Review of demographic studies on seabirds of the Dutch North Sea

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1 Summary

Aims and structure

This report represents one of three main work packages in a desk study on our current knowledge of distribution, diets and demography of coastal birds and seabirds in the Dutch part of the North Sea. It is an annex to the main report by Van Donk *et al.* (2025), but can be read separately.

Work Package 4 (WP4) of the MONS desk study on birds aimed to deepen our understanding of how seabird demography -encompassing survival, breeding productivity, and settlement- is influenced by at-sea conditions, particularly food availability. These relationships are critical in determining the carrying capacity of the North Sea for marine birds and can inform ecosystem models developed in other MONS projects. WP4 specifically focused on five seabird species with significant Dutch management responsibility because of national breeding populations: lesser black-backed gull, European herring gull, great black-backed gull, Sandwich tern and common tern. Additionally, information on seven other seabird species present in Dutch waters mainly outside the breeding season is included: black-legged kittiwake (with a small Dutch breeding population on offshore platforms), common scoter, red-throated diver, common guillemot, razorbill, northern fulmar and northern gannet.

The work package had two main objectives: (1) summarizing reported values of key demographic parameters of the focal species, and (2) reviewing studies linking these parameters to food resources. The key demographic parameters reviewed are annual survival in the adult, immature and first-year age classes, breeding productivity (mean number of fledged young per breeding pair per year), age at recruitment (age at first breeding), and adult breeding propensity (the reverse of ‘skipping’ of breeding years by adults). The review incorporated estimates from published literature, emphasizing mean values alongside variability measures -standard deviation among estimates (SD_e) and environmental stochasticity (SD_p)- to allow parameterisation of population models.

Demographic studies on gulls and terns

For the Dutch breeding species, information on breeding colonies in the Netherlands was summarised using information from Sovon’s abundance and breeding success databases, published reports and interviews with researchers. Monitoring has focused on two main regions: the southwestern Delta Area and the Wadden Sea. In these regions, long-term monitoring programs track breeding productivity since the early 1990s and 2004 respectively. Survival data predominantly derive from ringing studies, encompassing nearly 438,000 gulls and terns ringed between 1911 and 2023. More recent efforts have employed colour-ringing to increase resighting rates and expand the spatial scope of recoveries.

Various dedicated studies on the focal species have been conducted in the Netherlands. Lesser black-backed and herring gulls have been studied extensively, including reproductive success, survival, recruitment, diet, and spatial ecology. Studies on Sandwich terns and common terns have combined breeding productivity monitoring with observations on diet, colour-ringing and tracking of foraging movements and dispersal. By contrast, the great black-backed gull, with a population of just about 120 dispersed breeding pairs, has received little dedicated research. Internationally, similar demographic monitoring exists, including the German effort in TMAP and a dedicated long-term study on common terns at Wilhelmshaven, the UK Seabird Monitoring Programme, and Norway’s SEAPOP program.

Key demographic parameters

From the synthesis of available demography data, breeding productivity and adult survival rates emerge as the best-known key parameters across species, although even on these information is lacking for common scoter and red-throated diver. Of the key parameters, adult survival has the strongest influence long-term population growth, with immature survival, first-year survival, breeding productivity, and breeding propensity showing progressively less influence. While breeding productivity exhibits high interannual variability (which will affect shorter-term fluctuations in population size), particularly among gulls and terns, adult survival is relatively stable. This is consistent with life-history theory predicting that in long-lived species survival is prioritised over reproductive output when conditions are unfavourable. Cliff-nesting focal species such as auks, gannet and fulmar, which have an even slightly slower life-history than the gulls and terns, tend to show lower variability in both productivity and survival. Important information gaps remain for first-year and immature survival, age at recruitment and adult breeding propensity. Data on early survival and age at recruitment is probably embedded in existing datasets but not yet analysed. Remaining information gaps can be filled by intensive colour-ringing efforts, or the use of bird-borne devices such as geolocators to track breeding propensity over multiple years.

Relationships with food resources

The relationship between demography and food abundance has been investigated mostly from a breeding season perspective, and is unevenly understood across the focal species. For lesser black-backed and herring gulls, some studies indicate relationships between chick growth or productivity and the availability of discards, but quantitative links between food supply and survival, recruitment, or skipped breeding are lacking. Sandwich tern studies link settlement of breeders to indices of herring abundance in the southeastern North Sea and breeding productivity to prey delivery rates. Common tern research in the German Wadden Sea demonstrated strong correlations between breeding productivity and the abundance of key prey (herring/sprat and smelt), but not with adult survival, which seemed influenced more by conditions in the winter range. Black-legged kittiwake studies in the North Sea and Norway provide detailed evidence that sandeel and other forage fish (and sea butterflies) influence breeding productivity and/or adult survival. Results for common guillemot and (less extensively studied) razorbill are mixed, suggesting some flexibility in coping with fluctuating prey availability. Northern gannet appear the least sensitive to short-term prey variation, whereas few data exist for northern fulmar and virtually none for common scoter, red-throated diver, and great black-backed gull. Most published studies assessed food-demography relationships on the basis of broad-scale fish surveys and stock indices, which may not always accurately represent the prey conditions that birds encounter within their local foraging ranges, or on sampling of chick diets which themselves depend on prey abundance in an unknown way. Only a small number of studies incorporated targeted fish surveys in known foraging ranges.

Outlook

Future progress will profit most from integrated, multi-year research that simultaneously measures demographic rates (including intensive ringing and ring-resighting) and local food availability (by ship-based surveys or acoustic monitoring), guided by tracking to identify the areas where birds truly forage. Such studies will support the development of dose-effect relationships between food availability and demography, enabling more robust population and ecosystem modelling.

Nederlandse samenvatting

Dit rapport beschrijft één van de drie werkpakketten in een bureaustudie naar de huidige kennis over verspreiding, voedselkeuze en demografie van kust- en zeevogels in het Nederlandse deel van de Noordzee, in het kader van het programma MONS (Monitoring, Onderzoek, Natuurversterking en Soortenbescherming) geïnitieerd onder het Noordzeeakkoord. Het is een bijlage bij het hoofdrapport van deze bureaustudie (van Donk *et al*. 2025), maar kan afzonderlijk worden gelezen.

Werkpakket 4 (WP4) van de bureaustudie had als doel onze kennis te verdiepen over hoe de demografie van zeevogels —waaronder overleving, broedsucces en vestiging— wordt beïnvloed door omstandigheden op zee, met name de beschikbaarheid van voedsel. Deze relaties zijn essentieel voor het bepalen van de draagkracht van de Noordzee voor zeevogels en kunnen bijdragen aan ecosysteemmodellen die in andere MONS-projecten worden ontwikkeld. WP4 richtte zich specifiek op vijf zeevogelsoorten waarvoor Nederland een belangrijke verantwoordelijkheid heeft vanwege nationale broedpopulaties: kleine mantelmeeuw, zilvermeeuw, grote mantelmeeuw, grote stern en visdief. Daarnaast is informatie opgenomen over zeven andere zeevogelsoorten die voornamelijk buiten het broedseizoen in Nederlandse wateren voorkomen: drieteenmeeuw (met een kleine broedpopulatie op offshore-platforms), zwarte zee-eend, roodkeelduiker, zeekoet, alk, noordse stormvogel en Jan-van-Gent.

De hoofddoelen van WP4 waren: (1) samenvatten van gerapporteerde waarden van belangrijke demografische parameters van de focale soorten, en (2) een review van studies waarin deze parameters worden gekoppeld aan voedselbeschikbaarheid. De demografische parameters die zijn beschouwd zijn jaarlijkse overleving van adulte vogels, onvolwassen vogels en eerstejaars, broedsucces, recruteringsleeftijd, en de jaarlijkse kans dat volwassen vogels daadwerkelijk tot broeden overgaan. De review omvatte schattingen uit gepubliceerde literatuur, met nadruk op gemiddelde waarden en twee variatiematen — standaarddeviatie tussen schattingen (SD_e) en jaarvariatie onder invloed van omgevingsstochastiek (SD_p) — die kunnen worden gebruikt in populatiemodellen.

Voor de in Nederland broedende soorten zijn gegevens over broedkolonies samengevat met behulp van informatie uit de Sovon-databases over aantallen en broedsucces, gepubliceerde rapporten en interviews met onderzoekers. In het zuidwestelijke Deltagebied en in de Waddenzee volgen langlopende monitoringsprogramma's het broedsucces sinds respectievelijk begin jaren 1990 en 2004. Gegevens over overleving zijn voornamelijk afkomstig uit ringonderzoek, waarbij tussen 1911 en 2023 bijna 438.000 meeuwen en sterns zijn geringd. Meer recent zijn kleurringprogramma's opgestart die kunnen leiden tot betere overlevingsschattingen.

In Nederland zijn diverse gerichte studies uitgevoerd naar de besproken soorten. Kleine mantelmeeuwen en zilvermeeuwen zijn uitgebreid onderzocht, onder meer op reproductief succes, overleving, vestiging, dieet en ruimtelijk gedrag. Studies naar grote sterns en visdieven combineren monitoring van broedsucces met dieetobservaties, kleurringen en het volgen van foerageerbewegingen en dispersie. De grote mantelmeeuw, met slechts circa 120 verspreide broedparen, is daarentegen nog weinig onderzocht. Internationaal bestaan vergelijkbare demografische monitoringsprogramma's, zoals de Duitse inspanningen binnen TMAP en een langlopende studie aan visdieven bij Wilhelmshaven, het Britse Seabird Monitoring Programme, en het Noorse SEAPOP-programma.

Uit de review van beschikbare demografische gegevens blijkt dat broedsucces en volwassen overleving de best onderzochte parameters zijn, hoewel zelfs hierover informatie ontbreekt voor de zwarte zee-eend en de roodkeelduiker. Van de kernparameters heeft volwassen overleving de sterkste invloed op de lange-termijn populatiegroeisnelheid; daarna volgen overleving van onvolwassen vogels, eerstejaars overleving, broedsucces en de jaarlijkse broedkans. Broedsucces vertoont grote variatie tussen jaren (met invloed op korte-termijn-schommelingen in populatieomvang), vooral bij meeuwen en sterns, terwijl de volwassen overleving relatief stabiel is. Dit is verklaarbaar doordat langlevende soorten onder ongunstige omstandigheden hun overleving prioriteren boven reproductie. Op kliffen broedende zeevogels zoals alken, Jan-van-Genten en noordse stormvogels — die een nog iets trager levensgeschiedenis hebben dan meeuwen en sterns — vertonen iets lagere variabiliteit in zowel broedsucces als overleving. Belangrijke kennislacunes zijn er voor eerstejaars en onvolwassen overleving, recruteringsleeftijd en jaarlijkse broedkansen. Gegevens over onvolwassen overleving en rekruteringsleeftijd zijn waarschijnlijk al aanwezig in bestaande datasets, maar nog niet geanalyseerd. Verdere lacunes kunnen worden ingevuld met intensieve kleurringprojecten of door het gebruik van tracking technieken waarmee het broedgedrag van individuen over meerdere jaren is te volgen.

De relatie tussen demografie en voedselbeschikbaarheid is vooral onderzocht vanuit het perspectief van het broedseizoen, en is in verschillende mate begrepen voor de soorten. Bij kleine mantelmeeuwen en zilvermeeuwen wijzen beschikbare studies op relaties tussen de groei of uitvliegsucces van jongen en de beschikbaarheid van visserij-discards, maar kwantitatieve relaties tussen voedselaanbod en overleving, rekrutering of het overslaan van broedjaren ontbreken. Studies naar grote sterns koppelen vestiging van broedvogels aan variaties in de hoeveelheid haring en sprot in de zuidoostelijke Noordzee, en broedsucces aan de aanvoerfrequentie van vis voor de kuikens. Onderzoek naar visdieven in de Duitse Waddenzee toonde sterke verbanden tussen broedsucces en de abundantie van belangrijke prooien (haring/sprot en spiering), maar niet met volwassen overleving, die sterker leek beïnvloed door omstandigheden in het wintergebied. Voor drieteenmeeuwen in de Noordzee en Noorwegen is er veel bewijs dat zandspiering en andere kleine vissoorten (en zeevlinders) effect hebben op zowel broedsucces als overleving. Resultaten voor zeekoeten en —minder uitgebreid onderzocht— alken zijn wisselend, wat wijst op enige flexibiliteit in het omgaan met fluctuerende voedselbeschikbaarheid. Jan-van-Genten lijken het minst gevoelig voor korte-termijnschommelingen in prooiaanbod, terwijl voor de noordse stormvogel weinig gegevens bestaan en voor zwarte zee-eend, roodkeelduiker en grote mantelmeeuw vrijwel geen. De meeste gepubliceerde studies onderzochten voedselrelaties op basis van grootschalige vissurveys en bestandsschattingen, die niet altijd even representatief zijn voor het voedselaanbod dat vogels binnen hun lokale foerageergebieden tegenkomen, of op basis van voedselaanvoer naar de jongen, die zelf weer op onbekende wijze afhangt van de beschikbaarheid van prooien. Slechts weinig studies omvatten gerichte vissurveys binnen bekende foerageergebieden.

De meeste vooruitgang op de vele nog bestaande kennislacunes kan worden geboekt met geïntegreerd, meerjarig onderzoek waarin de verschillende demografische parameters gelijktijdig worden gemeten met lokale voedselbeschikbaarheid (door bemonstering van kleine pelagische vis met schepen of via akoestische monitoring), ondersteund door zenderonderzoek om de foerageergebieden te identificeren. Dergelijke studies kunnen dosis-effect-relaties tussen voedselbeschikbaarheid en demografie aan het licht brengen, die robuustere populatie- en ecosysteemmodellen ondersteunen.

2 Introduction

2.1 Background

The MONS (Monitoring, Onderzoek, Natuurversterking en Soortenbescherming) research program was established in 2021 by the North Sea Agreement (Noordzeeoverleg; NZO). The goal of MONS is to provide the parties involved in the NZO, and society more broadly, with insight into the changes that occur in the North Sea. The North Sea undergoes significant changes already now and these will continue in the coming decades due to the planned transitions in energy supply, food extraction, and nature conservation. In addition, various other changes in pressure factors are expected, related to climate (temperature rise, changing wind patterns, acidification), as well as changing policies, such as those concerning sand extraction and terrestrial nutrient management. Coastal birds and seabirds (together with marine mammals and large predatory fish) are important apex predators in the North Sea. This means they represent the higher trophic levels and are potentially highly sensitive to changes in the abundance and availability of lower trophic levels, ranging from phytoplankton through zooplankton to (small) pelagic fish, which generally form the staple food for most seabirds and coastal birds. In the NZO, agreements are made about an integrated and systematic monitoring program by the government, for measuring the health and development of coastal and seabird populations. MONS is co-financed by the ministries of Infrastructure & Water Management (I&W), Economic Affairs & Climate Policy (EZK), and Agriculture, Nature and Food Quality (LVVN).

2.2 Desk study on seabirds – general aims and structure

The MONS program includes three desk studies on seabirds. These desk studies are to serve as preparatory studies for field research that should fill important knowledge gaps identified by the desk studies. Eventually the bird studies in MONS must contribute to answering the following main questions:

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

The current report represents one of the three desk studies mentioned above. These have been combined in a single joint project, carried out by a consortium consisting of Wageningen Marine Research (WMR), Waardenburg Ecology (WE) and Sovon Dutch Centre for Bird research (Sovon). Within the project, five work packages have been identified. The first work package (WP1) was formed by the project plan and selection of 12 seabird species addressed in the study (table 1). The next three work packages involve the desk studies (reviews of available information and identification of gaps) into distribution and main foraging areas of seabirds in the southern North Sea (WP2), diet composition of the focal species including patterns in space and time (WP3), and demographic rates of

Table 1. Bird species covered in this study.

English name	Dutch name	scientific name	breeds in The Netherlands	winters in NL North Sea
lesser black-backed gull	kleine mantelmeeuw	*Larus fuscus*	X	X
European herring gull	zilvermeeuw	*Larus argentatus*	X	X
great black-backed gull	grote mantelmeeuw	*Larus marinus*	X	X
Sandwich tern	grote stern	*Thalasseus sandvicensis*	X	-
common tern	visdief	*Sterna hirundo*	X	-
black-legged kittiwake	drieteenmeeuw	*Rissa tridactyla*	x*	X
common scoter	zwarte zee-eend	*Melanitta nigra*	-	X
red-throated diver	roodkeelduiker	*Gavia stellata*	-	X
common guillemot	zeekoet	*Cepphus grylle*	-	X
razorbill	alk	*Alca torda*	-	X
northern fulmar	noordse stormvogel	*Fulmarus glacialis*	-	X
northern gannet	jan-van-gent	*Sula bassana*	-	X

* Although a small breeding population is present on offshore platforms in the Dutch sector of the North Sea, the kittiwake is treated as a non-breeding species in this report.

seabirds and their relationships with food abundance, with an emphasis on gulls and terns breeding in The Netherlands (WP4). In the main report of the desk studies (van Donk *et al.* 2025), results from WP's 2-4 are collated in a summarised form and a fifth work package is developed: proposals for (field) studies aimed at filling the information gaps identified. The full results of WPs 2-4 are presented in separate reports, as these take would take too much space in a single volume. The current report describes the work and results obtained in WP4.

2.3 Aims of work package 4 - demography

The main question for the research to be set up with input from this desk study is: How does the importance of key marine areas for seabirds affect their population dynamics through changes in survival, reproduction, and dispersal? This leads to the following research questions in WP4 of the desk study:

- Where in the Netherlands and elsewhere around the southern North Sea have population studies on this species group been conducted and what information have these, and other studies provided with respect to the main drivers of their population dynamics?
- Do structural gaps in knowledge exist that hamper our understanding of the relationships between the ‘important at sea areas’ and population dynamic parameters of the relevant species?

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 conditions in the at-sea areas important for them, with a clear focus on relationships with 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 clear in work packages 2 (foraging areas) and 3 (diets). The underlying aim is to incorporate this type of knowledge in (a series of) ecosystem models, enabling to explore in spatially explicit scenarios the potential consequences of various changes (anthropogenic or autonomous) in the system.

WP4 focuses on five species of gulls and terns among the selected species (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 them, however, utilise North Sea resources outside the breeding season as well, so conditions in other 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 included in this work package. Because it is not straightforward to initiate field studies in far-away breeding areas, the effort for these species was limited to a review of available international literature.

2.4 Report structure

2.4.1 Structure of this report

This report covers two main topics: (1) a summarising overview of measured values of key demographic parameters of the focal seabird species, and (2) a review of published studies on the relationships between these demographic parameters and abundance/availability of food resources. With respect to the coverage of species, a division is made between those that have breeding populations in The Netherlands (treated in chapter 4) and species that breed elsewhere but occur in the Dutch part of the North Sea during migration and wintering (treated in chapter 5). The black-legged kittiwake is treated here as a non-breeding species, although it does breed in small numbers on offshore platforms in the Dutch North Sea.

Chapter 3 introduces key choices made and concepts used, and describes the methods used in the review and the presentation of some of the results in digital annexes to the report. Chapters 4 and 5 contain the species accounts for breeding and non-breeding seabird species, respectively. These accounts have the following structure: (a) a short introduction to the species' distribution, migratory behaviour, and occurrence in The Netherlands; (b) a short description of demographic studies on the species, with emphasis on studies in The Netherlands (for breeding species); (c) summary and short discussion of available estimates of key demographic variables, and (d) review of published studies on the relationship between demographic variables and food resources. Chapter 4 on breeding species starts off with a description of general programmes for monitoring of breeding productivity and ringing effort yielding survival information in The Netherlands. In chapter 6, the findings in chapters 4-5 are summarised and existing gaps discussed, as well as avenues to fill these by future studies.

2.4.2 Information presented in the main report

The main report on the MONS desk study of birds (van Donk *et al*. 2025) integrates the results of the three separate desk studies and works out options for (field) research aimed to fill the information gaps identified. The information in the current report is summarised in chapter 4 of Van Dongen *et al*. (2025), and a proposal for field studies in a selection of breeding colonies of gulls and terns is elaborated in chapter 5. Otherwise, the main report does not contain detailed information not mentioned in the current report.

2.4.3 Worksheet annexes

The results of this study are presented in tables and text in this report, but also in the form of digital annexes (excel worksheet files) containing the underlying data. These files are:

- Five tables, one for each of the five breeding gulls and tern species, containing information on breeding colonies in the coastal provinces of The Netherlands: location, numbers of breeding pairs within the most recent 10-years period, data on breeding productivity in this period if available, and whether birds have been ringed there.
- Two tables containing data extracted during the review of demographic studies, one for the breeding species and one for the non-breeding species. These worksheets list per species the publication details (authors, titles, publication year and source, as well as url's where available online), subjects covered, geographical scope, and details of the studies' results: data on breeding productivity, survival, recruitment age, breeding propensity. For studies addressing food relationships the main results are described succinctly.

Box 1: Abbreviations and terms used in this report

Abbreviation/term	Explanation
breeding productivity	Number of fledged young produced per pair (fy/pr) per breeding season. Also alluded to as ‘reproductive output’ or ‘breeding success’.
breeding propensity	The probability that a surviving adult that already has bred at least once will breed in a given season. This is the compliment of the incidence of ‘skipped breeding’.
fy/pr	Fledged young per (breeding) pair; the primary measure of breeding productivity.
Holland Coast	The mainland coast of Noord- and Zuid-Holland between Den Helder and Hoek van Holland.
HPAI	Highly Pathogenic Avian Influenza; the severe form of ‘bird flu’
IBN-DLO	Instituut voor Bos- en Natuuronderzoek, nowadays part of Wageningen Environmental Research
INBO	Instituut voor Natuur- en Bosonderzoek, the research institute for nature of the government of Flanders, Belgium.
MWTL	Monitoring Waterstaatkundige Toestand des Lands; environmental monitoring program run by Rijkswaterstaat (https://waterinfo-extra.rws.nl/monitoring/)
NEM	Netwerk Ecologische Monitoring; national framework of ecological monitoring schemes, run by national ministries and provinces to inform policymaking and management (www.netwerkecologischemonitoring.nl/)
MONS	(Monitoring, Onderzoek, Natuurversterking en Soortenbescherming) Monitoring, Research, Nature enhancement and species protection – a research program of NZO
(age at) recruitment	(Age at which) The first breeding attempt (including at least egg-laying) in the life of a bird (is made).
SEAPOP	Long-term monitoring and mapping programme for seabirds in Norway, Svalbard and adjacent sea areas, established in 2005. (https://seapop.no/en/)
SD_e	Standard deviation of estimates. This is the s.d. over mean values (of demographic parameters) reported by different studies.
SD_p	Standard deviation of the environmental process. The ‘process’ is usually variation between years, but in some cases variation between sites or a combination.
SMP	The Seabird Monitoring Programme assesses the status of Britain and Ireland’s seabird populations by monitoring trends in their abundance and productivity at both coastal and inland sites (https://app.bto.org/seabirds/public/index.jsp).
survival	The probability that a bird alive at a give time is still alive at some later point in time. In this report, survival is always quantified as an annual probability, unless stated otherwise. This also applies when survival is reported for age categories including more than 1 year; e.g. when S=0.65 for age group “1st+2nd yr”, the actual probability to survive from fledging to age 2 is 0.65^2=0.42.
TMAP	Trilateral Monitoring and Assessment Programme; a joint monitoring programme in the international Wadden Sea by The Netherlands, Germany and Denmark (https://www.waddensea-worldheritage.org/trilateral-monitoring-and-assessment-programme-tmap)
WBAT	WideBand Autonomous Transceiver (WBAT), an echosounder that can record abundance and depth distribution of fish in the water column during extensive periods at a fixed site.
Wozep	Wind op zee ecologisch programma This research program addresses effects of offshore wind development on birds, bats and marine mammals and their habitat, for use in policy and management.

Box 2: Fish and invertebrate species mentioned in this report

Enlish name	Dutch name	scientific name
anchovy	ansjovis	*Engraulis encrasicolus*
Atlantic mackerel	makreel	*Scomber scombrus*
capelin	lodde	*Mallotus villosus*
cod	kabeljauw	*Gadus morhua*
herring	haring	*Clupea harengus*
pipefish	zeenaald	*Sygnathus spp.*
sandeel (sand lance)	zandspiering	*Ammodytes spp.*
saithe	koolvis	*Pollachus virens*
(brown) shrimp	garnaal	*Crangon spp.*
sea butterflies	zeevlinders	*Thecosomata*
sardine	sardine	*Sardina pilchardus*
smelt	spiering	*Osmerus eperlanus*
sprat	sprot	*Sprattus sprattus*
stickleback	stekelbaars	*Gasterosteus aculeatus*

3 Methods

3.1 Key demographic parameters and concepts

3.1.1 Key parameters reviewed in this study

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. Survival and reproductive output are key demographic parameters that need to be quantified in order to understand the dynamics of a population, for survival preferably separately for different age categories. In research studies a diversity of other features may be reported, sometimes serving as proxies for key demographic parameters that are less easily measured, sometimes because they convey additional information on ecological processes and causal pathways. For instance, the body condition (mass at age) of growing chicks may explain or predict variation in chick survival and breeding productivity, but mass at fledging may also affect the birds' survival over some time period thereafter, or even their 'quality' when adult, expressed in recruitment age or breeding success. These and other relationships form an intricate web of possibilities that can make summarising the literature on relationships between feeding conditions and demography a complicated task, unless a clear focus is chosen.

The background of the current study is the MONS programme, in which an ultimate aim is to develop a suite of models that feed into each other and allow exploring, for instance, how changes at any trophic level in the ecosystem affect the other levels, from producers and primary consumers up to top predators (seabirds and marine mammals). With such ecosystem models, the potential effects of various types of changes could be explored. Models describing the top predators in this chain cannot generally include complexities like the above example, but work with 'simple' relationships between the environment (e.g. abundance of a prey type) and key demographic parameters. For this reason, we focus in this review on the key parameters of matrix population models (Caswell 2025), the type of models most often used to describe the effect of environmental factors on populations of (higher) animals, including seabirds (e.g. Potiek *et al.* 2019, Soudijn *et al.* 2025).

In such models the size and development of a population is determined by the balance of two key demographic processes: reproduction and mortality (survival). Movement (immigration and emigration) can be an additional driving process, but this depends on the scale of the population in question, with influence diminishing from the local scale to an entire species range. As a result of this scale-dependence, quantifications of the movement process can usually not be generalised to situations other than where they were measured. Therefore we have largely ignored movement parameters in this review, but of course the possibility that net immi- or emigration occurs should be kept in mind in modelling studies. Of the species addressed in this report, some show very high site-fidelity (e.g. common guillemot), while others (e.g. Sandwich tern) do not.

In this report we focus on these key parameters describing reproduction and mortality:

1 **Age-specific annual survival probabilities**. Survival is the complement of (1 minus) mortality. The seabird species covered in this report are all long-lived (for birds in general), with high annual survival rates. Survival is usually lower in the first year after fledging, when young birds must learn to feed and survive independently. This process as well as their physical maturation can take several years, and therefore survival is described

separately for three age classes, ‘first-year’ (from fledging -or age at ringing- to 1 year old), ‘immature’ (second year or a few additional years, depending on the species; survival may increase gradually during this period but usually a mean value is provided), and ‘adult’ (generally from the age at which birds become physically capable of reproduction or actually start to breed). Although survival may still change over time in the adult category (e.g. through experience or ageing effects) this is often ignored in population models, if only because such information is lacking for most species. 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 for breeding productivity, although this will lead to some underestimation if clutch losses are followed by renesting within the same season (which is not common in most of the focal species, except perhaps in terns). As with survival, we disregard any age-related variation in the productivity of established breeders. This metric is 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: while the lower limit is set by the attainment of reproductive maturity, the chance for a bird to access into the breeding population may be constrained by competition for nest sites, mates, etc. Variation in the age at first breeding is one way in which density-dependence becomes apparent in seabirds. Matrix population models can either use a fixed mean age at recruitment or incorporate information on its distribution for greater accuracy; if the latter is available we report it.

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. Therefore it is important to quantify this ‘skipping’ using a parameter called breeding propensity, the probability that an adult will breed in any given year, and incorporate it in the population model, either by multiplying with the breeding productivity parameter or as a transition probability to a category of non-breeding adults.[1]

3.1.2 Parameter variability

In this report we present and summarise estimates of the key demographic parameters discussed above, extracted from published literature. These literature data 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. In summarising the results of our review, we report the means and two different measures of variability for these estimates, which can be used in different ways in matrix population models:

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[1] Note that even if skipping can be measured at breeding sites this may still overestimate the true average reproductive output per adult in the population if some birds never get to make a breeding attempt. Any such segment could remain largely ‘out of sight’ of researchers.

SD_e – the ‘standard deviation of estimates’ describes 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 distribution defined 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 time. (In case a model is constructed for a specific population in which demographic parameters actually have been measured or estimated, this ‘general parameter uncertainty’ does not apply and the standard error (SE) of the estimates obtained in the population at hand can be used to describe the parameter uncertainty instead. Because this will probably not often be the case, we do not reproduce these standard errors in the results tables; they should be retrieved from the original publications.)

SD_p – the ‘standard deviation of the environmental (time) process’ is used in stochastic population modelling to represent variability in demographic parameter values caused by stochastic (random) environmental fluctuations over time. (Often it is unknown what environmental factor(s) cause(s) this variability.) 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. For several species and parameters, multiple published studies 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.

3.2 Information on Dutch breeding colonies

The information on Dutch breeding colonies of gulls and terns, contained in the digital annexes (excel tables), is derived from Sovon’s databases on colonial breeding birds and breeding success of coastal birds. From the colony databases, all known colonies in Dutch provinces bordering the North Sea were extracted, and listed with colony name and site coordinates. For each colony, information on breeding numbers in the most recent 10 years is presented (a 10-year period was chosen as it is short enough for the mean colony size to represent the current situation, and long enough to represent the interannual variation). Information on breeding productivity in each colony was added from the breeding success database for those same years if available. The tables were further augmented by information on ringing and research activities, obtained from published reports and papers and from interviews with active researchers of breeding gulls and terns in The Netherlands.

3.3 Literature review

We conducted a literature search for Dutch and English-language publications on demography and food relationships in the focal species. The search for Dutch publications included ‘grey’ literature (reports), retrieved with the aid of the google search engine or obtained directly from researchers. International literature was searched with google, Web of Science, and an AI engine. The following key words were used:

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*

Returns of the searches were perused and relevant publications downloaded, with the main focus on publications about the North Sea and wider Atlantic region. Results from the Pacific region were mostly ignored. Data on key demographic parameters and summary lines on food relationships were extracted and entered into the literature tables.

In the species' accounts about key demographic parameters, the data in the excel literature files and data from Dutch breeding colonies are summarised in tables. For breeding productivity these contain a summary (means by region) of the data available from Dutch colonies in the past 10 years, augmented by results from a selection of earlier or long-lasting studies in The Netherlands, and from a selection of reviews and long-lasting studies in other countries. These tables in the main text do not contain all the information/studies available in the excel spreadsheet, but provide a representative summary. The same applies to information presented on survival rates. For age at recruitment and breeding propensity usually so few data were available that these are not tabulated but described textually. In addition to mean parameter values we present standard deviations across the means of different studies (SD_e) and standard deviation of interannual variability in the parameter values (SD_p; see §3.1.2 for explanation of these concepts).

4 Seabirds breeding in the Netherlands

4.1 Demographic monitoring in gulls and terns in The Netherlands

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. There have also been several (often multi-year) demographic studies with a higher research intensity and more specific research questions in a number of species and locations. These will be mentioned in the species accounts below. First, we briefly describe the more generic frameworks in which demographic data of seabirds breeding in The Netherlands are collected.

4.1.1 Monitoring of breeding productivity

Collecting data on the reproductive output (or ‘breeding productivity’ or ‘breeding success’) of coastal breeding birds in The Netherlands has a long history in certain species and sites (e.g. Sandwich Terns on Griend in the Wadden Sea), but became more widely established since the 1990s and 2000s. Currently, systematic monitoring of breeding success of terns and gulls is in place in both the southwestern Delta Area and in the Wadden Sea, the two main breeding regions for the species considered. The monitoring focuses primarily on estimating the number of fledged young per breeding pair. In some areas, data are also collected on success during the egg and chick phases, to gain insight into the stage of the breeding process at which any losses occur. 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 after hatching.

In the Delta Area, breeding productivity monitoring was initiated in the early 1990s by the (then) Dienst GetijdeWateren of Rijkswaterstaat, in the wake of monitoring of breeding numbers (e.g. Meininger *et al.* 1999, Schekkerman *et al.* 2017), and is currently carried on by Delta MilieuProjecten. Because assessing reproduction was initially not a formal part of the monitoring within the MWTL program, a method was developed that could be combined with colony surveys with limited extra effort. Since 2020 this work is fully included in MWTL, focusing on Sandwich, common, arctic and little terns and common, lesser black-backed, herring, great black-backed and Mediterranean gulls. Each year, breeding sites in the Voordelta, Haringvliet, Grevelingen, Oosterschelde, Veerse Meer, and Westerschelde are surveyed by a limited number of targeted visits. During the first visits the breeding stage of the colony is determined and follow-up visits are scheduled to make the most accurate count or estimate possible of the number of large, almost fledged chicks. Results are reported annually (e.g. Lilipaly & Sluijter 2024).

In the Wadden Sea region, breeding productivity of coastal breeding birds is monitored in the ‘Reproductiemeetnet Waddenzee’, started in 2004 and since 2010 part of the Trilateral Monitoring and Assessment Programme (TMAP) in de international Wadden Sea, and included in the national framework for ecological monitoring (NEM). 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, 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 international Wadden Sea is divided into 15 sub-areas, and the aim is to obtain at least one estimate of breeding success of each species occurring there. The annual results are reported at approximately three-year intervals (e.g. Koffijberg *et al.* 2021).

4.1.2 Survival studies

Information on the survival of birds is usually obtained through ringing studies: 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. Vogeltrekstation) generally yields dead recoveries, often reported by the general public, but can also yield live recaptures or resightings, often by dedicated researchers of the species involved. A suite of statistical methods has been developed to estimate survival rates from such data (e.g. Williams *et al.* 2002, Cooch & White 2025). If survival is estimated from live encounters, permanent emigration from the study area cannot be separated from death and the resulting estimate is a combination of survival and fidelity to the study site, termed 'apparent survival'. By using individual colour-marks that can be read in the field, the number of reports can be greatly increased and the 'local' study area expanded, leading to better estimates. Recoveries and live re-encounters can also be combined in joint analyses, which then yields estimates of both true survival and site fidelity. Ringing also provides information on dispersal, but a common problem in quantifying dispersal is that the probability that a ringed bird is reported from a location is dependent on observers being active there, and this can lead to spatial bias.

Ringing of gulls and terns has a long history in The Netherlands, partly because in these species several tens to a few hundreds of chicks can be ringed in a single visit to a breeding colony. As a result, a total of almost 438.000 individuals of the five breeding gull and tern species covered in this study was 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.

4.2 Lesser Black-backed Gull

4.2.1 Species introduction and population in The Netherlands

The lesser black-backed gull is a large gull with an extensive breeding distribution in western and northern Europe. Breeding birds from NW Europe migrate away in the autumn to winter in SW Europe and NW Africa; only small numbers remain in The Netherlands. In their feeding ecology, lesser black-backed gulls are more marine-oriented than herring gulls, but in the past decades foraging inland in agricultural and urban areas has increased.

The Dutch breeding population was estimated at approximately 82.500–86.000 pairs in 2024 (Boele *et al.* 2025). The species established as a breeding bird only in 1926, as part of an expansion in the North Atlantic region. After many decades of sustained increase, the national breeding population has been in decline since about 2010 (recent trend over 2013-2024: moderate decline; fig. 1).

Lesser black-backed gulls breed predominantly in large colonies on the Wadden Sea islands and in the SW Delta region, including the Port of Rotterdam and Maasvlakte. Former large colonies in the coastal dunes of Noord- and Zuid-Holland were vacated after Red Fox

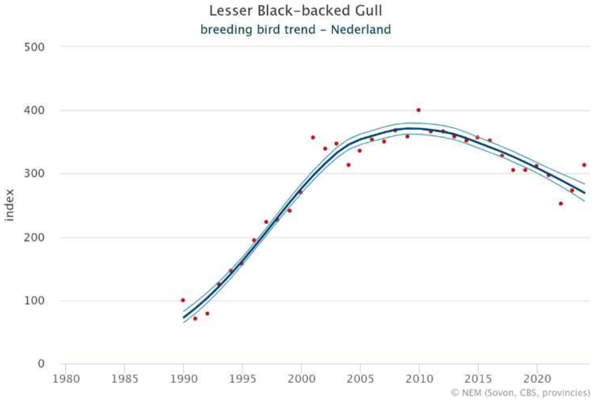

Fig. 1. Trend of lesser black-backed gull as a breeding bird in 1990-2024. Shown are the annual population-index, calculated from national totals or population in core breeding areas (red dots) and the trendline (dark blue line) with 95% confidence interval (light blue lines). Data is derived from the annual survey of colonial and rare breeding birds.

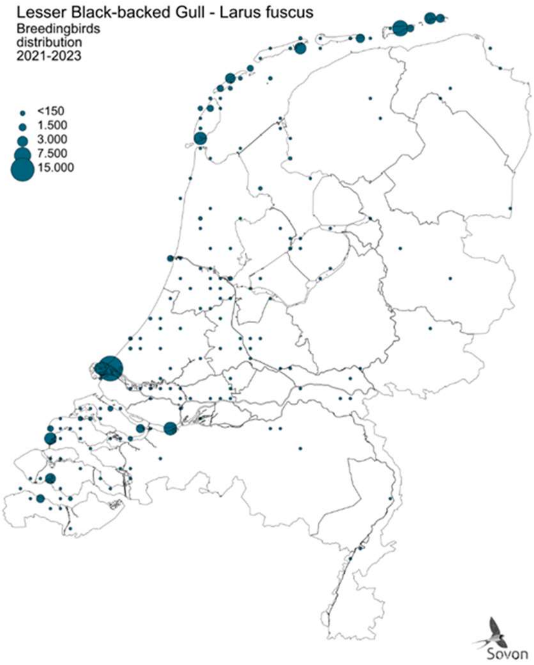

Fig. 2. Breeding distribution of the lesser black-backed gull in 2021-2023. For each atlas square of 5x5 km the highest counted number of breeding pairs is indicated. Data from the annual survey of colonial and rare breeding birds.

became established here in the 1980s. In 2013–2015, an estimated 50% of the national population bred in the Delta Area and c. 40% on the Wadden Islands (Sovon 2018). In recent decades, the breeding distribution has expanded inland, with colonies increasingly established on rooftops and artificial islands. Currently about 5–12% of the national population breeds on roofs, with the highest concentrations found in the Randstad conurbation (van Turnhout *et al.* 2023). This trend began in the late 1980s, when birds relocated from the dwindling dune colonies to cities in Noord- and Zuid-Holland (Vegelin 1989, Spaans 1998). Within the Delta region, a shift from the North Sea coast towards the eastern Delta has been observed, coinciding with a change in foraging habitats from marine habitats to agricultural grasslands, urban environments, and landfills (Meininger 2022).

4.2.2 Demographic studies

4.2.2.1 The Netherlands

In The Netherlands a number of demographic studies on lesser black-backed gulls has been ongoing, usually combined with studies on herring gulls as these species often form mixed colonies. Among the most detailed and wide-ranging is the study in the Kelderhuispolder dunes of Texel which was established in 2006 by Camphuysen and coworkers (NIOZ and University of Amsterdam), and is still ongoing. This study addresses reproductive success, annual survival, recruitment, diet and spatial foraging behaviour. Each year a suite of parameters is monitored in a standardised way during colony visits every third day. Breeding birds and large chicks are ringed with coded colour-rings, and adult birds have been tracked with GPS-tags to study colony attendance, spatial foraging behaviour and migration. This study has led to two PhD theses (Camphuysen 2013[2], van Donk 2019) and numerous publications (e.g. Camphuysen & Gronert 2012, van Donk *et al.* 2019, Camphuysen *et al.* 2024).

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[2] This PhD Thesis and literature references therein form the most comprehensive assembly of information on the ecology of lesser black-backed and herring gulls in the Netherlands up to 2013.

Earlier studies in the Wadden Sea region have been conducted by Spaans and coworkers (IBN-DLO) at the Boschplaat on Terschelling, mainly directed at unravelling the effects of (seasonal) food limitation, parental quality and (intraspecific) predation on breeding productivity (Brouwer *et al.* 1995, Bukacinska *et al.* 1996, Bukacinski *et al.* 1998).

Along the 'Holland Coast' between Den Helder and Hoek van Holland, the Forteiland ('fortress island') at IJmuiden harbours one of the larger remaining gull colonies. Here, breeding numbers and breeding success are followed by volunteer researchers since 2008 and adults and chicks are colour-ringed (connected to the Texel scheme). Tracking of adult and juvenile lesser black-backed gulls has also been undertaken from this colony, by NIOZ and the University of Amsterdam[3].

In the SW Delta Area, colour-ringing of large gulls has been ongoing for several decades. The largest ringing project has been conducted by Buijs Eco Consult, initiated at the port and industrial area of Moerdijk, later extended to Vlissingen-Oost, Rotterdam/Maasvlakte, Neeltje Jans and various other Natura 2000 areas in the Delta. The colour-ring resightings have been used to study foraging movements, e.g. to cities (e.g. Huig *et al.* 2016) and to obtain survival estimates (Schekkerman *et al.* 2021). In recent years, studies on large gulls in the Delta Area have been intensified with a view on potential effects of offshore wind energy development (Wozep programme), and have combined tracking of gulls with the collection of breeding data (Gyimesi *et al.* 2011, Vanermen *et al.* 2022, van Bemmelen *et al.* 2022). This work is carried out by researchers from INBO, Waardenburg Ecology and Buijs EcoConsult.

4.2.2.2 Other North Sea countries

In the Voorhaven (outer port) of Zeebrugge in Belgium, breeding lesser black-backed and herring gulls have been studied since 1999, when a colour-ringing project was started. From at least 2010 onwards, detailed studies into breeding ecology and life-history have been conducted by researchers from INBO (e.g. Bosman 2016). Elsewhere, lesser black-backed (and herring) gulls have been studied in multiple sites around the North Sea since the 1960s and 1970s. Several of those studies were initiated in response to the strong population increase in that era, which was viewed unfavourably and even led to massive culls (e.g. Harris *et al.* 1982). In Britain and Ireland, gull populations have been monitored within the Seabird Monitoring Programme (SMP) since 1986. Data on breeding numbers and breeding productivity at many sites are available from the SMP database[4]. At four 'Key Sites' within the program, additional data are systematically collected on phenology, diet and adult survival of seabirds: Isle of May (E Scotland), Fair Isle (Shetland), Canna (W Scotland) and Skomer (Wales). On the German Wadden Sea islands, monitoring of breeding productivity is part of the TMAP program, and a few colour-ring studies are in place yielding information on survival (e.g. Dierschke *et al.* 2021). In Norway, multiple gull colonies are included in the SEAPOP monitoring program running since 2005, in which breeding numbers, productivity and adult survival (based on colour-ringing) are monitored[5].

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[3] https://www.uva-bits.nl/projects/daily-movements-of-gulls-from-forteiland-ijmuiden/

[4] https://app.bto.org/seabirds/public/index.jsp

[5] https://seapop.no/en/

4.2.3 Key demographic variables

4.2.3.1 Survival

There is a good amount of information on survival of lesser black-backed gulls, both from The Netherlands and from various other sites in NW Europe, of which a selection is summarised in table 2. For the Netherlands, estimates from the Wadden Sea islands (Texel) and the SW Delta (including Zeebrugge, Belgium) conform fairly well except those for first-year birds. Estimates of adult survival from abroad are of the same magnitude as those from The Netherlands, and there is little evidence that older data yield systematically higher (or lower) estimates, although Schekkerman *et al.* (2021) noted a decline in adult survival in the SW Delta over 2003-2019. Overall, estimates of adult annual survival in table 2 vary from 0.82 to 0.94, with a mean of 0.89 and SD_e (variation among mean estimates) of 0.03. Reported standard deviations of between-year variability (SD_p) in adult survival vary around 0.06.

For survival of younger age classes fewer estimates are available, particularly from Denmark and Norway from where many lesser black-backed gulls migrating through the North Sea originate. A number of colour-ring projects has been in place in this region for a substantial time, and analyses of resightings in the breeding areas or along the European seaboard should allow useful estimates to be made. Those existing for first-year survival average 0.67 (SD_e 0.15). Survival of immatures is closer to that of adults than first-years: the mean is 0.87 (SD_e 0.03). Reported standard deviations of between-year variability (SD_p) vary around 0.09 for first-year survival and 0.05 for immatures, suggesting that annual variability is greater in young birds (c. 13% of the mean) than in immatures and adults (6-7%).

Table 2. Published estimates of annual survival probabilities for lesser black-backed gull. Standard deviations denote variability across years or across sites/years. More data for specific sites and years can be found in Annex IIa.

area	Period	adult	SD_p	imm.	SD_p	1st yr	SD_p	source
NL: Texel	2006-2011	0.91	0.05	0.83	.	0.31	0.08	Camphuysen 2013
NL/B: Delta Area	2003-2019	0.90	0.03	0.91	0.05	0.65	0.06	Schekkerman *et al.* 2021
B: Zeebrugge	1991-2012	0.91	.	.	.	.	.	Bosman *et al.* 2016
D: Helgoland	2006-2014	0.89[1]	0.05	.	.	0.80	0.07	Dierschke *et al.* 2021
D: Amrum	2006-2014	0.90[1]	0.05	.	.	0.67	0.13	Dierschke *et al.* 2021
DK: Langli	2009-2014	0.89[1]	0.05	.	.	0.72	0.09	Dierschke *et al.* 2021
UK: United Kingdom	Review	0.89[3]	0.02	.	.	0.82[2]	.	Horswill & Robinson 2015
UK, Isle of May	1989-1994	0.91	.	.	.	.	.	Wanless *et al.* 1996
UK, Isle of May	1966-1974	0.94	0.08	.	.	.	.	Chabrzyk & Coulson 1976
UK, Bristol	1991-2006	0.82	0.11	.	.	.	.	Rock & Vaughan 2013
UK, Skomer	1978-2019	0.88	0.07	.	.	.	.	Newman *et al.* 2021
NO: Horsvaer	2005-2023	0.88	.	.	.	.	.	SEAPOP; e.g. Fayet *et al.* 2025
NO: Vestland	2009-2024	0.85	.	.	.	.	.	SEAPOP; e.g. Fayet *et al.* 2025
NO: Rauna	2007-2024	0.83	.	.	.	.	.	SEAPOP; e.g. Fayet *et al.* 2025
Arctic Waters	model[4]	0.91	.	0.89	.	0.75	.	Frederiksen *et al.* 2025
Greater North Sea	model[4]	0.89	.	0.87	.	0.63	.	Frederiksen *et al.* 2025
Celtic Seas	model[4]	0.90	.	0.89	.	0.71	.	Frederiksen *et al.* 2025

[1] all birds >1st year; [2] 1st+2nd yr; [3] 3rd yr and later; [4] Baseline values taken from Robinson 2010, calibrated on observed breeding output and population development.

4.2.3.2 Recruitment and adult breeding propensity

Horswill & Robinson (2015) place age of first breeding at 5 years citing Harris (1970), who however commented that of the known-age breeders in his paper "many doubtless had bred a season or more before being caught". At Zeebrugge, Belgium, age at recruitment ranged between 3 and 7 years with a mean of 4.1 yrs (Bosman *et al.* 2016).

Rather little information is available on adult breeding propensity. Calladine & Harris (2008) found that in two years, 34% and 40% of birds ringed as breeders on the Isle of May that were seen in the (then growing) colony did not breed (average breeding propensity 0.63). Common amongst the intermittent breeders were smaller individuals, birds with low survival chances and less successful breeders. In the Kelderhuispolder on Texel, Camphuysen (2013) estimated an incidence of 22% 'skipped breeding seasons', but also noted that a significant proportion of the birds that made a nest did not lay eggs. Only 46% of adult lesser black-backed gulls returning to the colony were confirmed to breed (although some may have been missed). Depending on the definition used, breeding propensity was thus either c. 0.5 or 0.78.

4.2.3.3 Breeding productivity

Table 3 summarises data on breeding productivity of lesser black-backed gulls in The Netherlands for the recent period 2014-2023. It also shows results of a few Dutch studies dating further back in time, and of a selection of studies elsewhere in Europe. The recent mean breeding productivity in Dutch colonies was 0.51 fledged young per breeding pair. Lesser black-backs breeding on the Wadden Islands seem to be slightly more productive

Table 3. Summary of data on breeding productivity (young fledged per breeding pair) of lesser black-backed gull. The upper part of the table summarises data present in the breeding success database of Sovon, as the means (weighted by colony size) and standard deviations by region over colonies/years in 2014-2024. The middle contains published data from the Netherlands in a selection of earlier periods and well-studied sites. The lower part of the table contains a selection of published data from other countries in the North Sea region and elsewhere in Europe. More data for specific sites and years can be found in Annex Ia (for Dutch colonies) and Annex IIa.

Area	Period	N	fy/pr	SD_p	Source
Netherlands, all areas	2014-2023	95	0.51	0.31	Annex Ia
Wadden Sea islands	2014-2023	33	0.59	0.30	Annex Ia
SW Delta, coastal	2014-2023	58	0.48	0.28	Annex Ia
SW Delta, interior	2014-2023	23	0.44	0.38	Annex Ia
Texel, Kelderhuispolder	2006-2021	16	0.49	0.23	Camphuysen *et al.* 2024
Wassenaar	1980	1	1.77	.	Spaans 1998
Moerdijk	1997	1	1.50	.	Spaans 1998
Germany, Niedersachsen	2010-2012	5	0.65	0.31	Thorup & Koffijberg 2016
Germany, Schleswig-Holstein	2010-2012	7	0.25	0.17	Thorup & Koffijberg 2016
Denmark, Langli	2009-2012	4	0.59	0.62	Thorup & Koffijberg 2016
United Kingdom, nationla average	1986-2014	>100	0.53	0.33	Horswill & Robinson 2015
UK, England, North Sea coast	2015-2025	28	0.31	0.32	SMP database
UK, Wales, Skomer Island	1995-2021	27	0.40	0.22	Newman *et al.* 2021
Norway, North Sea colonies	2018-2024	13	0.72	0.29	SEAPOP, e.g. Fayet *et al.* 2025
Arctic Waters (OSPAR region I)	1986-2019	.	0.46	0.35	Frederiksen *et al.* 2023, 2025
Greater North Sea (OSPAR II)	1986-2019	.	0.70	0.29	Frederiksen *et al.* 2023, 2025
Celtic Seas (OSPAR region III)	1986-2019	.	0.34	0.20	Frederiksen *et al.* 2023, 2025

(0.59 fy/pr) than those in the SW Delta Area (0.44-0.48 fy/pr), in line with an increasing trend there over the period 2004-2019 reported by Koffijberg *et al.* (2021). Spaans (1998) alluded to breeding success formerly being higher in the Delta, and this seems to also have been the case in the mainland dunes before Red Foxes invaded. Some of the estimates from abroad are also somewhat higher than the recent Dutch ones, but most are in the same range.

The mean of the breeding productivity estimates in table 3 (excluding those based on one year's data) is c. 0.50 fy/pr (SD_e 0.14). SD_p values of interannual variation average around 0.30, which is 60% of the mean, indicating that breeding productivity is quite variable.

To put these productivity values in perspective, the mean annual breeding output necessary to obtain a stable population trend was estimated at roughly 0.63 fy/pr by Schekkerman *et al.* (2021) based on data from the Delta Area. Frederiksen *et al.* (2025) estimated it at 0.42-0.69 fy/pr, using population models calibrated on observed population trajectories and productivity data from three OSPAR regions, slightly lower age at recruitment and higher adult breeding propensity.

4.2.4 Relationships between demography and food resources

Studies on the dependency of breeding success in large gulls on food resources have been conducted in The Netherlands as well as elsewhere, but have not resulted in quantitative relationships between productivity and measures of food abundance, such as could be used directly in population models. This will be largely due to the difficulty of measuring food availability in opportunistic foragers with a wide prey spectrum like large gulls. We have found no studies relating survival rates, age at recruitment or breeding propensity of lesser black-backed gulls to (indices of) food abundance.

Breeding productivity

In the Netherlands, Spaans and coworkers investigated the role of food in the breeding ecology of Lesser-black backed gulls on Terschelling in the 1990s, while Camphuysen and colleagues addressed it as part of their multi-faceted population study on Texel after the turn of the century. On Terschelling, food resources seemed to limit productivity of lesser black-backed gulls to some extent, as evidenced by experiments in which additional food was provided (Bukacinski *et al.* 1998). Pairs whose chicks were fed with additional food until fledging had higher fledging success than control pairs. Food-supplemented chicks showed higher daily mass gains and higher fledging mass at an earlier fledging age. Starvation occurred only in control chicks and in fed chicks after food provisioning had stopped. When food was in short supply, fledging success was affected due to starvation (lower feeding rates) and higher (intraspecific) predation rate, arising from changes in the behaviour of both adults and chicks.

On Texel, lesser black-backed gulls are clearly more marine-oriented than herring gulls and their diet is dominated by discarded fish species (Camphuysen 2013). In Belgian waters as well, lesser black-backed gulls dominate scavenging flocks behind fishing vessels at greater distance from the coast (Sotillo *et al.* 2014). Scavenging for discards was the main foraging tactic of male lesser black-backed gulls on Texel; the smaller (and less competitive) females accessed a wider variety of resources, including on land and in the Wadden Sea (Camphuysen *et al.* 2015). The importance of discards as chick food was evidenced by cyclic fluctuations in growth rate; chicks gained less mass during weekends when the fishing fleet was in the harbour (Camphuysen 2013). The mean breeding productivity of lesser black-backed gull on Texel was low during the study years, and small and declining egg volumes, smaller hatchlings, declining mass at fledging and high levels of cannibalism indicated structural food stress (Camphuysen 2013, Camphuysen *et al.* 2024). Reductions of discards produced at sea since the heydays around 1990, mainly due to reductions in fishing effort, seem to play an important role in this.

The relationship with discards could perhaps be quantified further by explicitly relating measurements of breeding productivity to data on fishing activity within the colonies' foraging range (available from vessel tracking systems), but this seems not to have been done yet. Oro (1996) did compare the breeding ecology of lesser black-backed gull in the Ebro Delta in NE Spain in two breeding seasons affected by a trawling moratorium at sea. When trawlers operated, diet was dominated by fish from discards, while during the moratorium gulls fed from refuse tips and olive groves. Breeding phenology and mean clutch size did not change, but egg volume decreased. Breeding productivity was higher in the first year than in the second when the moratorium overlapped with the entire period of chick growth.

Despite the general importance of marine foods, lesser black-backed gull also forage in other habitats including intertidal areas, agricultural grasslands and urban environments. At Zeebrugge, chicks fed terrestrial or urban foods by their parents showed slower early growth than those fed marine foods, but this was due to food quantity rather than quality differences as chicks fed same foods *ad libitum* in the laboratory did not show growth differences (Sotillo *et al.* 2019). Lesser Black-backs breeding 30 km from the coast in the Haringvliet, N Delta Area, focused entirely on terrestrial food sources and reached relatively high breeding success (Gyimesi *et al.* 2016), and so did gulls breeding in a grassland area in Noord-Holland of which the diet comprised only about 20% marine prey (Camphuysen *et al.* 2005).

Other demographic variables

We have found no studies relating survival rates of lesser black-backed gulls, or age at recruitment or breeding propensity, to (indices of) food abundance. Hjernquist & Hjernquist (2010) reported that population size of lesser black-backed gulls (of the subspecies *L.f. fuscus*) on Lilla Karlsö in the Baltic Sea in 1974-2007 was associated with the abundance of sprat but not its age-related mean weight (a measure of prey quality).

4.3 European herring gull

4.3.1 Species introduction and population in The Netherlands

The herring gull is a large coastal gull with an extensive breeding distribution in western and northern Europe. W European breeding birds (*L.a. argenteus*) exhibit only limited migratory movements (e.g. Camphuysen *et al.* 2011), but in the non-breeding season numbers here are augmented by migratory Scandinavian breeders (*L.a. argentatus*). Herring gulls are opportunistic foragers but intertidal food sources (shellfish, crabs) are important in many areas, as well as landfills and fisheries discards.

The Dutch breeding population was estimated at 26,750–29,000 pairs in 2024 (Boele *et al.* 2025). The population increased strongly from 1970 onwards due to reduced persecution and the availability of abundant food at landfills and fishing vessels. A maximum of nearly 90,000 pairs was reached in the early 1980s (Spaans 1998). The subsequent decline is mainly a consequence of predators (Red Fox) invading mainland colonies and reduced food availability due to covering of landfills, decline of intertidal mussel beds, and possibly diminishing fisheries discards. The recent short-term trend (2013–2024) is still moderately declining.

Breeding colonies of herring gull are located primarily in the coastal provinces. Strongholds are the dunes of the Wadden Sea Islands (40–50% of the national population in 2013–2015; Koffijberg 2018b) and the Delta region (35% in 2024; Lilipaly *et al.* 2025). In 2024 the largest colony in the Delta Area was at Neeltje Jans with 1400 pairs, while in the Wadden Sea region the largest colony was in De Geul on Texel with 1200 pairs (Boele *et al.* 2025). Just like Lesser black-backed gulls and triggered by the same processes, herring hulls increasingly breed on rooftops in inland areas. It is estimated that 4–11% of the Dutch herring gull population currently breeds on roofs (van Turnhout *et al.* 2023).

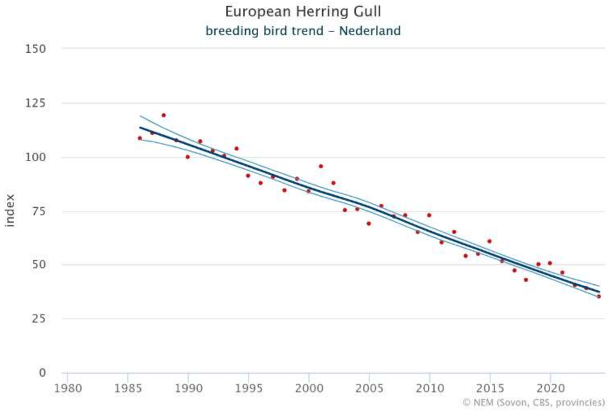

Fig. 3. Trend of the breeding population of European herring gull in 1990-2024. Shown are the annual population index, calculated from national totals or counts in core breeding areas (red dots) and the trendline (dark blue line) with 95% confidence interval (pale blue lines). Data from the annual survey of colonial and rare breeding birds.

Fig. 4. Breeding distribution of the European herring gull in 2021-2023. For each atlas square of 5x5 km the highest counted number of breeding pairs is indicated Data from the annual survey of colonial and rare breeding birds.

4.3.2 Demographic studies

Because they usually breed together in mixed colonies, demographic studies on herring gulls are often carried out in combination with studies on lesser black-backed gulls; see that species (§4.2.2) for the main existing projects. An early study not mentioned there 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 (and measured) in 12-14 colonies spread along the entire Dutch coast. The resulting resightings have yielded much information on seasonal movements (Camphuysen *et al.* 2011) and age-dependent and spatial patterns in survival (Kentie *et al.* 2023).

4.3.3 Key demographic variables

4.3.3.1 Survival

There is good information on survival of adult herring gulls, both from The Netherlands and from various other sites in NW Europe, of which a selection is summarised in table 4. These studies include both the resident or partly migratory W European subspecies *L.a. argenteus* and the Scandinavian form *L.a. argentatus*. No clear difference in adult survival is apparent between these.

Table 4. Published estimates of annual survival probabilities for European herring gull. Standard deviations denote variability across years or across sites/years. More data for specific sites and years can be found in Annex IIa.

area	**Period**	**adult**	**SD_p**	**imm.**	**SD_p**	**1st yr**	**SD_p**	**source**
NL: Texel	2006-2011	0.82	.	0.70	.	0.25	0.06	Camphuysen & Gronert 2012
NL: Delta Area	2003-2019	0.88	0.03	0.88	0.06	0.59	0.06	Schekkerman *et al.* 2021
NL: Wadden Islands	1986-2000	0.84	0.09[2]	0.89	0.03[2]	0.42	0.07[1]	Kentie *et al.* 2023
NL: Holland Coast	1986-2000	0.79	0.05[2]	0.89	0.02[2]	0.70	0.04[1]	Kentie *et al.* 2023
NL: Delta Area	1986-2000	0.74	0.07[2]	0.84	0.05[2]	0.63	0.05[1]	Kentie *et al.* 2023
B: Zeebrugge	2010-2015	0.75[2]	.	.	.	0.39	.	Bosman 2016
D: Amrum	2006-2014	0.82[2]	0.01	.	.	0.62	0.11	Dierschke *et al.* 2021
F: Crozon Peninsula	1983-1990	0.88	0.06	.	.	.	.	Pons & Migot 1995
UK, South Shields	1979-1985	0.91	0.08	.	.	.	.	Coulson & Butterfield 1986
UK, Isle of May	1989-1994	0.88	.	.	.	.	.	Wanless *et al.* 1996
UK, Skomer	1978-2019	0.82	0.09	.	.	.	.	Newman *et al.* 2021
UK, Bristol	1991-2006	0.83	0.14	.	.	.	.	Rock & Vaughan 2013
NO: Hornøya	2007-2024	0.86	.	.	.	.	.	SEAPOP, Fayet *et al.* 2025
NO: Vestland	2009-2024	0.82	.	.	.	.	.	SEAPOP, Fayet *et al.* 2025
NO: Rauna	2007-2024	0.83	.	.	.	.	.	SEAPOP, Fayet *et al.* 2025
UK, national	review	0.83[4]	0.03	.	.	0.80[3]	0.09	Horswill & Robinson 2015
Arctic Waters	model[5]	0.88	.	0.83	.	0.80	.	Frederiksen *et al.* 2025
Greater North Sea	model[5]	0.85	.	0.82	.	0.64	.	Frederiksen *et al.* 2025
Celtic Seas	model[5]	0.86	.	0.82	.	0.66	.	Frederiksen *et al.* 2025

[1] s.d. refers to between-colony variation; [2] all birds >1st year;; [3] 1st+2nd yr; [4] 3rd yr and older; [5] Baseline values taken from Robinson 2010, calibrated on observed breeding output and population development.

Kentie *et al.* (2023) reported substantial regional variation in survival within The Netherlands in the 1990s. Adults survived significantly better in northern (Wadden Sea Islands: 0.84) than southern colonies (Delta Area: 0.74). For first-year survival this spatial pattern was reversed (table 4). However, an analysis based on data from after 2003 from the Delta Area estimated adult survival at 0.88, even slightly higher than earlier in the Wadden colonies (although with a declining tendency), and an intermediate value for first-year survival (Schekkerman *et al.* 2021).

Overall, estimates of adult annual survival in table 4 vary from 0.74 to 0.91, with a mean of 0.84 and SD_e of 0.04. Reported standard deviations of between-year variability in adult survival (SD_p) vary around 0.06 (i.e. 6% of the mean value).

For survival of younger age classes far fewer estimates are available, and the recent Dutch studies contribute substantially to those. Surely a lot more information must be contained in colour-ring datasets elsewhere in Europe that have not yet been analysed or reported. Available estimates of first-year survival average around 0.59 (SD_e 0.17). Survival of immatures is closer to that of adults than first-years: the mean of estimates is 0.83 (SD_e 0.06). Reported standard deviations of between-year variability in survival (SD_p) vary around 0.06 for immatures and 0.08 for first-year birds (6-13% of the mean values).

4.3.3.2 *Recruitment and adult breeding propensity*

Horswill & Robinson (2015) place age of first breeding in herring gulls at 5 years citing Harris (1970), who however commented that of the known-age breeders in his paper "many doubtless had bred a season or more before being caught". Chabrzyk & Coulson (1976) and Coulson *et al.* (1982) provide detailed data from the Isle of May, Scotland, in two periods (table 5). After a massive cull that markedly reduced the local population size and breeding density, some 3-year and many more 4-year old birds started to breed than before the cull, resulting in a reduction of >1 year in the mean age at recruitment. Drost *et al.* (1961) found similar early recruitment in a new, growing colony at Wilhelmshaven (table 5). Vercruijsse (1999) reported that in the dunes of Schouwen most birds recruited at 5 or 6 years of age. These results indicate an average value of 4.9 years with SD_e of variation between studies of 0.6 years. Coulson *et al.* (1982) report no difference in the age at recruitment of male and female herring gulls.

Only scant information is available on adult breeding propensity. Calladine & Harris (2008) found that 33% and 37% of birds ringed as breeders on the Isle of May that were seen in the (growing) colony did *not* breed in 1993 and 1994 (average breeding propensity 0.65). Common amongst the intermittent breeders were smaller individuals, birds with low survival chances and less successful breeders. Camphuysen (2013) reported an incidence of 'skipped breeding seasons' of 15% on Texel, but also noted that a significant proportion of the birds that made a nest did not lay eggs; 63% of adult herring gulls returning to the colony were confirmed to breed (though a few may have been missed), which is similar to the Isle of May estimates. The high breeding propensity of 93-99% reported by Pons & Migot (1995) in a French colony is likely to be an overestimate, as non-breeders may have been elsewhere than on the local roost where such birds were identified.

Table 5. Published data on distribution of age at first breeding in herring gulls.

country,	**% recruiting at**		**age**	**(yrs)**		**mean**	**SD**	**source**
period	**3**	**4**	**5**	**6**	**7**	**age**	**age**	
UK 1966-1972	0%	14%	55%	23%	8%	5.25	0.80	Chabrzyk & Coulson 1976
UK 1973-1982	5%	60%	35%	0%	0%	4.30	0.56	Coulson *et al.* 1982
D 1948-1960	20%	25%	55%	0%	0%	4.35	0.80	Drost *et al.* 1961

4.3.3.3 *Breeding productivity*

Table 6 summarises data on breeding productivity of herring gulls in The Netherlands for the recent period 2014-2023. It also shows results of a few Dutch studies dating further back in time, and of a selection of studies elsewhere in Europe. The recent mean breeding productivity in Dutch colonies was 0.43 fy/pr. Herring gulls breeding on the Wadden Islands seem to be more productive (0.67 fy/pr) than those in the SW Delta Area (0.36-0.48 fy/pr). Earlier estimates from The Netherlands include both higher ones than the recent ones (Wadden Sea islands and Holland Coast early 1980s) and lower ones (Terschelling around 1990) (Spaans 1998). This is also the case in estimates made elsewhere in Europe, though higher values predominate, and are not confined to the previous century.

The mean of the breeding productivity estimates in table 6 is c. 0.73 fy/pr (SD_e 0.38). SD_p values of interannual variation range average around 0.30 (41% of the mean).

Table 6. Summary of data on breeding productivity (young fledged per breeding pair) of European herring gull. The upper part of the table summarises data present in the breeding success database of Sovon, as the means (weighted by colony size) and standard deviations by region over colonies/years in 2014-2024. The middle part contains published data from the Netherlands in a selection of earlier periods and well-studied sites. The lower part of the table contains a selection of published data from other countries in the North Sea region and elsewhere in Europe. More data for specific sites and years can be found in Annex Ib (for Dutch colonies) and Annex IIa.

Area	Period	N	fy/pr	SD_p	Source
Netherlands, all sites	2014-2023	30	0.43	0.41	Annex Ib
Wadden Sea islands	2014-2023	8	0.67	0.56	Annex Ib
SW Delta, coastal colonies	2014-2023	12	0.36	0.19	Annex Ib
SW Delta, interior colonies	2014-2023	10	0.48	0.51	Annex Ib
Texel, Kelderhuispolder	2006-2011	6	0.86	0.31	Camphuysen & Gronert 2012
Terschelling	1967-1969	3	1.37	0.06	Spaans 1998
Terschelling	1983-1984	3	0.29	0.17	Spaans 1998
Schouwen	1991-1994	4	0.68	0.23	Vercruijsse 1999
Germany, Niedersachsen	2010-2012	5	0.73	0.37	Thorup & Koffijberg 2016
Germany, Schleswig-Holstein	2010-2012	7	0.32	0.17	Thorup & Koffijberg 2016
Denmark, Langli	2009-2012	4	0.29	0.16	Thorup & Koffijberg 2016
France, Crozon Peninsula	1983-1988	5	1.37	0.10	Pons 1992
United Kingdom, national average	1986-2014	>100	0.92	0.48	Horswill & Robinson 2015
UK, England, E coast	2015-2025	34	0.47	0.49	SMP database
UK, Scotland, Isle of May	1989-1994	6	1.38	0.31	Wanless *et al.* 1996
UK, Shetland, Noss	2015-2025	9	1.56	0.56	SMP database
UK, Wales, Skomer Island	1995-2021	24	0.63	0.29	Newman *et al.* 2021
Norway, North Sea colonies	2018-2024	13	0.73	0.36	SEAPOP, e.g. Fayet *et al.* 2025
Norway, Barentz Sea colonies	2018-2021	5	0.30	0.21	SEAPOP, e.g. Fayet *et al.* 2025
Greater North Sea (OSPAR II)	1986-2019	.	0.80	0.33	Frederiksen *et al.* 2023, 2025
Arctic Waters (OSPAR region I)	1986-2019	.	0.70	0.48	Frederiksen *et al.* 2023, 2025
Celtic Seas (OSPAR region III)	1986-2019	.	0.72	0.25	Frederiksen *et al.* 2023, 2025

The mean annual breeding output necessary to obtain a stable population trend was estimated at 1.1 fy/pr by Schekkerman *et al.* (2021) based on data from the Dutch Delta. Frederiksen *et al.* (2025) estimated it to be 0.66-1.13 fy/pr, using population models tuned to the observed population trajectories in the in the North Sea, Celtic Seas and Bay of Biscay/Iberian coast.

4.3.4 Relationships between demography and food resources

Like for lesser black-backed gulls, several studies on the dependency of breeding success in herring gulls on food resources have been conducted in The Netherlands as well as elsewhere, but some of these have focused more on prey quality than on quantitative measures of food abundance. This will be largely due to the difficulty of quantifying food stocks in opportunistic foragers with a wide prey spectrum, such as the herring gull. Likewise, we have found no studies relating survival rates of herring gulls, or their age at recruitment or breeding propensity, to quantitative measures of food abundance.

Breeding productivity

Breeding herring gulls are significantly less marine-oriented in their foraging than lesser black-backed gulls. They do forage in significant numbers behind fishing vessels, but this is more restricted to the near-coastal zone (to 15-50 km; Camphuysen 2013, Sotillo *et al*. 2014). Herring gulls at Texel used intertidal resources (mussels, crabs etc) extensively and added fish to their diet during chick care. Among pairs, chick growth and fledging rates were positively related to the proportion of fish prey provided (Camphuysen 2013). Although growth rate of herring gull chicks showed similarly strong fishing-effort-related weekly fluctuations as observed in lesser black-backed gulls, the higher mean breeding productivity of herring gulls suggests that discard availability may have been less of a constraint for them. The fact that the productivity of herring gulls and lesser black-backed gulls on Texel was not significantly correlated over time also seems to indicate that different resources may be limiting (Camphuysen 2013).

Nevertheless, fish (often obtained behind fishing vessels) seems to be an important in the diet of herring gull chicks. In the 1990s, herring gull breeding success was studied in relation to time budgets and diet on Terschelling (Bukacinska *et al.* 1996). Successful pairs differed markedly in attendance patterns and diet from unsuccessful pairs. Unsuccessful pairs spent more time on the feeding grounds and left the territory unguarded more than successful ones. Successful pairs fed their chicks more often and these grew faster. They ate more fish and chicks of other gulls, while unsuccessful pairs ate more crabs and starfish. Chicks of pairs that did not change their diet at hatching suffered higher mortality than chicks of pairs that did. Similar observations were made by Van Donk *et al.* (2017) on Texel. Most pairs concentrated on bivalves and did not switch to energy-rich prey during chick rearing, but pairs feeding on energy-rich prey (domestic refuse and fishery discards) during chick rearing had higher reproductive success, even though they expended more energy during foraging for these prey (van Donk *et al.* 2019). O'Hanlon *et al.* (2017, 2023) sketch a somewhat different picture for herring gulls breeding in SW Scotland and N Ireland. These foraged mainly in intertidal zones and on terrestrial resources in built-up areas, and raised larger broods in colonies where they consumed more intertidal food.

On Canna, W Scotland, a correlation between detrended herring gull breeding numbers and detrended demersal fish landings provided evidence for a causal link between fishery discarding and gull breeding numbers (Foster *et al.* 2017).

Pons (1992) and Pons & Migot (1995) studied the effect of closure (80% reduction in food availability) of a rubbish dump near a herring gull colony in Brittany, France. After closure, mean clutch size and mean breeding productivity decreased by 6-7% and 49%,respectively. Spaans (1998) and particularly Camphuysen (2013) describe how the closure and covering of landfills in the Netherlands affected the size of numerous breeding colonies.

Survival and recruitment

We found just one study explicitly linking survival of herring gulls to measures of food abundance (Pons & Migot 1995). A gradual reduction of survival in the period that many refuse tips were closed off from foraging gulls (mainly in the 1980s-1990s) is often hypothesised to explain the shift from growth to declines in West-European herring gull populations (e.g. Spaans 1998, Camphuysen 2013). This does not seem unlikely given the numbers of gulls that foraged at such tips in winter, but the survival estimates summarised in table 4 do not clearly show a pattern of lower survival in recent than historical decades, at least not in The Netherlands. In the targeted study by Pons & Migot (1995) the closure of a refuse tip in Brittany was not followed by a significant decrease in adult survival, although the mean adult body weight decreased by 4-7%. Harris (1970) did link the increase of British herring gull populations in the mid-20th century to a very high adult survival estimate of 0.94, though based on a limited sample of ringed birds in one year.

Bosman *et al.* (2016) studied factors affecting first-year survival in herring gulls fledging at Zeebrugge in Belgium, and found that it was linked primarily to individual variation in growth rate of chicks, and also correlated with hatching date and rank order after brood reduction, pointing to carry-over effects of breeding season events on early survival. However, they did not relate juvenile survival to food abundance data.

4.4 Great Black-backed Gull

4.4.1 Species introduction and population in The Netherlands

Great black-backed gull is the largest extant gull, and breeds along all coasts of the northern Atlantic Ocean. The species is partly migratory; Scandinavian breeders seem to winter mainly in and around the North Sea, both along the coasts and offshore.

The species became an annual breeding bird in The Netherlands in 1993 (Boele *et al.* 2025), as part of a broader expansion along the southern margin of its European range. The growth of the Dutch breeding population was temporarily interrupted by avian influenza in 2022-2023 but thereafter resumed to 118–120 pairs in 2024 (trend over 2013-2024: moderate increase). However, at a global scale the species has shown a significant decline (Langlois Lopez *et al.* 2022), and the Dutch non-breeding trend also is negative on the long term (since 1991), although no further change is apparent in the most recent 12 years. Recent winter numbers in The Netherlands are estimated at 26.000-67.000 birds.

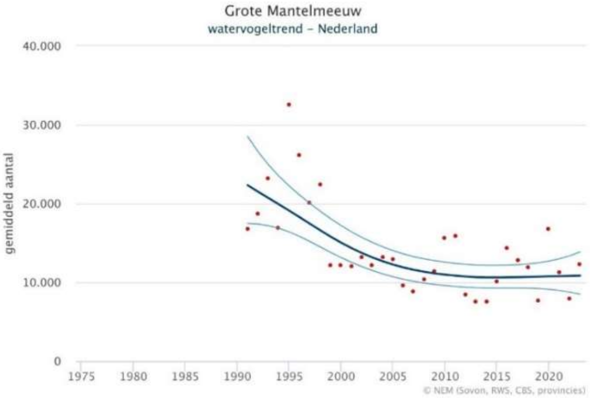

Fig. 4. Trend of wintering great black-backed gulls in The Netherlands in 1990-2024. Shown are the annual population index, calculated from aerial counts at sea and waterbird counts in coastal and inland areas (red dots) and the trendline (dark blue line) with 95% confidence interval (pale blue lines).

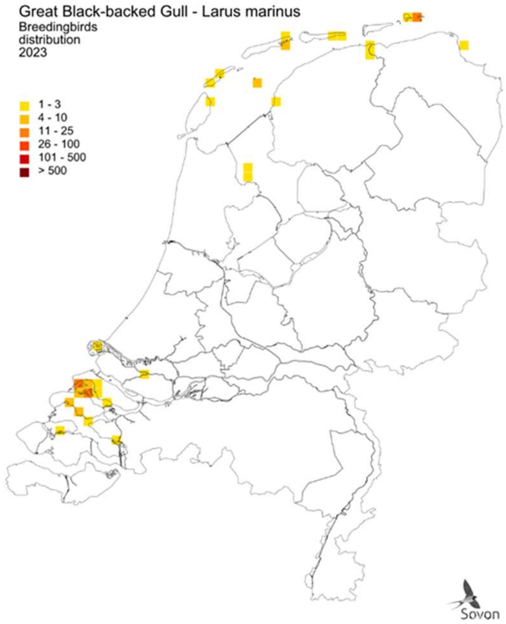

Fig 5. Breeding distribution of great black-backed gull in 2023. For each atlas square of 5x5 km the highest counted number of breeding pairs is given. Data from the annual survey of colonial and rare breeding birds.

The majority of Dutch great black-backed gulls breeds in the Delta Area (63 pairs in 2024) and the Wadden Sea region (53 pairs), while two pairs nested on De Kreupel in lake IJsselmeer. The species does not breed colonially but mainly in scattered pairs, although these may settle on the outskirts of colonies of other gulls. Nest sites include artificial stony habitats such as rubble foreshores as well as bare sandy substrates and saltmarsh (Sovon 2018).

4.4.2 Demographic studies

Great black-backed gull usually does not breed in large colonies but dispersed in smaller groups or as solitary pairs. The majority of the population breeds in relatively remote northern areas, where they are not perceived as a nuisance by humans as much as are herring and lesser black-backed gulls have been. This probably explains why very few dedicated studies of the ecology of this species have been carried out. As a result, basic information is lacking or very scant on several key demographic variables.

4.4.3 Key demographic variables

4.4.3.1 Survival

Very little published data is available on survival of great black-backed gulls (table 7). The background of the estimate by Glutz & Bauer (1982) is not very clear, and those of Frederiksen *et al.* (2025) were obtained by an indirect approach, by tuning to match observed breeding productivity and population trend data. The available estimates average at 0.86 (SD_e 0.05) for adult survival, 0.78 (SD_e 0.02) for immatures, and 0.48 (SD_e 0.13) for first-year survival. It is obvious that these can be improved upon, and given the significantly larger body size of great black-backs it is counterintuitive that they average not higher but slightly lower than survival rates of lesser black-backed and herring gulls. No published data at all is available on annual variability in survival. A number of colour-ring projects has been in place in this species for a substantial time (e.g. in Norway), and analyses of the available resightings in the breeding and non-breeding areas should allow to fill this knowledge gap.

Table 7. Published estimates of annual survival probabilities for great black-backed gull. Standard deviations denote variability across years or across sites/years. More data for specific sites and years can be found in Annex IIa.

area	period	Adult	s.d.	imm.	s.d.	1st yr	s.d.	source
Germany	.	0.93	.	.	.	.	.	Glutz & Bauer 1982
Norway, Hornøya	2001-2017	0.80	.	.	.	.	.	Layton-Matthews *et al.* 2024
North Sea countries	1990-2019	.	.	0.79	.	0.30	.	Collier *et al.* 2020
Arctic Waters	1986-2019 [2]	0.88	.	0.80 [1]	.	0.56	.	Frederiksen *et al.* 2025
Greater North Sea	1986-2019 [2]	0.85	.	0.77 [1]	.	0.48	.	Frederiksen *et al.* 2025
Celtic Seas	1986-2019 [2]	0.86	.	0.77 [1]	.	0.58	.	Frederiksen *et al.* 2025

[1] Mean of 2nd-4th years; [2] Baseline values taken from Robinson 2010, calibrated on observed breeding output and population development

4.4.3.2 *Recruitment and adult breeding propensity*

Horswill & Robinson (2015) place age of first breeding at 5 years citing Cramp (1985), who reports it as 4-5 years. We found no other information. No information is available on adult breeding propensity.

4.4.3.3 *Breeding productivity*

In The Netherlands, breeding productivity data on great black-backed gulls is available only from the Delta Area, and is limited as a result of the species' scarcity and dispersed breeding. Productivity seems to be above 1 fy/pr on average. Table 8 also lists estimates from a selection of studies elsewhere in Europe. All estimates combined average around 1.05 fy/pr (SD_e 0.40). SD_p values of interannual variation vary around 0.43, or 41% of the mean.

The mean annual breeding productivity necessary to obtain a stable population trend was estimated at 0.68-1.68 fy/pr by Frederiksen *et al.* (2025), using population models tuned to observed population trajectories in the in the North Sea, Celtic Seas and Bay of Biscay & Iberian coast.

Table 8. Summary of data on breeding productivity (young fledged per breeding pair) of great black-backed gull. More data for specific sites and years can be found in Annex Ic (for Dutch colonies) and Annex IIa.

Area	Period	N	fy/pr	s.d.	Source
Netherlands, Delta Area	2019-2023	4	1.22	0.23	Lilipaly *et al.* 2021, 2024
Netherlands, Delta Area	2006-2105	10	1.00	.	Schekkerman *et al.* 2017
United Kingdom, Skomer	1995-2021	26	1.36	0.36	Newman *et al.* 2021
United Kingdom, national average	1986-2005	66	1.14	0.53	Horswill & Robinson 2015
UK, Scotland, North Sea coasts	2015-2025	24	1.09	0.72	SMP database
Norway, Barentz Sea	2020-2021	4	0.25	0.25	SEAPOP; e.g. Fayet *et al.* 2025
Arctic Waters (OSPAR region I)	1986-2019	.	0.89	0.58	Frederiksen *et al.* 2023, 2025
Greater North Sea (OSPAR II)	1986-2019	.	1.41	0.47	Frederiksen *et al.* 2023, 2025
Celtic Seas (OSPAR region II)	1986-2019	.	1.07	0.26	Frederiksen *et al.* 2023, 2025

4.4.4 Relationships between demography and food resources

We found no published studies on these relationships for great black-backed gull.

4.5 Sandwich Tern

4.5.1 Species introduction and population in The Netherlands

The Sandwich tern is a medium-sized tern with a widespread breeding distribution along the seaboards of western and southern Europe, and winters mainly off western and southern Africa. The Dutch breeding population was estimated at 10,100–10,200 pairs in 2024 (Boele *et al.* 2025). In the 1960s, the population reached a low point due to the discharge of chlorinated hydrocarbons, but subsequently recovered gradually to approximately 18,000 breeding pairs. Since around 2010, however, this increase has stalled, and the recent short-term trend (2013–2024) indicates a moderate decline. In 2022 (and to a lesser extent in 2023), Sandwich terns were heavily affected by an outbreak of highly pathogenic avian influenza (HPAI), resulting in very high mortality among both adults and chicks (Rijks *et al.* 2022; Leopold 2023; Knief *et al.* 2024). Recovery of the population is expected to take considerable time, and to depend on whether further outbreaks occur and breeding productivity increases above that in the pre-HPAI years (Slaterus *et al.* 2022).

The breeding distribution of Sandwich tern is largely confined to a few large colonies in the Wadden Sea and the southwestern Delta Area, although a colony was also established in recent times along the Noord-Holland North Sea coast. In 2024 over 9700 pairs (96%) were concentrated in just four colonies: Utopia (2.930) and Prins Hendrik Zanddijk (2250) on Texel; the Slijkplaat in the Haringvliet (1785), and the Hooge Platen in the Westerschelde (2800). Larger (as well as smaller) colonies, however, exhibit considerable spatial dynamics and may relocate *en masse* from one year to the next in both the Wadden Sea (changing locations on Texel, vacation of formerly consistent settlement on Griend) and the Delta region (movement from Grevelingen towards Haringvliet, and between Hooge Platen, Zeebrugge harbour and recently developed Waterdunen in the Westerschelde mouth).

At the individual level, colour-rings and GPS-loggers revealed that adults from The Netherlands showed prospecting behaviour in other colonies around the S North Sea, up to over 850 km away, suggesting large-scale connectivity between NW European Sandwich tern colonies (Fijn *et al.* 2014).

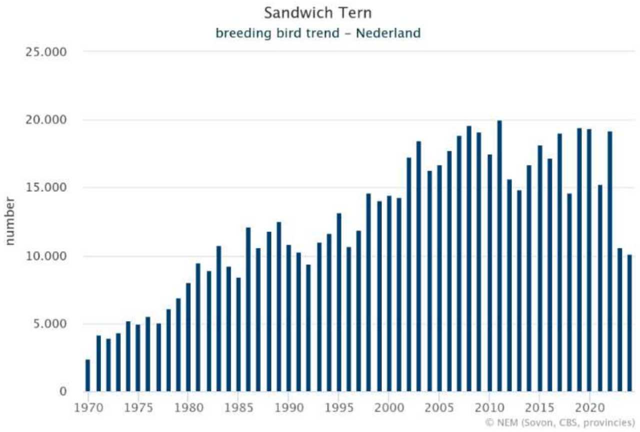

Fig. 6 (left). Development of numbers of Sandwich tern breeding in the Netherlands in 1970-2024. Data from the annual survey of colonial and rare breeding birds.

Fig 7 (right). Breeding distribution of Sandwich tern in 2023. Data from the annual survey of colonial and rare breeding birds.

4.5.2 Demographic studies

4.5.2.1 The Netherlands

Veen (1977) started a series of studies on breeding Sandwich terns on Griend in the Wadden Sea, investigating colony-nesting behaviour and the association with black-headed gulls as well as estimating nesting success and ringing of chicks. In later years, Klaassen *et al.* (1992, Klaassen 1992), focused here on the energetics of chick growth and Stienen & Brenninkmeijer (2002a,b, Stienen 2006) conducted detailed studies on food provisioning and revisited interactions with black-headed gulls. In the Delta Area, breeding success was followed since 1987 in the main colonies in the Grevelingen and the Westerschelde (Beijersbergen 2012, Derks & de Kraker 2005), and at nearby Zeebrugge in Belgium (Verstraete *et al.* 2024). Nowadays, reproduction is monitored annually in nearly all colonies in The Netherlands. In the past 15 years the scope of studies has been widened to assess potential impacts of offshore windfarms (Wozep programme), including diet studies and tracking of tern foraging locations and movements in and after the breeding season as well as their migration (Fijn *et al.* 2014, 2017, 2018, 2022, Fijn 2024). This also led to the initiation in 2012 of a colour-ringing program in the Delta that was later expanded to other colonies. Very intensive (sometimes daily) colour ring-reading at observable colonies (e.g. on Texel and at Camperduin) has yielded much new information on dispersal, prospecting behaviour and survival, the latter recently analysed by Courtens *et al.* (2021).

4.5.2.2 Other North Sea countries

Breeding success and ringing studies have been in place at various other localities around the North Sea. In the UK, most Sandwich tern breeding sites are covered within the Seabird Monitoring Program. Colonies with long data series are situated along the Norfolk and Suffolk coasts and in NE Scotland (Sands of Forvie). In the German Wadden Sea, breeding success has been followed on Hallig Norderoog. The outbreaks of HPAI in many W European breeding colonies in 2022-2023 have stimulated international contacts among researchers, on mitigation of future outbreaks and assessing the demographic consequences.

4.5.3 Key demographic variables

4.5.3.1 Survival

Data on survival of Sandwich terns are available mainly from The Netherlands and from the United Kingdom (table 9). The estimates from the UK are somewhat older and based on metal ring recoveries; those by Courtens *et al.* (2021) are based on an extensive Dutch and Belgian dataset of colour-ring resightings accumulated since 2012, combined with dead recoveries. Van der Jeugd *et al.* (2014) fitted an integrated population model to metal ring recoveries, breeding success data and breeding population counts in the Wadden Sea. Frederiksen *et al.* (2025) used the UK survival estimates as a baseline and 'tuned' these in a population model to match the observed breeding numbers and productivity at the scale of OSPAR regions.

Estimates of adult annual survival in table 9 vary from 0.87 to 0.95, with a mean of 0.91 and SD_e of 0.02. Reported standard deviations of between-year variability (SD_p) are around 0.07. None these estimates includes the year 2022, when mass mortality occurred in in adult breeders (and possibly non-breeders as well) due to Highly Pathogenic Avian Influenza (Knief *et al.* 2024).

Because young Sandwich terns usually stay near their wintering areas (where recovery probability is low) in their first and usually also second summer, and return to breeding areas only when 3-4 years old (Langham 1971), it is difficult to obtain separate estimates for survival in these first years. Those listed in table 9 are therefore mostly averages of 1st-3rd or 1st-2nd year survival; their mean value is c. 0.67 (SD_e 0.14; SD_p 0.17), but it is likely that survival is lower in the first than in subsequent years, and that of 2-year olds may already approach that of adults. Young adults aged 3-6 yrs, of which many do not yet breed, seem to have slightly higher survival than adult breeders.

Table 9. Published estimates of annual survival probabilities for Sandwich tern. Standard deviations denote variability across years or across sites/years. More data for specific sites and years can be found in Annex IIa.

area	**Period**	**adult**	**SD_p**	**imm.**	**SD_p**	**1st yr**	**SD_p**	**source**
NL: S Netherlands	1991-2020	0.92	0.06	0.65[3]	0.15	.	.	Courtens ea 2021[1]
NL: N Netherlands	1991-2020	0.91	0.07	0.70[3]	0.19	.	.	Courtens ea 2021[1]
NL: Netherlands	2012-2021	0.92	.	0.94[4]	.	0.65[5]	.	Courtens ea 2021[2]
NL: Wadden Sea	1991-2010	0.95	0.10	0.66[3]	.	.	.	vd Jeugd ea 2014
UK: United Kingdom	1990-2006	0.90	.	0.74[6]	.	0.36	.	Robinson 2010
UK: United Kingdom	1970-1990	0.87[7]	.	.	.	0.74	.	Jimenez-Munoz ea 2019
Greater North Sea	1991-2019[8]	0.90	.	0.84[6]	.	0.58	.	Frederiksen ea 2025
Celtic Seas	1991-2019[8]	0.90	.	0.82[6]	.	0.59	.	Frederiksen ea 2025
Bay of Biscay & Iberia	1991-2019[8]	0.90	.	0.87[6]	.	0.66	.	Frederiksen ea 2025

[1] Burnham model combining dead recoveries and live resightings; [2] CJS model (live resightings); [3] 1st-3rd year; [4] young adults in 4th-7th yr; [5] 1st-2nd year; [6] 2nd-3rd year; [7] all ages >1st year; [8] Baseline values taken from Robinson 2010, calibrated on observed breeding output and population development.

4.5.3.2 *Recruitment and adult breeding propensity*

We found no detailed quantitative information on the ages at which Sandwich terns recruit into the breeding population, but most individuals seem to do so in their 3rd or 4th, some not until the 5th summer (Cramp 1985). Horswill & Robertson (2015) give the age at recruitment as 3 years, but this seems somewhat optimistic. The colour-ring readings amassed in Dutch breeding colonies in recent years are likely to allow more precise quantification of age at recruitment.

No estimates are available on the incidence of skipping of breeding seasons in adults once recruited (breeding propensity). Estimating this is difficult in Sandwich terns as they exhibit low site fidelity, and may breed in distant colonies in different years, not all of which are monitored intensively for ringed birds. Tracking individuals over multiple years (e.g. with light-level storage tags) may be the only way to obtain good information on this parameter.

4.5.3.3 *Breeding productivity*

Table 10 summarises data on breeding productivity of Sandwich terns in The Netherlands for the recent period 2014-2023. It also shows results of a selection of Dutch studies that extend further back in time, and of studies elsewhere in Europe. The recent mean breeding productivity in Dutch colonies was 0.49 fledged young per breeding pair. Variation between regions was moderate, but colonies on the Wadden Sea islands seem more productive than those in the northern and particularly southern parts of the SW Delta, for unknown reasons. Estimates from abroad and for earlier periods in The Netherlands are of similar magnitude,

Table 10. Summary of data on breeding productivity (young fledged per breeding pair) of Sandwich tern. The upper part of the table summarises data present in the breeding success database of Sovon, as the means (weighted by colony size) and standard deviations by region over colonies/years in 2014-2024. The middle part contains published data from the Netherlands in a selection of earlier periods and well-studied sites. The lower part of the table contains a selection of published data from other countries in the North Sea region and elsewhere in Europe. More data for specific sites and years can be found in Annex Id (for Dutch colonies) and Annex IIa.

Area	**Period**	**N**	**fy/pr**	**SD$_p$**	**Source**
Netherlands, all sites	2014-2023	59	0.49	0.31	Annex 1d
Wadden Sea	2014-2023	28	0.56	0.32	Annex 1d
Delta Area N: Haringvliet, Grevelingen	2014-2023	16	0.43	0.28	Annex 1d
Delta Area S: Wester-, Oosterschelde	2014-2023	15	0.35	0.33	Annex 1d
Wadden Sea, all sites	2005-2019	15	0.49	0.15	Koffijberg *et al.* 2021
Wadden Sea, Griend	1991-2010	20	0.73	0.35	van der Jeugd *et al.* 2014[1]
Wadden Sea, Griend	1954-1991	20	0.70	0.23	Brenninkmeijer & Stienen 1992
Delta Area, all sites	1997-2016	20	0.50	0.20	Schekkerman *et al.* 2017
Delta Area, Grevelingen (Hompelvoet)	1980-1996	16	0.63	0.14	Brenninkmeijer & Stienen 1992, Derks & de Kraker 2005
D: Hallig Norderoog	2010-2023	14	0.50	0.25	Knief & Haupt 2023
UK: national average	1986-2014	>100	0.70	0.37	Horswill & Robinson 2015
UK: Norfolk & Suffolk	2015-2025	23	0.51	0.39	SMP database
UK: Scotland, Sands of Forvie	2015-2025	11	0.58	0.23	SMP database
Greater North Sea (OSPAR region II)	1986-2019	29	0.59	0.18	Frederiksen *et al.* 2023, 2025
Celtic Seas (OSPAR region III)	1986-2019	29	0.64	0.28	Frederiksen *et al.* 2023, 2025
Bay of Biscay & Iberia (OSPAR IV)	1986-2019	29	0.53	0.23	Frederiksen *et al.* 2023, 2025

but on average slightly higher, with mean values up to 0.73 fy/pr. This is partly due to the recent Dutch series including the years 2022-2023 when HPAI outbreaks caused high mortality in chicks. Schekkerman *et al.* (2021) did not find a significant change in productivity in the Delta Area over 1994-2019, nor did Koffijberg *et al.* (2021) in the Wadden Sea over 2004-2019.

The mean of all breeding productivity estimates in table 10 is c. 0.56 fy/pr (SD_e 0.11). SD_p values of interannual variation range from 0.14 to 0.39 with an average of 0.26, which is 46% of the mean, indicating that breeding productivity is quite variable over time.

To put the reported productivity values in perspective, the annual breeding productivity necessary to obtain a stable population trend was estimated at 0.46 fy/pr by Schekkerman *et al.* (2021) in the Dutch Delta Area. Frederiksen *et al.* (2025) estimated it to be 0.44-0.58 fy/pr, using population models tuned to the observed population trajectories and breeding productivity in the in the North Sea, Celtic Seas and Bay of Biscay/Iberian coast.

4.5.4 Relationships between demography and food resources

All published studies found on relationships between demographic rates of Sandwich terns 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 become available only recently. In several of the studies addressing breeding productivity this was related to observations on prey delivery to chicks, in the absence of direct measurements of fish abundance near the breeding location. At a 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.

In the breeding season, Sandwich tern (chick) diets are dominated by sandeel and ‘clupeids’: herring and sprat which are often not separated in diet studies (Stienen & Brenninkmeijer 2002a, Fijn *et al.* 2018, Courtens *et al.* 2022). Of these two main prey types, clupeids are the more profitable because of their higher energy (fat) content at a given size, and because they are less often than sandeels stolen by kleptoparasitising black-headed gulls (in whose vicinity Sandwich tern often breed) before they can be delivered to a chick. For these reasons, chicks on Griend in the Wadden Sea would be unable to fledge on a diet of sandeels alone (Stienen & Brenninkmeijer 2002a). As the chicks’ energy demand rises as they grow older, parent terns should increase the share of clupeids among prey delivered, but this was not the case on Griend, suggesting that the availability of profitable clupeids was limiting. In years when sandeel dominated the diet, parents increased their foraging effort and older chicks were left alone often (Stienen & Brenninkmeijer 2002a). In this same study, mass growth rate was highly variable and survival to fledging (at c. 26 days) was strongly connected to body condition (mass-at-age) at ages between 1 and 3 weeks, but not thereafter. Growth rate during the initial linear growth phase had no effect on the body mass at fledging. Chicks hatched second in the same nest survived much less well than their first-hatched siblings, but this difference disappeared at ages older than c. 15 days. Survival after fledging was investigated by analysing data of ringed chicks that were known to have fledged and were observed in the colony in later years. This measure of post-fledging survival was not related to body condition at hatching, but substantial differences existed between chicks fledged in different years (Stienen & Brenninkmeijer 2002b).

This all points to a possible effect of the availability of key food resources on breeding productivity, but no data were available on the availability of clupeids within the foraging range of the terns, which extends to the North Sea coastal zone above the central Wadden Islands. Stienen (2006) compared breeding data from Griend (1986-2004) and from the northern Delta Area (1989-2004) with clupeid abundance data from the International Bottom Trawl Survey (IBTS) in the southeastern North Sea. There was no obvious relationship between this index of prey abundance and Sandwich tern clutch size or breeding productivity in either region. However, when the expected growth of the breeding population was calculated for each year from average adult survival and breeding output three years earlier, deviations from this expectation correlated strongly with the IBTS index for the Wadden Sea population, but not for that in the Delta (fig. 8). It thus seems that clupeid abundance affects the number of Sandwich terns settling to breed in the Wadden Sea directly via effects on immigration/emigration and/or adult breeding propensity, more so than indirectly via an effect on breeding productivity. Why this effect on settlement is not apparent in the Delta Area remains unknown.

In the northern Delta Area, the breeding ecology of Sandwich terns was investigated as part of a study on compensation measures for the extension of the Maasvlakte (port of Rotterdam) by Fijn *et al.* (2018). No good data on fish abundance at sea were available; information on food availability was derived from observations on prey delivery to chicks. The survival of chicks to fledging and the average condition of fledged chicks were positively correlated with the mean length of clupeids fed to them (a proxy for prey quality), and fledging success was higher when herring were delivered at short intervals (proxy for high prey abundance). No such relationships were found for sandeel. The researchers concluded that chick condition and fledging success depend on the quality and quantity of food available in the Voordelta and beyond, particularly of clupeids. Sandeel constitute a 'second choice' prey, but are nevertheless important as a fallback when clupeids are not available. In addition, sandeel was the main food source for adult Sandwich terns during the first weeks of the breeding season. In a study on Sandwich terns breeding in the Westerschelde mouth in 2021, Courtens *et al.* (2022) observed that chicks were fed mainly very small herring and sandeel, but breeding productivity was nevertheless high, and hypothesised that this was enabled by a high abundance of small fish close to the colonies in this area.

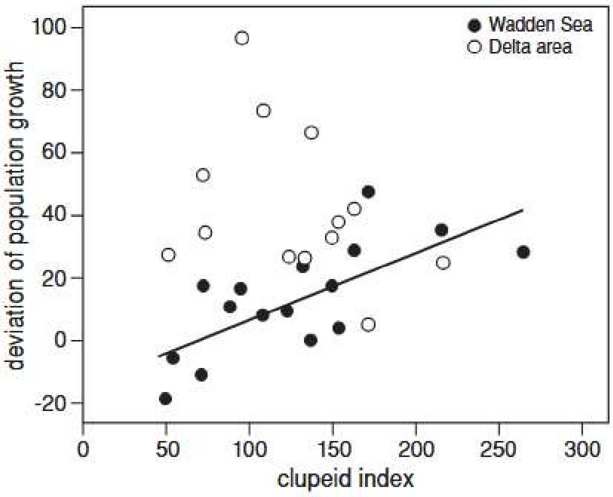

Fig. 8. Relationship between the IBTS index of clupeid abundance in the southeastern North Sea and the annual deviations of population growth of the Wadden Sea and Delta Area populations of Sandwich Tern expected from earlier breeding productivity and mean adult survival. From Stienen (2006).

4.6 Common Tern

4.6.1 Species introduction and population in The Netherlands

The common tern is the most abundant tern species in Europe with a widespread breeding distribution, both coastal and in freshwater habitats. Western and northern European breeding birds migrate towards (mainly West) African coasts for winter.

The Dutch breeding population was estimated at 16,500–19,000 pairs in 2024 (Boele *et al.* 2025). Current numbers are much lower than in the 1950s, when 30,000–40,000 pairs bred annually. Like other terns, the common tern suffered from poisoning by agricultural pesticides (Stienen & Brenninkmeijer 1992), and by the mid-1960s, only around 5.000 pairs remained (Teixeira 1979). Numbers partly recovered in the following decades, reaching c. 20,000 pairs in 2000–2010. Since then the population has again declined, due to multiple factors. Many natural breeding sites are only temporarily suitable, as vegetation succession leads to overgrowth and predator establishment; few areas exhibit sufficient natural dynamics to regularly reset these processes (Koffijberg *et al.* 2016, Schekkerman *et al.* 2021). In many areas, high predation pressure poses a problem. Breeding sites in saltmarshes along the mainland coast of the Wadden Sea were largely vacated after Red Fox became established here in the late 1990s (Stienen *et al.* 2009).

The breeding distribution is concentrated in the low-lying parts of The Netherlands, with strongholds in the Delta, Wadden Sea, and IJsselmeer regions, where all major colonies are located. In 2024, about 3100 pairs bred in the Wadden Sea and about 4500 pairs in the Delta Area. In 2024 the largest colony (1205 pairs) was situated at the construction site of the fish migration river at Kornwerderzand near the Afsluitdijk. Inland colonies are usually smaller and relatively few in number, although some may remain undetected. Several rooftop colonies with more than 100 pairs have been established on buildings in the western and northern provinces. Breeding birds from such colonies up to >20 km inland have been found to commute to forage in the Wadden Sea and North Sea (e.g. Manche *et al.* 2023).

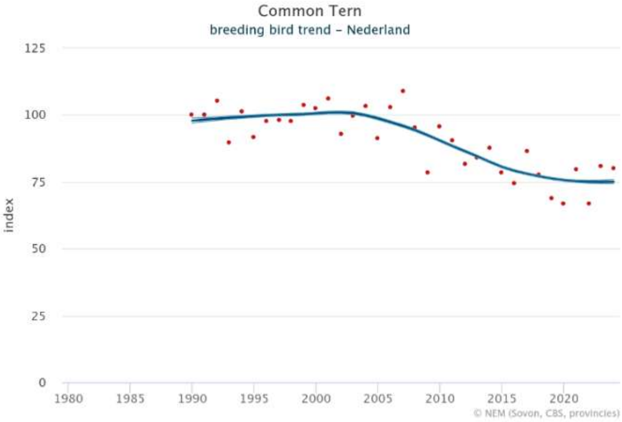

Fig. 9. Breeding bird trend of common tern in 1990-2024. Shown are the annual population index, calculated from national totals or counts in core breeding areas (red dots) and the trendline (dark blue line) with 95% confidence interval (pale blue lines). Data from the annual survey of colonial and rare breeding birds.

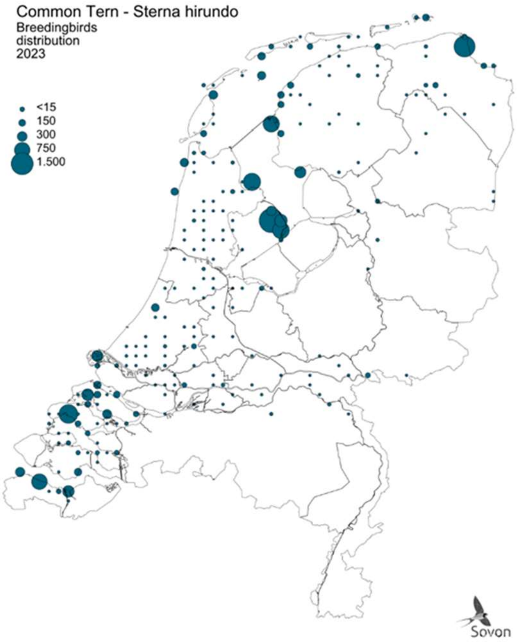

Fig. 10. Breeding distribution of common tern in 2023. For each atlas square of 5x5 km the highest counted number of breeding pairs is given. Data from the annual survey of colonial and rare breeding birds.

Since the late 20th century the breeding distribution has shown significant changes. In particular, numbers breeding on Griend and in saltmarshes along the mainland coast of the Wadden Sea have declined strongly, while newly created islands in the IJsselmeer area have attracted large colonies (Stienen *et al.* 2009, Sovon 2018).

4.6.2 Demographic studies

4.6.2.1 The Netherlands

Demographic information on common terns breeding in The Netherlands has been collected for several decades through generic monitoring of breeding productivity and ringing. Data on breeding success in a number of Wadden Sea colonies are collected within TMAP since 2005, and before that on Griend, while breeding success is estimated in most colonies in the Delta Area as part of the MWTL monitoring (§4.1). Breeding productivity is also measured in some colonies in the IJsselmeer area (van der Winden *et al.* 2019, 2021). Elsewhere, in the few colonies along the Holland Coast and those further inland, information on breeding success is collected only sporadically.

Generic ringing of common terns in breeding colonies has been ongoing for many decades and the resulting recovery data have been used to estimate survival rates, for the Wadden Sea region (van der Jeugd *et al.* 2014) and the SW Delta (Schekkerman *et al.* 2021). More recently, common terns have been fitted with engraved colour rings in several locations in all three major breeding regions. In some of these locations annual ringing and ring-reading effort as well as monitoring of breeding success (and in some cases also chick weights and prey choice) over multiple years amount to fairly comprehensive population studies. Examples are those on island Stern in the Eems estuary (e.g. de Boer 2025, Manche 2022) and on Kreupel and Marker Wadden in the IJsselmeer area (van der Winden *et al.* 2019, 2021), and earlier on Griend (Stienen *et al.* 2009). The survival information contained in the colour-ring resightings from these studies has not yet been analysed, but these data series are now becoming sufficiently long to obtain meaningful estimates.

4.6.2.2 *Other North Sea countries*

A very sophisticated long-term study on the population ecology of common tern has been ongoing since 1992 at Wilhelmshaven in the German Wadden Sea, by the Institute of Avian Research (Vogelwarte Helgoland) (e.g. Becker & Wendeln 1997, Bouwhuis 2025). In the Banter See directly adjacent to the Jadebusen bay, six artificial islands of 50m^2 provide breeding space for up to 700 pairs of common terns. Three times weekly checks of the colony yield information on reproductive performance of breeders. In 1992 and 1993 adult birds were caught and marked individually with both a legring and a subcutaneously injected transponder, and since then all local chicks are tagged similarly before fledging. Landing platforms on the islands' walls are equipped with weighing scales and antennas reading the transponder codes of both visiting and breeding individuals, and all marked breeders are additionally identified by placing an antenna around their clutch. The high site-fidelity of established breeders allows the assumption that these have died if they are not registered for two consecutive years. This study design and the in-depth analyses by the research group have unearthed a wealth of information on adult survival rates, prospecting behaviour, settlement, breeding phenology, breeding success, body condition, skipping of breeding years and other aspects of this species' life-history (e.g. Becker & Ludwigs 2004, Zhang et al 2015a,b, Vedder *et al.* 2021). Diets have also been studied and condition and survival of chicks have been related to regional and local fish stocks (Dänhardt & Becker 2011, Vedder *et al.* 2019, Cansse *et al.* 2024). More recently, the research was expanded beyond the breeding season by tracking the year-round migration with light-level geolocators, to study whether conditions in the wintering areas or *en route* (weather, food, pollutants) explain variation in survival or reproductive performance. In 2022-2023 the study colony was hit hard by outbreaks of avian influenza. The detailed information available on this population provides a unique opportunity to study the demographic details of both the resulting 69% decline in breeding pairs and the (hoped for) recovery (Bouwhuis 2025).

Breeding success and ringing studies have been in place at various other localities around the North Sea, but nowhere with a depth comparable to that at Wilhelmshaven. Common terns also breed on the eastern seaboard of North America, and here a few studies have quantified survival as well (Nisbet & Cam 2002, Breton *et al.* 2014, Palestis & Hines 2015).

4.6.3 Key demographic variables

4.6.3.1 Survival

Published estimates of annual survival of adult common terns are available mainly from The Netherlands, Germany, and the NE United States (table 11). They fall between 0.85 and 0.93, with a mean around 0.88 and SD_e of 0.03). Studies that have reported between-year variability in adult survival indicate that the standard deviation of annual values (SD_p) is c. 0.04. With respect to patterns over age, Breton *et al.* (2014) reported that annual adult survival in population in the eastern USA increased from 0.80 in 2-year-old birds to a maximum of 0.88 around 8 years and then declined to 0.76 at age 20 years. In the Wilhelmshaven population, survival was close to 0.90 between 2 and 6 years and then gradually declined to about 0.7 at 20 years of age (Vedder *et al.* 2021).

Because immature common terns stay near their (African) wintering areas (where recovery probability is low) in their first summer, and return to breeding areas only when nearly 2 or 3 years old, it is difficult to obtain separate estimates for first-year survival. Those listed in table 11 are therefore averages over the first and second years; it is likely that actual survival is lower in the first year than in the second. The mean of the estimates in table 11 is c. 0.65 (SD_e 0.11). Estimates for 3rd year birds approach those for adults (mean 0.80, SD_e 0.13). Survival shows somewhat greater annual variability in immature common terns than in adults (SD_p 0.04-0.13), but this may be confounded by smaller sample sizes and by birds prospecting and settling in different colonies.

Table 11. Published estimates of annual survival probabilities for common tern. Standard deviations denote variability across years or across sites/years. More data for specific sites and years can be found in Annex IIa.

area	**period**	**adult**	**SD_p**	**imm.**	**s.d.**	**1st yr**	**SD_p**	**source**
NL: SW Netherlands	1990-2019	0.93[2]	.	.	.	0.70[1]	.	Schekkerman *et al.* 2021
NL: Wadden Sea	1991-2010	0.89[2]	.	.	.	0.40[1]	.	vd Jeugd *et al.* 2014
D: Wilhelmshaven	1992-2021	0.86[2]	0.03	.	.	.	.	Bouwhuis 2025
D: Wilhelmshaven	2003-2012	0.85	0.05	0.78[3]	0.13	0.57[1]	0.11	Szostek & Becker 2015
D: Wilhelmshaven	1993-2002	0.90	0.04	0.88[3]	0.05	0.68[1]	0.04	Szostek & Becker 2015
D: Wilhelmshaven	2000-2001	.	.	.	.	0.67[1]	.	Braasch *et al.* 2009
Greater North Sea	1991-2019	0.88[5]	.	0.86[4,5]	.	0.68[1,4]	.	Frederiksen *et al.* 2025
Celtic Seas	1991-2019	0.88[5]	.	0.86[4,5]	.	0.67[1,4]	.	Frederiksen *et al.* 2025
Bay of Biscay & Iberia	1991-2019	0.93[5]	.	0.90[4,5]	.	0.79[1,4]	.	Frederiksen *et al.* 2025
USA: New Jersey	1995-1997	0.91	.	0.51[4]	.	.	.	Nisbet & Cam 2002
USA: Massachusetts	1983-2004	0.86	.	0.80[3]	.	.	.	Breton *et al.* 2014
USA: Massachusetts	2010-2014	0.88	.	.	.	.	.	Palestis & Hines 2015

[1] Estimates for 1st + 2nd year; [2] 3rd year and older; [3] 3rd year; [4] 3rd + 4th year;; [5] baseline values taken from Horswill & Robinson 2015, calibrated on observed breeding output and population development.

4.6.3.2 Recruitment and adult breeding propensity

Ludwigs & Becker (2002) reported that of the common terns that bred for the first time in the Wilhelmshaven colony, 6% did so at age 2 years, 57% at 3, 26% at 4, 9% at 5 and 1% at 6 years. Females tended to recruit at a slightly younger age (mean 3.2 yrs, SD 0.8, age proportions 12, 62, 21, 4, 1% respectively) than males (mean 3.6 yrs, SD 0.8). In 1992-2001, when the colony was growing, the mean age at recruitment was 3.3 yrs, whereas this increased to 3.9 yrs during a temporary population decline in 2002-2009 (Szostek & Becker 2012). Becker *et al.* (2001) reported that 3.5% of all common terns older than 5 years that visited the Wilhelmshaven colony in 1992-1998 did not breed. This may however not reflect the true incidence of non-breeding by adult birds, as some non-breeders may not visit the colony. Szostek & Becker (2012) estimated the annual transition probability from the state of breeder to non-breeder at 8% in this population, indicating a breeding propensity of 0.92. More information, including from other sites, would be valuable.

4.6.3.3 Breeding productivity

Table 12 summarises data on breeding productivity of common terns in The Netherlands for the recent period 2014-2024. It also shows for comparison results of a selection of studies in The Netherlands that extend further back in time, and of studies elsewhere in Europe. The recent mean reproductive output in Dutch coastal breeding colonies is c. 0.49 fledged young per breeding pair. There is substantial regional variation: in the Wadden Sea colonies situated on the island chain were less productive than colonies along the mainland coast and on Griend, and in the Delta region colonies close to the North Sea seem to do better than those at greater distances.

Table 12. Summary of data on breeding productivity (young fledged per breeding pair) of common tern. The upper part of the table summarises data present in the breeding success database of Sovon, as the means (weighted by colony size) and standard deviations by region over colonies/years in 2014-2024. The middle part contains published data from the Netherlands in a selection of earlier periods and well-studied sites. The lower part of the table contains a selection of published data from other countries in the North Sea region and elsewhere in Europe. More data for specific sites and years can be found in Annex Ie (for Dutch colonies) and Annex IIa.

Area	Period	N	fy/pr	SD_p	Source
Netherlands, all coastal regions	2014-2024	288	0.49	0.41	Annex Ie
Wadden Sea, island chain	2014-2024	40	0.13	0.29	Annex Ie
Wadden Sea, elsewhere	2014-2024	66	0.65	0.46	Annex Ie
W Delta Area (< 5 km from North Sea)	2014-2023	66	0.56	0.41	Annex Ie
NE Delta Area (fresh waters)	2014-2023	20	0.39	0.41	Annex Ie
SE Delta Area (Ooster- & Westerschelde)	2014-2023	96	0.40	0.40	Annex Ie
Wadden region: total	2005-2019	15	0.40	0.25	Koffijberg *et al.* 2021
Wadden region: Griend	1992-2007	15	0.39	0.32	Stienen *et al.* 2009
Delta Area: total	1994-2019	26	0.67	0.43	Schekkerman e.a. 2021
IJsselmeer: Kreupel	2005-2017	13	0.34	0.24	vd Winden *et al.* 2019
IJsselmeer: Marker Wadden	2017-2021	5	1.22	0.50	vd Winden *et al.* 2021
Germany: Nordrhein-Westfalen, inland	1984-1993	10	1.50	-	Becker 2008
Germany: Wadden Sea, Wilhelmshaven	1992-2021	29	0.82	0.44	Bouwhuis 2025
United Kingdom: national average	1986-2014	>100	0.76	0.47	Horswill & Robinson 2015
UK: Coquet Island, Northumberland	2015-2025	9	1.25	0.54	JNCC, SMP database
UK: Norfolk Coast	2015-2025	35	0.46	0.39	JNCC, SMP database
UK: Suffolk coast	2015-2025	15	0.64	0.58	JNCC, SMP database
Belgium: Zeebrugge	1977-2023	25	1.02	0.71	Verstraete *et al.* 2024
Greater North Sea (OSPAR region II)	1986-2019	34	0.52	0.19	Frederiksen *et al.* 2023, 2025
Celtic Seas (OSPAR region III)	1986-2019	34	0.68	0.21	Frederiksen *et al.* 2023, 2025
Bay of Biscay & Iberia (OSPAR region IV)	1986-2019	34	0.51	0.33	Frederiksen *et al.* 2023, 2025

It is noteworthy that none of the recent mean values for Dutch coastal regions exceed 0.65 fy/pr, whereas higher averages up to 1-1.5 fy/pr have been reported elsewhere, both in the Dutch IJsselmeer region and abroad. Similarly high breeding successes have been observed in the Delta Area before 2010 but not since then, and breeding productivity there declined significantly over 1994-2019 (Schekkerman *et al.* 2021). In the Wadden Sea such a decline was not apparent over 2004-2019 (Koffijberg *et al.* 2021), but data from Griend also indicate that poor breeding years occur more often nowadays than in the 1990s (Stienen *et al.* 2009).

Estimates of breeding productivity in table 12 vary around a mean of c. 0.67 fy/pr (SD_e 0.35). There is considerable variation between years as well as between sites; SD_P values of interannual variation often lie between 0.3 and 0.7, or 40-90% (average c. 65%) of the mean (table 12).

The mean annual breeding productivity necessary to obtain a stable population trend was estimated at c. 0.33 fy/pr by Schekkerman *et al.* (2021) based on the survival estimates for the Delta Area, which are among the highest reported. Frederiksen *et al.* (2025) estimated it to be 0.75-0.79 fy/pr, using lower survival values calibrated on the observed population trajectories in the North Sea and Celtic Seas (OSPAR) regions (see table 11), but in the same way obtained a value of 0.31 fy/pr for the Bay of Biscay and Iberian coast.

4.6.4 Relationships between demography and food resources

Published studies 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 strong 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 the W African wintering range. Although good data are available from the Wilhelmshaven study on age at recruitment and adult breeding propensity, these have not yet been comprehensively analysed in relation to indices of food abundance.

The Netherlands

Van der Winden *et al.* (2019) studied relationships between breeding of common terns and food resources on Kreupel in the freshwater lake IJsselmeer. The main prey base here is formed by a lake-locked population of smelt. Over 13 years, breeding success of the terns fluctuated strongly (from 0-0.8 fy/pr) and was significantly correlated with the size of the smelt stock in the preceding autumn. Despite the commercial fishery for smelt being stopped since 2012, the average breeding success in the following six years remained too low to maintain the population at a stable level.

In the northern Delta Area, breeding success and diet of common terns was investigated as part of a study on compensation measures for the extension of the Maasvlakte (port of Rotterdam) by Fijn *et al.* (2018). Due to the apparent diversity and flexibility of the common terns' diet, the lack of food availability data and the strong impact of factors not related to food (predation and vegetation succession), no clear conclusions could be drawn about the importance of food for the breeding success of common terns in that area. For common terns breeding at the Scheelhoek islands in the Haringvliet, freshwater fish expelled at the nearby Haringvlietsluizen were found to be a main food resource. In the Wadden Sea, low breeding success of common terns on Griend around 1990 has been linked retrospectively to a diet formed for a large part by low-energy prey types, including shrimp and crabs (Stienen *et al.* 2009). Maathuis *et al.* (2025) showed that the current diet of common tern chicks in the

Wadden Sea is dominated by herring, augmented by sprat, sandeel and small quantities of other species, and that the terns forage most in locations where small pelagic fish are abundant, but did not relate this to breeding success. In summary, direct quantitative relationships between breeding productivity and abundance of marine fish resources are not available for marine environments in The Netherlands, only for the freshwater lake IJsselmeer.

Studies elsewhere

In the common tern colony at Wilhelmshaven in the German Wadden Sea in 1992-2021, breeding productivity was positively associated with the ICES North Sea herring recruitment index, a 'global' measure of abundance of juvenile herring in the (southern) North Sea[6] (fig 11). This index explained 8% of the interannual variation in clutch size, 17% of the number of chicks hatched, and 25% of the number of fledglings (Bouwhuis 2025, confirming Dänhardt & Becker 2011). That this relationship becomes tighter in each consecutive phase of the breeding cycle indicates that high abundance of young herring brings several benefits, enhancing the condition of adults so that they lay more eggs and perform better during incubation (perhaps including nest defence), as well as increasing the survival of chicks to fledging. Juvenile herring makes up the largest share of the chick diet at Banter See (38%, Cansse *et al.* 2024), and laboratory experiments indicate that chicks grow faster when fed on herring/sprat than when fed less energy-rich prey like stickleback, pipefish or shrimp (Dänhardt *et al.* 2018). Vedder *et al.* (2019) showed that the effect on chick survival arises primarily through mortality of younger chicks being higher when young herring are scarce. This early mortality was highest, and occurred earliest (mainly in the first week), in third-hatched chicks in broods of three and in single chick broods. In common terns, full clutches usually contain three eggs but third (and to a lesser extent second) chicks do not often fledge and constitute a 'spare' that is sacrificed when foraging conditions are unfavourable, at relatively low cost to the parents (Vedder *et al.* 2019). The early mortality of single chick-

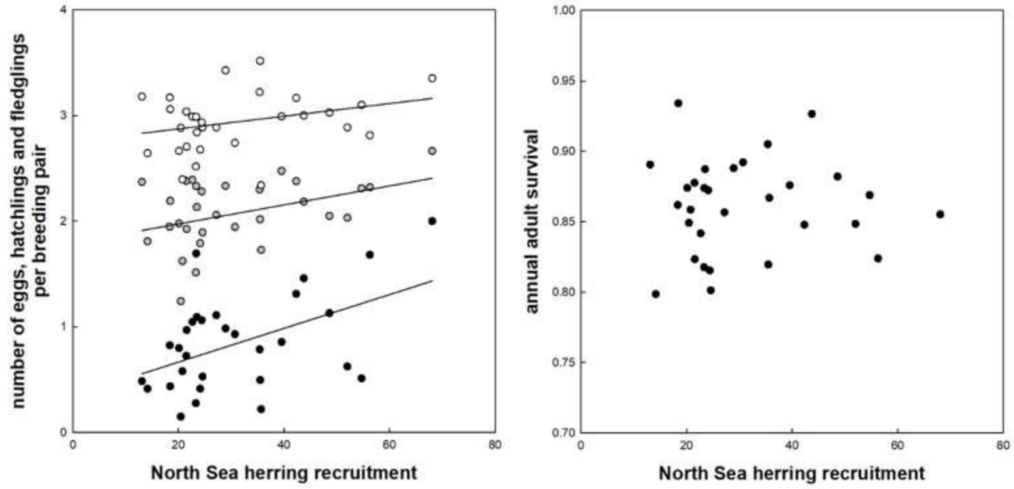

Figure 11. Annual reproductive performance (left; bottom to top eggs, hatchlings and fledged chicks per breeding pair) and survival (right) of Banter See Common Terns in 1992-2021 in relation to the ICES North Sea herring recruitment index. Reproduced from Bouwhuis (2025).

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[6] The ICES recruitment index for North Sea herring is the total abundance of juvenile herring (hatched in the previous winter) in the North Sea, measured with a fine-meshed pelagic trawl net as part of the International Bottom Trawl Survey conducted in January-March of each year.

broods may result from energetic constraints affecting both clutch size and quality of the chick, or from these parents limiting reproductive effort in order to safeguard their own survival when food is scarce. That parents may vary their effort strategically is also suggested by the lack of a relationship between the herring index and adult survival (fig 11).

The above relationships are between tern breeding productivity and an index of food abundance at the scale of the southern North Sea, obtained well before the breeding season commences. Apparently this ‘global’ metric is a predictor of food availability within the foraging range from the colony 2-4 months later. In 1991-2008, abundance of herring and sprat was also measured annually (in August) within the Wadden Sea, using a stow net (in Dutch: ankerkuil). In this period, in addition to the North Sea herring index, the abundance of sprat within the Wadden Sea also contributed to explaining variation in breeding productivity at Wilhelmshaven and on nearby Minsener Oldeoog (Dänhardt & Becker 2011). Together these two variables explained 75% of the variance in breeding success in that period. Notably, the stow net catches of herring correlated less well with tern breeding success than the large-scale ICES index. Also, herring and sprat abundance data explained more variability in breeding success than in growth rate and maximum weight of chicks.

These findings led Dänhardt & Becker (2011) to argue that herring and sprat are the key prey species for common terns. Somewhat contradictorily, Dänhardt *et al.* (2018) concluded from a project investigating the relationship between common terns and forage fish in the German Wadden Sea in 2006-2015 that among the tens of fish species occurring in the Jadebusen bay, only herring and smelt are essential as food for breeding terns, because these two species dominate the pelagic fish community and yield the highest energy return per unit foraging effort. Sprat was stated to constitute a valuable supplement of the prey base only in some years. In other regions, sprat has been indicated as a key prey species for breeding common terns. Jennings *et al.* (2012) reported that common tern breeding numbers in the Firth of Forth (E Scotland) were reduced when the sprat stock collapsed in the early 1980s after targeted fishing, but recovered during later decades when the stock was unfished. In contrast to herring and sprat, sandeel has not been identified as a key prey of breeding common terns, although it is consumed regularly. This species yields relatively little energy relative to its size, enabling single-prey-loading common terns to effectively provision their chicks only if it is available at very close range from the colony (Schekkerman *et al.* unpubl. data). Uttley *et al.* (1989) observed that in Shetland in 1988, common tern chicks grew well on a diet comprising for 80% of young saithe, while simultaneously in arctic terns feeding mainly on sandeel, chick growth was poor and mortality high.

Dänhardt *et al.* (2018) stressed that in addition to overall prey abundance, common tern chick development and breeding success can be strongly affected by a combination of weather conditions and factors driving the availability (rather than presence) of fish. In the Wadden Sea, high abundance of herring, smelt and sprat within the terns’ foraging range, winds between 3 and 6 Bft with no rain, and water temperatures below 22 °C support high reproductive success. Meteorological extremes such as heat, cold, strong winds and precipitation can affect foraging and chick provisioning to a point where chick mortality can increase drastically within days. For example, Becker *et al.* (1997) reported that in 1989 and 1992 uncommon mortality of fledglings was observed at Wilhelmshaven after lasting heat periods when sea water temperatures rose to >20 °C. The direct cause of this mortality was not heat stress, but food shortage due to herring leaving the Wadden Sea during the heat wave.

Relationships with survival

The survival of adult common terns at Wilhelmshaven did not show a relationship with the North Sea herring recruitment index during the entire study period (fig 11). Conditions outside the breeding season may be more important in shaping survival. Szostek & Becker (2015) linked estimates of survival and recruitment of birds tagged in the colony to environmental covariates potentially limiting during the wintering and migration periods, including the North Atlantic Oscillation, Southern Oscillation, fish abundance indices from commercial landings, and marine primary productivity (chlorophyll concentrations) in the W-African wintering area. Global indices (NAO, SO) were not linked strongly to these vital rates. Winter primary productivity (but not total landings of small pelagic fish in the same region) had the strongest effect on annual survival, especially in younger individuals. It was also positively associated with the probability of recruitment in the following breeding season, indicating that conditions during winter can have carry-over effects within the life cycle of individuals.

The only study investigating covariates of juvenile survival in common terns also comes from Wilhelmshaven. Braasch *et al.* (2009) investigated variation in survival over the first two years in chicks fledged from this colony, relating it not directly to food availability but to the birds' body condition at and after fledging. They found that the only predictor of juvenile survival was last post-fledging body mass recorded by the weighing scales at the colony islands, whereas fledging mass itself was of minor importance. This points to the importance of fish availability in the period directly after fledging, when the young terns are still partly fed by their parents but also have to learn to fish for themselves.

5 Seabird species overwintering in the Dutch North Sea

5.1 Black-legged kittiwake

5.1.1 Species introduction

The kittiwake is one of the most abundant seabirds of the Northern Hemisphere, breeding both in the Atlantic and Pacific regions, but its populations have declined severely, leading to Red-listing as ‘Vulnerable’ worldwide and as Endangered in the European Union (IUCN, Birdlife 2021). In the Dutch part of the North Sea the species is most abundant in autumn and winter, although the main wintering area of the European breeding population is located in Canadian waters of the NW Atlantic (Frederiksen *et al.* 2012). Nevertheless, up to a few hundred thousand kittiwakes can be present in Dutch waters. These include not only birds from North Sea colonies, but also (and perhaps in the majority) birds breeding in the Norwegian and Barents Sea regions (Furness 2016).

Small numbers of kittiwakes also breed on oil and gas platforms in the Dutch part of the North Sea since at least 2000 (Camphuysen & Leopold 2007; Camphuysen & de Vreeze 2005). All platforms occupied to date are situated near the Frisian Front, a marine area located approximately 50 km off the Wadden Islands. Because most platforms are not surveyed in every year, the current population size is uncertain, but reports since 2019 indicate that it involves several hundred pairs (Fijn *et al.* 2023). In 2024, at least five platforms were occupied, holding a minimum of 541 and up to 625 nests (R. Fijn, Waardenburg Ecology; M. Poot, WMR).

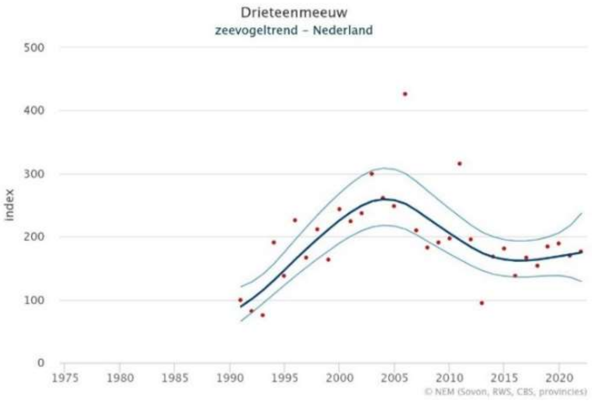

Fig. 12. Trend of mid-winter numbers of black-legged kittiwake in the Netherlands in 1986/87-2022/23. Shown are the annual population index (red dots) and the trendline (dark blue line) with 95% confidence interval (pale blue lines). Data from systematic aerial counts within the MWTL scheme.

Table 13. Published estimates of annual survival probabilities for kittiwake. Standard deviations denote variability across years or across sites/years. More data for specific sites and years can be found in Annex IIb.

area	**period**	**adult**	**SD_p**	**imm.**	**SD_p**	**1st yr**	**SD_p**	**source**
UK: United Kingdom	review	0.85	0.05	.	.	0.79	.	Horswill & Robinson 2015
UK: United Kingdom	review	.	.	.	.	0.63	.	Coulson 2011
UK: Tynemouth	1956-1996	0.82	0.07	.	.	.	.	Coulson & Strowger 1999
UK: Isle of May	1986-2002	0.88	0.09	.	.	.	.	Frederiksen *et al.* 2004
UK: Foula	1986-1997	0.81	0.13	.	.	.	.	Oro & Furness 2002
UK: Fair Isle	1986-1999	0.83	0.34	.	.	.	.	Rothery *et al.* 2002
UK: Skomer	1995-2020	0.84	0.08	.	.	.	.	Newman *et al.* 2021
UK: Skomer	1978-1994	0.87	0.06	.	.	.	.	Newman *et al.* 2021
UK: Canna	<2002-2019	0.85	0.02	.	.	.	.	O'Hanlon *et al.* 2021
UK: Colonsay	<2003-2019	0.90	0.02	.	.	.	.	O'Hanlon *et al.* 2021
UK: Lowestoft	1979-2014	0.79	0.02	.	.	.	.	O'Hanlon *et al.* 2021
UK: Anglesey	<2002-2019	0.85	0.01	.	.	.	.	O'Hanlon *et al.* 2021
DK: Bulbjerg	1992-2010	0.82	.	.	.	.	.	Lerche-Jørgensen *et al.* 2012
NO: Björnøya	2004-2024	0.88	.	.	.	.	.	SEAPOP, Fayet *et al.* 2025
NO: Hornøya	1999-2010	0.85	0.09	.	.	.	.	Reiertsen *et al.* 2014
NO: Barentz Sea	2015-2024	0.70	0.11	.	.	.	.	SEAPOP, e.g. Fayet *et al.* 2025
NO: Norwegian Sea	2015-2023	0.80	0.05	.	.	.	.	SEAPOP, e.g. Fayet *et al.* 2025
NO: Røst	2015-2023	0.76	0.05	.	.	.	.	SEAPOP, Fayet *et al.* 2025
NO: Runde	2011-2024	0.82	.	.	.	.	.	SEAPOP, Fayet *et al.* 2025
NO: Sklinna	2011-2024	0.80	.	.	.	.	.	SEAPOP, Fayet *et al.* 2025
F: Brittany	1987-1999	0.80	0.10[1]	0.67[2]	.	0.72	.	Cam *et al.* 2002
F: Brittany	1985-2012	0.81	0.05	.	.	0.65[3]	0.11	Acker *et al.* 2022
North Sea	1990-2019	.	.	0.82[4]	.	0.55	.	Collier *et al.* 2020
Arctic Waters	1986-2019	0.85	.	0.80[2]	.	0.56	.	Frederiksen *et al.* 2025[5]
Greater North Sea	1986-2019	0.85	.	0.79[2]	.	0.49	.	Frederiksen *et al.* 2025[5]
Celtic Seas	1986-2019	0.85	.	0.84[2]	.	0.52	.	Frederiksen *et al.* 2025[5]

[1] SD_p from Cam *et al.* 1998; [2] 2nd + 3rd year; [3] 1st + 2nd year; [4] 2nd year; [5] Baseline values taken from Robinson 2010, calibrated on observed breeding output and population development.

5.1.2 Key demographic variables

5.1.2.1 Survival

Adult survival was estimated from a review of the literature at 0.85 by Horswill and Robinson (2015), based mainly on studies at the Isle of May, Foula, and Skomer (all UK). Since then, a number of other estimates has become available, and these are listed in table 13 together with a number of older estimates from long-running studies in European waters. Overall, estimates of adult annual survival in table 13 vary from 0.70 to 0.90 with a mean of 0.83 and SD_e of 0.04. Reported standard deviations of between-year variability in adult survival (SD_p) vary around 0.08 (i.e. 10% of the mean value).

Perhaps remarkably in view of the extensive data on adult survival, very few estimates are available for survival of young kittiwakes. Horswill & Robinson 2015 give first-year survival as 0.79 based on Coulson & White's (1959, now rather dated) analysis of ring recoveries, but Coulson (2011) suggested that it is more likely to be around 0.63, which is close to the 0.65 observed by Acker *et al.* over a long time period at Cap Sizun, France. Collier *et al.* (2020) derived an even lower estimate from ring recoveries from countries around the North Sea, and modelling results by Frederiksen *et al.* (2025) are of the same magnitude. The mean of first-year survival estimates in table 13 is 0.61 (SD_e 0.10). For 'immatures' aged 1-2 years old, the mean is 0.78 (SD_e 0.07). We found just one report for temporal variability of survival in young birds: 0.11 (SD_p). These data weaknesses have not remained unnoticed and O'Hanlon *et al.* (2021) have explored the need for and potential of a large-scale colour-ringing effort in kittiwakes to fill the existing gaps. Their report includes a comprehensive review of the availability of quantitative demographic information on this species.

5.1.2.2 Recruitment and adult breeding propensity

The mean age at recruitment in kittiwakes is generally taken to be 4 years, although it can vary from 2 to 10 years, with part of this variation driven by the availability of nest sites (Cam *et al.* 2002; Coulson 2011). Acker *et al.* (2022) reported age-dependent recruitment rates from a long-term study in France; 14%, 39%, 28% and 18% of recruits bred first at 3-6 yrs respectively (mean 4.5 yrs, SD 0.9). At the North Shields (UK) colony mean age of first breeding of males decreased from 4.6 years in 1961-70 to 3.7 in 1981-90 (Coulson 2011). The estimates cited here vary around a mean of 4.3 yrs (SD_e 0.4).

Breeding propensity has been the subject of studies at Cap Sizun, Brittany. Here Danchin & Monnat (1992) reported annual breeding probabilities that were rather similar in a declining colony (0.79, SD_p 0.21) and an increasing colony (0.82, SD_p 0.19). In the same area but over a much longer time period Acker *et al.* (2022) reported it to be rather lower on average: 0.67 with interannual variability (SD_p) 0.04. Taken together these estimates average around 0.76 (SD_e 0.08, SD_p 0.14). Acker et al (2022) found breeding propensity to be positively associated with the mean quality of nesting habitat patches in the colony, and negatively with the number of competitors, indicating density dependence.

5.1.2.3 Breeding productivity

Breeding productivity of kittiwakes has been measured at many sites and in many years. It is highly variable, ranging from zero at colonies subject to severe food shortage up to a maximum of about 1.4 fy/pr where conditions are ideal (Furness 2016). Table 14 summarises mean estimates for a number of regions and a selection of well-studied sites. These average

Table 14. Summary of data on breeding productivity (young fledged per breeding pair) of black-legged kittiwake. The table contains a selection of published data from countries in the North Sea region and elsewhere in Europe. More data for specific sites and years can be found in Annex IIb.

Area	**Period**	**N**	**fy/pr**	**SD_p**	**Source**
United Kingdom: national average	1986-2008	>100	0.69	0.30	Horswill & Robinson 2015[1]
UK: North Sea mainland coasts	1986-2008	>100	0.82	0.33	Horswill & Robinson 2015[1]
UK: NE England	2009-2024	32	0.92	0.41	JNCC, SMP database
UK: Coquet Island	1990-2006	16	1.03	.	Coulson & Coulson 2008
UK: Firth of Forth , Isle of May	2009-2024	16	0.91	0.30	JNCC, SMP database
UK: Firth of Forth	1981-2003	19	0.59	0.19	Wanless *et al.* 2007
UK: Orkney	2009-2019	11	0.50	0.35	JNCC, SMP database
UK: Shetland	1986-2008	>100	0.41	0.48	Horswill & Robinson 2015[1]
UK: Shetland	2009-2019	11	0.40	0.32	JNCC, SMP database
UK: W Scotland & Irish Sea	1986-2008	>100	0.64	0.31	Horswill & Robinson 2015[1]
UK: Skomer	1995-2021	27	0.68	0.21	Newman *et al.* 2021
D: Helgoland	2015-2022	8	0.57	0.24	Dierschke 2022
NO: Björnøya & Svalbard	2018-2024	8	0.66	0.27	SEAPOP, e.g. Fayet *et al.* 2025
NO: Barentz Sea	2018-2023	10	0.26	0.39	SEAPOP, e.g. Fayet *et al.* 2025
NO: Norwegian Sea	2018-2024	24	0.52	0.26	SEAPOP, e.g. Fayet *et al.* 2025
F: Cap Sizun	1985-2012	28	0.65	.	Acker *et al.* 2022
Arctic Waters (OSPAR region I)	1986-2019	.	0.60	0.23	Frederiksen *et al.* 2023, 2025
Greater North Sea (OSPAR II)	1986-2019	.	0.72	0.19	Frederiksen *et al.* 2023, 2025
Celtic Seas (OSPAR region II)	1986-2019	.	0.66	0.18	Frederiksen *et al.* 2023, 2025

[1] mean and s.d. are by-region means of colony sd's; N sums of colony-years.

at 0.64 fy/pr (SD_e 0.19), slightly lower than averages for the UK reported by Horswill & Robinson 2015 (0.69) and Furness 2016 (0.67), due to low average productivity in colonies along the Norwegian coast. Estimates of annual variability of breeding productivity vary around 0.29 (SD_p), or 45% of the mean value.

5.1.3 Relationships between demography and food resources

Relationships between kittiwake demography and food resources have been studied extensively in the northwestern 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 effects of sandeel availability on breeding success as well as survival. Studies have also been made in Norway, where kittiwakes have strongly declined in the Norwegian Sea and Barents Sea regions. As a result, an extensive body of data is available on the dependency of breeding productivity on the regional abundance of forage fish (sandeel). Adult survival has been linked to prey abundance in both the breeding regions (North Sea and Barents Sea) and wintering regions (NW Atlantic). No data is available on the dependency of first-year survival, breeding propensity and age at recruitment on food stocks.

Breeding productivity

Because of their relatively restricted foraging range from the breeding colony (mainly within 50 km), kittiwakes are more likely to be affected by local changes in the abundance or availability of prey fish than wider-ranging seabirds (Furness & Tasker 2000). There is substantial evidence for a link between the observed declines of kittiwakes in the UK (NE England and Scotland) and lack of sandeels, with a causative role of both climate warming and fisheries. This has led to some (temporary and spatially restricted) closures of the fisheries, and eventually to a total moratorium on sandeel fishing in Scottish North Sea waters from 2024.

Kittiwake colonies in the UK can be grouped into regional clusters with similar patterns of variation in breeding success, and these clusters are consistent with sandeel population structure (Frederiksen *et al.* 2005). Cury *et al.* (2011) reported that kittiwake breeding productivity in Shetland in 1974-2005 was correlated with regional sandeel stocks, particularly in the lower 50% of the range of annual stock sizes. Adult survival rates were also correlated by sandeel abundance in Shetland (Oro & Furness 2002). Body condition at the end of the breeding season and availability of 0-group (< 1 yr old) sandeels positively influenced adult survival, whereas this was reduced when great skua productivity was high, pointing at a top-down effect of predation by skuas.

In eastern Scotland, Frederiksen *et al.* (2004) showed that both breeding productivity and adult survival were low when a sandeel fishery was active (1991–1998) and were also negatively correlated with winter sea temperature, with a 1-year lag for breeding success. Stochastic modelling indicated that the population was unlikely to increase if the fishery was active or sea temperature increased, and that it was almost certain to decrease if both occurred. Sandeel recruitment is reduced in warm winters, and this may explain the temperature effects on survival and breeding success.

To examine whether a (next) closure of the sandeel fishery off SE Scotland in 2000 benefitted seabirds, Daunt *et al.* (2008) compared fish consumption, at-sea distributions, and breeding success of seven sandeel-feeding seabird species to fishery removals and abundance of 1+ group (≥1 yr old) and 0 group (< 1 yr old) sandeels in 1996-2003. Breeding success of kittiwake was related to abundance of both 1+ group (targeted by the fishery) and 0 group sandeels. The proportion of 0 group sandeel consumed by kittiwakes and the proportion of the kittiwake population foraging in the area were linked to 0 group abundance. Frederiksen *et al.* (2008) evaluated the effects of sandeel fishery in the same

system on sandeel-dependent breeding seabirds. Controlling for environmental variation (sea surface temperature, abundance of larval sandeel, and size of adult sandeel), they found that, when the fishery was operating, breeding productivity was significantly depressed in the surface-feeding kittiwake, but not in four diving species. Kittiwake productivity among 12 colonies inside and outside the closure zone in a replicated BACI design was significantly depressed and negatively correlated with fishery effort in the closure zone when the fishery was active, whereas no effect was found in the control zone. Searle *et al.* (2023) broadly confirmed these findings in a later analysis using more years.

Regnier *et al.* (2024) investigated the effects of sandeel abundance and phenology on fledging success in five seabirds along the E coast of Scotland in 2000-2016. Breeding success in the late-breeding kittiwake was high when conditions favoured both high sandeel abundance and temporal synchrony between sandeel abundance and the chick-rearing period.

Sandeel have also been shown to affect breeding productivity of kittiwakes in the Norwegian Sea. On Anda, the proportion of sandeel in the diet was positively related to daily growth rate of chicks, and a high proportion of mesopelagic fish was associated with a decrease in their survival (Christensen-Dalsgaard *et al*. 2012). Both effects were strongest in the second chick in two-chick broods. However, Cury *et al.* (2011) showed that kittiwake breeding productivity on Røst in 1981-2010 was correlated to regional stocks of juvenile herring, particularly in the lower quarter of the range of annual stock sizes. In the Barents Sea region, capelin are the preferred food of kittiwakes and large stock fluctuations (including several collapses) had negative effects on the population (Barret *et al*. 2004, Barrett 2007).

Survival
As noted above, survival of kittiwakes breeding in Shetland and E Scotland has been shown to be affected by sandeel abundance and by climate variables (sea surface temperature).

In N-Norway, over a period of 22 years (1990-2011) the survival of adult kittiwakes correlated positively with both the biomass of capelin in the Barents Sea were the gulls stay between March and October, and with the density of sea butterflies (*Thecosomata*) in their main wintering region in the Grand Banks-Labrador Sea area (NW Atlantic). Together these two factors explained 53% of the variability in survival (Reiertsen *et al.* 2014). Thecosomata are planktonic sea snails that form an important food source for fish, seabirds and whales. They have an internal aragonitic shell which makes them sensitive to seawater acidification due to climate warming, a process that is expected to become serious in arctic waters. The NW Atlantic wintering areas are used by kittiwakes from most of the European breeding areas (Frederiksen *et al.* 2012). In a different study in the same region, Sandvik *et al.* (2015) found that rather than with capelin abundance, adult survival of Hornøya kittiwakes was correlated weakly positively with 0-group cod abundance, and more strongly but negatively with 1-group herring. However, a model including only effects of year performed best, indicating that other factors than the three fish species and some climatic indices considered affected survival most (e.g. the *Thecosomata* referred to above).

Recruitment age and breeding propensity
We found few studies on the potential dependence of recruitment or adult breeding propensity on food abundance. Oro & Furness (2002) found that on Foula, Shetland, in years of low sandeel abundance or high great skua predation kittiwakes did not refrain from breeding activity to buffer their survival at the cost of not rearing chicks.

5.2 Common Scoter

5.2.1 Species introduction

The breeding range of the Common Scoter extends from Iceland, Scotland and Ireland in the west through northern Scandinavia to Central Siberia. Wintering areas comprise the Baltic Sea and Atlantic coastal seas from SW Scandinavia down to Iberia; individual birds may visit multiple sites in this vast area, even in a single winter. Outside the breeding season, this seaduck exhibits a strong preference for shallow (<20-30 m) coastal waters and bays, where it forages on shellfish by diving to the seafloor. Recent tracking research indicated that most Common Scoters wintering in the Netherlands may breed in Russia, as far east as 80°E in Siberia (Camphuysen & van Lieshout 2024).

Numbers of Common Scoter wintering in Dutch waters are monitored by two aerial surveys per winter (MWTL/NEM; e.g. Sluijter *et al.* 2024). The national trend is classified as 'no change' on the long term (since 1986/87), and as 'uncertain' on the short term (2011/12–2022/23), both due to the large interannual variation in numbers. Nevertheless, numbers in the better years were higher in the 1990s than in the decade around 2010. Since then, the midwinter counts have fluctuated between 900 and 80,300 individuals (fig 13).

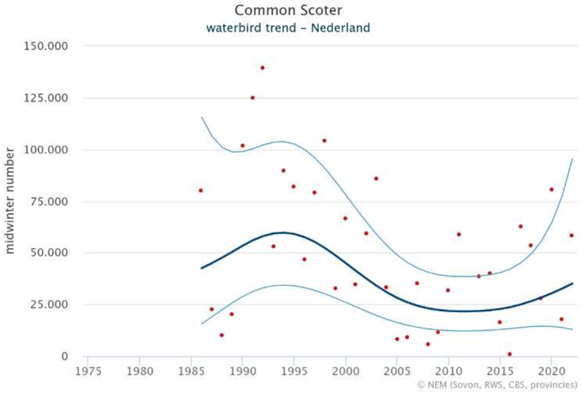

Fig. 14. Trend of mid-winter numbers of ommon scoter in the Netherlands in 1986/87-2022/23. Shown are the numbers of birds in January (red dots) and the trendline (dark blue line) with 95% confidence interval (pale blue lines). Data from aerial counts within MWTL, part of the waterbird monitoring scheme.

5.2.2 Key demographic variables

5.2.2.1 Survival

Probably due to the circumstance that common scoter breeds quite dispersed in a very large range in habitat that is often not easily accessible, very little information is available on demographic parameters. What is available is based on studies at lake Myvatn in Iceland, which is not the breeding area of most scoters wintering in the North Sea. Fox *et al.* (2003) estimated the mean adult survival rate at 0.78 based on old ringing data (1925-1958). No estimates are available for annual survival of younger scoters, nor for annual variability in adult survival.

5.2.2.2 Recruitment and breeding propensity

Age at first breeding is given as 3 years. No data are available on breeding propensity of adults.

5.2.2.3 Breeding productivity

Gardarsson & Einarsson (2004) reported a mean breeding productivity of 1.84 fledged young per breeding female at lake Myvatn in Iceland (SD_P 1.18).

5.2.3 Relationships between demography and food resources

The only study that reported a relationship between a key reproductive parameter (breeding productivity) and food resources in the common scoter addresses food abundance not at sea but in the breeding area, the freshwater lake Myvatn in Iceland. Gardarsson & Einarsson (2004) found that between-year variation in production of young ducks was strongly correlated with the abundance of aquatic insects (emerging midgets) at the lake's surface, affecting food availability for the young ducks.

For wintering scoters, the availability of concentrations ('banks') of shellfish of ingestible and profitable size and with a high flesh-to-shell-ratio at depths that can be easily exploited by the diving ducks has been shown to affect their distribution and numbers wintering in a region, but direct effects on key demographic parameters have not been shown. This is no surprise as estimates of mortality and breeding productivity are almost nonexistent for this species, and this is unlikely to change in the near future. Common scoters seem to make extensive within-season movements in their non-breeding range which would enable them to switch to other areas when local shellfish stocks are depleted (Camphuysen & van Lieshout 2024).

5.3 Red-throated Diver

5.3.1 Species introduction

The breeding range of the red-throated diver extends across the Arctic and boreal zones of Eurasia. The species breeds in (often small) mountain and tundra lakes and winters mainly along the coasts of Iceland and from the Baltic Sea southwards to the Bay of Biscay, with a concentration in the southeastern North Sea. Divers from this area migrate to breeding areas ranging from western Greenland to Taimyr, with a considerable proportion in Russia. The Dutch wintering population (present mainly between October and February) was estimated at 3000–11,200 individuals in 2016/17–2020/21 (Hornman *et al.* 2022), and is concentrated in the coastal zone off the Wadden Islands, the Holland Coast, and the Voordelta. Aerial surveys have revealed a regular occurrence also further offshore in the Dutch North Sea (Fijn *et al.* 2022). In 2023/24, counts in January yielded an estimated total of 14,500 birds across the whole Dutch North Sea (van Bemmelen *et al.* 2024).

The national trend of the red-throated diver as a non-breeding species shows a stable population development both in the long term (1991/92–2022/23) and in the short term (2011/12–2022/23).

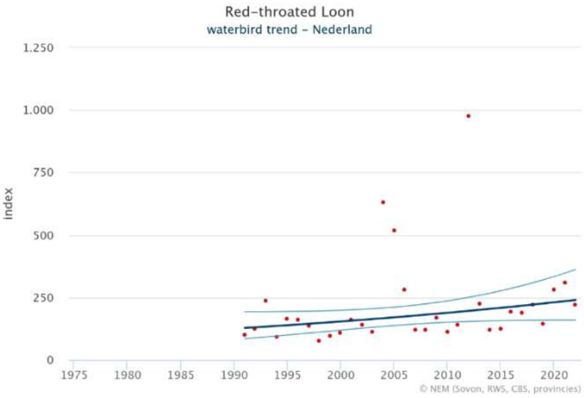

Fig. 16. Trend of numbers of red-throated diver in Dutch waters in 1986/87-2022/23. Shown are the annual population index (red dots) and the trendline (dark blue line) with 95% confidence interval (pale blue lines). Data from systematic seawatches made from shore and aerial counts within the MWTL scheme. .

5.3.2 Key demographic variables

Like common scoter, the red-throated diver breeds dispersed in a very large range in habitat that is often not easily accessible. As a result little information is available on its demography; most of this was summarised by Horswill & Robinson (2015).

5.3.2.1 Survival

The only published estimate of survival in divers was reported by Hemmingsson & Eriksson (2002) based on ringing data from Sweden: mean annual adult survival 0.84, second-year 0.62, first-year 0.60. No information is available on annual variability in survival.

5.3.2.2 Recruitment and adult breeding propensity

Age at recruitment is approximately 3 years. No data is available on skipping of breeding seasons.

5.3.2.3 Breeding productivity

Published data on breeding productivity come from the Shetland and Orkney islands, where the small British breeding population has been the focus of some studies. It is unknown whether these figures are at all representative for divers in the main breeding regions of birds migrating to the North Sea, in Scandinavia and Russia. The values in table 15 average at 0.58 fy/pr (SD_e 0.14, SD_p 0.17).

Table 15. Summary of data on breeding productivity (young fledged per breeding pair) of red-throated diver. The table contains a selection of published data from Europe.

Area	Period	N	fy/pr	SD_p	Source
United Kingdom: Shetland	1918-1983	.	0.45	0.08	Gomersall 1986
United Kingdom: Orkney	1973-1998	15	0.73	0.22	Booth 1999
United Kingdom, national average	1918-1998	.	0.57	0.22	Horswill & Robinson 2015

5.3.3 Relationships between demography and food resources

No studies were found that report on relationships between demography of red-throated divers and food resources.

5.4 Common Guillemot

5.4.1 Species introduction

Common Guillemot is a cliff-nesting alcid breeding widespread along the Atlantic coast of western (subspecies *U.a. albionis*) and northern Europe (*U.a. aalge*) and spends most of the non-breeding season at sea. It is among the most abundant seabirds in the North Sea, particularly in Dutch waters, where the highest numbers are recorded from August to February. In July-August, many father-chick pairs (with still flightless chicks) travel down from English breeding colonies to Dutch waters (Camphuysen 2002, van Bemmelen *et al.* 2025). Seasonal maximum numbers in the Dutch part of the North Sea were estimated at 190,000–570,000 individuals in the period 2016/17–2020/21 (Hornman *et al.* 2022). Birds in the southern North Sea include many of those from colonies in eastern England and Scotland, but also immatures from further north (Norway; Furness 2016, van der Vliet 2018).

Trends in Dutch waters are currently calculated for both guillemot and razorbill combined, as distinguishing these species during the aerial MWTL counts has been problematic until recently. This combined trend shows a moderate increase both since 1991/92 and in the short term (2011/12–2022/23). The common guillemot dominates this trend numerically, being present in larger numbers for longer periods. The increase in Dutch waters reflects one in the British breeding colonies (Harris *et al.* 2024).

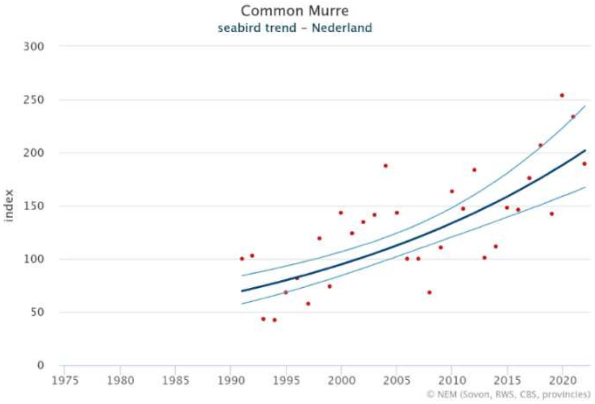

Fig. 17. Trend of numbers of non-breeding common guillemot on the Dutch North Sea in 1986/87-2022/23. Shown are the annual population index (red dots) and the trendline (dark blue line) with 95% confidence interval (pale blue lines). Data from systematic aerial counts within the MWTL scheme.

Table 16. Published estimates of annual survival probabilities for common guillemot. Standard deviations denote variability across years or across sites/years. More data for specific sites and years can be found in Annex IIb.

Area	**period**	**adult**	**SD$_p$**	**imm.**	**SD$_p$**	**1st yr**	**SD$_p$**	**source**
UK: Isle of May	1983-2002	0.97	.	0.88[1]	.	0.56	0.21	Harris *et al.* 2007
UK: national	review	0.94	0.02	0.86[2]	.	0.56	.	Horswill & Robinson 2015
NO: Hornøya	1989-2003	0.96	0.02	.	.	.	.	Sandvik *et al.* 2005
NO: Hornøya	1988-2024	0.98	0.01	.	.	.	.	SEAPOP, Fayet *et al.* 2025
NO: Hjelmsøya	2007-2024	0.91	0.05	.	.	.	.	SEAPOP, Fayet *et al.* 2025
NO: Sklinna	2008-2024	0.93	.	.	.	.	.	SEAPOP, Fayet *et al.* 2025
SE: Stockholm Arch.	1995-2014	0.90	.	.	.	.	.	Kadin *et al.* 2029
Arctic Waters	model	0.94	.	0.85[3]	.	0.65	.	Frederiksen *et al.* 2025[3]
Greater North Sea	model	0.91	.	0.79[3]	.	0.52	.	Frederiksen *et al.* 2025[3]
Celtic Seas	model	0.91	.	0.79[3]	.	0.51	.	Frederiksen *et al.* 2025[3]

[1] 2nd-4th years; [2] 2nd-3rd years; [3] 2nd year; [3] Baseline values taken from Robinson 2010, calibrated on observed breeding output and population development.

5.4.2 Key demographic variables

5.4.2.1 Survival

Table 16 summarises estimates of guillemot survival rates from a number of regions and long-running studies. Estimates of adult annual survival vary from 0.90 to 0.98, with a mean of 0.94 and SD$_e$ of 0.03. This conforms well to the value given by Horswill & Robinson (2015). Reported standard deviations of between-year variability (SD$_p$) vary around 0.03 for adult survival, just 3% of the mean.

For first-year guillemots there is only one study in which survival was actually measured; the other estimates in table 16 were derived in an indirect way. The mean of estimates is 0.56 (SD$_e$, 0.06). For immatures (2nd to 4th yr) the same caveat applies; the mean is 0.83 (SD$_e$ 0.04). Variability in first-year survival seems to be appreciably larger than in adults (c. 0.2).

5.4.2.2 Recruitment and adult breeding propensity

The BTO Birdfacts website gives the mean recruitment age as 5 years while Horswill and Robinson (2015) report 6 years. They pointed out that published information is fairly old, and differs regionally; e.g. on Skomer and the Isle of May the median age of first breeding seems to be 1-2 years earlier than on Canna.

Reed *et al.* (2015) studied skipping of breeding seasons in guillemots on the Isle of May in 1983-2013 and found its annual frequency to range between 0.02 and 0.14, with mean 0.07, i.e. a mean breeding propensity of 0.93 (SD$_p$ 0.03). We found no information for other locations.

5.4.2.3 Breeding productivity

Breeding productivity of common guillemots is monitored in numerous sites around the British Isles as well as in Norway. Table 17 summarises such data by region. Breeding colonies along the Norwegian coast (particularly of the Barents Sea) seem to be less productive than those in Britain and Ireland, where northern colonies (Shetland, Orkney,

Table 17. Summary of data on breeding productivity (young fledged per breeding pair) of common guillemot. The table contains a selection of published data from countries in the North Sea region and elsewhere in Europe. More data for specific sites and years can be found in Annex IIb.

Area	Period	N	fy/pr	SD_p	Source
United Kingdom, national	1986-2008	.	0.67	0.15	Horswill & Robinson 2015
United Kingdom, E coasts	1986-2008	.	0.66	0.13	Horswill & Robinson 2015
United Kingdom, N coasts	1986-2008	.	0.63	0.17	Horswill & Robinson 2015
United Kingdom, W coasts	1986-2008	.	0.82	0.06	Horswill & Robinson 2015
United Kingdom, Skomer	1994-2021	27	0.66	0.08	Newman *et al.* 2021
Norway: Norwegian Sea	2018-2024	7	0.58	0.27	SEAPOP, e.g. Fayet *et al.* 2025
Norway: Barentz Sea	2018-2024	11	0.23	0.31	SEAPOP, e.g. Fayet *et al.* 2025
Norway: Björnøya & Jan Mayen	2018-2014	10	0.66	0.10	SEAPOP, e.g. Fayet *et al.* 2025
Arctic Waters (OSPAR region I)	1986-2019	.	0.64	0.16	Frederiksen *et al.* 2023, 2025
Greater North Sea (OSPAR region II)	1986-2019	.	0.66	0.13	Frederiksen *et al.* 2023, 2025
Celtic Seas (OSPAR region III)	1986-2019	.	0.65	0.11	Frederiksen *et al.* 2023, 2025

N Scotland) also seem to do slightly less well than eastern and western sites. Entries in this table average at 0.62 (SD_e 0.14). Between-year variability in breeding output is moderate; it averages around 0.15 (SD_p), i.e. 24% of the mean, which is less than in many other N-Atlantic seabirds.

5.4.3 Relationships between demography and food resources

Published studies on the relationships between guillemot demography and variation in food resources paint a mixed picture; some found clear effects while others did not. Note that published estimates of both breeding productivity and adult survival show relatively low variability between years compared to most other species addressed in this report. This might suggest that guillemots are rather flexible in coping with fluctuations in the availability of prey species.

Abundance

Erikstad ea (2013) analysed variation in numbers of breeding common guillemots on Hornøya in NE Norway between 1987 and 2011 in relation to the variation in abundance (acoustic and trawl surveys) of important fish prey species in the Barents Sea: capelin, 1-group herring and 0-group cod. The guillemot population collapsed by more than 80% during the winter 1986/1987, when the abundance indices of all fish prey were very low, but has since steadily increased. The annual variation in population growth rate after the collapse was best explained by the variation in abundance of 0-group cod (unlagged), and the 0-group cod and capelin 6 and 4 yr earlier, respectively (the approximate age of maturation of guillemots). These results undermine earlier focus on the capelin stock as the main cause of the population crash in common guillemots. Hjernquist &Hjernquist (2010) reported that population size of common guillemots on Lilla Karlsö in the Baltic Sea was associated with the abundance of sprat but not their mean age-related weight (a measure of prey quality).

Breeding productivity

Cury *et al.* (2011) reported that common guillemot breeding productivity in Shetland in 1989-2005 correlated with regional sandeel stocks, particularly in the lower 30% of the range of annual stock sizes. Uttley *et al.* (1994) compared breeding performance of guillemots in Shetland in a year of high and a year of low food availability. They found no difference in reproductive success, although the rate of chick feeding, chick mass and fledging success were greater in the ‘good’ year. Adult Guillemots in the year of low food availability spent much less time resting at the colony and made twice as long foraging trips.

Wanless *et al.* (2005) reported that unprecedented breeding failures occurred at many seabird colonies on the east coast of Britain in 2004. Guillemots on the Isle of May showed very poor breeding success and low body mass at fledging. The main prey fed to chicks in 2004 was sprat rather than the usual sandeel, and parents increased the amount of time spent foraging, frequently leaving chicks unattended. Daily food intake of chicks did not differ markedly from previous years but fish collected from birds in 2004 had quite low energy value. Poor food quality appeared to be the proximate cause of seabird breeding failure in 2004. Wanless *et al.* note that single-prey loaders such as guillemots will be particularly sensitive to reductions in the energy value of food items.

Daunt *et al.* (2008) and Frederiksen *et al.* (2008), evaluating the effects of temporary closures of a sandeel fishery in SE Scotland, found no effects of sandeel abundance on breeding productivity in 3-6 other seabird species other than kittiwakes, including guillemots. Based on more years of data Searle *et al.* (2023) also found no evidence for negative effects of the fishery on guillemot breeding success, nor for positive effects arising from its closure. However, Regnier *et al.* (2024) investigated the effects of sandeel abundance and phenology on fledging success in five seabirds along the E coast of Scotland in 2000-2016, and found that fledging success of guillemots was positively influenced by both age-0 sandeel abundance and the overlap between age-0 sandeel availability and the chick-rearing period.

Kadin *et al.* (2012) examined how inter-annual variation in the quality (weight-at-age) and quantity of sprat influenced Baltic Sea guillemots during chick-rearing. Fledging success showed a positive relationship with sprat quality but none with their abundance. They found no relationship between sprat quality and parental behaviour or chick feeding parameters, but a negative relationship with trip duration.

Chivers *et al.* (2012) reported that despite substantial variation in the composition of guillemot chick diets over three years on Rathlin Island, N Ireland, their breeding productivity remained nearly constant.

Survival

Sandvik ea 2005 reported that in guillemots on Hornøya (NE Norway), adult survival rate was best explained (r^2=0.54) by climate variation (NAO index). Of three fish species considered (capelin, 1-group herring, 0-group cod), only herring abundance explained a significant part of this variation (r^2=0.34). Kadin *et al.* (2019) analysed a dataset on guillemots breeding on Stora Karlsö in the Baltic Sea and identified abundance and biomass of sprat as the main factor influencing adult survival.

5.5 Razorbill

5.5.1 Species introduction

The Razorbill is a cliff-breeding alcid that breeds widespread along the Atlantic coasts of western and northern Europe, often alongside common guillemots, and spends the non-breeding season at sea. Razorbills occurring in Dutch waters mainly originate from the western and northern coasts of Great Britain, Ireland, and Iceland. Birds migrate from UK colonies with many passing through the southern North Sea to wintering areas in southern English waters or southwards to southern Europe. Movements of immatures are more extensive than those of adults (Furness 2016). Seasonal maximum numbers on the Dutch part of the North Sea were estimated at 21,700–150,000 individuals in 2016/17–2020/21. Assessing the population trend of razorbill in Dutch waters is challenging due to its similarity during aerial counts to the more abundant guillemot, but it is likely increasing, reflecting developments in British colonies (Harris *et al.* 2024).

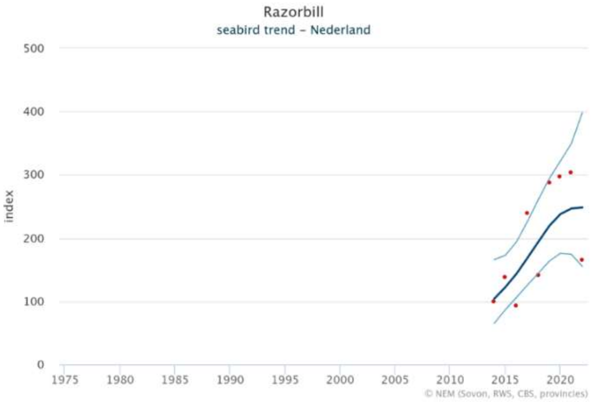

Fig. 18. Trend of mid-winter numbers of razorbill in the Netherlands in 1986/87-2022/23. Shown are the annual population index (red dots) and the trendline (dark blue line) with 95% confidence interval (pale blue lines). Data from systematic aerial counts within MWTL scheme. Before 2014, razorbills were usually not distin-guished from guillemots from the airplane

Table 18. Published estimates of annual survival probabilities for razorbill. Standard deviations denote variability across years or across sites/years. More data for specific sites and years can be found in Annex IIb.

Area	period	adult	SD_p	imm.	SD_p	1st yr	SD_p	source
UK: national	review	0.90	0.07	.	.	0.63[1]	.	Horswill & Robinson 2015
UK: Isle of May	1984-2007	0.90	0.06	.	.	.	.	Lahoz-Montfort *et al.* 2011
UK: Skomer	1970-2021	0.90	0.08	.	.	.	.	Newman *et al.* 2021
NO: Hornoya	1995-2003	0.92	0.03	.	.	.	.	Sandvik *et al.* 2005
NO: Hornoya	1995-2024	0.94	.	.	.	.	.	SEAPOP; Fayet *et al.* 2025
NO: Sklinna	2020-2024	0.90	.	.	.	.	.	SEAPOP; Fayet *et al.* 2025
Canada, Labrador	1981-1995	0.90	.	0.78[2]		.	.	Chapdelaine 1997
CAN: Gannet Island	1996-2006	0.93[3]	0.14	.		0.48[1]	.	Lavers *et al.* 2008
CAN: Machias Seal Isl.	1996-2006	0.94[3]	0.04	.		0.78[1]	.	Lavers *et al.* 2008
Arctic Waters	model[5]	0.89	.	0.88[4]	.	0.63	.	Frederiksen *et al.* 2025
Greater North Sea	model[5]	0.90	.	0.90[4]	.	0.68	.	Frederiksen *et al.* 2025
Celtic Seas	model[5]	0.90	.	0.90[4]	.	0.65	.	Frederiksen *et al.* 2025

[1] 1st-2nd year; [2] 1st-4th yr; [3] means of estimates for birds ringed as adults and as chicks; [4] 2nd – 4th yr; [5] Baseline values taken from Robinson 2010, calibrated on observed breeding output and population development.

5.5.2 Key demographic variables

Razorbill has far less often been the target of demography studies than common guillemot. Although there are similarities in ecology between these two species, there are also important differences, e.g. in distribution at sea, foraging mode and diet. In the key demographic features they are rather similar, but adult survival in razorbills tends to be slightly lower, possibly offset by an earlier age at first breeding.

5.5.2.1 *Survival*

Estimates of annual survival of adult razorbills are summarised in table 18 and vary from 0.89 to 0.94, with a mean of 0.91 and SD_e of 0.01. Reported standard deviations of between-year variability (SD_p) in adult survival vary around 0.07.

For first-year razorbills the mean survival value is 0.64 (SD_e 0.11), but the only two direct estimates based on ringing data are for first-and second-year birds combined (Lavers *et al.* 2008; the entry in Horswill & Robinson (2015) is the mean of these). There is also no direct estimate for immature survival; the one by Chapdelaine (1997) pertains to the first 4 years of age combined. The mean of values for immatures in table 18 is 0.87 (SD_e 0.06).

5.5.2.2 *Recruitment and adult breeding propensity*

Razorbills start to breed when 4 years old according to the BTO Birdfacts website, but at 5 years according to Horswill & Robinson (2015). More information is needed as age of first breeding may vary between colonies depending on factors such as nest site availability (Furness 2016).

Harris & Wanless (2007), cited in Horswill & Robinson (2015), reported an incidence of missed breeding of 3% on the Isle of May in 1982-1987 (breeding propensity 0.97), but remarked that some birds assumed to have died might have bred somewhere out of sight.

Table 19. Summary of data on breeding productivity (young fledged per breeding pair) of razorbill. The table contains a selection of published data from countries in the North Sea region and elsewhere in Europe. More data for specific sites and years can be found in Annex III.

Area	**Period**	**N**	**fy/pr**	**s.d.**	**Source**
United Kingdom, national	1986-2010	.	0.57	0.25	Horswill & Robinson 2015
United Kingdom, southern sites	1986-2010	.	0.64	0.27	Horswill & Robinson 2015
United Kingdom, mid-lat. Sites	1986-2010	.	0.64	0.06	Horswill & Robinson 2015
United Kingdom, northern sites	1986-2010	.	0.46	0.24	Horswill & Robinson 2015
United Kingdom, Skomer	1995-1921	26	0.48	0.15	Newman *et al.* 2021
Norway, Barentz Sea	2018-2024	8	0.30	0.23	SEAPOP, e.g. Fayet *et al.* 2025
Arctic Waters (OSPAR region I)	1986-2019	.	0.64	0.23	Frederiksen *et al.* 2025
Greater North Sea (OSPAR II)	1986-2019	.	0.61	0.09	Frederiksen *et al.* 2025
Celtic Seas (OSPAR region II)	1986-2019	.	0.53	0.17	Frederiksen *et al.* 2025

5.5.2.3 *Breeding productivity*

Table 19 summarises breeding productivity data for razorbill. Regional mean values vary between 0.30 in the Barents Sea to 0.65 in southern and mid-latitude British sites; the mean is 0.54 fy/pr (SD_e 0.11), with annual variability (SD_p) around 0.19, i.e. 35% of the mean.

5.5.3 Relationships between demography and food resources

Population size

Hjernquist & Hjernquist (2010) reported that population size of common guillemots on Lilla Karlsö in the Baltic Sea in 1974-2007 was associated with the abundance of sprat but not its mean age-related weight (a measure of prey quality).

Breeding productivity

Regnier *et al.* (2024) investigated the effects of sandeel abundance and phenology on fledging success in five seabirds along the E coast of Scotland, and found that fledging success of razorbills was positively affected by 1-group sandeel abundance, but that the amount of overlap of sandeel abundance with the chick-feeding period had no effect.

Daunt *et al.* (2008) and Frederiksen *et al.* (2008), evaluating the effects of temporary closures of a sandeel fishery in SE Scotland, found no effects of sandeel abundance on breeding productivity in 3-6 other seabird species other than kittiwakes, including razorbills. Based on more years of data Searle *et al.* (2023) also found no evidence for negative effects of the fishery on razorbill breeding success, nor for positive effects arising from its closure.

Chivers *et al.* (2012) reported that despite substantial variation in the composition of razorbill chick diets over three years on Rathlin Island, N Ireland, their breeding productivity remained nearly constant.

Survival

Sandvik ea 2005 reported that in razorbills on Hornøya (NE Norway), adult survival rate was not well explained by either climate variables (NAO index, sea surface temperature) or abundance of three fish species (capelin, 1-group herring, 0-group cod); the most plausible model assumed constant survival without covariate effects.

5.6 Northern Fulmar

5.6.1 Species introduction

The northern fulmar is a pelagic seabird from the tubenose family (also including albatrosses and shearwaters) that largely avoids the coastal zone. The majority of the North Sea population breeds on the Shetland and Orkney islands and in northern Scotland. Smaller numbers are found in England, Norway, Denmark, France, and on Helgoland (Germany). Breeding birds may forage at considerable distance (>100 km) from the colony. Birds from colonies around the North Sea disperse across the North Sea and the Atlantic Ocean until they begin breeding in May (Lloyd *et al.* 2010). Outside the breeding season, the North Sea also hosts breeding birds from more northern regions (Tasker *et al.* 1987). Seasonal maximum numbers in the Dutch part of the North Sea were estimated at 6600–39,100 individuals in the period 2016/17–2020/21 (Sovon 2025). The national trend of the fulmar as a non-breeding species has shown a strong decline since 1991/92 and a moderate decline in the short term (2011/12–2022/23). Reductions in fisheries discards may play a role in this decline, as well as climate change and mortality through bycatch in fisheries.

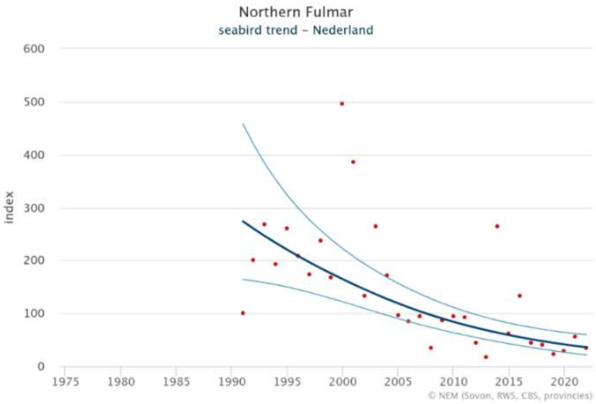

Fig. 19. Trend of mid-winter numbers of northern fulmar in the Netherlands in 1986/87-2022/23. Shown are the annual population index (red dots) and the trendline (dark blue line) with 95% confidence interval (pale blue lines). Data from systematic aerial counts within the MWTL scheme.

5.6.2 Key demographic variables

Compared to several other seabirds in the N Atlantic the demographics of northern fulmar are relatively poorly known. A long-term study has been ongoing on Eynhallow in the Orkney islands, UK.

5.6.2.1 Survival

Data on survival of fulmars is summarised in table 20. Estimates of adult annual survival vary within a narrow range around 0.93 (SD_e 0.01), with between-year variability (SDp) about 0.06 based on the Eynhallow study. There is no published direct estimate of survival of young northern fulmars; the value given by Horswill & Robinson (2015) is from a study on southern fulmars (*Fulmarus glacialoides*) in the southern hemisphere, and those in Frederiksen *et al.* were obtained by tuning that value to observed population trajectories and productivity data. For first-year birds the latter average 0.44 (SD_e 0.03), for immatures c. 0.90.

Table 20. Published estimates of annual survival probabilities for northern fulmar. More data for specific sites and years can be found in Annex IIb.

area	**period**	**adult**	**SD_p**	**imm.**	**SD_p**	**1st yr**	**SD_p**	**source**
UK: Eynhallow	1985-1994	0.92	0.07	.	.	.	.	Grosbois & Thompson 2005
UK: Eynhallow	1962-1984	0.95	0.05	.	.	.	.	Grosbois & Thompson 2005
NO: Jan Mayen	2014-2024	0.93	.	.	.	.	.	SEAPOP; Fayet *et al.* 2025
UK: national average	Review	0.94	0.06	.	.	0.41	.	Horswill & Robinson 2015
Greater North Sea	model [2]	0.94	.	0.90 [1]		0.46	.	Frederiksen *et al.* 2025
Celtic Seas	model [2]	0.92	.	0.89 [1]		0.45	.	Frederiksen *et al.* 2025

[1] 2nd to 6th year; [2] Baseline values taken from Robinson 2010, calibrated on observed breeding output and population development

5.6.2.2 Recruitment and adult breeding propensity

Horswill & Robison (2015) give the mean age at recruitment as 9 years, and Cramp & 1977 as 6-12 yrs, mean 9.2. Horswill & Robison (2015) caution that these are based on an older study from the time that the population was increasing, while it is declining nowadays. In southern fulmars a similarly high value (11 yrs, SD 4) has been reported.

No good data is available on adult breeding propensity, though skipping of breeding years seems to happen now and then (Horswill & Robinson 2015).

5.6.2.3 Breeding productivity

Table 21 summarises regional estimates and long-term studies of breeding productivity in northern fulmars in the NE Atlantic region. The mean of estimates in this table is 0.40 fy/pr (SD_e 0.05); the reported between-year variabilities vary around 0.12 (SD_p).

Table 21. Summary of data on breeding productivity (young fledged per breeding pair) of northern fulmar. The table contains a selection of published data from countries in the North Sea region and elsewhere in Europe. More data for specific sites and years can be found in Annex III.

Area	Period	N	fy/pr	SD_p	Source
United Kingdom: national average	1986-2006	414	0.42	0.13	Horswill & Robinson 2015 [1]
UK: North Sea coasts	1986-2006	91	0.38	0.14	Horswill & Robinson 2015
UK: N Scotland & Orkney	1986-2006	113	0.37	0.15	Horswill & Robinson 2015
UK: Shetland	1986-2006	105	0.40	0.08	Horswill & Robinson 2015
UK: W Scotland	1986-2006	74	0.47	0.10	Horswill & Robinson 2015
UK: Irish Sea	1986-2006	31	0.44	0.17	Horswill & Robinson 2015
UK: Orkney, Eynhallow	1985-2005	18	0.36	0.13	Lewis *et al.* 2009
UK: Orkney, Eynhallow	1958-1984	26	0.44	0.14	Lewis *et al.* 2009
D: Helgoland	2015-2022	8	0.30	0.19	Dierschke 2022
Greater North Sea (OSPAR II)	1986-2019	.	0.40	0.06	Frederiksen *et al.* 2023, 2025
Celtic Seas (OSPAR region III)	1986-2019	.	0.41	0.08	Frederiksen *et al.* 2023, 2025

[1] mean and s.d. are by-region means of colony sd's; N sums of colony-years;

5.6.3 Relationships between demography and food resources

Cury *et al.* (2011) reported that breeding productivity of fulmars in Shetland in 1986-2005 was correlated with regional stocks of sandeel, particularly in the lower 30% of the range in annual stock sizes. Sandeel made up 50-70% of the diet in this period. We found no other studies relating fulmar demographic rates to food resources. Lewis *et al.* (2009) investigated relationships between breeding productivity and environmental conditions (winter NAO) and intrinsic effects (colony size, pair bond duration, past breeding success rate) using data from the long-term study at Eynhallow. There was a negative trend in breeding success over time since 1950, and a negative relationship with winter NAO and 1-year lagged winter NAO, which themselves increased over the study period. The effects of lagged winter NAO remained after accounting for the linear trend.

5.7 Northern Gannet

5.7.1 Species introduction

Northern gannet is the largest seabird of the North Atlantic, breeding in large to very large colonies on sea stacks and cliffs from Canada via Iceland, the Faroe Islands, Norway, Great Britain, Ireland, Germany (Helgoland), to W France. Adult birds are colony-bound in March–October, from which they undertake foraging trips up to 600 km away, although most forage within 100 km from the colony. After the breeding season, birds migrate to more southern waters down to NW Africa, and numbers in Dutch waters decline. Birds from UK colonies tend to winter off southern Europe or W Africa. Birds in the North Sea in winter include a relatively high proportion of adults from Norwegian colonies (Furness 2016). Immature birds winter further away than adults on average, many to W Africa.

Seasonal maximum numbers in the Dutch part of the North Sea were estimated at 20.800–69.200 individuals in the period 2016/17–2020/21 (Hornman *et al.* 2022), mostly occurring in late summer and autumn. The national trend of the Northern Gannet shows a moderate increase in the long term (since 1991), and a moderate decrease on the short term (2011/12–2022/23). The recent decline is partly caused by very high mortality caused by avian influenza in many breeding colonies in 2022 (Lane *et al.* 2024; Matthiopoulos *et al.* 2025).

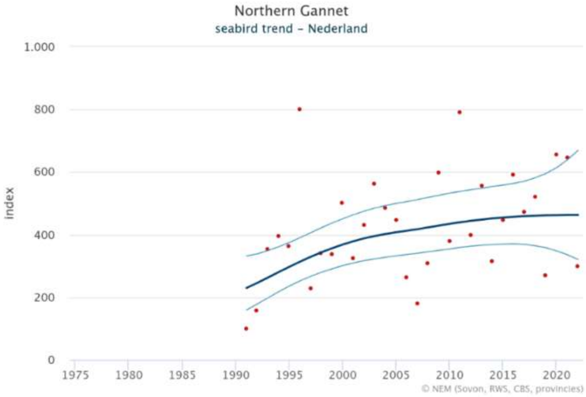

Fig. 20. Trend of mid-winter numbers of Northern Gannet in the Netherlands in 1986/87-2022/23. Shown are the annual population index (red dots) and the trendline (dark blue line) with 95% confidence interval (pale blue lines). Data from systematic aerial counts within the MWTL scheme.

5.7.2 Key demographic variables

Northern gannet is a well-studied species. Demographic monitoring, particularly of breeding productivity, is in place at most of the major colonies around the British Isles, in France and on Helgoland, as well as in some colonies in Norway.

5.7.2.1 Survival

Wanless *et al.* (2006) analysed survival in British and Irish gannets based on data from ten major colonies, and these are augmented by a few other estimates in table 22. The mean of estimates for annual survival is 0.93 (SD_e 0.01); annual variability was reported as 0.04 by Wanless *et al.* Estimates of first-year survival range around 0.54 (SD_e 0.10), while annual survival of immatures in their second to fourth year is about 0.90 (SD_e 0.04); no variability estimates are available for these younger age classes.

Note that none of the estimates extend to the year 2022 when massive mortality of adults, (as well as in other age classes at least to some extent) was caused by HPAI outbreaks in most European colonies (Lane *et al.* 2024). Matthiopoulos *et al.* (2025) estimated that 33% of the entire NE Atlantic metapopulation died during this outbreak, a mortality level three to four times that in ‘normal’ years.

5.7.2.2 Recruitment and breeding propensity

Gannets start to breed on average when 5 years old (Nelson 1978; BTO Birdfacts), with variation from 4-6 yrs (Cramp 1977). Information on the incidence of missed breeding seasons (adult breeding propensity) is lacking. This is probably due to the difficulty of reliably identifying ringed individuals in the dense and inaccessible colonies, but now that individuals can be followed over multiple years with tracking devices it should be possible to obtain information from these.

5.7.2.3 Breeding productivity

Table 23 summarises breeding productivity estimates for gannets. These average at 0.69 (SDe 0.06). Note that the year 2022, when HPAI outbreak hit many European gannet colonies, is included in the data series from Helgoland (where HPAI had large impact) and Norway (where breeding productivity was moderately affected), but not in those from the UK and France. Estimates of annual variability in breeding output (SD_p) vary around 0.09, i.e. 13% of the mean, indicating that gannet breeding success shows rather little annual variation.

Table 22. Published estimates of annual survival probabilities for northern gannet. More data for specific sites and years can be found in Annex IIb.

area	period	adult	SD_p	imm.	SD_p	1st yr	SD_p	source
United Kingdom	1959-2000	0.92	0.04	0.87 [1]	.	0.42	.	Wanless *et al.* 2006
Alderney, Channel Is.	1983-2010	0.95	.	0.96 [2]		0.57	.	Warwick-Evans *et al.* 2016
Arctic Waters	model	0.93	.	0.89 [1]	.	0.60	.	Frederiksen *et al.* 2025 [3]
Greater North Sea	model	0.93	.	0.90 [1]	.	0.65	.	Frederiksen *et al.* 2025 [3]
Celtic Seas	model	0.92	.	0.87 [1]	.	0.44	.	Frederiksen *et al.* 2025 [3]

[1] 2nd-4th years; 2 2nd-3rd year; [3] Baseline values taken from Robinson 2010, tuned to observed breeding output and population development.

Table 23. Summary of data on breeding productivity (young fledged per breeding pair) of northern gannet. The table contains a selection of published data from countries in the North Sea region and elsewhere in Europe. More data for specific sites and years can be found in Annex IIb.

Area	Period	N	fy/pr	SD$_p$	Source
United Kingdom, average	1986-2010	.	0.70	0.08	Horswill & Robinson 2015
United Kingdom, eastern coasts	1986-2010	.	0.70	0.07	Horswill & Robinson 2015
United Kingdom, western coast	1986-2010	.	0.71	0.11	Horswill & Robinson 2015
Germany, Helgoland	2015-2024	8	0.57[1]	0.11	Dierschke 2022
Norway, Bjørnoya	2015-2024	10	0.65	0.10	SEAPOP, Fayet *et al.* 2025
Norway, Runde	2015-2024	10	0.77	0.07	SEAPOP, Fayet *et al.* 2025
Arctic Waters (OSPAR I)	1986-2019	.	0.66	0.36	Frederiksen *et al.* 2025
Greater North Sea (OSPAR II)	1986-2019	.	0.68	0.04	Frederiksen *et al.* 2025
Celtic Seas (OSPAR region III)	1986-2019	.	0.72	0.11	Frederiksen *et al.* 2025

[1] Excludes year 2022, when breeding productivity was 0. 14 fy/bp due to HPAI outbreak

5.7.3 Relationships between demography and food resources

Breeding productivity

The low annual variation in breeding productivity of northern gannets might suggest that they can cope relatively flexibly with variations in abundance of certain prey species. Martin (1989) studied the food of young gannets on Hermaness, Shetland, between 1973 and 1988. Sandeel formed 90% of the diet of chicks in 1981 but declined steadily in importance thereafter due to a decline in availability. By 1988 herring and mackerel were the most common prey; apparently the gannets were able to switch to other prey with no loss of breeding success.

Hamer *et al.* (2007) investigated how the breeding productivity of North Sea gannets has remained remarkably stable whereas reproductive declines and large variation have become common in other seabirds. Over three years (1998, 2002-2003), gannets at Bass Rock exhibited great flexibility in both the species and sizes of prey consumed and in durations and ranges of foraging trips. They also showed high consistency in bearings of foraging trips and behaviour at sea. Nest attendance was low in years with long mean trip durations and chicks were left unattended and vulnerable to attack by conspecifics. While adults have so far been able to maintain high reproductive success in years of low prey availability, they may not be able to do so in future years if providing sufficient food for chicks entails any further increases in foraging effort. More recently, Daunt *et al.* (2008) did not find associations between breeding parameters of gannets in E Scotland and estimates of sandeel abundance in 1996-2003.

In response to the study by Cury *et al.* (2011) who showed that seabird breeding productivity generally starts to decline at about one third of maximum prey abundance, Guillemette *et al.* (2018) studied this in gannets breeding in the Gulf of St Lawrence, Canada. They also found a positive and non-linear relationship between fish (Atlantic mackerel) biomass and breeding success, but the latter only started to decline when prey abundance fell below c. 8% of the maximum.

D'Entremont *et al.* (2023) reported that along the Atlantic coasts of North America, northern gannet colonies near the species' southern limits are experiencing plateaued or declining population growth and poor productivity. These trends have been linked to reduced availability of Atlantic mackerel, linked to warming ocean temperatures and overfishing. At Cape St. Mary's, Newfoundland, declining mackerel availability (landings and biomass) due to warming sea surface temperatures and overexploitation has resulted in poor productivity. In more northern colonies, mackerel populations increase and range expansion coincides with gannet population growth. Jeglinski *et al*. (2024) reported a similar climate sensitivity in gannets in the European N-Atlantic, arising through a non-linear effect of temperature on breeding productivity (with an optimum at c. 11°C near-surface air temperature) and earlier density-dependent limitation of recruitment at higher temperatures, disadvantaging southwestern colonies whilst benefitting northern ones.

Other demographic parameters

We have found no other studies relating survival, age at recruitment or breeding propensity in northern gannets to food abundance.

5.8 Multi-species studies and reviews

Species-specific studies into relationships between demographic rates of seabirds and abundance of food resources were reviewed in the preceding paragraphs. Here we mention some major publications that either review the literature on certain food-related topics or use data from multiple studies on multiple species to identify general patterns.

Within the last category is the study by Cury *et al.* (2011), who quantified the effect of fluctuations in food abundance on seabird breeding productivity in a dataset consisting of 19 long time series of breeding productivity and stock sizes of the main prey species (fish and krill) of 14 seabird species. They identified a threshold in forage fish abundance below which seabirds experience both consistently reduced and more variable productivity (fig. 21). This decelerating response was common to all seven ecosystems examined within the Atlantic, Pacific, and Southern Oceans. The threshold approximated one-third of the maximum prey biomass observed in the long-term studies.

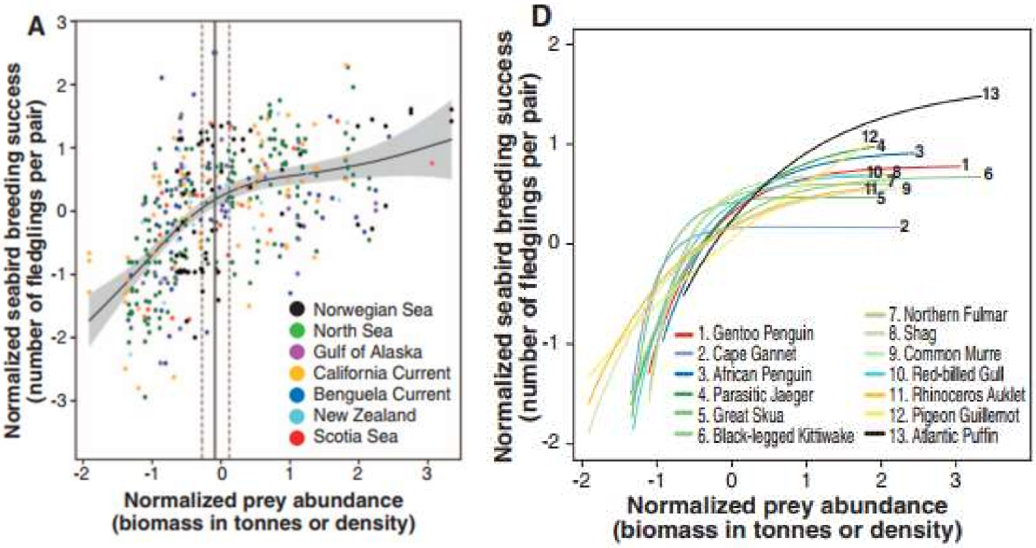

Fig. 21. (A) Relationship between annual breeding success of seabirds and prey abundance. Each (normalised) data point from all the time series was plotted with the predictions of a GAM model (solid line with grey 95% confidence interval). The threshold in the nonlinear relationship is represented by the black vertical lines. (D) Similar relationships (predictions of the best-fitting asymptotic model) per species. Reproduced from Cury et al. (2011).

The one-third threshold provides an indicator of the minimal forage fish biomass needed to sustain seabird productivity over the long term. It can for instance be used as a rule of thumb ('one third for the birds') to regulate catches of forage fish species in situations where more precise information of fish stock-bird demography relationships is absent, which is still the case in the majority of bird species-fish stock combinations. This study included data on some of the focal species of this report (as mentioned in the species sections): black-legged kittiwake, common guillemot and northern fulmar. Non-focal species included which occur in the North Sea are European shag, great skua, arctic skua, arctic tern and Atlantic puffin.

Another multi-species review study of interest with respect to the North Sea is that by Furness & Tasker (2000), who developed an index of expected vulnerability of seabird species' breeding productivity to reduced abundance of sandeels. The index is based on bird size, cost of foraging, potential foraging range, ability to dive, amount of 'spare' time in the daily budget, and ability to switch diet. Testing the index with empirical data from Shetland during periods of reduced sandeel abundance showed a close correlation between seabird breeding performance and predictions from the index. These authors also derived separate indices for four different sectors of the North Sea, among which the southern and southeastern parts, and for vulnerability to reductions in forage fish in general (instead of sandeel only). The latter vulnerability is particularly relevant because in the southern and eastern North Sea, sandeel form a much smaller part of the diet of many seabirds than in the west and north, and clupeids are predominant in many diets, suggesting that clupeid abundance may be more important in determining breeding success in this area than is sandeel abundance. Indeed this is the case for common and sandwich terns, as reviewed in paragraphs 4.5 and 4.6.

Other relevant recent reviews are those by Engelhard *et al*. (2014) on the ecosystem interactions that affect forage fish stocks in the North Sea, Votier *et al.* (2023) on the impacts of fishing on seabirds worldwide, and Piat *et al.* (2024) and Johnston *et al.* (2025) on how marine heat waves and climate change in general affect seabirds.

6 Discussion: main findings and information gaps

6.1 Key demographic parameters: summary and knowledge gaps

Table 24 summarises estimates of mean values of the key demographic parameters and associated SD_e and SD_p for the species covered in this report. These can be used in the parameterisation of population models for various purposes. The table also highlights for which aspects of species information is largely lacking (denoted by '?'), and where some information exists, but the confidence in its accuracy, actuality or representativeness for the species in general is lower, and 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 of this report. Not only are estimates available for just one or two of the parameters but some of these were also 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 (of all parameters other than breeding productivity), and northern fulmar is a fourth (survival of young age classes, age at first breeding and breeding propensity). In the other species, there is generally good information on breeding productivity and adult survival[7]. Less is often known about first-year and immature survival, and on (variation in) the age at recruitment. Generally least well-known is adult breeding propensity; for most species there is information for just one or two locations.

From the viewpoint of understanding population change it is particularly important to have reliable estimates of those parameters that have the largest influence on the species' population dynamics. In population modelling studies this influence is usually quantified as the elasticity, the proportional change of the predicted finite population growth rate (λ) in response to a given proportional change in a parameter. In table 25, elasticities are presented for the six key parameters of two of the focal species: herring gull and common guillemot. For birds in general, all our focal species are long-lived with high annual survival, and as is usual in such species (Sæther & Bakke 2000), 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, though considerably lower than that for adults. The empirical data base 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 in our species.

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[7] The (compared to other parameters) small values of SD_e and SD_p of adult survival rate may create the impression that this parameter is well known and not very variable in time, but note that the growth of a population is determined by the balance between reproduction and *mortality*, which equals 1-survival. So a survival estimate of 0.90 ± 0.03 may seem precise, but actually means that mortality may fall between c. 4% and 16% , a fourfold range!

Table 24. 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, taken from the species account texts. "?" denotes no data; values in italic print have a relatively weak data basis and require additional information.

parameter	lesser black-backed gull			European herring gull			great black-backed gull			Sandwich tern		
	avg.	SD_e	SD_p	avg.	SD_e	SD_p	avg.	SD_e	SD_p	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			black-legged kittiwake			common guillemot			razorbill		
	avg.	SD_e	SD_p	avg.	SD_e	SD_p	avg.	SD_e	SD_p	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	0.44	0.64	0.19	0.29	0.62	0.14	0.15	0.54	0.11	0.19

parameter	northern fulmar			northern gannet			common scoter			red-throated diver		
	avg.	SD_e	SD_p	avg.	SD_e	SD_p	avg.	SD_e	SD_p	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 25. 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 (taken from table 24) by -10% (except for age at recruitment +10%). The growth rate predicted by the base model is given in the last column. (Model structure copied from the herring gull model in Schekkerman et al. 2021).

species	breeding productivity	1st-year survival	immature survival	adult survival	recruitment 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 (fig. 22a). 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 (fig. 22). This difference can probably 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 long-lived birds to ‘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 terns at Wilhelmshaven breeding productivity was affected negatively by low herring abundance but adult survival was not (§4.6).

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 (fig. 22b). Although these effects were not statistically significant, it makes sense that as adults have more breeding years available 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.

Generally very little information is available in the literature on the amount of variability in age at recruitment and breeding propensity and first-year survival, even though the latter two have similarly large influence on the population growth rate as breeding productivity. It is likely that information on age at recruitment is embedded in multiple already existing datasets of breeding studies using ringed birds, but has just not yet been analysed and

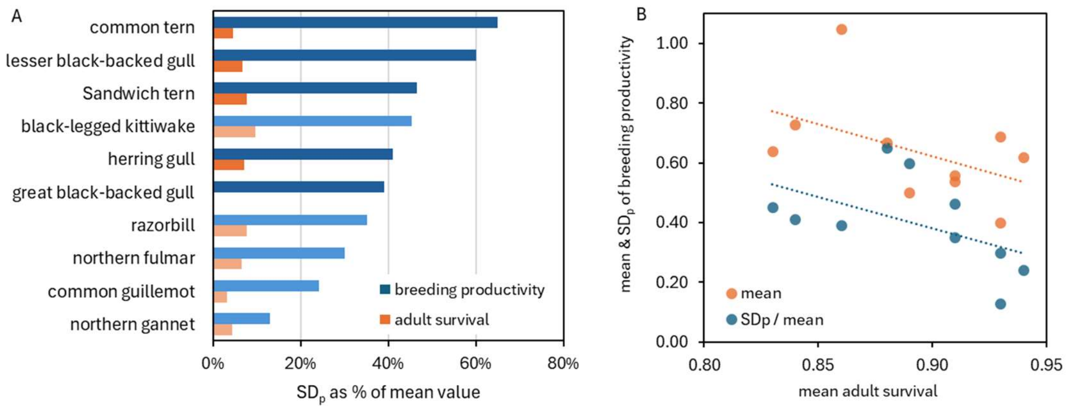

Figure 22. Summary comparison of variation in breeding productivity and survival among the focal seabird species of this study. A: Relative interannual variability (SD_p divided by the mean value) by species, ordered from largest to smallest relative variability in productivity. (Bars with darker colour 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).

reported, and therefore represents ‘low-hanging fruit’. Similarly, information on first first-year survival will be embedded in datasets of from colour-ring studies that have not yet been analysed for this purpose. However, natal dispersal and the tendency of the youngest age classes of some species to remain in remote wintering areas will provide challenges. If these parameters cannot be estimated from existing data, dedicated colour-ringing of near-fledged chicks could be initiated in multiple colonies, complemented by a network of observers, to fill this gap. Probably less ‘hidden information’ exists 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 in at a location can be observed. A promising approach is to use bird-borne devices to track individuals over multiple years, enabling the assessment of breeding status independent 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 have are relatively low cost, making them feasible for deployment on large samples of birds.

6.2 Dependency of demographic rates on food abundance

The relationship between demography and food abundance is unevenly understood across the focal species. For lesser black-backed and herring gulls, some studies indicate relationships between chick growth or productivity and the availability of discards, but quantitative links between food supply and survival, recruitment, or skipped breeding are lacking. Sandwich tern studies link settlement of breeders to indices of herring abundance in the SE North Sea and breeding productivity to prey delivery rates. Common terns exhibited strong correlations between breeding productivity and the abundance of key prey (herring/sprat and smelt), but not with adult survival, which seemed influenced more by conditions in the winter range. Kittiwake studies in the North Sea and Norway provide showed that sandeel and other forage fish (and sea butterflies) influence breeding productivity and/or adult survival. Results for common guillemot and razorbill are mixed, suggesting some flexibility in coping with fluctuating prey availability. Northern gannet appear the least sensitive to short-term prey variation, whereas few data exist for northern fulmar and virtually none for common scoter, red-throated diver, and great black-backed gull.

Table 26 enables a quick-and-dirty visual assessment of the availability of information per bird species and key parameter. In an ideal situation, all cells in the table would have an ‘A’, meaning that quantitative relationships are known between the parameters and metrics 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. (Note that the column for population size/growth probably underrepresents available studies, as we did not focus our search explicitly on studies directly relating changes in numbers to food stocks, but on the key demographic parameters driving such changes.) With respect to species, most information on food relationships is available for the kittiwake and the common tern. 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 26. 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; brackets () denote that available studies may have less relevance for North Sea populations; '-' denotes that no studies were found. Bold print indicates that studies from 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	-	-	-
Black-legged 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 point of view the situation is slightly less grave than suggested by table 26, because in our long-lived focal seabird species, adult survival shows much less variability than breeding productivity, as discussed above. 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 adults 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 27 summarises the use of different measures of food resources in the reviewed studies. In the great majority of studies, bird demography was related to fish data from general surveys conducted (usually annually) over long periods in extensive sea areas, such as those coordinated by ICES. Their overlap in space and time with bird foraging distribution and breeding seasons, and therefore possibly their power to reveal existing dependencies, varies among the bird species concerned. Only very few studies included targeted survey effort within the known foraging ranges of the focal 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 27).

Table 27. Summary of methods used to quantify availability of forage fish in the reviewed food-demography studies. Numbers in the cells denote how many study-bird species-parameter combinations reviewed used the relevant metric (if 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

6.3 Research needs

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 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 largely lacking is studies in which all these aspects are studied jointly within the same colony while simultaneously data on food availability are collected.

What is thus needed most to enhance our understanding of demography-food relationships in seabirds is studies where multiple demographic rates and the abundance of food within the foraging area of the study population are measured simultaneously, over a sufficiently long series of years to capture a representative range of environmental (food) conditions[8]. These provide the best basis to describe quantitative dose-effect relationships of the type required by predictive models like those to be developed in MONS.

This means that in the same colony or area, breeding productivity must be measured annually, and enough sufficient birds must be (colour-)ringed and resighted to be able to estimate survival, and data collected on breeding propensity (using colour-ring resightings or tracking devices over multiple years). Measuring the food resources can be an even greater challenge. Sometimes 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 local food availability, the foraging range of the study seabird study population must be known, and can be identified by tracking of foraging birds. Then, ship-based surveys of forage fish can be conducted within this area, or passive methods such as acoustic monitoring can be implemented at representative sites.

We propose to set up comprehensive studies as outlined above in lesser black-backed gull, Sandwich tern and common tern in at least one colony in each of the main breeding regions, the Wadden and Delta Area), and here address the topics listed below. Although we provide

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[8] What is 'sufficiently long' in this respect is hard to say in general, but think of a period of at least c. 10 years.

suggestions for relevant study techniques, final choices on which techniques are most appropriate must be made when study plans are developed further, and tailored to local needs and possibilities.

- Diet composition of both chicks and (where possible) parents, with attention to variability associated with laying date/chick age, between years, or other factors (e.g. weather, disturbance). Useful techniques include visual/camera registrations of prey delivered to the colony, analysis of visible remains or DNA in fecal samples.
- GPS tracking to determine foraging trips of nesting birds in various phases of the breeding cycle, at least during incubation and chick-rearing periods (but if feasible also during the (pre-)laying period). Combining such tracking with identification of prey delivered to chicks may yield additional information on the provenance of the resources for successful reproduction.
- Annual estimates of breeding productivity (and nest success and chick survival) 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 near the 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, followed up with a systematic ring-reading effort (including outside colonies) and statistical survival modelling.
- Estimates of age at recruitment and adult breeding propensity can be derived from resightings of colour-ringed birds that settle in the colony to breed. More accurate and global estimated of breeding propensity can be obtained by fitting samples of adult birds with light-storage tags (geolocators) and retrieving these after some years.
- Data on food availability at sea during key phases of the breeding season (at least during chick-rearing, but preferably also pre-laying and incubation periods). Sometimes 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 the latter food availability, the foraging range of the study seabird study population must be known. This can be identified by tracking of foraging birds. Then, ship-based surveys of forage fish within this area can be conducted(using nets and/or acoustic techniques, e.g. Baptist *et al.* 2010, Maathuis *et al.* 2025), or passive methods such as acoustic monitoring (WBATs; Sakinan *et al.* 2025) can be implemented at representative sites within the area (also allowing simultaneous measurement of potentially important environmental parameters like water temperature etc.). During ship-based surveys, observers can quantify densities and behaviour of foraging birds, including data on fish capture rates, that will aid in modelling the foraging process.. Information on the availability of fisheries discards can be obtained from data sources on commercial fishing vessel activity.

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Annexes

Digital annexes tot his report (excel format):

Ia: Colony table for lesser black-backed gull: lbb_gull.xlsx

Ib: Colony table for herring gull: herring_gull.xlsx

Ic: Colony table for great black-backed gull: gbb_gull.xlsx

Id: Colony table for Sandwich tern: sandwich_tern.xlsx

Ie: Colony table for common tern: common_tern.xlsx

IIa: LiteratureTable_Breeding_Species.xlsx

IIb: LiteratureTable_NonBreeding_Species.xlsx

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