Knowledge gaps and research options for coastal birds and seabirds of the Dutch North Sea

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Wageningen Marine Research
report: C093/25

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[3] Waardenburg Ecology

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Samenvatting

Het MONS-onderzoeksprogramma ontstond in 2021 vanuit het Noordzeeakkoord als een gecoördineerde inspanning om te begrijpen hoe de Noordzee verandert onder toenemende milieudruk en menselijke activiteiten. Nu de Noordzee ingrijpende transities doormaakt in energieproductie, voedselwinning en natuurbeheer, en tegelijkertijd te maken heeft met klimaatgedreven veranderingen zoals opwarming, gewijzigde windpatronen en verzuring, streeft MONS ernaar inzicht te bieden in de gevolgen van deze ontwikkelingen voor het ecosysteem.

Om de monitoring uit het Noordzeeakkoord te ondersteunen, heeft MONS drie bureaustudies naar zeevogels laten uitvoeren. Deze studies moeten de basis vormen voor toekomstig veldonderzoek door belangrijke kennislacunes te identificeren. Uiteindelijk richten zij zich op vragen over hoe energie- en voedseltransities de draagkracht van de zee beïnvloeden, welke gebieden in de zuidelijke Noordzee het belangrijkst zijn voor vogels, en welke ecologische factoren — zoals voedselbeschikbaarheid, verstoring en ruimtelijke samenhang — deze waarde en kwetsbaarheid bepalen.

Het huidige rapport biedt een inleiding tot en een samenvatting van de belangrijkste resultaten uit de drie werkpakketten over verspreiding, dieet en demografie van zeevogels, die elk uitvoeriger worden besproken in afzonderlijke rapporten (bijlagen). In dit rapport worden deze resultaten geïntegreerd en worden gerichte onderzoeksopties beschreven die bedoeld zijn om de kennislacunes in onze kennis van zeevogel-ecologie in een snel veranderende Noordzee te vullen.

Werkpakket 2 presenteert de verspreidingskaarten van twaalf soorten zeevogels, waaronder kaarten van actief foeragerende vogels in de Nederlandse Noordzee. Aanvullend geeft het rapport een overzicht van de beschikbare literatuur over foerageergebieden en, waar mogelijk, de omgevingsfactoren die het foerageergedrag van de geselecteerde kust- en zeevogelsoorten in de zuidelijke Noordzee beïnvloeden, met nadruk op Nederlandse wateren. Geolocator- en GPS-studies worden besproken voor zowel broed- als niet-broedseizoen. GPS-gegevens leveren gedetailleerde informatie op over ruimtelijk gedrag en omgevingsinvloeden, terwijl geolocators relatief grove data opleveren. Voor enkele soorten, zoals de kleine mantelmeeuw, bestaat veel informatie, maar andere soorten zijn nauwelijks onderzocht. Grote kennislacunes bestaan vooral voor onderzochte dwergmeeuw en zilvermeeuw en andere soorten zoals aalscholver, en grote jager buiten het broedseizoen. Belangrijke factoren die het foerageren beïnvloeden zijn abiotisch (stroming, temperatuurafwijkingen, troebelheid, maanstand), biotisch (prooidichtheden, gedrag, associaties met andere soorten) en antropogeen (o.a. windparken, visserij). Heel weinig studies gebruikten de directe abundantie en beschikbaarheid van prooivissoorten ("forage fish", zoals haring, sprot en zandspiering, als covariabelen in de modellen. Ondanks voortgang blijft modelonzekerheid groot en zullen aanvullende variabelen, zoals het aanbod en beschikbaarheid van "forage fish", helpen om betere voorspellingen te doen over reacties van zeevogels op veranderingen in de omgeving.

Werkpakket 3 richtte zich op het dieet van twaalf kust- en zeevogelsoorten in de zuidelijke Noordzee, met nadruk op Nederland. Naast een literatuurstudie werden nieuwe analyses uitgevoerd van maag- en darminhoud van dode vogels. Verschillen tussen seizoenen, leeftijdsklassen, jaren en de invloed van klimaatgerelateerde factoren werden onderzocht. Kustgebonden duikers zoals zwarte zee-eend en roodkeelduiker tonen contrasterende winterdiëten: zee-eenden eten vooral schelpdieren, roodkeelduikers vrijwel uitsluitend vis. Pelagische duikende soorten — zeekoet en alk — eten haringachtigen, kabeljauwachtigen en zandspiering; daarbij eten zeekoeten iets grotere prooien vergeleken met de alk en zij vertonen variatie in hun dieet afhankelijk van weer en lichaamsconditie. Pelagische soorten die minder diep duiken hebben allen een iets ander dieet: noordse stormvogels eten veel visserijafval & bijvangst (discards), jan-van-genten eten vooral energierijke pelagische vis maar eten ook discards, en drieteenmeeuwen eten kleine pelagische vis en benutten eveneens discards. Kennislacunes blijven bestaan rond winterdiëten, afhankelijkheid van discards en klimaatinvloeden. Grote stern en visdief eten vooral haringachtigen en zandspiering, maar visdieven vertonen meer flexibiliteit in hun dieet. Grote meeuwen combineren mariene prooien met afval en ander voedsel van

land, waarbij recente verschuivingen richting binnenland mogelijk samenhangen met een afname van discards. Over alle soorten heen zijn systematische, jaarrond studies nodig waarbij gangbare methodes gecombineerd worden met moderne technieken zoals DNA-metabarcoding.

Werkpakket 4 voerde een review uit van schattingen van demografische parameters van de twaalf soorten en onderzocht hoe demografische prestaties samenhangen met voedselbeschikbaarheid en -kwaliteit. De nadruk lag op vijf meeuwen en sterns die in Nederland broeden. De meest robuuste gegevens bestaan voor de overleving van volwassen vogels en broedsucces, dankzij langdurige monitoring en ringonderzoek. Overleving van juvenielen en subadulte vogels, leeftijd bij de eerste broedpoging en het overslaan van broedseizoenen door volwassen vogels zijn veel minder goed gedocumenteerd. Voor soorten zoals grote mantelmeeuw, zwarte zee-eend, roodkeelduiker en noordse stormvogel zijn bijzonder weinig gegevens beschikbaar. Het overzicht toont dat de relatie tussen voedsel en demografie sterk per soort verschilt. Grote stern en visdief vertonen duidelijke verbanden tussen broedsucces en de beschikbaarheid van kleine pelagische vis. Bij meeuwen bestaan aanwijzingen voor relaties tussen voedsel en kuikengroei, maar kwantitatieve verbanden tussen voedsel en overleving of rekrutering ontbreken. Bij drieteenmeeuwen is goed gedocumenteerd dat geringe beschikbaarheid van zandspiering zowel het broedsucces als de volwassenoverleving verlaagt. Voor alkachtigen, jan-van-genten en stormvogels is het bewijs zwakker of inconsistent. Een terugkerend fenomeen is dat veel studies gebruikmaken van grootschalige visbemonsteringen die niet automatisch representatief hoeven te zijn voor de lokale foerageercondities. Slechts weinig studies combineren demografie met gerichte vismetingen binnen met zenderstudies geïdentificeerde foerageergebieden.

Werkpakket 5 integreert de resultaten, identificeert kennislacunes en doet voorstellen voor toekomstig onderzoek. De drie thema's —foerageergedrag, dieet en broedprestaties— blijken sterk verweven. Vanuit deze geïntegreerde benadering worden grote kennisleemtes geïdentificeerd over hoe veranderingen in beschikbaarheid van "forage fish" de ecologie van zeevogels beïnvloeden, en wordt benadrukt dat gecoördineerde onderzoeksinspanningen essentieel zijn.

Voorstellen voor toekomstig onderzoek vallen uiteen in drie lijnen. De eerste richt zich op broedende zeevogels in Nederland — vooral kleine mantelmeeuw, grote stern en visdief — waar behoefte bestaat aan meerjarige, geïntegreerde studies die dieet, foerageren en broedsucces tegelijk volgen en koppelen aan voedselbeschikbaarheid op zee. De tweede richt zich op overwinterende soorten, waarbij hoge-resolutie tracking en dieetonderzoek belangrijke inzichten kunnen verschaffen. De derde richt zich op de verspreiding en beschikbaarheid van vis en de rol van visserijafval. Door dieetonderzoek te combineren met gerichte observaties rond vissersschepen en jaarrond metingen van vis en vogels kan de relatieve waarde van discards beter worden begrepen.

Summary

The MONS research programme emerged in 2021 from the North Sea Agreement as a coordinated effort to understand how the North Sea is transforming under growing environmental and human pressures. As the region faces profound shifts in energy production, food extraction, and nature conservation, alongside climate-driven changes such as warming waters, altered wind patterns, and acidification, MONS seeks to provide clarity on how these developments affect the ecosystem. Particular attention is placed on seabirds and coastal birds—key apex predators whose wellbeing reflects the condition of the food web beneath them.

To support the long-term monitoring commitments set by the North Sea Agreement, MONS, co-funded by several Dutch ministries, has commissioned three desk studies dedicated to seabirds. These studies are intended to lay the groundwork for future field research by identifying critical knowledge gaps. Ultimately, they aim to answer pressing questions about how energy and food transitions influence the sea's carrying capacity, which areas of the southern North Sea are most important for birds, and what ecological factor- -such as food availability, disturbance, and connectivity -shape the value and vulnerability of these areas.

The current report provides an introduction to and summarises the main results of the three main work packages focused on seabird distribution, diets and demography, each more comprehensively covered in separate reports (annexes). In this report, these results are integrated and targeted research options are described, designed to fill the gaps in our understanding of seabird ecology in a rapidly changing North Sea.

Work package 2 presents distribution maps of twelve selected seabird species including maps of actively foraging birds in the Dutch North Sea. These are complemented by an overview of published literature of the foraging areas and (where available) environmental factors that influence foraging among twelve coastal and seabird species in the southern North Sea, focusing where possible on Dutch waters. This chapter highlights geolocator and GPS studies in both the breeding and non-breeding season for all species, providing information about foraging behaviour and habitat use. While GPS data can provide detailed information about spatial ecology and environmental drivers (e.g. depth, sea surface temperature, chlorophyll-a, seabed morphology), geolocator data are coarse and limited. For some species such as lesser black-backed gull, extensive research exists, but others have scarcely been studied. Significant knowledge gaps remain, particularly for the little gull and European herring gull and other species such as great cormorant and great skua during the non-breeding season. Key factors influencing foraging include abiotic variables (currents, temperature anomalies, upwelling, turbidity, moon phase), biotic factors (prey abundance, behaviour, multi-species feeding associations), and anthropogenic impacts (e.g. offshore wind farms, fisheries). Very few studies included direct abundance and availability of forage fish (e.g. herring, sprat and sandeel), which have a key position in the North Sea food web, as covariates in the models. Despite advances, models remain uncertain due to multicollinearity, and integrating additional covariates, such as forage fish abundance and availability, will improve predictions of seabird responses to environmental changes and human activities in the (Dutch) North Sea.

Work package 3 aimed to improve understanding of the diet of twelve coastal and seabird species in the southern North Sea, focusing on Dutch waters. The study combined a literature review with new analyses of stomach and intestinal contents of dead birds. Key aspects included differences between breeding and non-breeding seasons, chick versus adult diet, interannual variation, prey profitability and the influence of climate-related factors. Coastal diving species such as common scoter and red-throated diver occur in winter and show contrasting diets: scoters feed mainly on bivalves, while divers are almost entirely piscivorous, switching to alternative prey when preferred fish are scarce or birds are in poor condition. Pelagic pursuit divers—common guillemot and razorbill—consume clupeids, gadoids and sandeels, with razorbills having a narrower diet. Guillemots diet varies with weather and body condition. More aerial pelagic species have more variation in their diet between species: northern fulmars rely heavily on fishery discards, while gannets mainly take high-energy pelagic fish such as mackerel and herring and opportunistically discards, while kittiwakes forage on small pelagic fish but also exploit discards. Knowledge gaps remain for winter diets, discard dependency and climate impacts. Among Dutch breeding species, Sandwich terns and common terns feed mainly on clupeids

and sandeels, while common terns show greater flexibility and include freshwater prey. Large gulls—herring, lesser black-backed and great black-backed—are opportunistic, combining marine prey with refuse and terrestrial food, with recent shifts towards inland resources potentially linked to reduced availability of discards. Across all species, systematic, year-round studies combining conventional methods with modern techniques such as DNA metabarcoding are needed to address gaps on seasonal variation, prey size and environmental drivers.

Work package 4 reviewed estimates of key demographic parameters of the 12 focal seabird species and examined how their demographic performance relates to the availability and quality of their food resources. The work package concentrated on five species of gulls and tern with breeding populations in The Netherlands while also incorporating information for focal species with non-breeding populations in the southern North Sea. Existing data on key demographic parameters of the focal species was reviewed: survival in three different life stages, breeding productivity, the age at first breeding and the tendency of adults to skip breeding in some years. The most robust information exists for adult survival and breeding productivity, supported by long-standing colony monitoring and extensive ringing datasets in the Netherlands and surrounding countries. In contrast, juvenile and immature survival rates, recruitment ages, and especially breeding propensity remain poorly documented. Several species —notably great black-backed gull, common scoter, red-throated diver, and fulmar— have particularly large gaps in demographic data. The review also synthesises what is known about how these demographic rates respond to food conditions. Evidence varies widely among species. Sandwich and common terns show clear links between their breeding success and the availability of small forage fish such as herring, sprat, and smelt. For gulls, some studies indicate relationships between chick growth or productivity and the availability of discards or natural prey, but quantitative links between food supply and survival, recruitment, or skipped breeding are lacking. Kittiwakes provide the best-studied example of food dependency: reduced sandeel availability has been shown repeatedly to depress both breeding productivity and adult survival. For auks, gannets, and fulmars, evidence of food-driven demographic change is weaker or inconsistent, with some of these species exhibiting relatively stable vital rates unless prey levels fall below critical thresholds. For great black-backed gull, common scoter, and red-throated diver no food-demography studies were retrieved at all. A recurring challenge across the literature is that most studies rely on broad-scale fish stock indices that may not accurately represent the prey conditions seabirds encounter within their local foraging ranges, or on sampling of chick diets which themselves relate to prey abundance in an unknown way. Only a small number of studies incorporate targeted fish surveys in tracking-informed foraging ranges. Future progress will profit most from integrated, multi-year research that jointly measures demographic rates and local food availability, ideally guided by tracking data that identify the areas where birds truly forage. Existing ringing datasets also hold untapped potential for estimating recruitment and early survival. Improving how prey distribution and abundance are measured—particularly at the spatial scales relevant to seabirds—is essential if ecosystem models are to capture the real mechanisms linking food conditions to seabird population dynamics.

In **work package 5** the results of the previous work packages are brought together, knowledge gaps identified and avenues for future research proposed. The previous chapters bring together three closely connected themes —seabird foraging behaviour, diet, and breeding performance— to understand how North Sea seabird populations respond to changing food conditions. These themes are shown to be deeply interdependent: what seabirds eat shapes where and how they forage, and both in turn influence their ability to raise young and sustain healthy populations. From this integrated view, the project identifies several major knowledge gaps relating to how shifts in forage fish availability affect seabird ecology. It is emphasised that coordinated efforts, both within MONS and with other national and international studies, are essential to address these gaps efficiently.

Future research recommendations are divided into three strands. The first focuses on seabirds breeding in the Netherlands —especially lesser black-backed gull, Sandwich tern, and common tern. Although much ecological information already exists, the main limitation is the lack of long-term, synchronised studies that monitor diet, foraging, and breeding productivity within the same colonies while simultaneously measuring food availability at sea. The report therefore proposes multi-year field studies combining colony monitoring, GPS tracking, dietary analysis, and detailed surveys of fish abundance. These efforts should be carried out in both key regions Wadden Sea and Delta Area, where environmental conditions differ and may shape seabird foraging strategies.

The second research strand targets non-breeding seabirds that winter in Dutch waters. High-resolution tracking, combined with diet sampling, stable isotope analysis, and environmental DNA, offers a way to map important feeding areas and understand the drivers behind seabird movements. Collaboration with international partners is essential because many of these species breed elsewhere. A third line of research examines fish distribution at sea and the role of fisheries discards, which many seabirds still use as a food source. By combining dietary analysis with targeted observations of seabirds around fishing vessels, it should be possible to shed light on the relative importance of discards versus natural prey fish. The report stresses the value of ship-based surveys and acoustic monitoring that simultaneously measure seabird presence and fish abundance throughout the year, capturing the dynamic and often unpredictable distribution of prey.

1. Introduction

1.1. Background

The MONS (Monitoring, Onderzoek, Natuurversterking en Soortenbescherming) programme was established in 2021 by the North Sea Agreement (Noordzeeoverleg-NZO) as a research and implementation programme. It 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 outlined in section 1.2. The MONS programme includes three desk studies on seabirds, which. These desk studies serve as preparatory studies for the field studies. This specification concerns the development of the research questions for these desk studies (work package 1 (WP1)), followed by the desk studies themselves (work package 2-4 (WP2-4)), and finally, a preview of follow-up field research (work package 5 (WP5)). The North Sea has undergone significant changes and will continue to experience changes in the coming decades due to the planned transitions in energy supply, food extraction, and nature conservation. Furthermore, various other changes in pressure factors are expected, such as those related to climate (temperature increase, changing wind patterns, acidification), as well as changing policies relating to e.g. sand extraction and terrestrial nutrient management. Coastal and seabirds (together with marine mammals and large predatory fish) are important apex predators in the North Sea. As such, they represent higher trophic level species that are potentially extremely sensitive to changes in the abundance and availability of lower trophic level species, ranging from phytoplankton through zooplankton to (small) pelagic fish, which generally form the staple food source for most seabirds and coastal birds.

1.2. Research questions and aim

Coastal and seabirds are being affected by major changes in the North Sea ecosystem, hence agreements were made in the aforementioned North Sea Agreement (NZA): "In the NZA, agreements have been made about an integrated and systematic monitoring programme by the government, for measuring the health and development of coastal and seabird populations".
This project contributes to answering the following key questions:

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

1.3. Results of the assignments

The delivered within this assignment are:

1. Action plan (delivered in March 2025)
2. ID 60 - Desk study on foraging areas of coastal and seabirds (WP2: ID 60 - Literature study and additional analyses on foraging areas of seabirds – knowledge gaps and recommendations, page 10)
3. ID 62 - Desk study and laboratory study on the food ecology of coastal and seabirds(WP3: ID 62 - Literature and laboratory studies on the diet of seabirds occurring in the Dutch North Sea, page 31)

4. ID 64 - Desk study on population studies of gulls and terns (WP4: ID 64 – Literature study on seabird demography with a focus on gulls and terns, page 44)
5. Research advice, final report and data delivery (Work package 5: Conclusions and future research, page 56)

Within this report, the main messages and knowledge gaps are shared for work packages 2-4. The full reports are published separately:

- WP2: Hannah Madden, Rob van Bemmelen, Tom van der Have & Ruben Fijn (2025) Foraging areas of coastal and offshore seabirds in the Dutch North Sea. An analysis of survey and tracking data. Report 25-134. Waardenburg Ecology, Culemborg.
- WP3: Susanne van Donk, Eileen Hesse, Michaël Kolman, Susanne Kühn, Mardik Leopold, Eleni Melis, Martin Poot & Fokje Schaafsma (2025) Diet of coastal birds and seabirds of the Dutch North Sea, Wageningen University & Research Report C092/25
- WP4: Hans Schekkerman, Petra Manche, André van Kleunen, Loes van den Bremer & Roos Reinartz (2025). Review of demographic studies on seabirds of the Dutch North Sea. Sovon-rapport 2025/115. Sovon Vogelonderzoek Nederland, Nijmegen.

1.4. Consortium

This project is carried out by a consortium of Wageningen Marine Research, Sovon, and Waardenburg Ecology.

1.5. Selection of species

Dozens of seabird species regularly occur in the North Sea, however it was outside the scope of this desk study to include them all. During the preparatory phase of the project we discussed which species to include, based on considerations such as abundance in the (Dutch part of the) North Sea, importance of the North Sea for international populations of the species, inclusion of both wintering and breeding birds, dependence on offshore vs. coastal food sources, diversity in feeding strategies and functional groups. Following extensive discussion with the partners and commissioners, we selected twelve species. An overview of the species is provided in Tabel 1-1. In the project plan, an extensive substantiation for the species list is provided (van Donk *et al* 2025).

Table 1-1 *Selected species within this project.*

English name	**Dutch name**	**scientific name**	**Func-tional group**	**Connec-tion to NL** [1]	**Conser-vation status** [2]	**% of fly-way pop. in NL** [4]
common scoter	*zwarte zee-eend*	*Melanitta nigra*	Coastal diving	M/W	VU	6-7%
red-throated diver	*roodkeel-duiker*	*Gavia stallata*	Coastal diving	M/W	F	~1%
common guillemot	zeekoet	*Uria aalge*	Pelagic diving	M/W	F	2-3%
razorbill	alk	*Alca torda*	Pelagic diving	M/W	F	15%
northern fulmar	noordse stormvogel	*Fulmarus glacialis*	Pelagic surface	M/W	MU	~1% (EU)
northern gannet	Jan-van-Gent	*Sula bassana*	Pelagic surface	M/W	F	~3%
black-legged kittiwake	drieteen-meeuw	*Rissa tridactyla*	Pelagic surface	(B), M/W	F	~2% (NE Atl.)
Sandwich tern	grote stern	*Thalasseus sandvicencis*	Coastal surface	B, M	*VU* F	15-25% (EU br)
common tern	visdief	*Sterna hirundo*	Coastal surface	B, M	*VU* VU	3-6% (EU br)
lesser black-backed gull	kleine man-telmeeuw	*Larus fuscus*	Coastal & pelagic surface	B, M/W	*F* F	35-40% (EU br)
European herring gull	zilver-meeuw	*Larus argentatus*	Coastal & pelagic surface	B, M/W	*VU* MU	~30% NW EU winter), ~3% br
great black-backed gull	grote man-telmeeuw	*Larus marinus*	Coastal & pelagic surface	B, M/W	*F* VU	5-10% (winter)

1 Connection to NL: B breeding, M migrant, W wintering
2 Conservation status (Staat van Instandhouding) in NL: italic: breeding, regular: non-breeding; F favourable, MU moderately unfavourable, VU very unfavourable
3 KEC: species considered in 'Kader Ecologie en Cumulatie'
4 Sources: Sovon Bouwstenen, Camphuysen et al. 1994, Wetlands International; BirdLife International

2. WP2: ID 60 - Literature study and additional analyses on foraging areas of seabirds – knowledge gaps and recommendations

2.1 Aim and structure

This work package aims to advance understanding of the spatial and temporal foraging patterns of coastal and offshore seabirds, focusing on the environmental and anthropogenic drivers that shape these behaviours. Key influencing factors include biotic variables such as prey abundance, availability, and behavioural dynamics, and abiotic conditions such as sea surface temperature, ocean currents, nutrient upwellings, turbidity, and lunar cycles. In addition, human activities - including offshore wind farms, fisheries, and shipping - introduce further complexity by altering habitat structure and prey accessibility. Foraging behaviour is likely governed by a complex interplay of these factors, yet existing studies often fail to capture the full extent of these relationships, leaving critical gaps in predictive capacity. In particular, the distribution and availability of prey species in the North Sea, such as forage fish, is seldom used as a covariate in distribution models, limiting our ability to model seabird responses to environmental changes in the North Sea. Addressing these gaps will require integrating high-resolution tracking data with comprehensive environmental datasets with direct information of forage fish abundance and availability to identify key foraging hotspots and the mechanisms driving habitat selection.

WP2 presents the distribution maps of twelve selected seabird species including maps of actively foraging birds in the Dutch North Sea. To date, the number of covariates included the models to generate distribution maps based on survey data is limited. Therefore, a literature review was carried out which focuses on compiling and synthesising existing geolocator and GPS tracking studies for the focal seabird species, covering both the breeding and non-breeding season and include a wide range of environmental covariates. While an extensive body of research exists for certain selected species (e.g. lesser black-backed gull), other species in the selection such as little gull and European herring gull remain poorly represented in the literature, which also applies to species outside the selection, such as great cormorant and great skua. This disparity is partly due to species-specific sensitivities to GPS logger deployment, which limits the use of high-resolution tracking for some birds. In such cases, geolocators are often the only viable option; however, these devices provide relatively coarse data, lacking critical parameters such as flight speed, altitude, and fine-scale location accuracy. Consequently, the insights derived from geolocator studies are restricted to broad spatial patterns and general behaviour, leaving significant gaps in understanding detailed foraging strategies, habitat selection, and responses to environmental and anthropogenic pressures. WP2 identifies these gaps, assesses the limitations of existing datasets, and highlights opportunities for integrating advanced tracking technologies to improve knowledge of seabird ecology across different life stages.

WP2 is structured as follows: following the introduction outlining the goal of the chapter (and the challenges in achieving this), the methods used for the literature review are briefly described. The results of the literature review are then summarised per logger type (geolocator, GPS) and by species, in alphabetical order. Per species we present: (1) a summary of the knowledge gaps that remain for geolocator studies and recommendations for future research; (2) a brief overview of GPS tracking and some of the analytical techniques that can be used to better understand foraging by the focal species; (3) distribution maps of the selected seabird species, including actively foraging birds and a summary of knowledge gaps based on aerial survey data and the distribution of foraging coastal/seabirds; and (4) a summary of the importance of forage fish for the focal species (and their vulnerability to a reduction in food abundance). In the conclusion, the findings from WP2 are summarised and existing knowledge gaps discussed.

2.2 Methods

We conducted a literature search for Dutch-and English-language publications (including 'grey' literature) on foraging areas and the factors that drive foraging among the focal species. We consulted Waardenburg Ecology's Endnote library for relevant publications; international literature was searched using Google Scholar, Seabird Group, and an AI engine, using the following key words:

For all species: foraging, feeding, consuming, North Sea, Dutch Continental Shelf, GPS, geolocator, tracking, tagging, spatial, seabird, coastal, offshore, forage fish, prey, fishing, discards, sandeel, habitat, SST, NAO.

Relevant publications were downloaded, with a preference for literature from the southern North Sea and – if relevant - wider Atlantic region.

2.3 Results

2.3.1 Tracking studies & geolocator studies - knowledge gaps

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. Despite the insights provided by some studies on certain species in the (southern) North Sea, significant knowledge gaps remain regarding their foraging behaviour and preferences. While geolocators can provide information on the large-scale spatial distribution of coastal and seabirds outside the breeding season, as well as behaviour, these data are coarse and often limited (i.e. speed and flight height 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 suited to GPS-tracking – which has several advantages over geolocators (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.

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. However, given that these species occupy inland habitats, such studies may not be relevant.

The number of geolocator studies available for the target species in general is far lower than GPS studies. In 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.* 2022; Militão *et al.* 2023; Thaxter *et al.* 2024).

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:

a) 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 (forage) 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 northwards 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 which marine habitats are selected for foraging.

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 changes in the NAO 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) and Sandwich Terns primarily forage at intermediate turbidities, where catchability of near-surface prey may peak (Baptist & Leopold 2010).

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).

a) 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 seabird distribution 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 3.7, adapted 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 of seabirds. 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 across larger temporal and spatial scales.

a) 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 (Schwemmer et al. 2011; Fliessbach et al. 2019).

2.3.2 Geolocator studies – 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 relative roles of adult survival and reproduction in population dynamics as a function of prey availability are not fully understood and require more attention. Vulnerability and sensitivity indices 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 nest monitoring with more refined survival models, which is crucial for effective seabird conservation, particularly in the context of fisheries management.

1.1.1. GPS tracking data and environmental data

In this section we provide a brief overview of GPS tracking, the target species selected for this study, and some of the analytical techniques that can be implemented to answer overarching research questions in relation to coastal and seabird spatial ecology.

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 to perform analyses on existing data to help explain the factors that influence specific foraging behaviours and distribution patterns among the already tracked target seabird species. It is also recommended, where feasible, carrying out GPS studies on those species where few data currently exist (i.e. common scoter, little gull and great skua) – to at least get descriptive data on distribution and movement behaviour.

To demonstrate what can be done with GPS-derived spatial data, 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 (spring, summer, autumn, winter) across 2024 and created four plots (Figure 2-1).

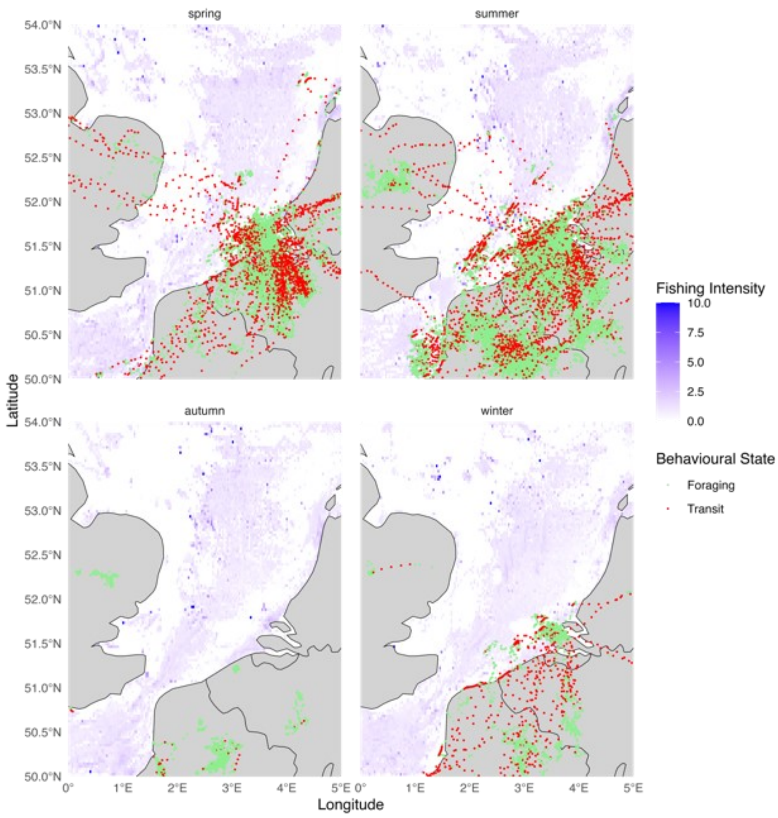

Figure 2-1 *Foraging (green dots) and transit (red dots) locations of 100 lesser black-backed gulls tracked in 2024 from Neeltje Jans in the Netherlands (Stienen et al. 2024) and fishing intensity (blue scale) in the North Sea, split according to season.*

From Figure 2-1 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 2-1), 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 tracking 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).

21As mentioned, 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 (ref Ecowende/BirdLife etc).

- It is recommended using these tracking 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 environmental variables (for example those that can be 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 2-2).

- 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 to better understand the factors that influence great black-backed gull foraging in the (southern) North Sea.

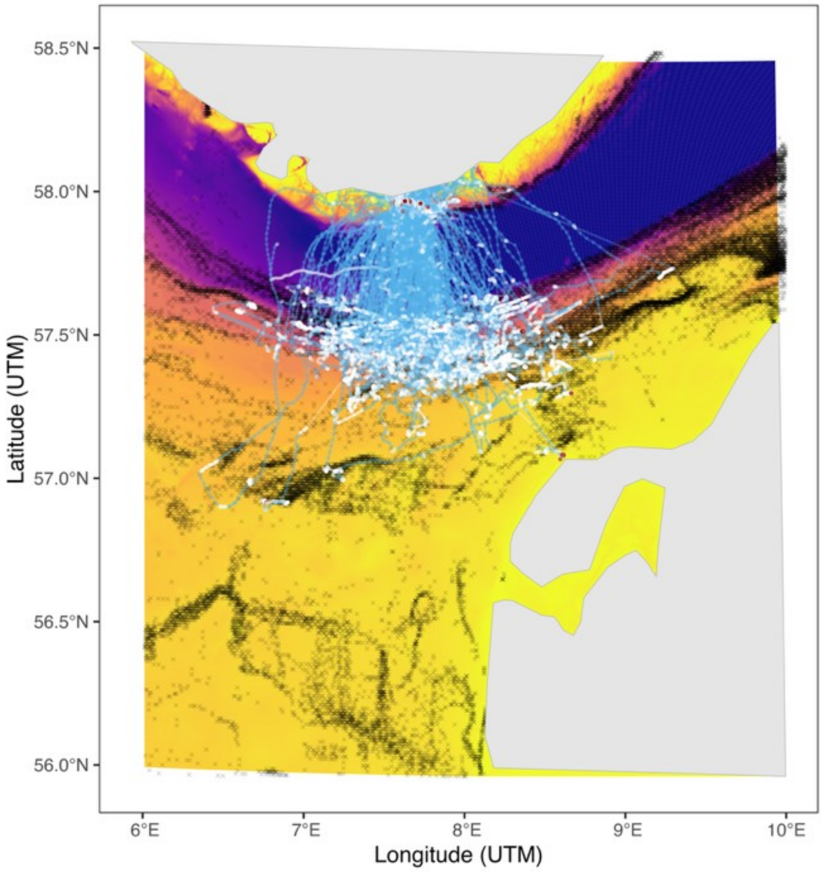

Figure 2-2 *GPS positions of Great Black-backed Gulls (n = 20), recorded during chick-rearing. GPS fixes were collected every 3 minutes. Grey areas are the landmasses of southern Norway, where the gulls breed, and north-western Denmark. White dots represent GPS fixes that were classified as foraging, 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 colours represent shallow areas; darker colours represent depth <400 m). Madden et al. 2025 in review.*

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 2-3). This map provides a hypothetical visual indication of the coastal habitats in which common terns might forage, and the plot suggests 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.

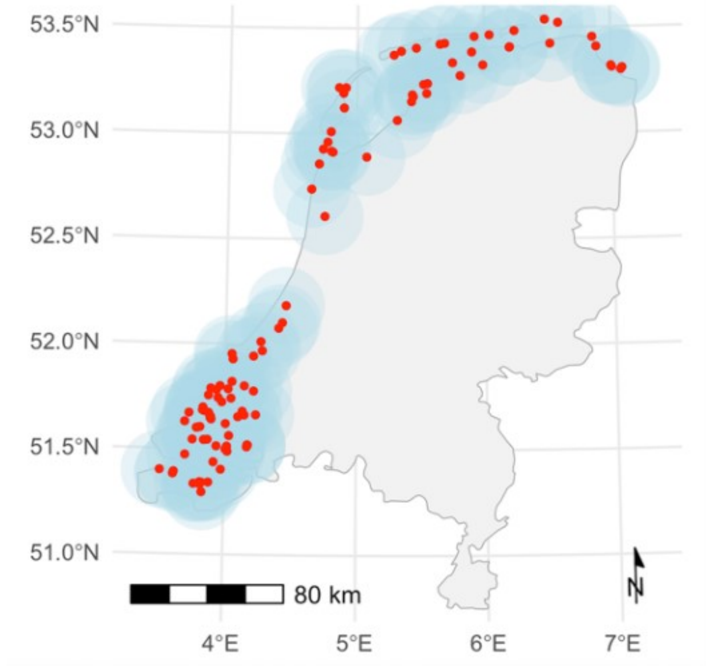

Figure 2-3 *Map of the Netherlands showing coastal breeding colonies (red dots) and the mean maximum foraging distances travelled by common terns (blue circles). Distance calculated based on data from a breeding colony at Maasvlakte II.*

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 2-1). Unfortunately for all datasets, these tracks may be viewed but not yet downloaded:

As shown in the examples above (Figure 2-1, Figure 2-2 en Figure 2-3), should these data become publicly available:

- It is recommended to use these data to produce maps showing the spatial distribution of the above-mentioned species, make inferences 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.

Table 2-1 *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	**Climate variable(s)**	**Population parameter(s)**	**Observed effect**	**Ref**
Black-legged kittiwake	SST, salinity	At-sea distribution	+/none	1
Black-legged kittiwake	SST	Hatching, fledging, breeding success	+	1
Common guillemot	SST, salinity	At-sea distribution	+	1, 2
Common guillemot	Stormy conditions	Foraging cost	+	3
Common guillemot	SST	Hatching, fledging, breeding success	none	4
Common tern	Salinity	At-sea distribution	-	2
Great black-backed gull	SST	Hatching, fledging, breeding success		4
Herring gull	Salinity	At-sea distribution	-	2
Herring gull	SST	Hatching, fledging, breeding success	+	4
Northern fulmar	SST, salinity	At-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	At-sea distribution	+	1

2.4 Survey data

2.4.1 Identification of knowledge gaps: general seabird distribution

Timing
The aerial surveys of the MWTL programme provide excellent data on the distribution of seabirds in 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 is estimated using the same methods, however this is currently not the case. For the species considered here, the distributions of northern fulmar and common tern were estimated using different methods than the remaining species. Although habitat modelling 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 the species' models may arise, however, since what (sets of) covariates may be relevant will likely differ between species and seasons.

Covariates – forage fish abundance
The most obvious improvement to current habitat models is likely additional 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). 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 distributions and 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 breeding 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, the effort in the coastal zone was rather limited - which is problematic for coastal species such as terns. This led to the 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 seabirds outside Dutch Continental Shelf (DCS)
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 in the DCS during summer, with their chicks, from breeding areas along the eastern coasts of England and Scotland. During summer and autumn, guillemots may leave the DCS. By focusing only on the DCS, important information about the movements of guillemots throughout the North Sea is missed. Although international at-sea seabirds surveys 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 interpret seabird distribution patterns within the DCS and link these to North Sea wide-patterns.

Disturbance
With the development of more offshore wind farms in the Dutch North Sea, shipping activity will increase - not only during construction but also during the operational phase due to maintenance. Hence, understanding the effects of marine traffic on seabird distributions is important. Initial attempts to estimate the effect of shipping lanes on e.g. alcids (van Donk *et al.* 2024; Mercker *et al.* 2021) have been made but additional studies are required, for example including fishing vessel activity data.

2.4.2 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 and 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). What drives settlement in Sandwich terns is poorly understood, however. 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 improve our understanding of the processes (e.g. settlement) and consequences (e.g. productivity) of the breeding strategies of lesser black-backed gulls and Sandwich terns.

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 upper meter 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) for driving 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). Pursuit-diving predators drive prey fish to the upper water layers, where they become available to surface-feeding seabirds. However, to what extent surface-feeding seabirds depend on such processes is uncertain. A first step would be to study the 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 surface-feeding seabird - were compared to those of common guillemot and razorbill - two pursuit-diving seabirds.

2.4.3 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) measures of 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 the possibility of including 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.

2.4.4 North Sea food web

The interactions between forage fish populations and coastal and seabird foraging ecology in the North Sea (See Figure 2-4 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).

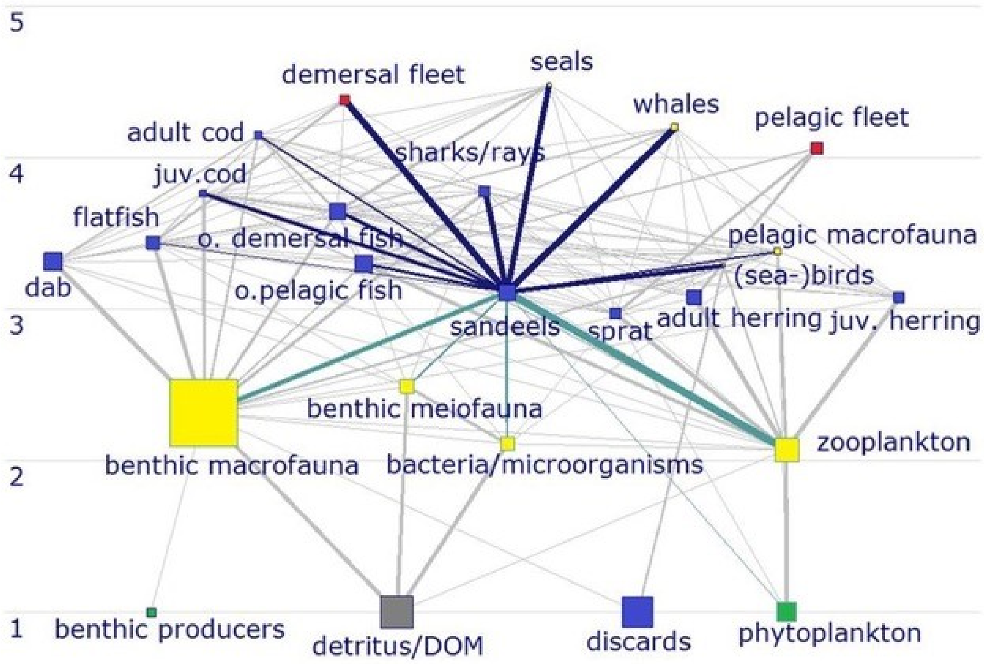

Figure 2-4 *Food web of the Southern North Sea showing the central position of sandeels, with the lines indicating the trophic flows and the numbers indicating the trophic level. The size of the squares is proportional to the biomass of a group, with grey representing detritus, green representing primary producers, blue representing fish, yellow representing marine organisms (except fish) and red representing fishing fleets (Otto et al. 2019).*

2.4.5 Distribution of forage fish

Since the 1990s, pelagic fish numbers have increased, potentially indicating a shift from demersal to pelagic dominance (Engelhard *et al.* 2011). The influence of other predators like seabirds and marine mammals on these fish populations is not well understood. It is unclear whether forage fish in the North Sea (Figure 2-5) are influenced more by natural ecosystem dynamics, or by fishing pressures. 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 zooplankton 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 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 due to a combination of climate change and fisheries effects; 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 slifted in English waters (Permanent Court of Arbitration 2025).

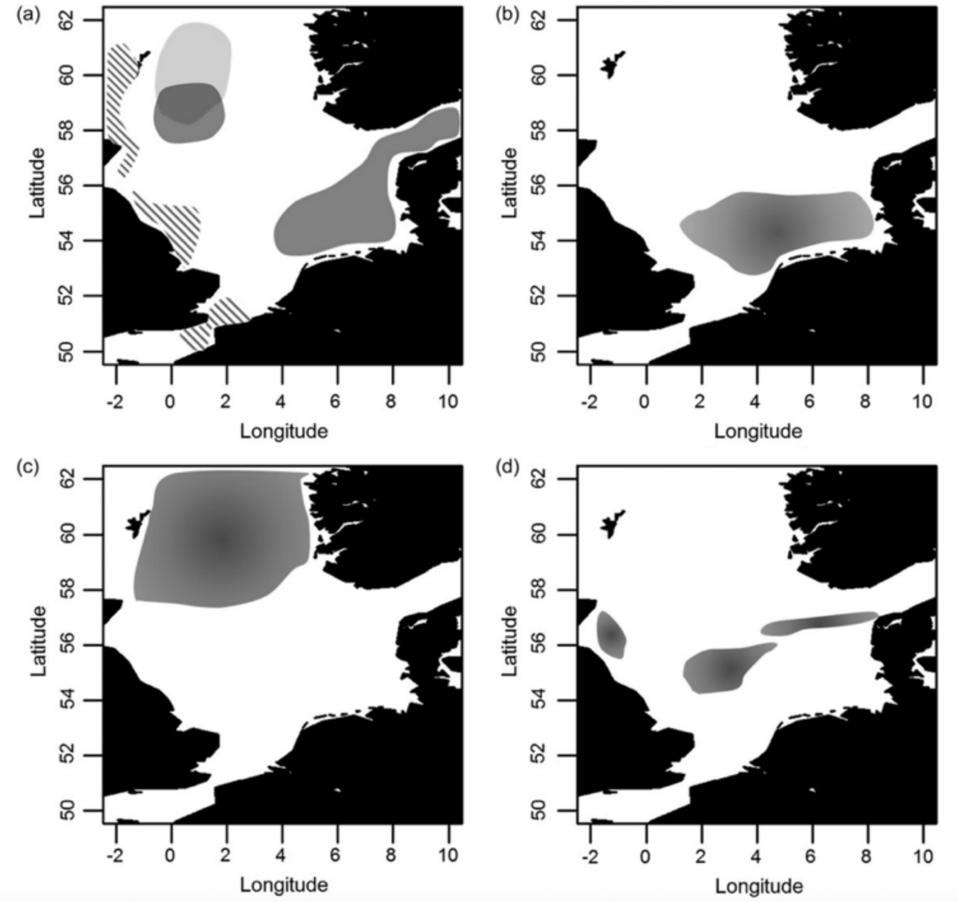

Figure 2-5 *Schematic distribution maps showing the areas of high concentrations within the North Sea for four forage fish species. A) herring, distinguishing between juveniles (dark grey), adult herring during summer (light grey), and autumn spawning areas (hatched); B) sprat; C) Norway pout; D) sandeel. 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). In the herring acoustic survey project, Wageningen Marine Research is a Dutch research partner (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 2-6).

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

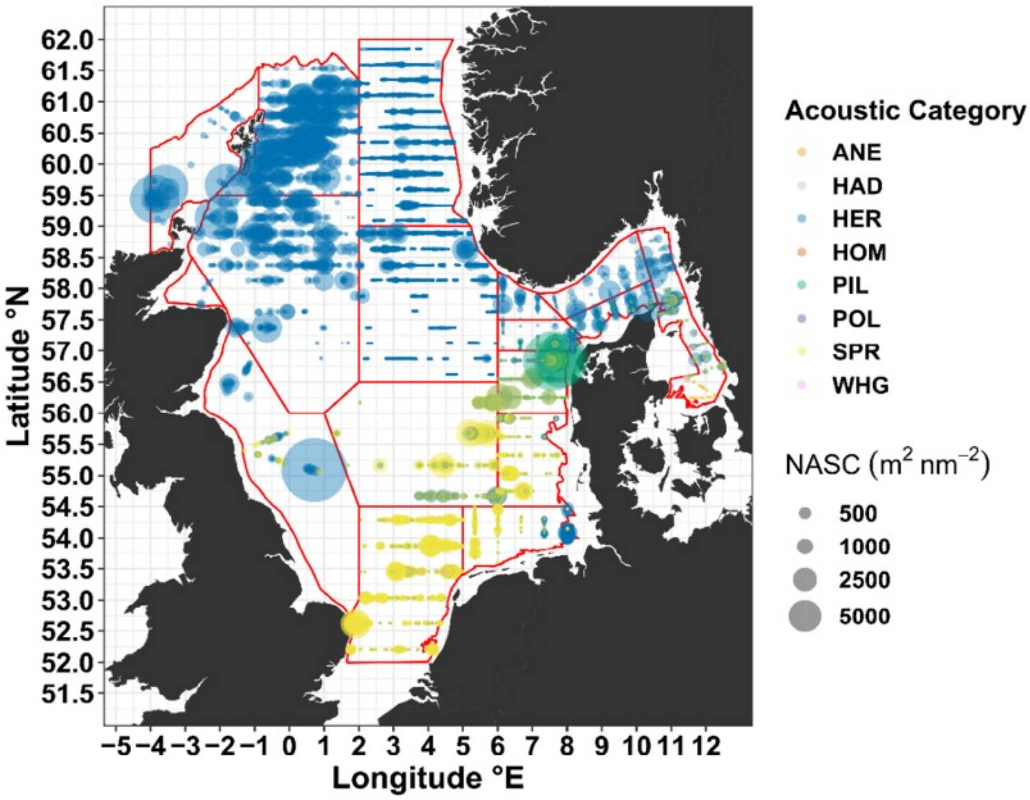

Figure 2-6 *Densities of small pelagic species (forage fish and young stages of haddock, pollock and whiting) determined by the HERAS survey, June 2023 – Disaggregated hydroacoustic categories assigned to hydroacoustic data after implementing the splitNASC-process in StoX software. Aggregated acoustic 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 2-7). While large fish trends are monitored using established indicators like the Large Fish Index, no similar index exists for small pelagic 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). 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. Analysing survey trends may reflect changes in catchability as much as changes in fish populations, which in turn may be influenced by environmental factors such as water clarity and temperature (Parmentier *et al.* 2025).

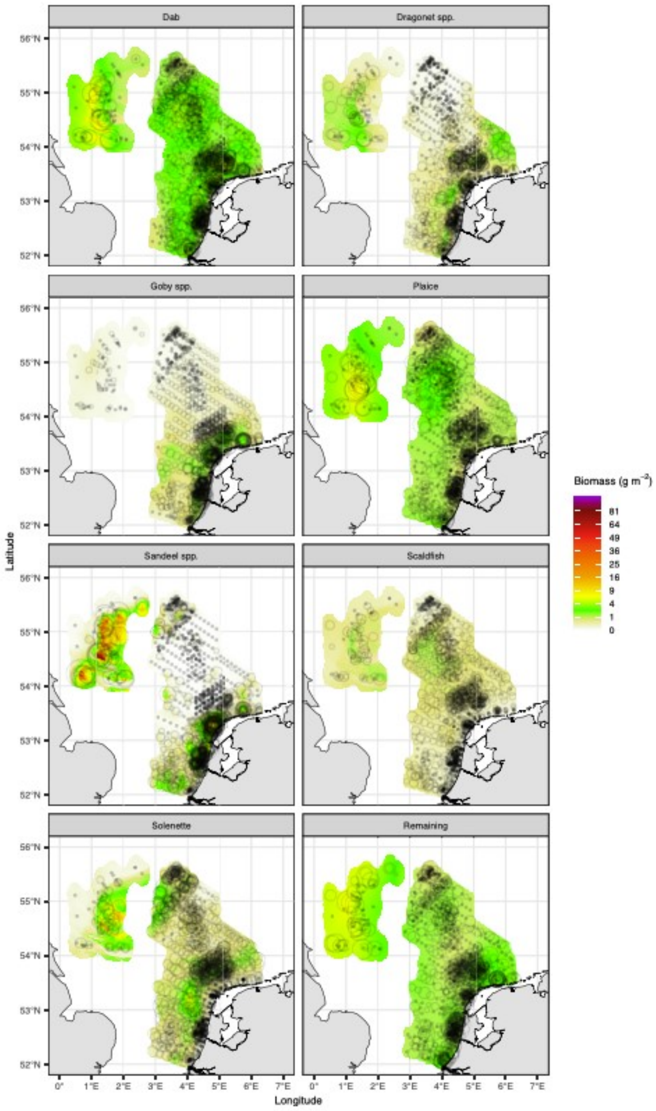

Figure 2-7 *Distribution of biomass per small (<30 cm) fish species and all remaining small fish pooled in the southern North Sea. Biomass estimates for the Dutch EEZ are a winter prediction, while estimates for the UK Dogger Bank reflect summer conditions. Size of black circles correspond with the observed 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).*

Small demersal fish are concentrated in the southern North Sea, with areas of high biomass identified in the western Dogger Bank. Spatial variation in overall 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 distributions shifting offshore and northward in, for example, juvenile flatfish (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 (Figure 2-8). 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).

These studies help improve our understanding of sandeel distribution in the Dutch EEZ, especially in areas that have been under-sampled in past research. However, it does not directly compare its 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 in the wider North Sea region 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).

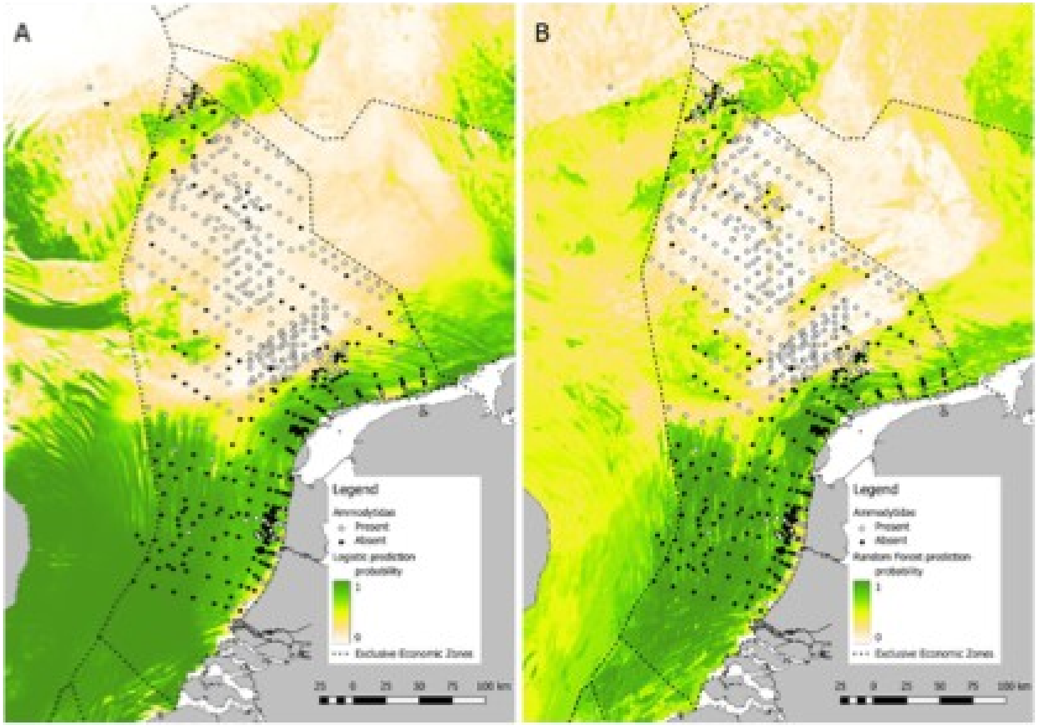

Figure 2-8 *Observed occurrence of sandeels in the Dutch EEZ, and model predictions by (A) logistic regression and (B) random forest regression. White open dots indicate samples with the species absence, Black filled dots represent presence. [Legends in figure are incorrect] Green-yellowish Shading represents predicted probability of occurrence from the models (Witbaard et al. 2024).*

Vulnerability of seabirds to fluctuations in forage fish abundance

As shown in (Table 2-2), 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 as they need to regularly return to their terrestrial nesting site. The high costs that come with such commuting flights, combined with small body size and lack of dietary flexibility, often means birds are reliant on fatty pelagic fish with high energy content, such as sandeel, particularly birds that forage in the northwestern North Sea where sandeel are highly abundant and easily accessible. In the eastern and southern North Sea, seabirds with limited foraging ranges are more likely to consume more clupeids (e.g. juvenile herring), which have lower energy content than sandeel (although this differs per location) (Furness & Tasker 2000; Maathuis *et al.* 2025; Stienen & Brenninkmeijer 2002). Thus, seabirds breeding in the Netherlands are particularly vulnerable to fluctuations in forage fish abundance due to ecological limitations and prey quality constraints. Any decline in local forage fish abundance could result in negative impacts on overall breeding success.

Table 2-2 *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
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]

Furness & Tasker (2000) 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 to avoid 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 2-3). 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 2-3 *Documented evidence of dependence on North Sea forage fish by marine birds (adapted from Engelhard et al. 2014). I, immobile year-round; IB, immobile during the breeding season only; M, mobile year-round.*

	Forage fish contribution to diet						
Species	**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	0.10-0.95	Low	0.10-0.95	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 (and adult survival) 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	0.7-0.25	No evidence reported
Northern fulmar	M	0	0.02	0.11	0.02	0.15	No evidence reported

Table 2-3 shows, per species, the levels of mobility; proportion of diet made up by each of four forage fish species, and all forage fish 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 localised prey shortages: 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)

Seabirds are among several key marine predators that exert significant pressure on forage fish populations, alongside predatory fish and marine mammals. Forage fish thus face substantial predation pressures, often exceeding the 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 (*Merlangius merlangus*) and grey gurnard (*Eutrigla gurnardus*) 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.

2.5 Conclusions

Despite decades of ongoing research, our understanding of seabird foraging dynamics in the North Sea remains incomplete, particularly in offshore areas and during non-breeding periods, limiting the development of effective conservation strategies. As the North Sea's ecosystem continues to undergo rapid transformation (via anthropogenic activities and natural shifts in the marine environment), prey availability will change, in turn affecting the long-term survival of marine birds. Comprehensive tracking and survey studies are therefore essential to more accurately determine core foraging areas and important migratory pathways. Linking spatial data to changes in forage fish availability and anthropogenic activities will provide critical insights that can guide national policy to ensure key foraging habitats are adequately protected in the North Sea. The monitoring and research efforts outlined in the MONS program are particularly timely given these 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. If food availability can be increased in key areas (e.g. coastal zones, Bruine Bank and Friese Front) or 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 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 whether these exhibit any temporal changes/trends. In addition, interactions between forage fish populations 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 necessary data for effective conservation of seabirds.

3. WP3: ID 62 - Literature and laboratory studies on the diet of seabirds occurring in the Dutch North Sea

3.1 Aim & structure

The aim of this work package was to improve knowledge about the diet of the focal seabird species, with a focus on the southern North Sea, both within and outside the breeding season. Our focus is on the (fish) species that were found in the diet and, when supported by published literature, we also discuss whether specific species select certain size categories. Together with the focus of the other two work packages on foraging areas and breeding ecology, this work package could contribute to ecosystem knowledge and models, that could be used to investigate the consequences of environmental changes.

This chapter summarises the results for WP3. The full results can be found in van Donk *et al.* (2025), which can be read as separate report but also as an annex to this report. Our results include a literature review but also new data on prey remains in the stomachs and intestines of seabirds. The chapter begins with a short method section in which we outline the focus of the literature review, and which new data were analysed. The results and knowledge gaps of the review and the analysis are presented together per species group as described in Table 1-1: coastal diving species, pelagic species and surface-feeders. For the pelagic species, we distinguish between those that mostly swim (pelagic diving) and those that are more aerial (pelagic surface).

3.2 Methods

3.2.1 Literature review

A more extensive explanation of the methods used can be found in van Donk *et al.* (2025). A short description is provided below. In this study, an overview of available knowledge about diet of the selected species of coastal- and seabirds in the Southern North Sea occurring in the Dutch North Sea are described. Since a literature review can be broad and extensive, we prioritised gathering information on:

- Literature (including “grey”) on the diet of the selected seabird species from the Dutch part of the southern North Sea and, if necessary (only in case of scarce literature for a certain species or if literature from abroad was considered crucial), relevant studies from neighboring countries were included.
- The difference in diet between the breeding and non-breeding season. During the breeding season, the foraging strategies of coastal and seabirds are characterised as “central place foraging”: individuals must find prey within a maximum range around the colony. It is therefore important to know whether chick diet differs from that of adults, and whether competition exists with other birds and/or colonies. When birds migrate or breed outside the Netherlands, the diet from this period is not included or is only briefly described.
- The difference in diet between years or seasons.

Some other subjects were described when time allowed and/or literature was available. For instance, we described the role of profitability. This could relate to the (chemical) quality of prey but can also mean how accessible (in deep or shallow, clear or turbid waters) prey is. For some species, we described to what extent the availability and quality of prey species is affected by parameters that vary due to climate change (temperature, weather patterns).

In diet and discard studies, prey species are often aggregated into broader categories because individual identification is not always possible. For instance, when analysing faecal remains or regurgitates, prey is frequently too digested to determine at species level. Consequently, researchers group prey by taxonomic Orders or Families, or by ecological characteristics. Common examples include herring (*Clupea harengus*) and sprat (*Sprattus sprattus*), which belong to the Clupeiformes order and are often referred to as 'clupeids', and various sandeel species grouped under Ammodytidae. Similarly, 'cod-like' fish such as Atlantic cod (*Gadus morhua*), haddock (*Melanogrammus aeglefinus*), and whiting (*Merlangius merlangus*) fall within the Gadiformes order. In discard studies, a distinction is made between flatfish—demersal species such as species that belong to Pleuronectidae or Soleidae family —and roundfish, which include all species that are not flatfish, rays, or sharks. Other useful aggregations relate to the position of species in the water column, distinguishing between pelagic and demersal fish. This distinction is ecologically relevant because it influences which seabird species can access these prey. Pelagic fish can become available near the surface and are typically taken by surface-feeding birds, whereas demersal species occur near the seabed and can be eaten by deeper diving birds or become available as discards from fisheries. An overview of the fish species, including their scientific names, Orders, Families, and whether they are grouped in other categories, is provided in Table 3-1.

Table 3-1 *Prey species mentioned in this report, their scientific name, order and family and different aggregation levels. A more elaborate Table can be found in van Donk et al. 2025.*

Species	scientific name	Order	Family	Species group names
horse mackerel/scad	*Trachurus trachurus*	*Carangiformes*	*Carangidae*	pelagic
common dab	*Limanda limanda*	*Carangiformes*	*Pleuronectidae*	demersal, flatfish
plaice	*Pleuronectes platessa*	*Carangiformes*	*Pleuronectidae*	demersal, flatfish
common/Dover sole	*Solea solea*	*Carangiformes*	*Pleuronectidae*	demersal, flatfish
tub gurnard	*Chelidonichthys lucerna*	*Chelidonichthys*	*Triglidae*	demersal
herring	*Clupea harengus*	*Clupeiformes*	*Clupeidae*	pelagic, forage fish, herring-like, clupeids
sprat	*Sprattus sprattus*	*Clupeiformes*	*Clupeidae*	pelagic, forage fish, herring-like, clupeids
anchovy	*Engraulis encrasicolus*	*Clupeiformes*	*Engraulidae*	pelagic, forage fish
Atlantic cod	*Gadus morhua*	*Gadiformes*	*Gadidae*	demersal, cod-like
haddock	*Melanogrammus aeglefinus*	*Gadiformes*	*Gadidae*	demersal, cod-like
whiting	*Merlangius merlangus*	*Gadiformes*	*Gadidae*	demersal, cod-like
Norway pout	*Trisopterus esmarkii*	*Gadiformes*	*Gadidae*	demersal, cod-like, forage fish
poor cod	*Trisopterus minutus*	*Gadiformes*	*Gadidae*	demersal, cod-like
transparant goby	*Aphia minuta*	*Gobiiformes*	*Gobiidae*	pelagic
Raitt's sandeel	*Ammodytes marinus*	*Labriformes*	*Ammodytidae*	demersal/pelagic, sandeel, forage fish
lesser sandeel	*Ammodytes tobianus*	*Labriformes*	*Ammodytidae*	demersal/pelagic, sandeel, forage fish
great sandeel	*Hyperoplus lanceolatus*	*Labriformes*	*Ammodytidae*	demersal/pelagic, sandeel, forage fish
glacier lantern fish	*Benthosema glaciale*	*Myctophiformes*	*Myctophidae*	pelagic
capelin	*Mallotus villosus*	*Osmeriformes*	*Osmeridae*	pelagic, forage fish
smelt	*Osmerus eperlanus*	*Osmeriformes*	*Osmeridae*	pelagic, forage fish
three-spined stickleback	*Gasterosteus aculeatus*	*Perciformes*	*Gasterosteidae*	demersal/pelagic
sand goby	*Pomatoschistus minutus*	*Perciformes*	*Gobiidae*	demersal
Atlantic mackerel	*Scomber scombrus*	*Perciformes*	*Scombridae*	pelagic
grey gurnard	*Eutrigla gurnardus*	*Perciformes*	*Triglidae*	demersal

3.2.2 Summarising literature results

To summarise the findings of the literature search, some figures were produced to show the prey types found in different studies. As diet studies are often hard to compare because of the different methods used, we categorised prey types based on whether they were rare (<5%), occasional (5-20%), common (20-50%) or very common (>50%). This was only done for the gulls and terns that were reviewed. For breeding birds of the Netherlands, we used Dutch studies whenever possible. If possible, frequency of occurrence was used for prey remains or stomachs, but if this was not presented, the % of total prey or % biomass was used. Studies that used isotopes were not included. Prey were mostly grouped by family, or otherwise by prey groups frequently used in studies for that seabird species. Many studies presented the data per year; in these cases, the average of the measured years were taken unless these were many years (~10 years) apart. In that case, the most recent years were selected. In some studies, a distinction could be made between adult and chick diet, in which case the diets of adults were selected. The figures are meant to provide a visual overview of the potential prey of a seabird species, but are highly dependent on the amount of suitable studies that could be included and whether these were executed in similar years or habitats.

3.2.3 Laboratory work

The second part of this working package was to disclose and/or analyse the stomach and intestine contents of dead birds. Valuable knowledge was available from previously gathered but not fully examined or analysed material. For two species, the red-throated diver and the northern fulmar, scientific manuscripts were completed within this project.

Besides data that were available in datasets but not yet disclosed (red-throated diver, common guillemot and northern fulmar), new data were gathered from dead common guillemots and Sandwich terns. An inventory has been made of material stored in freezers at NIOZ (in collaboration with Kees Camphuysen) and WMR (bird stomachs and intestines) from seabirds. This includes approximately 60 common guillemot stomachs and 240 stomachs and 237 intestines from Sandwich terns. Common guillemots were mostly collected on Texel and autopsies performed, documenting age class, sex, presumed cause of death, and stranding date. Sandwich Terns were collected during the 2022 bird flu outbreak during the breeding season.

3.3 Results

3.3.1 Coastal diving species

Diets of coastal diving species
Neither of the designated coastal diving species breed in the Netherlands but are present in relatively high numbers along the Dutch coast in winter. The diet of common scoters is relatively well studied, including prey selection as well as prey size. The diet of the red-throated diver is less well-studied, but within this study new data has been presented based on the analysis of a long-term dataset of beached birds. Although both species are coastal diving birds, their diets differ significantly.

For the common scoter, multiple studies have demonstrated that the distribution is primarily determined by the availability of ingestible bivalves, although other environmental and anthropogenic factors such as water depth, hydrographic conditions and disturbance from shipping, also play a significant role. Based on long term monitoring, it appears that the location of main foraging areas in the Netherlands may vary substantially within and between years. Nevertheless, three designated areas of primary ecological importance can be clearly identified, in descending order of significance: the Wadden Sea coastal zone, the Voordelta, and the North Holland coast in the vicinity of Petten (Leopold *et al.* 1995; Tulp *et al.* 2010; Fijn *et al.* 2017; van der Wolfshaar *et al.* 2023; Camphuysen & van Lieshout 2024).

Red-throated divers in the eastern North Sea, unlike common scoters, were found to be (almost) completely piscivorous (Figure 3-1). Healthy birds primarily consumed small clupeids (herring and sprat), and larger gadoids (mostly whiting and pouts). However, when faced with scarcity of their preferred prey, either locally or temporarily, or when birds became debilitated by sickness or by oil contamination, preventing them from pursuing these prey, they had plenty of fall-back options. Sick birds were able to move to more sheltered waters and/or switch to prey that were likely easier to catch, however this was at the expense of a lower caloric return per prey. Estuarine prey fish, such as smelt or stickleback were important for such birds, as were small demersal prey like gobies, sandeels or even flatfish. Diet studies on birds with a broad prey spectrum require large sample sizes and should include individuals that died from various causes in different micro-habitats to capture the full range of prey.

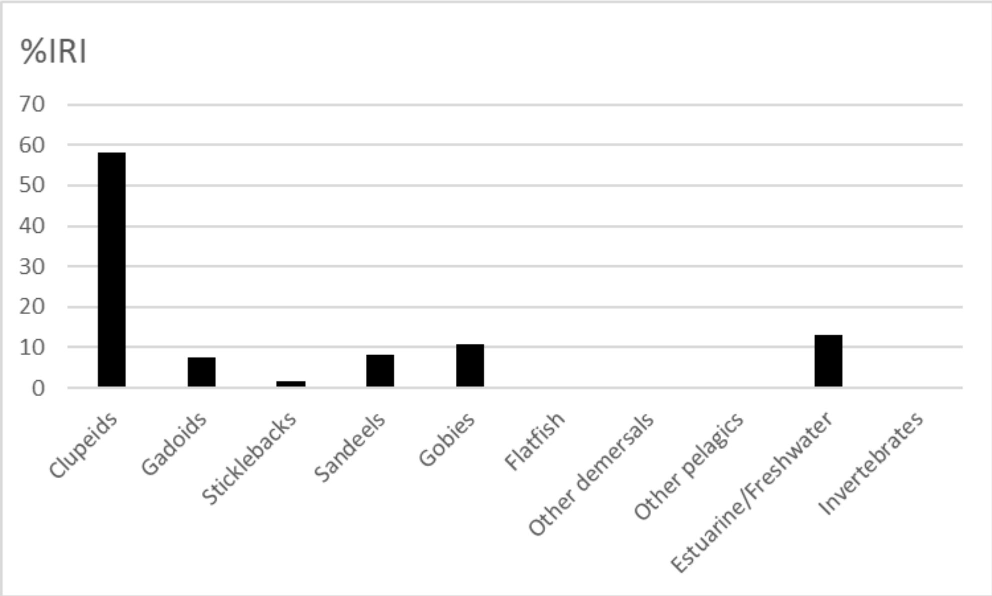

Figure 3-1 *The relative importance of 10 prey groups, found in 220 red-throated divers with non-empty stomachs, as the percent index of relative importance (%IRI).*

3.3.2 Pelagic species

Of the designated pelagic species, only the kittiwake breeds in the Netherlands, albeit in low numbers on artificial structures such as oil platforms. Studying the diet of seabird species that do not breed in the Netherlands (or that breed in difficult-to-reach places) is more challenging and therefore the information used for these reviews relies more heavily on international publications. For some birds, new data on beached birds collected along the shoreline are presented. We first discuss findings for the pelagic divers - guillemot and razorbill - followed by the more aerial pelagic species - northern fulmar, northern gannet and kittiwake.

Diet of pelagic divers
Common guillemots and razorbills share many ecological similarities and their diets also partly overlap, however razorbills in Dutch waters have a much narrower diet. The diet of guillemots in the Dutch North Sea is dominated by energy-rich clupeids, gadoids, and sandeels, although a wide variety of additional prey types has also been documented (Camphuysen 2006; Leopold *et al.* 2019; Leopold & Overmaat 2023), while the diet of razorbills primarily comprises small clupeids and sandeels (Camphuysen & Leopold 2005; Leopold & Camphuysen 1992; Ouwehand *et al.* 2004). Besides the slight differences in diet, guillemots and razorbills also seem to select slightly different fish sizes. Size selection in guillemots is also affected by weather and body condition: birds foraging in poorer weather or with a bad body condition consumed smaller fish (Finney *et al.* 1999; Leopold *et al.* 2019).Guillemots ingested, on average, larger fish than razorbills which often ingest fish < 10 cm (Ouwehand *et al.* 2004). For guillemots, more data are available compared to razorbills. Body condition appears to strongly influence dietary breadth and prey quality, with birds in poor condition adopting a more opportunistic foraging strategy (Camphuysen 2006; Leopold *et al.* 2019). Seasonal patterns for guillemots diverge somewhat from earlier studies, with sandeels occurring frequently in winter and early spring rather than during the breeding season. The long-term stomach content dataset analysed in this study provides valuable insights into diet composition, sex-specific patterns, and the potential role of fisheries discards in guillemot foraging (Figure 3-2). Our study adds valuable stomach content data to the dataset for recent years. The available data are largely derived from beach-washed, often oiled, birds with stomachs containing recent meals. Unlike guillemots, razorbills rarely consume gadoids and have a marked preference for smaller, slender fish, which likely reflects morphological constraints. While seasonal or long-term trends in Dutch razorbill diet remain poorly understood, studies elsewhere suggest strong reliance on sandeels during the breeding season and possible vulnerability to shifts in prey availability linked to climate change.

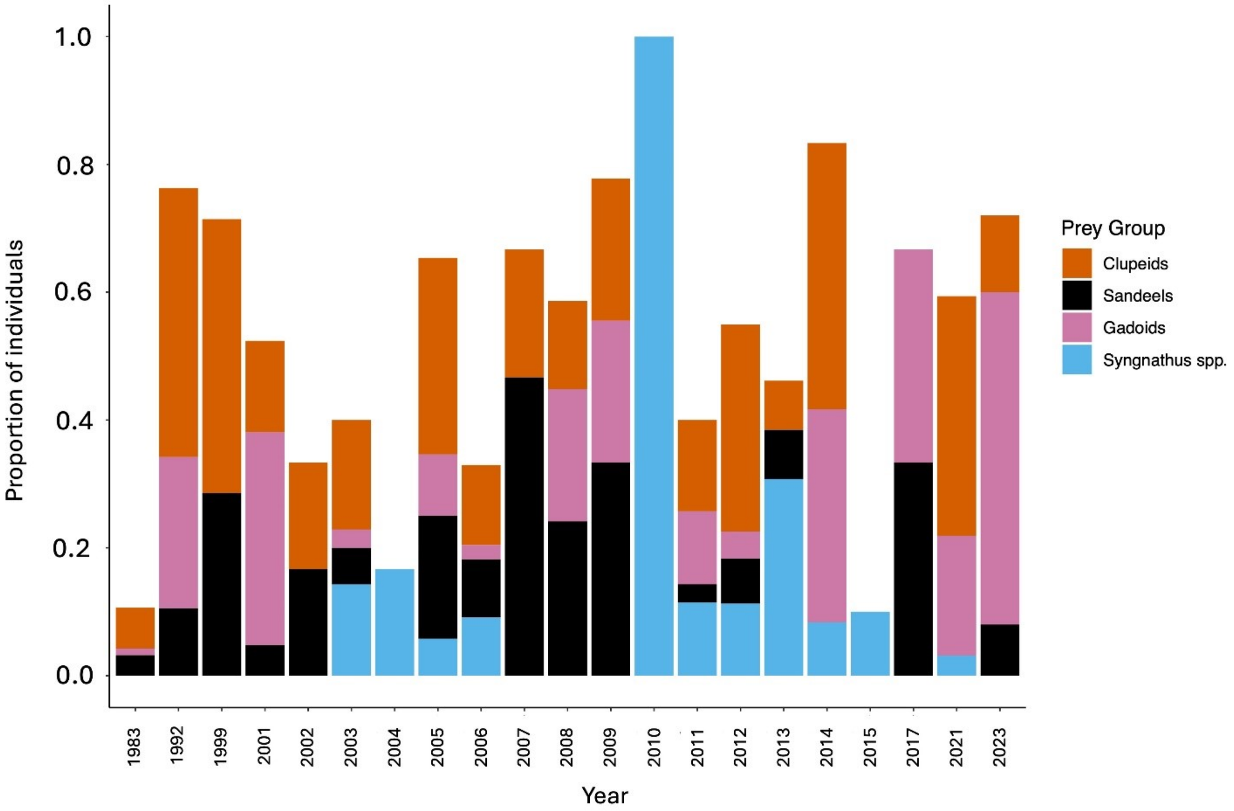

Figure 3-2 *Proportional frequency of occurrence of the four most common prey groups in the diet of the common guillemot across all years (1983–2023). Frequencies are scaled so that values range from 0 to 1 on the y-axis. The white space above each coloured bar represents the proportion of occurrence attributed to all other prey types not included among the top four groups.*

Diet of pelagic surface species

Very little literature on the diet of northern fulmars was available. Findings of new data (van Donk *et al.* 2025) suggest that much of the consumed prey, particularly gadoids such as whiting, poor cod, and Norway pout that live in deeper waters close to the seafloor, likely originated from fisheries discards. This is supported by the predominance of sub-minimum landing size individuals, which are typically not retained during commercial fishing activities. Other prey species such as horse mackerel, and glacier lanternfish are less likely to be discarded, suggesting direct predation. The presence of species such as glacier lanternfish, a mesopelagic fish mostly occurring outside the North Sea, indicates that some fulmars may not strictly forage within the southern North Sea, although they were found stranded along the Dutch coastline. Prey length varied per fish species and ranged from approximately 5 to 28 cm. A deeper analysis carried out in the context of this study investigated potential factors that could influence the amount of whiting in the diet, an important prey for Norther fulmars. Statistical analysis revealed that several factors influenced whiting biomass in the diet, such as sea surface temperature (SST), sex, age, season and year. Increased SST had a negative effect on whiting biomass, suggesting that warming may reduce prey availability or alter fulmar foraging patterns. Additional factors may include temporal shifts in whiting abundance, changes in discard availability linked to fisheries management or effort, and fluctuating fulmar foraging behaviour in response to prey distribution and accessibility. Within the current dataset, many gadoid prey items were under the minimum landing size (MLS), further emphasising dependence on discards. However, there appeared to be a gap between typically ingested sizes and current MLS thresholds. This gap may be caused by a highly specialised foraging method used by fulmars: while smaller fish may be swallowed completely (including fish heads and integrated otoliths), fulmars often use their sharp bills to rip open the body cavities of larger fish and forage on energy-rich intestines, such as the liver (Camphuysen 1994).

Historically, the diet of northern gannets in the southern North Sea has been dominated by high-energy pelagic fish species, such as Atlantic mackerel, Atlantic herring, and sandeels (Hamer *et al.* 2000; Lewis *et* *al.* 2003; Hamer *et al.* 2007). These prey types are especially important during chick-rearing, providing the high caloric value necessary for breeding success. Nevertheless, less energy-dense, gadoids such as whiting are also regularly consumed (Davies 2012; Hamer *et al.* 2007; Lewis *et al.* 2003). The average prey size consumed by gannets ranged from 8 to 40 cm, with most prey falling within the 15–30 cm range (Camphuysen 2011; Lewis *et al.* 2013). Within the North Sea, sandeel dominated gannet diets in the early 2000s, but by 2010 - 2011 their contribution had declined significantly, with mackerel becoming the main component of the diet (Guillemette *et al.* 2018). These changes are likely a response to prey availability influenced by environmental drivers, such as SST. Besides temperature, variations in gannet diet have been related to sex, age, prey availability, other environmental fluctuations, colony size and location of foraging (nearshore or offshore). Gannets also forage for fisheries discards, particularly during the non-breeding season and early in the breeding season (Furness *et al.* 1992). Here, they seem to prefer larger roundfish. During chick-rearing, however, they switch to pelagic fish. Research suggests that a diet of discards is sub-optimal for raising chicks. Importantly, northern gannet population growth in the North Sea does not appear to depend on discard availability (Leopold 2016), implying a degree of dietary flexibility that may buffer the species against ecosystem changes. Dietary patterns during migration and wintering periods remain less well understood, although stable isotope analyses have begun to shed light on these dynamics, with different dietary patterns near the shore and further offshore, possibly reflecting a more discards-focused diet offshore and a more forage fish focus nearshore. However, until now only two studies have examined the diet of gannets specifically in Dutch waters.

Depending on their location, kittiwakes forage on small pelagic fish such as gadoids, clupeids and sandeels. On the eastern coast of the UK, sandeel is the most common prey, followed by gadoids and clupeids, while in the southeastern North Sea, diet consists mainly of gadoid fish, specifically whiting and to a lesser extent clupeids and sandeels (Pearson 1968; Bull *et al.* 2004; Wanless *et al* 2018). Kittiwakes mainly catch small fish, < 10 cm during the breeding season, but size in the diet ranges from 6-32 cm. Larger fish are considered discards, while clupeids ranged from 6-17 cm. Kittiwakes are commonly observed behind fishing vessels, foraging on discards and offal. In discard experiments, kittiwakes showed a preference for fatty roundfish with a median size of ~14 cm and their dependence on discards varied according to location and season, with more birds documented around fishing vessels in the southern North Sea during winter (Camphuysen 1994). However, data availability on kittiwake diet in Dutch waters is restricted and findings are therefore mostly from neighbouring countries.

Pelagic species primarily feed on forage fish as gadoids, clupeids and sandeels, but many other fish species also appear in the diet. Each species targets different size classes, partly influenced by its own size. Fishery discards are consumed mainly by northern fulmars, northern gannets and kittiwakes, but not by pursuit divers. However, recent insights into the diet of Dutch guillemots reveal some prey items that likely originated from discards.

3.3.3 Coastal surface feeders; terns and large gulls

All designated surface feeders in this study also breed in the Netherlands. However, the great black-backed gull breeds in very low numbers and its breeding diet in the Netherlands has not been studied. In contrast, the other species have been studied more extensively due to their higher presence in the Netherlands.

Diet of coastal surface feeders
Both Sandwich tern and common tern breed in the Netherlands in large numbers. Although the diet of both species contains small pelagic marine fish such as Clupeidae (herring, sprat), their dietary preferences differ (*Figure 3-4*). For Sandwich terns, the importance of Clupeidae and Ammodytidae (sandeel spp.) throughout the chick-rearing period is evident, both for adults and chicks (van Bemmelen et al., 2022). Particularly for adult Sandwich terns, other prey species such as ragworms (Nereididae), and different flatfish and round fish species can supplement their diet (Brabant, 2004; Brenninkmeijer *et al.* 2002; Courtens *et al.* 2017; Hoffmann 2000; Stienen 2006; van Bemmelen *et al.* 2022; van der Beek 2017). However, the respective importance of the different prey groups is likely influenced by chick age, variability in food availability due to daily and seasonal effects, variability between years and colony location, and different environmental factors at the foraging location. Sandwich terns eat mainly small fish (ranging from 5-14 cm), but prey length increases with growing chicks (Engels 2015; Stienen & Brenninkmeijer 1994, 2002; van Bemmelen *et al.*

2022; van der Meer 2018). New results of stomach contents from individuals that died from avian influenza in the Dutch Delta area and Wadden Sea showed that sandeels and clupeids were the most abundant prey, followed by gadoids, gobies and estuarine roundfish (Figure 3-3). Prey ranged from 5-23 cm.

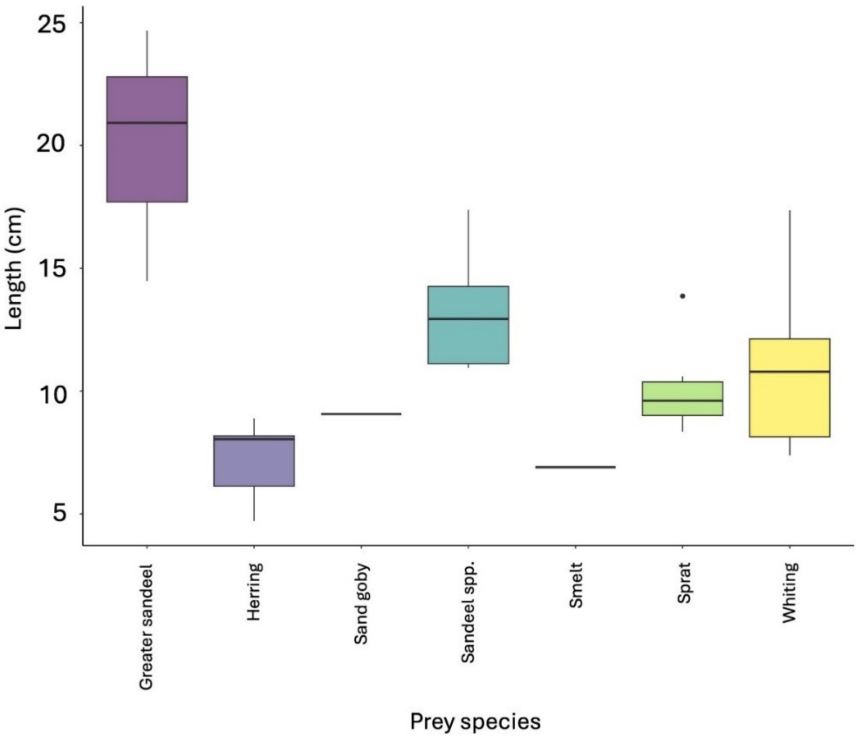

Figure 3-3 *Boxplot showing the median estimated length of prey species (cm) (black line). Solid lines without a box are single individuals.*

For the common tern, a wider variety of prey types can be important during the breeding season. Prey species in the diet include freshwater species like stickleback, and marine species like Clupeidae, particularly herring, Ammodytidae (sandeels), smelt and shrimp (Becker & Ludwigs 2004). Common terns predominantly feed on small fish < 15 cm in length. Prey composition seems to vary depending on several variables, such as stage of the breeding season (courtship, egg or chick phase, breeding success or failure). For instance, studies collectively show that adult common terns predominantly target energy-rich fish such as clupeids and smelt during the courtship period, although prey choice differs per location (Dänhardt *et al.* 2011; Dänhardt *et al.* 2018; van der Winden *et al.* 2009). Additionally, older chicks often receive larger or more energy-rich prey items. However, prey choice also depends on the location of the breeding site (e.g. near freshwater or marine habitat), prey availability per year, and individual specialisation. For example, at the Banter See colony, stickleback and smelt were key components of the diet during courtship feeding, yet showed high interannual and individual variation (Dänhardt *et al.* 2018; Wendeln *et al.* 1994). Pairs or individuals may adopt different foraging strategies - some focusing on sticklebacks, others on marine species - pointing to flexible, pair-specific preferences beyond mere prey availability.

All large gulls are generalist species; they utilise a variety of resources and/or foraging areas although they often exhibit individual specialisation. Gulls make use of a variety of habitats, including land-based resources like landfills and agricultural land (Isaksson *et al.* 2015). Although the three focal gull species selected for this work package show similarities, there are also differences in their feeding patterns (*Figure 3-4*, *Figure 3-5*). For the herring gull and lesser black-backed gull, diet studies that were (mainly) executed in the Netherlands are highlighted, while for the great black-backed gull, most of the literature originated from outside the Netherlands.

Herring gulls have a broad diet that includes both terrestrial and marine prey. Herring gulls are more coastal-bound compared to the other two gull species, but they can be found further offshore, mainly attracted to fishing vessels, or inland in cities and refuse dumps. The most common prey documented during the breeding season are shellfish (Camphuysen 2013; Van Donk *et al* 2017; Spaans 1971). However, depending on the colony location other prey can also be important e.g. crustaceans (shore crabs and shrimp), starfish, marine fish, as well as other prey of minor importance e.g. mammals, birds, insects, plant matter, polychaetes and freshwater fish. Diet composition is dependent on location of the breeding colony and prey availability. Herring gulls can opportunistically forage on prey that are unpredictable and ephemeral, but individuals often show specialisation or repeatability in their foraging strategies (van Donk *et al.* 2019). Diet appears to vary between adult gulls and their chicks; chick diet contained more fish and - depending on colony location and the method used to measure diet - more bread, shrimp and refuse, and less shellfish (Camphuysen 2013; Spaans 1971). This suggests that parents feed their chicks prey with a higher nutritional value. Furthermore, it is possible that chicks, especially when they are young, require soft prey. The diet of herring gulls in winter is less well documented. The majority of herring gulls remain close to the coast or travel more inland, also in winter. However, some studies were conducted with a focus on behaviour and selectivity around fishing vessels and discards at sea, both during and outside the breeding season, where herring gulls often preferred roundfish and offal over flatfish and invertebrates (Camphuysen, 1994). During feeding experiments, herring gulls selected relatively small flatfish with a width <8 cm. Depending on the type of roundfish, the average length of fish eaten fell between 12-23 cm but fish < 30 cm were sometimes consumed as well. (Garthe & Huppop 1994). However, the majority of herring gulls remain close to the coast or travel more inland, also in winter. Other research studied prey remains in faeces at roosting locations, but whether this came from the herring gull or great black-backed gull could not be determined.

Lesser black-backed gulls have traditionally relied on marine prey in colonies around the Wadden Sea and along the Belgian and Dutch coasts, where they supplemented their diet with agricultural and urban food sources (Camphuysen 2013; Garthe & Scherp 2003; Isaksson *et al.* 2015; Schwemmer *et al.* 2013; Sotillo *et al.* 2014). Common prey species in the diet of Dutch breeding gulls included marine roundfish and marine flatfish, insects, refuse, mammals, freshwater prey, birds and marine crustaceans, and to a lesser extent plants, oligochaetes, marine polychaetes and intertidal prey. Similar to the herring gull, chick diet differed slightly from that of adults. In a breeding colony on Texel, chick diet contained (besides mostly flatfish) a relatively high percentage of fatty pelagic fish such as sprat and sand lances (Camphuysen 2013). At a more inland colony, boluses of chicks contained fewer beetles but more domestic waste like bread and waste meat compared to adults, again suggesting selectivity in soft or energy-rich prey for the chicks (Gyimesi *et al* 2016). During feeding experiments at sea, lesser black-backed gulls selected flatfish with a width <8 cm but roundfish were taken that ranged between 13-24 up to ~30 cm (Camphuysen 1994; Garthe & Hüppop 1994). Diet is largely dependent on location, given the difference in diet between colonies and prey availability around the colony. Recent shifts in foraging behavior show a growing reliance on terrestrial resources (Bicknell *et al.* 2013), with some colonies even fully focusing on food sources from land (Gyimesi *et al.* 2016). However, diet has only been studied from a couple of colonies in the Netherlands, and of these the amount of information gathered is sometimes limited. The change in diet observed at some colonies could be driven by a change in marine food resources, for instance due to a decline in the availability of fishery discards and/or changes in opportunities inland. If marine prey and discards continue to decline, gulls may shift further away from marine ecosystems, which could reduce their presence at sea as top marine predators and scavengers. However, lesser black-backed gulls have also been observed foraging at sea without the 'help' of fishing vessels (Baptist *et al.* 2019). This behaviour has only been studied occasionally, and the extent to which lesser black-backed gulls forage naturally in the Dutch seas and what they catch remains largely unknown.

The great black-backed gull is a large, opportunistic generalist predator with a highly varied diet that includes marine prey (fish, invertebrates), birds, mammals, refuse, and anthropogenic food sources (Farmer & Leonard 2011; Rome & Ellis 2004; Washburn *et al.* 2013; Westerberg *et al.* 2019). During the breeding season, marine prey typically dominates the diet, supplemented by terrestrial and anthropogenic items (Borrmann *et al.* 2019; Gotmark 1984; Lopez 2023). Diet composition varies by location and colony, with some populations focusing heavily on seabirds or specific fish species. The species shows strong associations with fishing vessels, often dominating competitive interactions with other large gull species over discarded fish (Camphuysen 1994). However, detailed dietary studies for the Netherlands are limited by the scarcity of breeding pairs and difficulties in distinguishing diet components from mixed gull roosting spots.

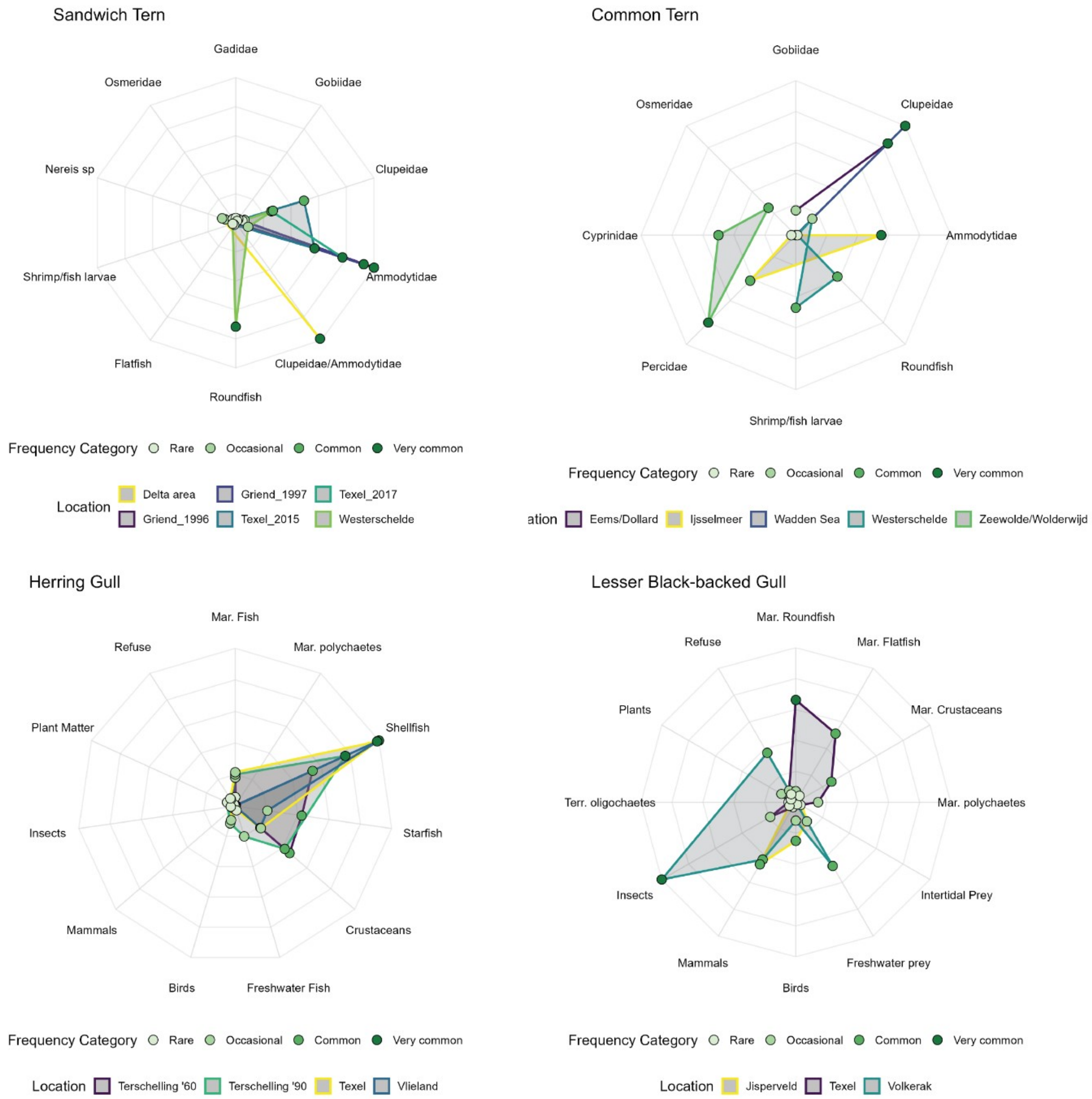

Figure 3-4 *Summary of the literature of diet of surface feeding breeding birds of the Netherlands. Only Dutch studies were used for these figures.*

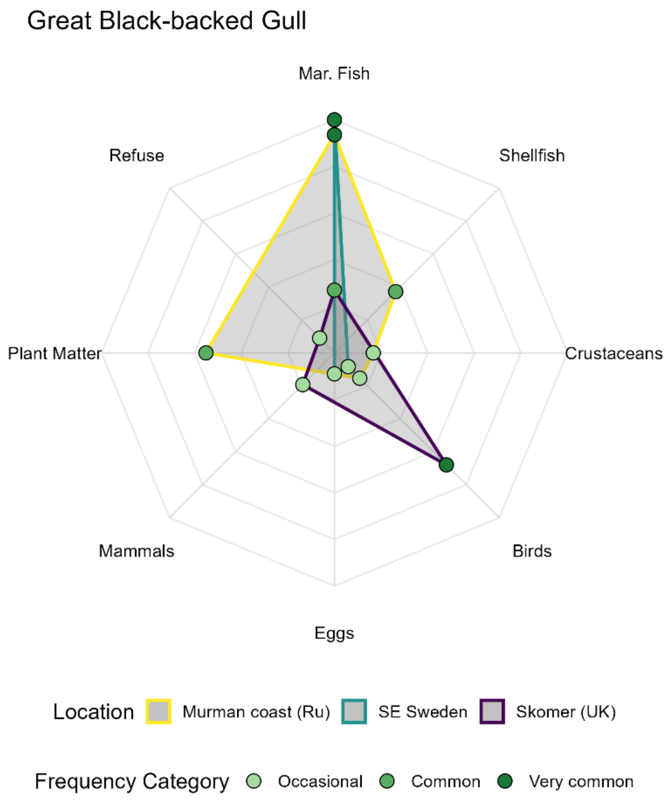

Figure 3-5 *Summary of the diet of the surface feeder great black-backed gull breeding mainly outside the Netherlands. Only European studies were used for these figures, no Dutch data were available.*

3.4 Recommendations & knowledge gaps

3.4.1 Coastal diving species

In the Dutch coastal zone, common scoters switched to feeding on the established American razor clam following the decline of the cut through shell after 2000. However, with the recovery of the cut through shell since 2015, it is plausible that scoters have reverted to this preferred prey species, as indicated by their current distributional patterns and a tentative increase in numbers. These observations underscore the strong reliance of common scoters on suitable bivalve prey and their ability to adapt foraging strategies in response to shifts in benthic community composition (Schwemmer *et al.* 2019). Future research should therefore aim to refine habitat models by incorporating prey dynamics, hydrodynamic drivers, and potential anthropogenic impacts as advocated by Schwemmer *et al.* (2019) and Wolfshaar *et al.* (2023).

The new results presented in this report on the diet of red-throated divers demonstrate an intriguing relationship between body condition and prey choice. This relationship confirms the adaptability of birds while highlighting how different variables affect prey selection. The findings raise questions about the drivers of habitat shifts: whether they reflect active choices or result from deteriorating body and/or environmental conditions. The current diet study relied on stranded or bycaught individuals, which may bias interpretations of population-wide foraging ecology. This reinforces the need for non-invasive, live-animal tracking or dietary sampling to assess prey choice across the full range of habitats and health states. Such approaches could also provide deeper insights into foraging behaviour in relation to fine-scale habitat features, such as frontal zones or prey patchiness, especially under varying weather or tidal conditions.

3.4.2 Pelagic species

Pelagic divers
Whilst some information exists on the diet of pelagic species, substantial knowledge gaps about their diet and factors that influence foraging remain.

Although guillemots are relatively well-studied compared to other seabird species in the Dutch EEZ, several knowledge gaps persist. Specifically, most dietary data originate from beach-washed or oiled individuals collected outside the breeding season, potentially biasing the results toward opportunistic foraging or a shift in dietary profiles. Observed seasonal patterns, such as the frequent occurrence of sandeels in winter and early spring, diverge from findings near breeding colonies elsewhere, where sandeel dominate in summer. However, given that neither guillemots nor razorbills breed in the Netherlands, the lack of breeding season data from Dutch waters is to be expected and cannot easily be addressed. To help resolve seasonal dietary trends, continued collection of individuals found dead or bycaught during summer months is recommended, although such opportunities are likely rare and restricted to non-breeding individuals. To date, prey size distribution and nutritional values are poorly documented, which constrains our understanding of prey profitability under different ecological conditions. In contrast to guillemots, razorbills are understudied in the Netherlands, with information on seasonal or long-term dietary trends in Dutch waters lacking. Their dietary flexibility and response to changes in prey availability remains poorly understood. Given their strong reliance on sandeels during the breeding season, as observed in other parts of their range, razorbills and guillemots may be particularly vulnerable to climate-driven changes in prey distribution and availability. Reports of reduced breeding success and a shift in foraging behavior in response to declining sandeel availability elsewhere underscore the need to better understand how such changes may affect razorbills using the Dutch EEZ. Overall, more systematic, year-round data collection, including from bycaught individuals, which are usually in good condition, would help refine our understanding of the foraging ecology of both species in Dutch waters.

Pelagic surface species
Northern fulmar research revealed the potential importance of prey such as squid, crustaceans, and polychaete worms and other soft prey, however, these were not structurally sampled or quantified in terms of biomass, potentially underrepresenting their dietary importance. To further evaluate the importance of these prey types, stable isotope analysis or DNA sampling is recommended.

Despite the relative abundance of research and insights for the northern gannet, numerous knowledge gaps remain. For instance, the diet of wintering and migrating gannets in Dutch waters is poorly understood. There is also limited information on intra-individual diet variability (Daunt *et al.* 2008), the role and accessibility of fisheries discards (Lewis *et al.* 2003), and the impact of climate change on prey availability and quality (Franci *et al.* 2015). Additional unknowns include the degree of individual dietary specialisation (Bodey et al. 2018), the nutritional quality of prey (Käkelä *et al.* 2007), and the foraging ecology of gannets in different spatial environments (Hamer *et al.* 2000). The role of non-commercial prey in gannet diets also requires further investigation (d'Entremont *et al.* 2022). Furthermore, data availability on the diet of northern gannets in Dutch waters is very limited. Northern gannets exhibit considerable dietary flexibility, influenced by environmental conditions, prey availability, age, colony size, and geographic location. However, significant gaps in knowledge - particularly concerning winter diet, the importance of discards as a food source and the effects of environmental change - underscore the need for further research in this field, also in the Dutch North Sea.

To better understand the dependence of kittiwakes on the Dutch waters and its associated food resources, additional research on 'Dutch' kittiwake diet is recommended. Newly colonised artificial structures within the Dutch EEZ offer excellent opportunities to sample kittiwake diet during the breeding season. Through its central location within the North Sea, kittiwake diet can reflect local fish abundancies and serve as an indicator for ocean health.

3.4.3 Coastal surface feeders

Despite this general understanding of the diet of breeding terns and gulls, substantial knowledge gaps remain.

Although large numbers of Sandwich terns migrate through Dutch waters (Camphuysen *et al.* 1983; Platteeuw *et al.* 1994), dietary studies predominantly focus on the breeding season (March–June/July), when adults regularly return to their nests to provision chicks. In contrast, little is known about the species' diet during migration. Stomach content analysis of stranded individuals may offer additional insights into foraging during this phase, provided suitable specimens are available. To date, for Sandwich terns, differences in chick diet composition between colonies or study years have not been statistically quantified and remain descriptive. Furthermore, the relationship between at-sea food availability and seasonal patterns in chick diet composition is often not studied. Closing these knowledge gaps would provide greater insights into the differences in chick diet composition, as well as the driving factors behind such observed variability.

For the common tern, general information on prey size during the breeding season is scarce, highlighting the need for further research to better understand the energy intake of adult common terns. Furthermore, in Dutch freshwater colonies and the Wadden Sea, long-term chick diet data are absent, making regional comparisons difficult. German colonies provide more continuous data, but direct comparisons between regions or years are rarely statistically quantified. Due to high local variability in prey availability, a comparison between German and Dutch colonies might be challenging to quantify. While some studies document temporal diet shifts across the breeding season or chick developmental stages, most provide only snapshots of diet composition or average their results across the entire study period.

Besides recent studies investigating the effect of prey availability in the Dutch Wadden Sea, the influence of environmental factors on common tern diet is poorly understood. While it is possible that the opportunistic feeding strategy of common terns makes them less reliant on specific environmental conditions for foraging success and to meet their energetic demands, studies from the 1980s and 1990s suggest different environmental factors affect their diet. The impacts of climate change and increasing weather variability, factors that may further alter tidal dynamics, prey distribution and availability, and foraging opportunities for common terns, are important knowledge gaps. Renewed research is required to assess how such environmental changes may influence common tern foraging ecology and the potential impacts of these at population level e.g. breeding success. Studies combining prey availability data and diet studies for different developmental ages at a large spatial scale such as the Dutch Wadden Sea (see e.g., Maathuis *et al.* (2025)), in combination with environmental data, are a solid approach to help address these knowledge gaps.

Over the past decades, significant changes in food availability for large gulls have occurred. Drivers of this reduction include the closure and coverage of open refuse sites and reduced availability of fisheries discards. For instance, in the 1970s, there were over 100 open refuse sites in just three northern Dutch provinces. Fisheries discards likely decreased due to the introduction of discard regulations (although the effects are not fully understood), but also due to fleet reductions and improved catch efficiency. While a reduction in fishing pressure could theoretically increase natural food availability, it may simultaneously reduce the amount of accessible fisheries waste and affect breeding success and population trends. The extent to which current fishing pressure affects prey availability for surface-feeding gulls remains uncertain.

Some knowledge gaps that need to be addressed are more species-specific. The diets of breeding herring gulls and lesser black-backed gulls have only been examined thoroughly in a handful of studies, some of which are relatively old (Spaans 1971; Camphuysen 2013). For the herring gull, all studies have been conducted along the Wadden Sea coast. To obtain a broader impression of Dutch breeding colonies, more diet studies should be executed at colonies in different locations, for instance near cities. Even less is known about the diet of herring gulls that overwinter in the Netherlands. This could potentially be studied by collecting faeces at roosting spots, using DNA analysis. This method could help to better understand the diet of juvenile gulls, about which even less is known.

For the lesser black-backed gull, recent changes in diet that have been observed in several colonies are remarkable. However, the underlying drivers of these temporal dietary changes, including the decline in marine prey and increased reliance on anthropogenic food sources, remain unclear. Moreover, the consequences of these dietary shifts at population level—such as their effects on survival, reproductive success (partly studied in Belgium), and overall colony dynamics—have not been thoroughly investigated.

There is a scarcity of detailed diet studies on great black-backed gulls in the Netherlands, both during the breeding and non-breeding season, leading to reliance on data from other North Sea and Baltic populations. Studying the (few) breeding birds in the Netherlands could shed light on foraging behaviour and diet preferences. Furthermore, faeces from roosting locations could be studied using DNA analysis. At sea, the relative importance of fishery discards versus naturally caught fish in the marine environment in great black-backed gull diet remains unclear. The impact of reduced fisheries discards on diet, foraging behavior, and body condition over time requires further investigation, especially given the recent changes in fishing practices.

All species would benefit from diet studies that use methods such as DNA metabarcoding that enhance the resolution of dietary studies and reduce the bias that is often introduced by other sampling methods. Overall, a more coordinated, multi-colony monitoring approach—including standardised sampling methods and statistical comparisons across years, colonies, and chick age classes—is required to fully understand the drivers of chick diet variation and its implications for chick growth and survival. Many other knowledge gaps remain, such as inter-annual variability in prey size, differences between (freshwater and marine) sites, factors influencing prey size, and the diet of non-breeding and juvenile individuals.

4. WP4: ID 64 – Literature study on seabird demography with a focus on gulls and terns

4.1 Aims and structure

This work package as well as the desk study as a whole aims to improve our knowledge of relationships between the key demographic drivers of bird populations (survival, breeding productivity, settlement) and the at-sea conditions that are important for them. It focuses on the relationships between demography and food availability and food quality, as these are paramount to shaping the carrying capacity of the North Sea for marine birds. This focus is also evident in work packages 2 (foraging areas) and 3 (diets). The underlying idea is that if this type of knowledge can be incorporated in (a series of) ecosystem models, it will become possible to explore the potential consequences of various changes (anthropogenic or autonomous) in the system in spatially explicit scenarios.

WP4 focuses on the gulls and terns among the focal species of this desk study: lesser black-backed gull, European herring gull, great black-backed gull, Sandwich tern and common tern. This emphasis arises from the specific management responsibility of the Netherlands for this group, and from the existence of management potential at national level. The Netherlands hosts nationally and internationally important breeding populations for four of these five species.

Several of these breeding species, however, utilise North Sea resources outside the breeding season as well, so conditions in those parts of the year may also affect their populations. In addition, the Dutch sector of the North Sea provides resources for multiple seabird species that do not breed there but utilise it during migration and/or wintering. The ecosystem-oriented modelling in other MONS projects also requires information on relationships between food availability and bird demography for these species, and consequently they are mentioned in this work package.

This chapter summarises the results for WP4, which are described more extensively in the report by Schekkerman *et al.* (2025), that forms an annex to this report. WP4 covered two main topics: a summarising overview of measured values of key demographic parameters of the focal seabird species, and a review of published studies on the relationships between these parameters and food resources. Species that have breeding populations in the Netherlands are discussed in more detail than non-breeding species. The black-legged kittiwake is included here as a non-breeding species, although it does breed in small numbers on offshore platforms in the Dutch sector.

This chapter is structured as follows. After an introduction outlining the key choices and concepts used, the methods applied in the review are briefly described, as well as the digital annexes that were produced during this project. The results of the review are then summarised by species, starting with the breeding gulls and terns. These accounts present: (1) a summary description of demographic studies on the species, with emphasis on studies in the Netherlands; (2) summary of available estimates of key demographic variables, and (3) a summary of published studies on the relationship between demographic variables and food resources. In the final paragraph, the findings from chapters 4-5 are summarised and existing gaps discussed, as well as avenues to fill these gaps through future field studies.

4.2 Methods

4.2.1 Key demographic parameters and concepts

The demography of a species or population encompasses many different aspects, and a multitude of parameters can be thought of that describe or influence these aspects. This makes summarising the literature on relationships between feeding conditions and demography a complicated task, unless a clear focus is chosen. The current study is part of the MONS programme, through which a suite of models will be developed that feed into each other to explore how changes in any trophic level in the ecosystem affect the other levels. In this review, we focus on the key parameters of matrix population models (Caswell 2025), the type of models most often used to describe the effects of environmental factors on populations of animals, including seabirds (e.g. Potiek *et al.* 2019; Soudijn *et al.* 2025). In such models the size and development of a population is ultimately determined by a balance between reproduction and mortality (survival). Movement - immigration and emigration - can be considered an additional driving process, but this depends on the scale of the population in question. We have largely ignored movement parameters in this review, but the possibility that net immigration or emigration occurs should be kept in mind in model studies. In this report we focus on the following key parameters describing reproduction and mortality:

1. **Age-specific annual survival probabilities**. Survival is the complement of (1 minus) mortality and is described separately for three age classes, '**first-year**' (from fledging [or age at ringing] to one year old), '**immature**' (second year and possibly a few additional years, depending on the species), and '**adult**' (the age at which birds become physically capable of reproduction or actually start breeding). In this report, survival is quantified as an annual probability (that a bird alive at a given time is still alive one year later) unless stated otherwise. This convention also applies when survival is reported for age categories including more than one year; e.g. when S=0.65 for age group "1st+2nd yr", the actual probability to survive from fledging to age two is 0.65^2=0.42.

2. **Breeding productivity**. In this review, breeding productivity is defined as the average number of fledged young produced per breeding pair (fy/pr) per year. In practice, the number of young fledged per nest (breeding attempt) is often used as a proxy, although this will lead to some underestimation of productivity if clutch losses are followed by renesting within the same season. As with survival, we disregard any age-related variation in the productivity of established breeders. This metric is sometimes also referred to as 'breeding success'.

3. **Age at recruitment** – This is the age at which birds make their first breeding attempt involving the production of a clutch. In population models this age is often included as a fixed value, but in reality it usually varies among individuals and can also be influenced by local conditions. Matrix population models can either use a fixed mean age at recruitment or incorporate information on its distri-bution for greater accuracy.

4. **Breeding propensity**. Even after recruiting as breeders, birds may not initiate a breeding attempt every year, and such 'skipping' reduces the mean reproductive output of adults in the population compared to that measured in breeding pairs. Hence, it is important to quantify this 'skipping' using a parameter called breeding propensity, the probability that an adult individual will breed in any given year.

The summaries of estimates of the key demographic parameters extracted from published literature include mean values reported by studies obtained at different sites or in different time periods, as well as the separate year-estimates in single studies or summaries (standard deviations) of these. We report the means and two different measures of variability for these estimates, which can be used in different ways in matrix population models:

SD_e – the 'standard deviation of estimates' refers to the variability among mean values obtained from studies conducted at different sites or averaged over different time periods at a site. Demographic parameters are rarely fixed within a species; even mean values can vary across sites and periods, and SD_e describes this variation. When parameterising a population model for a population different from the one where estimates were obtained - or for birds of unknown or mixed origin - it is uncertain which estimate best describes the model population. This uncertainty can be addressed by running multiple simulations, each drawing parameter values from a probability distri-bution described by the mean and SD_e of each parameter. These values are then used to construct the projection matrix, which remains constant within each run while iterating over all time steps.

SD_p – the 'standard deviation of the environmental (time) process' is used in stochastic population modelling to represent variability in parameter values caused by stochastic (random) environmental fluctuations over time. This is addressed in matrix models by resampling from probability distributions defined by the mean and SD_p of each parameter at every time step. Multiple studies often reported levels of annual variability. For use in 'general' models, such as those for different or unknown populations, we report the mean of these values as SD_p.

4.2.2 Breeding colonies in The Netherlands

Tables listing information breeding colonies of gulls and terns in The Netherlands are contained in the digital annexes (excel worksheet files) of the WP4 report. This information is derived from Sovon's databases on colonial breeding birds and coastal bird breeding success. They include breeding numbers in a recent ten-year period, breeding productivity in those years (if available), and notes on ringing and research activities at the sites, obtained from publications and interviews with active researchers.

4.2.3 Literature review

We conducted a literature search for Dutch-and English-language publications (including 'grey' literature) on demography and food relationships in the focal species. International literature was searched with Google Scholar, Web of Science, and an AI engine, using as key words:

For demographic parameters: <or>: Breeding success, breeding productivity, breeding output, reproduction, reproductive success, breeding propensity, floaters, skipping/skipped breeding, survival, survivorship
For food relationships: <or>: Food availability, food quantity, food quality, food abundance, diet quality, provisioning, prey abundance, prey availability, prey quality, prey quantity

Relevant publications were downloaded, with the main focus on material from the North Sea and wider Atlantic region. Data on key demographic parameters and summary lines on food relationships were extracted and entered into excel worksheets (available as digital annexes to the WP4 report). In the species' accounts about key demographic parameters in the WP4 report, the data extracted from published literature and breeding productivity data from Dutch breeding colonies are summarised in tables. These contain mean values by region of recent Dutch productivity data, augmented by results from a selection of previous or long-term studies in the Netherlands, and from a selection of reviews and long-term studies in other countries. They do not contain all the information/studies available in the excel annexes but provide a representative summary. In the WP4 report, the data in these tables are summarised as the mean of all estimates for the key demographic parameter in question, together with the associated SD_e and mean SD_p. In the current chapter, all information on the key demographic parameters is again consolidated into a single table.

4.3 Results

4.3.1 Studies on demography of breeding seabird species

4.3.1.1 General monitoring of demography

Demographic information on gulls and terns breeding in the Netherlands has been collected for many decades, in the generic form of estimates of reproductive output in breeding colonies and ringing of birds, yielding recoveries and recaptures that inform about survival and movements. Currently, systematic monitoring of breeding productivity of terns and gulls takes place in both the south-western Delta Area and in the Wadden Sea, being the two main breeding regions for seabirds and coastal birds in The Netherlands. The monitoring focuses primarily on estimating the number of fledged young per breeding pair (fy/pr). Methods vary between sites, from 'quick and crude' counts of the number of large chicks present in a colony, to erecting enclosures around a sample of nests so that the survival, growth and condition of (ringed) chicks can be followed post-hatching. In the Delta Area, this work was initiated in the early 1990s, using methods that can be combined with surveys of population size with limited extra effort. Since 2020 this has been fully included in the MWTL programme. Results are reported annually (e.g. Lilipaly & Sluijter 2024). In the Wadden Sea region, breeding productivity of coastal breeding birds is monitored under the 'Reproductie-meetnet Waddenzee', which started in 2004 and since 2010 is part of the Trilateral Monitoring and Assessment Programme (TMAP) in the international Wadden Sea. In TMAP, the breeding success of 10 bird species representative of habitats and food groups in the international Wadden Sea is monitored (Koffijberg *et al.* 2011). Of these species, lesser black-backed and herring gull and Sandwich, common and arctic tern depend mainly or partly on the North Sea for their food supply. The annual results are reported at approximately three-year intervals (e.g. Koffijberg *et al.* 2021).

Information on the survival of birds is usually obtained through ringing studies, that yield reports of ringed individuals found dead or re-encountered when still alive. Ringing of birds with numbered metal rings (issued by national ringing centres, e.g. Vogel-trekstation) generally produces dead recoveries, often reported by the general public, but can also yield live recaptures or resightings, often by dedicated researchers of the species. By using individual colour-marks that can be read in the field, the number of reports can be greatly increased and the study area expanded, leading to better estimates. Ringing of gulls and terns has a long history in the Netherlands, and a total of almost 438,000 individuals of the five breeding gull and tern species covered in this study were ringed in the Netherlands between 1911 and 2023, ranging from 423 great black-backed gulls to 182,000 common terns. This has yielded 77,200 reported recoveries and re-encounters (Vogeltrekstation 2023). Historically, mostly chicks of the focal species were ringed, but few older birds. Since the 1980s, however, adult gulls have been ringed with individual colour-rings in addition to metal rings in several colonies, and more recently colour-ringing programmes have also been established for tern species.

4.3.1.2 Dedicated studies

In the Netherlands various demographic studies on **lesser black-backed gulls** are ongoing, usually combined with studies on herring gull as these species often form mixed colonies. The most detailed and wide-ranging study has been ongoing since 2006 in the Texel dunes by Camphuysen and coworkers (NIOZ). This study encompasses reproductive success, annual survival, recruit-ment, diet and spatial foraging behaviour, and has led to two PhD theses and numerous publications. Earlier studies in the Wadden Sea region have been conducted by Spaans and coworkers (IBN-DLO) on Terschelling, mainly aimed at disentangling the effects of (seasonal) food limitation, parental quality and (intraspecific) predation on breeding productivity. Along the 'Holland Coast' between Den Helder and Hoek van Holland, the Forteiland ('fortress island') at IJmuiden supports one of the largest remaining gull colonies. Here, breeding numbers and reproductive success have been monitored by volunteer researchers since 2008, and adults and chicks are also colour-ringed. Since 2019, the movements of individual gulls have also been GPS-tracked from this colony. In the SW Delta Area, colour-ringing of large gulls has been ongoing for several decades, by Buijs Eco Consult and others. Resighting data have been used to study foraging movements and to obtain survival estimates. In recent years, studies on large gulls in the Delta Area have been intensified within the framework of offshore wind energy development (Wozep programme), combining tracking of gulls with the collection of breeding data. This work is being carried out by researchers from INBO, Waardenburg Ecology and Buijs EcoConsult. In the nearby Voorhaven at Zeebrugge in Belgium, breeding lesser black-backed and herring gulls have been studied since 1999, when a colour-ringing project was initiated. From at least 2010 onwards, detailed studies into breeding ecology and life-history have been conducted by researchers from INBO. Outside the Netherlands, lesser black-backed (and herring) gulls have been studied at multiple sites around the North Sea since the 1960s and 1970s. In Britain and Ireland, the size and breeding productivity of gull populations have been monitored under the Seabird Monitoring Programme (SMP) since 1986. At four key sites within the programme, additional data are systematically being collected on seabird breeding phenology, diet and adult survival: Isle of May (E Scotland), Fair Isle (Shetland), Canna (W Scotland) and Skomer (Wales). On the German Wadden Sea islands, monitoring of breeding productivity falls under TMAP, and a few colour-ring studies are in place yielding information on survival. In Norway, multiple gull colonies are included in the SEAPOP monitoring programme that has been running since 2005, through which breeding numbers, productivity and adult survival are monitored.

Because they commonly breed together in mixed colonies, demographic studies on **herring gull** are often carried out in combination with studies on lesser black-backed gulls. An early project not mentioned for that species, as it focused specifically on herring gulls, was initiated by A.L. Spaans (IBN-DLO) in 1986-1988. In each of those years c. 100 chicks were colour-ringed in 12-14 colonies spread along the entire Dutch coast. The resulting resightings have yielded extensive information on seasonal move-ments and age-dependent and spatial patterns in survival.

The Dutch population of **great black-backed gull**, which is no more than 120 pairs, breed primarily (semi) solitarily. Elsewhere, the species also exhibits relatively dispersed breeding, often in remote areas where they are not perceived as a nuisance by humans. This likely explains why, to date, very few dedicated studies of this species' ecology have been carried out.

Studies on breeding **Sandwich terns** were initiated by J. Veen in the 1970s, on Griend in the Wadden Sea. Here, in later years, Klaassen and coworkers from the University of Groningen studied the energetics of chick growth, and Stienen and Brenninkmeijer at IBN-DLO investigated food provisioning of chicks and interactions with black-headed gulls. In the Delta Area, breeding success has been monitored since 1987 in the main colonies in Westerschelde and Grevelingen, and at nearby Zeebrugge in Belgium. Nowadays, reproduction is monitored in nearly all Sandwich tern colonies in the Netherlands. Over the past 15 years the scope of studies has been widened to assess the potential impacts of offshore windfarms (Wozep programme), including diet, tracking of tern foraging locations and spatial ecology within and outside the breeding season, as well as their migration. This also led to the initiation of a colour-ringing program in the Delta in 2012 that was later expanded to other colonies. Very intensive (sometimes daily) colour ring-reading at observable colonies has yielded extensive novel information on dispersal, prospecting behaviour, and survival. Outside the Netherlands, breeding productivity and ringing studies are in place at various other localities around the North Sea. In the UK, most Sandwich tern breeding sites are monitored under the Seabird Monitoring Programme. Colonies with long-term data series are situated along the North Norfolk and Suffolk coasts and in NE Scotland (Sands of Forvie). In the German Wadden Sea islands, breeding success has been monitored on Hallig Norderoog.

Demographic information on **common terns** breeding in the Netherlands has been collected for several decades through breeding productivity monitoring programmes and general ringing effort. Generic ringing of common terns in breeding colonies has been ongoing for many decades, and the resulting recovery data have been used to estimate the survival rates of terns from the Wadden Sea region and SW Delta. More recently, common terns have been fitted with engraved colour rings at several locations in all three major breeding regions. At some locations, e.g. the Eems estuary, the IJsselmeer area, Haringvliet, and previously on Griend, annual ringing and ring-reading effort as well as monitoring of breeding success over multiple years amount to relatively comprehensive population studies. In the German Wadden Sea, a detailed long-term study on the population ecology of common terns has been ongoing since 1992 at Wilhelmshaven (Bouwhuis 2025). A combination of field visits, sophisticated monitoring, and identification of visiting birds fitted with a transponder (PIT tag) in early life has led to a unique dataset on breeding performance, survival, recruitment, and other aspects of the terns' life history. Diet has also been studied, and the condition and survival of chicks has been related to regional and local fish stocks. More recently, the research was expanded to outside the breeding season by tracking year-round migration with light-level geolocators. Breeding success and ringing studies have been in place at various other locations around the North Sea, but not to the same level of detail as that achieved at Wilhelmshaven.

4.3.2 Key demographic parameters: summary and information gaps

Table 4-1 presents a summary of the mean values of key demographic parameters for the 12 focal species, along with their associated SD_e and SD_p. These values can be used to parameterise population models for various purposes. The table also highlights where species-specific information is largely lacking (denoted by '?'), and where some data exist but confidence in their accuracy, actuality or representa-tiveness for the species as a whole is lower. In such cases, additional studies or analyses of existing data are needed (denoted by *italic* print).

Common scoter and red-throated diver are the least well-studied of the focal species in this report. Not only are estimates available for just one or two key parameters, but some of these were obtained in regions where few birds breed that migrate to the North Sea. Great black-backed gull is a third species for which few data are available (all parameters other than breeding productivity), and northern fulmar is a fourth (survival of young age classes, age at first breeding and breeding propensity unknown). For the other species, there is generally reliable information on breeding productivity and adult survival. Less is generally known about first year and immature survival, and on (variation in) the age at recruitment. Least well-known is adult breeding propensity: for most species there is limited information on from just one or two locations and/or a few years.

From the viewpoint of under-standing population change, it is particularly important to have reliable estimates of the parameters that have the greatest influence on the species' population dynamics. In population models, this is usually quantified as elasticity, the proportional change of the predicted finite population growth rate (λ) in response to a given proportional change in a parameter. In table 4-2, elasticities are presented for the six key parameters, for herring gull and common guillemot. For birds in general, all the focal species are long-lived with high annual survival, and as is usual in such birds the highest elasticity is associated with the adult survival rate. Fortunately, relatively good data are available for this parameter. Immature survival shows the next highest elasticity, although considerably lower than that for adults. The factual basis for this parameter is relatively weak, but its potential range can be narrowed down using available information on adult and first year survival, as immature survival is typically intermediate or close to that of adults. Elasticities for first year survival, breeding productivity and breeding propensity are lower and almost identical, as they all exert the same quantitative effect on the number of one-year-olds in the population the following year. While extensive data exist on breeding productivity for our focal species, information on first year survival, and particularly on adult breeding propensity, is far more limited. Improving knowledge of these parameters is thus relevant, and slightly more so than for variation in the age at recruitment. The latter is not well documented but has the smallest impact on population development.

Table 4-1 *Summary of key demographic parameters for the focal seabird species in this report. Listed are the means over the selections of studies tabulated in the species accounts, the standard deviation of these estimates (SD_e) and the mean standard deviation of variability between years (SD_p), if available. Values in italic print have a relatively weak data basis and require additional information.*

parameter	lesser black-backed gull avg. SD_e SD_p	European herring gull avg. SD_e SD_p	great black-backed gull avg. SD_e SD_p	Sandwich tern avg. SD_e SD_p
adult survival	0.89 0.03 0.06	0.84 0.04 0.06	*0.86 0.05 ?*	0.91 0.02 0.07
immature survival	*0.87 0.03 0.05*	*0.83 0.06 0.06*	*0.78 0.02 ?*	*0.82 0.06* .
1st-year survival	0.67 0.15 0.09	0.59 0.17 0.08	*0.48 0.13 ?*	0.67 0.14 0.17
age at recruitment	4.5 0.5 ?	4.9 0.6 ?	*5 ? ?*	*3-4(5) ? ?*
breeding propensity	*0.62 0.16 ?*	*0.71 0.12 ?*	*?*	*?*
breeding productivity	0.50 0.14 0.30	0.73 0.38 0.30	1.05 0.40 0.41	0.56 0.11 0.26

parameter	common tern avg. SD_e SD_p	black-legged kittiwake avg. SD_e SD_p	common guillemot avg. SD_e SD_p	razorbill avg. SD_e SD_p
adult survival	0.88 0.03 0.04	0.83 0.04 0.08	0.94 0.03 0.03	0.91 0.01 0.07
immature survival	0.80 0.13 0.09	*0.78 0.07 ?*	*0.83 0.04 ?*	0.87 0.06 ?
1st-year survival	0.65 0.11 0.08	*0.61 0.10 ?*	*0.56 0.06 0.20*	*0.64 0.11 ?*
age at recruitment	3.4 0.8 ?	4.3 0.4 ?	*5-6*	*4-5*
breeding propensity	*0.92 ? ?*	*0.76 0.08 0.14*	*0.93 ? 0.03*	*0.97 ? ?*
breeding productivity	0.67 0.35 0.50	0.64 0.19 0.29	0.62 0.14 0.15	0.54 0.11 0.19

parameter	northern fulmar avg. SD_e SD_p	northern gannet avg. SD_e SD_p	common scoter avg. SD_e SD_p	red-throated diver avg. SD_e SD_p
adult survival	0.93 0.01 0.06	0.93 0.01 0.04	*0.78 ? ?*	*0.84 ? ?*
immature survival	*(0.90) ? ?*	0.90 0.04 ?	*?*	*0.62 ? ?*
1st-year survival	*0.44 0.03 ?*	0.54 0.10 ?	*?*	*0.60 ? ?*
age at recruitment	*9 (6-12)*	*5(4-6)*	*3 ? ?*	*(3) ? ?*
breeding propensity	*?*	*?*	*?*	*?*
breeding productivity	0.40 0.05 0.12	0.69 0.06 0.09	1.84 ? 1.18	0.58 0.14 0.17

Table 4-2 *Sensitivity (elasticity) of the predicted population growth rate to key demographic parameters in matrix population models, for herring gull and common guillemot. The parameter elasticities were calculated by decreasing (one by one) the base values (Schekkerman et al. 2025) by 10% (except for age at recruitment +10%). The growth rate (λ) predicted by the base model is given in the last column.*

species	breeding productivity	1st-year survival	immature survival	adult survival	recruit-ment age	breeding propensity	(λ base model)
herring gull	0.07	0.08	0.21	0.69	0.04	0.06	(0.936)
common guillemot	0.06	0.06	0.18	0.76	0.02	0.06	(1.020)

Although survival is the parameter with the greatest effect on the long-term population growth rate in these seabirds, breeding productivity is also influential, particularly for shorter-term fluctuations, because it shows much greater between-year variability than survival (Figure 4-1a). Among the species considered in this study, annual variability in breeding success is particularly large in the common tern and the lesser black-backed gull, and smallest in the common guillemot and especially the northern gannet. More generally, the tern and gull species (with breeding population in The Netherlands) show more annual variability in breeding success than the cliff-nesting seabirds that overwinter in the southern North Sea. This can probably be explained by the slightly 'faster' life history strategies of the gulls and terns, with slightly lower survival rates and age at recruitment and higher mean clutch size. Life-history theory predicts that long-lived birds should 'defend' their survival at the cost of breeding success when conditions are unfavourable. Birds that have many opportunities (seasons) to reproduce during their lives should better skip a breeding season or allow a chick to die when food is scarce than work hard in the current year and thereby jeopardise their future options to breed. This 'rule' can explain for instance why in the common tern population at Wilhelmshaven breeding productivity was affected negatively by low herring abundance, but adult survival was not (Bouwhuis 2025). Even though all the focal species in this study are long-lived birds, auks, fulmars and gannets are slightly more so than gulls. Among the 10 species for which estimates are available, there is a tendency for both the mean and the relative annual variability of breeding productivity to be lower in species with a higher mean adult survival rate (Figure 4-1b). Although these effects were not statistically significant, it makes sense that as adults have more breeding years available as they need to produce fewer young in each of those to replace themselves in the population. Why the breeding output would be less variable over time in the longer-living species in our sample is less straightforward, however.

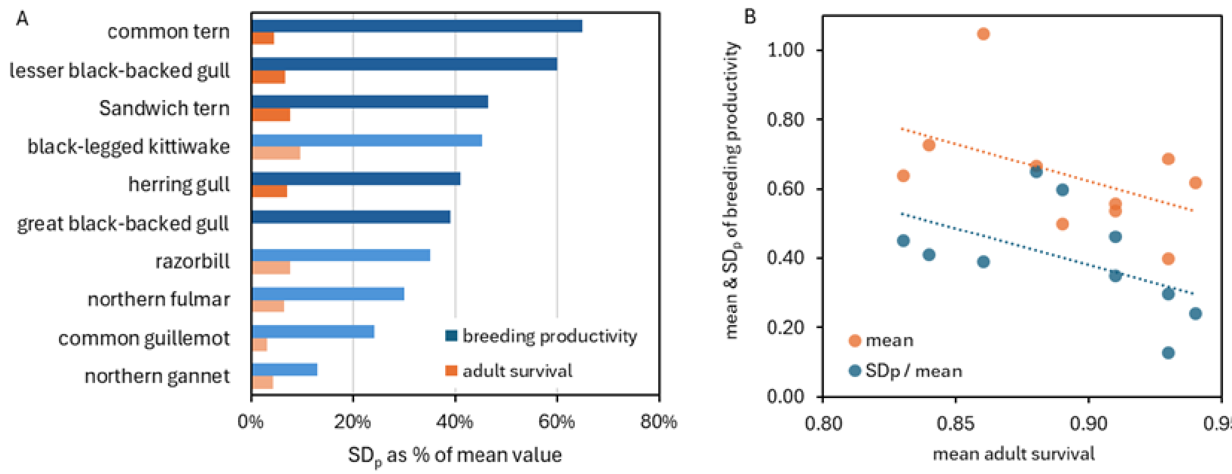

Figure 4-1 *Summary comparison of variation in breeding productivity and survival among the focal seabird species of this study. A: Relative interannual variability (SD_p divided by the mean value) by species, ordered from largest to smallest relative variability in productivity. (Bars with darker colour denote species breeding in The Netherlands.) B: There is a tendency for both the mean and the relative annual variability of breeding productivity to be lower in species with a higher mean adult survival rate, but this is not statistically significant (P = 0.16 and 0.12, respectively).*

Generally, very little information is available in published literature about the amount of variability in age at recruitment and breeding propensity and first-year survival, even though the latter two exert a similarly large influence on the population growth rate as breeding productivity. It is likely that 'hidden' information on age at recruitment is already contained in multiple datasets of breeding studies using ringed birds, but has not yet been analysed or reported on, and therefore represents 'low-hanging fruit'. Similarly, existing information on first year survival will be embedded in datasets from colour-ring studies that have not yet been analysed for this purpose. However, challenges remain due to natal dispersal and the tendency of the youngest age classes of some species to winter in remote areas. If such data cannot be extracted, dedicated colour-ringing of near-fledged chicks across multiple colonies could be initiated to fill this gap, complemented by a network of observers. In contrast, there is probably less 'hidden information' on breeding propensity (skipping of breeding seasons), which is a difficult parameter to measure unless breeding site fidelity is very high and all marked birds breeding at a location can be observed. A promising approach is to use bird-borne devices to track individuals over multiple years, enabling assessment of breeding status regardless of their location. In particular, light-level storage tags ('geolocators') allow incubation behaviour to be inferred from light-dark schedules (van Bemmelen *et al.* 2024) and are relatively low cost, making them feasible for deployment on large samples of birds.

4.3.3 Relationships between demographic rates and food abundance

Detailed results of our review of published studies on the dependence of seabird demographic variables on food resources are discussed in the WP4 report (which see for literature references). Here we present a summary focusing on the availability (or absence) of studies that describe such relationships, particularly those offering quantitative insights that are useful for modelling.

For **lesser black-backed gull** and **herring gull,** studies on the dependency of breeding success on food resources have been conducted in The Netherlands as well as elsewhere, but have not resulted in quantitative relationships that could be incorporated directly into population models. This is largely due to the difficulty in measuring food availability in these generalist foragers with a wide prey spectrum. In the lesser black-backed gull its high frequency of foraging behind fishing vessels may provide an avenue to explore such a relationship further; chick growth rates and fledgling mass have been shown to be correlated with fishing fleet activity. Growth of herring gulls on Texel showed a similar correlation, nevertheless herring gulls seem somewhat less sensitive to discard availability than lesser black-backed gulls. We found no studies relating survival rates, age at recruitment or breeding propensity of these two gull species to food abundance indices.

All published studies we found on relationships between demographic rates of **Sandwich tern** and food resources were carried out in The Netherlands, and all pertain to reproduction. No studies have examined factors affecting adult (or juvenile) survival, possibly because good survival estimates have only recently become available. In several of the studies addressing breeding productivity, this was related to observations of prey delivery to chicks, in the absence of direct measurements of fish abundance near the breeding location. At a fairly large spatial scale, abundance of key prey species (herring/sprat) seems to affect settling decisions of adults more strongly than local breeding productivity, in this species with low adult breeding site fidelity.

Published studies on **common tern**, particularly long-term research conducted at Wilhelmshaven in Germany, have found clear relationships between annual variation in common tern breeding productivity and the abundance of certain energy-rich key fish species, particularly herring, sprat and smelt. There is no indication that food resources in the breeding season have a notable influence on annual (adult) survival, but survival has been associated with variation in primary productivity in their West African wintering range. Although sufficient data on age at recruitment and adult breeding propensity are available from this study, these have not yet been analysed comprehensively in relation to food abundance indices.

Relationships between demographic parameters of **black-legged kittiwake** and food resources have been studied extensively in the NW part of the North Sea (E Scotland and Shetland), in the light of strong reductions of seabird breeding productivity since the 1990s, which were linked to reduced availability of sandeel, the main prey of several seabird species breeding in this region. These studies have considered the effects of sandeel availability on breeding success as well as survival. Studies have also been published in Norway, where kittiwakes have strongly declined in the Norwegian Sea and Barentsz Sea regions. As a result, an extensive body of data is available on the dependency of kitiwake breeding productivity on the regional abundance of forage fish (sandeel, herring, capelin). Adult survival has been linked to prey abundance in both the breeding (North Sea and Barentsz Sea; sandeel and capelin) and wintering regions (NW Atlantic; sea butterflies). No data are available on the dependency of first-year survival, breeding propensity or age at recruitment on food stocks.

Published studies on the relationships between **common guillemot** breeding productivity and variation in food resources paint a mixed picture; some found clear effects while others did not. Published estimates of both breeding productivity and adult survival in this species show relatively low variability between years compared to most of the other focal species in this report. This might suggest that guillemots are relatively flexible in coping with fluctuations in prey species availability. To a lesser extent this might also apply to **razorbill**, but far fewer studies on this species are available than for guillemots.

The only published study retrieved on **northern fulmar** was the multi-species study by Cury *et al.* (2011), who reported that breeding productivity of fulmars in Shetland correlated with regional sandeel stocks, particularly in the lower 30% of the range in annual stock sizes.

The low annual variation in breeding productivity of **northern gannet** might suggest that northern gannets can cope relatively well with variations in abundance of certain prey species. Published studies have yielded some support for this idea, but it has been cautioned that adult gannets may not be able to maintain high reproductive success when low prey availability requires further increases in foraging effort, and effects of mackerel abundance on breeding productivity have been observed in Canada.

For three of our focal species, i.e. **common scoter**, **red-throated diver** and **great black-backed gull**, we have found no published studies on demography-food relationships.

The results are summarised in tables 4-3 and 4-4. Table 4-3 provides a quick visual assessment of the availability of information per bird species and parameter. Ideally, all cells in the table would have an 'A', indicating that quantitative relationships are known between the parameters and measures of food abundance. The actual situation is obviously far from ideal: for most species, information on food relationships exists only for breeding productivity. Data on the dependence of adult survival on food resources is available for about half of the species, but in several cases this pertains to studies in populations that do not or rarely visit the North Sea, limiting their representativeness. For the other key parameters, almost no information is available. A further clear pattern is that the great majority of food-demography studies have focused on food resources available in the breeding season and breeding areas, rather than in migratory staging and wintering regions.

Table 4-3 *Summary of availability of published studies on relationships between seabird key demographic variables of seabird species and abundance of food resources. Symbols indicate the nature and quality of information available. 'A' denotes that quantitative relationships with key demographic parameters have been reported, 'B' that the available information is comparative only or pertains to proxies for the key parameter; () denote that available studies may have less relevance for North Sea populations; '-' denotes that no studies were found. Bold print indicates that studies in The Netherlands or Belgium are available.*

species	breeding productivity	adult survival	immature survival	breeding propensity	age at recruitment	population size/growth
lesser black-backed gull	**B**	-	-	-	-	-
European herring gull	**B**	-	-	-	-	-
great black-backed gull	-	-	-	-	-	-
Sandwich tern	**B(A)**	-	**B**	-	-	**A**
common tern	A	A(o)	B	-	-	-
blacklegged kittiwake	A	A	-	-	-	A
common scoter	(B)	-	-	-	-	-
red-throated diver	-	-	-	-	-	-
common guillemot	A	(A)	-	-	-	A
razorbill	A	(A)	-	-	-	(A)
northern fulmar	A	-	-	-	-	-
northern gannet	(A)	-	-	-	-	-

From a modelling perspective the situation may be slightly less grave than suggested by table 4-3, because in our long-lived focal seabird species, adult survival shows much less variability than breeding productivity (see above, Figure 4-1). This means that in the absence of information on survival, a model that uses a known productivity-food relationship but assumes constant survival may in many cases produce reasonable results. However, at some point along the food availability axis, adult birds will no longer be able to uphold their survival, and then this has large consequences for the population growth rate (high elasticity value), so this assumption comes with a risk.

Table 4-4 summarises the use of different measures of food resources in the reviewed studies. In the great majority, bird demography was related to fish data from general surveys conducted (usually annually) over expensive time-series in extensive sea areas, such as those coordinated by ICES. Their overlap in space and time with the foraging distribution and breeding seasons of the birds varies among the studies concerned. Only very few studies were based on targeted survey effort within the known foraging ranges of the focal bird species. The second-most used method was to use the composition of chick diet as a proxy for resource abundance. This assumes that variation in diet composition reflects variation in the availability of one or two preferred prey types, but the strength and shape of these relationships remain unknown. On the other hand, this metric is likely to reflect the conditions encountered in the foraging area of the birds at the time they are there. Other metrics have been used less often (Table 4-4)

Table 4-4 *Summary of methods/metrics used to quantify availability of forage fish in the reviewed studies relating demography of seabirds to food resources. Numbers in the cells are the number of study-parameter combinations mentioned in each species' review paragraph that have used the relevant metric (i.e. when a study relates both breeding productivity and survival to food resources it is counted as 2).*

species	lesser b-b gull	herring gull	Sandwich tern	common tern	kittiwake	guillemot	razorbill	fulmar	gannet	total
experimental food provisioning	3	.	.	.	.	.	.	.	.	3
composition of food delivered to chicks	2	4	2	2	1	2	1		1	15
rate of food delivery to chicks	.	.	1	.	.	1	.	.	1	3
presence-absence (discarding ships, refuse tip)	2	3	.	.	.	.	.	.	.	5
open vs closed fishery, or fishery effort	.	.	.	1	3	2	2	.	1	9
fish monitoring surveys, large spatial scale	1	.	1	2	11	10	6	1	3	35
targeted fish surveys, in bird foraging area	.	.	.	1	.	.	.	.	.	1
landings from commercial fishery	.	1	.	1	.	.	.	.	.	2
primary productivity metrics (chlorophyll)	.	.	.	1	.	.	.	.	.	1
total	8	8	4	8	15	15	9	1	6	74

4.3.4 Research needs

To enhance our understanding of the relationships between seabird demography and food availability, the most critical need is for studies that measure multiple demographic rates alongside food abundance within the foraging area of the study population. These measures should span a sufficiently long time series to be able to capture a representative range of environmental (food) conditions. These provide the best basis to describe quantitative dose-effect relationships of the type required by predictive models, but as can be seen in table 27 such studies have been conducted only rarely.

This means that in the same colony or area, breeding productivity must be measured annually, and sufficient birds (colour-)ringed and resighted to be able to estimate survival, as well as collecting data on breeding propensity (using colour-ring resightings or geolocators). Measuring food resources can be an even greater challenge. Some existing standard fish survey programmes can be utilised to obtain a global proxy, but these may not accurately represent food availability at the study location. To be able to measure food availability, the foraging range of the study seabird population must be known, which can be done through tracking birds. Then, ship-based surveys of forage fish within this area can be conducted, or passive methods such as acoustic monitoring (WBATs) can be implemented at representative sites within the area.

4.4 Conclusion/summary

This work package reviewed estimates of key demographic parameters of 12 focal seabird species and examines how their demographic performance relates to the availability and quality of their food resources. The work package concentrated on five species of gulls and tern with breeding populations in The Netherlands while also incorporating information for focal species with non-breeding populations in the southern North Sea.

Existing data on key demographic parameters of the focal species was reviewed: survival in three different life stages, breeding productivity, the age at first breeding and the tendency of adults to skip breeding in some years. The most robust information exists for adult survival and breeding productivity, supported by long-standing colony monitoring and extensive ringing datasets in the Netherlands and surrounding countries. In contrast, juvenile and immature survival rates, recruitment ages, and especially breeding propensity remain poorly documented. Several species —notably great black-backed gull, common scoter, red-throated diver, and fulmar— have particularly large gaps in demographic data.

The review also synthesises what is known about how these demographic rates respond to food conditions. Evidence varies widely among species. Sandwich and common terns show clear links between their breeding success and the availability of small forage fish such as herring, sprat, and smelt. For gulls, some studies indicate relationships between chick growth or productivity and the availability of discards or natural prey, but quantitative links between food supply and survival, recruitment, or skipped breeding are lacking. Kittiwakes provide the best-studied example of food dependency: reduced sandeel availability has been shown repeatedly to depress both breeding productivity and adult survival. For auks, gannets, and fulmars, evidence of food-driven demographic change is weaker or inconsistent, with some of these species exhibiting relatively stable vital rates unless prey levels fall below critical thresholds. For great black-backed gull, common scoter, and red-throated diver no food-demography studies were retrieved at all.

A recurring challenge across the literature is that most studies rely on broad-scale fish stock indices that may not accurately represent the prey conditions seabirds encounter within their local foraging ranges, or on sampling of chick diets which themselves relate to prey abundance in an unknown way. Only a small number of studies incorporate targeted fish surveys in tracking-informed foraging ranges.

The chapter concludes that future progress will profit most from integrated, multi-year research that jointly measures demographic rates and local food availability, ideally guided by tracking data that identify the areas where birds truly forage. Existing ringing datasets also hold untapped potential for estimating recruitment and early survival. Improving how prey distribution and abundance are measured—particularly at the spatial scales relevant to seabirds—is essential if ecosystem models are to capture the real mechanisms linking food conditions to seabird population dynamics.

5. Conclusions and future research

Below are the three core questions posed by MONS regarding knowledge gaps relating to seabirds. The current report has contributed, to the best extent possible, to improve knowledge on the questions below:

1. What are the consequences of the energy and food transitions for the ecological carrying capacity of functional groups of marine and coastal birds (and marine mammals) in the North Sea, expressed in terms of environmental conditions and food availability?
2. Which areas are of key importance to seabirds (both offshore and coastal waters across the international southern North Sea), how do these areas function, and what are their vulnerabilities (i.e. what are the main areas used for foraging and resting)?
3. Which factors—such as food availability, food accessibility, undisturbed resting areas, and connectivity with areas serving other functions—determine the ecological importance of these key areas, and how vulnerable are these factors to the impacts of the energy and food transitions?

This WP5 concludes the project, integrating Work Packages 2 to 4 (5.1), formulating research gaps (5.2) and providing recommendations for future field-based research (5.3). With its focus on the anticipated changes and potential impacts of the energy and food transitions on seabirds, and based on the new insights acquired during this project, WP5 identifies research that will be necessary to adequately address the three core questions posed above.

We believe MONS should prioritise establishing a broad research framework compared to other programmes. This would involve broad-scale temporal and spatial tracking of seabirds using telemetry, collection of diet samples both in breeding colonies and at sea, and monitoring of important demographic parameters - such as breeding success and mortality - through ringing programmes in colonies. This broad framework will, in the short term, help identify correlations between various aspects of seabirds ecology, thereby improving our understanding of the factors and processes that affect populations. However, the time frame of MONS itself (up to 2028) is too short to capture the full extent of environmental variability. Therefore it would be valuable to extend parts of the suggested work beyond 2028, ideally as part of other programmes.

In addition, we offer several suggestions for knowledge development based on existing data relating to forage fish (see also chapter 5.2: knowledge gaps). We further propose that targeted forage fish research is conducted in parallel with seabird studies. This way, MONS could evolve into a comprehensive, overarching research initiative capable of capturing detailed, long-term ecological changes compared to simply counting birds at sea using aerial monitoring.

5.1 Integration of work packages

The knowledge we have gained and the gaps identified are visualised in Figure 5-1. This figure illustrates the integration of three interrelated work packages (WPs) within an ecological research framework focused on seabird foraging and breeding dynamics. **WP2 (Foraging Distribution)** examines when, where, and how seabirds forage, including factors such as prey availability and oceanographic conditions. **WP3 (Diet)** investigates what seabirds eat, how diet varies by age or breeding status, and size selection or quality of prey. **WP4 (Breeding & Demography)** explores how foraging and diet influence breeding success, survival, and population dynamics.

The arrows between the WPs highlight their strong interdependence: foraging distribution is influenced by diet, while both foraging and diet impact breeding outcomes. This integrated approach allows for a more comprehensive understanding of the ecological drivers of seabird populations and informs effective conservation strategies. Based on the integration of the three work packages, we identified knowledge gaps that were evident across all packages. In the formulations of the research plan (Options for future research), we propose future studies that address these gaps, ensuring a coordinated approach to filling critical information needs.

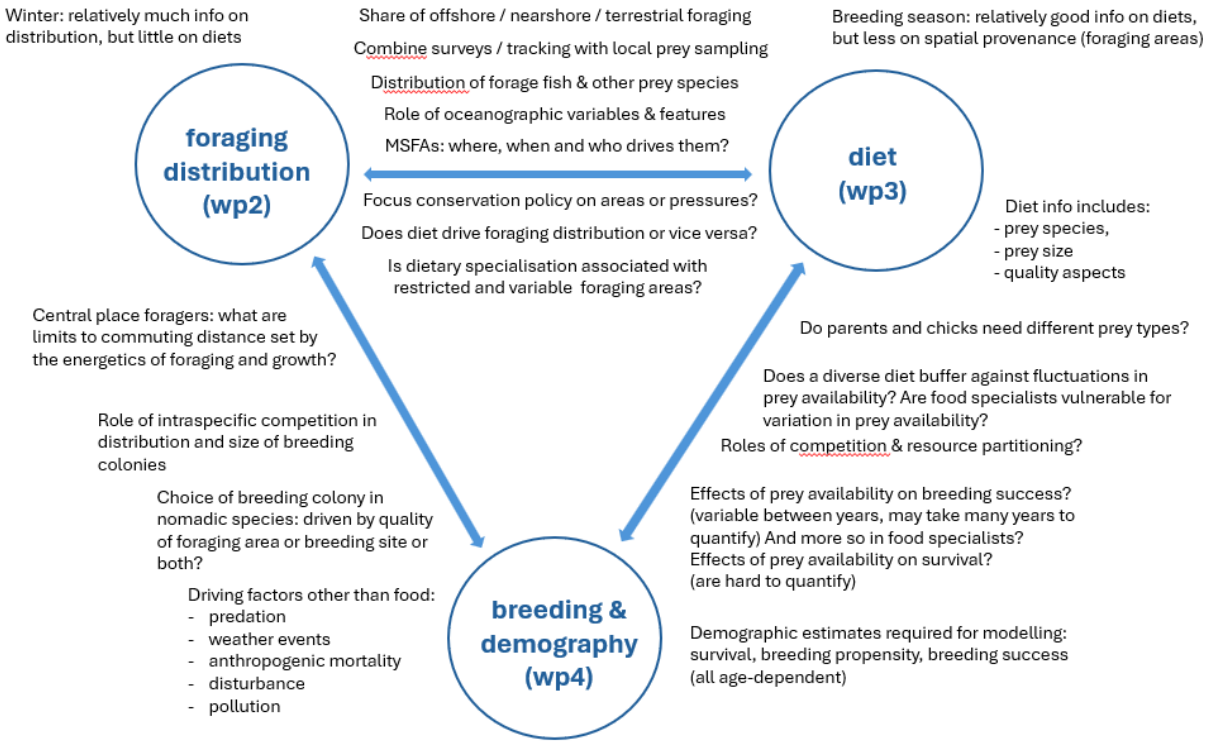

Figure 5-1 *Conceptual view of how the knowledge in the three work packages comes together and overlaps.*

5.2 Knowledge gaps

Below, we provide an overview of the key knowledge gaps based on existing knowledge and unpublished data available to the consortium. These identified gaps form the foundation of the research proposals in chapter 5.3. In addition, some suggestions for research to fill these gaps are made.

We have provided a prioritisation of research needs, taking into account ongoing and upcoming research initiatives. Evidently, the most significant knowledge gaps concern the relationship between changing food availability and the ecology of the focal seabird species. However, some of these gaps are potentially be addressed by other major research programmes. To organise an efficient synergy and cooperation between other relevant MONS-research projects, such as (forage) fish distributions, sufficient time should be allocated to both the fish and seabird projects.

The overall research theme of the three MONS projects relates to the factors that determine seabird foraging distribution based on their position as top predators in the food web. This theme can be broken down into four general categories (Table 5-1): diet studies; (2) energetic needs and foraging costs; (3) forage fish availability and accessibility; (4) seabird populations in the future.

These categories are directly linked to the above-mentioned core questions of this project. Understanding the consequences of the energy and food transition requires specific knowledge about the diet and energetic needs of seabird species. To understand the importance of foraging habitat, and why, knowledge about forage fish availability and the factors that influence their availability and accessibility is missing. This information can help us better understand which at-sea factors are of ecological importance for seabirds, as well as the processes and improvements required for seabird conservation in the future.

For each knowledge gap, detailed topics and research questions are outlined. Table 5-1 describes the knowledge gaps, and whether filling these gaps would require additional desk or field studies (offshore or colony work). We also list, to the best of our knowledge, potential overlap with other programmes.

Table 5-1 *Overview of knowledge gaps and research questions, and whether these can be answered with a desk study, fieldwork offshore and/or fieldwork in a breeding colony.*

	What determines foraging seabird distribution - a synthesis					Potential overlap with other programmes
1	**Diet studies of seabirds**		Desk	Field offshore	Field colony	
a	Gathering specific diet information of seabirds	What are the temporal and spatial differences in food choice?	X	X	X	
b	Factors determining distribution of (foraging) seabirds, and their prey	Which factors determine the distribution of (foraging) seabirds? Prey types and densities that contribute to breeding success		X	X	
2	**Energetic needs and costs of foraging**					
a	Estimating energetic requirements of seabirds	What are the energetic needs of seabirds overall and the costs of foraging in particularduring summer and winter?		X		Wozep
b	Forage fish requirements of seabirds	What is the total forage fish requirement at population level to reach and conserve a favourable conservation status?	X			
3	**Forage fish availability and accessibility**		Desk	Field offshore	Field colony	
a	Factors influencing forage fish availability	Which factors determine forage fish availability for seabirds?	X	X	X	MONS fish
b	Foraging fish distribution and its temporal variability	What is the spatial and temporal variation in forage fish densities and qualities based on the results of existing monitoring in HERAS/MONS?	X			MONS fish, MONS mammals, Wozep, KEC
c	Effects of changing forage fish availability on seabird species	How does variation in forage fish availability affect seabird populations?	X			
d	Effects of climate change on seabird prey	How do increasing water temperatures caused by climate change affect forage fish populations, distribution, nutritive quality and catchability?		X	X	MONS fish, … Project Karen vd Wolfshaar

e	Disturbance by shipping and fishing vessels & offshore windfarms	What is the effect size of disturbance caused by shipping and fishing vessels and vessels sailing to and from offshore windfarms? What are the direct and indirect effects of offshore wind farms on forage fish distribution and consequently on seabirds?		X	X	NWA, Wozep, OSPAR/ MSFD indicator D1C5
f	Spatial and temporal trends in discard availability	What are the temporal and spatial variations in discard availability and which seabird species are affected?		X		
9	Multiple Species Feeding Associations (MSFA)	What are the spatial and temporal patterns in MFSAs? Which seabird species are involved? Which non-bird species? What proportion of diet is obtained through MSFAs in various bird species?		X	(X)	No-regrets
4	**Seabird populations in the future**					
a	Modelling seabird populations in the future under different scenarios		X			MONS projects 20, 30 and 132

1) Diet information

For many species, information on diet, particularly in Dutch waters and during the non-breeding season, is scarce. Up-to-date information on diet would benefit research and management plans for all the target seabird species. As the North Sea environment continues to change due to climate effects and offshore structures, so too do the marine species that inhabit its waters. Examining the diet of seabirds is crucial in understanding whether these species are being forced to adapt their consumption preferences in a changing marine environment. To what extent does diet change between seasons based on temporal changes in prey availability, and what do seabirds consume depending on their location? Knowledge about the diet of non-breeding birds in particular is scarce, and in this report we propose several diet studies. Novel methods to study diets have been developed, such as the use of DNA in faeces, using eDNA to monitor fish abundance, and the application of cameras and AI technology in colony monitoring. However, existing techniques remain valuable, such as gathering and examining the stomachs and intestines of seabirds washed ashore (Leopold *et al*. 2019).

a) Gathering specific diet information per species

- Herring gulls not breeding on the Wadden islands
- Diet of kittiwakes breeding on oil platforms in the southern North Sea
- Diet of Northern gannets in the Netherlands, for instance by gathering stranded individuals on the beach by Waterstaat
- Diet of common terns in the Netherlands; most data originate from Germany.

b) Diet in relation to breeding success

- Diet studies in combination with GPS loggers for breeding birds in the Netherlands, such as terns and gulls, to better determine their foraging areas.
- Diet studies in colonies in relation to prey availability in the surrounding waters, for instance combining GPS tracking with cameras to record prey and forage fish distribution in single-prey loaders like Sandwich terns (Fijn *et al.* 2024).
- Changes in chick/adult diet during and between breeding seasons, coupled with effects on breeding success.

2) Energetic needs and costs of foraging

While some information exists on diet choice and energetic requirements of seabirds (partly presented in this report), details on their year-round energetic needs and the potential effects of fluctuating food conditions are less well understood. This information is needed to better quantify the effects of climate change or anthropogenic disturbances, such as wind farms, in different periods of the year. The effects of disturbance - when food is scarce or its availability decreases due to environmental changes, resulting in increased foraging costs - can be stronger than during periods with favourable foraging conditions. It is therefore important to assess year-round body condition and the relationship between overall energy expenditure and the foraging costs of seabirds combined with food availability.

a) Estimating energetic costs of foraging

Energetic costs can be estimated using data collected by GPS loggers throughout the year, yielding information about the duration of foraging trips and associated bird behaviour (flight and submersion times). This is only possible for birds that are large enough to carry GPS devices and spend the winter in the North Sea. Because setting up tracking studies is challenging, it is advisable to link research to already existing GPS tracking studies (great black-backed gull, lesser black-backed gull, herring gull). Northern gannets have been tracked from UK and German breeding colonies but GPS studies from the Netherlands are lacking (in the absence of breeding colonies). A closer option for Northern gannets is to conduct a study from e.g. Helgoland where there are sufficient breeding pairs. Researchers also started investigating the possibility of using GPS tracking to study common guillemots at sea. Information on body mass and at-sea bird composition should also be collated (e.g. data from post-mortem analyses of acutely oiled, storm-wrecked and other beached birds), or could be collected in the field (trapping of birds at sea) to gain insight into nutrient stores and individuals’ capacity to sustain periods of negative energy balance.

b) Forage fish requirements of seabirds

The 'net' food requirements of seabirds are determined by their energy expenditure for self-maintenance and reproduction, both at individual and population level. However, (by far) not every fish in the sea is available to a foraging bird due to constraints such as capture accessibility and competition – both among seabird species and with other predators, including human fisheries. Consequently, the 'required total availability of forage fish' is a very different metric than the 'individual energy requirement of seabirds translated to fish biomass'. At the population scale, this requirement is larger by several orders of magnitude.

This raises key questions: How much forage fish is required for seabirds to achieve or maintain a favourable conservation status? How does this compare to extraction and collateral mortality by fisheries and other predators, such as large fish and marine mammals? These questions can be addressed by studying population-level responses (specifically demographic processes such as reproduction and survival) under varying levels of resource availability.

3) Forage fish availability and accessibility

Almost all the target seabird species consume fish, particularly forage fish (mostly small shoaling fish species occurring in the pelagic zone). Therefore, questions regarding food availability relate to forage fish stocks in these areas. To date, no specific comprehensive forage fish density maps have been created for seabirds, and this would be a significant step forward in quantifying the spatial distribution of seabirds. Potential factors assumed to influence forage fish abundance are pelagic fisheries (direct), demersal fisheries (indirect: survival of immature fish and habitat quality for sandeels), zooplankton abundance, climate, species interactions and predator-prey relationships. Furthermore, it is unclear whether forage fish in the North Sea are primarily influenced by natural ecosystem dynamics, fishing pressures, or other external factors.

Prey density is likely important for seabird survival and reproduction, but this is only part of the story. Other factors can affect prey availability and accessibility at sea, for example environmental conditions such as turbidity and weather conditions. Furthermore, several factors can affect the catchability and availability of forage fish. For instance, the construction of wind farms might alter stratification (Carpenter *et al.* 2016), climate change might affect the swimming speed of forage fish and thus the success of seabirds foraging on them (Domenici *et al.* 2019).The extent of fisheries, and regulations around discards, affect the availability of food that is normally out of reach for many species (Bicknell *et al.* 2013); disturbance by vessels can scare away species from potentially optimal foraging habitat (Fliessbach *et al.* 2019).

To study forage fish densities and availability, several study directions can be considered:

a) Availability of forage fish & environmental conditions

To address the relationship between environmental conditions and forage fish availability, fieldwork should be conducted in various areas at different times of the year. One option is to use a shoot net (available at WMR). This net can be used to sample the first two metres of the water column: this area is crucial for species that forage on or near the surface. Other monitoring techniques could include hydroacoustics or acoustic sensor buoys (combined with environmental sensor buoys) while simultaneously measuring environmental conditions and (human) changes to the environment over time.

b) Spatial and temporal maps of forage fish

To study changes in forage fish densities in time and space, we recommend using spatially comprehensive surveys (maps) of forage fish distribution, such as those collected through internationally coordinated HERAS monitoring (since 1979, for small pelagic species including herring, sprat, anchovy, sardines) within the ICES framework (Couperus *et al.* 2024). These maps should be supplemented with distribution maps of sandeel and other small species (Parmentier *et al.* 2025; Witbaard *et al.* 2024). Within the consortium, there is sufficient in-house expertise to develop such maps. This work could be integrated into/developed simultaneously with existing MONS projects, such as those focusing on food availability for harbour porpoises. While it is important to develop density maps of forage fish, we also propose research into the various factors that influence the availability and catchability of these fish for target seabird species.

c) Effects of changing forage fish availability on seabird species

The impacts of changes in forage fish availability may vary depending on the diets of different seabird species. For example, specialist species such as common guillemot, razorbill and Northern gannet are highly dependent on specific forage fish (e.g. sandeel, sprat and/or herring). A decline in these prey populations could significantly affect the breeding success and/or chick and adult survival of specialist seabird species that are less able to switch to alternative food sources, especially compared to more generalist feeders (e.g. gulls). The extent to which changes in forage fish availability would affect the spatial distribution/survival of different seabird species could be addressed through prey selectivity index studies that quantify seabird preference for certain forage fish species relative to their availability/abundance in the marine environment. This could be achieved by combining hydroacoustic/trawl surveys to study prey availability/abundance/distribution and simultaneous pellet/regurgitate/stable isotope analysis of seabird diets in nearby colonies. Additionally, GPS tracking could be used to link spatial with prey distribution data.

d) Forage fish and climate change

Over the past 50 years, the North Sea has experienced significant warming. These climate changes have led to increased primary productivity and changes in phytoplankton communities in the southern North Sea. At the same time, zooplankton populations have shifted, with cold-temperate species declining drastically—resulting in a 70% reduction in zooplankton biomass—while warm-temperate species and meroplankton have increased. These ecological shifts have likely affected the productivity of forage fish through changes in the availability of their own food sources (Engelhard *et al.* 2014). Due to their short lifespans and rapid reproduction, forage fish are highly sensitive to climate changes, particularly in relation to plankton availability (Engelhard *et al.* 2014). Potential research avenues could include modelling work as well as monitoring schemes to follow trends in forage fish abundance and behaviour, especially around colonies and when breeding birds are tied to a central place.

e) Displacement by offshore windfarms and disturbance by shipping

Recent studies have reported extensive impact ranges of offshore wind farms in red-throated divers, common guillemots and razorbills (Garthe *et al.* 2023; Grundlehner *et al.* 2025; Peschko *et al.* 2024; Szostek *et al.* 2024). These species, and in particular the common scoter, are also vulnerable to disturbance by shipping traffic including fishing vessels (Fliessbach *et al.* 2019; Kaiser *et al.* 2006; Schwemmer *et al.* 2011). Increasing numbers of offshore wind farms will increase shipping activity by Crew Transport Vessels (CTVs) to and from the wind farms and will also alter vessel movements, particularly those of the fishing industry, with the possibility of increased vessel traffic density around wind farms. This development should be addressed by future KEC6.0 studies, together with more quantitative information on effect size. However, the combined disturbance effect of offshore wind farms and associated vessel traffic remains poorly understood. Consequently, further research is needed to disentangle these drivers. Research should also address the mechanisms of the disturbance caused by the different sources, and in this way can provide indications and supporting evidence for potential species-specific mitigation measures.

Zeyl *et al.* (2023) recently demonstrated that seabirds that catch their prey during underwater pursuit have specifically adapted ears (i.e. middle ear cartilage and bone structures) compared to other seabirds. These adaptations likely enhance underwater hearing, where visual and olfactory cues are likely insufficient for efficient prey capture. This implies that underwater noise could potentially be an underlying mechanism for the marked displacement impacts observed, acting through as-yet-unknown effects on the foraging efficiency of these birds. Such questions are fundamental in nature, yet at the same time can be ecologically applied. Nevertheless, they can only be addressed through robust, long-term scientific research. Work on this topic is currently being further developed in scientific project proposals that will be submitted outside the MONS framework (see Table 5-1).

The construction of offshore wind farms in the (Dutch) North Sea has resulted in changes in fisheries, whereby bottom-trawling fishing vessels are no longer permitted to enter certain areas. This has increased fish abundance and distribution within offshore wind farms, in particular hard substrate-associated demersal species (Methratta & Dardick 2019). Furthermore, turbine bases in the marine environment create an indirect food source (e.g. algae, barnacles, anemones), essentially becoming artificial reefs with large, mobile fauna, such as Crustacea and fish (Langhamer 2012). These structures increase habitat complexity, increasing total biomass and aggregating forage fish and large fish populations. These developments may alter the presence of seabird species that feed on them. This requires monitoring of fish populations within and in the vicinity of wind farms to quantify their spatial and temporal distribution, combined with seabird monitoring to assess to what extent fish aggregations attract seabirds (Methratta 2021).

Discards availability

For many Dutch breeding seabirds and several wintering species, fisheries discards play an important role in their diet (Camphuysen & Garthe 1997; Hüppop & Wurm 2000; Sotillo *et al.* 2014). Discard availability is in decline due to bycatch regulations (discard ban, landing obligations), but more so due to the long-term decline in the number of fishing vessels in many areas (Sherley *et al.* 2020). However, spatial trends in discard availability have not yet been thoroughly examined. One approach would be to calculate the relationship between fishing effort (EMODnet maps; Global Fishing Watch) and average bycatch/discards per fleet type. Identifying trends and changes in bycatch /discards is important as it may highlight that some species are being forced to shift to natural or alternative prey sources, which must be available within protected areas such as Natura 2000 sites. In consultation with the client, we should explore whether this work could be executed within an existing MONS project, for instance MONS projects 28 and 29 on fisheries discards.

f) Multi-species Feeding Associations

Different seabird species forage together, exploiting patchily distributed prey such as sandeel and sprat with positive interactions. These associations allow surface feeders and plunge divers (e.g. gannets, kittiwakes) and pursuit divers (e.g. guillemots, razorbills) to jointly exploit transient prey concentrations. Seabird species that are unable to dive deep depend on processes that bring prey to the surface, where they become available for capture. Such processes can be anthropogenic (e.g. fishery discards) or natural, such as the formation of multi-species feeding associations (MSFAs). In MSFAs, deep-diving predators drive fish to the water's surface, where they become available to surface-feeding seabirds. A frequently observed MSFA is where kittiwakes join foraging razorbills and/or common guillemots.

Understanding consumption patterns and how seabirds partition prey during feeding, as well as spatial overlaps in diet and abundance across species, provides a broader assessment of prey communities in the North Sea. In a recent study, Van Bemmelen *et al.* (2025) analysed ship-based and aerial survey observations and found that kittiwakes preferentially joined razorbills over guillemots, that larger alcid flocks were more likely to be joined by kittiwakes, and that large-scale distributions of kittiwakes overlapped that of both alcids (but slightly more so for razorbill) more so than expected by chance. This exercise can be repeated for all seabirds recorded in the MWTL aerial survey scheme, providing insights into which seabird species co-occur more often than expected by chance. Such a study would become even more powerful by including data (maps) on fish distributions. We could then, for example, determine to what extent kittiwake distribution is explained by alcid presence or forage fish availability.

4) Seabird populations in the future

Modelling studies can use the findings of the fieldwork and desk studies described above to examine and predict the effects of human disturbance such as fisheries and wind farms, and climate change on bird distribution and populations. For example, the effects of offshore wind farms on the prey base can be direct (negative impact of noise, loss of spawning habitat, positive impact of fishery exclusion) or indirect (changes in stratification, phytoplankton abundance). For these modelling studies, specific data on foraging behaviour are required to be able to make better predictions on the potential impacts of human interventions, such as year-round energy expenditure, spatial and temporal changes in catchability of prey, turbidity changes over time, and the effect of turbidity on foraging success. In addition, modelling studies could provide a better understanding of the effects of climate change and help predict changes in forage fish abundance and composition over time. This work could be executed within an existing MONS project, for instance MONS projects 20, 30 and 132 on climate and OWFs on fish productivity.

5.3 Options for future research

The broader knowledge gaps are brought together below in more focused recommendations for future research. Here, we distinguish between a research plan for birds breeding in the Netherlands (H5.3.1) and for birds wintering in the Netherlands (H5.3.2). We added a third research plan to study the effects of discards as these are used by both breeding and wintering birds (H5.3.3). In the focused future recommendations, we also propose a more suitable study for MONS seabirds, and we excluded study proposals/subjects that may be better suited under a different research umbrella or topic. We end the chapter with a rough estimate of time and effort required to execute these research plans (H5.3.4).

5.3.1 Research options for breeding birds

The Netherlands supports important breeding colonies of herring gull, lesser black-backed gull, Sandwich tern and common tern, and the Wadden Sea, Delta region, and various coastal islands and estuaries are internationally recognised (e.g. Natura 2000, EU Birds Directive, Ramsar Convention on Wetlands). Kittiwakes breed on platforms in Dutch waters, but their numbers and ecological importance are as yet unknown. Great black-backed gulls also breed in the country, but in small numbers and are not concentrated in larger colonies. In general, the breeding distribution of these species in the Netherlands is separated into two major regions together harbouring the majority of national populations: the Wadden Sea and the southwestern Delta region. The area in between (Hoek van Holland to Den Helder, denoted here as 'coastal Holland') generally supports fewer breeding seabirds, but with some exceptions. These species are integral components of the Dutch coastal ecosystem, and their population trends serve as key indicators of the overall health of the marine environment.

In this section, we propose field studies on breeding gulls and terns in the Netherlands that integrate the various questions addressed in MONS but will also be relevant and valuable if continued beyond the projected time scope of the MONS programme (in line with the abbreviation 'M' of Monitoring).

Available/existing knowledge and projects relating to breeding seabirds
Information outlined in Work Packages 2-4 concluded that many aspects of the ecology of these seabird species in the Netherlands have been studied to some extent, yet important knowledge gaps remain.

For all species, some information is available on foraging areas during the breeding season, based on aerial counts of birds at sea, colour ring resightings and/or tracking of tagged birds to determine foraging behaviour. The latter method yields the most useful information as it is spatiotemporally the most precise and least prone to biases in habitat coverage and observer effort. Some tracking studies have been conducted on all the species mentioned, but coverage has been uneven with respect to the different regions of the Netherlands. Lesser black-backed and herring gulls have been tracked from colonies in the SW Delta and Western Wadden Sea (Texel), but less extensively from Wadden Sea islands further east or along the 'Holland coast' (except for lesser black-backed gulls breeding at IJmuiden). Sandwich terns have been tracked mainly from colonies in the Delta area, while tracking of common terns has been less extensive with an emphasis on the Wadden Sea region (mainly within the Wadden Sea itself, although these birds frequently forage in the tidal deltas between the main islands). Diet during the breeding season has also been studied in all species except great black-backed gull, but with large differences in extent between species (least extensive in common tern), geographical regions, and stages of the breeding cycle.

For all species, information exists on breeding success from the two major regions. In the SW Delta this mainly stems from monitoring work by Delta Milieuprojecten financed under the MSFD (KRM); in the Wadden Sea area this work falls mainly under the Trilateral Monitoring and Assessment Program (TMAP). TMAP covers a subsample of all colonies in the Wadden Sea (particularly in gulls) but does not include the great black-backed gull. In the SW Delta, breeding success is often quantified in relatively crude classes due to time constraints. Generally, it is not always possible to measure breeding output precisely, limiting the potential to establish the effects of fluctuations in environmental conditions such as food availability.

Similarly, some information is available on survival rates for Dutch breeding populations of all the target species except great black-backed gull. Extensive colour-ringing programmes are already in place for herring and lesser black-backed gull and sandwich tern populations, and data from these programmes have been analysed to estimate annual survival rates. In common terns, a colour-ring programme was established more recently, and existing survival estimates have mainly relied on recoveries of metal rings across the Netherlands. For all species, these estimates can still be improved, particularly in terms of precision, timeliness and potential geographical variation) by incorporating the most recent resighting data and conducting a joint analysis of all available data.

While at least some data exist on most aspects of the ecology and demography of the focal breeding seabird species in the Netherlands, one main gap from in relation to modelling under the MONS programme is that different topics have usually been studied separately in various colonies/regions and years for any given species. **What is still lacking are studies in which all these aspects are studied synchronously within the same colony over a period of several years, while simultaneously collecting data on food availability.** Through these kinds of studies it will be possible to obtain a comprehensive understanding of how variations in food availability influence the demographic performance of breeding populations. These dependencies form a key component of the 'model train' envisaged in MONS.

Choice of study species

Of the five seabird species breeding along the Dutch coast, herring gull and great black-backed gull are the least dependent on food resources gathered in the North Sea during the breeding season. Results of tracking and diet studies suggest that herring gull occupies an almost strictly coastal niche during this period, feeding mainly in the intertidal zone (tidal flats, dikes and breakwaters) and inland (cities, landfills), but rarely foraging further out at sea. Though less well-known, great black-backed gulls also appear to retrieve most of their food from similar areas including fresh and tidal waterbodies in the SW Delta. Both species are much more dependent on North Sea food resources outside the breeding season, particularly wintering migrant populations. Moreover, the low numbers and dispersed breeding distribution of great black-backed gulls in the Netherlands prohibit intensive studies with appropriate sample sizes.

We therefore propose to limit these comprehensive field studies to lesser black-backed gull, Sandwich tern and common tern. These three species represent a range in prey choice, foraging ecology, dependence on fisheries discards (mainly lesser black-backed gull), and pelagic vs. coastal feeding distribution. In addition it would be valuable to establish a similar study on kittiwakes breeding in the Dutch North Sea (since few studies have been conducted on kittiwakes breeding on offshore platforms), although we acknowledge that this will present greater logistical challenges than studies of onshore-breeding species.

Outline of proposed (field) research on breeding seabirds

To help fill the main knowledge gaps identified above, we propose to establish a series of comprehensive studies in a limited number of Dutch breeding colonies/regions of each species in the coming years. Each of these field studies should include the following activities/topics:

- Colony work on diet and breeding success, and colour ringing to measure survival.
- GPS tracking of adults in various phases of the breeding cycle (where possible combined with identification of prey brought to chicks).
- Quantification of at-sea food availability through dedicated surveys.

The components of these studies are outlined in more detail below:

Studying breeding populations

For the lesser black-backed gull, Sandwich tern and common tern, monitoring of breeding populations should include quantifying breeding populations, colour ringing chicks and adults, and estimating breeding success https://www.waddensea-worldheritage.org/trilateral-monitoring-and-assessment-programme-tmap. Long-term assessment of breeding populations provides essential data on population size, dynamics, and trends, whereby declines, expansions, or shifts in distribution can be detected. Sandwich and common terns are highly sensitive to environmental changes and anthropogenic disturbance, hence changes in food availability can impact breeding success or colony size. Populations of the lesser black-backed gull have fluctuated in the Netherlands over recent decades, possibly linked to changes in fisheries discards, landfill policies, and climate-driven shifts in prey availability (Camphuysen 2013).

Quantifying breeding success is a crucial component in understanding population viability. Poor breeding success over multiple seasons can signal underlying issues such as food scarcity. Colour ringing allows researchers to track individuals across years and geographic locations without the need to recapture birds, providing essential data on survival, dispersal, migration routes, site fidelity, and age at first breeding (e.g. Schekkerman *et al.* 2021). The importance of this work is amplified in the context of climate change and other external pressures, e.g. offshore wind developments in the North Sea.

Geographical scope

Comprehensive studies of the kind proposed here are not possible in many colonies, for practical and financial reasons. It is, however, important to establish studies in at least one colony/area in both the main 'ecological regions' SW Delta and Wadden Sea, as habitat distribution and environmental conditions likely differ in important ways between these regions.

It would also be valuable to study all species in the intermediate region of 'coastal Holland', again because of its contrasting environmental conditions, however very few colonies/breeding sites of the focal species in this region are amenable to intensive study. The single most important coastal breeding concentration of terns near Camperduin has not been occupied by Sandwich terns in recent years, and only by limited numbers of common terns. Most common terns that forage at sea in this region breed in widespread colonies further inland but these are often relatively small and situated on building roofs, and as such are inaccessible. A notable exception is the colony of lesser black-backed gulls at IJmuiden ('forteiland') which is accessible to researchers (in fact, breeding success and ringing studies have been conducted here for many years by volunteers - (Cottaar *et al.* 2023) situated centrally in the coastal Holland region (and close to a research institute).

The exact choice of study site locations falls outside the scope of this proposal and will be made when outlining further details of a research plan. It seems logical, however, to consider sites where research activities currently are or have been carried out recently, to make efficient use of existing data, practical arrangements, established numbers of ringed birds, et cetera.

Diet and prey availability

Understanding the diet, foraging ecology and food availability of these species is key in interpreting trends in breeding success and population dynamics. The lesser black-backed gull, Sandwich tern and common tern rely heavily on marine food webs, and their foraging ecology is strongly linked to the availability of small pelagic fish ('forage fish'). Common and Sandwich terns forage primarily on sandeel, sprat and herring, often within a short distance (<30 km) of their breeding colonies (Fijn *et al.* 2024; Manche *et al.* 2022, 2023). Lesser black-backed gulls are more opportunistic feeders, consuming a range of food sources such as discards, offshore fish or anthropogenic waste (Langley *et al.* 2023). These birds can travel much further (<200 km) from their breeding sites, sometimes foraging far into the North Sea.

Forage fish availability in the North Sea and coastal waters is influenced by seasonal and other factors. Forage fish stocks (e.g. sandeel, sprat) are sensitive to changes in sea surface temperature, salinity and nutrient availability (Lindegren *et al.* 2018). When forage fish availability decreases, breeding success is negatively impacted, especially among terns. The common tern, a single prey-loading species, is particularly energetically constrained by its limited ability to carry fish (Fijn *et al.* 2024). During periods of forage fish scarcity, terns must make longer foraging trips and are away from the nest longer, increasing the risk of chick starvation/mortality.

Monitoring these species throughout the breeding season (e.g. quantifying chick provisioning rates, prey analysis/availability) combined with tracking studies (GPS/geolocator) will provide in-depth information about the health of the marine food web and its impacts on coastal bird population survival. Here, research on forage fish availability and accessibility (described in more detail in the chapter above) should be executed (research topics 3a-h). Fish availability could be mapped and monitored in the surroundings or foraging range of breeding birds using several techniques, for instance shoot nets, or hydroacoustic or acoustic monitoring with vessels or buoys (WBATs), while simultaneously measuring environmental conditions and (human) changes to the environment over time.

A suitable location for a study on forage fish in relation to seabirds could be defined according to known distribution patterns from aerial surveys and tracking data from breeding Sandwich terns and lesser black-backed gulls. A suitable location could be chosen based on its representativity and spatially manageable setting, as well as access to facilities and potential benefits from local study programmes of gull and tern colonies.

Elements of the studies per colony

Comprehensive studies in a limited number of breeding colonies are proposed to address the topics listed below. Although we provide suggestions for relevant study techniques, final choices on which techniques are most appropriate must be made at a later stage when study plans are further refined and tailored to local needs and possibilities.

- Diet composition of chicks and (where possible) parents, with attention to variability in laying date/chick age, years, or other factors (e.g. weather, disturbance). Useful techniques include visual/camera registration of prey delivered to the colony or to nests, analysis of visible remains or DNA in faecal samples accompanied by stomach content research on dead birds.
- GPS tracking to determine foraging trips of nesting birds in various phases of the breeding cycle, at least during incubation and chick-rearing, but if feasible also during the (pre-)laying period (which may require logger-mounted harnesses lasting multiple breeding seasons). Combining such tracking with identification of prey delivered to chicks may yield additional information on the provenance of resources for successful reproduction.
- Annual estimates of breeding productivity (hatched eggs and fledged young per pair), with adequate sample size and precision. Ideally these will be based on samples of nests situated within enclosures, or observations of individually marked breeding pairs. Data on development of the physical condition of chicks (body mass and structural growth) should also be collected, particularly around fledging age.
- Annual survival estimates for different age classes within the population. Data to be generated by colour-ringing of sufficiently large samples of breeding birds and fledged young, supported by a systematic ring-reading effort (including outside colonies) and statistical survival modelling.
- Data on at-sea food availability during key phases of the breeding season (at least during chick-rearing, but preferably also pre-laying and incubation periods). Dedicated ship-based surveys specifically designed to simultaneously monitor seabirds and forage fish could be carried out within the potential foraging range of the study colonies (see below), using techniques including side-scan sonar and stationary wide band acoustic transducers (WBAT), as well as fishing with net types suitable for sampling small pelagic fish near the surface (e.g. Baptist *et al.* 2010, Maathuis *et al.* 2025). During these cruises, observers can quantify the densities and behaviour of foraging birds, including data on fish capture rates, that will aid in modelling the foraging process. For instance, small pelagic fish monitoring in the coastal zone that recently commenced under the MONS programme could be redirected by including top predator counts and concentrated to improve coverage in the study areas. Prey type will also be relevant for lesser black-backed gulls, although their diet also includes terrestrial food sources and fisheries discards. Information on availability of the latter can be obtained from data sources on commercial fishing vessel activity (e.g. Global Fishing Watch).
- Based on the above information, selectivity studies can be performed: how selective are birds compared to what is available? This could be done for seabirds breeding in the Netherlands or wintering birds. For breeding birds, Dutch colonies can be compared and combined with prey availability information at the different locations (focusing on adult and chick diet) in single-prey loaders: common tern and Sandwich tern. For these species, fish lengths can be estimated in the field; for other species, diet can be assessed by identifying otoliths from stomach contents/regurgitations and through eDNA-methods. Information on selectivity throughout the breeding season can be used to improve modelling work.

A general first step

A first step for all three species at a general level, rather than per-colony, is energetic modelling to explore the maximum foraging distances parents must travel within the constraints of a foraging day to meet the energetic needs of their chicks (and themselves). As ‘central place foragers’ that must operate from and return to a central place (their nest), chick-rearing gulls and terns experience constraints in addition to the exploitation of at-sea resources compared to non-breeding birds. Exploring foraging energetics will yield useful insights into the relative potential importance of different prey characteristics: species, size, and nutritional quality (energy density). It will also help identify the spatial range (distance to study colonies) of the foraging trips referred to above in relation to sampling of forage fish availability. Data on the energetic requirements of growing chicks are available for all three study species, and such modelling has already been performed for common terns breeding in the Wadden Sea (Schekkerman *et al.* in prep.). Energetic modelling is also ongoing elsewhere in MONS, and mutual benefits can be gained from collaborating in this work.

5.3.2 Research options for overwintering birds

Several seabird species that do not breed in the Netherlands migrate to the North Sea during autumn and winter. These birds spend the winter months foraging in the North Sea, which means that we also need information about the spatial and temporal availability of prey in those areas. In this section, we propose field studies on species that occur in Dutch part of the sea during the non-breeding season that integrate the various questions addressed in MONS and will also be relevant and valuable when continued beyond the time scope of the MONS programme.

Tracking and diet studies combined
To map key foraging and resting areas for marine birds in the southern North Sea, tracking studies (either using GPS loggers or geolocators) are the most appropriate in terms of data resolution and accuracy. GPS studies in particular produce high-resolution data that can provide critical information about the spatial distribution of marine birds and the impacts of offshore structures and other environmental changes. By linking information on food availability with at-sea behaviour, the importance and vulnerabilities of these factors in relation to the energy and food transition can be quantified and important (foraging) habitat can be identified.

We propose an annual tracking campaign targeting key non-breeding species. Considerable preparatory work is required to develop effective protocols and secure permits. We propose two complementary approaches: tagging individuals in Dutch breeding colonies, as well as the UK and other relevant countries, and capturing birds at sea during the non-breeding season within the Dutch North Sea, particularly at night when they are accessible and catchable on the water. During these offshore capture efforts, we also intend to collect stomach contents and faecal samples to conduct dietary analyses. This integrated approach will allow us to link individual movement and behaviour in relation to forage fish use, thereby increasing our understanding and filling MONS knowledge gaps relating to seabird foraging ecology.

Choice of study species
The razorbill and common guillemot are abundant in the North Sea from October – April and depend heavily on forage fish in offshore waters. These species are often spatially restricted to areas of high food density, making them natural indicators of ecosystem health. Light-level geolocators or leg-ring GPS devices could be used to track individuals to determine key foraging areas and examine how prey availability influences their temporal and spatial distribution (see knowledge gap 3b). A recent GPS study is being conducted on guillemots by a French research team to investigate their spatial ecology and key foraging areas (Cadiou et al.).

To date, only a few GPS tracking studies exist on great black-backed gulls from the North Sea region, all of which are restricted to the breeding season and limited to a small number of birds (see e.g. Borrmann 2019; Langlois Lopez *et al.* 2024). In 2024, a long-term study commenced that will track 100 adult birds from two breeding locations in Norway and data are in the early phases of being analysed. These open access GPS data from breeding colonies in Norway (Madden *et al.* unpublished data) could be integrated with data from other studies to better understand great black-backed gull foraging ecology and diet outside the breeding season. Based on preliminary data, tracked birds from Norway appear to have variable migration strategies, with some individuals remaining entirely offshore during winter while others select coastal areas. GPS data can also help determine whether the species is affected by (or becomes habituated/attracted to) offshore structures, and if so, to what extent.

The herring gull is a highly mobile, generalist species that consumes both natural and anthropogenic food sources. Understanding the species' foraging decisions and to what extent these are influenced by fishing activities, OWFs, or other external factors is important for its long-term conservation.

The black-legged kittiwake is a species of conservation concern whose breeding success is strongly influenced by the availability of forage fish such as sandeel. The recent closure of sandeel fisheries in the UK may have implications for prey availability and the survival of breeding kittiwake populations. By building on existing discards data and supplementing this with diet analysis from faecal samples and/or stable isotope analysis, the foraging ecology and diet of kittiwakes outside the breeding season can be better understood. The Northern fulmar is another species of conservation concern due to its steep decline in recent years (Sovon.nl). Fulmars feed primarily on fish, squid, plankton and fisheries discards, making them vulnerable to changes in prey availability, pollution and discard bans (Camphuysen & Garthe 1997). Long-term population data combined with novel information on diet composition and key foraging areas will help elucidate the factors that influence the fulmar's survival.

The Northern gannet consumes larger marine prey and has already been widely studied through GPS tracking (see e.g. Hamer *et al.* 2000, 2007; Camphuysen 2011; Corman 2015). The geographic scope of these studies could be expanded, possibly in conjunction with ongoing research at Bempton Cliffs in the UK (see Langston and Boggio 2011; Langston *et al.* 2013). The diet of these species in the Dutch North Sea is largely unknown.

Geographical scope
Since some of the above-mentioned species do not breed in the Netherlands, we propose the formation of international collaborations with researchers that are already working on those species in their home countries, e.g. Bernard Cadiou on guillemots (France), RSPB in the UK for northern gannets, BirdLife Norway for great black-backed gulls etc. While the common scoter and red-throated diver are already being studied in coastal areas, their spatial distribution and foraging ecology can be further examined within the broader context of this project.

Analysis of tracking data
High-resolution GPS data can be analysed using Markov Models to infer behavioural states, i.e. resting, foraging, or in transit. This will allow us to map foraging hotspots and link those areas to food availability, environmental variables, such as sea surface temperature, primary productivity, bathymetry, and so on. For example, we have demonstrated that great black-backed gulls forage in shallower waters off the southern Norwegian coast during the breeding season (Madden *et al.* in review), but the effects of other environmental variables on foraging outside the breeding season are yet unknown.

Similarly, tracking data can help us quantify the impacts of offshore structures and other anthropogenic effects on the at-sea behaviour of marine birds (habituation, avoidance, attraction, habitat loss, and so on). This is particularly relevant for the energy transition as species that avoid offshore wind farms may lose key foraging habitat, or travel greater distances to reach it, resulting in increased energetic costs (Masden *et al.* 2010). In the case of attraction, seabirds may fly into rotor blades, resulting in increased mortality (Fox *et al.* 2006). Tracking data can also be overlayed with fishing activity (open access data from Global Fishing Watch) to examine whether birds forage in association with fishing vessels, a common practice especially among large gulls (Garthe *et al.* 1996).

Linking spatial data to prey availability and distribution can provide deeper insight into the ecological drivers that shape seabird foraging strategies and their broader role in marine ecosystems. Data from ICES can be used to correlate seabird foraging with (short term and long term) prey abundance in the southern North Sea, providing a deeper understanding of how marine birds respond to changes in prey across different scales (temporally and spatially). Responses of birds to prey abundance and/or diversity may differ between years or habitats. Again, this can be linked to the energy transition and changes in the North Sea ecosystem over time.

Combining tracking with other techniques
Recently, methods have been developed by Lauret *et al.* (2025) and Blackwell & Matthiopoulos (2024) to combine tracking data with spatial abundance data, such as aerial and boat counts (MWTL; van Donk *et al.* 2024). A key innovation of this proposal is the integration of tracking (GPS/geolocator) technologies with analysis of eDNA collected from faeces and stable isotopes in feathers. This would involve collecting faecal

samples and feathers from live birds, caught at sea with nets, from offshore platforms or from their breeding grounds. These approaches will help to map key foraging areas combined with data on prey consumption. Stable isotope analysis can also provide information about the trophic ecology of the target species as well as competition, whereas eDNA analysis (metabarcoding) provides a higher dietary resolution than traditional methods like stomach content analysis.

Beached birds
We also propose to systematically collect seabird carcasses found on beaches to investigate diet and interactions with offshore fisheries. Dead birds can be collected and their stomach contents analysed (hard parts and metabarcoding) to identify dietary preferences. If any of the birds have colour rings, data relating to their previous observed locations can be used to try to identify where they might have foraged. This is especially interesting for Northern gannets, which are large and can easily be spotted and gathered before degradation while traveling by car on the beach. This approach could use existing resources as long-term monitoring schemes for dead seabirds are already in place e.g. OSPAR monitoring of oiled seabirds (Camphuysen 2024) and OSPAR monitoring of plastics in fulmars (Kühn *et al.* 2024).

Ship-based surveys specifically designed to simultaneously monitor seabirds and forage fish
To assess the ecological requirements of overwintering non-breeding seabirds in the Dutch North Sea, repeated and seasonally stratified at-sea surveys are essential, particularly for diving species such as common guillemots and razorbills. Importantly, the non-breeding season encompasses several distinct phases, including late summer/autumn, mid-winter, and early spring, each of which may present different energetic demands and prey field characteristics. Surveys should therefore be designed to capture this intra-seasonal variability, also spanning a range of meteorological conditions and tidal phases to reflect the dynamic availability and vertical distribution of pelagic prey. These prey fields can fluctuate considerably in response to wind speed forcing, current regimes, water clarity, and fish behaviour. Continuous Seabird-At-Sea counts should accompany the fish surveys to detect ecologically important feeding areas of seabirds throughout the year.

A primary objective is to quantify the abundance and depth distribution of small pelagic fish species that form the core dietary component for these seabirds during winter. This requires systematic ship-based surveys using methods such as side-scan sonar and stationary wideband acoustic transducers (WBAT), complemented by net sampling techniques optimised for capturing epipelagic forage fish (Baptist *et al.* 2010; Geelhoed *et al.* 2014; Maathuis *et al.* 2025). Repeated sampling over time and under varying oceanographic conditions will allow for the assessment of temporal variability in prey fields and provide insight into the mechanisms driving prey accessibility in the water column.

As with during the breeding season, we recommend a reassessment of the current MONS pelagic fish monitoring programme during winter. This programme, which recently began surveying small pelagic fish in the broader Dutch coastal zone, would benefit from a spatially refined and integrated study design focused on key areas used by common guillemots and razorbills, to effectively address the MONS research questions concerning forage fish availability for seabirds. Depending on the temporal and spatial scale of the monitoring effort, this approach may also yield valuable insights for other species, including black-legged kittiwakes and Northern gannets.

A suitable location for a study on forage fish in relation to wintering seabirds could be defined according to known distribution patterns from aerial surveys and tracking data from, for instance, common guillemot. A suitable location could be chosen based on its representativity and spatially manageable setting, as well as access to facilities and potentially benefiting from local study programmes of gull and tern colonies.
A suitable study area for research on forage fish in relation to wintering seabirds includes coastal and offshore waters featuring a clear depth gradient. This gradient is linked to variations in water clarity, current velocity, and sediment characteristics which, together with tidal phase and time of day, influence the distribution, availability, and detectability of forage fish for pursuit-diving species such as the common guillemot. The area should furthermore be ecologically representative and manageable.
By integrating prey data with seabird distribution patterns, a more mechanistic understanding can be gained into how oceanographic conditions, shaped by weather, tidal cycles, and water clarity, influence fish distribution and, in turn, prey availability in the water column. This will significantly enhance our ability to

understand habitat use by seabirds during the non-breeding season and assess the potential effects of environmental changes, such as those driven by climate change or anthropogenic activities, on the North Sea ecosystem.

5.3.3 Fisheries discards versus natural forage fish in the diet of gulls, Northern fulmars and Northern gannets

Understanding the relative importance of fisheries discards compared to natural prey, including key forage fish such as sandeel, in the diets of gulls, Northern fulmars, and Northern gannets requires an integrated, year-round research approach. This applies to both the breeding season, when adults provision chicks at colonies, and the non-breeding season, when birds are widely dispersed at sea and dietary patterns may differ substantially. We propose a combined approach via diet composition reconstruction and large-scale aerial and ship-based field observations to improve our understanding of the ecological role of fisheries waste in marine ecosystems.

Dietary composition should be assessed for both adult and juvenile birds through the systematic collection of regurgitated pellets and faecal samples across seasons. To ensure a comprehensive picture, environmental DNA (eDNA) analysis will be employed, as certain prey taxa may be underrepresented in pellet samples due to digestion bias. To complement dietary data, field-based assessments will be conducted to evaluate the degree to which fishing vessels act as foraging opportunities for the target species.

We are considering dedicated aerial surveys to estimate the abundance of birds in proximity to fishing vessels. The exact survey design remains under discussion, but it will account for temporal patterns as foraging on natural prey is known to peak during crepuscular periods. This is likely linked to the diel vertical migration of forage fish and other prey, which become more accessible at the water's surface around dusk and dawn. Where available, high-resolution GPS tracking data will also be used to identify and quantify seabird interactions with fishing vessels across different seasons. Furthermore, during ship-based surveys that integrate forage fish and seabird research, targeted observations will be collected on seabird distribution, foraging behaviour and prey availability in relation to fishing activity. This will enable direct comparison between the occurrence of forage fish schools and seabird aggregations, helping to disentangle the respective importance of discards versus natural prey.

5.3.4 Planning of research and means

We have estimated the potential effort required to implement the above research plans. Here, we chose to estimate the time that will be spent on fieldwork in work days per species and colony (ifor breeding-related research) (see Tables 5-2, 5-3). Here, we estimate that the total time spent on a project can be calculated by multiplying the time spent on fieldwork multiplied by five. We also made a rough indication of resources required for materials (Table 5-4).

These estimates could be reduced when combining existing projects with our research plans (e.g. combining bird observations with fish monitoring on vessels, working in breeding colonies that are already being monitored). We anticipate higher costs for work relating to black-legged kittiwakes due to increased ship time; to compensate for higher travelling cost it may require fewer trips and reduced sampling, potentially supplemented with camera monitoring. It is important to clarify that various options are possible (e.g. with or without GPS tagging or colour ringing, choices of species or number of colonies sampled). The time and effort required to catch birds at sea in winter is currently difficult to estimate.

Tagging/colour ringing and colony research combined with diet sampling
We recommend commencing research in January 2026 until the end of 2028, financed through MONS. However, some activities may need to continue thereafter. In particular, spatial data are likely to be collected over several years and analysis of these data (and reporting results) will take longer. Example:

- GPS loggers are deployed in 2026 breeding season (April/May)
- Data analysis (determine key foraging areas during chick-rearing) begins late 2026; report early 2027.

- Data analysis (determine key foraging areas/behaviour outside the breeding season) begins in 2027; report end 2027.

These tasks will repeat (bi)annually (assuming loggers remain on birds longer than one year), with work continuing beyond 2029/30. Flight height data can also be extracted and used to run and improve existing collision risk models.

Colour-marking of birds and ring-reading for estimating survival is another example of a type of research requiring longer time periods. For example, to obtain annual survival estimates for a single year will require three years of research activities (one year for marking and two for resighting birds), but improving the precision of estimates and capturing interannual variability will require data collection over a longer period. At-colony diet and nest research would take place leading up to and during the breeding season. Analysis of these data and reporting could be completed in the same year. While three years of research will provide a reasonable dataset, ideally these activities would continue over a longer period (minimum five years) to be able to quantify the relationship between breeding success, chick provisioning rates and diet to forage fish availability and environmental factors.

Combined field research forage fish and seabirds

Multiple steps must be taken to improve knowledge on the relationship between forage fish and seabirds in both seabirds that breed and those that overwinter in the Netherlands. At present, these surveys are conducted twice annually, in summer and winter, following a zigzag transect design that predominantly covers the coastal zone. Within the framework of the MONS programme, the goal is to carry out at least one pilot survey in February 2026 to conduct seabird observations from the same survey vessel, and MWTL aerial counts concurrently, enabling integrated analyses of fish and seabird data. At this stage, it is not yet possible to develop a fully detailed research plan to study of seabird occurrence and behaviour combined and with pelagic (prey) fish availability, as the pilot survey will be essential to establish the methodological, spatial, and analytical framework. A pilot study with WBATs has demonstrated the potential of using stationary WBAT instruments to provide high temporal resolution data on the biomass and depth distribution of forage fish. WBAT systems can furthermore act as robust indicators of ecosystem function and prey availability when used in combination with spatial simulations and complementary environmental data.

Against this background, as an alternative to ornithologists joining the current pelagic fish surveys twice a year, it is possible to revise the current ship-based survey design. By reducing spatial coverage and reallocating resources to conduct repeated transects perpendicular to the coastline within a smaller, well-defined area, it will be possible to capture tidal and diel patterns in prey availability for seabirds (for instance prey availability for Sandwich terns and common guillemots, see Tables 5-2 & 5-3). This would also enable direct investigation of the relationship between seabird foraging behaviour, foraging success, and prey availability.

Below, we present an overview of recommended species, breeding colonies, research type, individuals and person-days required to adequately fulfil fieldwork requirements. We also present suggestions for complementary methods to study diet, duration of the proposed research, and the names of in-country partners/potential collaborators.

Table 5-2 *Breeding season – Estimation of fieldwork hours, methods required, duration and potential partners. WE = Waardenburg Ecology, RSPB = Royal Society for the Protection of Birds, NINA = Norwegian Institute for Nature Research, BLN = BirdLife Norway, WMR = Wageningen Marine Research, UvA = University of Amsterdam, NIOZ = Royal Netherlands Institute for Sea Research, BTO = British Trust for Ornithology.*

Species	Colony	Research type	Min. # required	# person days required per colony	Minimum methods required + duration	Partner(s)
Black-legged kittiwake	France, UK, Norway, NL offshore platforms (K1 Alpha)	GPS (catching) diet + analysis Color-ringing for survival breeding	20-30 GPS + nests	14 15 14 2 (installing cameras) plus crew ship	Stable isotope analysis, regurgitate/faecal samples, DNA metabarcoding 3-5 years	WE, RSPB, Uni de Montpellier, NINA, BLN, platform owner(s)
Common tern	Netherlands (Delta, Wadden Sea)	GPS diet + analysis ringing for survival breeding success prey availability around colonies & discard availability	20-30 GPS + nests	15 15 15 30 6 days of surveying, 2 bird observers, 3-4 fish researchers, crew	Stable isotope analysis, regurgitate/faecal samples, DNA metabarcoding 3-5 years	WE, SOVON, WMR
Lesser black-backed gull	Netherlands (Neeltje Jans, Maasvlakte II, Delta, Wadden Sea)	GPS diet + analysis ringing for survival breeding success prey availability around colonies & discard availability	20-30 GPS + nests	15 15 15 30 6 days of surveying, 2 bird observers, 3-4 fish researchers, crew	Stable isotope analysis, regurgitate/faecal samples, DNA metabarcoding, forage fish/discards research 3-5 years	WE, UvA, SOVON, WMR
Sandwich tern	Netherlands (Delta & Wadden Sea), UK	GPS diet + analysing ringing for survival breeding success prey availability around colonies & discard availability	20-30 GPS + nests	15 15 15 30 6 days of surveying, 2 bird observers, 3-4 fish researchers, crew	Cameras at nest site, regurgitate/fecal samples, DNA metabarcoding, forage fish research 3-5 years	WE, WMR, SOVON, NIOZ, BTO

Table 5-3 *Non-breeding season – fieldwork hours, methods required, duration and potential partners. WE = Waardenburg Ecology, RSPB = Royal Society for the Protection of Birds, NINA = Norwegian Institute for Nature Research, BLN = BirdLife Norway, WMR = Wageningen Marine Research, UvA = University of Amsterdam, NIOZ = Royal Netherlands Institute for Sea Research, UKCEH = UK Centre for Ecology & Hydrology.*

Species	Colony	Research type	Min. # required	# person days required	Minimum methods required + duration	Partner(s)
Common guillemot	UK, Germany, Norway	GPS (catch at sea) Diet – gathering & analysing beached birds prey availability in non-breeding areas	20-30 GPS tagged per colony, over multiple seasons	14 10 21 days (per year) of surveying, 2 bird observers, 3-4 fish researchers, crew	regurgitate/fecal samples, DNA metabarcoding 3-5 years	WE, WMR, NINA, BLN, UKCEH
Great black-backed gull	Norway	GPS Diet - Faecal samples roosting & platforms	25 per year over 2 years	14 14	Stable isotope analysis, regurgitate/fecal samples, DNA metabarcoding 3-5 years	WE, Ecowende, BLN
Northern gannet	Netherlands	GPS? Diet – gathering & analysing beached birds	20-30 GPS	14 10	Stable isotope analysis, stomach content analysis regurgitate/fecal samples, DNA metabarcoding 3-5 years	WE, NIOZ, WMR
Razorbill	France, UK	GPS (catch at sea) Diet – gathering & analysing beached birds	20-30 GPS	14 10	Stable isotope analysis, regurgitate/fecal samples, DNA metabarcoding 3-5 years	WE, SEATRACK, FAME/STAR, WMR

Table 5-4 *Annual cost estimates for materials*

Item	**Cost estimate (EUR)**	**Quantity**	**Total EUR (per year)**
GPS logger + data transfer	1000-1,750 depending on size	210	Maximum of 367,500
Harness + other equipment	50	210	10,500
Cameras	500	32	16,000
Lab material DNA faeces/regurgitates per colony	5000-10,000		
Field material breeding per colony	1500		
Transport shipping	**10,000 per day**		

6. References

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7. Quality Assurance

Wageningen Marine Research utilises an ISO 9001:2015 certified quality management system. The organisation has been certified since 27 February 2001. The certification was issued by DNV.

8. Justification

Report: C093/25
Project Number: 4315100243

The scientific quality of this report has been peer reviewed by a colleague scientist and a member of the Management Team of Wageningen Marine Research

Approved: ir. S.C.V. Geelhoed
Researcher

Signature:

Date: November 28, 2025

Approved: C.J. Wiebinga, PhD
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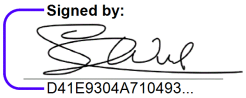
Signature:



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