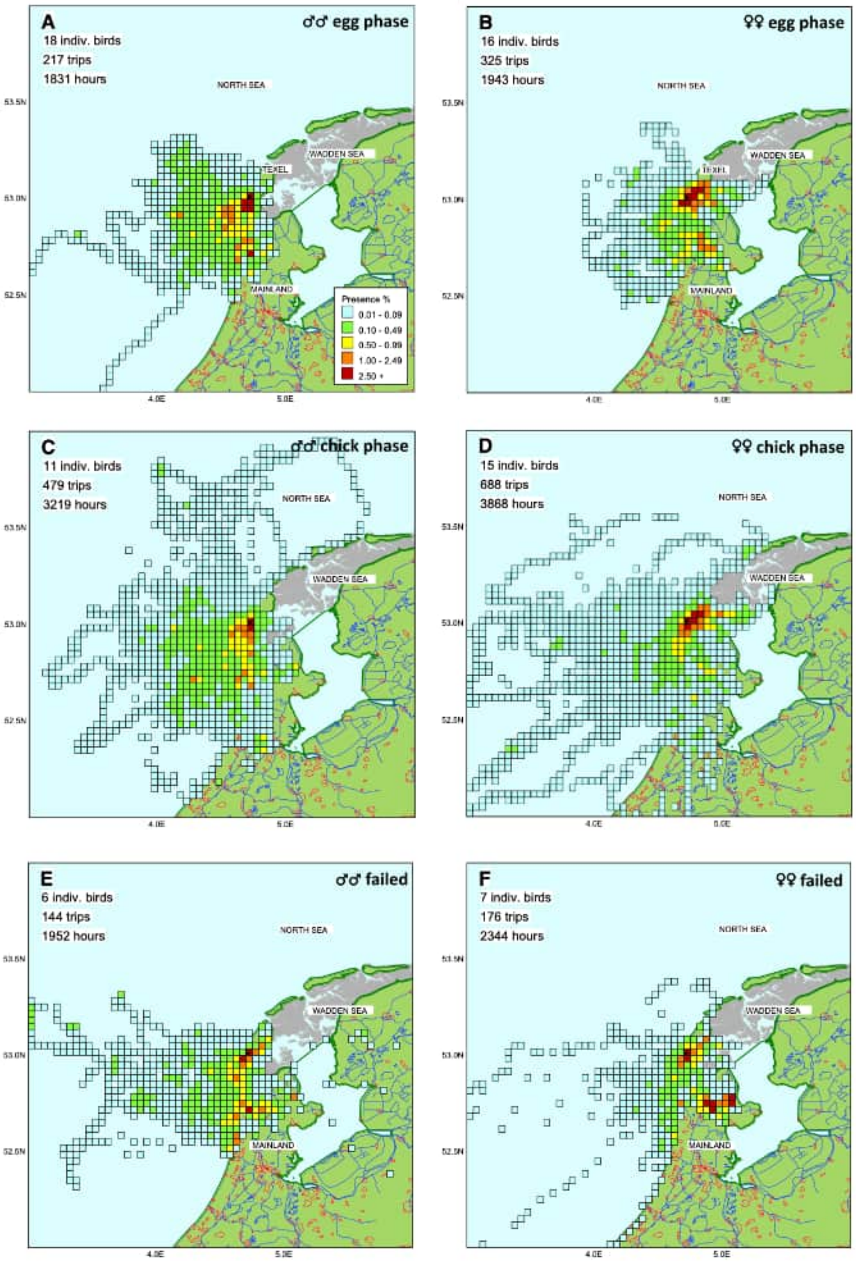


Figure 3.30 Foraging locations of lesser black-backed gulls breeding in the Netherlands based on sex and breeding status (Camphuysen et al. 2015).

Corman & Garthe (2014) tracked incubating lesser black-backed gulls from two colonies in Germany to better understand flight heights of the species. Birds typically flew at low altitudes, with most flights occurring below 20 meters. Lower flight heights at sea could be attributed to the gulls' opportunistic foraging behaviour, where flying closer to the sea surface may allow them to access food quickly (Figure 3.31). The authors also found that gulls flew higher during the day, likely due to better visibility. At night they often scavenged at lower altitudes, particularly behind fishing vessels or in illuminated sites, suggesting a reliance on anthropogenic food sources after dark (Corman & Garthe 2014).

Gulls travelling between foraging sites or within the colony flew at higher altitudes, whereas foraging flights occurred at lower altitudes. Occasional extreme flight heights observed midway through trips could represent orientation phases, where gulls had either finished foraging or were searching for the next site (Corman & Garthe 2014). The authors did not find a significant effect of wind on flight height, possibly due to the coarse resolution of wind measurements and the fact that most tracked flights were at low altitudes, where wind speed is less influential (Corman & Garthe 2014).

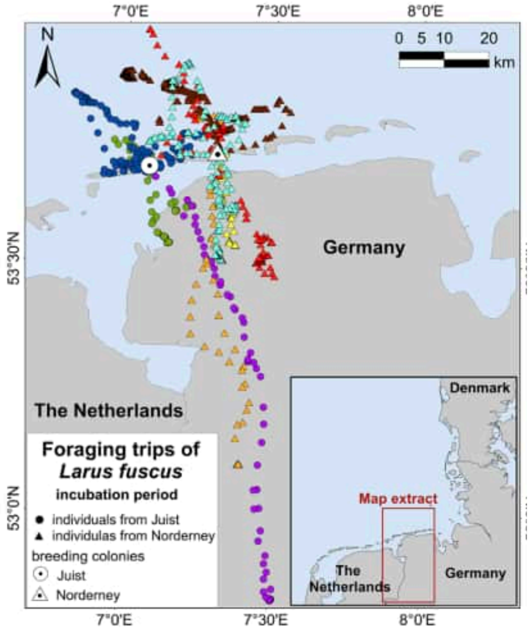


Figure 3.31 Foraging trips of lesser black-backed gulls from Germany during incubation (Corman & Garthe 2014).

Of the foraging trips recorded, nearly half (48.1%) were exclusively at sea, 43.5% were focused on inland areas, and a small percentage (6.5%) involved both sea and land (Garthe *et al.* 2016). Offshore trips were more variable in duration and distance, often consisting of very short and very long trips (Figure 3.32). Very little foraging occurred on the tidal flats in the Wadden Sea (Garthe *et al.* 2016). Food items identified from pellets included: grass, insects, fish (grey gurnard (*Eutrigla gurnardus*), cod (*Gadus morhua*), unidentified gurnards/gadids, scad (*Trachurus trachurus*), and unidentified flatfish), litter, earthworms, crustaceans (*Liocarcinus* spp.), mammals, bivalves, seeds, polychaetes and eggs. All species identified to group level were discards (Garthe *et al.* 2016).

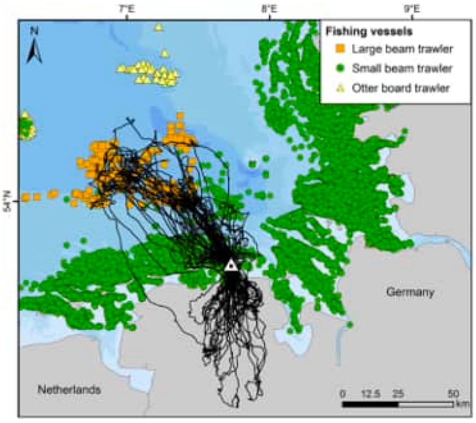


Figure 3.32 *Distribution of fishing vessels and lesser black-backed gull tracks from May-June 2010. Black lines show flight tracks of lesser black-backed gulls. Triangle represents breeding colony in Germany (Garthe et al. 2016).*

Kentie *et al.* (2024) examined the behavioural effects of GPS logger deployment on incubating lesser black-backed gull foraging and habitat choice over multiple years in the Netherlands. While there was no direct relationship between return rates and time spent at sea, the study found a decrease in the proportion of time individuals spent at sea in the years following deployment, suggesting a change in foraging strategies (Kentie *et al.* 2024).

To account for potential external factors, the study compared the behaviour of newly tagged individuals with those tagged in previous years. Newly tagged gulls spent a higher proportion of time at sea compared to gulls with older tags, suggesting that the devices caused a shift away from foraging at sea (Figure 3.33), rather than the discard ban that could have reduced food resources from trawlers (Kentie *et al.* 2024).

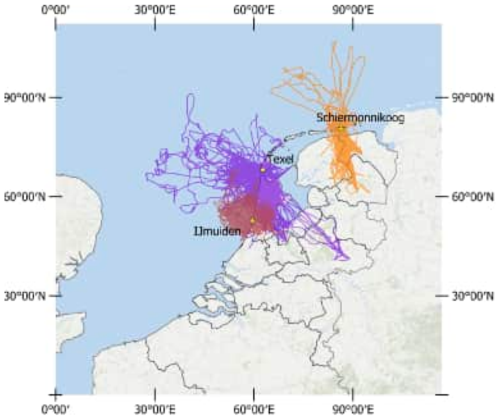


Figure 3.33 *Locations of lesser black-backed gull breeding colonies (yellow stars) in the Netherlands and tracks of all GPS-tagged individuals between 2019 and 2021 (Kentie et al. 2024).*

Camphuysen *et al.* (2024) identified prime foraging locations from a breeding colony of lesser black-backed gulls in the Netherlands based on GPS tracking data. Most foraging occurred within a 72 km radius of the colony, with 50% of foraging time spent within 28 km (*Figure 3.34*). Birds utilised a variety of habitats, from pelagic to coastal and terrestrial zones (Camphuysen *et al.* 2023). In the North Sea, gulls engaged in extensive searches or followed trawlers for discards.

The diet of these gulls was diverse, containing over 300 unique prey species. The majority (82.2%) was marine (roundfish, flatfish, whiting, horse mackerel, grey gurnard, plaice, dab and dover sole, as well as swimming crab and marine polychaetes). The former are typically demersal fish, often available as discards from large beam trawlers. Prey from intertidal zones and freshwater were rare. Lesser black-backed gull dietary patterns also appeared to reflect seasonal and individual preferences, with some variation in foraging based on tidal, lunar, and diurnal cycles (Camphuysen *et al.* 2023).

During the breeding cycle, there were notable shifts in the types of prey consumed. From the pre-laying stage to incubation and chick-rearing, lean fish species (e.g. *Gadidae*, *Syngnathidae* and *Trachinidae*) and bony fish species (e.g. *Belonidae, Bothidae* and Pleuronectidae) were less frequently consumed in favour of fatty, small pelagic fish (e.g. *Ammodytidae*, *Clupeidae*, *Osmeridae* and *Scombridae*), particularly during chick-rearing. The availability of swimming crabs and marine polychaetes varied throughout the season, suggesting that gulls adjusted their foraging strategies in response to shifts in prey abundance (Camphuysen *et al.* 2023).

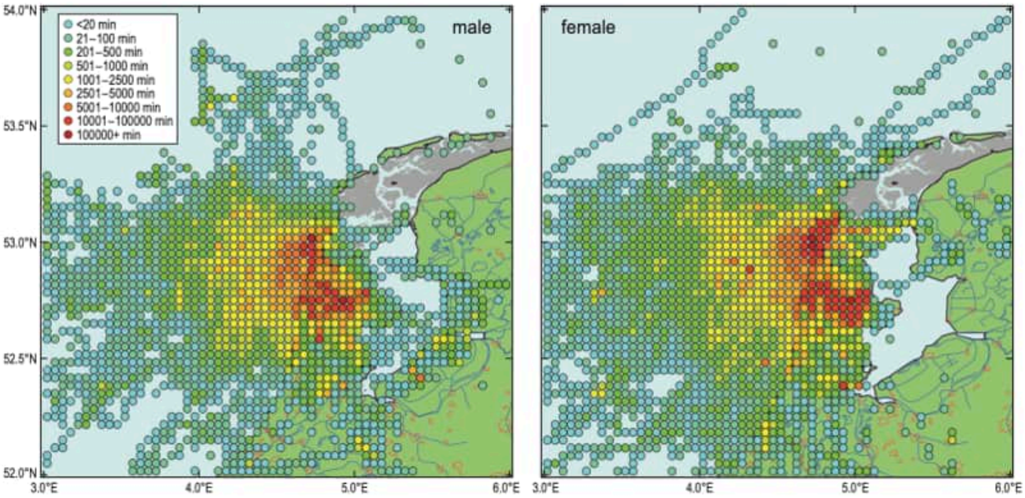


Figure 3.34 *Prime foraging distribution based on GPS tracking data for adult male (n = 24) and female (n = 27) lesser black-backed gulls breeding on Texel, the Netherlands (Camphuysen et al. 2023).*

Elsewhere in the Netherlands and in Belgium, Kavelaars *et al.* (2020) used GPS tracking data to determine how lesser black-backed gulls adjust their foraging behaviour after relocating to another colony due to habitat destruction. The authors concluded that relocated individuals did not efficiently adapt to their new environment. Despite their ability to exploit both marine and terrestrial food sources, relocated gulls did not visit foraging sites close to their new colony, instead re-using familiar areas near their original colony (Figure 3.35) (Kavelaars *et al.* 2020).

The relocated birds shared a large portion of their foraging range with resident birds in Belgium, suggesting they continued to rely on known foraging areas. This implies that site fidelity is a significant factor, even if it involves higher costs such as longer travel distances. The authors also suggest that competitive exclusion (i.e. difficulty accessing high-quality foraging sites) may be a factor in the gulls' reluctance to switch to new foraging sites. These findings emphasise the high cost and difficulty of adapting to new foraging areas later in life for lesser black-backed gulls (Kavelaars *et al.* 2020).

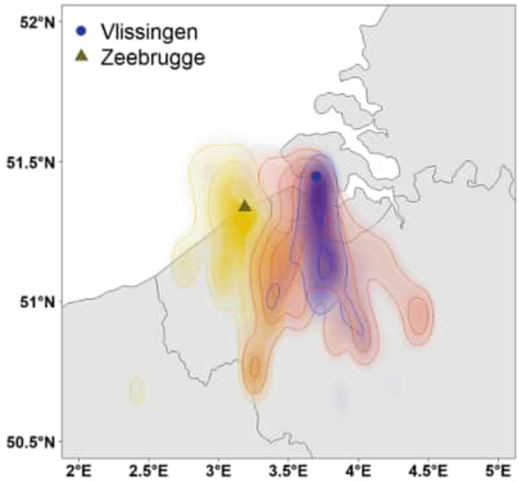


Figure 3.35 Autocorrelated kernel density distribution of lesser black-backed gulls in Vlissingen, the Netherlands (blue dot): relocated birds (vl zb, red, n = 8), resident birds of new population (vl vl, blue, n = 8); in Zeebrugge, Belgium (yellow triangle): resident birds of old population (yellow, n = 29). Isopleths represent 25, 50, 75, and 95% of space use by the gulls (Kavelaars et al. 2020).

Another Belgian study (Vanermen *et al.* 2020) tracked lesser black-backed gulls breeding in Zeebrugge and Ostend. The authors found that distance to the edge of a wind farm significantly influenced the presence of flying and non-flying birds. In areas without man-made structures, non-flying bird activity steadily increased up to 2 km from the edge. However, where turbines and platforms were present, there was a sharp increase in activity from the centre to the edge of the wind farm. Across the wind farm, the majority (86%) of birds were non-flying, higher than in the control area. Of the 31 tracked gulls that entered the wind farm, 16 were recorded near the turbines or transformer platform (Vanermen *et al.* 2020). On average, the gulls spent 56% of their time within 100 m of these structures, although individual use varied greatly. The model indicated that outer turbines had 6.5 times more bird activity than inner ones, and predicted a sharp decline in presence with increasing distance from the coast.

Sage & Shamoun-Baranes (2022) used GPS loggers to determine foraging areas and year-round at-sea distribution of lesser black-backed gulls from Schiermonnikoog, the Netherlands. The authors concluded that the tagged gulls only spent 3.2% of their time foraging in the North Sea, although this varied between years over the study period (Sage & Shamoun-Baranes 2022). In contrast, similar studies (Ens *et al.* 2008; Stienen *et al.* 2016; Shamoun-Baranes *et al.* 2017; Baert *et al.* 2018) have showed extensive use of the

North Sea by lesser black-backed gulls migrating from other areas of the Netherlands (Figure 3.36).

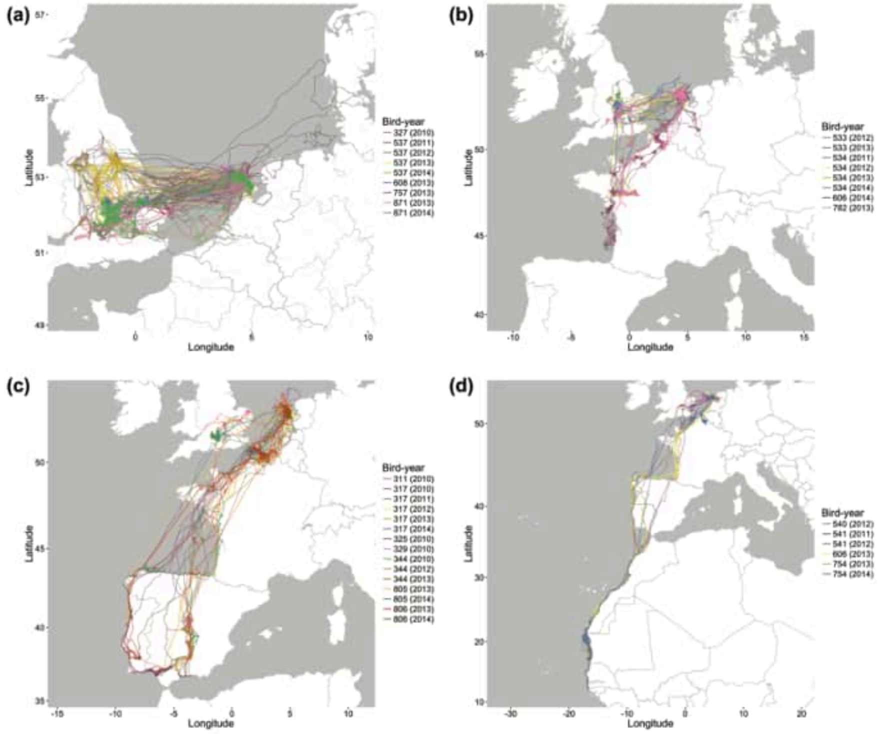


Figure 3.36 *Migration routes of lesser black-backed gulls per bird-year and migration strategy (a) Great Britain (GB), (b) western France (F), (c) Iberian Peninsula (IP), (d) west Africa (WA), from 2010 to 2015. Each line represents a bird-year subset (Shamoun-Baranes et al. 2017).*

The authors determined that the tracked gulls spent little time at sea, suggesting that many individuals rely heavily on inland resources for foraging (Figure 3.36). While foraging strategies during the breeding season vary per individual, those outside the breeding season remain unexplored. Understanding these differences, particularly in relation to foraging and prospecting behaviour, is crucial for assessing cumulative distances travelled. Ultimately, a deeper understanding of year-round foraging behaviour could shed light on the fitness costs associated with different foraging strategies (Shamoun-Baranes *et al.* 2017).

Sommerfeld *et al.* (2016) deployed GPS loggers on incubating lesser black-backed gulls from Helgoland, Germany, to assess foraging behaviour in relation to beam trawl fisheries in the southern North Sea. Approximately one-third of foraging trips showed overlap with fishing vessels, with the birds exhibiting search behaviour within 5 km of vessels (Figure 3.37), indicating they were utilising discards (Sommerfeld *et al.* 2016). The authors also highlighted that gulls from Helgoland travelled further and spent more time away from the colony when feeding on discards compared to those that did not. This is likely due to the higher energetic value of predictable fishery discards, despite the increased flight costs. The longer foraging trips of the tracked gulls were likely due to Helgoland's offshore location and distant fishing zones, although they could still successfully exploit prey near the colony during shorter trips (Sommerfeld *et al.* 2016).

The study's dietary analysis confirmed that individuals rely on discards, ruling out the theory that gulls and fishing vessels were simply overlapping in productive areas (Sommerfeld *et al.* 2016). Birds may compensate for a reduction in discards by feeding on more swimming crabs, however these are low-energy compared to other food sources. Swimming crabs are abundant near the shore or as bycatch, meaning lesser black-backed gulls from Helgoland might face a net energy loss when travelling long distances to forage for them, especially in the absence of discards. The lack of other natural prey in the gulls' diet suggests limited availability of alternative food resources. A long-term reduction in discards will therefore negatively impact the Helgoland population (Sommerfeld *et al.* 2016).

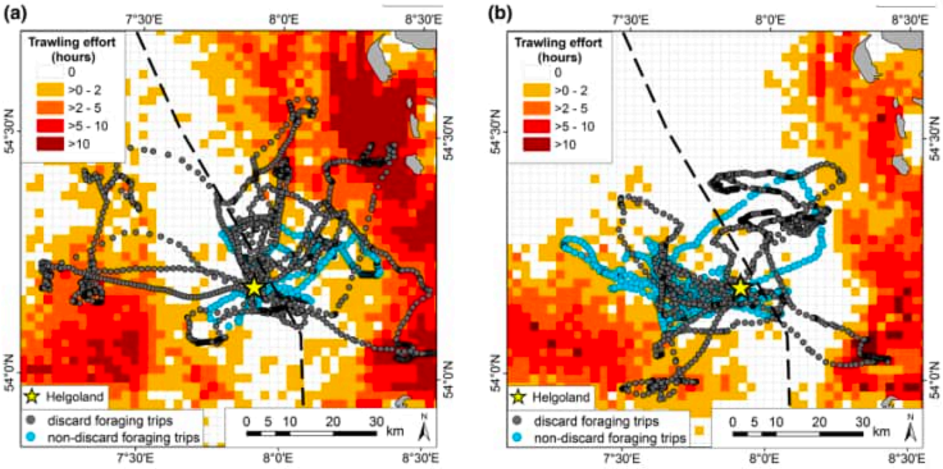


Figure 3.37 *Discard (grey) and non-discard (blue) foraging trips of lesser black-backed gulls from Helgoland, Germany, in a 2008, b 2009. Trawling effort (h) is represented by the colour ramp (shrimp and flatfish fisheries combined). Black dashed line denotes spatial separation between the near shore shrimp fishery (east of dashed line) and the offshore flatfish fishery (west of line). Yellow star represents the colony (Sommerfeld et al. 2016).*

A study by Sotillo *et al.* (2019) on breeding lesser black-backed gulls from Belgium found that marine foraging trips generally involved higher energetic costs but shorter time investments compared to terrestrial trips. As chicks grew older, the proportion of marine trips decreased, trip duration increased, and energy costs per trip became lower (Figure 3.38). During the chick rearing period, trip frequency increased initially but decreased after about 20 days (Sotillo *et al.* 2019).

While energy costs varied among individuals, marine foragers tended to spend less time away from the colony on average. Males were more likely to engage in marine foraging, particularly on weekdays, with the prevalence of offshore foraging decreasing as chick age increased. The active foraging on weekdays and reduction in marine foraging on weekends might be due to decreased fishing activity, with some gulls foraging on naturally occurring prey such as swimming crabs (Sotillo *et al.* 2019). Marine foraging trips were more energy-demanding but shorter in duration. Despite this, there were no clear trends in energy expenditure between marine and terrestrial foragers, suggesting that offshore foragers might compensate for higher energy costs by resting more near the colony or optimising time to reduce chick-guarding constraints (Sotillo *et al.* 2019).

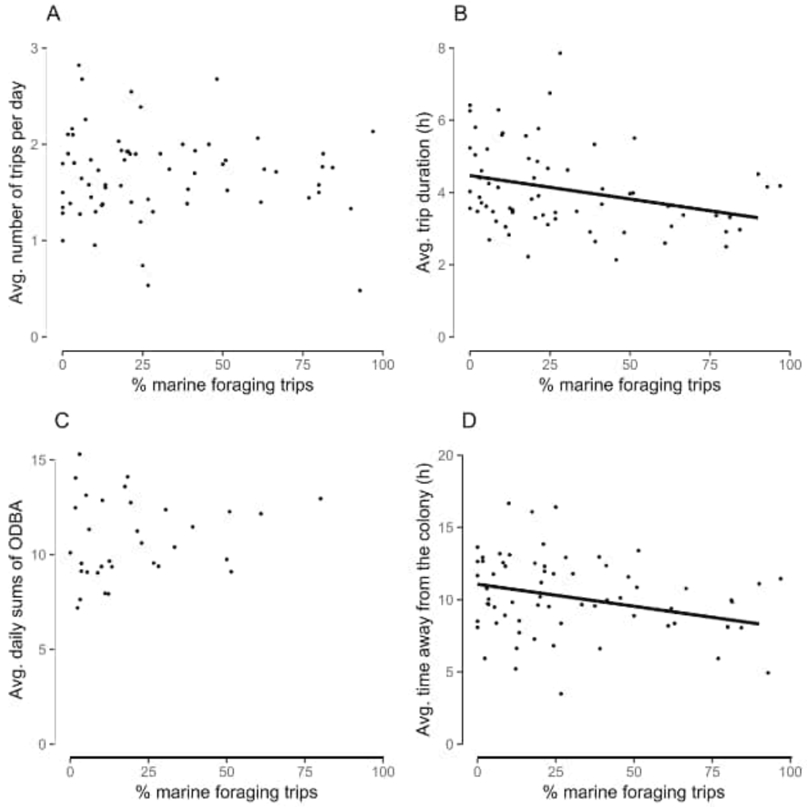


Figure 3.38 *Time and energy costs averaged per individual over the chick rearing period, plotted against the individual's proportion of marine foraging trips. a) average number of foraging trips per day, b) average trip duration, c) average of the total daily sums of ODBA and d) average time spent outside the colony in a day. Regression lines are plotted for significant relationships (Sotillo et al. 2019).*

Ens *et al.* (2008) studied the movements of lesser black-backed gulls and herring gulls from the Netherlands to examine their habitat use during breeding and post-breeding. The authors found that habitat use differed between gull species (Figure 3.39). Herring gulls most frequently used island habitat, followed by the tidal area and North Sea beach. The mainland was rarely used, and the Wadden Sea and North Sea were seldom visited by most individuals. Interestingly, even though herring gulls often stayed on the North Sea beach, they did not fly onto the North Sea, although they did traverse the Wadden Sea. In contrast, lesser black-backed gulls most frequently used the North Sea, followed by island and mainland habitats (Figure 3.39). The Wadden Sea, tidal area, and North Sea beach were less frequently visited by these gulls (Ens *et al.* 2008).

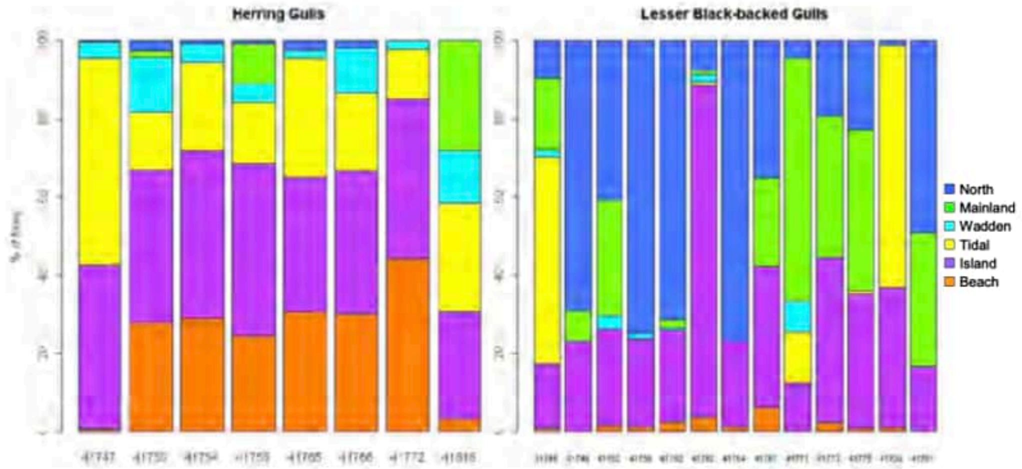


Figure 3.39 Habitat use by individual herring gulls (left) and lesser black-backed gulls (right) breeding in the Netherlands (Ens et al. 2008).

Lesser black-backed gulls did not use habitats in proportion to their availability. They preferred island and North Sea beach habitats, with islands being most favoured. The North Sea, Wadden Sea, and tidal area were not preferred, and the mainland was avoided, however individuals exhibited variability in habitat selection. While these gulls are not typically marine invertebrate specialists in the Wadden Sea, the majority of visits occurred during low tide, suggesting that they were feeding on marine invertebrates rather than scavenging from fishing vessels during high tide (Ens *et al.* 2008). Lesser black-backed gull trips to the North Sea are likely driven by the presence of potential food sources such as pelagic fish and discards from fishing vessels, but could also be a strategy to avoid competition with herring gulls.

The authors highlighted a near-total partitioning of food resources between herring gulls and lesser black-backed gulls. Herring gulls rarely visited the North Sea or mainland, while lesser black-backed gulls used these habitats frequently. This aligns with findings by Kubetzki & Garthe (2003) who observed similar differences in habitat use at two breeding colonies in northwest Europe. They found that lesser black-backed gulls more frequently occupied neritic areas (like the North Sea) compared to intertidal areas (Kubetzki & Garthe 2003). Lesser black-backed also showed high intra-specific variation, with individuals visiting all habitat types in different ways, suggesting more flexible and varied foraging strategies than those of herring gulls (Ens *et al.* 2008).

Also in the Netherlands, Camphuysen *et al.* (2008) collected pellets to study diet and deployed GPS loggers on lesser black-backed gulls and herring gulls breeding on Texel (Figure 3.40). The data collected confirm the significance of the open sea, use of specific food sources at sea, and the primary foraging areas of both species. Lesser black-backed gulls exhibited a strong preference for marine species during the breeding season, with a wide variety of fish species making up the majority of their diet. GPS data showed frequent visits to fishing vessels at sea, and the authors recommended investigating what proportion of the gulls' diet is composed of fish caught independently at sea, and what proportion comes from discards (Camphuysen *et al.* 2008).

Nevertheless, the prey species identified point to a major commonality between both species: the lesser black-backed gull primarily consumed marine fish, supplemented with swimming crabs, polychaete worms, and some terrestrial prey species, whereas the herring gull consumed food from estuaries or the intertidal zone along the coast, with a preference for bivalves (mussels), supplemented with shore crabs, fish, and other items (Camphuysen *et al.* 2008).

Figure 3.40 *Combined tracks of all GPS locations from lesser black-backed gulls breeding at the Kelderhuispolder (orange dot), each individual indicated with its own colour (Camphuysen et al. 2008).*

3.3.9 Northern fulmar

A GPS tracking study of 102 breeding northern fulmars from the UK and Ireland found a significant relationship between foraging fulmars and fishing vessels (Darby *et al.* 2021). This suggests that anthropogenic food sources, such as discards, offal and bait play an important role in fulmar diet, especially for incubating and chick-rearing individuals. Vessel interactions likely expand the fulmar's diet by providing access to prey that would otherwise be out of reach. However, such associations also raise concerns about elevated bycatch rates for fulmars compared to other seabirds (Darby *et al.* 2021).

While the tracked birds from this study did not forage in the southern North Sea, the authors suggest that anthropogenic fishing effort is a stronger predictor of fulmar foraging habitat preference than traditional oceanographic variables. Nevertheless, fulmars still foraged on natural prey, and environmental factors such as chlorophyll-a concentration, SST, seabed roughness and stratification did contribute to their foraging behaviour (Figure 3.41). These factors indicate that fulmars may also benefit from areas where zooplankton and other prey are aggregated by complex water flow patterns, often in regions unsuitable for demersal fisheries (Darby *et al.* 2021).

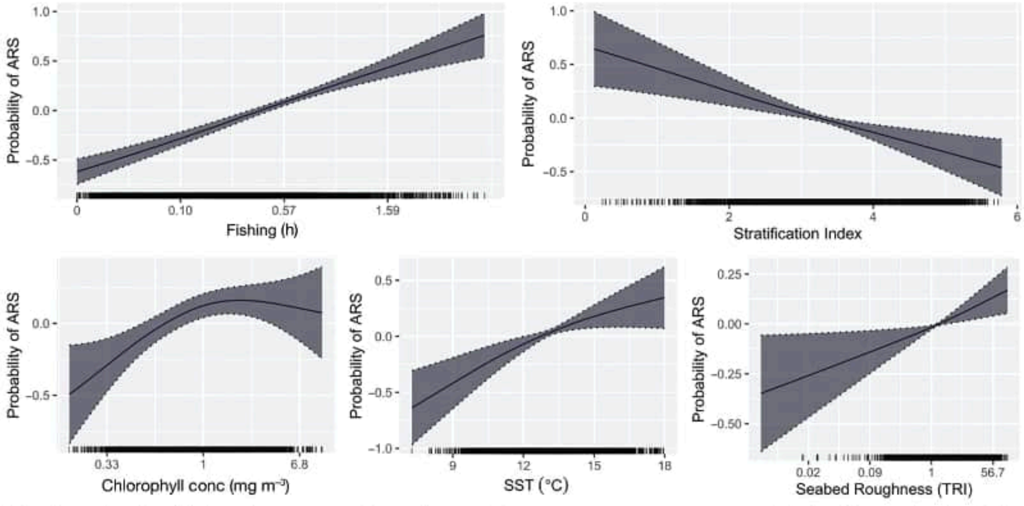


Figure 3.41 *Marginal effects of model covariates on the probability of foraging in northern fulmars. Dotted lines and shaded grey represent 95% confidence interval (Darby et al. 2021).*

3.3.10 **Northern gannet**

A study from the UK combined GPS tracking with regurgitate sampling from northern gannets (Hamer *et al.* 2007). The authors highlighted the adaptability and varied foraging strategies of adult gannets, being able to exploit a wide range of prey species and sizes, as well as scavenging fishing discards. The proportions of prey species in their diet varied annually, but sandeels consistently formed a key component.

Gannets foraged across large areas, and their foraging trips showed significant annual variation in duration, range, and distance travelled (Figure 3.42). Trips were longest in 2002, when sandeel abundance in the North Sea was exceptionally low. Gannets also displayed marked directional preferences for foraging, particularly to the northeast and southeast, with fewer trips due east. This change over the years might reflect a decline in the quality of prey at lower latitudes, particularly in terms of size and lipid content (Hamer *et al.* 2007).

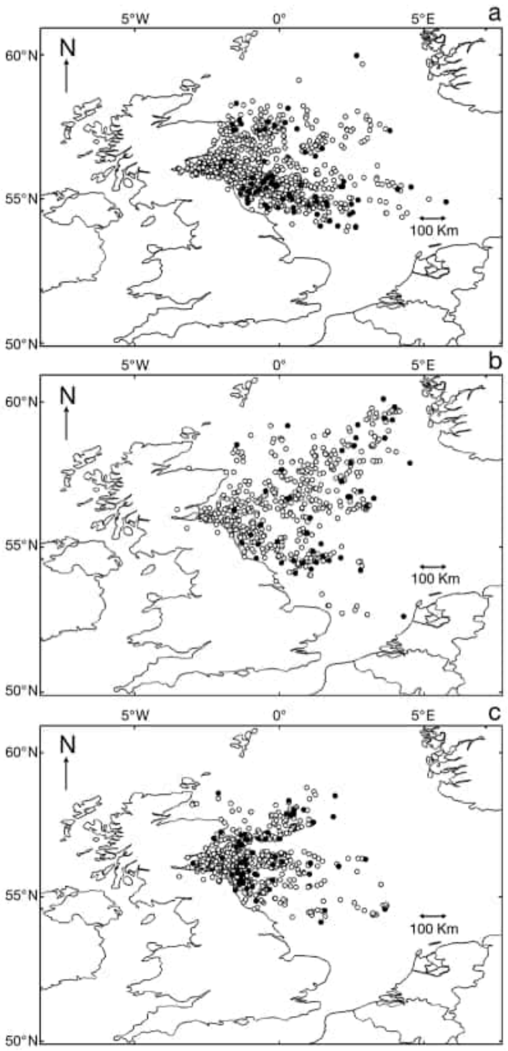


Figure 3.42 *Northern gannet foraging ranges and destinations of foraging trips from Scotland in a) 1998, b) 2002 and c) 2003 based on GPS tracking data (Hamer et al. 2007).*

A second study from the same area (Grecian *et al.* 2018) revealed important differences in foraging specialisation and proficiency between adult and immature gannets. Adults had a narrower foraging range and exhibited higher Individual Foraging Site Fidelity (IFSF), whereby they returned repeatedly to productive foraging areas. These birds were more likely to shift from transiting to foraging modes when encountering ocean fronts. In contrast, immature gannets had a wider foraging distribution and lower IFSF. They foraged more broadly across the North Sea and showed a weaker response to ocean fronts, suggesting they were still learning and exploring foraging sites (Grecian *et al.* 2018).

The authors found that adults primarily foraged to the northeast and southeast of the colony, while immature birds ventured much further, including areas like the Norwegian Trench. Despite this, there was some overlap in the foraging ranges of adults and immatures, suggesting they may target similar resources. Immature gannets appeared less constrained by the breeding season and can exploit under-used habitats, thereby reducing intraspecific competition (Grecian *et al.* 2018).

Similarly, a tracking study on gannets from the same colony during the non-breeding season highlighted the significant threats faced by adults and juveniles from offshore wind farms and fishing activities in the southern North Sea (Lane *et al.* 2021). Adults may be more vulnerable, as they appear to migrate further offshore compared to juveniles (Figure 3.43), thus encountering more wind turbines, whereas juveniles are susceptible to bycatch and the impacts of prey depletion (Lane *et al.* 2021).

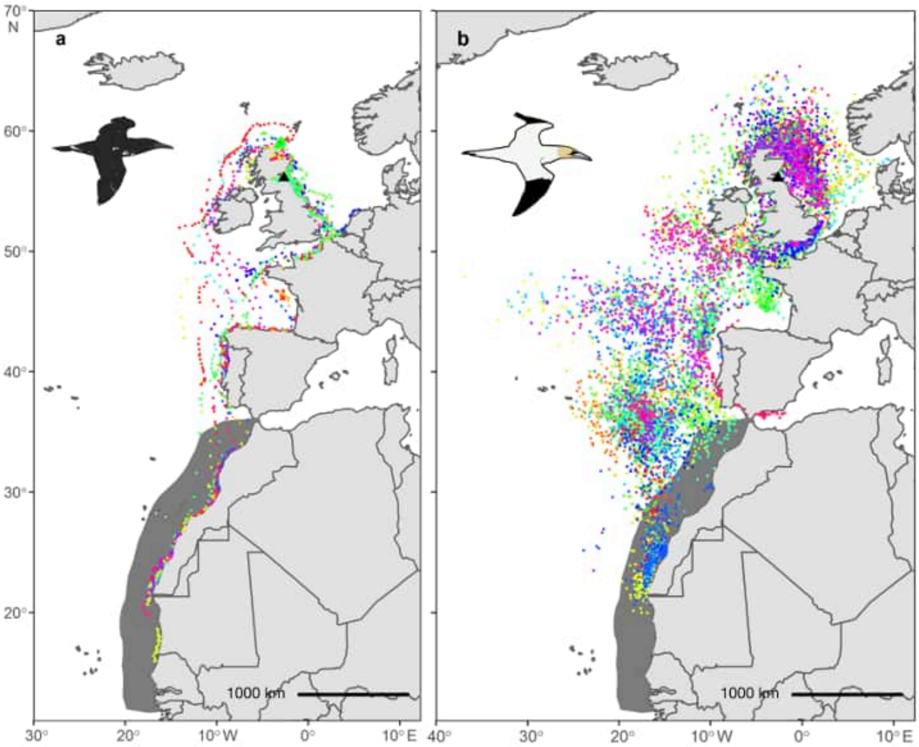


Figure 3.43 (a)GPS locations of 41 juvenile gannets tracked from Bass Rock (black triangle) between September and November 2018 and 2019; (b) GLS locations of 35 adults tracked from Bass Rock between September and January 2018−19 and 2019−20. Individual birds identified by colour. Shaded area in (a) and (b) shows the Canary Current Large Marine Ecosystem (Lane et al. 2021)

A small study from Helgoland, Germany, on seven chick-rearing northern gannets revealed that birds avoid areas where wind turbines were installed in the southern North Sea, despite the areas having been regularly visited prior to installation (Garthe *et al.* 2017a). This avoidance behaviour has two key implications for gannets. First, avoiding wind turbines reduces the risk of direct mortality, as gannets flying at higher altitudes (above 50m) could be at risk of colliding with turbine blades. Second, this avoidance might lead to habitat loss due to displacement from wind farm areas, a potential problem if more wind farms are constructed. Although this study does not provide direct information about foraging areas, it shows that the impacts of OWFs on gannets could extend beyond the wind farm areas themselves, possibly affecting buffer zones and wind turbine wake zones, particularly for birds commuting to and from breeding colonies (Garthe *et al.* 2017a).

A second publication by the same authors analysed gannet dive positions in relation to fixed habitat parameters (distance to colony, water depth, and distance to coast). Most dives occurred within 50 km of the colony (Figure 3.44), with dive frequency decreasing as distance increased. However, the proportion of dives increased at the greatest distances, suggesting that gannets might specifically target these distant foraging areas (Garthe *et al.* 2017b).

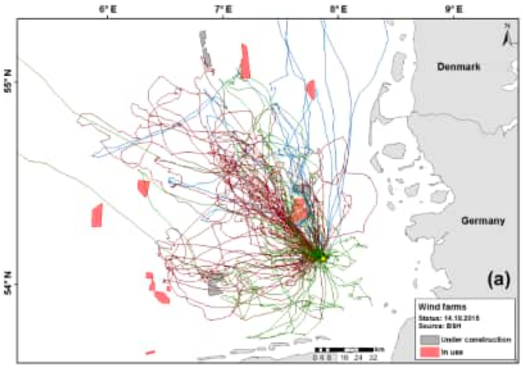


Figure 3.44 *Overlap of flight patterns for the three northern gannets with the locations of wind farms in the German Bight* (Garthe *et al.* 2017b).

3.3.11 Red-throated diver

Dorsch *et al.* (2019) used stable isotope analysis to examine the trophic relationship of red-throated divers within their marine food webs in the North Sea and Baltic Sea. They used PTT tags to study the birds' migration movements from their breeding grounds. Of the 45 individuals sampled, 53.3% (n = 24) performed their autumn moult in the Baltic Sea and 46.7% (n = 21) in the North Sea (Figure 3.45) (Dorsch *et al.* 2019).

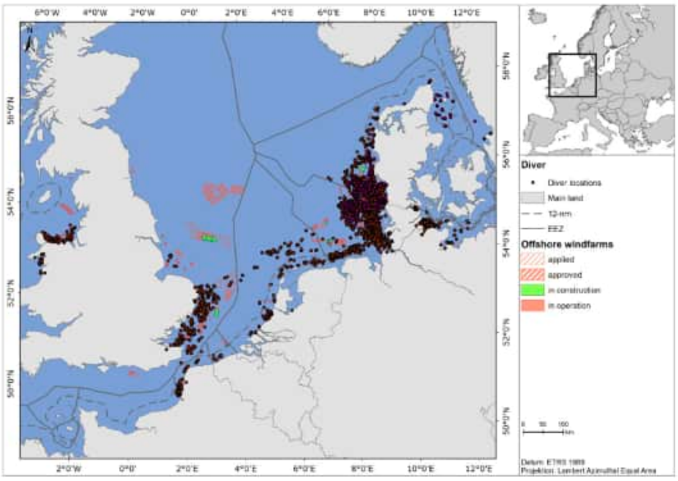


Figure 3.45 *Red-throated diver wintering areas used for home range analyses (Dorsch et al. 2019).*

The authors found that about half of the birds captured in the German North Sea wintered there, while the remainder travelled to nearby waters, using the eastern German Bight for staging and moulting during migration. The authors concluded that the tracked individuals from different breeding regions used various wintering sites, with no consistent migration patterns (Dorsch *et al.* 2019).

The study also observed relatively high site fidelity among red-throated divers; many birds consistently used the same wintering, spring staging, breeding, and moulting areas from year to year. High site fidelity may make the species more sensitive to disturbances, taking them longer to adapt to environmental changes (Dorsch *et al.* 2019). The ability to adapt depends on the availability of alternative habitats. In the eastern German Bight, some individuals used multiple core areas, suggesting a high exchange between sites within the larger wintering area. Environmental factors such as wind conditions (Figure 3.46) can lead to some flexibility in stopover sites during migration, with similar patterns observed in other seabirds relating to ocean productivity (Péron & Grémillet 2013).

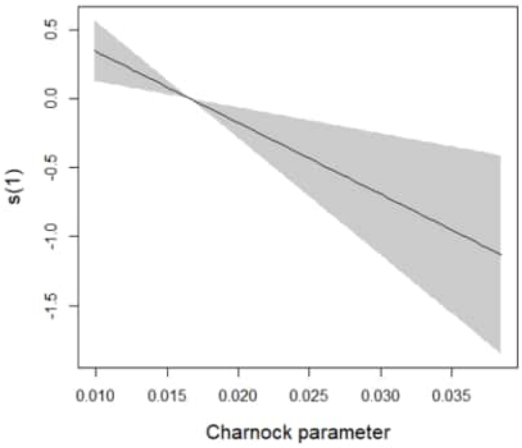


Figure 3.46 GAMM response curve showing that red-throated divers were less likely to migrate when Charnock parameter values, characterising sea surface roughness, were increasing during spring migration (Dorsch et al. 2019).

Linked to the above study, a DNA metabarcoding analysis was conducted on red-throated diver fecal samples collected during at-sea capture and PTT deployment in the German Bight (Kleinschmidt *et al.* 2019). The authors found an exclusively piscivorous diet, with no evidence of cephalopod or crustacean consumption, and a similar prey spectrum between two consecutive sampling years (Figure 3.47).

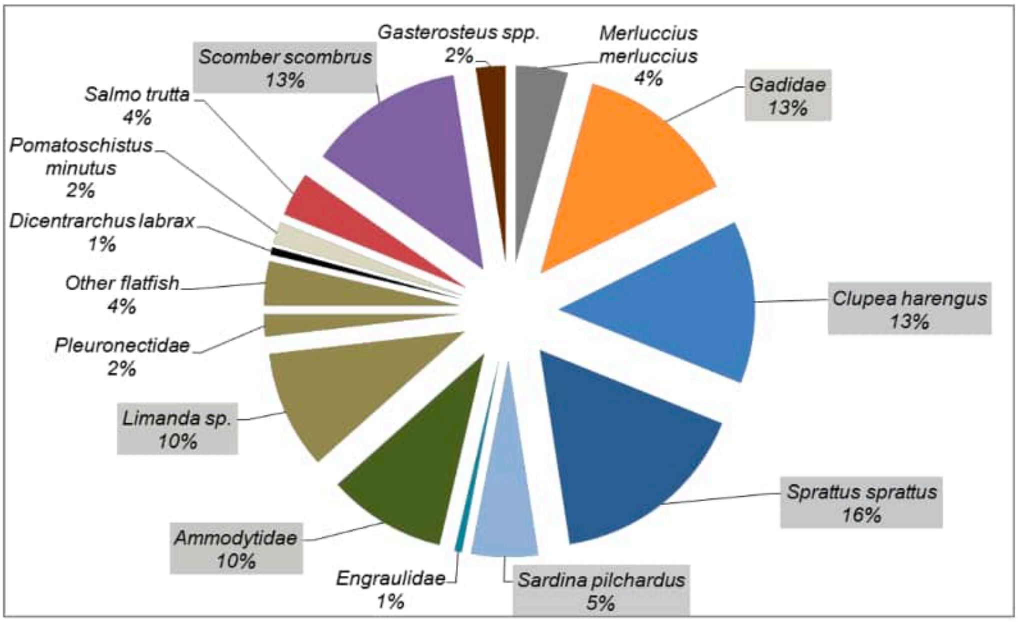


Figure 3.47 The occurrence of molecular operational taxonomic units (n = 169) in all red-throated diver fecal samples (n = 29) assigned for fish prey: blue = clupeids, orange = gadoids, grey = hake, brown = sticklebacks, violet = mackerels, red = salmonids, beige = sand gobies, black = seabass, grey = light-brown flatfish and green = sand lances. Captions of prey groups with highest proportions (> 5%) are highlighted (Kleinschmidt et al. 2019).

Red-throated divers consumed a broad range of fish species, both pelagic and benthic. Primary prey included clupeids, mackerels, flatfish, gadoids, and sand lances, with no single species dominating their diet (Kleinschmidt *et al.* 2019). Sprat and juvenile herring were the most frequent prey items; these species are high in energy and abundant in the German Bight during spring, aligning with the study's sampling period. Prey size also influenced selection, with juvenile herring (<20 cm) and smaller sprat (<16 cm) being most commonly consumed. European sardine and anchovy were found less frequently, corresponding with their Mediterranean origin and recent expansion into the North Sea. Red-throated diver distribution is therefore closely linked to the availability of prey, particularly in frontal zones (Kleinschmidt *et al.* 2019).

Flatfish, particularly juvenile common dab, were also found in the diet, though in smaller quantities, possibly due to their wide-bodied shape. Gadoids, particularly cod, were less frequently consumed by red-throated divers. Sand lances, an important prey species for seabirds in the North Sea, occurred frequently in the diet in 2015 but were less common in 2016 (Kleinschmidt *et al.* 2019). This aligns with commercial catch data that showed fluctuations in sand lance abundance over the study period. Previous studies (Madsen 1957; Guse *et al.* 2009) also observed varying frequencies of sand lances in red-throated diver diets, suggesting that this is closely tied to their availability in the environment. Other species such as sea trout, hake, stickleback, bass and sand goby were recorded infrequently. Thus, overlap exists between the prey species of red-throated divers and commercially fished species such as herring and mackerel (Kleinschmidt *et al.* 2019).

Oceanographic conditions were similar between the two sampling years, whereby diver diet appeared relatively stable, reflecting prey availability. The diet samples also included expanding species like European sardine and anchovy, as well as recovering species such as mackerel, suggesting flexibility in prey consumption (Kleinschmidt *et al.* 2019). However, the authors recommended collecting additional data over a longer period to fully support this conclusion. They also stressed that energy expenditure and resource partitioning are poorly understood during the non-breeding season. Reliable energy intake during winter is vital for red-throated diver survival and migration, and disruptions in prey availability could negatively impact their ability to meet these demands (Kleinschmidt *et al.* 2019).

3.3.12 Sandwich tern

Fijn *et al.* (2024) combined GPS tracking with video monitoring and visual observations of Sandwich terns breeding in the Netherlands to study the spatial distribution of prey items and foraging trip energetics of the tracked birds. The authors found that terns captured smaller prey closer to their colony, while high-energy prey was obtained on longer trips (Figure 3.48) (Fijn *et al.* 2024).

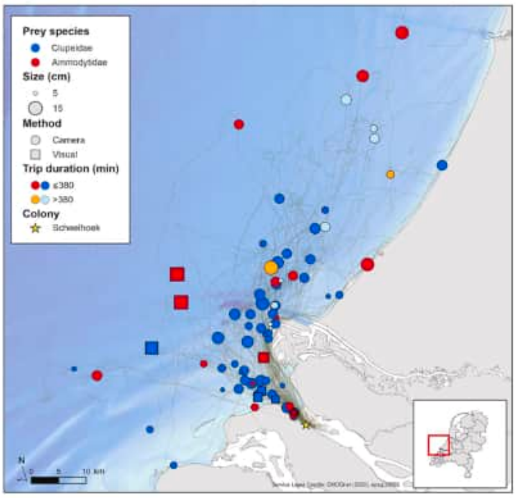


Figure 3.48 *Spatial distribution of capture locations of prey items brought to the colony by Sandwich terns with GPS loggers in 2012, 2013 and 2017. Prey size is to scale and colour indicates prey species. Faded colours indicate prey items left out of the regression analysis (Fijn et al. 2024).*

In the study, 79% of all prey items were delivered to chicks, closely aligning with the 86% found during visual observations reported by another study elsewhere (Stienen *et al.* 2001). Prey lengths of provisioned items were similar between tagged and non-tagged birds in 2012 and 2013. Prey items comprised primarily *Clupeidae* and *Ammodytidae* (Fijn *et al.* 2024). Fish monitoring in the area confirms that larger individuals of these species are found further from the coast (Waardenburg Ecology unpublished data). Abiotic factors such as tide and weather conditions also likely influence prey availability (Fijn *et al.* 2017).

Larger prey items captured further from the colony by Sandwich terns suggest a spatial pattern in prey size distribution and greater energetic investment by adults to acquire prey (Fijn *et al.* 2024). Such investment for higher caloric prey implies that parents may have to work harder when chick energy demands increase later in the season. This increased energy expenditure is likely compensated by the adults' ability to self-provision during foraging trips (Fijn *et al.* 2024).

Comparative tracking studies on Sandwich terns breeding in the same area showed core foraging areas up to 40 km from the coast, or 60 km from the colony (Figure 3.49) (Fijn *et al.* 2014; Fijn *et al.* 2017). The authors found substantial year-to-year variation in foraging ranges, although prey availability, tides and local feeding conditions around the colonies are known to drive variation in foraging ranges. There was a significant positive relationship between average prey length and trip duration (Fijn *et al.* 2017).

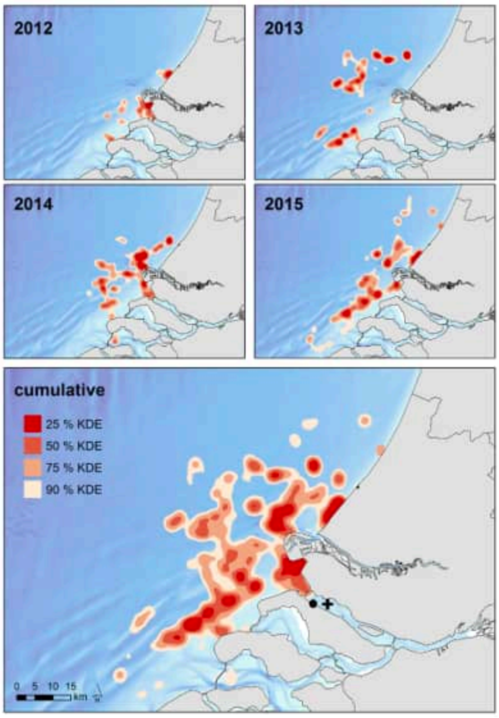


Figure 3.49 Kernel density estimates calculated for foraging Sandwich terns (21 birds, 154 trips) using location data collected in four consecutive breeding seasons with GPS loggers on birds breeding in two different colonies (Scheelhoek: 2012, 2013 and 2015 [dot], Slijkplaat: 2014 [cross]). (Fijn et al. 2017).

A similar study by Fijn *et al.* (2022a) found that breeding Sandwich terns foraged in highly dynamic marine habitats in the North Sea where environmental conditions varied temporally across different scales. Foraging was strongly influenced by sediment grain size, suggesting that even in such a dynamic habitat, sediment type is crucial in determining the likelihood of foraging (Figure 3.50). Salinity, wave period, and water depth showed a small but consistent effect (Fijn *et al.* 2022a). These findings highlight the complexity of seabird foraging behaviour in response to environmental cues and suggest that both long-term habitat features and short-term conditions contribute to Sandwich tern foraging strategies.

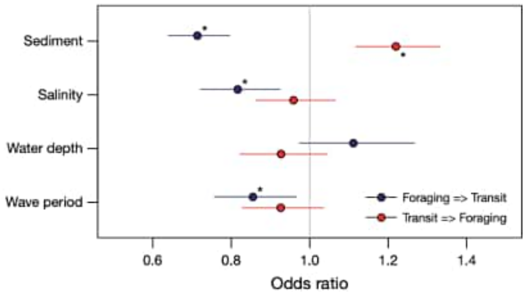


Figure 3.50 Parameter estimates ranked by value for Sandwich tern transition from transit to foraging. Positive values = probability of switching behaviour. Covariates were standardised. Error bars: 95% CI; asterisks: significant (Fijn et al. 2022a).

The main prey of Sandwich terns were forage fish, specifically from the uppermost 1.5–2.0 meters of the water column. Sediment grain size was linked to the presence of sandeel, an important prey for Sandwich terns throughout the breeding season. Sandeel are visual feeders found in the water column during the day but buried at night, often in coarser, sandy sediments (Fijn *et al.* 2022a). Thus, Sandwich terns were more likely to forage in areas with coarser sediments as these areas have a higher sandeel abundance. Given that sandeel form a key part of the diet for many seabird species in the North Sea, many seabird species are also expected to target areas with coarser sediments (Fijn *et al.* 2022a).

Furthermore, salinity is linked to the presence, growth, and survival of sandeel (van der Kooij *et al.* 2008; Bonisławska *et al.* 2014; Tien *et al.* 2017). Sandwich terns were more likely to forage in areas with higher salinity, possibly reflecting higher sandeel abundance. In addition, herring and sprat (Clupeidae) are important prey items for Sandwich terns, especially later in the breeding season (Fijn *et al.* 2022a). While herring and sprat may be associated with specific seafloor habitats, their preference for sediment type is less pronounced than that of sandeel. Nevertheless, herring distribution and growth has been linked to higher salinity, which might explain why Sandwich terns are more likely to forage in areas with higher salinity (Baxter *et al.* 2011; Fijn *et al.* 2022a).

A study from the UK revealed clear spatial patterns in the distribution of Sandwich tern foraging and commuting behaviour. A distinct commuting flight path was observed between the breeding colony and the foraging areas, with two frequently visited OWFs falling within the foraging area. These coincide with important nursery grounds for sandeel and herring, key prey species for Sandwich terns and linked with areas containing coarser sediments (Thaxter *et al.* 2024).

The authors found a marked reduction in the use of OWFs between the first (2018) and second (2019) years of operation. The mechanisms behind these changes are still unclear but could include increased densities of predatory fish, changes in vibrational sensitivity, and potential negative biotremological effects, similar to those seen in terrestrial environments for earthworms (Thaxter *et al.* 2024). Nevertheless, this reduction in OWF use could reflect an impact on the terns' prey base, particularly the availability of sandeel. Sandwich terns are especially sensitive to changes in the abundance of sandeel near their breeding colonies, which are predicted to decrease within OWFs in the long term (Thaxter *et al.* 2024; van Bemmelen *et al.* 2024).

Finally, van Bemmelen *et al.* (2022b) predicted the at-sea area use of breeding Sandwich terns in the southern North Sea based on GPS tracking, annual colony counts, and environmental variables. Distance to the colony had the greatest impact on foraging habitat use, with birds generally preferring areas closer to their breeding colony. Terns also showed a preference for shallow waters and finer sediments (Figure 3.51). However, these covariates likely only capture part of the habitat selection process, as terns are known to target dynamic and ephemeral phenomena such as thermal fronts (Baptist & Leopold 2010), and specific ocean conditions like clarity and temperature (Grecian *et al.* 2018).

The authors further suggest that frontal systems could be integrated into the model using advanced techniques like remotely sensed finite-time lyapunov exponents (Boffetta *et al.* 2001). Tidal cycles could also play a role in shaping at-sea habitat selection (Trevail *et al.* 2019), thus influencing foraging behaviour. Offshore habitat selection was assumed to be similar across years, however foraging distribution could change in response to variations in prey availability and the needs of adults and chicks throughout the breeding season (van Bemmelen *et al.* 2022).

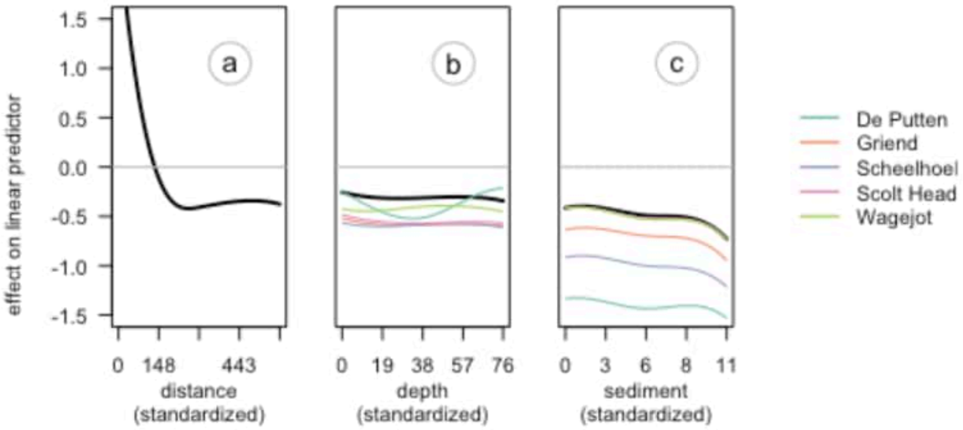


Figure 3.51 *Effects of distance to colony, water depth and sediment grain size on at-sea area use by Sandwich terns. Coloured lines show colony-specific effects estimated through random intercepts and slopes (van Bemmelen et al. 2022).*

4 Seabird distribution in the North Sea with survey data

4.1 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. In this chapter, the most recent estimates of the spatial and temporal distribution of seabirds on the Dutch continental shelf are summarized and reviewed. In addition, we present a preliminary analysis of observations of actively foraging seabirds, focusing on whether consistent patterns in the spatial distribution of foraging behaviour excist. Finally, we discuss important knowledge gaps, recommend research themes, and suggest a priorisation in studies.

We focus on the following species: northern fulmar *Fulmarus glacialis,* northern gannet *Morus bassanus* , black-legged kittiwake *Rissa tridactyla*, great black-backed gull *Larus marinus*, herring gull *Larus argentatus*, lesser black-backed gull *Larus fuscus*, Sandwich tern *Thalasseus sandvicensis,* common tern *Sterna hirundo,* razorbill *Alca torda*, common guillemot *Uria aalge*.

4.2 Spatial and temporal distribution of seabirds

Many studies have attempted to estimate and model seabird distribution in the (Dutch) North Sea (e.g. Stone *et al.* 1995; Camphuysen & Leopold 1994; Waggitt *et al.* 2019; Donk *et al.* 2024). The earlier studies were based on pioneering surveys of seabirds from vessels and calculated observed 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; it is also usually not accompanied by estimates of variation or uncertainty.

Observed and estimated densities

Density maps can also be generated by spatial modelling, offering the potential to further our understanding of the drivers of seabird distribution by including covariates describing abiotic and biotic factors and human activities. Studying the relative importance of static versus dynamic environmental covariates on seabird distributions may also shed light on the consistency of seabird distributions in space and time - and thus what future changes in covariates and consequently 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, food availability, fishing activity), 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 planning of offshore wind farms and assignment of marine protected areas, where decisions may have consequences over multiple decades.

Table 4.1 Data and covariates (with sources and frequency) that were used or explored in the analyses of van Donk et al. (2024), with slight adaptations.

Type of data	Source Time period	Frequency
ESAS counts raw data (number of birds)	ESAS (ICES datacenter) 1991-2022 MWTL data, not open. https://sovon.nl/ or https://waardenburg.eco/	Date time stamp for every observation
Sediment (percentage mud and sand)	Working Group on Spatial Fisheries Data (outputs from nvt 2021 meeting https://www.ices.dk/community/groups/pages/wgsfd.asp	One value for all years
Depth (m)	x	One value for all years
Distance to (nearest) coast (km)	x	One value for all years
Sea surface temperature (SST, C)	Marine Copernicus. SST: January 1982 to https://doi.org/10.48670/moi-00153, December 2020, Chl-a:	monthly and annually
Chlorophyll A (Chl-a; Mg/l)	https://doi.org/10.48670/moi-00058 January 1993 to June 2022	monthly and annually
Distribution other species	Waggitt, James (2019), Data from: Distribution maps of nvt cetacean and seabird populations in the North-East Atlantic, Dryad, Dataset, https://doi.org/10.5061/dryad.mw6m905sz	One value for all years
Breeding sites (distance to nearest breeding site, km)	UK breeding sites downloaded from Measurements done https://app.bto.org/seabirds/public/index.jsp. Other between 2013-2017 breeding sites taken from https://ebba2.info/	number of breedings pairs, One value for all years
Shipping lanes (distance to nearest shipping lane, km)	RWS (2017), Scheepvaart verkeersscheidingsstelsel Version of 2017 Noordzee (Nederlands Continentaal Plat) update 1-juni-2017 https://www.nationaalgeoregister.nl/geonetwork/srv/dut/catalog.search#/metadata/5996e444-f7f3-40d2-b485-8b9af6e8aa89?tab=relations	One value for all years
Distance to neareast mining platforms	Human activities, oil & gas platforms, boreholes and 1950-now offshore installations. https://emodnet.ec.europa.eu/geoviewer/	month-year of completion of construction
Distance to nearest offshore windfarms	To be requested via Wozep - Offshore Wind Ecological Programme OWPdata_HabLoss500mBuffer.gpkg, Soudijn, F. H., Hin, V., Wal, J. T. van der, & Donk, S. van. (2021). Cumulative population-level effects of habitat loss on seabirds “Kader Ecologie en Cumulatie.” Wageningen Marine Research report C070/21, IJmuiden, September 2021, https://doi.org/doi.org/10.18174/553775	year of completion of construction
Fishing activity (seafloor swept x times per year)	VMS data via WMR	Annual data between 2009-2020

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 estimated density maps for the Dutch sector of the North Sea for a set of seabirds based on ship-based and aerial survey data, 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 ecosystem of the North Sea. Both Waggitt *et al.* (2019) and van Donk *et al* (2024) included environmental and human activity 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).

Covariates

Donk *et al.* (2024) selected a range of covariates based on a literature review and expert knowledge about the drivers of seabird distribution. The final selection of covariates was initially limited by what environmental data were available for the greater North Sea. Prey abundance and availability was identified as an important driver, but data in a relevant format on the scale of the North Sea are currently lacking. Therefore, proxies for habitat and/or prey availability were used including 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 review and/or expert judgement) to have an effect on the species' distribution. The lack of data on prey abundance and availability was also apparent in the review of tracking studies in the North Sea area (Chapter 3).

The report by van Donk *et al.* (2024) provides a short overview of the results per study species; a table with environmental and human activity covariates showing which covariates were retained in the final models (Table 4.1), conditional plots of the effect of water depth, and the resulting density maps. The main aim of the project was 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. Furthermore, model selection was performed, which is primarily developed for prediction rather than inference. 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, the resulting seabird density maps and our understanding of the drivers of seabird distributions.

Estimated density distribution maps

In appendix A, we present the most recently developed distribution maps with estimated densities. In most cases, these texts and maps originate from van Donk *et al.* (2024) and have been estimated using habitat modeling techniques, using aeral survey data collected within the MWTL program. However, two species were not included in the study by van

Donk *et al.* (2024) and have been sources from other studies. These are northern fulmar and common tern. For the northern fulmar, Waggitt *et al.* (2019) provides the most recent distribution map for the DCS, on a monthly basis, using habitat models and aerial and ship-based seabird surveys covering the northeast Atlantic between Norway and northern Portugal. For common tern, the most recent maps were prepared by Wageningen Marine Research for the KEC project, using inverse-distance weighing of aerial survey data from the MWTL program (Susanne van Donk *in litt*). Here, we discuss these maps, with special attention to the results presented by van Donk *et al.* (2024), aiming to suggest potential additional covariates, or combinations of covariates, that may improve future modelling and our understanding of seabird distributions. Several statistical aspects were already highlighted in the discussion by van Donk *et al.* (2024) and will not or only shortly be repeated here.

Explained variation

Van Donk *et al.* (2024) succinctly discussed the model results per species, mainly focusing on summarising which covariates were retained after model selection. It is important to realise at the outset of a discussion on the effects of covariates that the random spatial-temporal field explained much more 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 proportion of the observed densities. This indicates that there are important drivers of seabird distribution that were not included as covariates in the models – for a long list of potential reasons, 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 a literature review, apart from water depth, which was included in all models. Water depth likely captures a key component of the large-scale habitat selection of species, for example whether they occur primarily nearshore (e.g. Sandwich tern) 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. Other covariates considered were sand percentage of bottom sediments, sea surface temperature, chlorophyll-a concentration, distance to the nearest large breeding colony and distance to shipping lanes and fishing vessel activity. The literature review which formed the basis for the initial selection of covariates generally appeared complete. However, while shipping lanes were considered for the two alcids, fishing vessel activity may also disturb alcids and would be interesting to include in future modelling exercises.

Within species, the selection of variables in the final model differed 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 and availability, the seasonality of whether they are included may suggest seasonal changes in diet, the link between prey and the covariates, or both.

Correlation between covariates

It should be noted that the set of covariates initially considered by van Donk *et al.* (2024) was based on a literature review and already rather extensive. Several of the initially considered covariates could not be included in the models. Variables that were excluded were salinity, wind force, the occurrence of other seabird species, offshore platforms, offshore wind farms and currents. An important reason for not including certain covariates was collinearity, for example the correlation 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 were 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/cetaceans) and what would be used for predictions (in this case: the modeled average densities of seabirds/cetaceans). After all, robust predictions require gridded data of relevant covariates with suitable resolution across at least the Dutch North Sea and preferably the whole North Sea basin. Similarly, the attraction of seabirds to active fishing vessels can have a huge local effect on observed densities, but fishing activity data are usually only available as fishing intensities averaged over a much longer time frame than the observations.

Static and dynamic environmental covariates

When studying the temporal consistency of seabird distributions, an important issue is the relative roles of static versus dynamic environmental variables. Ideally, for this approach, sufficient static and dynamic variables should be included in the models. In the models by van Donk *et al* (2024), only a 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 and effect sizes (after standardising the covariates) 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 (e.g. stratification and depth distribution of prey). 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 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 (Felicísimo *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 distribution in other ways, such as has been tested elsewhere in this report, for the Frisian Front and the distribution of common guillemots.

Feeding associations with seabirds and cetaceans

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 metre 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.

Temporal resolution

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 five-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.

Besides large-scale ship-based and aerial surveys, drivers of seabird distributions can also be studied using tracking data from individual birds, which is discussed elsewhere in this report (Chapter 3). 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. Recently, methods have been developed for the integration or joint interference of telemetry (spatial and temporal) and survey (spatial) data (Blackwell and Matthiopoulos, 2024; Lauret *et al.* 2025).

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 (see below in section 4.4). 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.

4.3 Species-specific concerns: Northern Fulmar and Common Tern

The maps by Waggitt *et al.* (2019), shown here only for the northern fulmar, were developed using survey data stored in the ESAS database (which includes the MWTL aerial survey data) and collected during 1980-2018. These maps give a general overview of seabird distribution at very large scales. As such, the maps by Waggitt *et al.* (2019) have a much lower spatial resolution than those by van Donk *et al.* (2024). They provide monthly estimates whereas virtually all of the survey effort in recent years has come from the aerial surveys of the MWTL program, which have not been carried out monthly but since 2014 in six months of the year in January, February, April, June, August and November.

The maps for common tern were developed using inverse-distance weighing. This method does not provide uncertainty estimation and may be especially sensitive to very high values. Sample size would permit habitat modelling: high numbers are recorded annually during the MWTL aerial surveys In April, June and August (Bemmelen *et al.* 2023).

5 Distribution of foraging seabirds

At small spatial scales, seabirds often aggregate where foraging opportunities arise. Hence, at spots where many seabirds are present, a large proportion is expected to show behaviour indicating foraging - either just before actual feeding (e.g. searching behaviour, or homing in towards a feeding frenzy), during feeding (diving, scavenging, etc.) and potentially just after feeding (resting on the water in flocks). However, at larger spatial scales, the link between the distribution of seabirds and the likelihood of foraging may be decoupled or weakened. At larger scales, seabirds are likely distributed according to the *potential* to find foraging opportunities. Hence, at such large scales, the proportion of birds foraging may show a much weaker increase with seabird densities than at small scales. Therefore, areas with higher proportions of foraging seabirds may not align, or only weakly, with areas of higher seabird abundance.

Here, we studied the relationships between seabird abundance and the probability of foraging at small spatial and temporal scales (along 5 km transect segments, within surveys) and at larger temporal and spatial scales (20 x 20 grid cells, across all surveys during 2014-2024), using ten years of aerial surveys on the DCS. In particular, we aim to study whether areas are associated with higher-than-average probability of foraging behaviour, and whether these overlap with areas of higher bird densities.

5.1 Methods

The MWTL aerial surveys provide good coverage of the Dutch sector of the North Sea - in particular since the adoption of a new survey design in 2014. For as many sightings as possible, observers note the behaviour and association, for example with cetaceans, according to standardised protocols (Camphuysen & Garthe 2004). For further details on the survey methods, see van Bemmelen *et al.* (2023).

Per 5 km segment and per focal species, the total number of individuals was summed, as well as the number of individuals recorded as foraging (where this was noted), namely where behaviour was either: dipping, diving/foraging, kleptoparasitising, kleptoparasitised, scavenging, wheeling, searching, or associating with the surf, a line in the sea, a front or floating seaweed. Note that this excludes birds that associated with fishing vessels. We also calculated seabird densities, dividing the number of observed individuals by the 'effectively surveyed area', which is calculated by multiplying the number of observed sides of the plane by the length of the segment and the effective strip width (ESW). We used the most recent estimates of ESWs for this dataset (van Bemmelen *et al.* 2023). This procedure accounts for decreasing detectability of birds at larger distances from the transect. In each analysis, only surveys with at least 50 sightings were included.

We then analysed the data per species in three steps. First, the probability of showing behaviours associated with foraging was modelled as a function of the natural log of bird density. The number of foraging birds was taken as the response, with the total number of observed birds as the number of 'trials' in a binomial generalised linear model (GLM). Per survey, a random intercept and a spatial random field were included to account for temporal and spatial correlation. Only segments with sightings were included, as there is the probability of observing foraging birds is zero when there are no birds present.

Second, the probability of foraging was modelled only spatially to explore whether foraging was consistently more likely in some areas. The number of foraging birds was taken as the response, with the total number of observed birds as the number of ‘trials’ in a binomial GLM. Now, the model included a single random spatial field. Random intercepts were added per survey. Whether areas were associated with higher-than-average probabilities of foraging behaviour was assessed by taking 1000 draws (samples) from the model and calculating the lower boundary of the 95% confidence interval; if this was higher than the intercept (i.e. the mean probability), areas were considered to have foraging birds more often than expected.

Third, we spatially modelled abundance using a negative binomial model with the number of observed birds per 5 km segment as the response, with an intercept, random intercepts per survey and the log of the effectively surveyed area as an offset. We chose this approach rather than the more sophisticated distribution maps by van Donk *et al.* (2024) to make sure 1) that abundance and foraging probability were based on exactly the same data and 2) that predictions were not affected by environmental covariates - so that abundance estimates will be closely linked to observed numbers. For each species, we then fitted a simple regression model with of the predicted foraging probability (second model) as a function of the predicted density (third model), with random intercepts per survey. For both predictions, we used values at the scale of the linear predictor of each model (thus, at the logit and log scales, respectively) to allow the use of Gaussian models.

All models were fitted using the sdmTMB package (Anderson *et al.* 2024) in R (R Core Team 2023).

5.2 Results

Based on aerial surveys, almost no alcids (razorbill and common guillemot) were recorded actively foraging (<1%, n = 22,120 and 95,679, respectively), whereas for the other species the fraction of individuals recorded as foraging ranged between 22% (northern fulmar) and 58% (common/Arctic tern, species that are considered together here as they are frequently recorded to group level in the data).

The results presented here should be interpreted with caution, as some binomial models showed signs of poor fit; potentially caused by large numbers of zeros. This requires further exploration and testing - for example adjusting the spatial resolution of the mesh or using more informative priors.

At small scales - i.e. the scale of 5 km segments - the probability of foraging decreased with the natural log of the density of conspecifics for black-legged kittiwakes and common/Arctic terns, whereas it increased for most the remaining species (Figure 5.1). For great black-backed gull and razorbill, confidence intervals overlapped with zero, thus the absence of an effect of seabird densities could not be excluded.

For each species, the probability of foraging showed spatial variation (Figure 5.2), with some areas containing a substantially higher proportion of foraging birds compared to the average (i.e. where the lower boundary of the 95% confidence interval was higher than the mean; Figure 5.3). However, the spatial patterns were generally erratic, and not linked to areas of high general abundance: confidence intervals of nearly all slope estimates overlapped with zero (Figure 5.4). For example, the distribution of common/Arctic terns showed generally high probabilities of foraging across the DCS, although their distributions are usually largely restricted to the nearshore zone and - especially in late-summer - the Frisian Front area. Two exceptions were Sandwich tern, which showed a positive relation between abundance and probability of foraging, and, surprisingly, razorbill, which was only rarely observed foraging (Figure 5.4).

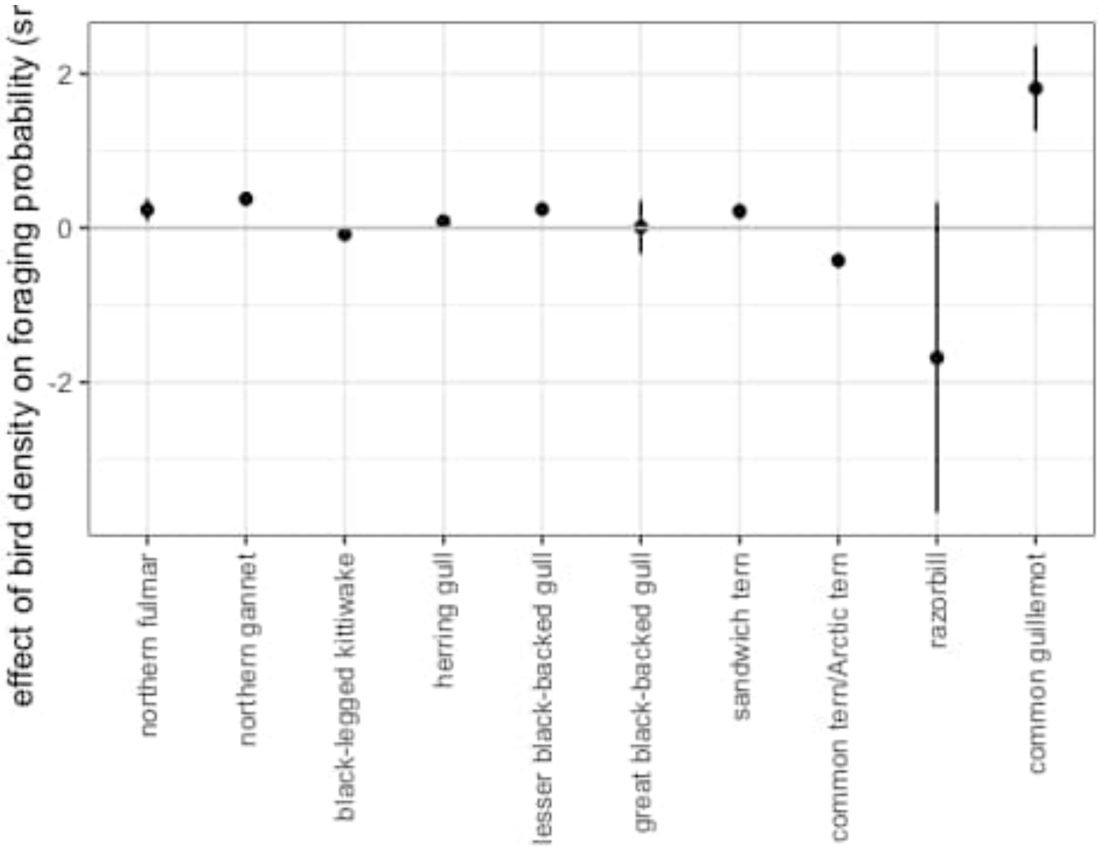


Figure 5.1 *Slope estimates of the effect of seabird densities on the probability of foraging, per species, at the scale of 5 km transect segments. The horizontal line at 0 represents no effect; estimates and 95% confidence away from this line indicate 'significant' effects. Note that the confidence intervals for razorbill were truncated at -0.04 and 0.04, whereas they extended to -0.27 and 0.22, respectively.*

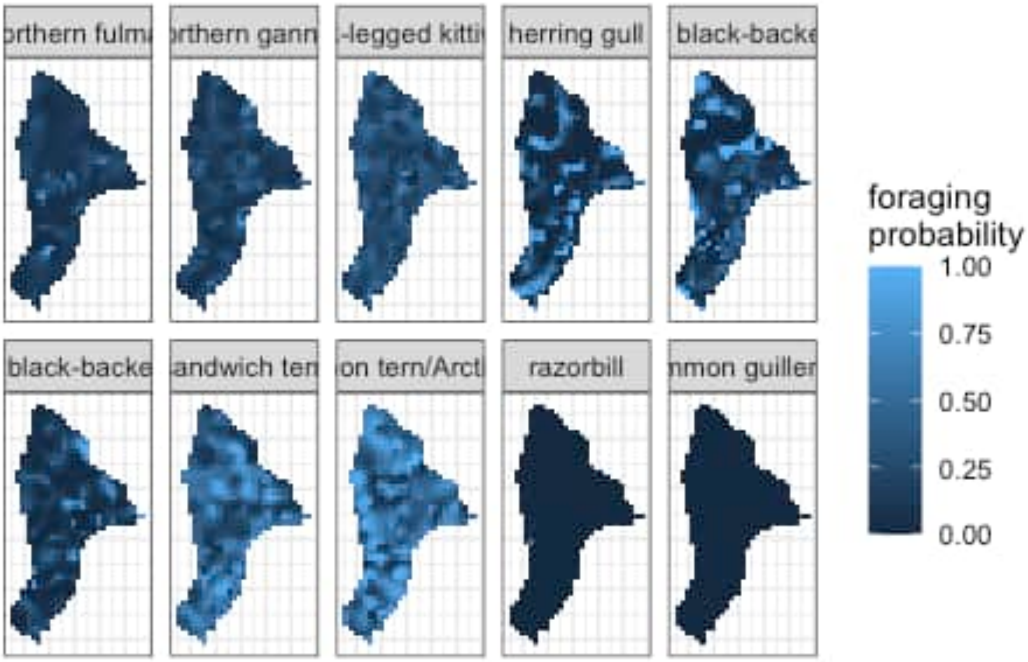


Figure 5.2 *Spatial pattern of the foraging probability of bird flocks, based on aerial surveys conducted in 2014-2024.*

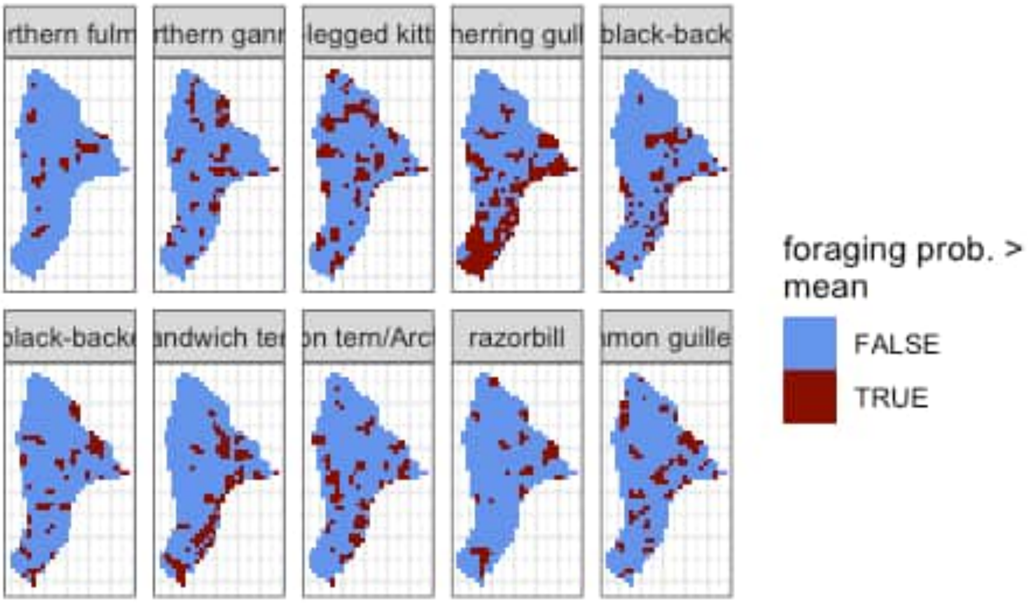


Figure 5.3 *Significance of the spatial pattern of foraging, assessed by whether the lower border of the 95% confidence interval is above the overall intercept (i.e. the overall mean probability) per species.*

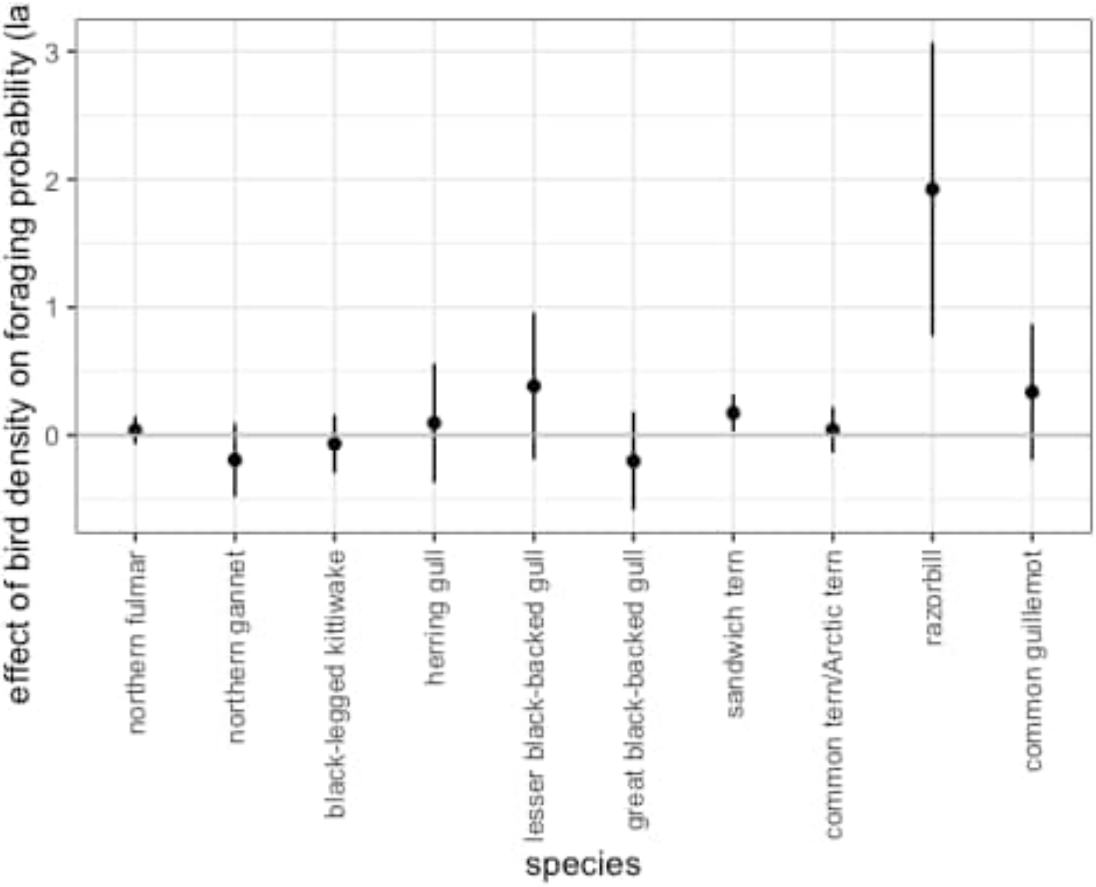


Figure 5.4 *Relationship between model-predicted abundance and model-predicted probability of foraging per grid cell, per species. The y-axis is on the scale of the linear predictor.*

Discussion

For most species, sightings were regularly accompanied by notes on behaviour and/or associations. However, this was not the case for the two alcids, razorbill and common guillemot, both pursuit-divers. Diving behaviour may thus indicate foraging, but also regularly occurs in response to the approaching ship or plane. Hence, diving behaviour of alcids is rarely recorded during ship-based or aerial surveys and may be ambiguous if noted. The scant sightings of actively foraging alcids explains why the confidence intervals of parameters for these species (especially for razorbill) are large (Figure 5.1 and Figure 5.4), and why there is no spatial pattern discernible for these species (Figure 5.2).

At the scale of 5-km transect segments, Sandwich terns, common/Arctic terns and black-legged kittiwakes were less likely to forage when there were more conspecifics observed; however, for northern fulmar, herring gull, lesser black-backed gull, great black-backed gull and common guillemot, this relationship was reversed. The confidence intervals for northern gannet and razorbill overlapped with zero, hence no conclusion can be drawn for these species. The differences between species are remarkable.

Although we found some support for patches with a higher-than-average probability of foraging in the remaining species, these patches were generally small (Figure 5.2) (and were not related to areas with higher abundance (Figure 5.4) , with the potential exception of Sandwich tern and razorbill (but see above for notes on that species). Considering that the modelled probability of foraging for a given location will depend on cases where the species is actually observed, erratic results in areas with lower densities were likely the result of too few observations. Together, these results suggest that at large temporal and spatial scales, and for most if not all species, foraging is likely to occur at all locations where a species is present - irrespective of its abundance. This suggests that when aiming to identify areas of high importance for seabirds, for example to delineate potential marine protected areas, using only the proportion of foraging birds may not necessarily lead to delineation of areas of high abundance. Using seabird densities as a proxy for food, therefore, may be untenable.

On the other hand, our analysis may have missed patterns of consistent foraging at small scales associated with static (physical) environmental properties. For example, Sandwich terns breeding in the Haringvliet area and tracked using GPS loggers mainly foraged along the surf and within a depth band further offshore parallel to the coast of South- and North-Holland (Fijn *et al.* 2022). At-sea surveys, with transects usually running perpendicular to depth gradients, may have limited effort per depth layer to capture such small-scale variations, whereas GPS tracking is more suitable to identify such phenomena.

In our analysis, we did not distinguish between different types of foraging behaviours (e.g. scavenging, pursuit diving) or associations (e.g. fronts, cetaceans). We also ignored foraging with fishing vessels. Furthermore, we did not explore potential seasonal or inter-annual variation. Potentially, areas with higher foraging activity may occur only in certain periods or are linked to specific phenomena such as fronts.

6 Knowledge gaps and recommendations

Table 6.1 provides a summary of seabird distribution maps, based on MWTL survey data, which are presented in Appendix I, together with tables showing which covariates were included in the final models. The maps show the general distribution of seabirds as described in chapter 4. The foraging distribution maps are discussed and included in chapter 5. Table 6.1 also shows how many studies were found and included in the review of geolocator and GPS logger studies.

Table 6.1 Target species within this project, with functional group, and indication of whether a general distribution map and/or foraging distribution map is presented in Appendix I and the number of tracking studies with Geolocators (#GLS) and GPS logger (#GPS) found in the literature review.

Species	Functional group	General map	Foraging map	#GLS	#GPS
Common scoter	Coastal diving	N	N	1	1
Red-throated diver	Coastal diving	N	N	1	1
Common guillemot	Pelagic	Y	Y	7	3
Razorbill	Pelagic	Y	Y	3	2
Northern fulmar	Pelagic	N	Y	2	1
Northern gannet	Pelagic	Y	Y	6	7
Black-legged kittiwake	Pelagic	Y	Y	4	5
Sandwich tern	Surface feeders	Y	Y	0	9
Common tern	Surface feeders	Y	Y	4	0
Lesser black-backed gull	Surface feeders	Y	Y	0	19
European herring gull	Surface feeders	Y	Y	0	6
Great black-backed gull	Surface feeders	Y	Y	1	2

6.1 Tracking studies

6.1.1 General knowledge gaps

Despite the insights provided by the above-mentioned studies on the target species in the (southern) North Sea, significant knowledge gaps remain regarding their foraging behaviour and preferences. While geolocators can provide information on the spatial distribution of coastal and seabirds outside the breeding season, these data are coarse and often limited (i.e. speed, flight height and other data are absent, and locations have large error margins). Furthermore, no geolocator studies exist for the great cormorant, little gull, European herring gull or great skua in the non-breeding season, in part since most of these species are larger and therefore more suited to GPS studies (the exception being little gull, which is challenging to study). Information on foraging site selection, feeding ecology and interactions with anthropogenic structures/activities, particularly OWFs and fisheries, is therefore still limited for these species.

The number of geolocator studies available for the target species in general is far lower than GPS studies. Of the studies that do exist, few environmental data were examined in association with the spatial data collected, leaving large knowledge gaps about the specific factors that drive foraging among these species. For example, only SST has been linked to the foraging behaviour of common guillemots (Dunn *et al.* 2020), great black-backed gulls (Layton-Matthews *et al.* 2024) and northern gannets (Atkins *et al.* 2023) in the non-breeding season. Models with additional covariates used to predict seabird distribution had issues with multicollinearity and were thus uncertain in relation to future climatic scenarios (Fauchald *et al.* 2021). Nevertheless, high SST is linked to large sandeel aggregations, and low SST to sandeel growth and recruitment, a main prey species for many seabirds (Hunt & Furness 1996; Hamer *et al.* 2007; Robertson *et al.* 2014; Fijn *et al.* 2022a; Militão *et al.* 2023; Thaxter *et al.* 2024).

Geolocator and GPS tracking studies are crucial in addressing knowledge gaps, providing (high-resolution) data on spatial and temporal foraging patterns, and revealing how marine birds utilise different marine habitats and are influenced by oceanographic conditions at different times of the year. For some species (e.g. lesser black-backed gull) there is an abundance of data (Ens *et al.* 2008; Corman & Garthe 2014; Camphuysen *et al.* 2015; Corman *et al.* 2016; Garthe *et al.* 2016; Sommerfeld *et al.* 2016; Shamoun-Baranes *et al.* 2017; Baert *et al.* 2018; Sotillo *et al.* 2019; Kavelaars *et al.* 2020; Vanermen *et al.* 2020; Sage & Shamoun-Baranes 2022; Camphuysen *et al.* 2023; Kentie *et al.* 2024), whereas for others (e.g. great black-backed gull) only a limited number of studies have been conducted (Borrmann *et al.* 2019; Madden *et al.* in review). For many of the target species, a suite of environmental variables have been linked to foraging based on GPS data (e.g. depth, SST, chlorophyll-a, sediment type/grain size, seabed morphology, water stratification/slope, salinity, wave activity, wind, tides, ocean fronts, distance to colony/coast, trip duration/direction, time of day, diet, prey length, fisheries) that provide a better understanding of why certain species forage in a particular area.

The foraging ecology of common scoter, little gull and great skua during the breeding season has not been studied successfully using GPS technology, leaving knowledge gaps about their responses to changes in prey availability in coastal and offshore zones in the North Sea.

6.1.2 GPS tracking data and environmental data

GPS tracking provides high-resolution data that can be combined with environmental or other data to better quantify the factors that influence foraging among marine birds. It is recommended, where feasible, carrying out GPS studies on those species where few data currently exist (i.e. common scoter, little gull and great skua). It is also recommended to perform analyses on existing data to help explain the factors that influence specific foraging behaviours among the already tracked target seabird species.

To demonstrate this, we downloaded publicly accessible GPS data of 100 lesser black-backed gulls tracked from Neeltje Jans in the Netherlands (Stienen *et al.* 2024) and extracted all locations from 2024. We resampled all data to 20-minute intervals and ran a Hidden Markov Model to infer behavioural states (stationary, foraging or in transit) based on step length and turning angle, calculated from the GPS positions. After filtering out stationary points, we then downloaded open access data from Global Fishing Watch (www.globalfishingwatch.org) from the same time period, and created a map showing lesser black-backed gull foraging/travelling in the North Sea and overlap (if any) with fishing intensity. To better assess whether lesser black-backed gulls foraged in association with fishing vessels throughout 2024, we split the data into seasons across 2024 and created four plots (Figure 6.1).

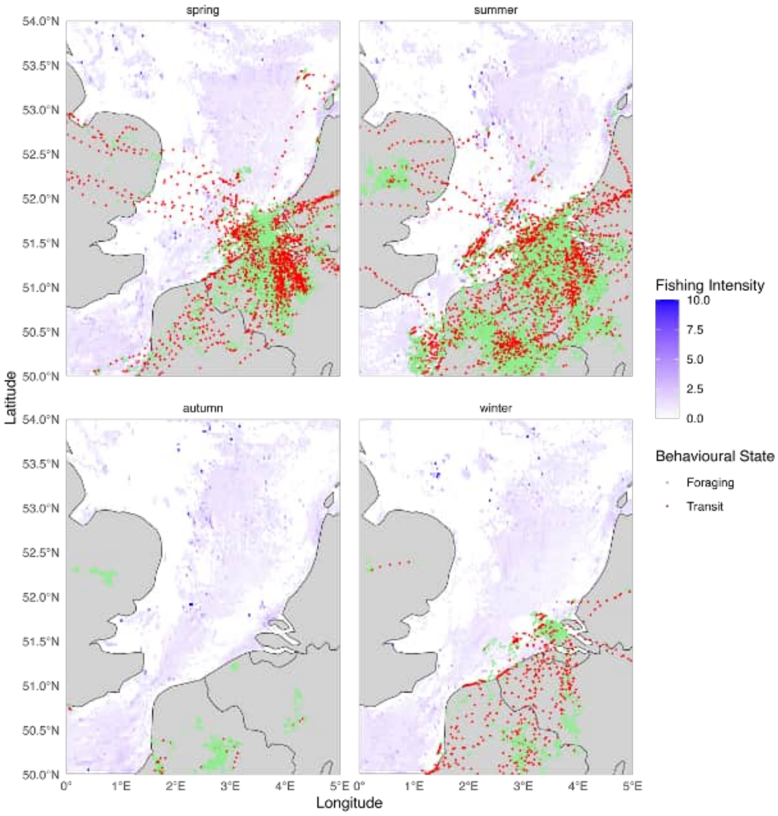


Figure 6.1 *Foraging (green dots) and transit (red dots) locations of 100 lesser black-backed gulls tracked in 2024 from Neeltje Jans in the Netherlands (Stienen et al. 2024) and fishing intensity (blue scale) in the North Sea, split according to season.*

From Figure 6.1 it can be inferrred that during 2024, lesser black-backed gulls nesting at Neeltje Jans foraged more on land than at sea, especially during autumn and winter. Specifically during autumn the birds had left the nest site and there was virtually no at-sea activity, whereas during winter marine foraging occurred primarily in the vicinity of the nest site (Figure 6.2), possibly in combination with local trawler activity. In the spring and summer, at-sea activity extended further from the nest site and there is a clear overlap between transit/foraging points and vessel activity, suggesting that lesser black-backed gulls follow trawlers to scavenge on discards.

- It is recommended to link these data with environmental variables obtained from Movebank to show whether the latter influence the probability of lesser black-backed gulls switching states (i.e. from foraging to transit or vice versa).

For the common tern, we obtained colony locations from SOVON (H. Schekkerman pers. comm.) and calculated the mean of the maximum foraging trip distance (20.4 km, based on data collected at the Maasvlakte breeding colony). We then plotted the foraging ranges (blue circles) of the common tern from coastal breeding colonies in the Netherlands located <8 km from the coast (Figure 6.2). This map provides a hypothetical visual indication of the coastal habitats in which common terns might forage and the plot suggests that there may be considerable overlap in foraging areas between colonies located in the south and north of the country, including the islands in the Wadden Sea.

- It is recommended to use this approach in new studies into prey availability and breeding success.

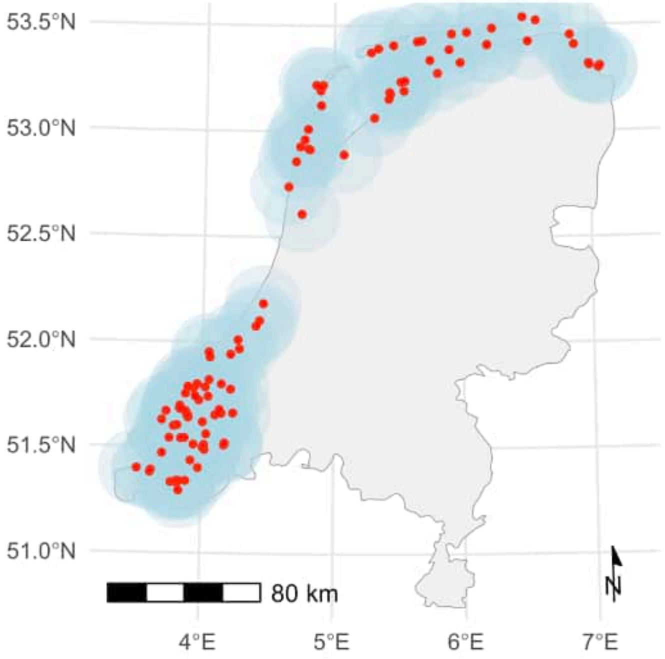


Figure 6.2 *Map of the Netherlands showing coastal breeding colonies (red dots) and the mean maximum foraging distances travelled by common terns (blue circles). Distance calculated based on data from a breeding colony at Maasvlakte II.*

As mentioned under §3.3.5, high-resolution data are being collected via GPS loggers on great black-backed gulls breeding in Norway. The data will be publicly available via Ecowende's Ecological Data Repository (predicted launch date: end 2025). These data will provide critical information about the spatial and temporal ecology of this species over at least five years (https://ecowende.nl/en/news/great-black-backed-gulls-tagging-with-gps/).

- It is recommended using these data, to determine year-round movements of breeding adults both within and outside the breeding season, their migration routes, and behaviour over the North Sea (e.g. interactions with fishing vessels, and meso/macro/micro-avoidance of or habituation to OWFs).

Additionally, combining these data with remotely sensed environmental variables accessed via Movebank will help explain what factors influence the probability of a bird foraging in or transiting over a particular area. For example, do great black-backed gulls forage preferentially in deep or shallow waters? In waters with higher salinity, primary productivity and/or SST? An example is provided below from the 2024 breeding season off the Norwegian coast that shows great black-backed gulls forage in shallow, highly productive waters, possibly in combination with fishing vessels (Figure 6.3).

- It is recommended to create North Sea foraging maps, similar to the one provided above for the lesser black-backed gull, based on these data.

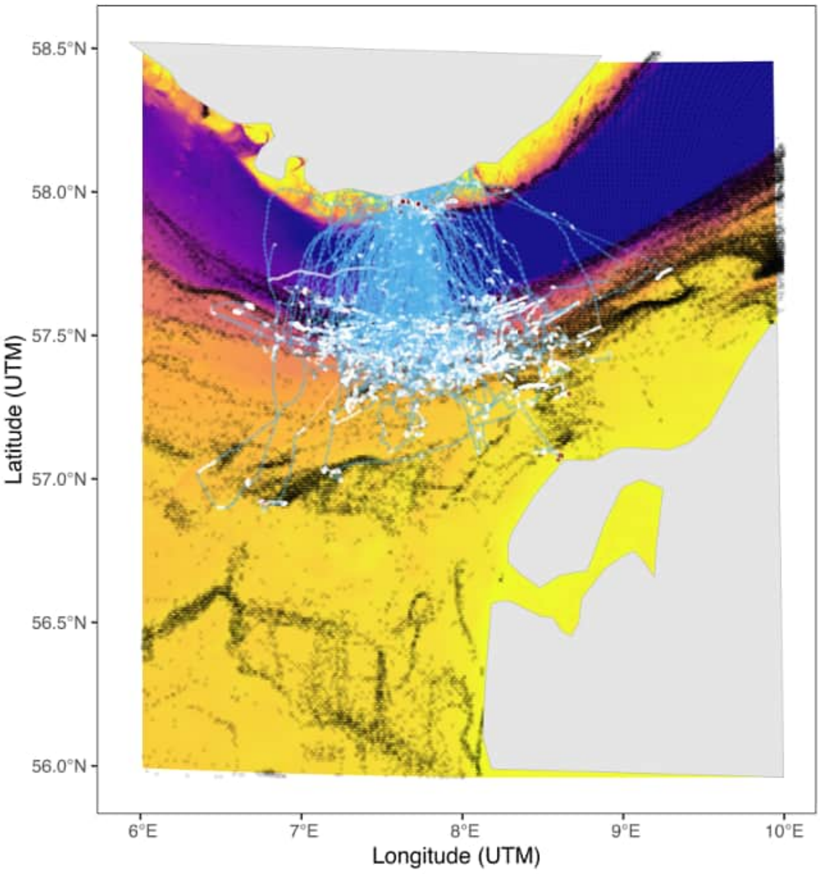


Figure 6.3 *GPS positions of Great Black-backed Gulls (n = 20), recorded during chick-rearing. GPS fixes were collected every 3 minutes. Grey areas are the landmasses of southern Norway, where the gulls breed, and north-western Denmark. White dots represent GPS fixes that were classified as foraging, blue dots represent flying, i.e. birds in transit between the colony and foraging areas, and red dots show where the birds were stationary. Apparent fishing effort (black) is based on changes in vessel speed and direction gained from the Automatic Identification System (AIS). Copyright 2024, Global Fishing Watch, Inc., www.globalfishingwatch.org. This map is overlayed with a raster showing bathymetry (source: General Bathymetric Chart of the Oceans; lighter colors (yellow) represent shallow areas; darker colours (blue) represent depth <400 m). Madden et al. 2025 in review.*

A number of unpublished studies are stored in Movebank's animal tracking database (www.movebank.org).

- It is recommended to explore the use of these ongoing projects that are not yet publicly available, tracking data that are being collected but are not yet published, or data that will not published by the owners (Table 6.2). Unfortunately for all datasets, these tracks may be viewed but not yet downloaded:

*Table 6.2 Overview of GPS tracking studies visible in Movebank's animal tracking database (www.movebank.org). * tracks may be viewed but not downloaded; ++ multiple species in same study*

Species	**Location**	**No. of tracked birds [tags]**	**First deploy-ment date**	**Last deploy-ment date**	**Contact person**	**Study name/summary**
Black-legged kittiwake*	Germany	29 [34]	2016	2021	Stefan Garthe	FTZ
Black-legged kittiwake*	Germany	22 [22]	2017	2022	Stefan Garthe	FTZ BfN MONTRACK
Black-legged kittiwake* ++	France	673 [1467]	2022	2025	Fréderic Jiguet	Migratlane/Tracking seabirds and terrestrial migrants to identify foraging, resting, dispersal and migratory pathways to advise offshore wind farm planning in the Channel and East Atlantic, off France
Great black-backed gull*	Germany	25 [21]	2016	2024	Stefan Garthe	FTZ Great black-backed gull North Sea
Northern fulmar* ++	France	673 [1467]	2022	2025	Fréderic Jiguet	Migratlane/Tracking seabirds and terrestrial migrants to identify foraging, resting, dispersal and migratory pathways to advise offshore wind farm planning in the Channel and East Atlantic, off France
Northern gannet* ++	France	673 [1467]	2022	2025	Fréderic Jiguet	Migratlane/Tracking seabirds and terrestrial migrants to identify foraging, resting, dispersal and migratory pathways to advise offshore wind farm planning in the Channel and East Atlantic, off France
Northern gannet*	Germany	42 [36]	2017	2020	Stefan Garthe	FTZ BfN MONTRACK
Razorbill* ++	France	673 [1467]	2022	2025	Fréderic Jiguet	Migratlane/Tracking seabirds and terrestrial migrants to identify foraging, resting, dispersal and migratory pathways to advise offshore wind farm planning in the Channel and East Atlantic, off France

As shown in the examples above (Figure 6.2, Figure 6.3), should these data become publicly available. These GPS-data contribute to a wider range of research questions than the spatial and temporal extent of foraging distributions, which is one of the focal questions in this study.

- It is recommended to use these data to produce maps showing the spatial distribution of the above-mentioned species, make inferences possible about their behaviour (e.g. travelling, foraging), migration movements, and to better understand the environmental factors (e.g. salinity, SST, depth, primary productivity) that influence behaviour in addition to foraging distributions.

6.1.3 Recommendations for further research

With the above knowledge gaps in mind, below we present some recommendations for further research to better understand coastal and seabird foraging in the (southern) North Sea.

Prey availability and adult survival

The relationship between adult survival and prey availability is not fully understood and requires more attention to complement data on breeding success. Vulnerability and sensitivity indices (see Table 6.3 and Table 6.4 are valuable tools for predicting seabird breeding success in relation to prey availability, especially sandeel. While these indices are well-supported by some localised data, their broader applicability and ability to predict impacts on survival in the wider North Sea require further investigation.

- It is recommended to combine ongoing monitoring with more refined models, which is crucial for effective seabird conservation, particularly in the context of fisheries management. See § 6.3.

In addition to the above-mentioned variables, several others could help provide a more nuanced understanding of the factors that influence coastal and seabird foraging in the North Sea:

Abiotic covariates

a) *Ocean currents*: seabirds often forage in areas where ocean currents converge, which can concentrate prey. *Calanus finmarchicus*, a copepod crucial to the grazing food web and populations of many fish species, is in decline in the North Sea partly due to changing currents (Frederiksen *et al.* 2013). Since the breeding success of seabirds such black-legged kittiwakes and common guillemots is correlated with the presence of *C. finmarchicus*, if this copepod shifts northward it will have consequences for seabird populations in this area (Frederiksen *et al.* 2013). Including data on currents (both surface and subsurface) could improve understanding of foraging behaviour.
b) *Temperature anomalies*: in addition to SST, incorporating temperature anomalies (e.g. the North Atlantic Oscillation index) could highlight how changes in sea temperature due to climate variation impact seabird foraging. For example, reported effects of the NAO on zooplankton abundance suggest that it may influence seabird populations (Durant *et al.* 2004).
c) *Nutrient upwelling*: areas where nutrient-rich water upwells are often hotspots for marine life. Including upwelling indices could reveal important foraging areas. For example, GPS tagged great black-backed gulls breeding in southern Norway foraged primarily in a shallow, highly productive marine area characterised by mixed depth waters (Madden *et al.* in review).
d) *Turbidity*: many marine areas have become more turbid due to climate change, which may affect the ability of marine birds to detect prey. For example, Manx shearwaters fitted with GPS loggers were more likely to forage in waters with low turbidity (Darby *et al.* 2022).
e) *Moon phase:* seabird (nocturnal) foraging behaviour may be influenced by lunar cycles, especially those species that rely on visual cues or hunt at night. Including the moon phase or light intensity could be beneficial. For example, common guillemots switched

from foraging on sandeels during the breeding season to nocturnal prey species during winter, possibly influenced by moonlight availability (Dunn *et al.* 2020).

Biotic covariates

f) *Prey abundance and distribution*: while prey length is mentioned, more direct measurements or proxies for prey abundance and distribution (such as zooplankton or specific fish species density) could enhance models. For example, sandeel are a critical food source for many of the target species; a reduction in their abundance in the North Sea (either through fisheries or natural factors) will negatively impact seabird breeding performance (Table 6.3 and Table 6.4), adpated from (Furness & Tasker 2000).
g) *Prey species behaviour and diel patterns*: seabird foraging could be influenced by the behaviour of prey, such as migratory patterns, vertical movements, or diel activity (active during the day vs. at night), which could be coupled with GPS tracking. For instance, northern gannets exhibit diurnal foraging to capture prey located near the surface (Garthe *et al.* 2014).
h) *MSFAs*: surface-feeding seabirds may depend on other species (e.g. large fish, marine mammals) to drive prey to the water's surface. While such feeding associations are frequently observed during surveys (Camphuysen & Webb 1999), it is unclear to what extent these species depend on each other.

Human activities

i) *Human activity* (e.g. shipping lanes, OWFs, oil/gas operations)**:** the influence of anthropogenic factors in the North Sea, such as proximity to shipping routes or industrial activities, is likely to affect seabird foraging behaviour.

6.2 Survey studies

6.2.1 Identification of knowledge gaps: general seabird distribution

Timing

The MWTL programme's aerial surveys provide excellent data on the distribution of seabirds over the Dutch North Sea. However, the timing of surveys (January, February, April, June, August and November), is sub-optimal for the northern gannet and great skua *Stercorarius skua* (a species not considered here, but of high conservation concern); numbers of these species in the DCS peak in September-October, when no aerial surveys are carried out (Fijn *et al.* 2021).

Modelling

Ideally, the distribution of all species would be estimated using the same methods, but this is currently not the case. For the species considered here, northern fulmar and common tern distribution were estimated using different methods than for the remaining species. Although habitat modeling techniques may not be feasible for some species due to low numbers (e.g. skuas), this is not the case for the species considered here: all are relatively abundant (Bemmelen *et al.* 2023). Variation between species' models may arise, however, since what (sets of) covariates may be relevant will likely differ between species and season.

Covariates – forage fish abundance

The most obvious improvement to existing habitat models is likely the addition of information on the distribution and abundance of forage fish (herring, sprat, sandeel). At the time of the study by van Donk *et al* (2024), this was (deemed) impossible, as gridded data on forage fish distribution were not available. A first attempt to model the distribution of sandeel species *Ammodytes* - which form a critical food source for many seabirds - has recently been undertaken (Witbaard *et al.* 2024). A recent study focussing on small fish (<30 cm) showed that the flatfish dab and plaice are important contributors to fish biomass in the DCS, while sandeel dominates the Dogger Bank region (Parmentier et al., 2025; Figure 3.54). A next step would be to model the distribution of other forage fish species such as sprat *Sprattus sprattus* and herring *Clupea harengus* based on the HERAS and MONS fish surveys (Couperus *et al.* 2024).

Understanding the drivers of forage fish population dynamics and distribution would further improve understanding of seabird distribution and thus our ability to develop effective management strategies for seabird conservation. In addition, it may improve our understanding of the breeding distribution of a species with low site fidelity, such as the Sandwich tern, as well as our ability to explain productivity in (other) breeding seabirds (e.g. lesser black-backed gull and common tern).

Coastal zone coverage

Poot & Fijn (2016) concluded that in the first few years of the 'new' MWTL aerial surveys, effort in the coastal zone was rather limited - which is problematic for coastal species such as terns. This led to adjustment of the survey design, based on advice by Statistics Netherlands (CBS; CBS 2019), which was adopted in January 2020. Hence, survey effort has only been adequate for a few years. With the continuation of the MWTL aerial surveys, survey effort in the coastal zone will increase, which will provide more robust distribution maps of coastal zone species.

Distribution of seabirds outside the Dutch Continental Shelf

A major drawback of the current maps is that they do not extend beyond the borders of the DCS, whereas all birds using this area will spend part of their annual cycle outside the DCS. For example, common guillemots arrive with their chicks in the DCS during summer from breeding areas along the eastern coasts of England and Scotland. During summer and autumn, however, guillemots may leave the DCS. By focusing only on the DCS, important information on the movements of guillemots across the entire North Sea is missed. Although international at-sea seabird data are collected in the ESAS database, the amount of survey effort stored in the database for the past *ca.* ten years, has been very limited for large parts of the North Sea outside the DCS. It is essential that data collected during this period, but held back by private parties, become available to the scientific community to allow interpretation of seabird distribution patterns within the DCS and link these to North Sea-wide patterns.

Disturbance

With the development of additional offshore wind farms in the Dutch North Sea, shipping activity will increase - not only during construction but also the operational phase due to maintenance. Hence, it is important to better understand the effects of marine traffic on seabird distribution. Initial attempts to quantify the effects of shipping lanes on e.g. alcids (van Donk *et al.* 2024) have been made but additional studies are required, for example including fishing vessel activity data.

6.2.2 Identification of knowledge gaps: distribution of foraging seabirds

Breeding site fidelity

A notable dichotomy exists between two major seabird species breeding along the Dutch coast: lesser black-backed gull and Sandwich tern. Both are long-lived species that only breed at a few locations, but in (very) large colonies. The two species differ markedly in their breeding site fidelity: whereas lesser black-backed gulls usually breed in the same location in the same colony year after year (Camphuysen 2013), Sandwich terns may breed in different locations, even when re-nesting in the same year (Fijn & Bemmelen 2023). The factors that drive settlement in Sandwich terns are currently poorly understood. Conceivably, besides breeding habitat availability, settlement is largely driven by prey fish availability, the presence of predators, and social cues. Annual data on prey fish distribution may help elucidate our understanding of the processes (e.g. settlement) and consequences (e.g. productivity) that influence the breeding strategies of lesser black-backed gulls and Sandwich terns. Refer also to WP4 for issues relating to egg/chick predation.

Multi-species feeding associations

Another relevant topic is the dependence of seabirds on other seabird species to find food in the marine environment. Surface-feeding seabirds depend on fish availability in the uppermost metre of the water column. Pursuit-diving predators, such as alcids or cetaceans, can drive fish to the surface where they become available for surface-feeding seabirds (Camphuysen & Webb 1999). To date, the importance of such multi-species feeding associations (MSFAs) to drive the distribution of seabirds has received little attention (Veit & Harrison 2017).

Furthermore, the interplay between seabird species and other offshore marine predators is a relevant but understudied topic (Camphuysen & Webb 1999, Veit & Harrison 2017). As mentioned above, pursuit-diving predators drive prey fish to the upper water layers where they become available to surface-feeding seabirds. However, the extent to which surface-feeding seabirds depend on such processes is uncertain. A first step would be to study large-scale associations between species distributions, for example using the approach described by Bemmelen *et al.* (2025) where the distributions of black-legged kittiwake, a pelagic feeding seabird, were compared to those of common guillemot and razorbill - two pursuit-diving seabirds.

6.3 The importance of forage fish for coastal and offshore seabird foraging

Our review of c 75 tracking studies and several survey studies shows that very few tracking and survey studies of seabirds in the North Sea have used (direct) prey abundance as a covariate to explain or predict seabird distribution in general, and foraging seabirds in particular. This was identified as a knowledge gap in both tracking and survey studies. Therefore, it was recommended to explore possibilities to include forage fish abundance in tracking and survey studies of seabirds in the North Sea. This paragraph briefly reviews the importance of forage fish for coastal and offshore seabirds and the availability of data on forage fish abundance in the North Sea and the Dutch part in particular.

6.3.1 North Sea food web

If possible, the interactions between forage fish populations and coastal and seabird foraging ecology in the North Sea (See Figure 6.4 for the food web in the Southern North Sea) should be investigated. Over the past 50 years, the North Sea has experienced significant warming, with temperatures rising by approximately 0.18°C over the past century. These climatic shifts have led to increased primary production and changes in phytoplankton communities in the southern North Sea. Concurrently, zooplankton populations have shifted, with cold-temperate species like *Calanus finmarchicus* declining sharply - resulting in a 70% reduction in zooplankton biomass - while warm-temperate species and meroplankton have become more prevalent. These ecological changes have likely impacted the productivity of forage fish due to altered prey availability (Engelhard *et al.* 2014).

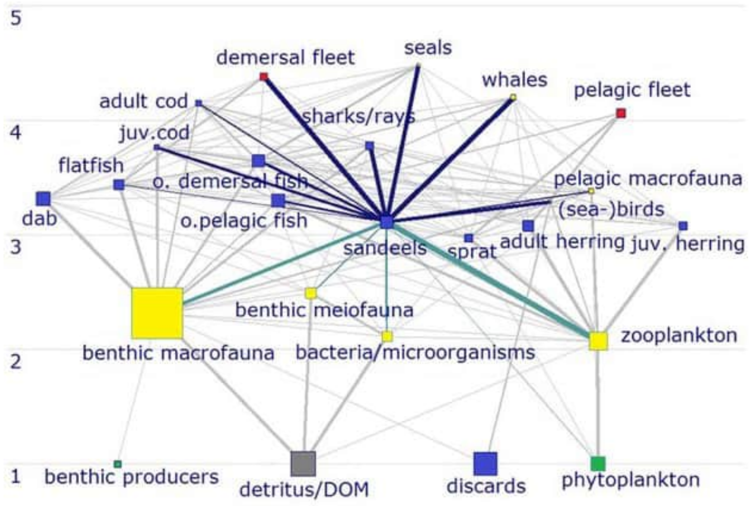


Figure 6.4 *Food web of the Southern North Sea showing the central position of sandeel, with lines indicating the trophic flows and numbers indicating trophic level. The size of squares is proportional to the biomass of a group, with grey representing detritus, green representing primary producers, blue representing fish, yellow representing marine organisms (except fish) and red representing fishing fleets (Otto et al. 2019).*

6.3.2 Distribution of forage fish

It is unclear whether forage fish in the North Sea (Figure 6.5) are influenced more by natural ecosystem dynamics, or by fishing pressures. Since the 1990s, pelagic fish numbers have increased, potentially indicating a shift from demersal to pelagic dominance (Engelhard *et al.* 2011). However, the influence of other predators like seabirds and marine mammals on these fish populations is not well understood. Four main drivers of forage fish dynamics have been identified: climate and environment, species interactions, predator-prey relationships, and fisheries. With their short lifespans and quick reproduction, forage fish are sensitive to climate change, especially in relation to plankton availability. The authors posit that recruitment in herring and other forage fish species may be linked to large-scale climate patterns such as the Atlantic Multidecadal Oscillation, however evidence remains limited (Engelhard *et al.* 2014).

It should be noted, however, that the above-mentioned study is based solely on trawl catches and not on ICES stock estimates. Trawl catch data demonstrate that there were large stocks of herring and sprat before the 1970s, which plummeted drastically following the introduction of industrial fishing. Thanks to improved quotas and enforcement, stocks have increased since the 1970s but are still well below their original levels. Fishing pressures on forage/pelagic fish are therefore still extremely high. Near Scotland, for example, almost the entire stock of sandeel was wiped out; this is no longer the case since the closure of the sandeel fishery in 2025. Recently, a ruling in arbitration between the EU and UK ordered the closure of the sandeel fishery (for recovery of seabird populations) in Scottish waters to remain in place, but to be reversed in English waters (Permanent Court of Arbitration 2025).

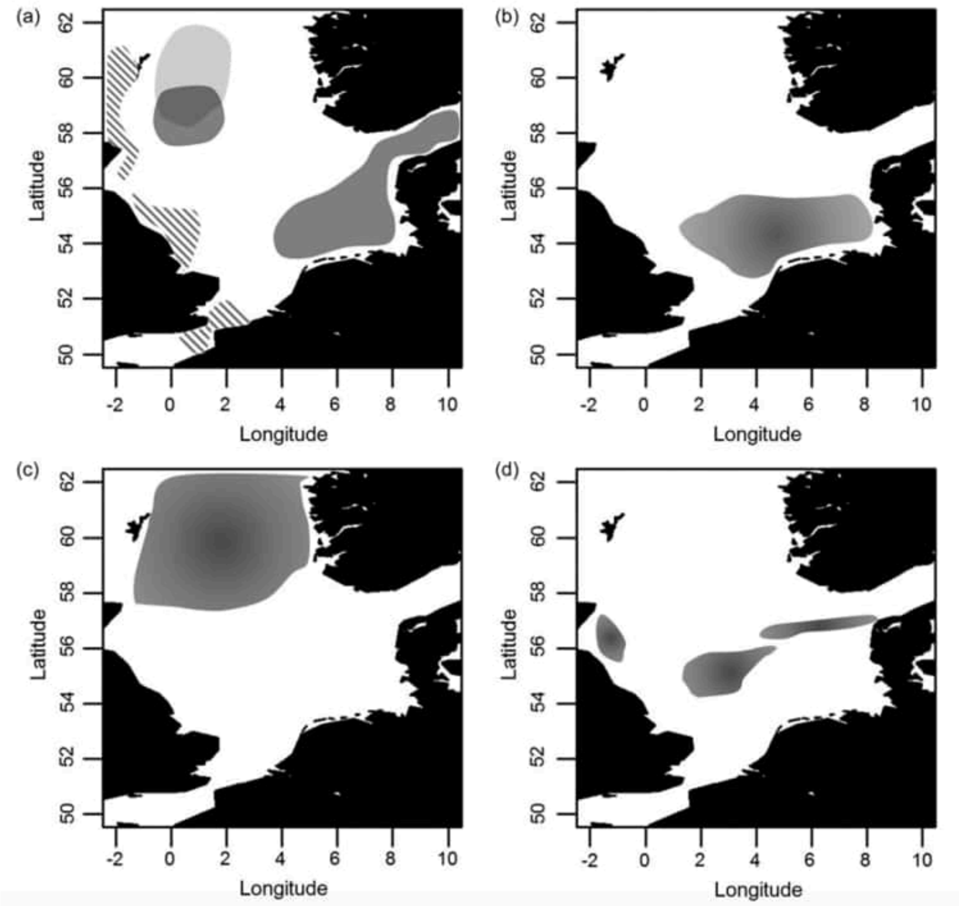


Figure 6.5 *Schematic distribution maps showing the areas of high concentrations within the North Sea for four forage fish species. A) herring, distinguishing between juveniles (dark grey), adult herring during summer (light grey), and autumn spawning areas (hatched); B) sprat; C) Norway pout; D) sandeel. The sketches are based on a combination of data from the International Bottom Trawl Surveys (IBTS), acoustics, and commercial catches (Engelhard et al. 2014).*

Herring, the most extensively studied forage fish in the region, shows varying responses to changing temperatures depending on life stage. Whereas cooler conditions support larval survival, juveniles benefit from warmer temperatures for growth, and adults require specific environmental cues to successfully spawn. These age-dependent responses highlight the complex environmental needs across the herring's life cycle (Engelhard *et al.* 2014). Wageningen Marine Research is a Dutch research partner in the herring acoustic survey project (https://www.wur.nl/en/research-results/research-institutes/marine-research/about-us/research-blogs/herring-acoustic-survey.htm), together with other research institutions from Ireland, Germany, Scotland, Norway and Denmark (Couperus *et al.* 2024). This international collaboration involves collecting (hydro)acoustic data combined with surf zone monitoring to estimate the herring stock size in the North Sea (Figure 6.6).

- It is recommended to use these monitoring data to create forage fish density maps. These maps can be used to include prey density as a covariate to analyse GPS tracking data.

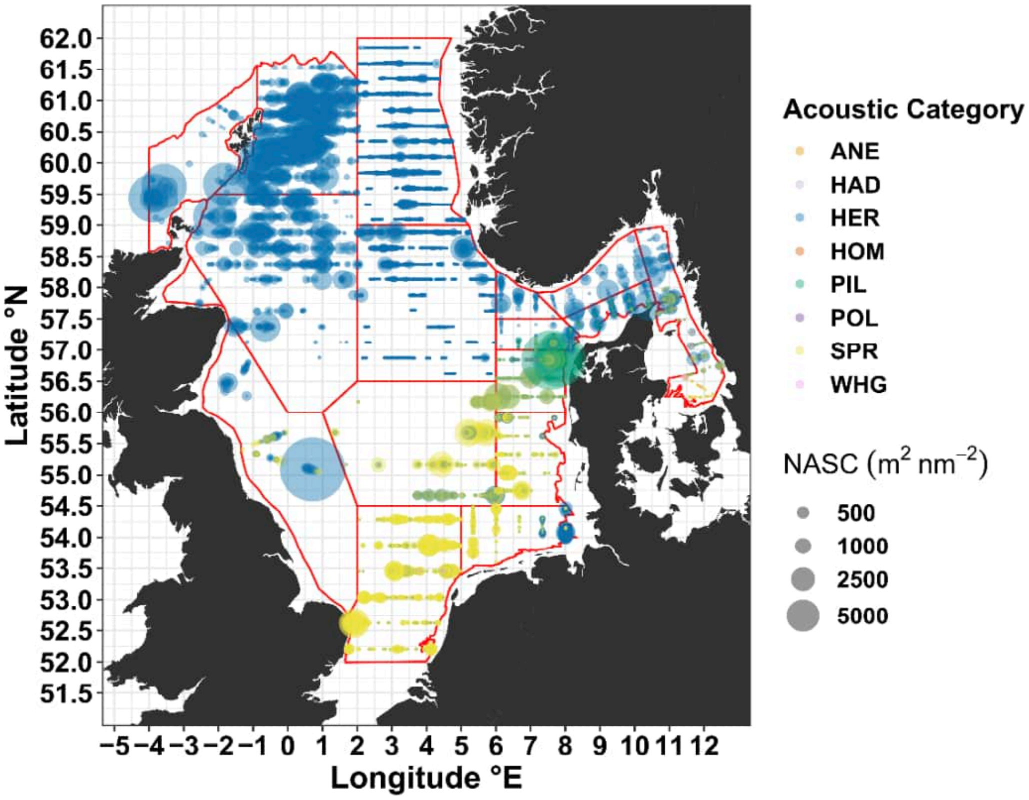


Figure 6.6 *Densities of small pelagic species (forage fish and young stages of haddock, pollock and whiting) determined by the HERAS survey, June 2023 – Disaggregated hydroacoustic categories assigned to hydroacoustic data after implementing the splitNASC-process in StoX software. Aggregated acoustic categories: CLU – Clupeids. MIX – Clupeids plus various other fish species. Disaggregated acoustic categories: ANE – anchovy. HAD – haddock; HER – herring; HOM – horse mackerel; PIL – pilchard; POL – pollock; SPR – sprat; WHG – whiting (Source: Couperus et al. 2024).*

Small fish abundance

A more recent study focusing on small (<30 cm) fish found that dab and plaice are the main contributors to fish biomass in the Dutch EEZ, while sandeel dominates in the Dogger Bank (Parmentier *et al.* 2025; Figure 6.7). While large fish trends are monitored using established indicators like the Large Fish Index, no similar index exists for small fish. Triple-D gear captured fish communities similar in composition to those sampled by a 2-meter beam trawl but with significantly higher biomass. This suggests that Triple-D gear is more effective - likely due to its fine mesh, fast towing speed, and ability to collect fish hidden in sediment (Parmentier *et al.* 2025).

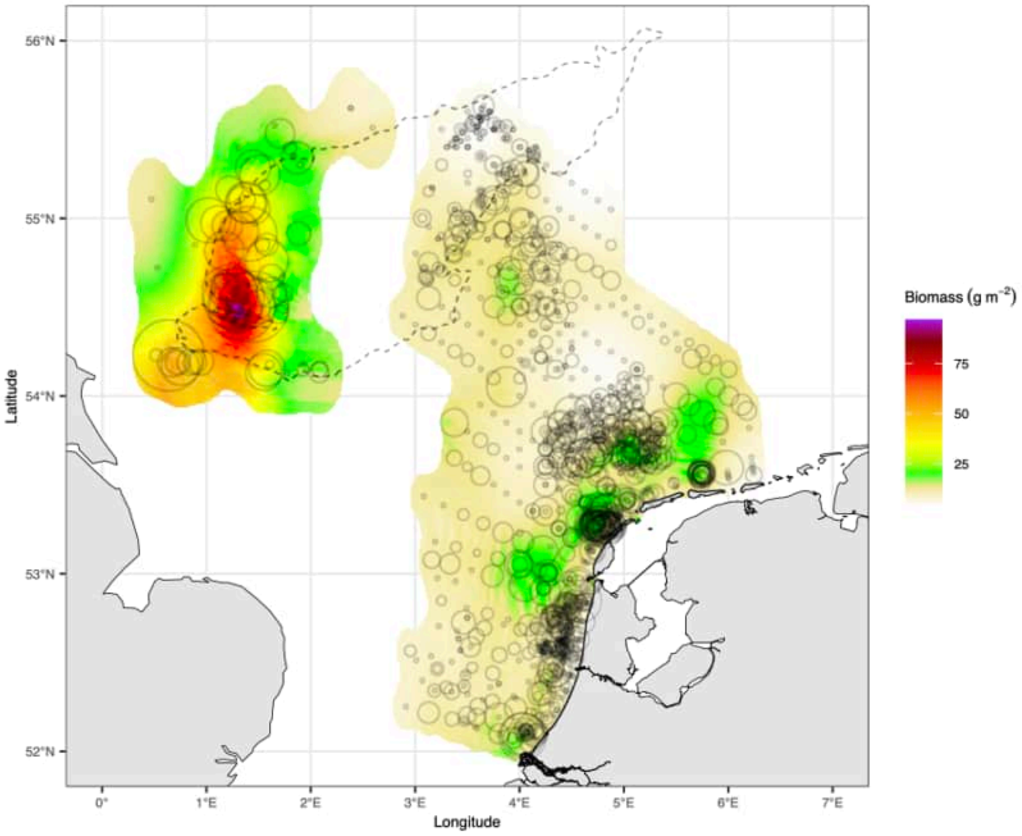


Figure 6.7 *Distribution of biomass per small (<30 cm) fish species and all remaining small fish pooled in the southern North Sea. Biomass estimates for the Dutch EEZ are a winter prediction, while estimates for the UK Dogger Bank reflect summer conditions. Size of black circles correspond with the observed biomass densities per station (corrected for haul distance and sorting fraction). The 40-m-depth contour of the Dogger Bank is indicated by the black dashed line (Parmentier et al. 2025).*

Compared to previous studies using different gear types (Greenstreet *et al.* 2007; Aarts *et al.* 2019), Triple-D gear consistently recorded higher small fish biomass, even when sandeel were excluded. These differences highlight the limitations of traditional survey methods, especially in catching small or buried fish. Survey trends may reflect changes in catchability as much as changes in fish populations, influenced by environmental factors such as water clarity and temperature (Parmentier *et al.* 2025).

Small demersal fish are concentrated in the southern North Sea, with high biomass identified in the western Dogger Bank. Spatial variation in fish biomass is likely due to the patchy distribution of species such as sandeel. The distribution patterns of the most abundant species in this study align well with earlier survey data, supporting evidence of species such as juvenile flatfish shifting offshore and northward (Parmentier *et al.* 2025). Unlike sedentary invertebrates, fish are mobile and show strong seasonal and annual variability in abundance and distribution. Day-of-year effects revealed seasonal trends, with biomass generally peaking in summer and declining in winter (Parmentier *et al.* 2025). Witbaard *et al.* (2024) published a first attempt to model the distribution of sandeel species

Ammodytes sp. - which form a critical food source for many seabirds - has recently been undertaken (Figure 6.8).

These studies improve understanding of sandeel distribution in the Dutch EEZ, especially in areas that have been under-sampled in past research. However, they do not directly compare sandeel data with ICES stock assessments or other dedicated sandeel studies, limiting broader interpretation. In areas sampled multiple times, seasonal differences were more substantial than annual variations. For instance, fish biomass in some locations tripled between seasons, emphasising the importance of accounting for such shifts (Parmentier *et al.* 2025). Areas with hard substrates, such as rocky reefs, shipwrecks, and wind farms, were excluded due to gear limitations. These locations likely support different fish communities and potentially higher biomass, thus total small fish biomass in the North Sea is thought to be higher than was estimated in this study (Parmentier *et al.* 2025).

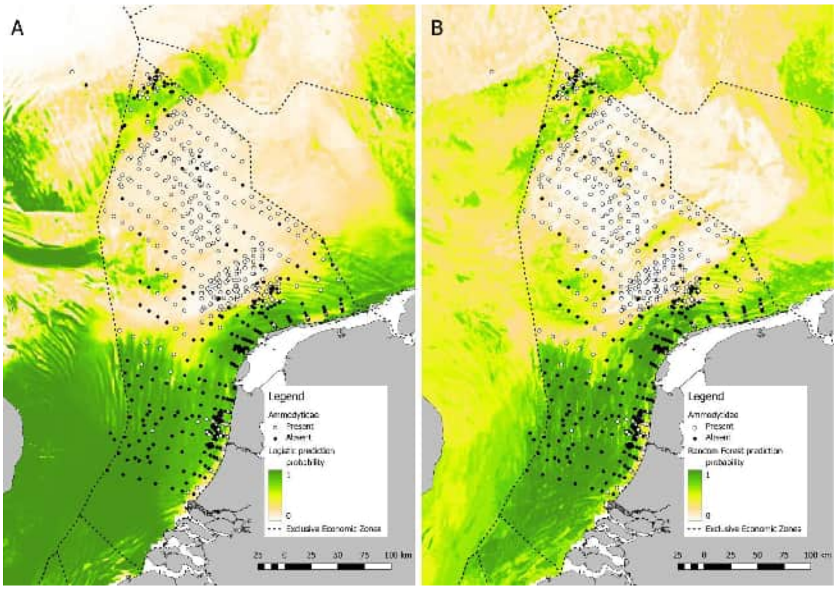


Figure 6.8 *Observed occurrence of sandeel in the Dutch EEZ, and model predictions by (A) logistic regression and (B) random forest regression. White open dots indicate samples with species absence, Black filled dots represent presence.* [Legends in figure are incorrect] *Green-yellowish shading represents predicted probability of occurrence from the models* (Witbaard et al. 2024).

Vulnerability of seabirds to forage fish abundance

As shown in (Table 6.3), common tern, Sandwich tern and black-legged kittiwake are particularly vulnerable to a reduction in food abundance, especially sandeel which form a significant proportion of their diet (Furness & Tasker 2000). Sandeel are harvested by industrial fisheries in the North Sea, with extractions being capped at 1 million tonnes to ensure sustainability of the species. During the breeding period, marine birds have a limited foraging range and limited time to forage. These high foraging costs, combined with small body size and lack of dietary flexibility, often means birds are reliant on sandeel, particularly in the northwestern North Sea. In the eastern and southern North Sea, seabirds consume more clupeids (e.g. juvenile herring) (Furness & Tasker 2000).

Table 6.3 *Vulnerability of breeding success of different seabird species to reduced abundance of food in vicinity of colonies (ranked by vulnerability score) (Furness & Tasker 2000).*

Species	**Small size**	**High cost of foraging /unit time**	**Constrained to short foraging range**	**Little ability to dive**	**Lack of spare time in daily budget**	**Low ability to switch diet**	**Score**	**Sensitivity to sandeel abundance (S & S.E. North Sea) [proportion sandeel in diet]**
Common tern	3	4	4	3	4	2	20	8 [0.4]
Sandwich tern	3	4	3	3	3	3	19	11 [0.6]
Black-legged kittiwake	2	2	1	4	4	3	16	10 [0.6]
Razorbill	1	3	2	1	2	3	12	7 [0.6]
Red-throated diver	0	3	4	0	2	3	12	0 [-]
Lesser black-backed gull	1	2	2	4	1	1	11	4 [0.4]
Herring gull	1	2	3	4	1	0	11	1 [0.1]
Great black-backed gull	0	2	3	4	1	0	10	4 [0.4]
Common guillemot	1	3	1	0	2	2	9	4 [0.6]
European shag	0	3	3	0	0	2	8	5 [1.0]
Great cormorant	0	3	4	0	0	0	7	8 [0.1]
Northern fulmar	1	0	0	4	2	0	7	1 [0.2]
Northern gannet	0	2	0	2	1	0	5	1 [0.2]

The above-mentioned study focused on breeding success and did not study adult or juvenile survival, immigration, or other factors. Life-history theory suggests that marine birds buffer against food shortages by reducing reproductive effort versus sacrificing their own survival (Cairns 1988; Furness 1996). However, black-legged kittiwake survival may decrease when the demands of chick-provisioning are particularly high (Golet *et al.* 1998; Golet & Irons 1999).

Top predators in the North Sea thus rely heavily on forage fish, often experiencing strong bottom-up effects where prey availability affects health and reproduction (Table 6.4). These effects are most pronounced in specialist species (e.g. kittiwakes), or during critical life stages such as the breeding season (Engelhard *et al.* 2014). Species with limited foraging ranges are especially vulnerable to local prey shortages; restricted movements can limit population sizes due to inter- or intraspecific competition, making it difficult to respond to changes in prey distributions (Furness 2002).

Table 6.4 Documented evidence of dependence on North Sea forage fish by marine birds (adapted from Engelhard et al. 2014).

Tab	Mobility	Herring	Sprat	Sandeel	Norway pout	Forage fish total	Reported effects of low forage fish abundance
Sandwich tern	I	High	High	High	Low	0,99	Highly vulnerable to changes in local food supply (esp. clupeids); reproductive performance, breeding numbers and breeding distribution [1]
European shag	I	Low	Low	High	Low	0,98	Reproductive output probably limited by local sandeel availability at Isle of May (UK) [2]
Great skua	IB	Low	Low	10-95%	Low	10-95%	Reproductive success influenced by local sandeel availability [3]
Guillemot	IB	0,14	0,15	0,42	0	0,7	Provisioning of chicks influenced by local abundance and quality of sandeel and sprat [4]
Razorbill	IB	0,09	0,22	0,37	0,01	0,68	Reproductive output probably limited by local sandeel availability at Isle of May (UK) [5]
Black-legged kittiwake	IB	0,02	0,06	0,28	0	0,36	Reproductive performance strongly dependent on local sandeel availability [6]
Northern gannet	IB	0,11	0,04	0,18	0	0,34	No evidence reported
Lesser black-backed gull	M	High	Low	Low	Low	7-25%	No evidence reported
Northern fulmar	M	0	0,02	0,11	0,02	0,15	No evidence reported

The able above shows, for each predator species, the levels of mobility; proportion of diet made up by each of four forage fish species, and all species combined; and documented cases of effects of low forage fish abundance on top predators. Mobility describes the potential of the predator to relocate to different feeding areas in response to localized prey shortages: I, immobile year-round; IB, immobile during the breeding season only; M, mobile year-round. Diet proportions refer to the percentage composition by mass of a particular prey type, averaged over 1 year and over the North Sea: note that local and seasonal percentages can be substantially higher or lower. Literature sources: [1] Stienen (2006); [2] Rindorf *et al.* (2000); [3] Furness (2007); [4] Wanless *et al.* (2005); [5] Mitchell *et al.* (2004); [6] Frederiksen *et al.* (2004).
(Rindorf *et al.* 2000; Frederiksen *et al.* 2004; Wanless *et al.* 2005; Stienen 2006; Furness 2007; Mitchell *et al.* 2011)

Forage fish face also substantial predation pressures, often exceeding natural mortality estimates commonly used in stock assessments. While fishing contributes to mortality, natural predators account for a larger share of total removals (Engelhard *et al.* 2014). Regionally, no single predator species currently exerts strong top-down control, however localised impacts can be significant. For example, whiting and grey gurnard are known to cluster around high-density sandeel areas (e.g. Dogger Bank). Such "aggregative responses" suggest that localised predator pressure may still be intense even when broader-scale influences are limited.

6.3.3 Conclusions

As the North Sea's ecosystem continues to undergo rapid transformation, our understanding of how coastal and offshore seabirds utilise the area for foraging remains too limited for the development of effective conservation measures. Marine birds are highly sensitive to changes in prey availability, which in turn are influenced by both anthropogenic activities and natural shifts in the marine environment. Comprehensive tracking and survey studies are therefore essential to more accurately determine core foraging areas and important migratory pathways. Linking spatial data with changes in marine resource availability and anthropogenic activites will provide critical insights that can guide national policy to ensure core foraging habitats are adequately protected in the North Sea.

The monitoring and research efforts outlined in the MONS programme are particularly timely given these and other substantial knowledge gaps. Nevertheless, based on studies to date, it is evident that some species (common tern, Sandwich tern and black-legged kittiwake) are extremely vulnerable to a reduction in prey abundance close to their breeding colonies, especially sandeel. If food availability can be increased in key areas (e.g. Bruine Bank and Friese Front) or in the wider southern North Sea, prey species might disperse to other areas in the North Sea.

Understanding the factors that affect coastal and seabird foraging requires insight into the food availability of breeding and visiting bird populations in the (southern) North Sea. Limited information is currently available about the abundance and availability of forage fish stocks, therefore a first step is to map forage fish and sandeel abundance and distribution over multiple years, and determine whether these exhibit any temporal changes/trends. In addition, interactions between forage fish populations and coastal and seabird survival and foraging ecology in the North Sea should be investigated, as well as the various environmental factors that influence the presence and abundance of these species. This will provide the data necessary for effective conservation of seabirds.

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Appendix I. Seabird distribution maps 2025-2020

Below, the most recent distribution maps for the period 2015-2020 based on the methods used in the study of van Donk *et al*. (2024). The latter study covers a longer time period (1999-2020).

Maps are included for 10 of the 12 species selected for this study: Northern Fulmar (based on Waggitt *et al.* 2019; figure A.1), Northern Gannet (figure A.2), Black-legged Kittiwake (figure A.3), Great Black-backed Gull (figure A.4), Herring Gull (figure A.5), Lesser Black-backed Gull (figure A.6), Sandwich Tern (figure A7), Common Tern (using invers-distance weighing, figure A.8), Common Guillemot (figure A.9), Razorbill (figure A.10). For red-throated diver and common scoter no suitable data are available for similar distribution maps.

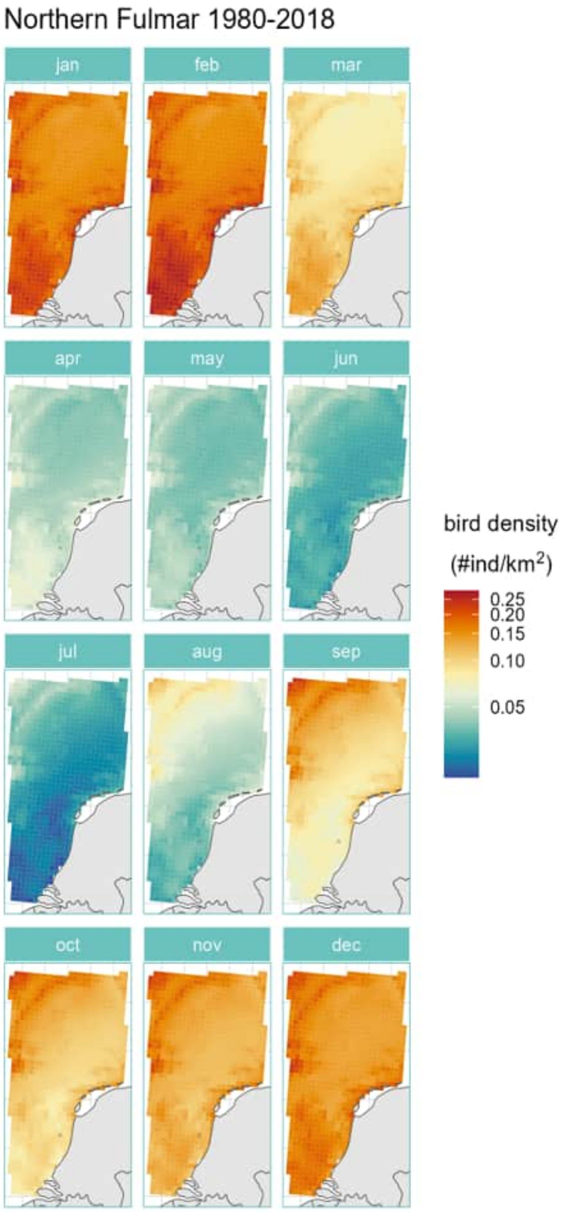


Figure A.1 *Monthly distribution of Northern Fulmar Fulmarus glacialis, based on habitat modelling by Waggitt et al. (2019). Note that densities are plotted on the natural log scale so allow visibility of details.*

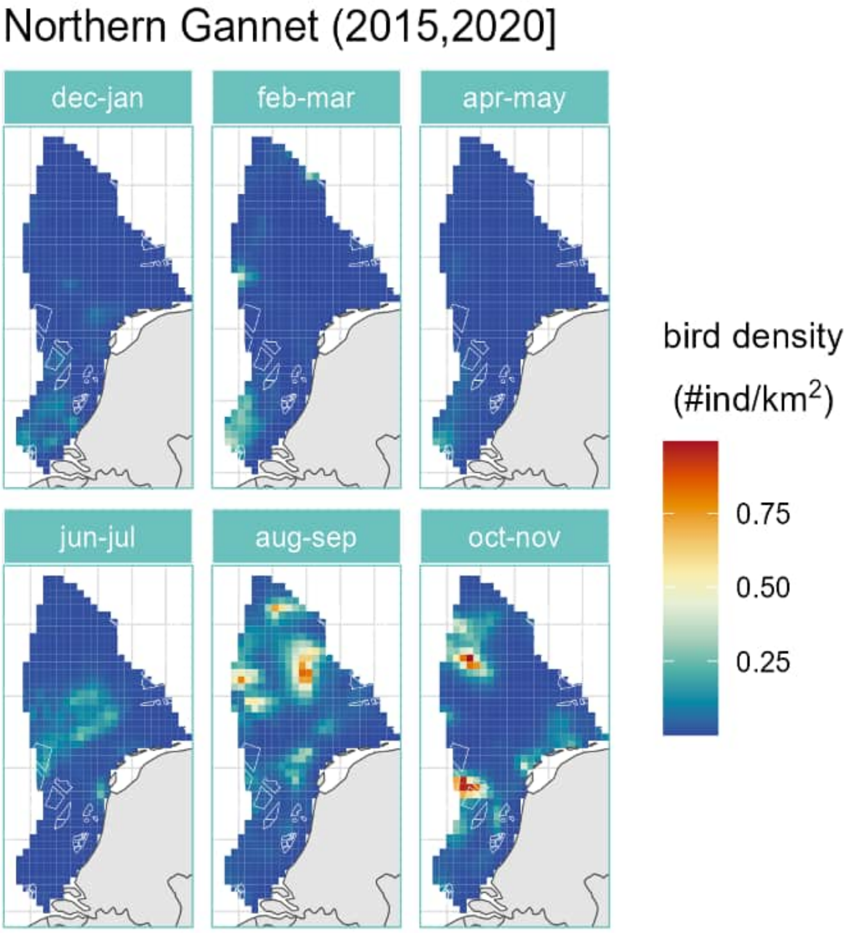


Figure A.2 *Bimonthly distribution of Northern Gannet Morus bassanus, based on habitat modelling by van Donk et al. (2024).*

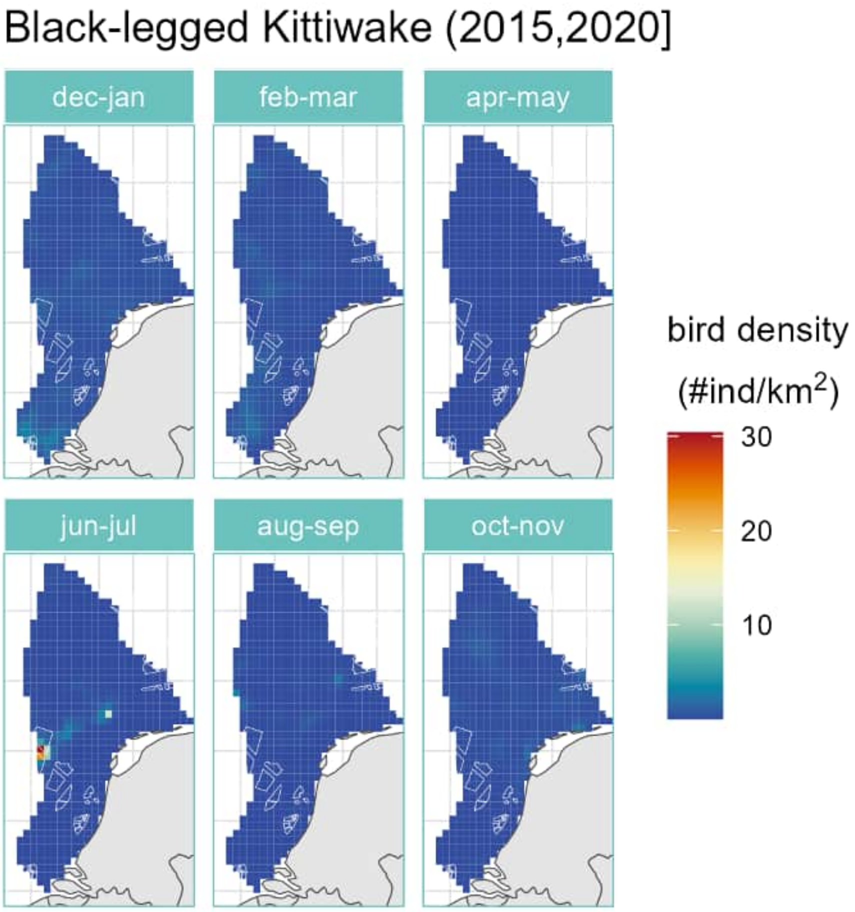


Figure A.3 *Bimonthly distribution of Black-legged Kittiwake Rissa tridactyla, based on habitat modelling by van Donk et al. (2024).*

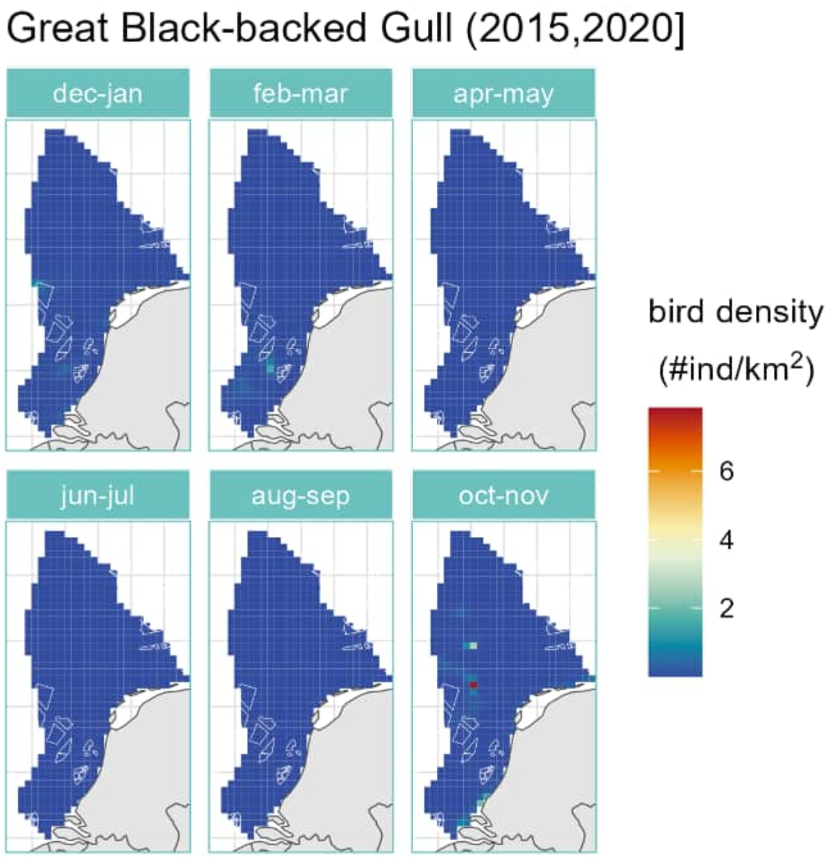


Figure A.4 *Bimonthly distribution of Great Black-backed Gull Larus marinus, based on habitat modelling by van Donk et al. (2024).*

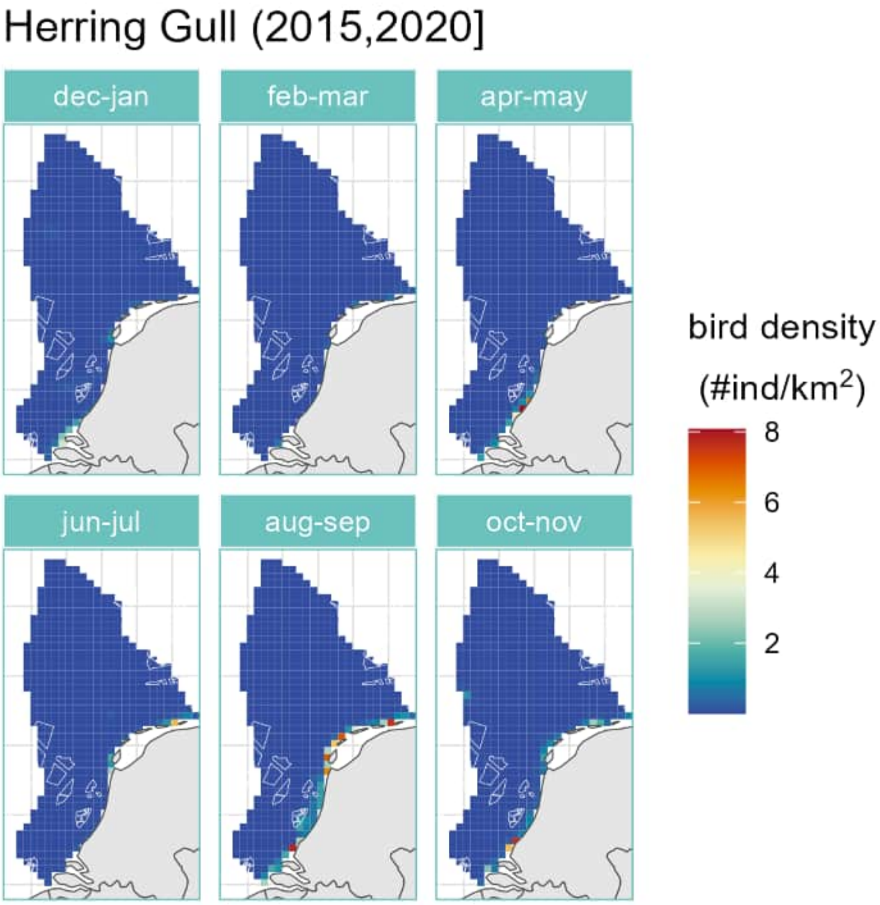


Figure A.5 *Bimonthly distribution of Herring Gull Larus argentatus, based on habitat modelling by van Donk et al. (2024).*

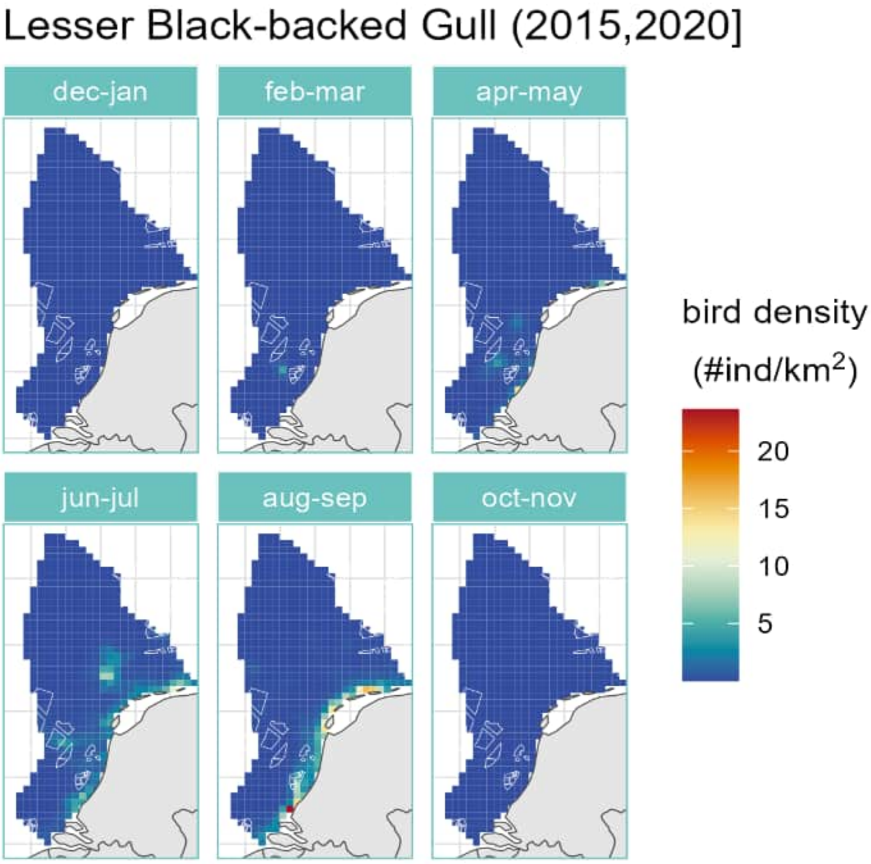


Figure A.6 *Bimonthly distribution of Lesser Black-backed Gull Larus fuscus, based on habitat modelling by van Donk et al. (2024).*

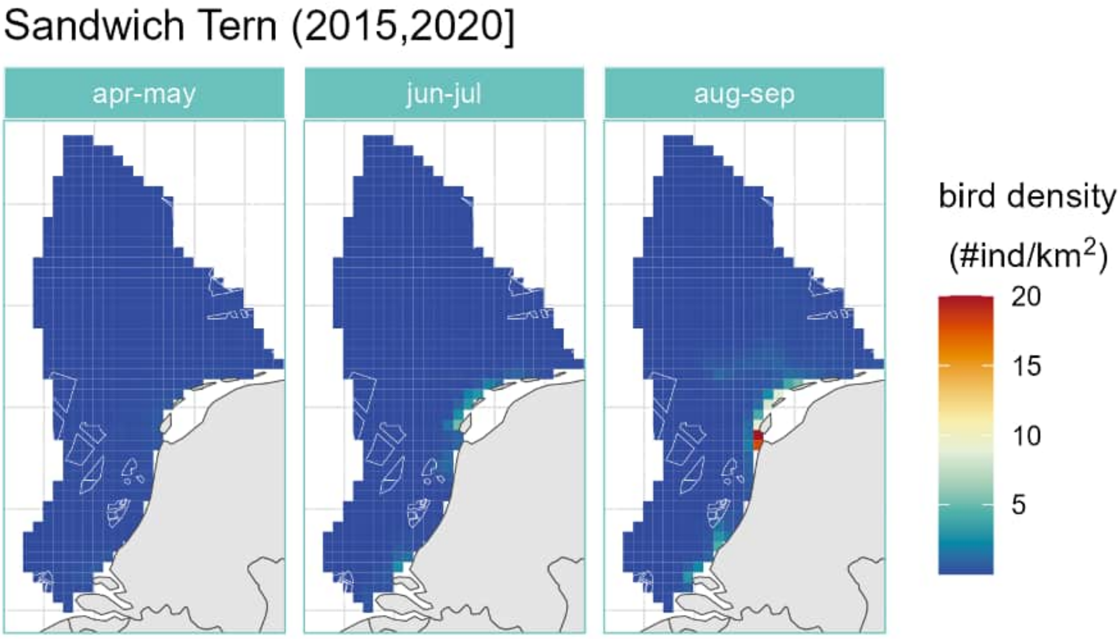


Figure A.7 *Bimonthly distribution of Sandwich Tern Thalasseus sandvicensis, based on habitat modelling.*

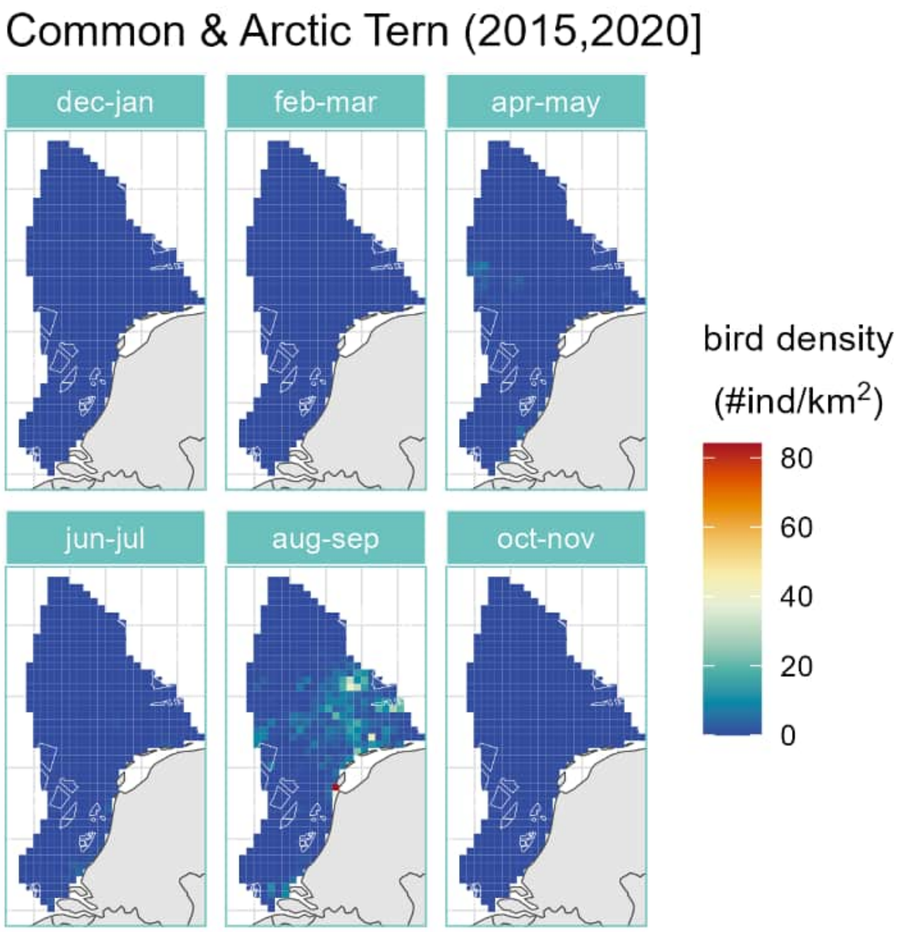


Figure A.8 *Bimonthly distribution of ‘commic terns’, Common Sterna hirundo and Arctic Tern S. paradisaea, based on inverse-distance weighting of observations.*

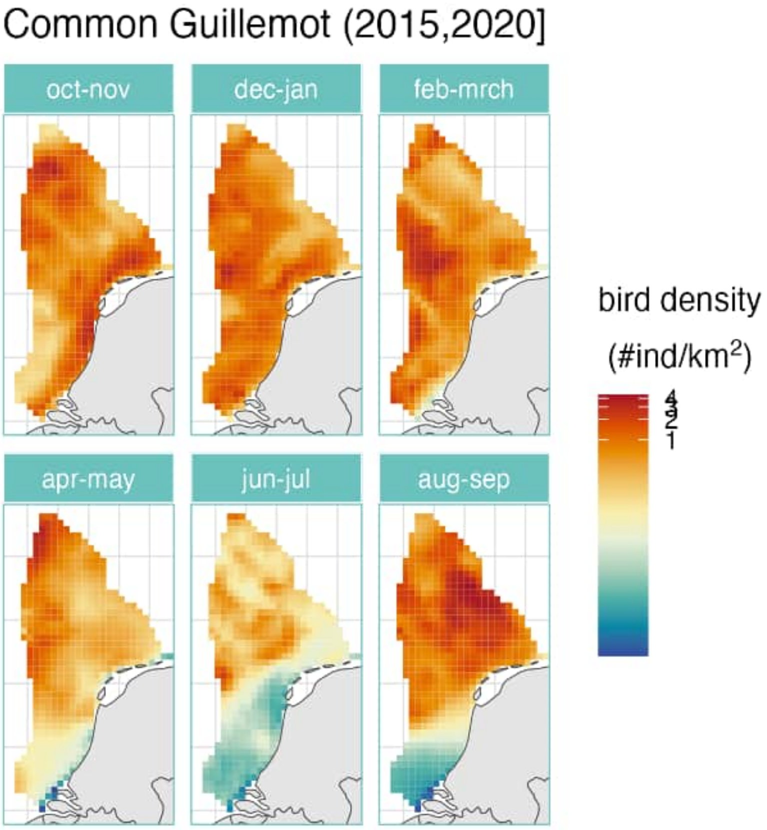


Figure A.9 *Bimonthly distribution of Common Guillemot Uria aalge, based on habitat modelling.*

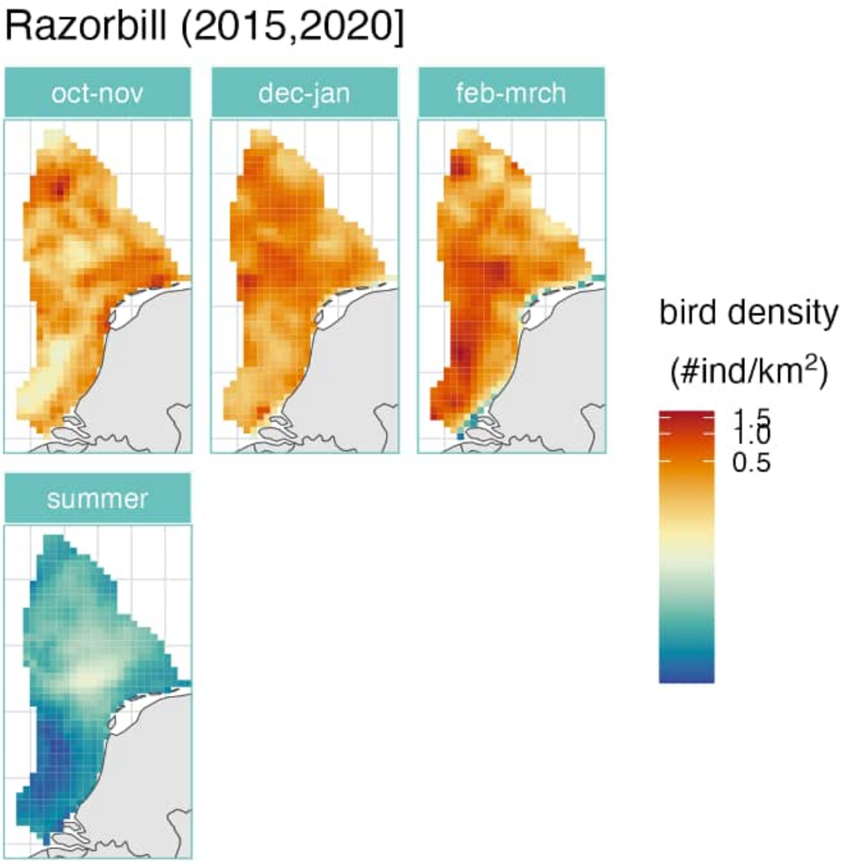


Figure A.10 Bimonthly distribution of Razorbill Alca torda, based on habitat modelling.

Appendix II Seabird distribution maps 1999-2020

All maps and texts in Appendix II were copied and slightly adapted from van Donk, van Bemmelen, Chen, Tulp & Melis (2024). This study covers the period 1999-2020.

Maps are included for 10 of the 12 species selected for this study:

Northern gannet (figure A.11),
Black-legged kittiwake (figure A.12),
Great Black-backed gull (figure A.13),
Herring gull (figure A.14),
Lesser Black-backed gull (figure A.15),
Sandwich tern (figure A.16),
Common guillemot (figure A.17),
Razorbill (figure A.18).
Northern fulmar (figure A.19).
Red-throated diver (figure A.20).

6.4 Northern Gannet

Density distribution models of the Northern Gannet show that sea surface temperature and chlorophyll-a improved the models in almost all bimonthly periods, while percentage of sand was only significantly important in some (Table A.1). As depth did not form part of model selection and was always included in the models, we showed the conditional effect of this variable. It appears that in all bimonthly periods, Gannet densities are low along the relatively shallow coastline (Figure A.11).

Table A.1 Covariates included in the Northern Gannet final model.

Bimonthly period	Depth	Proxies for prey			Distance to breeding site	Distance to shipping lane	Fishing intensity	Time period
		Sand %	SST	Chl-A				
Dec-Jan	x	x	x	x				5-year
Feb-Mrch	x	x		x				5-year
Apr-May	x		x	x				5-year
Jun-Jul	x	x	x	x				5-year
Aug-Sep	x		x					5-year
Oct-Nov	x		x	x				5-year

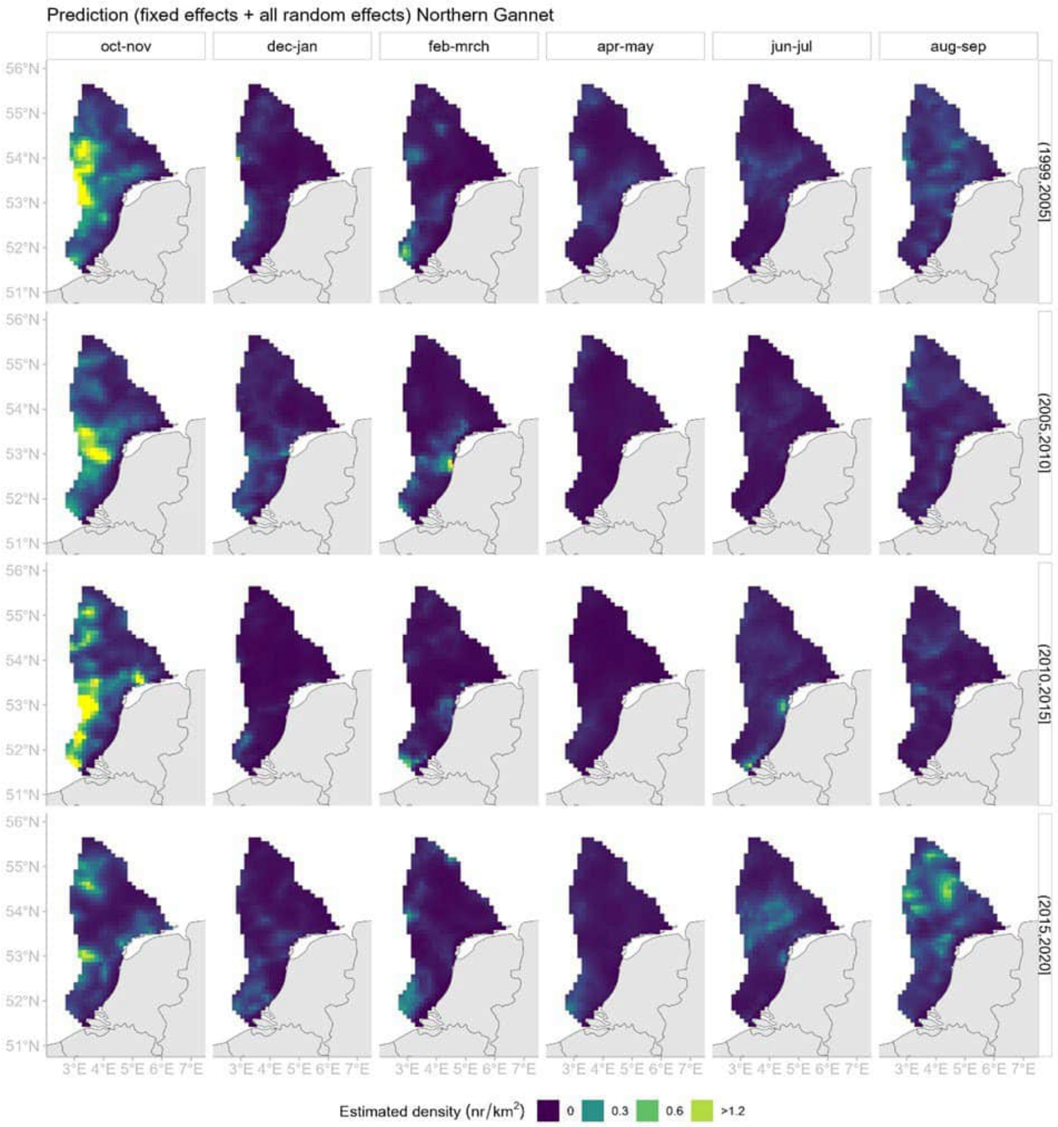


Figure A.11 *The predicted density for Northern Gannet per bimonthly period for the time periods 2000 to 2005 (1999,2005], 2006 to 2010 (2005,2010], 2011 to 2015 (2010,2015] and 2016 to 2020 (2015,2020].*

6.5 Black-legged kittiwake

The final models used for the black-legged kittiwake prediction map are provided in Table A.2. The table shows that sea surface temperature, chlorophyll-a and fishing intensity improved the model in all bimonthly periods, while percentage of sand was only significant in some bimonthly periods. Distance to breeding site did not improve the model. Black-legged kittiwakes are a common species in the North Sea during the colder months (October-March). During the breeding season, densities are usually a bit lower as most larger breeding sites are located further away from the Dutch North Sea (Figure A.12).

Table A.12 Covariates included in the Black-legged Kittiwake final model.

Bimonthly period	Depth	Proxies for prey			Distance to breeding site	Distance to shipping lane	Fishing intensity	Time period
		Sand %	SST	Chl-A				
Dec-Jan	x		x				x	5-year
Feb-Mrch	x	x	x	x			x	5-year
Apr-May	x		x	x			x	5-year
Jun-Jul	x		x	x			x	5-year
Aug-Sep	x		x	x				5-year
Oct-Nov	x	x	x	x				5-year
		x					x	

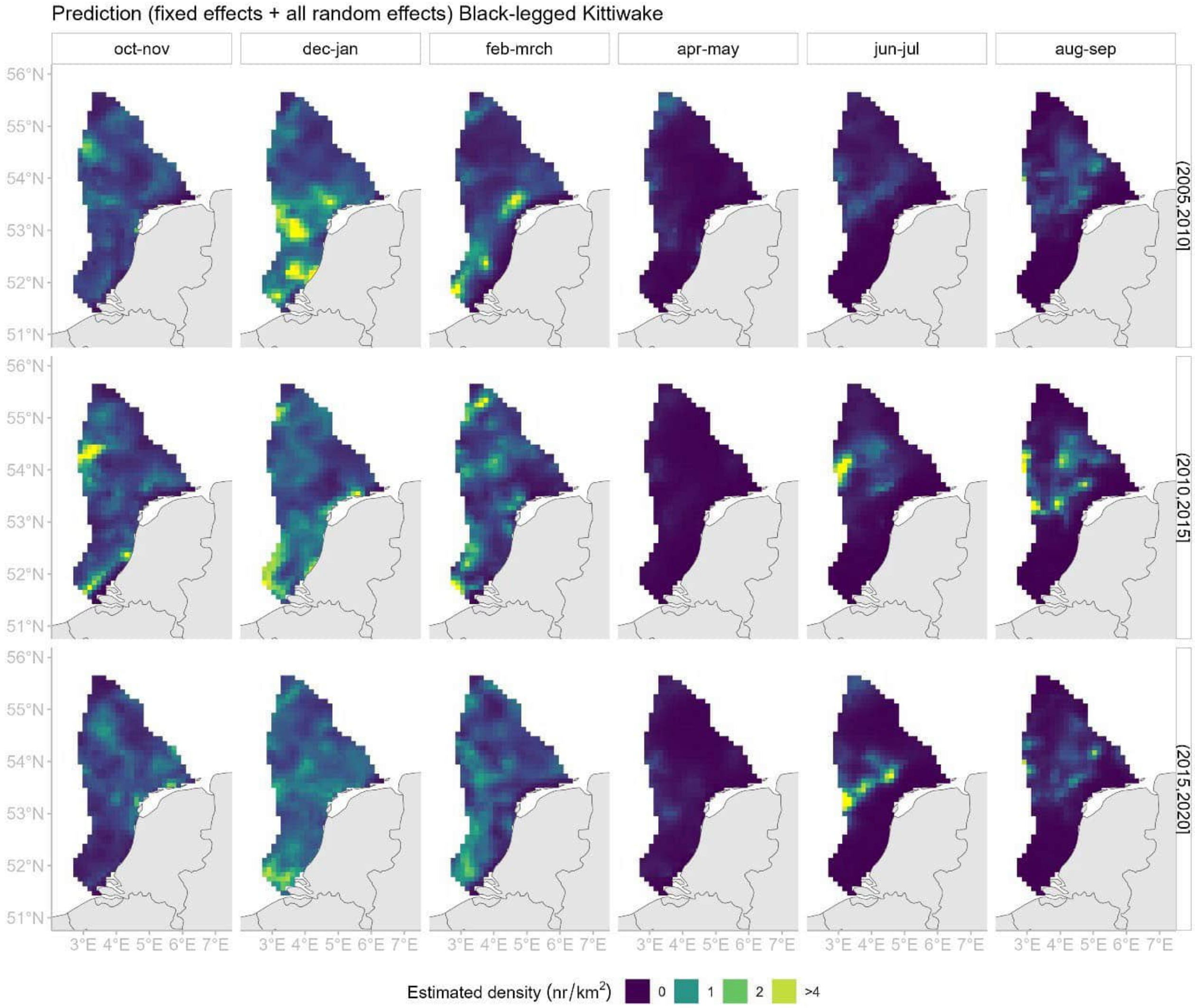


Figure A.12 *The predicted density for the Black-legged Kittiwake per bimonthly period for the time periods 2006 to 2010 (2005,2010], 2011 to 2015 (2010,2015] and 2016 to 2020 (2015,2020]. Time period 2000 to 2005 (1999,2005] is not predicted, as for this period fishing intensity is not available.*

6.6 Great black-backed gull

The density distribution models for the great black-backed gull show that the covariates sea surface temperature and chlorophyll-a had opposite effects (Table A.3). When SST was included, chlorophyll-a was not. Fishing intensity was significant in the models in the period December to July. Distance to breeding site was included in the models from April to September but was excluded during model selection. As depth was not part of model selection and was always included in the models, we show the conditional effect of this variable. There was no clear pattern between great black-backed gull density and depth. Great black-backed gulls densities were generally low but predicted to be slightly higher in the south-western part of the Dutch North Sea (Figure A.13). Densities were close to zero during the breeding season (April-August).

Table A.13 Covariates included in the Great Black-backed Gull final model

Bimonthly period	Depth	Proxies for prey			Distance to breeding site	Distance to shipping lane	Fishing intensity	Time period
		Sand %	SST	Chl-A				
Dec-Jan	x		x				x	5-year
Feb-Mrch	x			x			x	5-year
Apr-May	x		x				x	5-year
Jun-Jul	x						x	5-year
Aug-Sep	x			x				5-year
Oct-Nov	x		x					5-year
				x				

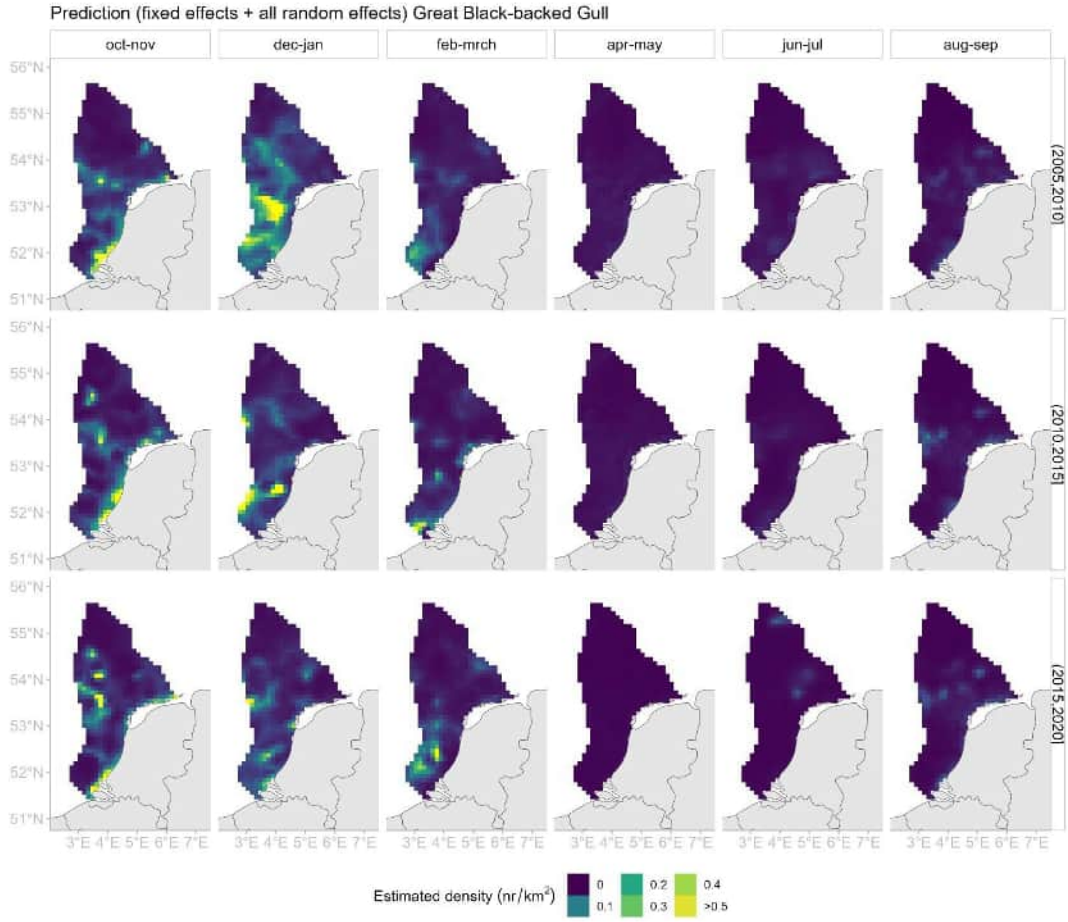


Figure A.13 *The predicted density for the Great Black-backed Gull per bimonthly period for the time periods 2006 to 2010 (2005,2010], 2011 to 2015 (2010,2015] and 2016 to 2020 (2015,2020]. Time period 2000 to 2005 (1999,2005] is not predicted, as for this period fishing intensity is not available.*

6.7 Herring gull

Density distribution models of the herring gull show that the covariates SST and chlorophyll-a improved the model in almost all bimonthly periods (Table A.4). Fishing intensity improved the models in most bimonthly periods, apart from April to July. In this period, herring gulls probably foraged, when at sea, very close to the coast and breeding colony and in the Wadden Sea which is not counted by MWTL. As depth was not part of model selection and was always included in the models, we show the conditional effect of this variable. It appears that in all bimonthly periods, herring gull densities were slightly lower in relatively deep areas of the Dutch Sea (Figure A.4). Densities of herring gulls were higher along the coast, especially during the breeding season (April-August) (Figure A.14). In winter, the predicted maps showed also higher densities further at sea (for instance in Dec-Jan).

Table A.4 Covariates included in Herring Gull final model.

		Sand %	SST	Chl-A	breeding site	shipping lane	intensity	period
Dec-Jan	x		x				x	5-year
Feb-Mrch	x		x					5-year
				x			x	
Apr-May	x							5-year
			x	x				
Jun-Jul	x							5-year
				x				
Aug-Sep	x							5-year
				x				
Oct-Nov	x							5-year
				x				
			x				x	
			x				x	

Sand % = percentage of sand of seafloor substrate, SST = Sea Surface Temperature, Chl-a = Chlorophyll-a

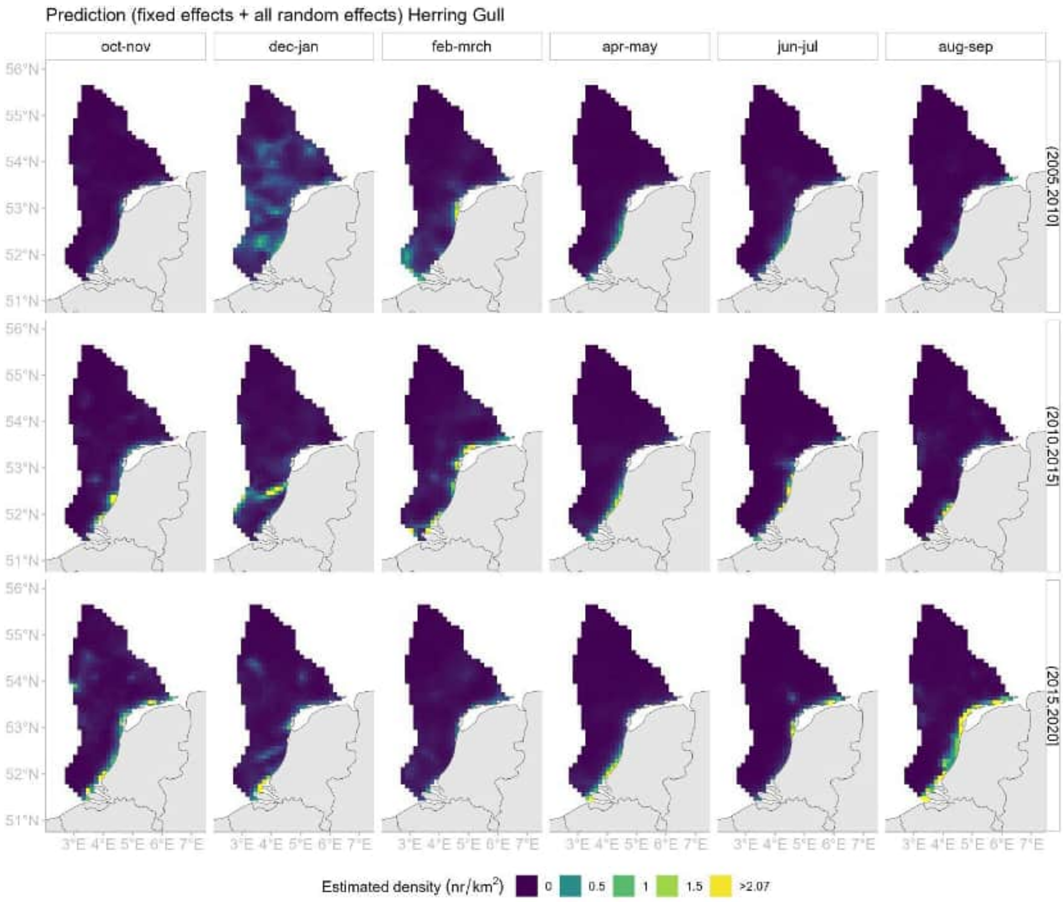


Figure A.14 *The predicted density for Herring Gull per bimonthly period for the time periods 2006 to 2010 (2005,2010], 2011 to 2015 (2010,2015] and 2016 to 2020 (2015,2020]. Time period 2000 to 2005 (1999,2005] is not predicted, as for this period fishing intensity is not available.*

6.8 Lesser black-backed gull

The models for the density distribution of the lesser black-backed Gull show that sea surface temperature and Chlorophyll-A improved the model in almost all bimonthly periods (Table A.5). Both percentage of sand and fishing intensity was of importance in the model in the warmer months (resp. April till July, April till September). As depth was not part of the model selection and was always left in the models, we showed the conditional effect of this variable. It appears that in the colder bimonthly periods, Lesser Black-backed Gull densities were slightly lower in relatively deep areas of the Dutch Sea. Densities of Lesser Black-backed Gulls were concentrated along the coast, especially during the breeding season (April-August) (Figure A.15). In winter, densities were close to zero when Lesser Black-backed Gulls migrated to their winter areas.

Table A.5 Covariates included in final model Lesser Black-backed Gull.

Bimonthly period	Depth	Proxies for prey			Distance to breeding site	Distance to shipping lane	Fishing intensity	Time period
		Sand %	SST	Chl-A				
Dec-Jan	x		x	x				5-year
Feb-Mrch	x		x	x				5-year
Apr-May Jun-Jul	x x	x	x x				x	5-year 5-year
Aug-Sep	x	x	x	x			x	5-year
Oct-Nov	x		x	x			x	5-year
				x				

Sand % = percentage of sand of seafloor substrate, SST = Sea Surface Temperature, Chl-a = Chlorophyll-a

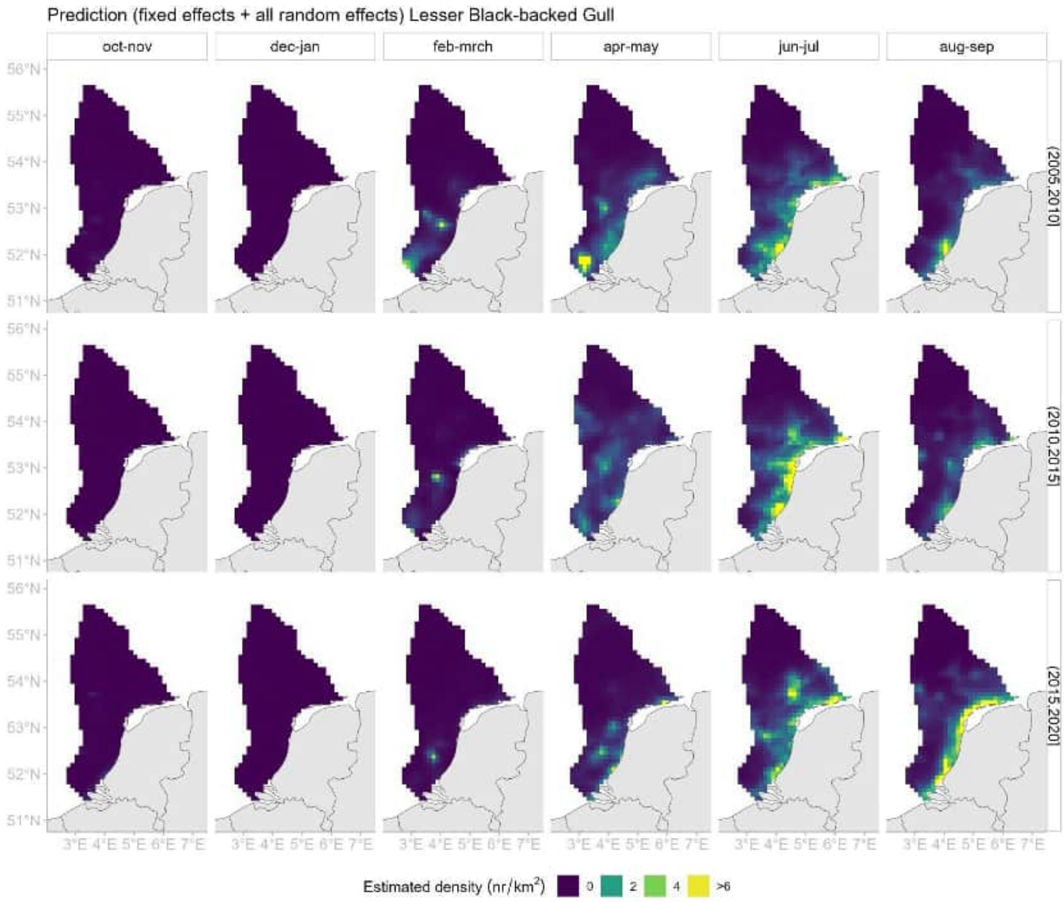


Figure A.15 *The predicted density for Lesser Black-backed Gull per bimonthly period for the time periods 2006 to 2010 (2005,2010], 2011 to 2015 (2010,2015] and 2016 to 2020 (2015,2020]. Time period 2000 to 2005 (1999,2005] is not predicted, as for this period fishing intensity is not available.*

6.9 Sandwich tern

Due to too few non-zero datapoints, the winter months between December and March could not be not modelled. The density distribution models of the sandwich tern show that when SST was included in the best model, chlorophyll-a was not, except in Apr-May (Table A.6). The sandwich tern is a coastal bird, whereby all bimonthly periods show that densities were high along the coastline and close to breeding colonies (Figure A.16).

Table A.6 The covariates included in Sandwich tern final model.

Bimonthly period	Depth	Proxies for prey			Distance to breeding site	Distance to shipping lane	Fishing intensity	Time period
		Sand %	SST	Chl-A				
Apr-May	x		x	x				5-year
Jun-Jul	x	x	x					5-year
Aug-Sep	x							5-year
Oct-Nov	x	x		x				5-year
			x					

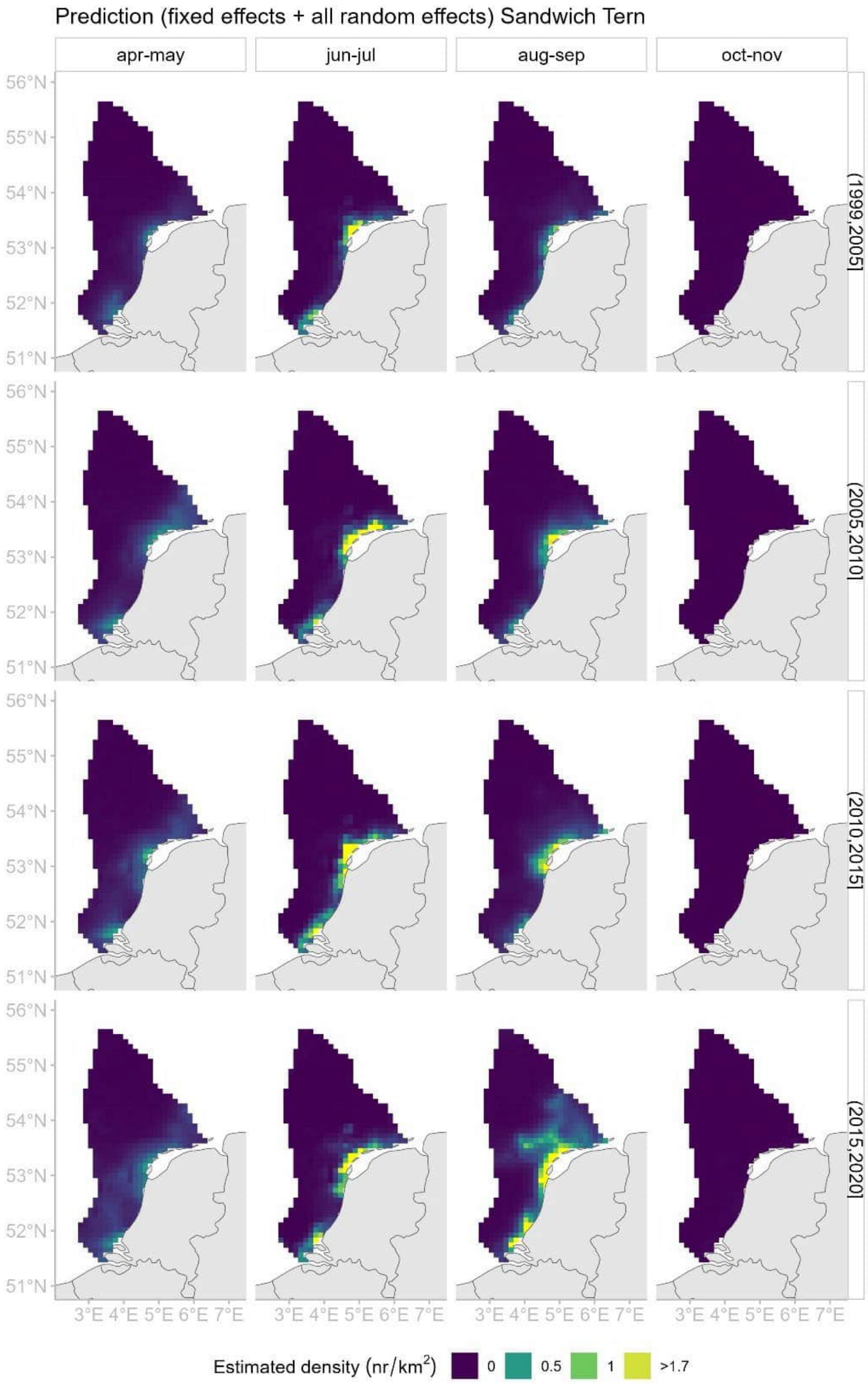


Figure A.16 *The predicted density for the Sandwich Tern per bimonthly period for the time periods 2000 to 2005 (1999,2005], 2006 to 2010 (2005,2010], 2011 to 2015 (2010,2015] and 2016 to 2020 (2015,2020].*

6.10 Common guillemot

The density distribution models for the common guillemot show that SST and chlorophyll-a contrasted each other (Table A.7). When SST was included in the best model, chlorophyll-a was not apart from Oct-Nov. Distance to breeding site was included in the models from April to September, but was only included in the model of Aug-Sep. Percentage of sand and distance to shipping lane seemed to be of minor importance as both covariates only improved one model.

It appears that in all bimonthly periods, guillemot densities were low along the relatively shallow coastline (Figure A.17). There were some strikingly large areas with high densities, for instance in Aug-Sep 2018 and Feb-Mrch 2019. Densities were usually low in Jun-Jul.

Table A.17 Covariates included in the Common Guillemot final model.

Bimonthly period	Depth		Proxies for prey		Distance to breeding site	Distance to shipping lane	Fishing intensity	Time period
		Sand %	SST					
Dec-Jan	x			x		x		1-year
Feb-Mrch	x			x				1-year
Apr-May	x		x					1-year
Jun-Jul	x							1-year
Aug-Sep	x	x		x				1-year
Oct-Nov	x		x		x			1-year
			x	x				

Sand % = percentage of sand of seafloor substrate, SST = Sea Surface Temperature, Chl-a = Chlorophyll-a

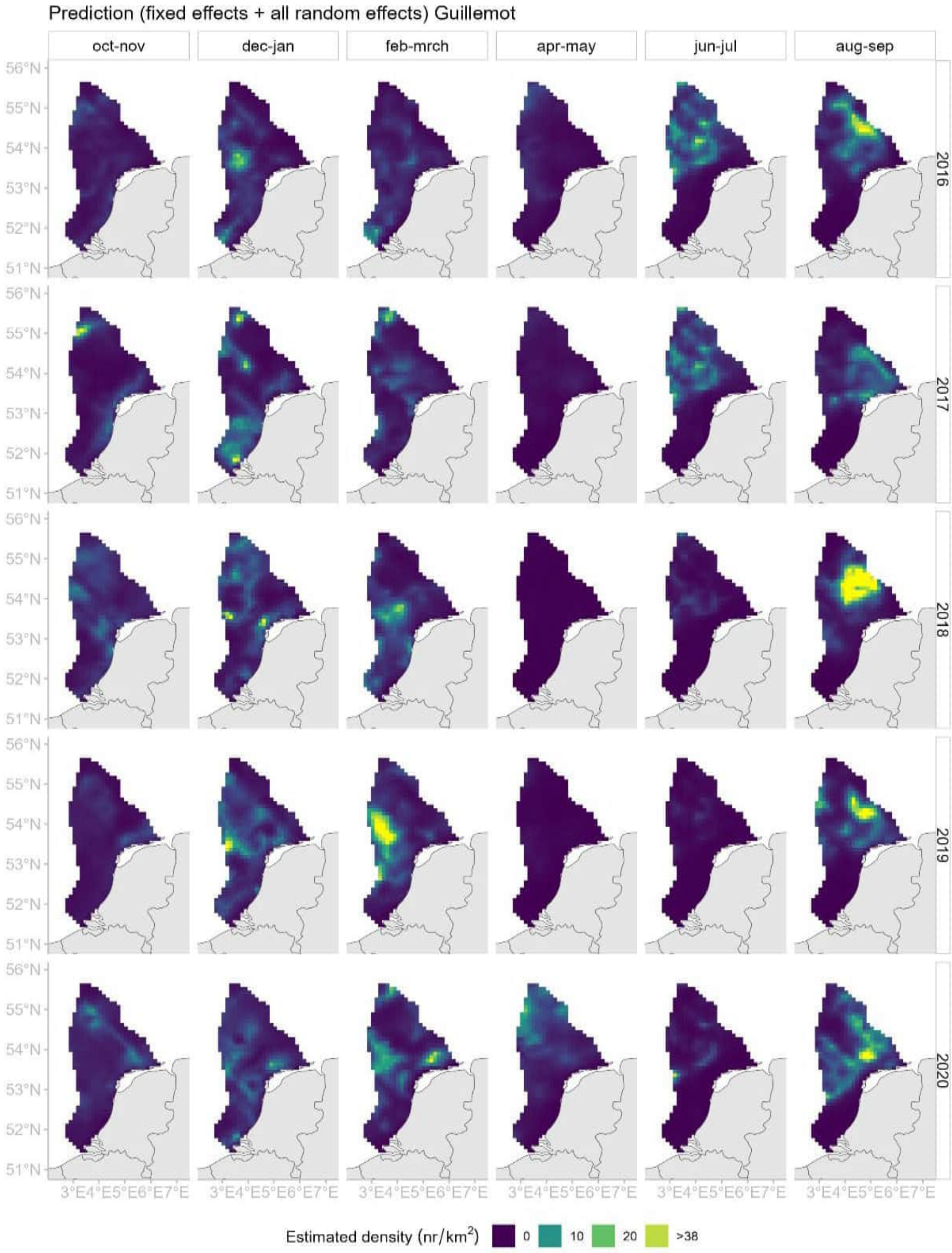


Figure A.17 *The predicted density for Common Guillemot per bimonthly per year.*

6.11 Razorbill

The density distribution models of the razorbill show that SST and chlorophyll-a only improved one model, while percentage of sand improved the model in most cases (Table A.8). Distance to shipping lane was not included in the models due to low non-zero values and models that did not converge. Due to too few non-zero datapoints, the months April to September were merged into a single model (summer).

It appears that in all bimonthly periods and the period 'summer', razorbill densities were low along the relatively shallow coastline (Figure A.18). Densities were close to zero during the breeding season (April-August).

Table A.8 Covariates included in the razorbill final model.

Bimonthly period	Depth	Proxies for prey			Distance to breeding site	Distance to shipping lane	Fishing intensity	Time period
		Sand %	SST	Chl-A				
Oct-Nov	x	x						1-year
Dec-Jan	x	x		x				1-year
Feb-Mrch	x							1-year
Summer	x							1-year
		x	x					

Sand % = percentage of sand of seafloor substrate, SST = Sea Surface Temperature, Chl

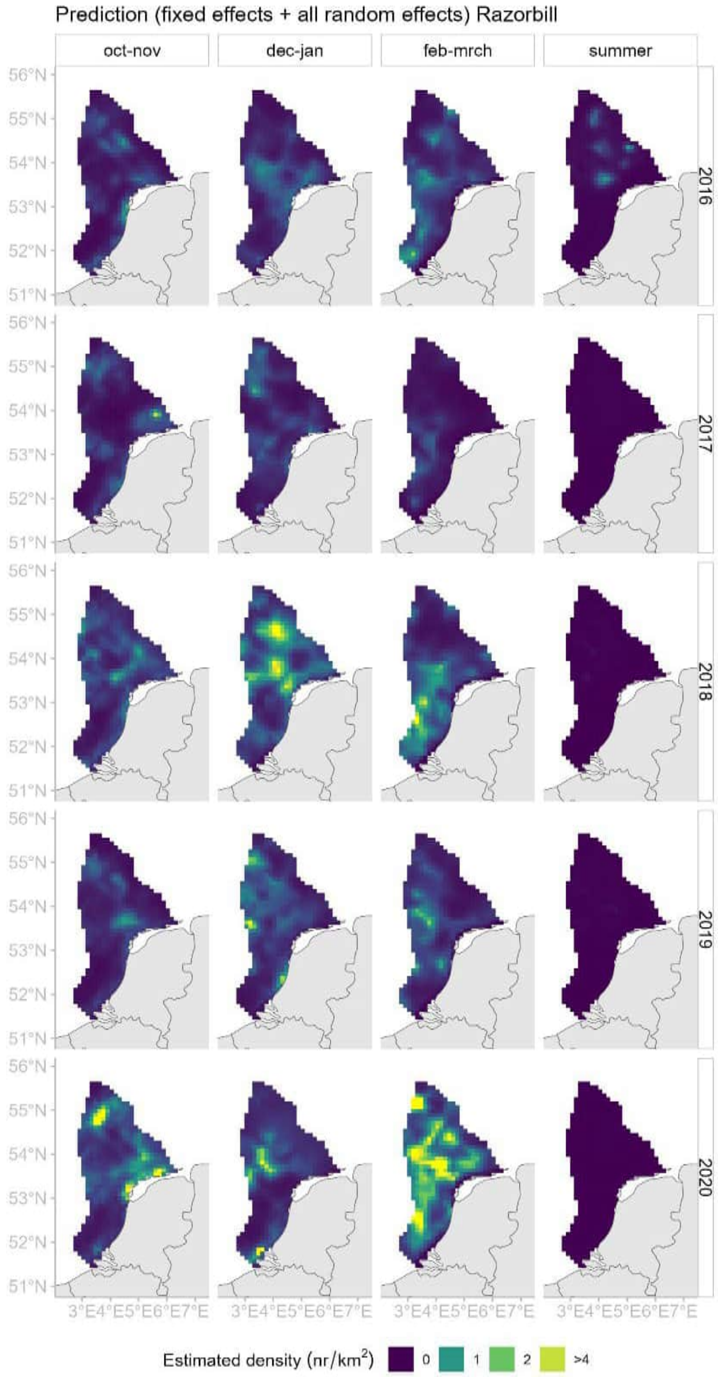
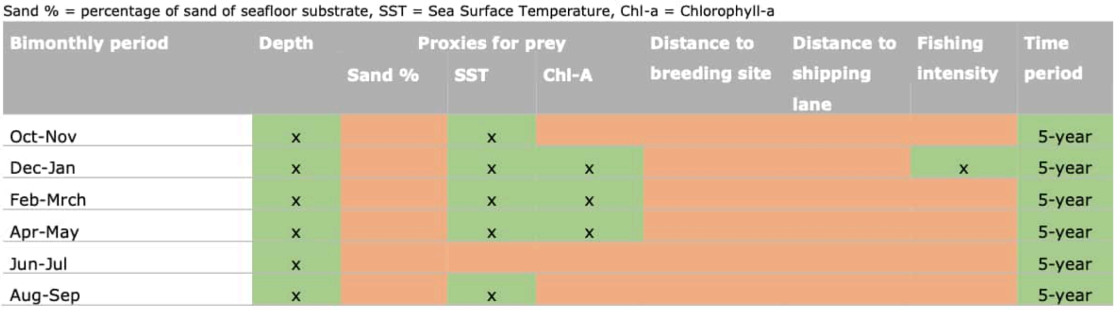


Figure A.18 The predicted density for the Razorbill per bimonthly period per year.

6.12 Northern fulmar

The density distribution models of the northern fulmar included all 6 bimonthly periods. SST was included in almost all final models, sometimes together with chlorophyll a (Table A.9). As depth was not part of the model selection and was always included in the models, we showed the conditional effect of this variable. All bimonthly periods show that fulmar densities were lower in relatively shallow areas of the Dutch North Sea (Figure A.9). In areas that are deeper than the average depth, there is no clear pattern anymore in fulmar densities. This is also visible in the maps of predicted densities, which were very low along the coastline (Figure A.19).

Table A.9 Covariates included in northern fulmar final model.



Sand % = percentage of sand of seafloor substrate, SST = Sea Surface Temperature, Chl-a = Chlorophyll-a

Bimonthly period	Depth	Proxies for prey			Distance to breeding site	Distance to shipping lane	Fishing intensity	Time period
		Sand %	SST	Chl-A				
Oct-Nov	x		x					5-year
Dec-Jan	x		x	x			x	5-year
Feb-Mrch	x		x	x				5-year
Apr-May	x		x	x				5-year
Jun-Jul	x							5-year
Aug-Sep	x		x					5-year

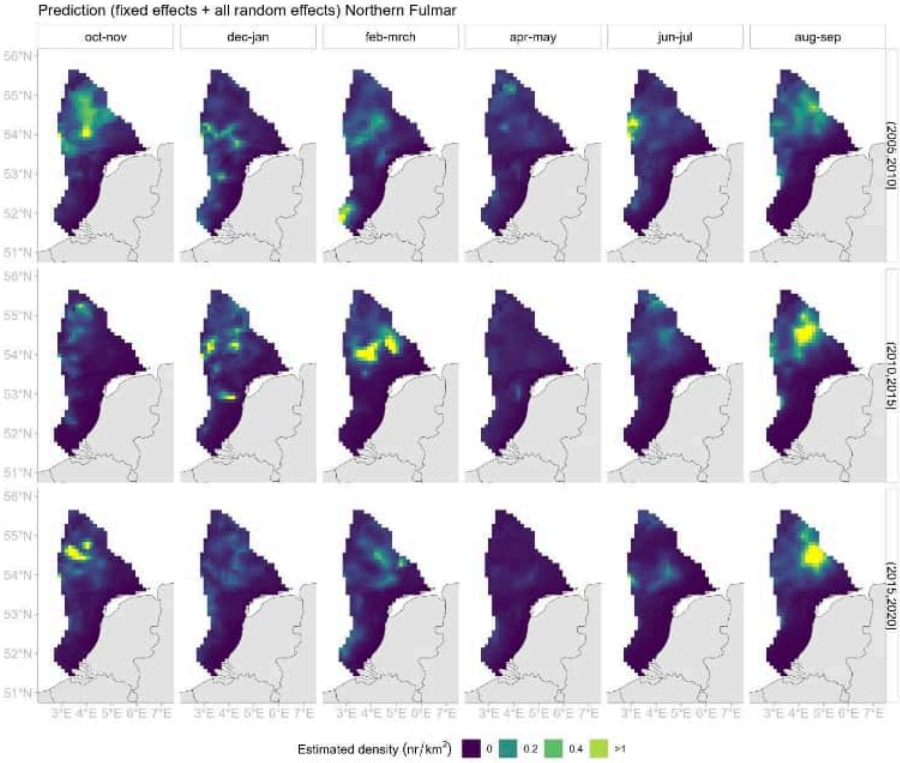
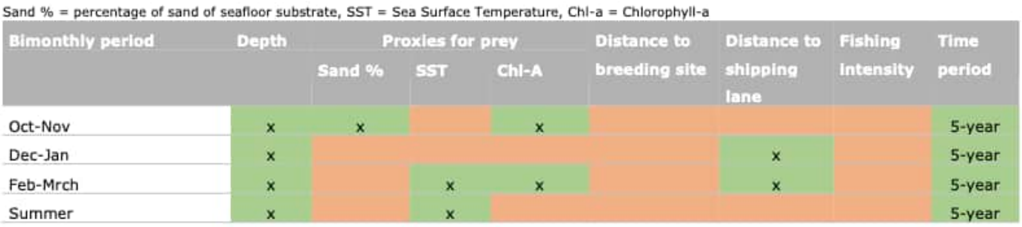


Figure A.19 *The predicted density for the northern fulmar per bimonthly period for the time periods 2006 to 2010 (2005,2010], 2011 to 2015 (2010,2015] and 2016 to 2020 (2015,2020]. Time period 2000 to 2005 (1999,2005] is not predicted, as for this period fishing intensity is not available.*

6.13 Red-throated diver

Due to too few non-zero datapoints, the summer months between April and September were modelled together. The red-throated diver density distribution models show that percentage sand, SST and chlorophyll a are irregularly included or excluded from the models (Table A.10). The Red-throated Diver is a clear coastal bird, all bimonthly periods in winter and the combined summer months show that densities were higher and strongly clustered in relatively shallow areas of the Dutch North Sea (Figure A.10).

Table A.20 The covariates included in red-throated diver final model.



Sand % = percentage of sand of seafloor substrate, SST = Sea Surface Temperature, Chl-a = Chlorophyll-a

Bimonthly period	Depth	Proxies for prey			Distance to breeding site	Distance to shipping lane	Fishing intensity	Time period
		Sand %	SST	Chl-A				
Oct-Nov	x	x		x				5-year
Dec-Jan	x					x		5-year
Feb-Mrch	x		x	x		x		5-year
Summer	x		x					5-year

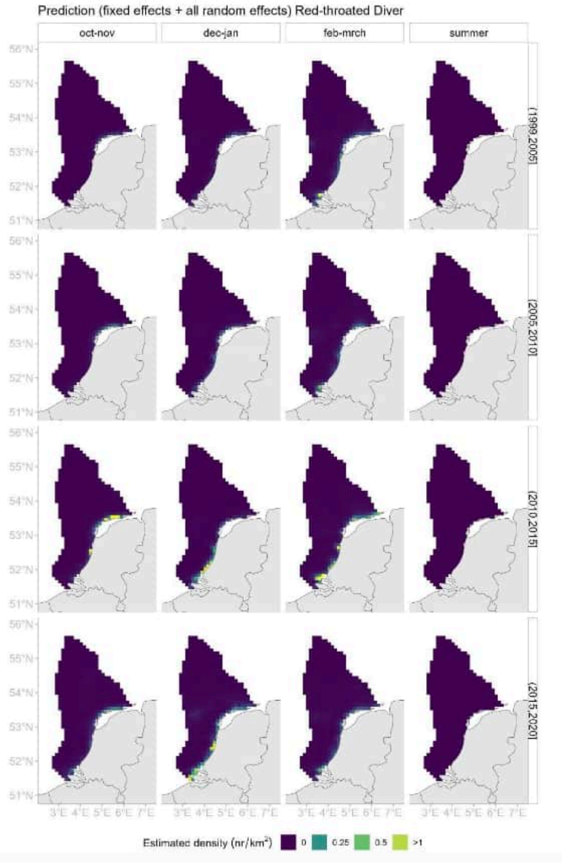


Figure A.20 *Red-throated diver predicted densities for the per bimonthly period for the time periods 2000 to 2005 (1999,2005], 2006 to 2010 (2005,2010], 2011 to 2015 (2010,2015] and 2016 to 2020 (2015,2020].*