Diet of coastal birds and seabirds of the Dutch North Sea

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Wageningen Marine Research
report: C092/25

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Wageningen Marine Research
Den Helder, November 2025

Wageningen Marine Research report: C092/25

Keywords: Diet, seabirds, stomach analysis

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KvK nr. 09098104,
WMR BTW nr. NL 8065.11.618.B01.
Code BIC/SWIFT address: RABONL2U
IBAN code: NL 73 RABO 0373599285

A_4_3_2 V36 (2025)

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Summary

This report aims to enhance understanding of the diet of coastal and seabird species in the southern North Sea, both during and outside the breeding season. The research combined a literature review with new analyses of stomach and intestinal contents of dead birds. The study reviewed available knowledge on the diet of twelve coastal and seabird species in the southern North Sea, focusing on the Dutch sector. Priority was given to literature (including grey sources) from Dutch waters, supplemented by studies from neighbouring countries where necessary. Key aspects examined include differences in diet between breeding and non-breeding seasons, chick versus adult diet, and interannual variations. Where possible, additional topics were addressed, such as prey profitability—linked to prey quality and accessibility—and the influence of climate-related factors like temperature and weather patterns on prey availability and quality. The laboratory component examines previously collected and newly obtained samples from species including red-throated diver, northern fulmar, common guillemot, and Sandwich tern, providing valuable additional insights into seabird diets.

Coastal diving species such as common scoter and red-throated diver do not breed in the Netherlands but occur along the Dutch coast in winter, with markedly different diets. Common scoters primarily feed on bivalves, and their distribution is strongly influenced by prey availability and environmental factors, with key foraging areas identified off the Wadden Sea, North Holland coast and in the Voordelta. In contrast, red-throated divers are almost entirely piscivorous, mainly consuming clupeids (herring, sprat) and gadoids, but switch to alternative prey such as gobies, sandeels or estuarine fish when preferred prey is scarce or birds are in poor condition. Recent findings highlight adaptability in prey choice linked to body condition and underscore knowledge gaps regarding habitat shifts and foraging behaviour, calling for non-invasive methods to better understand diet across health states and environmental conditions.

Common guillemots and razorbills are pelagic pursuit divers with overlapping diets, though razorbills exhibit a narrower prey spectrum. Guillemots primarily consume energy-rich clupeids, gadoids and sandeels, while razorbills mainly feed on small clupeids and sandeels. Guillemots generally ingest slightly larger fish than razorbills. Size selection in common guillemots is influenced by weather and body condition, with poorer conditions leading to smaller prey being taken and a broader prey spectrum. Seasonal patterns show sandeels occurring frequently in winter and early spring rather than during breeding. Recent stomach content analyses provide insights into sex-specific patterns and a (small) potential role of fisheries discards in guillemot foraging. For both guillemots and razorbills, long-term trends remain unclear, but studies elsewhere indicate strong reliance on sandeels during breeding and a possible vulnerability to climate-driven shifts in prey availability and prey quality.

More aerial pelagic species, such as northern fulmars, northern gannets and kittiwakes exhibit different dietary patterns in the southern North Sea. Fulmars rely most on fishery discards with gadoids such as whiting, poor cod and Norway pout—alongside occasional direct predation on species like horse mackerel and mesopelagic fish. The presence of species such as glacier lanternfish, a mesopelagic fish mostly occurring outside the North Sea, indicates that some fulmars that end up in Dutch waters had foraged far away from the southern North Sea, carrying prey fragments with them to our shores. Fulmar diet appears influenced by factors including sea surface temperature, sex, age and discard availability, with warming negatively affecting whiting biomass. In contrast, gannets primarily consume high-energy pelagic fish such as mackerel, herring and sandeels, particularly during chick-rearing, while opportunistically taking discards, particularly outside the breeding season. Long-term trends indicate shifts from sandeels to mackerel dominance, likely driven by environmental change. Black-legged kittiwakes forage mainly on small pelagic fish, with regional variation: sandeels dominate along the eastern UK coast, while gadoids—especially whiting—are most common in the south-eastern North Sea, alongside clupeids. Kittiwakes frequently exploit discards and offal from fishing vessels, particularly in winter. Significant gaps remain in understanding the diets of these species in Dutch waters, particularly during winter and migration. For fulmars, the role of prey other than fish, such as squid, crustaceans and polychaetes is poorly quantified, warranting further investigation using

stable isotope or DNA analysis. Gannets require more research on the diet away from the breeding colonies, e.g., in Dutch waters, on discard dependency, individual dietary specialisation and the effects of climate change on prey availability and quality. For kittiwakes, data from Dutch waters are scarce; targeted studies at newly colonised artificial structures in the Dutch EEZ could provide valuable insights into breeding-season diet and local prey dynamics. Overall, integrated approaches combining diet sampling, prey availability data and environmental variables are recommended to address these gaps and improve understanding of species' foraging ecology under changing conditions.

Sandwich terns and common terns, both breeding in large numbers in the Netherlands, primarily feed on small pelagic fish such as clupeids and sandeels, though their dietary preferences differ. Sandwich terns rely heavily on clupeids and sandeels during breeding, with adults occasionally supplementing their diet with ragworms, flatfish and roundfish. Prey size typically ranges from 5–15 cm but increases as chicks grow, and recent stomach analyses confirm sandeels and clupeids as dominant prey, followed by gadoids and gobies. Common terns have a more varied diet, including sticklebacks, clupeids, sandeels, smelt and shrimp, with prey size generally ~15 cm. Their diet shifts across breeding stages and varies by location, prey availability and individual foraging strategies, indicating high flexibility. Despite existing studies, knowledge gaps remain regarding seasonal and interannual variability, prey size, and the influence of environmental factors such as climate change, underscoring the need for integrated research combining diet, prey availability and environmental data.

Large gulls in the Netherlands are highly opportunistic and have flexible diets, combining marine prey with terrestrial and anthropogenic food sources. Herring gulls are more coastal-bound and commonly consume shellfish during the breeding season, supplemented by crustaceans, fish and refuse, while chick diets tend to include relatively more softer, energy-rich prey such as fish and refuse. Lesser black-backed gulls historically relied on marine prey but increasingly exploit inland resources, with marked variation between colonies and evidence of dietary shifts linked to potentially reduced discard availability and changing prey availability. Great black-backed gulls are generalist predators feeding on fish, invertebrates, birds and refuse, often dominating competitive interactions at fishing vessels. Across all gulls, diet composition varies by location, season and prey availability, with recent declines in fisheries discards and closure of refuse sites likely driving behavioural changes. Significant knowledge gaps remain regarding winter diets, colony-specific trends and the ecological consequences of these shifts, underscoring the need for systematic studies across sites and colonies, potentially using modern techniques such as DNA analysis of faeces.

To address existing knowledge gaps, all species would benefit from long term studies combining conventional methods with relatively new dietary methods such as DNA metabarcoding, which improve taxonomic resolution and reduce biases inherent in traditional sampling. For breeding species in the Netherlands, a coordinated, multi-colony monitoring approach using standardised methods and statistical comparisons across years, colonies and chick age classes is essential to understand drivers of chick diet variation and its implications for growth, survival and population development. In contrast, studying species that do not breed in the Netherlands—or breed in inaccessible locations—is more challenging and relies heavily on international literature, supplemented by new data from beached birds collected along Dutch shores. This difference in approach reflects the feasibility of sampling: for local breeders, detailed colony-based studies are possible, whereas for wintering species, opportunistic sampling and literature synthesis remain the primary sources of information.

1 Introduction

1.1 Background

The MONS (Monitoring, Onderzoek, Natuurversterking en Soortenbescherming) programme was established in 2021 by the North Sea Agreement (Noordzeeoverleg-NZO) as a research and implementation programme. It is co-financed by the ministries of Infrastructure & Water Management (I&W), Economic Affairs & Climate Policy (EZK), and Agriculture, Nature and Food Quality (LVVN). The current project is part of a coherent set of MONS bird research projects and serves as preparation for future field studies that will contribute to answering the main questions outlined in section 1.2. The MONS programme includes three desk studies on seabirds, which. These desk studies serve as preparatory studies for the field studies. This specification concerns the development of the research questions for these desk studies (WP1), followed by the desk studies themselves (WP2-4), and finally, a preview of follow-up field research (WP5). The North Sea has undergone significant changes and will continue to experience changes in the coming decades due to the planned transitions in energy supply, food extraction, and nature conservation. Furthermore, various other changes in pressure factors are expected, such as those related to climate (temperature increase, changing wind patterns, acidification), as well as changing policies relating to e.g. sand extraction and terrestrial nutrient management. Coastal and seabirds (together with marine mammals and large predatory fish) are important apex predators in the North Sea. As such, they represent higher trophic level species that are potentially extremely sensitive to changes in the abundance and availability of lower trophic level species, ranging from phytoplankton through zooplankton to (small) pelagic fish, which generally form the staple food source for most seabirds and coastal birds.

This report presents the results of work package 2 and can be read separately, but has also links to the main report that brings all work packages together and presents knowledge gaps and fieldwork plans more elaborate (van Donk et al. 2025; MONS ID 60, 62, 64). Two other reports contributed to the main report (Madden et al. 2025; Schekkerman et al. 2025).

1.2 Research questions and aim

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

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

1.3 Selection of species

Dozens of seabird species regularly occur in the North Sea, however it was outside the scope of this desk study to include them all. In the preparatory phase of the project we discussed which species to include,

based on considerations such as abundance in the (Dutch part of the) North Sea, importance of the North Sea for international populations of the species, inclusion of both wintering and breeding birds, dependence on offshore vs. coastal food sources, diversity in feeding strategies and functional groups, etc..
After discussion with the partners and commissioners, we selected twelve species. An overview of the species is given in Table 1-1. In the project plan, an extensive substantiation for the species list is provided (van Donk et al. 2025). There are several ways to classify seabirds into groups, such as by functional group, breeding status or feeding guild (see Table 1-1 and Leopold et al. 2025). However, the choice of grouping has limited impact on this report, as most species are discussed individually. Nevertheless, these classifications should be kept in mind when interpreting results, as they provide useful ecological context.

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

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

1 Connection to NL: B breeding, M migrant, W wintering

2 Conservation status (Staat van Instandhouding) in NL: italic: breeding, regular: non breeding; F favourable, MU moderately unfavourable, VU very unfavourable

3 KEC: species considered in ‘Kader Ecologie en Cumulatie’

4 Sources: Sovon Boustenen, Camphuysen et al. 1994, Wetlands International; BirdLife International

2 Methods - Literature and laboratory studies on diet of seabirds occurring in the Dutch North Sea

2.1 Literature review

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

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

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

2.1.1 Common fish species

In diet and discard studies, prey species are often aggregated into broader categories because individual identification is not always possible. For instance, when analysing faecal remains or regurgitates, prey is frequently too digested to determine at species level. Consequently, researchers group prey by taxonomic Orders or Families, or by ecological characteristics. Common examples include herring (*Clupea harengus*) and sprat (*Sprattus sprattus*), which belong to the *Clupeiformes* order and are often referred to as 'clupeids', and various sandeel species grouped under *Ammodytidae*. Similarly, 'cod-like' fish such as Atlantic cod (*Gadus morhua*), haddock (*Melanogrammus aeglefinus*), and whiting (*Merlangius merlangus*) fall within the *Gadiformes* order. In discard studies, a distinction is made between flatfish—demersal species such as species that belong to *Pleuronectidae* or *Soleidae* family —and roundfish, which include all species that are not flatfish, rays, or sharks. Other useful aggregations relate to the position of species in the water column, distinguishing between pelagic and demersal fish. This distinction is ecologically relevant because it influences which seabird species can access these prey. Pelagic fish can become available near the surface and are typically taken by surface-feeding birds, whereas demersal species occur near the seabed and can be eaten by deeper diving birds or become available as discards from fisheries. An overview of the fish species, including their scientific names, Orders, Families, and whether they are grouped in other categories, is provided in Table 2-1. Scientific names of species are not mentioned in the rest of this document anymore.

Table 2-1 *Prey species mentioned in this report, their scientific name, order and family and different aggregation levels in which these species are named in the text.*

Species	scientific name	Order	Family	Species group names
greater argentine	*Argentina silus*	*Argentiniformes*	*Argentinidae*	pelagic
saury	*Scomberesox saurus*	*Beloniformes*	*Scomberesocidae*	pelagic
horse mackerel/scad	*Trachurus trachurus*	*Carangiformes*	*Carangidae*	pelagic
common dab	*Limanda limanda*	*Carangiformes*	*Pleuronectidae*	demersal, flatfish
plaice	*Pleuronectes platessa*	*Carangiformes*	*Pleuronectidae*	demersal, flatfish
common/Dover sole	*Solea solea*	*Carangiformes*	*Pleuronectidae*	demersal, flatfish
solenette	*Buglossidium luteum*	*Carangiformes*	*Soleidae*	demersal, flatfish
tub gurnard	*Chelidonichthys lucerna*	*Chelidonichthys*	*Triglidae*	demersal
herring	*Clupea harengus*	*Clupeiformes*	*Clupeidae*	pelagic, forage fish, herring-like, clupeids
sprat	*Sprattus sprattus*	*Clupeiformes*	*Clupeidae*	pelagic, forage fish, herring-like, clupeids
anchovy	*Engraulis encrasicolus*	*Clupeiformes*	*Engraulidae*	pelagic, forage fish
-		*Cypriniformes*	*Cyprinidae*	freshwater, minnow
bream	*Abramis brama*	*Cypriniformes*	*Leuciscidae*	freshwater
common roach	*Rutilus rutilus*	*Cypriniformes*	*Leuciscidae*	freshwater
Atlantic cod	*Gadus morhua*	*Gadiformes*	*Gadidae*	demersal, cod-like
haddock	*Melanogrammus aeglefinus*	*Gadiformes*	*Gadidae*	demersal, cod-like
whiting	*Merlangius merlangus*	*Gadiformes*	*Gadidae*	demersal, cod-like
blue whiting	*Micromesistius poutassou*	*Gadiformes*	*Gadidae*	cod-like
Norway pout	*Trisopterus esmarkii*	*Gadiformes*	*Gadidae*	demersal, cod-like, forage fish
poor cod	*Trisopterus minutus*	*Gadiformes*	*Gadidae*	demersal, cod-like
transparant goby	*Aphia minuta*	*Gobiiformes*	*Gobiidae*	pelagic
Raitt's sandeel	*Ammodytes marinus*	*Labriformes*	*Ammodytidae*	demersal/pelagic, sandeel, forage fish
lesser sandeel	*Ammodytes tobianus*	*Labriformes*	*Ammodytidae*	demersal/pelagic, sandeel, forage fish
great sandeel	*Hyperoplus lanceolatus*	*Labriformes*	*Ammodytidae*	demersal/pelagic, sandeel, forage fish
glacier lantern fish	*Benthosema glaciale*	*Myctophiformes*	*Myctophidae*	pelagic
capelin	*Mallotus villosus*	*Osmeriformes*	*Osmeridae*	pelagic, forage fish
smelt	*Osmerus eperlanus*	*Osmeriformes*	*Osmeridae*	pelagic, forage fish
dragonet	*Callionymus lyra*	*Perciformes*	*Callionydae*	demersal
sculpins		*Perciformes*	*Cottidae*	demersal
three-spined stickleback	*Gasterosteus aculeatus*	*Perciformes*	*Gasterosteidae*	demersal/pelagic
sand goby	*Pomatoschistus minutus*	*Perciformes*	*Gobiidae*	demersal
ruffe	*Gymnocephalus cernua*	*Perciformes*	*Percidae*	freshwater
pikeperch	*Sander lucioperca*	*Perciformes*	*Percidae*	freshwater
perch	*Perca fluvialitis*	*Perciformes*	*Percidae*	freshwater
Atlantic mackerel	*Scomber scombrus*	*Perciformes*	*Scombridae*	pelagic
grey gurnard	*Eutrigla gurnardus*	*Perciformes*	*Triglidae*	demersal
European eelpout	*Zoarces viviparus*	*Perciformes*	*Zoarcidae*	demersal
common dragonet	*Callionymus lyra*	*Syngnathiformes*	*Callionymidae*	demersal
lesser pipefish	*Syngnathus rostellatus*	*Syngnathiformes*	*Syngnathidae*	demersal/pelagic

2.1.2 Summarizing literature results

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

2.2 Laboratory work and analysis of new diet data

In the Netherlands, the primary source of information on seabird winter diets derives from research on the stomachs and intestines of dead birds. Valuable knowledge was available from previously gathered but not fully examined or analyzed material. New data is presented in this report for the red-throated diver, common guillemot, northern fulmar and Sandwich tern. For two species, the red-throated diver and the northern fulmar, scientific manuscripts are in progress, which will provide new insights on diet in the Dutch part of the North Sea. A summary with the new findings of these species are presented in the chapters of respective species. In the next sections, the methods used for these species are summarised.

2.2.1.1 Red throated diver

Dead red-throated divers were collected by volunteers, during beached bird surveys. In addition, some birds were received from bird rehabilitation centres, but these were only used if they had not been fed during rehabilitation (i.e., when they had died soon after arriving at the centre or arrived dead). Finally, three batches of birds (n=8, 7 and 29 birds, respectively) that had died in drowning incidents with bottom set-nets were collected. Each bird was autopsied and standard biometrics were taken (c.f., Camphuysen 2007a). Body mass was recorded when corpses were reasonably clean and complete. Age and sex of each bird were determined by inspecting the gonads and the *Bursa fabricii* (cf., van Franeker & Camphuysen 2007). Stomach and gut contents were collected, washed and sorted under a binocular microscope. Fish hard parts were identified, paired if possible, measured, their size corrected for wear and subsequently used to determine size and mass of each prey (full process cf., Guse et al. 2009 and Leopold et al. 2015).

The nutritional condition of each bird was determined by assigning scores ranging from 0 (absent) to 3 (well-developed) for pectoral flight muscles, subcutaneous and intestinal fat, adding up to a condition index from 0 (totally emaciated) to 9 (in excellent body condition) (cf., Hope Jones et al. 1982; van Franeker 2004; van Franeker & Camphuysen 2007). Birds with a condition index between 0-3 were considered to be in “poor condition”, birds with a condition index between 4 and 6 were considered “lean” and birds with a condition index of 7-9 were in “good condition”.

Cause of death was determined for each bird, if possible, based on both external and internal examination of the corpse. Apparently healthy birds in good body condition, that were found dead along the North Sea coast, without any signs of contamination, were considered to have drowned in bottom-set gill nets (cf., Leopold & Overmaat 2023).

For each bird that was suitable for diet analyses and that contained identifiable prey remains, the minimum number of prey and total prey mass per prey group were determined. The diet was described by four indices: percent frequency of occurrence (%FO), percent number (%N), percent mass (%M), and, combining these three: percent index of relative importance (%IRI). The first three indices are often used in diet studies, but all come with specific biases. The index that combines these three, %IRI, is believed to best balance these biases (see: Liao *et al*. 2001; Barrett *et al*. 2007). For these indices: $\%FO_i$ is the percentage of birds (with non-empty stomachs) in which remains of prey type i were present and $\%N_i$ and $\% W_i$ are, respectively, the relative contributions of prey type i in terms of total number of prey and total reconstructed prey mass across all birds. IRI and %IRI are calculated as:

$$IRI_i = \%FO_i \cdot (\%W_i + \%N_i) \qquad (1)$$

$$\%IRI_i = 100 \cdot IRI_i / \Sigma_{i..n} \qquad (2)$$

Differences in diet between groups of birds were examined in three steps, using prey numbers, grouped into nine main prey categories. The most striking differences between particular groups of birds were visualised in a Non-metric Multidimensional Scaling (NMDS) plot (Kruskal 1964; Clarke & Warwick 2001) and in a modified Costello diagram (Amundsen et al. 1996). To investigate similarities and dissimilarities of stomach contents between individual birds, ordination by Non-metric Multidimensional Scaling (NMDS), based on a Bray-Curtis dissimilarity matrix of untransformed numerical stomach content data was performed (Kruskal 1964; Clarke & Warwick 2001). Statistical differences between groups with different body condition, sex or age were further analysed using the non-parametric Analysis of Similarities (ANOSIM) based on Bray-Curtis dissimilarity and 999 permutations, which compares the mean ranked dissimilarities between groups with the mean ranked dissimilarities within groups (Clarke & Warwick 2001). Analysis was performed in R version 4.4.1 (R Core Team 2024) using packages "vegan" (Oksanen et al. 2025) and "ggplot2" (Wickham 2016). Dietary niche overlap between groups of birds with various body conditions was further assessed using the Schoener's Overlap Index (D):

$$D = 1 - 0.5\ (\textstyle\sum_{i=1}^{n} |p_{ij} - p_{ik}|) \qquad (3)$$

where p_{ij} is the proportion of prey type *i* in the diet of group *j* and p_{ik} is the proportion of prey type *i* in the diet of group *k*. The index ranges from 0 (no overlap) to 1 (complete overlap), and a value higher than 0.6 is considered to indicate that two groups have the same dietary niche (Schoener 1970; Wallace 1981). Modified Costello diagrams show the percentage of birds containing a specific prey group along the X-axis, against the contribution to the total prey mass of that prey group along the Y-axis. In these graphs, prey that are important for the majority of birds and constitute a large proportion of total prey mass end up in the upper right corner of the graph (Amundsen et al. 1996).

2.2.1.2 Common guillemot

As part of the diet study, we conducted stomach content analyses, including newly performed analyses as well as a first-time evaluation of previously collected but unexamined guillemot stomach content data. An inventory of dead seabirds has been made of material stored in freezers at NIOZ (in collaboration with Kees Camphuysen). This included approximately 60 common guillemot stomachs. The evaluation of unexamined guillemot stomach data consisted of birds that were collected over a period of nearly 40 years, dating back to the early 1980s, and sourced both at sea and from beaches. The newly performed analyses of stomachs, were mostly from guillemots collected on Texel and autopsies performed, documenting age class, sex, presumed cause of death, and stranding date. Condition was estimated based on the development of the breast muscle, as well as subcutaneus and intestinal fat deposits (e.g. Van Franeker et al. 2004; Camphuysen et al. 2007). These are scored between code 0 (totally absent) to code 3 (fully developed). The sum of these three parameters is given as Condition Index between 0 (total emaciated) to 9 (good body condition with plenty of fat deposits). The majority of individuals were collected outside the breeding season (September to February), with the highest samples in October and February. A total of 691 guillemot stomachs, collected between 1983 and 2023, were examined, of which 290 stomachs were empty.

2.2.1.3 Northern fulmar

In the Netherlands, northern fulmars have been collected for plastic research by volunteers since the 1980s (van Franeker et al. 2021). Since 2002, the fulmar is an OSPAR indicator species for plastics in the Netherlands and surrounding countries. While the focus of this long-term monitoring was on ingested plastics, natural diet remains were also identified, counted and partly collected. However, the lack of funding hampered the analysis of these samples so far.

All fulmars were dissected according to the standard protocol (Van Franeker 2004; OSPAR 2015; Van Franeker & Kühn, in review), developed to monitor plastic in stomach contents. As focus was on plastics, fish otoliths were only collected and stored.

The collected otoliths were identified to species according to Härkönen (1986), Leopold et al. (2001) and Camphuysen et al. (2017). Otoliths found in each stomach were paired to estimate the minimum number of fish. The length of each otolith was measured using a Zeiss Discovery.V8 SteREO microscope with AxioCam MRc5 and ZEN 3.0 measuring software and correction for wear of otoliths in the stomachs was applied (Leopold et al. 2015). By using linear regressions, total fish length and mass were estimated (Leopold et al. 2001).

Given the importance of whiting, both in terms of numbers and biomass, a generalized additive mixed model (GAMM) was applied to disentangle which factors possibly influence whiting biomass in northern fulmars. The model included also sea surface temperature (SST), age, sex and seasonality and a Gamma distribution with a log link was used.

2.2.1.4 Sandwich tern

An inventory of dead seabirds has been made of material stored in freezers at WMR (bird stomachs and intestines). This included 240 stomachs and 237 intestines from Sandwich terns. Sandwich terns were collected during the 2022 bird flu outbreak on Texel (n = 166) and in the Delta area (n = 82) in the breeding season. Only ringed birds were kept, and autopsies were performed, with the exact age known for most birds (approx. 3-30 years); many were adult breeding birds. It is not always known where these birds had their last meal or whether it was "normal" food or low-quality prey due to illness. Therefore, it is important to consider the condition and cause of death of all the studied birds. Condition is estimated based on the development of the breast muscle, as well as subcutaneus and intestinal fat deposits (e.g. Van Franeker et al. 2004; Camphuysen et al. 2007). These are scored between code 0 (totally absent) to code 3 (fully developed). The sum of these three parameters is given as Condition Index between 0 (total emaciated) to 9 (good body condition with plenty of fat deposits).

3 Results of literature review & laboratory work

In this section, a description of the literature found per seabird species is provided. Species were discussed in the order as presented in Table 1-1. All literature reviews shortly introduce the species, followed by a description of the diet in the breeding season, diet outside the breeding season, and, if literature allowed, information on temporal or spatial variation in diet (for instance difference in diet choice throughout the winter or over years), information on size or quality in the diet and other variables influencing diet choice. Depending on when the species are present in Dutch waters, the emphasise of the review lies on either the breeding season or the winter period. When available, the reviews focus with literature from the Netherlands, but were sometimes supplemented with literature outside the Netherlands. If additional laboratory work was done, this was included in the section of that species. The conclusions are provided in chapter 4 Conclusion/summary diet seabirds.

3.1 Common scoter

Common scoters breed in the boreal and subarctic parts of Eurasia from Iceland far into Russia. They winter in marine, coastal, temperate waters from the Baltic Sea to NW Africa (del Hoyo et al. 1992), where they feed in large flocks, largely on bivalve shellfish up to 20 m deep (Durinck et al. 1994; Skov et al. 1995; Fox 2003). In the North Sea coastal zone of the Netherlands, cut trough shells (*Spisula subtruncata*) were the main food in the 1990s (Leopold et al. 1995). This food source declined sharply thereafter, simultaneously with the colonization by the American razor clam (*Ensis leei*). Small individuals of the latter, energetically less profitable species, have become an important food source ever since, both in the Netherlands (Tulp et al. 2010; Poot et al. 2014) and in other parts of the eastern North Sea (Freudendahl & Jensen 2006; Skov et al. 2008; Kottsieper et al. 2019; Schwemmer et al. 2019).

In the 20th century, locations with aggregations up to tens of thousands wintering scoters varied in the Netherlands (Leopold et al. 1995). The North Sea coast off the Wadden Sea Islands, particularly along the east-west oriented islands in the northeast of the country were often important. The Voordelta, the shallow waters off the Delta area, SW-Netherlands were important in the 1970’s and 80’s; the Wadden Sea in the 1960’s. Occasionally, large groups also occurred off the mainland Holland coast (Leopold et al. 1995; Fijn et al. 2017a). Wintering numbers in Dutch waters are now lower than in the early 1990s. The wintering function of both the Voordelta and the Wadden Sea has declined sharply and at present, the largest numbers of wintering scoters are found north of the Wadden Sea islands. The Voordelta is now mainly a spring staging area, probably for migrants wintering further south en route to their breeding grounds (Poot et al. 2014; Dirksen et al. 2016).

In mid-winter, a peak number of 80,000 common scoters currently is reached in the coastal zone, being less than half in the early nineties. In 1991, wintering numbers peaked at 139,000 individuals (Leopold et al. 1995; Sluijter et al. 2021). The long-term trend is negative. During the past twelve winters (2010/2011–2021/2022), aerial surveys recorded an average of 46,470 individuals, representing an increase of more than 48% compared with the mean count from the winters of 2002/2003–2011/2012 (31,360 individuals) (Hornman et al. 2024). Changes in the availability of ingestible benthic fauna is a likely important driving factor, but other factors like disturbance may play a role (van de Wolfshaar et al. 2023). Whether shifts in distribution occur due to milder winters within Europe is unknown due to a lack of an overview in total abundances along the flyway and the overall population trend. The coasts of western Europe are among the most disturbed marine habitats by human activities and common scoters are disturbance sensitive birds that have large escape distances from approaching vessels (Fliessbach et al., 2019).

The ducks are protected under the EU Bird Directive (79/409/EEC). Under Dutch national legislation the conservation status of the scoter wintering population is unfavourable and conservation efforts aim to maintain a carrying capacity of 68,500 wintering individuals (Ministry of Agriculture Nature and Food Quality, 2008). However, although this number of wintering ducks was reached 6 times in the years 1993–2004 since the start of monitoring in 1993, it was only reached once in the years 2005–2021 (Sluijter et al. 2021).

3.1.1 Diet during the breeding season

Only limited information is available on the diet during the breeding season. The seaducks are inland breeders that forage near their breeding location in freshwater habitats. Here, molluscs likewise in the non-breeding areas dominate the diet; however, in the breeding areas, insects are also captured in considerable numbers, and apparently, fleshy plant parts such as the rhizomes of amphibious bistort (*Polygonum amphibium*) and various pondweeds (*Potamogeton* spp.) are taken more or less regularly. The composition of the summer diet remains poorly investigated (Glutz von Blotheim & Bauer 1982). It is known that in summer females are dependent on chironomid larvae and cladocerans, while ducklings initially take seeds and adult insects from water surface, before switching to the same diet as females (Carboneras & Kirwan 2020). Specific information on the diet of males in this period is not available.

3.1.2 Diet outside the breeding season

Common scoters outside the breeding season forage usually on any locally abundant bivalve that usually have a round or oval shape and are present in shallow waters (Fox 2003, Kaiser et al. 2006, Leopold et al. 2013). Species that are eaten are usually relatively small and abundant in shallow waters (Leopold et al., 1995). Locally, depending on the marine benthic community, common scoters might prefer some prey over others (Fox 2003). Bivalve species that were found in common scoter' diet along the west coast of Europe (Belgium-Denmark) are for instance cockles (*Cerastoderma edule)*, cut trough shell (*Spisula subtruncata)* but also soft-shell clams (*Mya arenaria)* and blunt gaper (*Mya truncata)*, ocean quahog *(Arctica islandica)*, blue mussels (*Mytilus edulis)* and white furrow shell (*Abra alba)* and bean-like tellin *(Fabulina fabula)* (Durinck et al. 1993; Meissner and Brager 1990; Figure 3-1). Although bivalves clearly are the most important prey in the diet, in addition, some other prey might be consumed as well, for instance sea snails, marine worms, starfish and fish (e.g. Kaiser et al. 2006,Table 3-1).

Table 3-1 *Overview of studies presented in Kaiser et al. (2006).*

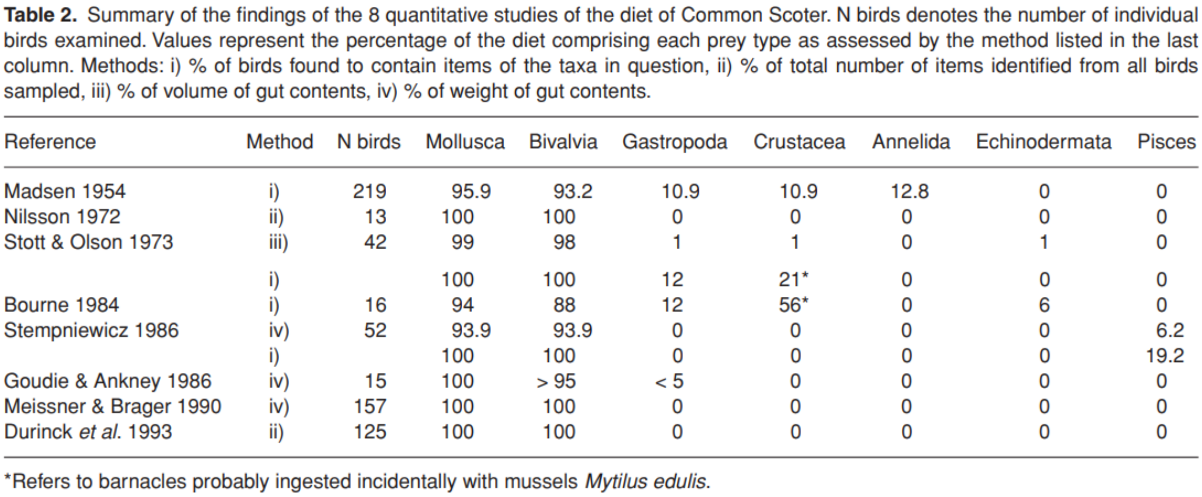


Table 2. Summary of the findings of the 8 quantitative studies of the diet of Common Scoter. N birds denotes the number of individual birds examined. Values represent the percentage of the diet comprising each prey type as assessed by the method listed in the last column. Methods: i) % of birds found to contain items of the taxa in question, ii) % of total number of items identified from all birds sampled, iii) % of volume of gut contents, iv) % of weight of gut contents.

Reference	Method	N birds	Mollusca	Bivalvia	Gastropoda	Crustacea	Annelida	Echinodermata	Pisces
Madsen 1954	i)	219	95.9	93.2	10.9	10.9	12.8	0	0
Nilsson 1972	ii)	13	100	100	0	0	0	0	0
Stott & Olson 1973	iii)	42	99	98	1	1	0	1	0
	i)		100	100	12	21*	0	0	0
Bourne 1984	i)	16	94	88	12	56*	0	6	0
Stempniewicz 1986	iv)	52	93.9	93.9	0	0	0	0	6.2
	i)		100	100	0	0	0	0	19.2
Goudie & Ankney 1986	iv)	15	100	> 95	< 5	0	0	0	0
Meissner & Brager 1990	iv)	157	100	100	0	0	0	0	0
Durinck *et al.* 1993	ii)	125	100	100	0	0	0	0	0

*Refers to barnacles probably ingested incidentally with mussels *Mytilus edulis*.

Studying the diet of common scoters at sea is challenging, as they remain at sea during the whole winter. Studying diet via the analysis of faeces at roosting areas is therefore not a possibility for this species (unlike eider ducks). In the Netherlands, two methods have been used to study the diet of common scoters; an indirect and direct method. The first method compares the occurrence of common scoters with the occurrence of potential prey species. This method is also used to try to reconstruct the historical diet of common scoters (Leopold et al. 1995). The second method is the analysis of stomach contents of dissected beached birds that mainly died because of oil spills or the analysis of regurgitates/faeces of caught individuals. As oil spills decreased, the number of collected beached birds also decreased over time (Tulp et al. 2010).

We first discuss the indirect research done on the diet of common scoters. One of the first studies trying to reconstruct the most possible diet of common scoters in the Dutch part of the North Sea is Leopold et al. (1995). The diet was reconstructed based on comparing the spatial distribution of potential prey species with the distribution of common scoters. Large groups of common scoters were present in the Western part of the Wadden Sea in the sixties. They probably foraged mostly on cockles and blue mussels as these were the most common bivalves in the Wadden Sea (Leopold et al. 1995). During a large oil spill in 1969, that affected many common scoters in the North Sea near Terschelling, also a large number of banded wedge shell (*Donax vittatus)*, bean-like tellins (*Abra tenuis)* stranded at the island of Terschelling indicating that these two species were potentially in the diet of common scoters. In the eighties, after a period of low common scoter presence in this area, the cut trough shell was potentially an important prey. From that period onwards, many cut trough shells washed ashore, and it was also found to be the more dominant species in the benthic sampling programs correlating with increased numbers of common scoters (van Scheppingen & Groenewold 1990, Offringa 1991, Den Hollander 1993).

Along the west coast of the Netherlands, the cut trough shell has probably also been an important prey species since the seventies. This bivalve species washed ashore in remarkably large numbers in both 1978-79 as in 1986-87. Besides, soil samples off the coast of North Holland confirmed that a large group of a minimum of 10,000 common scoters that were observed were seen above a bank of cut trough shells (Leopold et al. 1995). At the coastal waters near the province of Zeeland (Voordelta), the diet probably consisted of cockles in the eighties, given the location (mouth of the Haringvliet) where common scoters were seen (Craeymeersch et al. 1991). In another period the birds moved to the coast near Schouwen, an area that contained high densities of bean-like tellin and thin tellin *(Macomangulus tenuis)* (Seip & Brand, 1987), but later (beginning of the nineties) also high densities of cut trough shells (Leopold 1988; Offringa 1991).

Common scoters that were counted in the winter of 2011/12 north from the Dutch Wadden islands, used areas that contained mainly small razor clams and Baltic tellins. Densities were not extremely high, and the size classes of the razor clam were relatively small. Also the Baltic tellin is a relatively small prey for the common scoter (Leopold et al. 2013).

Another study that used aerial counts and observations from the coast to relate to the presence of large common scoter number to potential food, suggested that local rich benthos stocks dominated by cut trough shells determined the distribution of common scoters at the coast near Petten, along the coast of the province of North Holland. In the year of this study (2016), the razor clam was not abundant (Fijn et al. 2017a).

A GPS study that was executed in the winter of 2017/19 also showed that 23 tagged common scoters seemed to be attracted to areas with razor clams and cut trough shells. However, other factors seemed to be important as well, as shellfish beds with high densities of cut trough shells were only partly visited. Other factors that determine where the common scoters go might be disturbance by vessels and depth. However, this study did not conduct a statistical analysis on the data (Camphuysen and Lieshout 2024).

The following focuses on the second approach to assessing diet composition, namely the analysis of stomach contents. Stomach analyses partly confirm the above reconstructions of presumed diet of common scoters. In 1993, 31 scoters were found dead on the beach of Terschelling, of which 23 had prey remains in their stomachs. All stomachs of these birds contained cut trough shells. Besides, one bird also had remains of cockles in its stomach and two birds had remains of banded wedge shells and Baltic tellins but in all birds, the cut trough shells were the main prey (Tulp et al. 2010). The stomach analysis of a large group of stranded scoters that beached in the southwest of the Netherlands after a large oil wreck (1988) showed a slightly more varied diet. Although the stomachs (n = 383) also mainly consisted of cut trough shells (55%), they also contained blue mussels (14%), cockles (12%) and Baltic tellins (2%) (Offringa 1991).

Later, another bivalve became important in the diet of Dutch common scoters, the razor clam (*Ensis directus)* which was introduced in Europe in 1978 originally coming from North America. Razor clams, having an elongated shape, differ from other prey species that are more or less round, and are therefore potentially harder to handle compared to other prey (Fijn et al. 2017a). Nevertheless, in the beginning of the 2000s, observations of scoters foraging on razor clams, were done in the southwest of the Netherlands, for instance a common scoter that retrieved a razor clam of 7-10 cm (2003) and a year later a group of scoters was observed foraging for razor clams estimated between 6-8 or 10-12 depending on location (Leopold & Wolf 2003; Wolf & Meininger 2004). In 1995, 33 oiled common scoters were collected on the beach of Terschelling. Although the majority of scoters with prey remains in their stomachs had eaten cut trough shells (13 out of 23, 10 stomachs were empty), a few of these stomachs also had fragments of razor clams (Tulp et al. 2010). Between 2001-2007 only 19 beached common scoters were collected on the Wadden Sea islands. The razor clam was found in 5 of these birds. The stomach of one bird contained, next to razor clam, also fragments of blue mussels. One other bird that had consumed razor clam, also ate banded wedge shell and cut trough shell (Tulp et al. 2010). In 2010, another common scoter was found on the beach, with its stomach filled with fragments of small razor clams and remains of 1 banded wedge shell (Leopold, 2010). There is now also evidence of the consumption of razor clams by common scoters in nearby areas like for instance the German Wadden Sea (Kottsieper, 2020). Although the razor clam might be a profitable and numerous prey, it is possible that common scoters still prefer prey that are easier to handle, like cut trough shells (Fijn et al. 2017a).

A more recent study analysed prey remains in faeces (9x) and regurgitate (1x) of eight common scoters caught at sea for a GPS study, and the stomach content of one beached bird, in the winter of 2017/19 (Camphuysen & Lieshout 2024). The main prey that was found were cut trough shells (6 times), one *Spisula elliptica*, razor clams (3 times), a fragment of a banded wedge shell, an unknown bivalve and some rubbish like nylon and a plastic sponge. The beached bird had remains of razor clams in its stomach Camphuysen & Lieshout 2024).

In addition to prey composition and quality, prey density is an important aspect for common scoters. To meet their energetic needs, common scoters eat hundreds to thousands of bivalves per day and the foraging costs of diving to the bottom of the sea in cold temperatures are high (Leopold et al. 1998). Prey should therefore preferably be energetically rich, predictable and in shallow water at a location with little disturbance (Leopold et al. 2013; van de Wolfshaar et al. 2023).

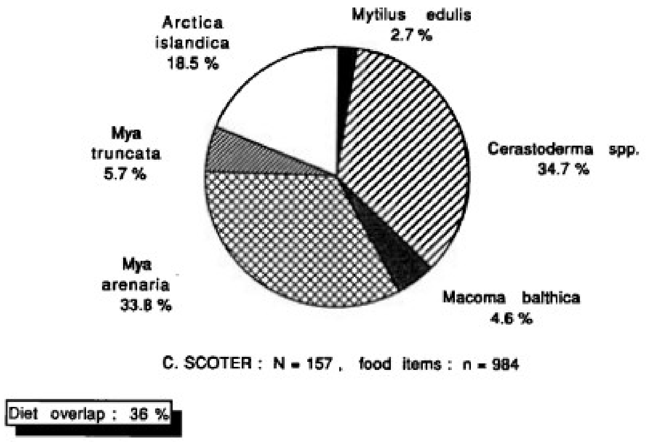


Figure 3-1 *Percentage of weight of different prey found in stomachs of drowned common scoters in fishing nets, figure taken from Meissner & Brager (1990).*

3.1.3 Selection in size and/or quality

Unlike some other seabird species, size selection of prey is quite well researched for common scoters. Shell length or width can often be estimated using shell remains that are found in faeces and stomachs, by using the known relationship between hinges and shell length. It seems that common scoters select individual bivalves between 5-20 mm in length, with outliers to 40 mm (Fox 2003).

The razor clam, a more recent prey in the diet of common scoters, is an exception. Observations that were done estimated the length of ingested razor clams between 60-120 mm (Leopold & Wolf 2003; Wolf & Meininger 2004). Common scoters can eat razor clams of 100 mm but they prefer clams of 40-80 mm. Smaller ones are probably not profitable, while bigger ones might be dangerous to ingest (Tulp et al. 2010). Razor clams of this size class are mostly zero-one year old, which means that only the small individuals of all available razor clams are ingestible and suitable as prey. However, some years there are large amounts of this size class present in winter and razor clams are an important prey for winter times, especially when cut trough shells are not present in large quantities (Leopold et al. 2013).

Results of other studies that looked into size selection fit in the range mentioned above. For instance, research to stomach contents of common scoters estimated that the birds ate shells with a length between 30 and 90 mm (Tulp et al. 2010). Another study used shell thickness of cut trough shells to estimate shell length as measurable hinges were not present (Leopold et al. 2007). In 1995 near Terschelling ducks were feeding on a rich *Spisula* stand that was mainly composed of 14–21 mm long individuals. Although these were probably also mostly taken by the scoters, evidence was found that larger (older) Spisula of 25–30 mm were taken disproportionably often (Leopold et al. 2007). Shell remains that were found in faeces of caught common scoters showed shell sizes for cut trough shells between 21-25 mm and one *Spisula elliptica* of 24 mm supporting the above mentioned shell range selection (Camphuysen & Lieshout 2024).

A Danish study showed that sizes of cockles and cut trough shells found in the stomachs of drowned common scoters in fishing nets fell in the same size categories as mentioned above (Durinck et al. 1993). Cockles that were found were between 8-15 mm and most of them (~55%) fell in the size category of 11-13 mm. Cut trough shells were between 9-19 mm and most of them (~53%) fell in the size category of 14-16 mm. Size selection of prey did not differ between males and females (Durinck et al. 1993).

Some studies also investigated the profitability of different prey that were present in areas of common scoters. In the German Wadden Sea, benthos sampling was done in the areas were common scoters moult and where they spent most of the winter (Kottsieper et al. 2019). The most common species differed between these areas: the American razor clam was most common in the moulting area, while the bean-like tellin was most common in the wintering area. Other potential prey in the area were Baltic tellins, cockles and white furrow shell. Overall, the wintering area had fewer species and lower abundances. However, both areas had similar mean ash-free-dry masses and flesh-to-shell ratios in both areas, which suggests that both regions are profitable foraging areas. Prey differs in how profitable they are. The razor clam was both abundant and has a good food quality (flesh-to-shell ratio) and is therefore a profitable prey for common scoters in the moulting period in this area (Kottsieper et al. 2019). Although energetic profitability of prey is probably important for common scoters, the time birds must forage might be a more limiting factor to maintain its energetic balance, for instance when birds are disturbed (van de Wolfshaar et al. 2023).

Fox (2003) provides an insightful evaluation of size selection in common scoters, noting that variation in reported prey size distributions may suggest an absence of selection below an upper digestive limit. However, without simultaneous measurements of available benthic prey and reconstructed diets, it remains impossible to determine whether observed differences simply reflect spatial or temporal variation in prey profitability. Such concurrent studies would likely reveal patterns of size selection, like by Leopold et al. (2007) as one of the few examples, and enhance understanding of scoter foraging ecology.

3.1.4 Other variables affecting diet choice

Common scoters are known to be very sensitive to disturbance by ships and low flying aircrafts and already take flight at considerable distances from approaching vessels (Offringa & Leopold 1991; Kaiser et al. 2006; Krijgsveld et al. 2008, 2022; Schwemmer et al. 2011), a behavioural trait that may render food resources, although abundant, less accessible when they are frequently disturbed (Houziaux et al. 2011, De Mesel et al. 2011).

Several researchers studied the distribution of common scoters and modeled these to variables like shellfish beds, environmental conditions and anthropogenic disturbances. The literature strongly suggests that common scoters forage on suitable prey in areas with coarse sandy substrates with water less than 20m deep (Fox 2003). A modelling study that investigated the explanatory factors of common scoter presence in Germany, found that depth and prey abundance explained most of their presence (Schwemmer et al. 2019). However, in this modelling study an important other factor in scoter distribution in the Netherlands, did not increase the explanatory power: disturbance. Another study looked at the relationship between counts and potential prey as these studies give additional information on the potential diet of common scoters. It seems that common scoters avoid places with a lot of disturbance of for instance shipping lanes (Camphuysen & Lieshout 2024). Other disturbances can come from sand nourishments or fisheries (Philippart et al. 2023).

Also, Fijn et al. (2017) emphasised that, in addition to the availability of sufficient food resources, the absence of disturbance is an important factor (e.g. Einars-son & Gardarsson 2004). In line with this, Leopold et al. (2015) concluded that, besides the presence of adequate edible shellfish, the absence of vessel traffic in the area may have contributed to recent concentrations of Common Scoter. Earlier studies at Terschelling (Dirksen et al. 2005) and in the Voordelta (Poot et al. 2014, Zuur et al. 2014) likewise demonstrated that disturbance was an important explanatory factor for spatial distribution.

3.2 Red-throated diver

The red-throated diver is the smallest of the five living species of divers (*Aves*, family *Gaviidae*; Sprengelmeyer 2014; Winkler et al. 2020). The species has a circumpolar, holarctic breeding distribution, in boreal and tundra habitats with small lakes (Voous 1960). Red-throated divers were classified as Least Concern by the IUCN Red List due to the species' extremely large range (Birdlife International, 2025). The trend in the Netherlands is stable since 1991 and the conservation status of in the Netherlands is favourable (SOVON, 2025). The main wintering range in Europe comprises relatively shallow marine waters, in the Baltic Sea, the North Sea, the Black Sea and the Atlantic seaboard from Norway to Spain (Cramp & Simmons 1977; Durinck et al. 1994a; Skov et al. 1995; O'Brien et al. 2008). In Dutch North Sea waters, some 10,000 Red-throated divers are thought to winter (Camphuysen & Leopold 1994).

3.2.1 Diet during the breeding season

It's diet during the breeding season consists largely of fish, taken both in freshwater lakes and at sea, in nearshore, shallow waters. Prey species vary, depending on location. Important freshwater prey are percids, carps and minnows and sticklebacks. Important marine prey of breeding birds are herrings, smelts, salmonids (*Salmonidae*), gadoids, sticklebacks, sculpins, pricklebacks (*Stichaeidae*), gunnels (*Pholidae*) and sandeels (Bergman & Derksen 1971; Davis 1972; Norberg & Norberg 1976; Cramp & Simmons 1977; Reimchen & Douglas 1984; Eriksson et al. 1990; Eriksson 1994; Ruggles 1994). After breeding, red-throated divers migrate and largely become coastal seabirds (Skov et al. 1995; Gray et al. 2015; Kleinschmidt et al. 2022) and they are thus adapted to both freshwater and marine feeding, as well as to long distance migration (Gayk et al. 2018).

3.2.2 Diet outside the breeding season

During over-land migration, the diet at stop-overs will consist mainly of freshwater fish, as illustrated by the stomach contents of 28 birds that were bycaught in autumn in fishing nets in two freshwater reservoirs in Poland: these had eaten mostly *Cyprinidae* and *Percidae* (Gwiazda et al. 2020).

Few studies of winter diets of red-throated divers have been carried out and most of these studies were based on rather small sample sizes. Such studies are unlikely to find all prey species for a given region (Ouwehand et al. 2004). Only two larger study are known: Madsen (1957) examined stomach contents of 203 red-throated divers that had been shot in the seas around Denmark in winter (October-February) in the

1940s. Of 173 birds that had food remains in their stomach, 158 came from northern and eastern Danish waters (Kattegat, Belt Seas, Baltic Sea) and 15 from western Denmark. Seventeen different fish species could be identified across these stomachs. Atlantic cod was the most important prey, present in 71% of the birds with non-empty stomachs and comprising roughly 54% of the total prey numbers found. Three more prey taxa, herring, sticklebacks (mostly *Gasterosteus aculeatus*) and gobies (*Gobiidae*, probably more than one species) were of secondary importance and 13 more species of fish, including flatfish, and both demersal and pelagic roundfish, were found incidentally.

Several decades later, Atlantic cod had apparently vanished from the diet, both in the Baltic and in the North Sea. Guse et al. (2009) found that birds wintering in the Pomeranian Bight (SW Baltic, Germany; n=82 immature birds, drowned in bottom-set nets, November through April 2001-2005) sustained themselves largely on pike-perch and ruffe in winter, but switched to fatter, more profitable herring as these migrated into the area in spring. Across winter and spring, 15 different prey fish were found in this study. In a smaller study further east in the Baltic, Zydelis (2002) found remains of six different prey fish in the stomachs of 19 birds that had drowned in nets set off the Lithuanian coast. Clupeids and European smelt Osmerus eperlanus were the main prey of these birds, a finding later corroborated by a study using stable isotopes in blood samples of 7 wintering birds caught alive in the same region (Morkūnė et al. 2016). In the stomachs of eight birds drowned in the Skagerrak (northern Denmark) remains of 10 different prey fish were found, with clupeids, gadoids (whiting and blue whiting) and sticklebacks as the dominating prey (Durinck et al. 1994b). Interestingly, not a single Atlantic cod was found in any study after Madsen (1957), excepting that some cod, among other gadoids, were detected in a study using DNA metabarcoding on faecal samples from 34 birds caught alive in the German Bight of the North Sea from late winter through spring (February-April), 2015-2016 (Kleinschmidt et al. 2019). Gadoids (whiting and pouts *Trisopterus sp*., but no cod) were the main prey found in a small sample of stomachs (n=19, but only six with food remains) of red-throated divers killed in the Sea Empress oil spill, in Wales, UK, in February 1996 (Weir et al. 1997).

Red-throated divers thus appear to be flexible foragers with diets that vary between locations and over time, depending on local food sources. Diets in the North Sea are still largely unknown, based on small samples from Limfjorden, western Denmark (Madsen 1957), from the Skagerak (Durinck et al. 1994b) and from the German Bight (Kleinschmidt et al. 2019). In all three studies, sampled birds were freshly dead (shot, drowned or caught alive). Birds that died from other causes, such as oil contamination, have only been used in one study, in another region (Weir et al. 1997) and may thus present yet another picture, for various reasons. The studies based on stomach contents analyses indicated a broad diet across the species, but rather narrow individual diets, with mostly one or two, rarely three to four, and very rarely more than four prey species found in single stomachs. However, a metabarcoding study of Kleinschmidt et al. (2019), indicated that individual birds may have a broader prey spectrum than indicated by just the hard prey remains, of presumably their last meal(s) in their stomach. In faecal samples from only 34 birds DNA of 19 fish taxa was detected. The diet was apparently dominated by clupeids, but DNA of gadoids, sandeels, flatfishes and mackerel was also found. Diet studies using metabarcoding often find a wider prey spectrum than studies using prey hard parts (e.g., Stavenow et al. 2022), at least when a limited number of predators is examined. Studies based on prey hard parts in dead birds would thus benefit from large sample sizes (Ouwehand et al. 2004).

3.2.3 Temporal and spatial patterns

In the Pomeranian Bight (German Baltic Sea) set net victims that were largely in good condition (Guse et al. 2009) showed a clear seasonal pattern in diet, with the birds switching from a diet dominated by estuarine/freshwater prey in winter (zander) to clupeids (herring) when the latter moved into the region in spring. Likewise, birds wintering further east in the Baltic were also found to take mainly estuarine prey (European smelt) and clupeids (Zydelis 2002; Morkūnė et al. 2016). However, such patters are not set in stone and may change over time as the prey base in a given region may change. Madsen (1957) found Atlantic cod to be the main prey of divers shot around Denmark but this prey species had nearly completely disappeared from more recent diet in the region, including one on set net victims in the Skagerrak (northern Denmark) and one in the Danish North Sea (Durinck et al. 1994b). Other gadoids, whiting and blue whiting had replaced Atlantic cod and became the dominant prey group alongside with clupeids. The smallest prey spectrum was found in a study on oil victims in Wales, but sample size was small (n=6 stomachs with food remains, Weir et al. 1997), suggesting that large sample sizes are required to find the full prey spectrum (c.f., Ouwehand et al. 2004).

3.2.4 New insights into the diet of Dutch red-throated divers from unpublished data

Between November 1991 and October 2023, 276 birds were examined, with 259 of these (93.8%) found in the winters 1995/96 to 2014/15 (Figure 3-2). Before 2010, the majority of the birds found had died from so-called chronic oil pollution, but with increasing measures to stop the deliberate discharging of oil from ships and offshore production installations, considerably fewer seabirds, including Red-throated divers, died from getting oiled in the North Sea in the most recent decade (Camphuysen 2022). Most birds that were found oiled had less than 20% of their plumage contaminated and had probably survived for some time after contamination, wasting away. These birds were mostly emaciated with severe loss of fat, muscle and body mass. A relatively small number (n=11) of birds was found to be totally covered in heavy fuel oil, during the Tricolor incident in January 2003 (see: Camphuysen & Leopold 2004). Six of these were in good body condition but the other five were not, suggesting that they may have been contaminated lightly at first, wasting away until they got contaminated again by a heavier load. Besides oil pollution, one other lethal pollutant was found on several birds: poly-isobutylene. This substance is very sticky (Camphuysen et al. 1999), totally covering 6 birds found between 1988 and 2010. One might expect that these birds would have died shortly after having been contaminated, but all six were emaciated, suggesting that they may have died earlier, and had only become contaminated after death.

A second major batch of birds consisted of fisheries bycatches (bottom set-nets). Most of these birds stemmed from three specific incidents: 5 birds found in Noord-Holland (Dutch mainland coast) in November 2012; 8 birds found floating closely together at sea off the Zuid-Holland coast in December 2012, and 29 birds that were handed in by a fisherman, who had caught them in nearshore waters off Noord-Holland in January 2014. Besides, there was a trickle of 15 birds with characteristics of bycatch (see: Leopold & Overmaat 2023) that stranded in different winters between 1998-99 and 2021/22. Most of the remaining birds had starved (but were not oiled), sometimes with clear signs of disease (internally, n=22) or of entanglement in floating debris, mostly small parts of ghost netting (n=11).

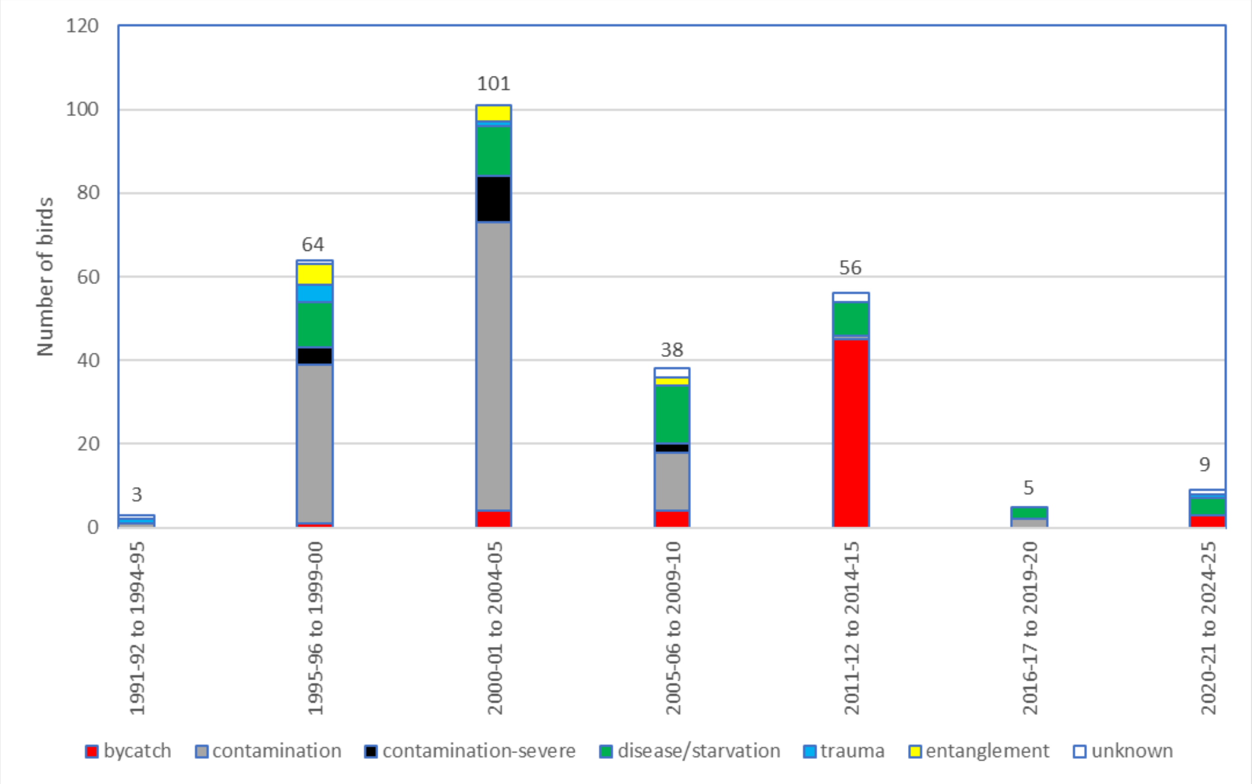


Figure 3-2 *Numbers of birds examined per five year period (shown on above each bar), for different causes of death. Note that the first and last samples cover only four winters.*

Biometry

Red-throated divers showed considerable variation in body dimensions. Males were on average 5% (1st winters) to 8% (adults) larger than females in the measurements taken (Table 3-2) and differed most in bill depth (gonys: 10-15%) and least in wing length (4%). First winter birds tended to be smaller than immatures and these were, on average, still smaller than adults. Within any sex/age class, the largest birds were 25-30% larger than the smallest and these differences were most pronounced in bill measurements (21-45%).

Likewise, males with body conditions "good" and "lean" were circa 15% heavier than females of the same age class; males in "poor" condition were even 23% heavier than females in poor condition. Completely starved (poor) birds were circa 40% lighter than birds in good condition (Table 3-3).

General diet

Several of the 276 birds studied were not suitable for diet study, for various reasons. Six birds had been badly scavenged and had their stomach and intestines missing, two birds lacked data on place or date and six had been fed in captivity. Of the remaining 262 birds, 42 (16%) did not contain identifiable prey hard parts. Most birds were found in the winter months; there was no trend in the percentage of birds with no prey remains against month (Figure 3-3). In the 220 divers in which prey hard parts were found in the stomach and/or intestines, remains of 2,291 fishes were identified, varying from fish with a mass of less than 1 gram, to a whiting of 195 gram (Table 3-4). Remains of invertebrates were rare and their summed reconstructed mass was negligible: in total only jaws of three small nereid worms were found (in two birds, together with remains of gobies); jaw fragments of two small sepiolid squids were found in two birds (together with remains of whiting) and tail fragments of a shrimp were found in one bird (together with whiting). As these invertebrates were all probably eaten by fish and thus only secondary prey in the divers, these were further ignored.

Overall, clupeids (herring and sprat) were the most important prey: these were found in 6 out of 10 birds and constituted nearly half (44.7%) of total reconstructed prey mass. Gadoids represented a quarter 24.6% of total reconstructed prey mass but these preys were found in less than 3% of the birds. Sandeels, gobies and estuarine & freshwater fishes were each found in nearly one in three birds; gadoids and sticklebacks in one in five. Other prey groups were relatively unimportant (Table 3-4). Combining the indices: %FO, %N and %M in %IRI (Figure 3-4) shows the overall importance of clupeids as prey, medium importance of gadoid, sandeels, gobies and estuarine / freshwater fishes, minor importance of sticklebacks, while the contribution of other prey groups (flatfish, other demersals and pelagics and invertebrates) is insignificant.

Table 3-2 *Biometry of the dissected birds for which both sex and age were determined. Average bill length (exposed culmen and nostril to bill tip), bill depth at the gonys angle, total head (head plus bill length), tarsus and wing (flattened, straightened chord) are all given in mm; both the left and right tarsus and wing were measured in each bird (unless one was missing, badly damaged or for wings: moulting. Figures are mean ± SD; range (min-max) and number of observations (n)*.

Sex	**Age**	**Culmen tip to feathers**	**Culmen tip to nostril**	**Gonys**	**Total head**	**Tarsus**	**Wing**
Male	Adult	55.46 ± 3.12 48.41-61.17 (59)	41.11 ± 2.59 34.67-47.00 (57)	10.49 ± 0.75 8.90-12.55 (57)	132.85 ± 5.47 118.97-145.20 (57)	75.83 ± 4.65 70.60-106.5 (60)	297.50 ± 9.80 266.50-329.50 (52)
Male	Immature	54.65 ± 3.51 45.43-61.43 (30)	40.18 ± 2.60 35.81-45.39 (29)	9.92 ± 0.78 7.95-11.50 (30)	132.23 ± 7.12 113.50-145.40 (29)	75.40 ± 2.99 68.66-79.77 (31)	293.61 ± 11.36 271.50-311.50 (27)
Male	First winter	52.42 ± 3.17 48.23-57.96 (9)	38.10 ± 2.81 34.36-41.69 (9)	9.64 ± 0.68 8.66-10.83 (9)	126.60 ± 5.43 117.50-134.25 (9)	73.68 ± 1.86 70.85-77.68 (9)	286.50 ± 8.53 272.5-296.00 (9)
Female	Adult	51.71 ± 2.74 45.93-57.91 (73)	38.23 ± 2.31 33.54-43.94 (72)	9.16 ± 0.52 7.92-10.61 (69)	125.01 ± 5.04 113.80-138.30 (67)	70.78 ± 2.80 63.97-78.19 (74)	285.64 ± 10.74 249.00-306.50 (70)
Female	Immature	51.34 ± 2.54 44.95-56.78 (63)	37.68 ± 2.19 33.81-43.28 (61)	9.03 ± 0.56 7.79-10.42 (60)	123.64 ± 4.23 112.24-133.80 (61)	70.85 ± 2.51 66.29-76.89 (62)	278.80 ± 9.26 240.50-297.00 (53)
Female	First winter	50.25 ± 2.49 44.06-54.69 (15)	36.85 ± 2.20 32.24-40.22 (15)	8.62 ± 0.72 7.67-10.07 (14)	121.80 ± 2.98 116.10-128.50 (14)	70.76 ± 1.99 67.40-73.25 (14)	274.54 ± 8.32 262.00-285.00 (13)

Table 3-3 *Body mass of (reasonably) clean and intact Red-throated divers in this study. Note that body masses may be slightly overestimated as some birds were wet, or slightly oiled. Birds in good, lean, and poor condition had, respectively, body conditions 7-9, 4-6, and 0-3.*

Age	Male-Good	Male-Lean	Male-Poor		Female-Good	Female-Lean	Female-Poor
Adult	2188 ± 243 1820-2510 (6)	1529 ± 503 1133-2640 (7)	1366 ± 169 1067-1800 (30		1911 ± 305 1430-2520 (11)	1319 ± 98 1185-1460 (6)	1113 ± 153 900-1600 (37)
Immature	2127 ± 444 1775-2625 (3)	1446 ± 424 1260-1670 (6)	1351 ± 111 1185-1565 (16)		1730 ± 163 1478-2030 (9)	1210 ± 257 960-1550 (7)	1094 ± 161 794-1456 (33)
First winter	2150 ± 358 1860-2550 (3)	- -	1153 ± 549 958-1400 (6)		1729 ±49 1675-1770 (4)	1436 1207-1665 (2)	1046 ± 197 910-1333 (4)

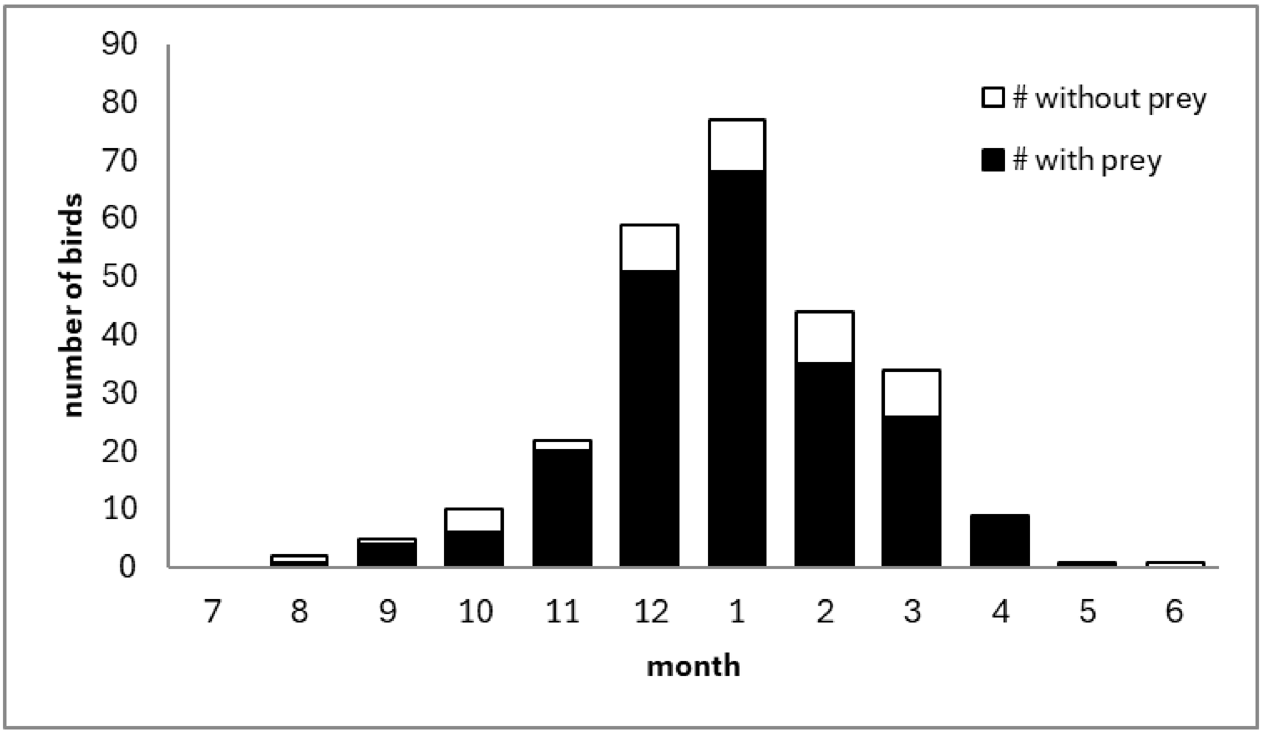


Figure 3-3 *Numbers of birds examined, with (black) and without (white) prey hard parts per calendar month, 1991-2023 (July through June).*

Table 3-4. *Reconstructed total numbers of prey and total prey mass of nine prey groups in all 220 Red-throated divers with non-empty stomachs/guts, with their relative contributions to the diet in terms of percent frequency of occurrence (%FO), percent prey numbers (%N), percent prey mass (%M), and percent index of relative importance (%IRI).*

Prey group	N birds	N prey	Total Mass		%FO	%N	%M
Clupeids	135	656	6741.43		61.36	28.56	44.71
Gadoids	47	65	3702.30		21.36	2.83	24.56
Sticklebacks	40	143	176.31		18.18	6.23	1.17
Sandeels	65	266	1439.86		29.55	11.58	9.55
Gobies	67	542	585.72		30.45	23.60	3.89
Flatfish	8	12	172.43		3.64	0.52	1.14
Other demersals	5	6	63.91		2.27	0.26	0.42
Other pelagics	16	41	479.85		7.27	1.78	3.18
Estuarine/Freshwater	62	560	1709.00		28.18	24.38	11.34
Invertebrates	5	6	6.44		2.27	0.26	0.04

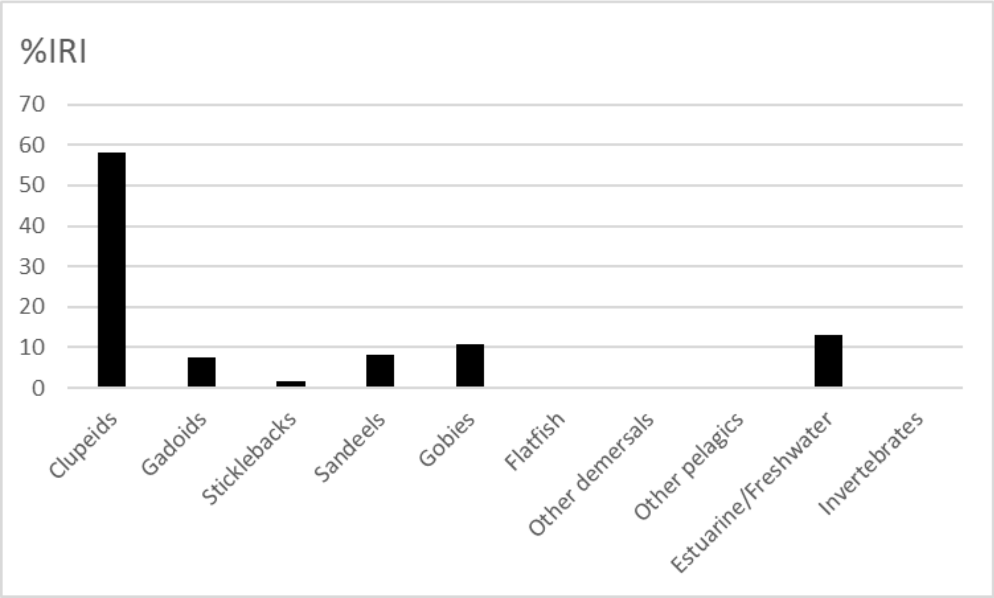


Figure 3-4 *The relative importance of 10 prey groups, found in 220 red-throated divers with non-empty stomachs, as the percent index of relative importance (%IRI).*

Selection in size and/or quality

The majority of the prey that had been consumed were small (Figure 3-5): some 50% had total lengths ≤ 7 cm and weighed less than 2 grams; 95% were under 15 cm long and under 23 gram. Peaks in fish lengths were found around 4 cm (gobies, sticklebacks), 8 cm (smelts, clupeids), 11 cm (clupeids, sandeels) and 17 cm (sandeels, whiting). Only four fishes (0.2%) were over 25 cm long (all whiting) and only 14 whiting and 1 bass (128 g) were over 100 gram (0.7% of all fish prey). The largest prey found was a 195 gram whiting, that was 29 cm long.

In total, 28 different fish species were identified as prey, as well as four invertebrates. Given that red-throated divers winter mostly in North Sea coastal waters and are found to a much lesser extent in the Wadden Sea and in the estuarine Delta area in the southwest of the country, a remarkable group of prey are the estuarine and freshwater fishes, mostly smelt, percids and cyprinids (13% IRI). These prey fish must have originated from freshwater bodies, where red-throated divers do not normally go in winter when healthy (Schekkerman 2018). However, oiled and otherwise weakened birds may seek more sheltered estuaries where they find fishes that got washed out to sea with the volumes of freshwater that are discharged through the large sluices in the northwest and southwest of the country.

Differences in prey size

As red-throated divers show a large variation in body size, and particularly in bill dimensions (Table 3-2), it is conceivable that larger birds eat larger fish. Therefore, the effects of sex, age and size on average prey size and on maximum prey size were first investigated. In contrast to expectation, older (larger) birds had taken smaller prey on average than had first winter birds (but note that numbers of juvenile birds were comparatively small; Table 3-5). Even if the largest prey was found in an adult bird, this adult was a bird of average size. Average prey mass of all adults, including two birds of unknown sex) (5.72 ± 12.47 g; n=1423) was significantly smaller (T-test, $P<0.01$) than that of immatures (7.57 ± 14.60 g; n=731); average prey mass of immatures did not differ from that of juveniles (10.15 ± 15.65 g; n=137; $0.05<P<0.1$).

Prey found in males (6.07 ± 12.47 g; n=1092) on average had a smaller mass than those found in females (7.16 ± 14.46 g; n=1159), but due to the large variation in prey sizes, this difference was not significant (T-test, $0.05<P<0.1$). Considering all birds together for which the measure total head could be taken as a proxy for both the overall structural size of the bird and of the size of its feeding apparatus, no correlation was found between bird size and either the average or the maximum prey mass (n= 203 birds with fish remains; Figure 3-7).

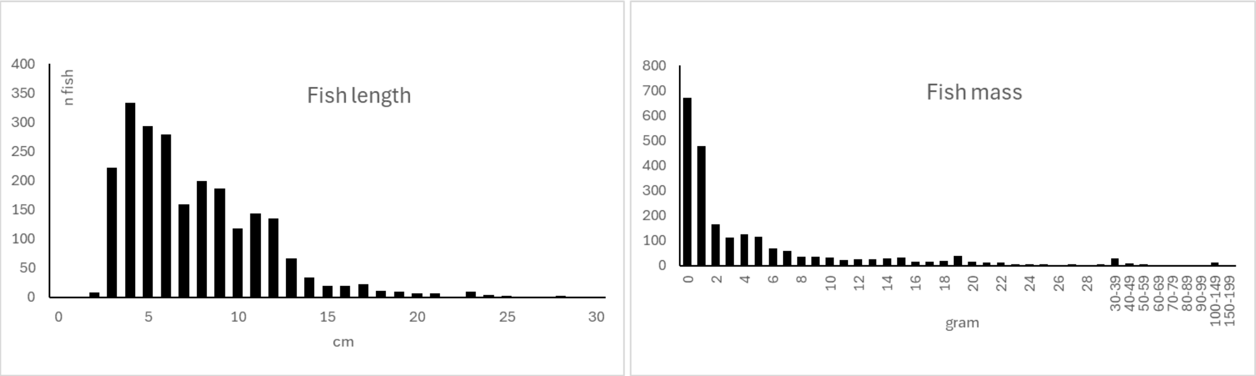


Figure 3-5 *Frequency distributions of prey fish length (cm, left) and mass (gram, right).*

Table 3-5 *Number (n fish), length (cm) and mass (g) (average, SD, maximum) of prey fish found in adult, immature and first winter (juvenile) male and female red-throated divers with non-empty stomachs/intestines.*

Age/Sex	**N fish**	**Avg fish length ± SD**	**Avg fish mass ± SD**	**Max fish length**	**Max fish mass**
Adult male (n=51)	761	7.28±3.79	5.16±11.54	24.96	128.44
Adult female (n=62)	664	7.96±3.71	6.36±13.43	28.99	194.93
Immature male (n=27	289	8.65±3.95	7.59±14.30	24.31	113.04
Immature female (n=49)	442	8.76±3.90	7.57±14.81	26.00	139.15
Juvenile male (n=8)	82	8.57±3.73	7.97±10.57	17.85	43.56
Juvenile female (n=12)	71	10.19±3.35	10.89±18.85	25.31	128.02

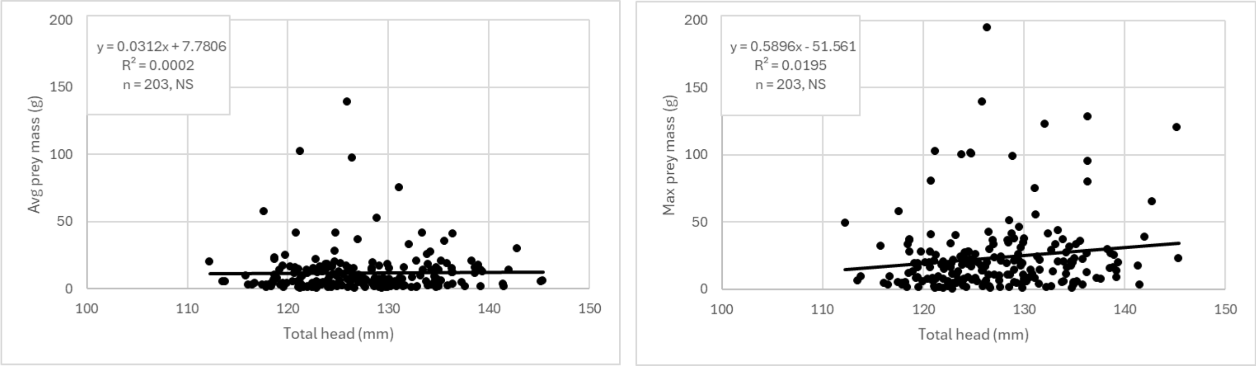


Figure 3-6 *Average and maximum prey fish mass (gram) per bird, as a function of the structural size of the birds, taken here as total head (mm).*

Other variables affecting diet choice

Similarity in the diet between birds with different characteristics was assessed using NMDS ordination. First, the diets of males and females, and of adult, immature and juvenile red-throated divers were compared. These completely overlapped, indicating that birds of both sexes and of all ages ate the same prey species and in similar relative quantities (Figure 3-7). However, birds that had died with a good body condition (mostly set-net victims) had a diet that was clearly different from the diets of birds in lean and poor condition (Figure 3-7). Birds in poor (severely emaciated) condition had the widest prey spectrum, but this overlapped considerably with that of birds in slightly better condition ("lean" birds). Birds in good condition had a much narrower diet spectrum, suggesting that when birds became emaciated, they were no longer able to eat their preferred prey (clupeids) and diversified their diet. Although diet composition was still similar between groups of different body condition according to ANOSIM (R=0, P=0.56), the Schoener's Overlap Index indicated that the diets of birds in good condition were different from birds in lean and poor condition (D < 0.6; Table 3-6). The diets of birds in lean or poor condition overlapped Figure 3-6.

Birds, of all age classes, in poor condition tended to have remains of more fish in their stomachs and guts than did birds in good condition; lean birds tended to be intermediate in this respect. Reconstructed prey massed tended to be higher in adult birds than in younger birds. Combining birds of all ages, birds in good body condition had, on average, higher reconstructed prey masses than lean and poor birds (combined: T=1.99, df=201, P<0.05), but lower prey numbers (T=-4.49, df=201, P<0.001), in other words: birds in good condition had eaten, on average, larger fishes than emaciated birds (Table 3-7).

The body condition of 41 (out of 43) birds with empty stomachs and guts could be assessed. Three birds, out of 50 in good body condition (6%) had empty stomachs and guts, while 38 birds out of 194 (20%) in lean of poor body condition had empty stomachs and guts.

Figure 3-6C shows a clear difference in diet between birds in good condition and birds in lean or poor condition. Birds in the first group likely had died quickly while, or shortly after feeding, as these got trapped in bottom-set gill nets during a dive, presumably during foraging, or when they became heavily oiled. Birds that got fouled by smaller quantities of oil had wasted away slowly, as had diseased birds, and, clearly, birds that had starved for reasons that could not be ascertained. The sudden death group had relatively fewer males (30%, n=46)) than the slow death group (45%, n=155); both groups had equal proportions of adult birds (54%).

The diets of the two groups are summarised in modified Costello diagrams (cf., Amundsen et al. 1996; Figure 3-7). These graphs show the percentage of birds containing a specific prey group (% Frequency of occurrence) along the X-axis, against the contribution to the total prey mass (%Mass) of that prey group along the Y-axis. The birds that had died in good condition contained mostly remains of clupeids, while gadoids were the second-important prey group in terms of prey mass. The main prey were thus a mixture of fatty clupeids and comparatively large gadoids. Clupeids decreased considerately in importance, from 89% Mass to 37% Mass, but remained the main prey in the lean and poor body condition birds, while the relative importance of gadoids did not change much. Clupeids were partly replaced by estuarine/freshwater fish, and by sandeels, gobies and sticklebacks. With the exception of the sandeels, these replacement preys are generally less fatty and thus lower in energy density than the clupeids (Massias & Becker 1990; Pedersen & Hislop 2001; Schreckenbach et al. 2001; Temming & Herrmann 2003).

Table 3-6 *Schoeners's Overlap Index (D) between groups of birds in various condition.*

	Lean	**Poor**
Good	0.35	0.32
Lean		0.72

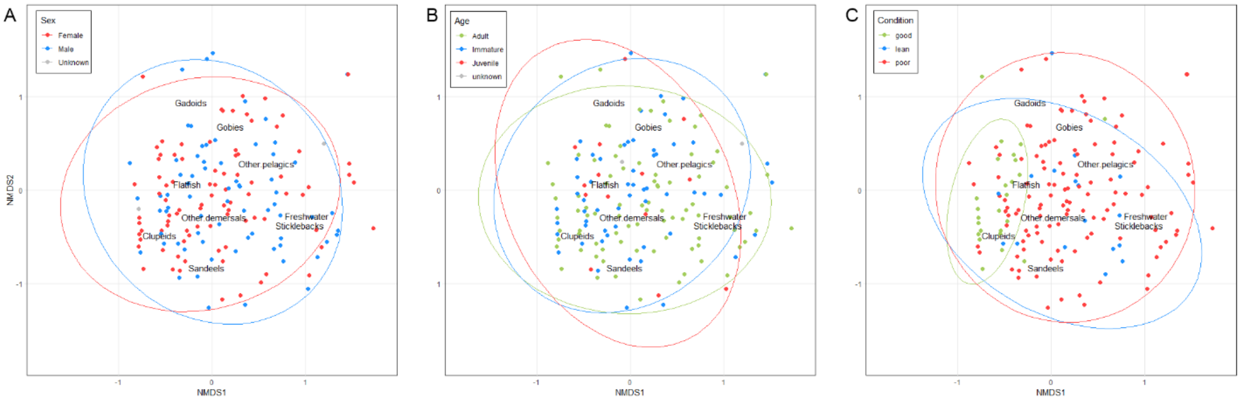


Figure 3-7 *Non-metric multidimensional scaling (NMDS; stress = 0.16) plots of the stomach contents of all birds with non-empty stomachs/guts. A: males versus females; B: bird of three different age classes; C: birds of different body condition. To assess differences between groups, individual birds (points) are coloured according to sex (A), age (B) and body condition (C) and groups are annotated using ellipses.*

Table 3-7 *Average (AVG) and standard deviation (SD) of the summed reconstructed mass (g) and numbers of prey fish found in red-throated divers of different age and nutritional condition. Age and body condition could not be established in some birds, due to scavenging.*

Age	Condition	N birds	AVG fish mass/bird	SD mass	N fish	N fish/bird	SD (N fish/bird)
Adult	**good**	25	127.66	144.93	163	6.5	5.52
Adult	**lean**	13	56.12	62.65	135	10.4	7.14
Adult	**poor**	70	57.77	62.37	1056	15.1	20.69
Adult	**ND**	7	25.43	23.66	68	9.7	5.62
Immature	**good**	13	52.22	43.02	48	3.7	2.43
Immature	**lean**	9	82.18	126.42	51	5.7	4.90
Immature	**poor**	51	75.06	70.05	543	10.6	14.12
Immature	**ND**	3	96.84	89.30	89	29.7	24.54
Juvenile	**good**	8	83.77	67.03	32	4.0	1.93
Juvenile	**good**	1	14.83	-	5	5.0	-
Juvenile	**poor**	11	39.99	42.75	67	6.1	8.85
Juvenile	**ND**	1	1.08	-	1	1.0	-
ND	**good**	1	66.33	-	4	4.0	-
ND	**poor**	1	9.75	-	4	4.0	-
ND	**ND**	6	31.43	38.30	24	4.0	3.46
All	**good**	47	98.02	115.12	247	5.3	4.46
All	**lean**	23	64.52	90.74	191	8.3	6.51
All	**poor**	133	62.57	64.55	1670	12.6	17.72
All	**lean+poor**	156	62.86	68.68	1861	11.9	16.61
All	**All**	220	68.50	81.13	2290	10.4	14.83

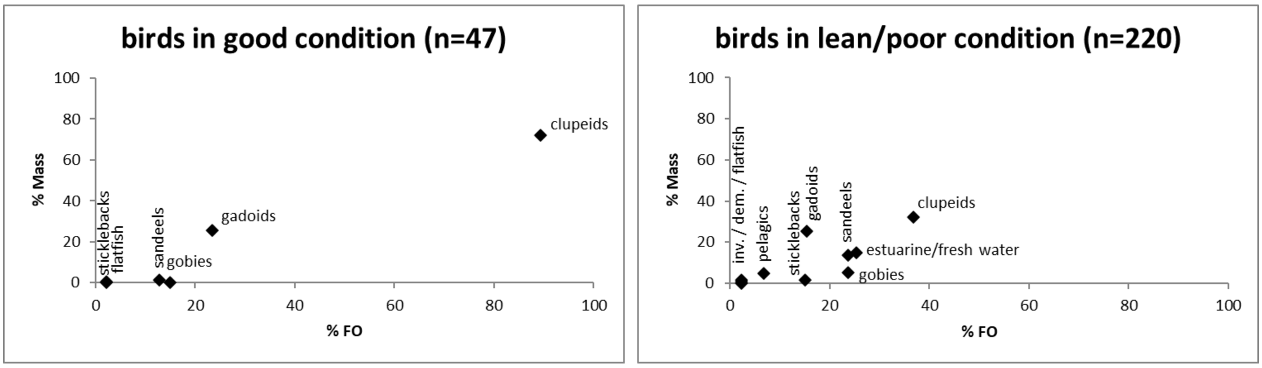


Figure 3-8 *Modified Costello diagram of various prey fish groups, found in red-throated divers that in good body condition that presumably had died quickly (left) or that had been starving before death (right).*

3.3 Common guillemot

Common guillemots (hereafter ‘guillemot’) are small pelagic seabirds of the auk family (*Alcidae*) (Photo 3-9). Their distribution ranges from the North Atlantic to the North Pacific and the Arctic Ocean. In the Atlantic, their southern distribution limit is Gibraltar on the eastern part and the northern coasts of the US on the western side. They also occur on the eastern coast of Greenland, Svalbard and the Barents Sea (BirdLife 2018). Guillemots were classified as Least Concern by the IUCN Red List due to its extensive range and large population size (Birdlife International, 2025). Guillemots are cliff-breeders and share narrow ridges with many conspecifics and razorbills. Like other members of the alcid family, guillemots hunt their prey, mostly schooling fish, by diving. Maximum diving depth can be 230 metres (BirdLife 2018), almost twice the depth razorbills can reach. Guillemots do not breed in the Netherlands but are common in the Dutch EEZ throughout the year, mainly during winter. Parts of the Dutch EEZ (e.g., the Frisian Front) are used as nursery area by fledglings and accompanying fathers in summer (De Gee et al. 1991).

Photo 3-9 *Common guillemots breed on narrow ridges of rocky cliffs. Photo: S. Kühn.*

3.3.1 Diet during the breeding season

As guillemots do not breed in the Netherlands, this is review focused on winter diet. However, diet in the summer near colonies is dominated by sandeel spp. (Blake 1984; Blake et al. 1985; Halley et al. 1995; Sonntag & Hüppop 2005).

3.3.2 Diet outside the breeding season

In the Netherlands, diet studies of guillemots mostly rely on dead beach-washed corpses. As guillemots spend much of their lives swimming at sea, they are highly vulnerable to oil pollution. Most wrecks occurred during winter and, besides oil, a lack of suitable food and/or bad weather are the most common causes of mortality (Camphuysen et al. 1999). Oiled seabirds often die quickly. These birds are usually in a good body condition with plentiful fat reserves and often full stomachs with recent meals. Therefore, most studies on guillemot’ diet were published during the period of chronic oil pollution between 1985 and 2003. Following a strong decline in oil pollution along Dutch coasts, opportunities to study diet became scarcer (Camphuysen 2022). The percentage of oiled guillemots on beaches is monitored continuously as OSPAR EcoQ Indicator and annual reports are published (see Camphuysen (2024) for the most recent update). While natural diet is not part of the standard monitoring, diet of the guillemot belongs to the best-studied seabird species in the Netherlands and outcomes present plenty of information on dietary preferences in guillemots and the habitat use of the Dutch EEZ.

All available guillemot diet studies in the Netherlands reported three groups of fish as dominant prey (Table 3-8): clupeids (mostly sprat and herring), gadoids (such as whiting), Atlantic cod, and poor cod and sandeel species. However, some studies mention a large variety of prey species, including gobies (*Gobiidae*), horse mackerel, pipefish (*Sygnathidae*) etc. Occasionally, invertebrates such as squid, polychaetes, crustaceans and small gastropods are also reported, but these invertebrates are often considered secondary prey, i.e. remains of prey fish diet (e.g. Halley et al. 1995; Sonntag & Hüppop 2005).

Table 3-8*. Overview of diet studies of guillemots in Dutch waters.*

Year	Month	Location	Sample size	Nonad/ ad/ unk	Cause of Death	Dominant prey species	Notes	Reference
1985	Apr / May	NH	47	Almost all young	Beached; oiled; fat	Sandeel (93% of otoliths), gadoids, clupeids	Sandeel length: 133 mm (55-187 mm)	Camphuysen 1990
1989	Sep / Okt	Friese Front	25	12/13/0	Shot; condition unknown	Sprat, Horse mackerel, whiting	all ad birds male; sprat size: 67 mm; horse mackerel: 20-40 mm; Whiting: 174-214 mm; meals size: <100 gr	Geertsma 1992
1990	Nov	NH	41	9/30/1	Beached; oiled; mixed condition	Clupeid, gadoid, sandeel, squid, stickleback	Most prey 12-15 cm, clupeid: 7-10 cm	Camphuysen & Keijl 1994
1991	Dec	Zeeland	38	27/11/0	Beached; oiled; mostly fat	Clupeid; gadoid; sandeel	8-12 cm	Camphuysen 1995
1992	Feb	Texel	76	64/12/0	Beached; oiled; fat	Clupeid; gadoids, sandeel; many other species, especially in young guillemots	Clupeid: 8-17 cm; gadoids: 13-27 cm; sandeel: 8-20 cm	Leopold & Camphuysen 1992
2003	Jan	All coasts	235	40/95/100	Beached; oiled; Poor: 38 / Mod.: 71 / fat: 119	Clupeids; gadoids, sandeel, many other species	Clupeids: 7.5-27.6 cm; gadoids: 10.7-27.1 cm; sandeel: 5-31.6 cm	Ouwehand et al. 2004
2004 / 2005	Winter	NH	12	1/11/0	Beached; not oiled; mostly emaciated	Sandeel, clupeids, gobies		Camphuysen & Leopold 2005
2005	Aug	NH	1	1/0/0	Beached; not oiled; emaciated	Insects, debris	Recently fledged, likely foraged on surface	Camphuysen 2006
2017	Jan	ZH	15	15/0/0	Bycatch; not oiled; fat	Clupeids (mostly sprat), gadoids	Sprat size: 7-15 cm (average 12 cm)	Leopold & Overmaat 2023
2019	Jan	All coasts	123	116/7/0	Beached; 2 ind. oiled; emaciated	Clupeid, pipefish, sandeel and many other small species	Most fish < 10 cm	Leopold et al. 2019

3.3.3 Temporal and spatial patterns

For guillemots, clear seasonal patterns have been observed in the Netherlands and elsewhere. In the Netherlands most fish consisted of clupeids (mostly sprat) in winter, while in summer, more sandeels were found (Camphuysen 1990; Camphuysen & Keijl 1994). Similar patterns were observed closer to breeding colonies in Germany and the UK with a sandeel-dominated diet in summer and a shift towards clupeids and gadoids in winter (Blake 1984; Blake et al. 1985; Halley et al. 1995; Sonntag & Hüppop 2005). The shift from sandeel in summer to clupeids and gadoids is most likely driven by the scarcity of sandeel outside the breeding season (Blake 1984).

In the Netherlands, no long-term temporal changes in diet composition of guillemots were observed in the available literature, however, after the decrease in oil pollution, studies on diet became scarce. In the UK, however, Harris et al. (2022) noted differences in the diet of guillemot chicks after forty years of research (1980s-2020s). While sandeel was fed to chicks throughout the entire breeding season in early years, the decline of sandeel restricted this period to the early breeding season when sandeel was replaced by mostly sprat.

3.3.4 Selection in size and/or quality

In contrast to razorbills, guillemot showed a much more variable diet and ingested, on average, larger fish than razorbills that often ingest fish < 10 cm (Ouwehand et al. 2004).

Size selection was affected by weather condition and body condition. Under stormy weather conditions around the Scottish colonies, smaller sandeel was delivered to chicks which negatively affected overall breeding success (Finney et al. 1999). Emaciated guillemots had smaller prey in their stomachs compared to healthy guillemots (Leopold et al. 2019).

3.3.5 Other variables affecting diet choice

Prey of seabirds in bad body condition may differ from that of healthy birds, due to decreased energy expenditure during foraging. Oiled or bycaught birds in good body condition mostly foraged on energy-rich clupeids, sandeels and gadoids (e.g. Camphuysen 1990, 1995; Leopold & Overmaat 2023). However, the stomach contents of emaciated guillemots also contained several lean fish species such as pipefish, gobies and sticklebacks (Camphuysen 2006; Leopold et al. 2019), indicating a more opportunistic feeding strategy on less favourable prey species. Leopold et al. (2019) described a diet shift towards smaller prey in 123 emaciated guillemots collected from Dutch beaches in 2019, in contrast to healthy birds that died due to oil pollution.

3.3.6 New insights into the diet of Dutch guillemots from unpublished data

As part of the diet study, we conducted stomach content analyses, including newly performed analyses as well as a first-time evaluation of previously collected but unexamined guillemot stomach content data (see Methods).

Overall, 46 distinct fish and invertebrate prey species were identified, spanning several prey groups.
The most frequently occurring prey across all years were sandeels, clupeids, gadoids and pipefish (*Syngnathus spp.*) (Figure 3-10). However, sample size varied over the years and may have inflated the occurrence of pipefish (Figure 3-10). Other species, such as three-spined stickleback, common dragonet, smelt, and poor cod, were dominant in individual years only. Also, invertebrates, such as polychaetes, and squid were found. Notably, benthic prey species such as the common dragonet are likely obtained as fishery discards, underscoring the significant role of discards in the diet. This is particularly evident for whiting, which occurs frequently in the samples and is probably acquired through access to discards.
Of the 691, 21 guillemots were killed as bycatch in nets and thus in a very good body condition. Among the bycaught birds, only clupeids and a single pipefish (*Syngnathus* spp.) were identified, confirming a narrower dietary profile compared to emaciated individuals.

Seasonally, sandeels were most frequently found from December to April, although data were missing for May and June. Herring dominated in August, *Syngnathus* spp. in September, whiting in October, and sprat in November, likely reflecting prey availability throughout the year. This finding is not in line with previous studies on the diet of guillemots in the Netherlands and elsewhere. Most studies found sandeels to be the main prey type during the breeding season whereas we found the opposite. Though Dutch studies were mainly conducted outside the breeding season, most other studies took place during the breeding season, with access to colonies, possibly distorting the dietary profile image.

Diet composition differed between sexes. Among females, the top three prey species in terms of frequency of occurrence were sandeels (n = 30), sprat (n = 27) and clupeids that could not be identified to species level (n = 25). Among males, sandeels and whiting were equally frequent (n = 32), followed by herring and sprat (both n = 29).

Bird condition varied from 0 (emaciated) to 9 (good fat reserves), with the majority of birds in condition classes 0 and 1, indicating predominantly poor to moderate body condition. Comparison of diet composition across different body conditions revealed distinct patterns in prey selection and diversity (Figure 3-11). Birds in poor condition (scores 0 - 3) predominantly consumed sandeels, whiting, sprat, and herring, collectively representing the main prey taxa within this group. In individuals assessed to be in moderate condition (scores 4 - 6), whiting constituted the most frequently occurring prey, while sandeels and herring were of equal importance and contributed similarly to diet composition. In contrast, birds in good condition (scores 7 - 9) primarily consumed sprat, followed by herring, and sandeels.

Overall, prey species diversity was substantially higher in birds in poor condition, with almost twice as many prey types recorded compared to birds in good condition. In contrast, birds in moderate condition preyed on only ten different species, although this finding should be interpreted with caution given the relatively low number of moderately conditioned individuals represented in the dataset. These observations suggest that birds in poor nutritional state may adopt opportunistic foraging strategies, consuming a wide range of prey items regardless of quality - potentially including low-energy ‘junk food’. In comparison, birds in better condition appear to target more profitable, energy-dense prey and supplement their diet with alternative items only when they are readily accessible.

Finally, it is important to note that the current diet assessment remains limited by the high number of unidentified clupeid species. Thus, prey composition estimates may shift as identifications improve, and seasonal patterns are further resolved. A further assessment will also allow to estimate prey size ranges.

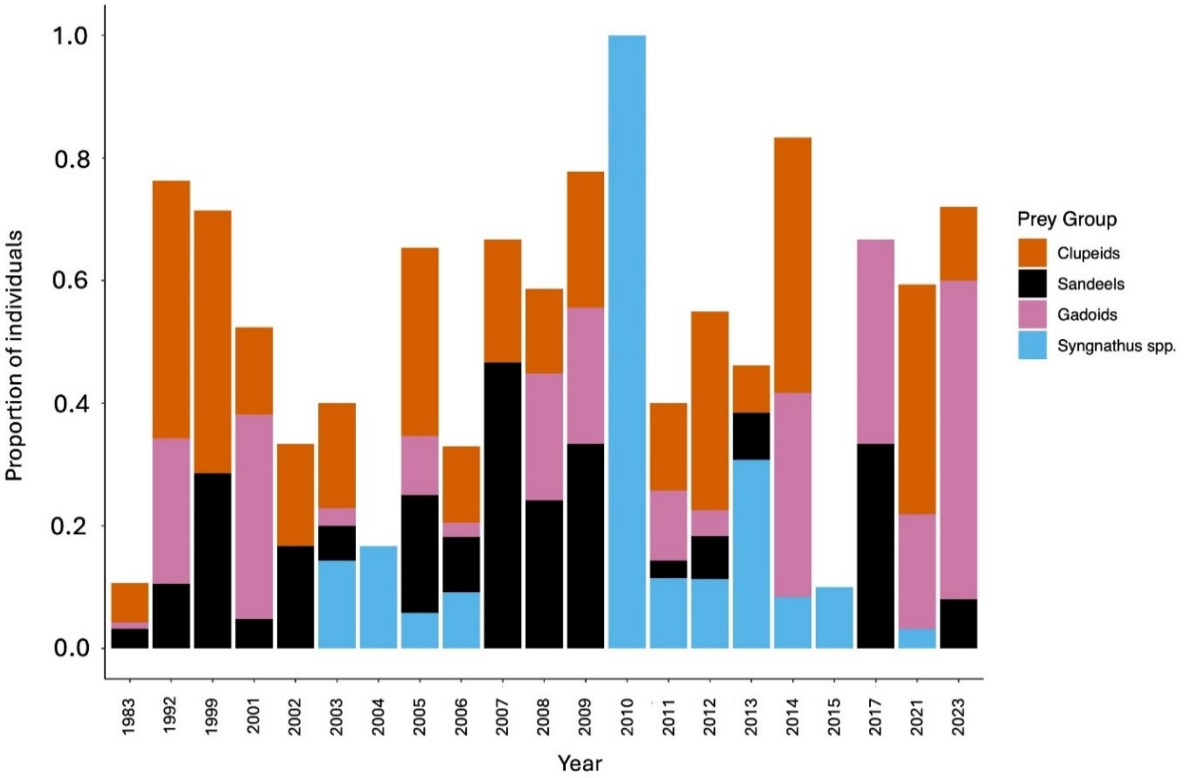


Figure 3-10 *Proportional frequency of occurrence of the four most common prey groups across all years (1983–2023). Frequencies are scaled so that values range from 0 to 1 on the y-axis. The white space above each colored bar segment indicates the proportion of occurrences attributed to all other prey types not included among the top four groups. Numbers in grey on top of each bar segment are sample sizes.*

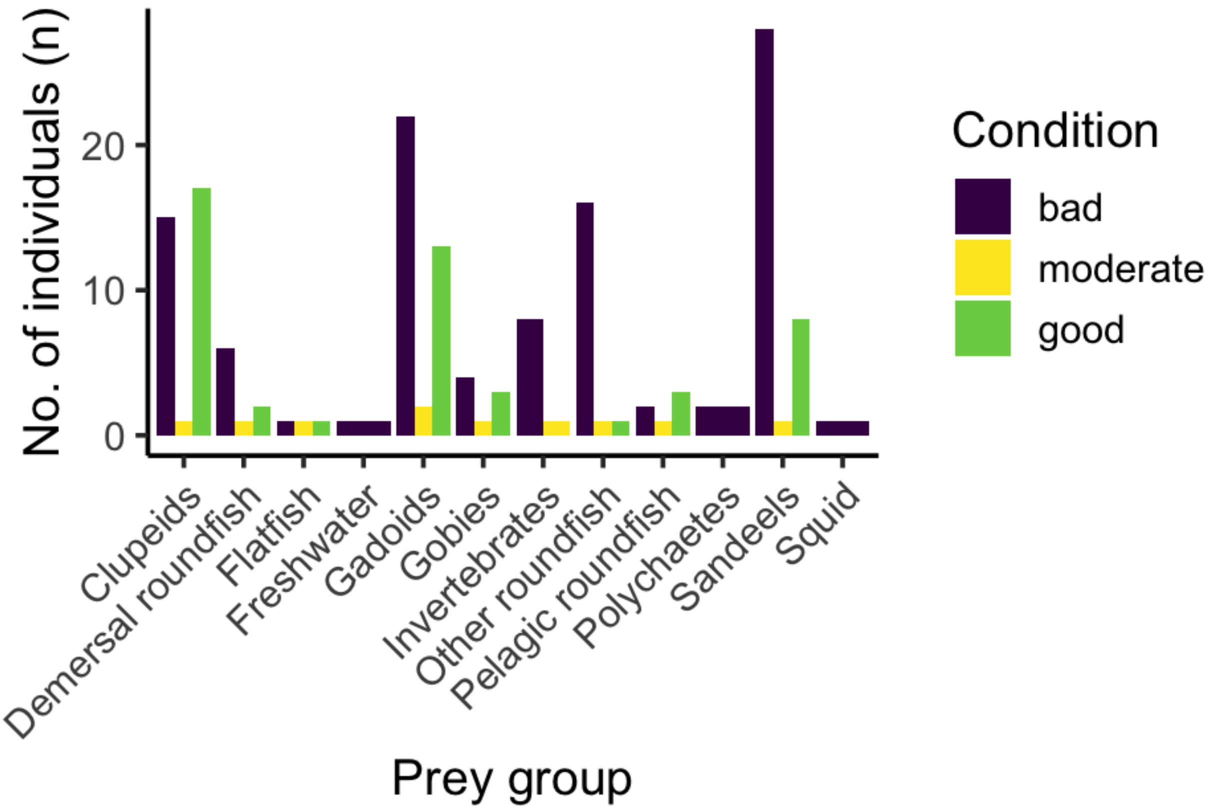


Figure 3-11 *Prey species found in the diet shown per body condition class: poor condition (scores 0-3), moderate condition (scores 4-6) and good condition (scores 7-9).*

3.4 Razorbill

The razorbill is a small pelagic seabird species from the Alcidae family (Photo 3-12). Razorbills occur among the North Atlantic, from sub-tropical to boreal and Arctic regions (BirdLife 2021). They breed on cliffs, often together with Common guillemots. Like other members of the alcid family, razorbills hunt their prey, mostly schooling fish, by diving. In contrast to the deep-diving guillemot, razorbills ‘only’ reach depths of 120 m (BirdLife 2021). None of the alcids breed within the Netherlands (as there is no suitable breeding habitat), the closest colonies are located at the eastern UK coast and on the island of Helgoland, Germany. They utilise the Dutch EEZ throughout the year, but mainly outside the breeding season and prefer waters around 20-30 m water depth (Camphuysen 1998).

Photo 3-12 *Razorbill sitting on a cliff, close to its nesting site. Photo: S. Kühn.*

3.4.1 Diet during the breeding season

As Razorbills do not breed in the Netherlands, this review focused on winter diet. However, in the UK, chick diet consisted mainly of sandeel followed by herring and sprat (Wagner 1997; Harris & Wanless 1986). In northern Norway, razorbill chick diet consisted mostly of sandeel, also when other suitable fish species were abundant. This preference was attributed to the more inshore distribution of sandeel at shallower water depth (Barrett 2003).

Harris & Wanless (1986) compared the diet of razorbills on the isle of May with other alcid species (guillemot and Atlantic puffin (*Fratercula arctica*)), and although all three species depended heavily on sandeel, guillemot presented a richer variety of other fish species (clupeids and gadoids) to their chicks, while puffins often returned with smaller (but larger numbers of) sandeel to the colony.

During the breeding season, razorbills feed their chicks by transporting mostly one, but sometimes several fish in their bill. Therefore, available studies rely on direct observations of delivered food and focus entirely on chick diet, which may deviate from food eaten by the adult itself. Fish size depended on chick size and increased throughout the breeding season.

3.4.2 Diet outside the breeding season

In the Netherlands, diet studies of razorbills mostly rely on dead beach-washed corpses. Similar to guillemots, they are vulnerable to oil pollution. Due to their sudden death, oiled seabirds are suitable for diet research as their stomachs are often filled with their most recent meals. While there is plenty of data on guillemot diet, data on razorbill diet is surprisingly limited (Table 3-9).

Compared to the guillemot, razorbills had a much narrower prey spectrum, mainly consisting of clupeid fish (herring-like fish, mostly sprat and herring and sandeel species (*Ammodytes* sp.). Gadoids (cod-like fish species) and other fish species were rarely encountered. Leopold et al. (2011) observed an unusual event of hundreds of razorbills (plus kittiwakes and guillemots) foraging behind a ship in the coastal area of Egmond aan Zee in 2012. These birds were most likely hunting for herring and sprat, although simultaneously beached emaciated razorbills were found to contain three-spined stickleback, a fish species usually consumed in the absence of more energy-rich food. Likely, and similar to guillemots, razorbills switch to lean and unprofitable food when sick or weak.

Table 3-9 *Overview of diet studies of razorbills in Dutch waters.*

Year	month	Location	Sample size	Nonad/ ad/ unk	Cause of Death	Dominant prey species	Notes	Reference
1977-1997	winter	All coasts	95	mixed	Beached; emaciated	Stickleback; sandeel; sprat	Mostly empty stomachs	Camphuysen 1998
1992	Feb	Texel	10	9/1/0	Beached; oiled	Clupeid; sandeel	Mostly empty stomachs; fish <10cm	Leopold & Camphuysen 1992
2003	Jan	All coasts	156		Beached; oiled; fat	Clupeids (72% by number); sandeel (24%)	fish <10cm	Ouwehand et al. 2004
2004 / 2005	winter	NH	6	4/6/0	Beached; not oiled; mostly emaciated	Clupeid; sandeel		Camphuysen & Leopold 2005

3.4.3 Temporal and spatial patterns

From the Netherlands, no information is available on seasonal changes in diet. Winter diet in razorbills from the Belgian coast were similar to those from the Netherlands. DePooter (2010) observed mostly sandeel remains, followed by clupeids and gobidae. Similar to data from the Netherlands, no gadoids were found, and the prey spectrum was much more restricted than in guillemots.

For the North Sea, no data on long-term changes in diet of razorbills are available. However, on Gannet Island in Canada, a major shift from the Arctic fish species capelin to the more boreal sandeels was observed (Lavers & Jones 2007). The absence of capelin however, likely contributed to low fledging success in razorbills and may have caused a previously unobserved feeding technique of kleptoparasitism in razorbills, whereby fish was stolen by conspecifics. Climate change may have also led to a northward shift of sandeel, followed by a temporal colonization of razorbills on the Arctic Coats Island (Canada), as described by Gaston & Woo (2008), indicating some flexibility with regard to climate change.

3.4.4 Selection in size and/or quality

Compared to guillemots, fish size selection was restricted in razorbills to smaller fish, with most fish measuring <10 cm (Ouwehand et al. 2004). In an experimental setup, razorbills showed a preference for smaller fishes, even if larger ones were offered. More important than fish length was fish 'height' (Swennen & Duiven 1977). During the breeding season on the Isle of May (Scotland, UK), delivered fish was on average less than 10 cm in size, however sometimes larger fish (>14 cm) were observed as well (Harris & Wanless 1986).

3.4.5 Other variables affecting diet choice

Some niche segregation was observed on Skomer Island (Wales, UK) between male and female razorbills when feeding their chick (Wagner 1997), with some females specialised on clupeid fish, but also here, sandeel dominated the diet.

3.5 Northern fulmar

The northern fulmar (hereafter fulmar; Photo 3-13) is a seabird species occurring in the North Atlantic, North Pacific and the Arctic Ocean. Within the North Sea, cliff-breeding fulmars have colonies along the coasts of the United Kingdom, southern Norway and the island of Helgoland. In the Netherlands, fulmars do not breed, due to the absence of suitable breeding habitat, however, they occur year-round in the Dutch part of the EEZ. While fulmars were classified as Least Concern by the IUCN Red List due to its extremely large range (Birdlife International, 2025), most local population counts in the North Atlantic and Arctic indicate strong declines. This decline includes colonies in Germany (Dierschke et al. 2022), the UK and Ireland (Burnell 2023), the Faroe Islands (Hammer et al. 2014), Norway (Anker-Nilssen et al. 2021), Iceland (Garðarsson et al. 2011) and the Canadian Arctic (Mallory et al. 2020). Davies et al. (2023) predict a further population decline of 70% until 2050. Reasons are unclear, but authors mainly refer to climate change and associated shifts in prey availability and fisheries including bycatch (e.g., Dias et al. 2019; Dierschke & Garthe 2022). Also in the Netherlands the number of fulmars at sea is decreasing since the 2000s (Sovon.nl). The conservation status in the Netherlands is classified as unfavourable.

Photo 3-13 *Northern fulmar foraging on fish factory waste in northern Iceland. Photo: S. Kühn.*

3.5.1 Diet during the breeding season

As fulmars do not breed in the Netherlands, no information on diet during the breeding season is available. However, diet research of fulmars from the North Sea has mainly focused on samples collected in colonies during the breeding season (e.g., Furness & Todd 1984; Hamer et al. 1997; Ojowski et al. 2001) and discard studies conducted at sea (e.g., Garthe & Hüppop 1994; Camphuysen & Garthe 1997). Fulmars are considered opportunistic predators, exclusively foraging at the sea surface. Known prey includes fish, squid, zooplankton and floating carrion (Mallory 2012), but also fish offal, discards and bait from longline fishing (e.g., Kühn et al. 2025), although the dependency on fishing operations is debated and may differ locally (Phillips et al. 1999).

3.5.2 Diet outside the breeding season

For the Netherlands, almost no diet data of fulmar diet is available: a single fulmar stomach was studied by Leopold & Camphuysen (1992), who found six heavily worn otoliths of poor cod. At sea (including the Dutch part of the North Sea), Camphuysen (1998) observed fulmars pecking on jellyfish, likely also foraging on associated big-eye amphipods (*Hyperia galba*). However, new information is presented in Chapter 3.5.5.

During discard experiments, fish of different species and sizes were offered to ship-following seabirds, among fulmars. Data presented by Garthe & Hüppop (1994) show that during summer, fulmars followed the fishing vessel mainly in the northern and central North Sea, but fulmars were also observed in the Dutch part

(Camphuysen et al., 1995). Fulmars foraged on all offered roundfish species like different species of the gadid and clupeid orders. Flatfish offered in discard experiments were usually ignored by fulmars. In winter, more fulmars were encountered in the southern part of the North Sea although birds remained well offshore (Camphuysen 1994).

3.5.3 Temporal and spatial patterns

As there is almost no literature on fulmar diet in the Netherlands, no seasonal or temporal patters are known. However, new information is presented under 3.5.5.

3.5.4 Selection in size and/or quality

The six heavily worn otoliths of poor cod found in one stranded fulmar were indicated a fish size of 11 cm (Leopold & Camphuysen 1992). In discard experiments in the Southern North Sea, fulmars foraged on all offered roundfish with length ranging from 10 – 30 cm with some exceptional cases of whiting <43 cm (Garthe & Hüppop 1994). New information on size selection is presented under 3.5.5 (Figure 3-15).

3.5.5 New insights into the diet of Dutch fulmars from unpublished data

In the framework of the current MONS project, unpublished raw data were analysed and preliminary results are presented here (see methods).

Photo 3-14 *Fulmar found dead on the beach of Texel, The Netherlands. This fulmar was included in the OSPAR monitoring of plastics in fulmar stomachs. Photo: S. Kühn.*

Otoliths stored from a total of 111 stomachs of northern fulmars, found in the Netherlands between 1989 and 2023, were analysed. Of these birds, 39 were males, 70 females and 2 with an unknown sex. Most individuals were adult (n = 67), followed by immature (n = 20) and juvenile (n = 13) birds. The remaining birds were either two-year olds (n = 9) or could not be assigned to an age category (n = 2). Most individuals were emaciated; more than two-thirds of the birds had a poor condition index of 0-3 out of 9. The majority of individuals were found between December and March 12, 20, 23 and 15 individuals, respectively. In all other months (April and November), two to eight birds were found.

In total, 20 different fish species were identified (Table 3-10). The most commonly consumed fish prey, in terms of number of individuals, were all members of the family *Gadidae*: whiting, poor cod, poor cod/bib (*Trisopterus minutus/luscus*), and Norway pout. Additional prey species belonged to diverse ecological guilds, including demersal roundfish, flatfish, clupeids, sandeels, gobies, pelagic roundfish, and mesopelagic fish. Prey species other than fish were recorded only by number per stomach and frequency of occurrence. Among the

111 fulmars analysed, 59 contained squid species (e.g., *Loligo* spp.), 12 had *Nereis* polycaetes, and 8 contained crustacean species, in addition to fish.

Whiting accounted for the largest proportion of reconstructed prey biomass across all samples (65.24%), followed by poor cod (9.98%). All other species contributed less than 5% individually to total biomass.
Fish prey length ranged from approximately 5 to 28 cm. The smallest prey species were glacier lantern fish (4.95 ± 0.36 cm) and gobies - specifically sand goby (5.57 ± 0.93 cm) and transparent goby (6.54 ± 0.53 cm). The largest prey species included greater argentine (27.5 cm), greater sandeel (25.1 cm), tub gurnard (23.6 cm), and whiting (19.34 ± 4.87 cm). Notably, an examination of the length distribution of the four most frequently consumed species - whiting, poor cod/bib, and poor cod - revealed that three of these species regularly exceeded 20 cm in length. In particular, large whiting >30 cm were also consumed (Figure 3-15).

Table 3-10 *Number of prey species (n) recovered from the stomachs of 111 northern fulmars from the Netherlands and their mean length (cm) ± standard deviation (SD) and reconstructed biomass (g).*

Prey species		**n**	**mean length (cm) ± SD**	**biomass (g)**
Whiting	*Merlangius merlangus*	81	19.34 ± 4.87	5469.34
Poor cod	*Trisopterus minutus*	26	13.14 ± 4.45	836.83
Poor cod-Bib	*Trisopterus minutus/luscus*	15	11.59 ± 4.95	380.46
Atlantic horse mackerel	*Scomber scombrus*	6	15.2 ± 7.26	299.42
Norway pout	*Trisopterus esmarkii*	26	11.16 ± 2.12	259.24
Atlantic cod	*Gadus morhua*	4	16.47 ± 7.2	257.16
Dab	*Limanda limanda*	3	18.6 ± 3.43	219.04
Greater argentine	*Argentina silus*	1	27.5 -	154.97
Tub gurnard	*Chelidonichthys lucerna*	1	23.6 -	139.93
Herring	*Clupea harengus*	6	12.68 ± 3.33	105.44
Sandeel sp.	*Ammodytes spp.*	9	15.12 ± 3.14	100.78
Great sandeel	*Hyperoplus lanceolatus*	1	25.1 -	39.75
Gurnard sp.	*Triglidae spp.*	1	14.19 -	30.40
Sole	*Solea solea*	3	9.93 ± 0.27	24.32
Silvery pout	*Gadiculus argenteus*	1	14.17 -	24.10
Sprat	*Sprattus sprattus*	1	12.51 -	14.50
Solenette	*Buglossidium luteum*	3	7.35 ± 0.65	12.11
Sand goby	*Pomatoschistus minutus*	5	5.57 ± 0.93	8.03
Transparent goby	*Aphia minuta*	2	6.54 ± 0.53	5.04
Glacier lantern fish	*Benthosema glaciale*	2	4.95 ± 0.36	2.09

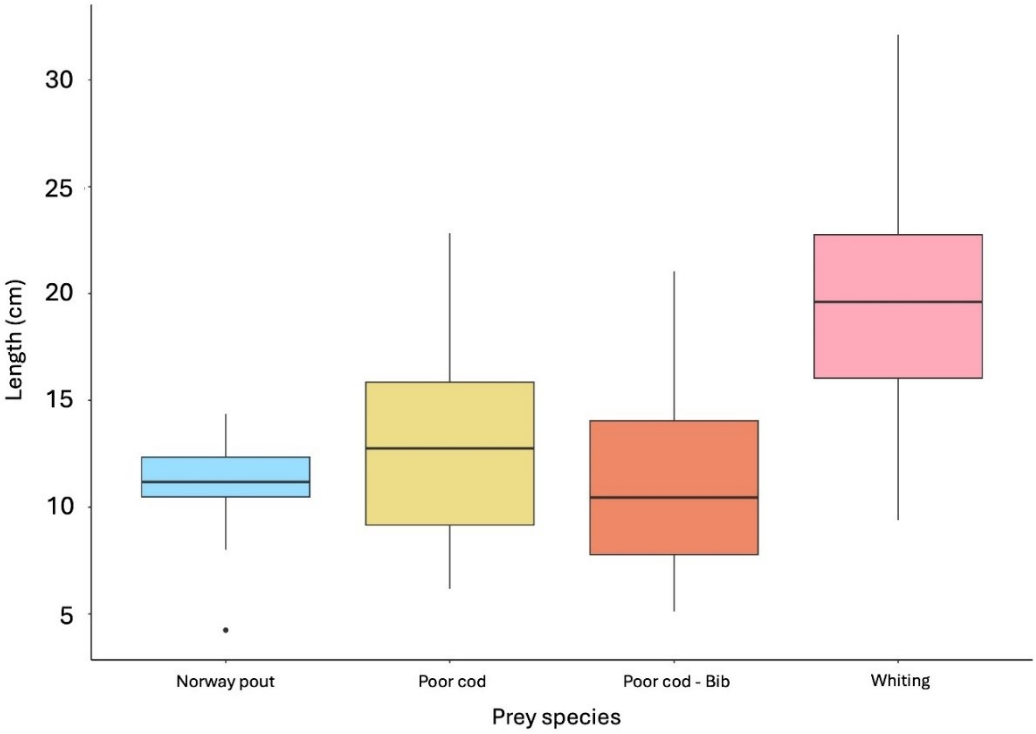


Figure 3-15 *Length distribution (in cm) of the four most common prey species recovered from the stomachs of northern fulmars from the Netherlands.*

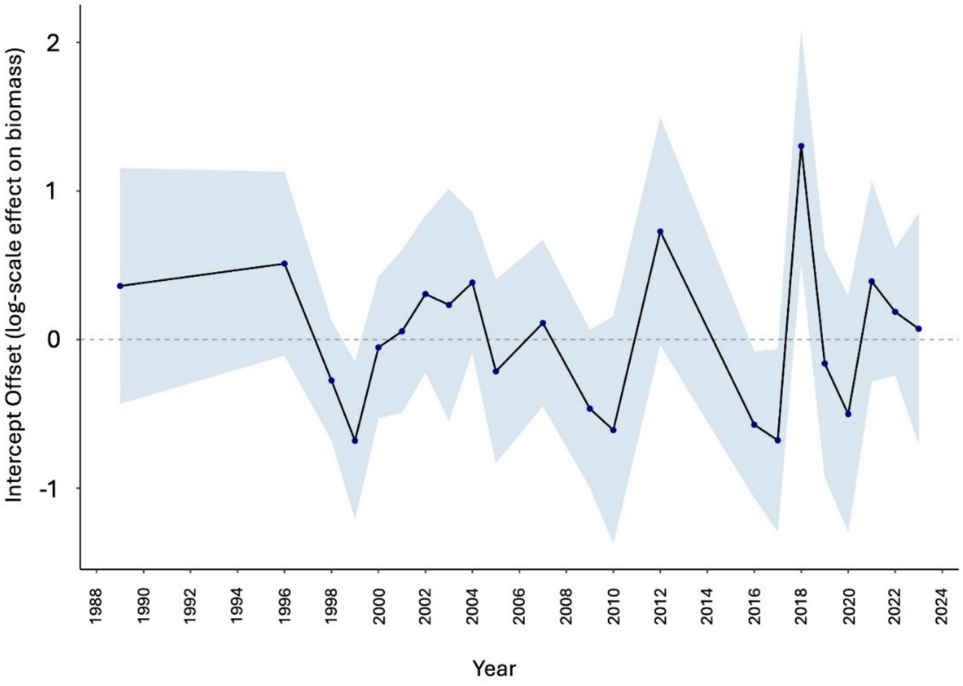


Figure 3-16 *Random intercepts of the variable year, included in the model to describe the amount of whiting biomass (g) in northern fulmars from the Netherlands. Data points above the intercept offset (dotted line) are years with an above average whiting biomass, and data points below the intercept offset are years in which whiting biomass was lower than the average.*

Given the importance of whiting, both in terms of numbers and biomass, a generalized additive mixed model (GAMM) was applied to disentangle which factors possibly influence whiting biomass in northern fulmars. The model, using a Gamma distribution with a log link, revealed that mean sea surface temperature (SST) had a negative, though marginally non-significant, effect on whiting biomass ($\beta = -0.099$, $p = 0.074$). Sex also played a role, with males consuming significantly more whiting than females ($\beta = 0.45$, $p = 0.019$). Age differences were pronounced: subadults ($\beta = -0.73$), immatures ($\beta = -1.16$), and juveniles ($\beta = -1.55$) all consumed significantly less whiting than adults ($p < 0.005$ for all). Seasonality was evident through a significant cyclical smooth term for month (edf = 0.90, F = 11.08, $p = 0.004$), with whiting biomass peaking mid-year. Additionally, a random effect for year (SD = 0.59) captured substantial interannual variation. Notably, whiting biomass exhibited distinct peaks and troughs over time, with higher-than-average values during 1990–1994, 2012, and 2018, and lower-than-average values in 1998–1999, 2010, 2016, and 2020 (Figure 3-16). Some years (e.g., 2018) showed wider uncertainty, likely due to low sample sizes or greater residual variance. Collectively, these patterns suggest genuine ecological variability in whiting consumption by northern fulmars that cannot be fully explained by SST, sex, age, or season alone.

While our model accounted for known drivers of diet composition - including SST, age, sex, and seasonality - some limitations remain. The dietary dataset was relatively sparse, averaging only 2.5 data points per year, although the model structure helped mitigate issues related to sample size. SST had a negative effect on whiting biomass, suggesting that warming may reduce prey availability or alter fulmar foraging patterns. Age-related differences likely reflect ontogenetic variation in prey handling and/or energetic needs. However, the significant interannual variability in whiting consumption cannot be fully explained by these predictors (Woehler & Hobday 2024). Additional factors may include temporal shifts in whiting abundance, changes in discard availability linked to fisheries management or effort, and fluctuating fulmar foraging behaviour in response to prey distribution and accessibility.

The presented data confirms the strong dependence on discards by fulmars foraging in the Dutch North Sea, such as whiting and other gadoid fish species that are considered demersal and therefore otherwise out of reach of the surface-feeding fulmar.

Photo 3-17 *Northern fulmars foraging on discarded fish. In large fish, or when massive amounts of fish are available, fulmars focus on the energy-rich intestines rather than swallowing the entire fish. Photo: S. Kühn.*

3.6 Northern gannet

Northern gannets (Photo 3-18) are part of the pelagic functional group in terms of diet and are currently listed as Least Concern on the IUCN Red List, with their formal conservation status deemed 'favourable' (BirdLife International 2018, SOVON 2024a). However, they have recently experienced exceptionally high mortality due to highly pathogenic avian influenza (HPAI), which may prompt a re-evaluation and potential downgrade of their conservation status (Lane et al. 2023). The current North East Atlantic breeding population consists of 390,000 pairs, of which the majority are found in the UK (van Bemmelen et al. 2024). In Dutch coastal waters, the majority of northern gannets are non-breeding, passage migrants, occurring year-round in the Southern Bight in variable numbers (Camphuysen 2001). Their abundance typically increases after March, peaking in the autumn months from September to November (Camphuysen & Leopold 1994). Most recent estimates suggest between 22 (April) and 1,577 (November) Northern gannets in Dutch coastal waters between August 2023 and June 2024, with peak numbers in autumn. For offshore waters (Dutch Continental Shelf) northern gannet numbers were between 3,466 (January) and 47,098 (August), with high abundances in February, April and August. According to the latest CBS trend analysis based on MWTL data, northern gannet numbers in the North Sea have shown a slight increase since 1991/1992, increasing by 2% per year ($p < 0.01$). Since 2014/2015, the slightly increasing trend has remained, with a 5% annual increase ($p < 0.01$) (van Bemmelen et al. 2024). Breeding populations in Europe, such as those from Bass Rock, Scotland, exhibit diverse migratory strategies: some winter in the North Sea and English Channel, others in the Bay of Biscay, Celtic Sea, or the Mediterranean, while a significant proportion - up to 45% - migrate as far as the waters off West Africa (Kubetzki et al. 2009). Migration distances vary substantially, ranging from several hundred to over 4,600 km (Kubetzki et al. 2009). Dutch coastal waters thus play an important role as both a passage and wintering area within this broad migratory network (Camphuysen 2001, Kubetzki et al. 2009).

Photo 3-18 *Northern gannets near the island of Helgoland, Germany – a gannet breeding colony in the southern North Sea. Picture Eileen Heße.*

3.6.1 Diet during the breeding season

Prey types like Atlantic mackerel, Atlantic herring, and sandeels are important during chick-rearing periods, providing the high caloric value necessary for breeding success (Hamer et al. 2000; Lewis et al. 2003; Hamer et al. 2007). Nevertheless, less energy-dense, gadoids such as whiting are also regularly consumed and may represent a significant portion of the diet by frequency (Davies 2012; Hamer et al. 2007; Lewis et al. 2003). Besides, gannets are known to consume fisheries discards, although mostly during the non-breeding period. They exploit discards early in the breeding season (Furness et al. 1992) but shift to pelagic fish once chick-rearing begins. Research on the Cape gannet (*Morus capensis*) indicates that a discard-dominated diet leads to reduced breeding success (Pichegru et al. 2007; Grémillet et al. 2008). Discards seem to be suboptimal for reproduction (Leopold 2016).

3.6.2 Diet outside the breeding season

Understanding the diet of northern gannets in the southern North Sea is complicated by a lack of region-specific data, especially along the Dutch coast. Most available information originates from studies conducted during the breeding season at major colonies such as Bass Rock in Northeast Scotland - the largest known northern gannet colony globally (Murray et al. 2014) - and Saltee Island off Southeast Ireland. Additional research primarily comes from the Western North Atlantic, including Canadian waters (e.g., Garthe et al. 2011; Guillemette et al. 2018; Montevecchi 2007). These sources, although informative, pose challenges when used to infer dietary habits of gannets in the Dutch sector of the North Sea.

Much of the data referenced in this review were collected over a decade ago. Consequently, changes in sea surface temperatures, the development of offshore wind farms (OWFs), a reduction in fisheries effort, and the closure of sandeel fisheries in parts of the North Sea may have substantially altered northern gannet foraging patterns and diet since these studies were conducted.

To date, only two studies have examined the diet of gannets in Dutch waters directly. Camphuysen (2007) analysed the stomach contents of eight dead gannets found in April 2006. Seven of the eight gannets were in good condition and one individual, suffering from oil, was rather emaciated. Five of these birds had ingested prey, consisting primarily of flatfish (European plaice (n = 17) and common dab (n = 12)) and sandeels (n = 8). These findings suggest that the birds were foraging on fishery discards near beam trawlers. One individual had an unusually full stomach (995 g of reconstructed prey biomass) with mostly flatfish, indicating substantial intake from discard sources. European plaice accounted for 44.2% and common dab for 46.6% of the total mass (Figure 3-19, adapted from Camphuysen, 2007). Given the relatively intact condition of the stomach contents, it is likely that foraging occurred close to the Dutch coast. An earlier study from 1992 analysed the stomach contents of oil victims along the Texel coastline (Leopold & Camphuysen 1992). Among these were four northern gannets from which it was possible to perform stomach content analysis. No fish remains were found in any of the stomachs, but in two stomachs the operculum (protective plate) of a whelk (*Buccinum undatum*) was found.

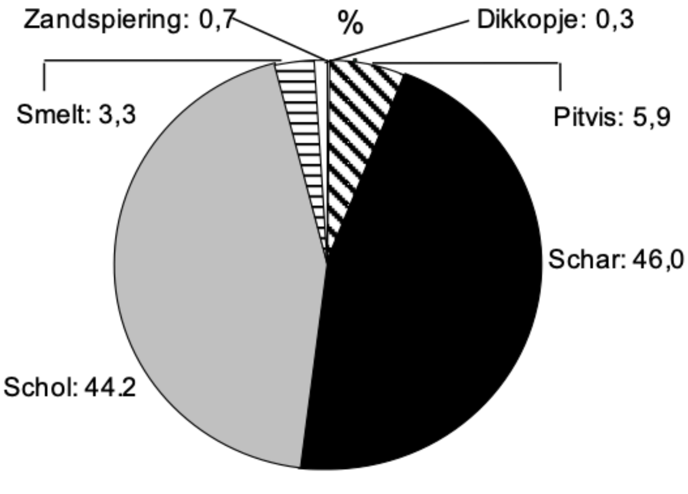


Figure 3-19 *Biomass (in percentages) of consumed prey species of one Northern gannet with a particularly full stomach in Camphuysen 2007b.*

Observational data from the mid-1980s further underscore the possible importance of prey availability in Dutch waters. In 1985–1986 near Texel, up to 1,075 gannets per hour were recorded foraging during autumn. This coincided with seasonal peaks in juvenile herring and cod populations. Favourable weather conditions and high water clarity likely enhanced prey visibility and accessibility. These observations suggest that gannets can exploit opportunistic feeding opportunities during favourable years (Camphuysen & van Dijk 1983; Leopold & Platteeuw 1987).

The diet of northern gannets in the southern North Sea as a whole has been historically dominated by high-energy pelagic fish species, notably Atlantic mackerel, Atlantic herring, and sandeels (Hamer et al. 2000; Lewis et al. 2003; Hamer et al. 2007). Nevertheless, less energy-dense, gadoids such as whiting are also regularly consumed and may represent a significant portion of the diet by frequency (Davies 2012, Hamer et al. 2007, Lewis et al. 2003). Gannets are also known to consume fisheries discards, particularly during the non-breeding season, although to a lesser extent than large gulls (Camphuysen 2011). In northern gannets, discards may support adult survival during winter (Leopold 2016). However, northern gannet population growth in the North Sea does not appear to depend on discard availability (Leopold 2016), implying a degree of dietary flexibility that may buffer the species against ecosystem change.

Stable isotope analyses have begun to shed light on dietary patterns during migration and winter. Grecian et al. (2019) identified two distinct winter dietary clusters for gannets in the Northeast Atlantic: one offshore cluster associated with higher trophic level prey (evidenced by higher $\delta^{15}N$ and lower $\delta^{13}C$ values), likely consisting of demersal fish or discards, and another inshore cluster reflecting the consumption of small forage fish, indicated by lower $\delta^{15}N$ and higher $\delta^{13}C$ values. Notably, 84% of individuals remained within the same dietary cluster across multiple years, while 16% switched, often with associated improvements in body condition. These results suggest a potential link between dietary flexibility and individual fitness. Additionally, some sex-specific differences were observed, with females more likely to switch to higher trophic prey.

Photo 3-20 *A young northern gannet swallowing a large fish discarded during fisheries research on the North Sea. Picture Susanne Kühn.*

3.6.3 Temporal and spatial patterns

Temporal variations in gannet diet have been widely documented, influenced by prey availability, environmental fluctuations, and colony size (e.g., Davies 2012; d’Entremont et al. 2022). Long-term shifts include a decrease in the dominance of sandeels and an increasing reliance on mackerel and herring. Martin (1989) first documented a decline in sandeels and the rise of other prey species. In Canadian populations, mackerel comprised 91% of the diet in 1974 but this has dropped to 54% in recent decades, likely reflecting changing ocean conditions (Guillemette et al. 2018). These changes in prey composition have been closely linked to SST anomalies (d'Entremont et al. 2022; Franci et al. 2015). Within the North Sea, sandeels dominated gannet diets in the early 2000s, but by 2010 - 2011, their contribution had declined significantly, with mackerel comprising 79% of dietary biomass in 2011 (Davies 2012). These changes are likely a response to prey availability influenced by environmental drivers.

Differences in foraging strategies and diet between nearshore and offshore environments further illustrate the species' adaptability. In the North Sea, nearshore foraging often involves multi-species feeding associations (MSFAs), in which gannets collaborate with guillemots and razorbills to drive sandeels to the surface, facilitating capture through surface-feeding techniques, including pelican-style scooping (Camphuysen 2011). Conversely, offshore foraging relies more heavily on plunge diving, targeting fish such as mackerel and herring, often driven to the surface by marine mammals (Camphuysen 2011). Offshore trips tend to be longer, especially for individuals from larger colonies, as demonstrated by comparisons between Bass Rock (Scotland) and Great Saltee (Ireland) (Lewis et al. 2001; Lewis et al. 2002; Lewis et al. 2003; Camphuysen 2011).

3.6.4 Selection in size and/or quality

The average prey size consumed by gannets ranges from 8 to 40 cm, with most prey falling within the 15–30 cm range (Camphuysen 2011; Lewis et al. 2003). Experimental studies further suggest that gannets select larger discarded roundfish (Camphuysen 2011).

Prey profitability is central to gannet foraging decisions. At Bass Rock, individuals delivered 34% more energy-rich prey than those at Great Saltee, despite having a 32% lower feeding rate. This suggests that the energetic benefits of high-quality prey can offset the costs of long-distance foraging (Lewis et al. 2001; Lewis et al. 2002; Lewis et al. 2003).

3.6.5 Other variables affecting diet choice

Colony size has a notable impact on foraging behaviour. Birds from large colonies like Bass Rock undertake longer trips but compensate by delivering higher-energy prey. In contrast, birds from smaller colonies such as Great Saltee travel shorter distances and tend to consume lower-energy fish, supporting the hypothesis that foraging range and prey quality are tightly coupled with colony dynamics (Lewis et al. 2001; Lewis et al. 2002; Lewis et al. 2003).

Age also plays a significant role in dietary habits and foraging strategies. Juveniles and immatures, particularly those under three years old, typically forage farther from breeding colonies and avoid areas within roughly 150 km of high adult density, likely to reduce competition with experienced, central-place foraging adults (during the breeding season) (Pettex et al. 2019). In their first two years, immatures disperse widely at sea, while older immatures (2 - 4 years) begin returning to the vicinity of colonies and may form foraging groups known as "clubs" (Nelson 2002; Pettex et al. 2019).

In the British and Norwegian North Sea, adults mainly target energy-rich pelagic fish such as mackerel, herring, and sandeels during the breeding season (Lewis et al. 2003; Camphuysen 2011; Pettex et al. 2015). It is thought that juveniles likely forage on species or sizes not targeted by adults, reflecting both their broader spatial range and lower competitive ability, as supported by isotopic niche segregation (Votier et al. 2011; Pettex et al. 2019). While adults show some dietary specialization and sex-specific differences in foraging, immatures exhibit generalist and flexible strategies without clear sexual segregation, possibly as a response to competition and developing foraging skills (Stauss et al. 2012; Pettex et al. 2019).

Environmental conditions, particularly SST, are significant drivers of dietary change. For example, in 2012, high SSTs in the Gulf of St. Lawrence, Canada, were associated with poor reproductive success and signs of nutritional stress in gannets (Franci et al. 2015). Warmer years often coincide with prey shortages, forcing birds to undertake longer trips and increasing chick mortality rates (Wanless et al. 2005). Shifts in prey timing and abundance due to temperature changes can alter dietary composition and reproductive outcomes. For instance, SST anomalies have been shown to displace mackerel distributions northward in warmer years (Franci et al. 2015). Interestingly, SST increases during the later stages of chick-rearing tend to be most detrimental, whereas earlier warming may improve access to certain prey types (d'Entremont et al. 2022). A clear example of such binary dietary switching is observed in Newfoundland, Canada, where northern gannets predominantly feed on saury in warm years and on capelin in colder years (Montevecchi 2007).

3.7 Black-legged kittiwake

Black-legged kittiwakes (hereafter 'kittiwake') are small pelagic gulls occurring throughout the northern boreal and Arctic regions, including the North Pacific, North Atlantic and the North Sea (Photo 3-21). The black-legged kittiwake is classified as Vulnerable by the IUCN Red List due to its strong decline over the past three generations (Birdlife International, 2025). These birds breed on (artificial) cliffs and rely entirely on marine diet. They acquire food at the sea's surface mainly through shallow plunge-diving and surface dipping (Coulson 2011). Kittiwakes are opportunistic feeders and their main diet consists of fish and marine invertebrates, but they can also often be found behind fishing vessels. Kittiwakes are found year-round in the Dutch EEZ, but peaks are observed in winter months (e.g., Camphuysen 1994). In absence of cliffs in the Netherlands, breeding kittiwakes have only recently been observed on oil rigs within the Dutch EEZ (Camphuysen & de Vreeze 2005; Camphuysen & Leopold 2007; Geelhoed et al. 2011; Van Bemmelen et al. 2025). Diet data of kittiwakes in the Netherlands is very limited, therefore the greater diet picture of the North Sea and beyond is discussed where necessary.

Photo 3-21 *Adult black-legged kittiwake in flight. Clearly visible are the completely back wing tips, a unique feature in North Sea gull species. Photo: S. Kühn.*

3.7.1 Diet during the breeding season

Kittiwakes were first described breeding in the Netherlands in 2000 when breeding birds were discovered on oil platforms within the Dutch EEZ (Camphuysen & de Vreeze 2005; Photo 3-22). Therefore, within the Netherlands, only a few stomach contents have been studied during the breeding season. During a platform visit in June 2005, Camphuysen & de Vreeze (2005) found 45 apparently occupied nests on a platform ca. 35 nm northwest of Texel. By now, it is estimated that ~350 pairs breed on oil platforms in Dutch waters (SOVON 2025). The diet of these birds has not been studied in detail, however in 2005, four faecal samples were collected, and the diet mainly consisted of sandeels and sprat. The remains of a single flatfish (solenette) suggested foraging on discards (Camphuysen & de Vreeze 2005). During an earlier wreck of juvenile kittiwakes in summer 1987, an estimated 2000 birds died on Dutch shores and starvation was the primary cause of death. Of the 20 stomach contents analysed, none contained any food remains, only non-nutritious items (plastic, stones, shell fragments and seaweed) (Camphuysen 1989).

Photo 3-22 *Oil platform PE-L7-PB based in the Dutch part of the North Sea, colonised by kittiwakes in July 2024. Photo: H. Verdaat.*

Given the scarcity of available data from the Netherlands, details on changes in time (throughout the breeding season and within years), potential competition and differences between colonies and diet selection by age must be derived from neighbouring colonies located in Germany (Helgoland) and the eastern coast of the UK. Here, more details of kittiwake diet are known, as diet can be studied in ‘traditional’ breeding colonies.

Since the 1960s the diet of kittiwakes has been studied in UK colonies. On the eastern coast, sandeel has always been the dominant prey species, followed by juvenile clupeid and gadoid fish species and, to a small extent, planktonic crustaceans and polychaetes (Bull et al. 2004; Pearson 1968). Whereas in June and July sandeels were the dominant food source, in July the diet shifted slightly towards clupeid fish, which was explained by the movements of juvenile fish from coastal waters to more offshore areas where kittiwakes forage. Although sandeel remained the dominant prey, Wanless et al. (2018) detected a significant decrease in the proportion of sandeel in kittiwake diet between 1986 and 2015, with clupeid fish gaining importance. The authors also observed a significant decrease in juvenile sandeel length within that period. No temporal trend was observed in the energy value of sandeel. The dependence on sandeel along the eastern coasts of the UK has made the kittiwake vulnerable to population fluxes of this species, related to changes in climate and fishing pressure (Arnott & Ruxton 2002; Frederiksen et al. 2004). During the breeding season, kittiwakes compete for similar sized fish with other seabirds such as auks and terns, however, as razorbills and guillemots can only transport one fish per feeding trip, kittiwakes can extend their search for food for longer periods, on average 2 hours, or 60-90 km from the colony (Coulson 2011).

In times of food scarcity, however, less profitable food is consumed. For example, pipefish were described as part of kittiwake diet during periods sandeel was less abundant/scarce/available (Harris et al. 2007; Kloppmann et al. 2007; Turner 2010; Wanless et al. 2018). Besides having a very low nutritional value, observations of kittiwake chicks choking on these bony fishes have been documented (Harris et al. 2007), while adult birds often regurgitate pipefish without digestion (Kloppmann et al. 2007). In northern Norway, in years of capelin scarcity, this dominant fish species was replaced by herring by kittiwakes. However, as herring was more difficult to catch, breeding success declined even though herring is considered an energy-rich fish (Barrett 2007).

On Helgoland, an island 40 nm off the German coast, where kittiwakes have bred since the 1950s, the diet of kittiwake chicks was studied during the breeding season. In an experimental study, Voss et al. (1987) estimated that one kittiwake chick consumes <5 kg of fish before fledging. In contrast to the eastern UK coast, diet in the southern North Sea consisted mainly of young gadoids and clupeids, but sandeels were of less importance (Vauk-Hentzelt & Bachmann 1983; Prüter 1986; Maul 1994; Markones et al. 2009). Although gadoid fish in surface-feeding seabirds is generally considered to originate from discards, Markones et al. (2009) indicate that the young whiting found (average length 9 cm), may be caught directly from the water's surface, as vertical migration of young whiting has been described in the southern North Sea. Gadoids found in 113 chicks between 1980-82 had a size range of 6-32 cm, the larger fish being considered discards. Clupeids ranged from 6-17 cm (Vauk-Hentzelt & Bachmann 1983). Low numbers of polychaete worms were present in all studies, however notably in the unusually warm summer of 2006, whiting was absent in stomach contents and the diet switched towards polychaetes (Markones et al. 2009). With the exception of that year, kittiwake diet has remained stable since the 1980s, with gadoid fish being the dominant species (Markones et al. 2009).

3.7.2 Diet outside the breeding season

During the winter period, diet studies are more difficult to conduct, due to the low accessibility of seabirds outside their breeding colony. In the Netherlands where data are scarce, two sources of information are available: the diet of dead birds collected during 'Beached Bird Surveys', and data from (discard) studies on ships.

Beached Bird Surveys have been conducted since the late 1970s (although earlier data exist), and traditionally focussed on oil in seabird feathers as an indicator for oil pollution at sea (Camphuysen 2022). While chronic oil pollution is almost absent recently (Camphuysen 2024), Beached Bird Surveys have proven their relevance as an indicator for other threats to the marine environment and seabirds generally, including plastic and chemical pollution (Kühn et al. 2024; Camphuysen et al. 2010) and diseases (Caliendo et al. 2024). Kittiwakes are commonly found during Dutch Beached Bird Surveys with 0.2 birds/km for the period 1977-2023 (Camphuysen 2024). However, kittiwakes tend to be scavenged quickly and, once found on beaches, often no stomachs remain. After a ship lost 350 containers during a storm in 2019, plastic contents in seabird stomachs were evaluated (Van Franeker & Kühn 2020). During that study, four intact non-adult kittiwakes were collected during Beached Bird Surveys, three of which were found on Ameland and one was collected in Zeeland. All birds were emaciated, but two birds from Ameland contained some food remains. One bird contained fish bones but these could not be identified; the other bird had ingested one whiting, a pipefish and four gobies (*Gobiidae*; S. Kühn unpublished data). Diet data obtained from beached birds is often biased towards hard prey items that are slowly digested and may overestimate this component in contrast to softer prey items that are quickly digested (Barrett et al. 2007). In emaciated birds there is also the risk of a non-representative diet spectrum, as starving birds may switch to prey that can be caught without exerting much energy (Markones & Guse 2009). Nevertheless, given the scarcity of data, even this small sample size contributes to the knowledge of diet composition of 'Dutch' kittiwakes. At a wider scale, diet studies conducted during winter on Helgoland (partly on hunted birds and partly on beached birds) show similar results: kittiwakes hunted in winters between 1968 and 1972, contained mainly sand gobies followed by sprat (Vauk & Jokele 1975). Remarkably, even this early reference noted the presence of plastic items in the diet of kittiwakes. Prüter (1986) analysed the stomach contents of 79 kittiwakes, hunted in the winter months between 1983-85. The majority of fish consisted of sprat and herring, followed by gadoid fish (mostly whiting) and to a lesser extent sandeel. A more recent study reports the diet of beached kittiwakes in winter 2006/07. Of 23 emaciated kittiwakes, Markones & Guse (2009) found prey remains in 13 birds. Hard prey remains consisted of sprat, gobies, three-spined sticklebacks, cod-like fish (*Gadiidae*) and sandeels. They also found invertebrate remains of polychaetes, shrimp and insects.

Other studies on kittiwake diet in Dutch waters rely on studies conducted on ships. Kittiwakes are commonly observed behind fishing vessels, targeting discards (undersized or non-target fish) and offal (fish waste) thrown overboard (Camphuysen 1994). During a seabird survey off Egmond aan Zee in January 2012, Leopold et al. (2011) observed more than 100 kittiwakes following the survey vessel foraging on what appeared to be herring. To study the dependence of seabirds on fishing activities, seabirds were observed around fishing (research) vessels and the fate of fish of known species and length was observed during discard experiments. In the southern North Sea, the reliance on discards and offal seems to be stronger during the winter months. In the UK, the consumption of discards during the breeding season was associated with the absence of sandeel, indicating that discards may be a less favourable food source (Harris & Wanless 1997). Due to their smaller size, they cannot compete with larger gull species (Larus, spp.), northern fulmars or gannets, but their small size and manoeuvrability allows them to catch fish close to the vessel. During discard experiments Camphuysen (1994) showed a preference for smaller roundfish above flatfish and benthic invertebrates, as roundfish have a high energy content and are easier to swallow. Kleptoparasitic behaviour has also been observed, where kittiwakes (and other species) steal caught discards or offal from other kittiwakes (Camphuysen 1994; Leopold et al. 2011). Consequences of the discard ban in North Sea waters were discussed by Leopold (2016) and it was expected that a consequent implementation of the discard ban could have given rise to decreased food resources and increased competition with large gulls.

3.7.3 Selection in size and/or quality

Kittiwakes mainly catch small fish. During the breeding season they usually fish up to 10 cm are caught (Coulson 2011). Gadoids found in 113 chicks between 1980-82 at Helgoland had a size range of 6-32 cm, the larger fish being considered discards. Clupeids ranged from 6-17 cm (Vauk-Hentzelt & Bachmann 1983).

During discard experiments Camphuysen (1994) showed a preference for smaller roundfish of median size ~14 cm and max. size 27 cm. These fish have a higher energy content compared to flatfish and benthic invertebrates. Similar fish sizes were reported in kittiwake stomachs by Maul (1994) during the breeding season, but see Tasker et al. (1999) who report fish size <36 cm.

Photo 3-23 *Kittiwakes beach regularly on Dutch coasts. However, most of the times not more than the wings with the conspicuous black wing tips remain, making it difficult to collect stomach contents in sufficient numbers. Photo: S. Kühn.*

3.8 Sandwich tern

The Sandwich tern is a medium-sized migratory seabird, primarily feeding on small pelagic fish (BirdLife International 2024; van Bemmelen et al. 2022; Photo 3-24). It is found to breed along the Dutch coast, particularly in the Wadden Sea and the Delta region, with an estimated 10,650 breeding pairs recorded in 2023 (BirdLife International 2024; SOVON 2024b). In the Netherlands, they are predominantly found in their breeding colonies between late March and August (SOVON, 2024b). Prior to migrating to the wintering areas along the coast of western Africa (Tree 2011), Sandwich terns disperse around their Dutch breeding colonies as well as to neighbouring countries (Fijn et al. 2014). In 2019, the Sandwich tern was classified as Least Concern by the IUCN Red List due to its extensive range and large population size (BirdLife International 2019b). However, within the Netherlands, its conservation status is listed as Quite Unfavourable due to the low number of breeding pairs in the Netherlands compared to the favourable reference value (*Gunstige Referentiewaarde*), insufficient habitat quality to sustain the favourable reference value, and a predicted decline in population numbers as consequence of the avian influenza outbreak in 2022 (SOVON, 2024b).

Since 1980, the Dutch breeding population has experienced a significant increase. However, the population has experienced a significant decline over the short term (2011–2023;(SOVON 2024b).

Photo 3-24 *Ringed Sandwich tern on Texel. Photo H. Verdaat*

3.8.1 Diet during the breeding season

In the following section, the results of the literature review on the diet of adult Sandwich terns are presented, followed by an overview of chick diet. Adult diet studies typically rely on faecal analysis, as described in more detail in Courtens et al. (2017), allowing more precise identification of prey species. In contrast, chick diet is mostly assessed through visual observations of prey items delivered by parents, where the distinction between similar species can be difficult or impossible in the field.

3.8.1.1 Adult diet

Faecal sample analyses consistently show that adult diet predominantly consists of clupeids and *Ammodytidae*. The latter typically includes lesser sandeel, Raitt's sandeel, and great sandeel (e.g., Brenninkmeijer et al. 2002; Courtens et al. 2017; Hoffmann 2000; van der Beek 2017). For instance, van Bemmelen et al. (2022) reported that clupeids and *Ammodytidae* combined accounted for 90±8% of the diet of adult Sandwich terns in the Dutch Delta colonies between 2013 and 2021. However, they reported a significant year-to-year variation in the clupeid-to-*Ammodytidae* ratio as well as differences in species ratios between the different Delta colonies (van Bemmelen et al. 2022).

In addition to these two dominant prey groups, varying amounts of other prey species have been reported to supplement adult diet. Where more detailed (species-level) identification was possible, these additional prey items included ragworms (*Nereididae*), sand goby, European common squid (*Alloteuthis subulata*), three-spined stickleback, gadids, and invertebrates such as brown shrimp (*Crangon crangon*) (Brabant 2004; Brenninkmeijer et al. 2002; Courtens et al. 2017; Hoffmann 2000; Stienen 2006; van Bemmelen et al. 2022; van der Beek 2017). In the Dutch Delta colonies, *Nereididae*- a family of polychaete worms -were the most common additional food source for adult Sandwich terns (van Bemmelen et al., 2022). Their importance as a supplementary resource, however, varied greatly. On average, *Nereididae* accounted for 9±8% of adult Sandwich tern diet in the Delta area (van Bemmelen et al. 2022).

In earlier studies on Griend in the Dutch Wadden Sea, *Ammodytidae* overwhelmingly dominated adult diets in both 1996 (91.2%) and 1997 (84.4%), followed by comparatively low amounts of clupeids (3.6–5.8%). On Griend, the proportion of *Nereididae* (2.4–6.9%) in the adult diet was comparable to that of clupeids (Hoffmann, 2000). In Texel's Utopia colony, Engels (2015) reported a more balanced prey composition between the two main prey groups for the breeding period between 19 May and 8 June 2015, with 52% *Ammodytidae* and 45% clupeids found in adult faeces samples. The remaining proportion consisted of flatfish and gobies.

Most studies focus on adult diet throughout the entire breeding and chick-rearing period. However, adult diet composition has been described to vary considerably throughout the breeding period (Engels 2015; van der Beek 2017). Engels (2015) monitored adult diet composition in the Utopia colony on Texel from the incubation period (prior to 19 May 2015) through the first week of June 2015 (Figure 3-25). Before 19 May, *Ammodytidae* dominated adult diet (72%), followed by a relatively high proportion of other prey species (21%) which consisted mainly of lesser pipefish. At this point, clupeids made up only 7% of the adult diet. In the following week (19–26 May), when some chicks had hatched but many eggs were still being incubated, the clupeid proportion in adult diet increased to 23%, *Ammodytidae* remained relatively stable at 75%, and the proportion of other prey dropped to 2%. More diverse species were found compared to the week before. This included *Nereididae*, lesser pipefish, sand goby, three-spined stickleback, and *Sepiola* species. By the third week (26 May–1 June), when nests contained both young and more developed chicks, diet composition shifted drastically. Clupeids now made up 75% of adult diet, while the proportion of *Ammodytidae* dropped to 23%, coinciding with an *Ammodytidae*-dominated chick diet high proportion of *Ammodytidae* in chick diet. Other prey in adult diet included sand gobies, pipefish and *Sepiola* spp., as well as flatfish, and anchovies. In the final week of the study (1–9 June 2015), when chicks became more mobile, the adults' diet reverted to being *Ammodytidae*-dominated (69%), with clupeids comprising 28% of the diet. Other species in adult diet were lesser pipefish, sand gobies, anchovy, and plaice.

In 2017, van der Beek (2017) documented a similar seasonal shift at the colonies Wagejot and Utopia on Texel. During the courtship period (11–28 May 2017), courtship prey items delivered to the colony were recorded and their group ratio analysed. Van der Beek (2017) observed an *Ammodytidae*-dominated courtship prey composition (70.4%), followed by 23.5% clupeids, and 6.1% other species. When most of the nests contained one or two eggs (13–20 May 2017), adult diet consisted of 73.7% *Ammodytidae*, 10.2% clupeids, and 16.1% other prey, including *Nereididae*, sand goby, and European common squid. This indicates a slight difference between courtship items delivered and prey items actually consumed (van der Beek 2017). After hatching began (20–28 May), the *Ammodytidae* proportion in adult diets declined to 58.9%, clupeids increased to 33.5%, and additional prey items, including flatfish, whiting, and three-spined stickleback, accounted for 7.6% of the diet. One week later (28 May–4 June), when small chicks were present in the nests but not yet fledged, clupeids became the dominant prey group (54.4%) and the proportion of *Ammodytidae* dropped to 38.3%, coinciding with an *Ammodytidae*-dominated diet of young chicks (van der Meer, 2018). Other species accounted for the remaining 10.3%, and contained e.g., *Nereididae*, flatfish, three-spined stickleback, and European common squid. Although the temporal change in prey composition was less pronounced in 2017 compared to findings by Engels (2015) two years prior, the general pattern, i.e., a decline in the dominance of *Ammodytidae* and a concurrent increase in clupeids with progressing chick age, was consistent.

Comparable to the low *Ammodytidae* proportions recorded by Engels (2015) and van der Beek (2017) in late May, van Bemmelen et al. (2022) reported adult consumption of 10–20% *Ammodytidae* and on average 75±8% clupeids for the Dutch Delta colonies during incubation (late May and early June 2013–2021). They further reported average *Nereididae* proportions of 9±8% during the incubation phase (van Bemmelen et al. 2022). Earlier results from Hoffmann (2000) detected similar *Nereididae* proportions in the diet samples taken from adult birds on Griend in the Dutch Wadden Sea in 1996 (2.4%) and 1997 (6.9%). Courtens et al. (2017) also reported comparable proportions of *Nereididae* in adult diet across four Dutch colonies and one Belgian colony monitored from 2009–2015, and in 2007 and 2008, respectively. In these five colonies, *Nereididae* accounted for, on average, 10.1±14.4% of adult Sandwich tern diet (Courtens et al. 2017). While *Nereididae* were consistently detected in adult diet across all colonies, only in 2010 they accounted for a substantial part of the adult diet in two of the Dutch Delta area colonies (57.0% at Scheelhoek and 23.8% at Markenje), leading the authors to suggest that *Nereididae* may be a common prey item during the incubation period in that specific region (Courtens et al. 2017). These results suggest that *Nereididae* have been part of adult Sandwich tern diet for at least three decades in Dutch colonies. Although usually consumed in lower proportions compared to the dominant groups of clupeids and *Ammodytidae*, *Nereididae* can play a locally significant role during incubation.

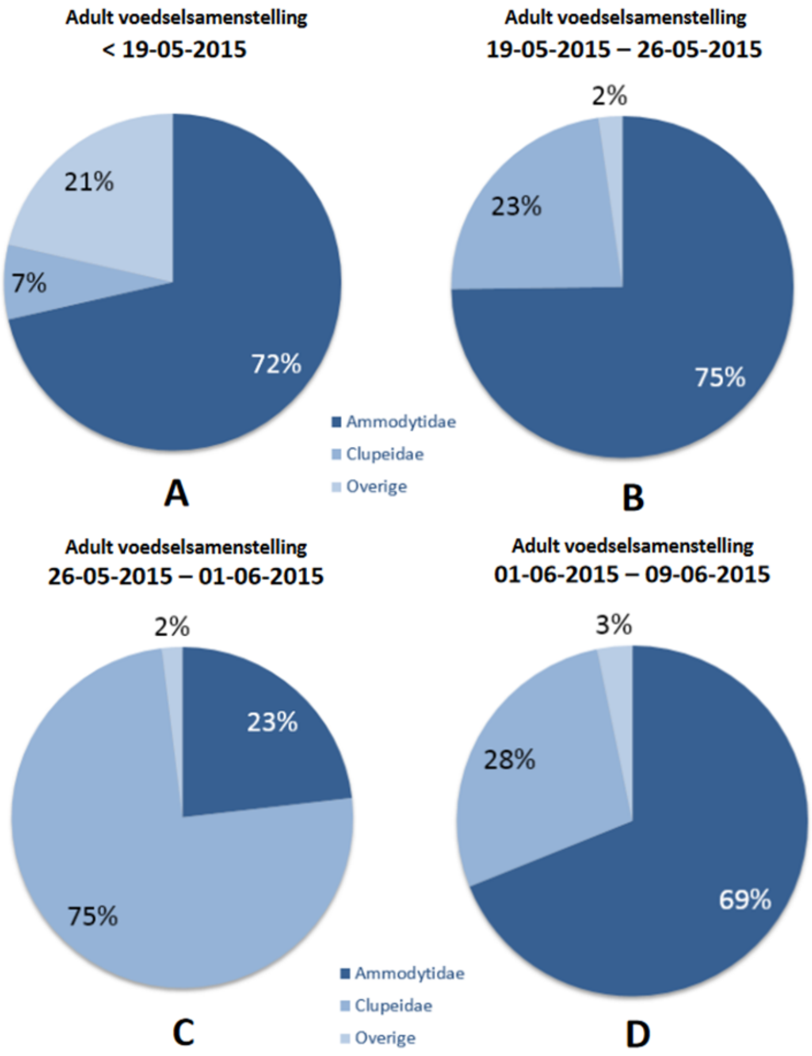


Figure 3-25 *Adult Sandwich tern diet composition at the Utopia colony on Texel, NL, from prior May 19 until June 9 2015 by Engels (2015). Diet items were categorised as Ammodytidae (dark blue), clupeids (Clupeidae; medium blue), and Other (Overige; light blue).*

3.8.1.2 Chick diet

Chick diet is generally assessed through visual observations of prey items delivered to the nest by the parents. For over 30 years, Sandwich tern chick diet has been reported to consist predominantly of clupeids and *Ammodytidae*. Between 1992 and 2021, multiple studies conducted in the different colonies along the Dutch coast, ranging from the Dutch Delta area in the south of the Netherlands to the Dutch Wadden Sea islands of Griend, Texel, and Ameland, analysed Sandwich tern chick diet composition. Averaging across all study years and locations, about 97% of the chick diet consisted of clupeids and *Ammodytidae*. However, variation in prey group ratios is described in most studies, either over the course of the chick-rearing period or between years and/or between colonies (de Graaf 2016; Engels 2015; Fijn et al. 2017b, 2024; Stienen 2006; Stienen & Brenninkmeijer 1994; van Bemmelen et al. 2022; van der Meer 2018).

Prey other than clupeids or *Ammodytidae* are provisioned to chicks in relatively low quantities. The proportion of non-clupeid and non-*Ammodytidae* prey ranged from as little as 0.08% on the island of Texel in June 2017 (van der Beek, 2017) to an average of 7.2% between May and the end of July 2017 at the Scheelhoek colony in the Dutch Delta area (Fijn et al., 2024). In studies in which more detailed taxonomic identification was conducted, the category of other prey items was found to primarily consist of various fish species, including cod, European eelpout (Stienen, 2006; Stienen & Brenninkmeijer, 1994), sand goby or other species within the family *Gobiidae*, as well as some flatfish species (Engels 2015; Stienen 2006; Stienen & Brenninkmeijer 1994; van der Meer 2018).

The diet composition of Sandwich tern chicks varies throughout the chick-rearing period and is influenced by both temporal and spatial factors such as year and colony location. In the early days post-hatching, diet is typically dominated by *Ammodytidae*. For instance, at the Utopia colony on Texel, during their first week after hatching (26 May to 1 June 2015) chicks received 83% *Ammodytidae* and 16% clupeids (Engels, 2015). However, in the second week post-hatching (1–9 June), this composition shifted significantly: *Ammodytidae* dropped to 51%, while the proportion of clupeids provisioned increased to 47%. Other prey species were only provisioned in negligible quantities (1-2% of the diet) in both weeks (Engels, 2015).

Building on data from Engels (2015) and van der Beek (2017), van der Meer (2018) identified a consistent dietary shift for Sandwich tern chicks around the second week of June (approx. 9 June). Early in the chick-rearing phase, *Ammodytidae* were the dominant prey species. However, clupeids became the more prevalent prey in subsequent weeks after 9 June. This shift aligns with findings by Stienen & Brenninkmeijer (2002), who showed that 14 days post-hatching, *Ammodytidae* were insufficient in energetic value to support the chicks' growth, even at a minimal level. Given that *Ammodytidae* have a lower energy content than clupeids (Hoffmann 2000), a transition to a clupeid-dominated diet appears to be beneficial with increasing chick age.

However, this temporal shift may not be universal. Contrary to the findings of Engels 2015), de Graaf (2016) found chick diet to be relatively balanced between 47.5% herring and 46.5% lesser sandeel on Texel in late May (25–30 May 2016). On Griend in 1992, Stienen & Brenninkmeijer (1994) observed stable daily provisioning rates of both *Ammodytidae* and clupeids throughout the entire chick-rearing period. Interestingly, in 1993, two colonies on Griend showed differing patterns: in one colony, provisioning shifted towards increased clupeid-proportion with increasing chick age, while provisioning did not exhibit a clear trend or shift towards one or another prey species at the second colony (Stienen & Brenninkmeijer 1994). In contrast to the clupeid-dominant diet approximately two weeks post-hatching described in Stienen & Brenninkmeijer (2002) , van Bemmelen et al. (2022) reported a strong proportional increase of *Ammodytidae* from around 13% in late May to 97% in the end of June. These findings suggest inter-annual variation in chick diet composition, as well as local or regional differences in food availability.

De Graaf (2016) compared chick diet between two colony locations on the islands Ameland and Texel in the Dutch Wadden Sea in 2016. Their findings showed that chicks on Texel received a relatively balanced diet of *Ammodytidae* and clupeids (46.5% and 47.5%, respectively), while chicks from Ameland received a clupeid-dominated diet comprising 72% herring and 23% lesser sandeel. This difference in diet composition between locations was found to be statistically significant (p <0.001). However, it is important to consider the timing of the dietary observations: on Ameland, data collection took place during the first week of June 2016, while observations were conducted both in the last week of May (May 30 –June 6, 2016) and in the third week of June (15–21 June) on Texel. As diet composition can vary throughout the chick rearing period (e.g., van der Meer, 2018), this should be accounted for in future studies.

In addition to the reported differences in chick diet between colonies (de Graaf, 2016), variability in local food availability is suggested to affect diet composition and could further explain the observed inter-colonial differences described earlier. Van der Meer (2018), for instance, reported relatively high proportions of flatfish (approx. 5%) in the diet of chicks on Texel. Although other studies have also documented prey items other than clupeids and *Ammodytidae* being provisioned to chicks (e.g., Engels 2015; Fijn et al. 2024; Stienen & Brenninkmeijer 1994; van Bemmelen et al. 2022; van der Beek 2017), none reported similarly high proportions for any single alternative prey type. This observation of relatively high flatfish ratio was attributed to the intense shrimp fisheries in the area, which produce substantial bycatch of small-sized flatfish that are subsequently discarded. These discards may represent an easily accessible resource for provisioning Sandwich terns (van der Beek 2017), highlighting the influence of local prey type availability on chick diet.

3.8.2 Diet outside the breeding season

The overall focus of diet research in the Netherlands lies on the breeding season (May–June/July) when birds are present in the Dutch colonies, as information on diet during migration and in their wintering areas is scare to completely lacking.

3.8.3 Selection in size and/or quality

Several studies from different Dutch colonies consistently report that provisioned prey length increases as chicks grow older (Engels 2015; Stienen & Brenninkmeijer 1994, 2002; van Bemmelen et al. 2022; van der Meer 2018). This trend likely reflects the increasing energy demands of growing chicks (van der Meer, 2018) which requires an increased biomass provisioned to them (Stienen & Brenninkmeijer 1994) to meet their energetic needs. For instance, van Bemmelen et al. (2022) found that the mean length of clupeids increased from 4.9±1.4 cm one week post-hatching to 12.4±1.9 cm in week five (near fledging). Similarly, average *Ammodytidae* lengths increased from 9.2±1.4 cm to 13.9±3.5 cm over the same period (van Bemmelen et al. 2022). While prey size patterns and mean lengths are reported to vary by year (Stienen & Brenninkmeijer 1994) and colony location (Engels 2015; van Bemmelen et al. 2022), *Ammodytidae* were generally provisioned at longer lengths than clupeids (Brabant 2004; Engels 2015; Stienen 2006; Stienen & Brenninkmeijer 1994; van Bemmelen et al. 2022). Overall, proportions of age class composition in adult and chick diet varied, with a strong selection for larger age classes reported for provisioning (van Bemmelen et al. 2022).

These dietary patterns may not only reflect prey selection by adult terns for provisioning but also shifts in local prey availability. For example, data from the Wagejot colony on Texel indicate that the average length of *Ammodytidae* increased from April to June in both 2021 and 2022 (Leopold, n.d., unpublished data). This suggests that seasonal growth in local fish populations may contribute to observed trends in chick diet, highlighting the need to consider both biological demand and food availability when interpreting prey provisioning dynamics.

3.8.4 Other variables affecting diet choice

Foraging trip duration can vary depending on prey species and length of the prey item brought back to the nest (Hoffmann 2000; Stienen & Brenninkmeijer 2002). Overall, foraging trips tend to increase in line with increasing chick age (Hoffmann 2000; Stienen & Brenninkmeije, 2002) which may be linked to the reported increase in prey size provisioned to chicks as they grow older (e.g., Hoffmann 2000; Stienen & Brenninkmeijer 1994, 2002; van Bemmelen et al. 2022; van der Meer 2018).

Sandwich terns exhibit diet shifts and changes in provisioning rates depending on different environmental factors such as wind speed, tidal stage, water transparency, time of day, and prey accessibility related to habitat features.

On Griend (1992–1998), provisioning rates remained relatively stable for wind speeds between 3 m/s and 14 m/s, but were reduced at both higher and lower wind speeds (Stienen 2006). Sandeel deliveries to the colony increased with wind speed up to 14 m/s, but strongly decreased at wind speeds between 17–20 m/s.

In contrast, clupeid deliveries declined steadily with increasing wind speed, from about 65% clupeids provisioned at low wind speeds to under 50% for wind speeds at 16 m/s (Stienen 2006). With conditions of high wind speeds, young chicks (under six days old) were increasingly fed less nutritious prey such as gobies and brown shrimp (Stienen 2006). On Ameland, prey size also changed with wind: both clupeids and *Ammodytidae* increased in size up to a wind speed of 5 m/s; this pattern was not found on the island of Texel (de Graaf 2016).

Tidal stage further influenced prey composition and prey size for Sandwich tern chicks. On Griend, *Ammodytidae* provision rates peaked around high tide, while clupeid provision rates peaked some hours later (Stienen 2006). Provisioned *Ammodytidae* tended to be longest around high tide, while clupeids were found to be slightly but significantly longer during incoming tide (Stienen 2006). On Ameland in 2016, similar patterns in provisioned *Ammodytidae* sizes were found as on Griend, with largest *Ammodytidae* provisioned directly after high tide (de Graaf 2016). On Texel, however, these patterns were found to differ. Here, the largest clupeids were provisioned directly after high tide and the smallest about four hours after high tide (de Graaf 2016). *Ammodytidae* were found to be largest before high tide, compared to at high tide on Ameland (de Graaf 2016).

Water transparency and turbidity were also found to play an important role in prey capture probability and likely consequently diet composition for Sandwich tern chicks. Off southern Texel in June/July in 2007, prey capture probability was found to be highest at a Secchi transparency between 1.5 m and 2.0 m, with an optimum at 1.74 m (Baptist & Leopold 2010). Very clear water reduced capture success, possibly because prey fish species remained in deeper waters or had better chances of evading foraging Sandwich terns. Higher concentrations of total suspended matter (>15 mg/L) as a measure of turbidity also lowered prey capture probability for Sandwich terns (Baptist & Leopold 2010).

Diurnal patterns also shaped the composition of prey delivered to Sandwich tern chicks. On Griend, *Ammodytidae* delivery peaked around midday, while clupeids were mostly delivered early in the morning and late in the evening, likely reflecting diel vertical migration patterns of this group (Stienen 2006).

Lastly, prey accessibility and therefore also diet composition for chicks can be influenced by habitat characteristics such as water depth, water temperature, and sediment. GPS-tracking of Sandwich terns from the Haringvliet colony in the Dutch Delta area showed that the likelihood of adult Sandwich terns switching from commuting to foraging increased over shallower, cooler waters, and coarser sediments (van Bemmelen et al. 2022). These habitat features are likely tied to prey availability. In particular, sediment grain size is suggested to be linked to *Ammodytidae* availability. Water depth is further likely to affect both prey distribution and detectability (van Bemmelen et al. 2022).

Selection of prey size and species appear to play a role regarding the risk of kleptoparasitism by for instance Black-headed gulls (*Chroicocephalus ridibundus*) that the provisioning Sandwich terns experience. Larger fish, especially herring, appear to be more likely to be stolen than smaller items or sandeel (Stienen & Brenninkmeijer 2002). Despite the higher energetic value and lower theft risk of small herring, no clear dietary shift towards them was observed on Griend from 1992–1998, suggesting that the (local) availability of small herring may have been insufficient to compensate for the losses through kleptoparasitism (Stienen & Brenninkmeijer 2002). While breeding alongside Black-headed gulls may offer some colony protection for Sandwich terns by deterring predators (Veen 1977), their role as food competitors may increase energetic costs for Sandwich tern parents who tend to increase foraging efforts to compensate for the experienced losses in food (Stienen & Brenninkmeijer 2002).

3.8.5 New insights into the diet of Dutch Sandwich terns from unpublished data

A total of 244 stomachs of individuals that died of avian influenza were examined. Prey remains were found in stomachs of 27 (11.06%) individuals, of which 15 were females, 11 males and one sex undetermined. The age of individuals with prey remains varied between 5 and 28 years with an average of ten years. Of the 27 birds with prey remains, ten were from the Delta area and 17 from the Wadden Sea. The number of birds that still had prey remains was higher at the beginning of June and decreased around mid-June with one exception on 19 June 2022 (Figure 3-26).

Seven different prey species were found, belonging to the prey guilds sandeels, clupeids, gadoids, gobies, and estuarine round fish; listed in declining frequency of occurrence (FO) (Table 3-11). The average number of prey species per individual was 1.33 (range 1–3). Prey size ranged between 4.7cm and 23.4cm (Figure 3-27). Prey species composition in the Delta and the Wadden Sea was rather similar with herring, sprat, great sandeel, sandeel spp. And whiting being found in individuals from both areas. However, remains of smelt were encountered in one individual and sand goby was found in another individual from the Wadden Sea area and in no individuals from the Delta. Most of the birds (n = 19) were in a bad condition (score between 0 and 3). Their diet did not differ significantly from the diet of the birds in moderate (score 4 – 6) or good condition (score 7 – 9). Given that two individuals were in good condition (score 8) but had prey remains of only two prey items each, it suggests that they were unable to forage sufficiently prior to death, whereas birds in a worse condition were likely unable to find enough prey for a longer period of time.

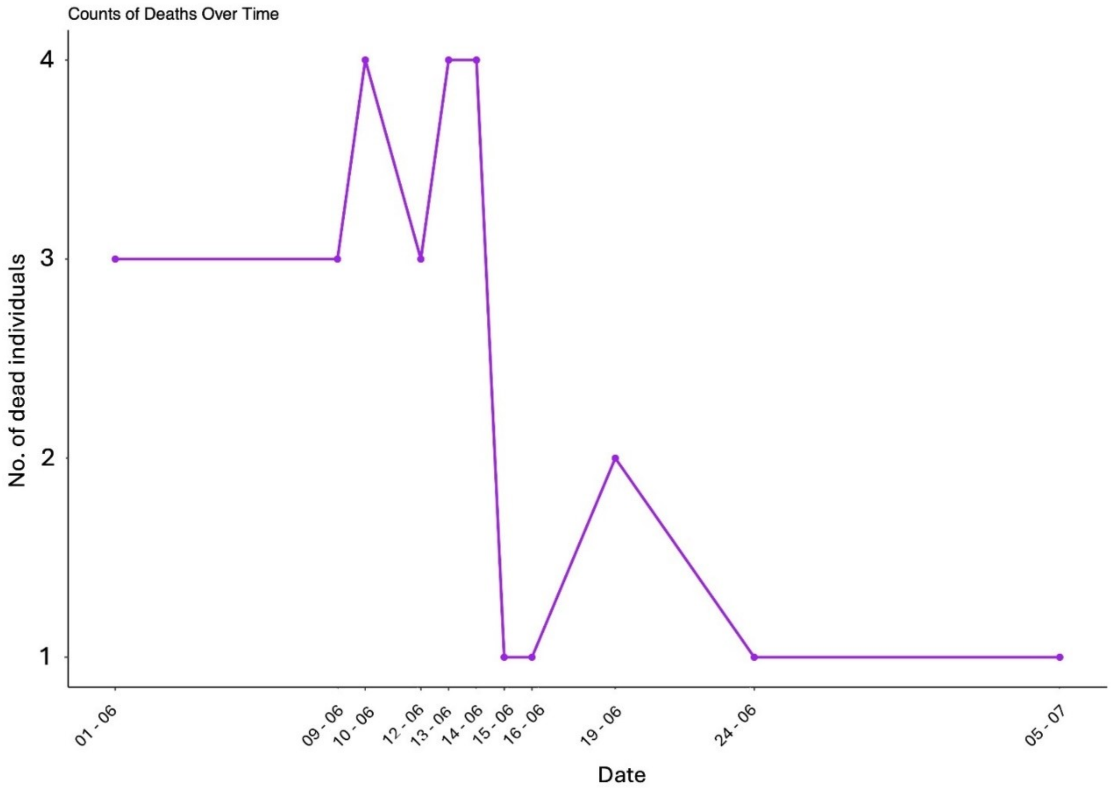


Figure 3-26 *Number of individuals that died of avian influenza with prey remains in their stomachs, recorded between 1 June and 5 July 2022.*

***Table 3-11**. Number of prey species (n) found in stomachs of sandwich terns, their frequency of occurrence (FO), as well as minimum, maximum, and mean length in centimetres.*

Species		**n**	**FO**	**Mean length (cm)**	**Min length (cm)**	**Max length (cm)**
Herring	*Clupea harengus*	5	4	7.19	4.71	8.89
Sprat	*Sprattus sprattus*	6	6	10.1	8.35	13.87
Smelt	*Osmerus eperlanus*	1	1	6.9	-	-
Whiting	*Merlangius merlangus*	6	6	11	7.38	12.41
Sand goby	*Pomatoschistus minutus*	1	1	9.07	-	-
Great sandeel	*Hyperoplus lanceolatus*	3	3	20.02	14.48	24.67
Sandeel spp.	*Ammodytes spp.*	10	9	12.17	10.95	17.37
Other		5	4	-		
TOTAL		**37**	**27**			

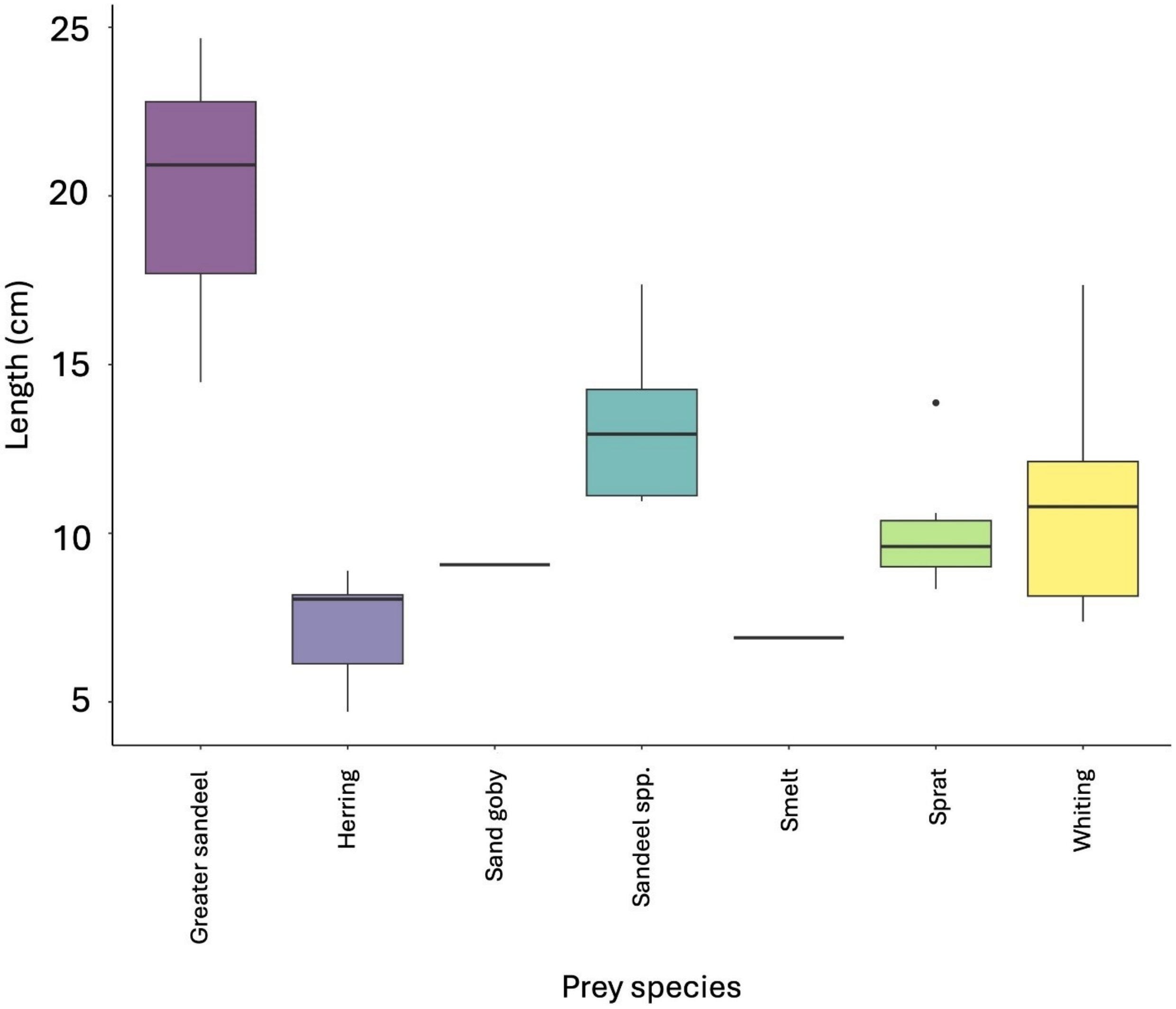


Figure 3-27 *Boxplot showing the median estimated length of prey species (cm) (black line). Solid lines without a box are single individuals.*

3.9 Common tern

The common tern is a medium-sized migratory seabird, characterised by a generalist feeding strategy primarily focused on small marine and freshwater fish and aquatic invertebrates (Becker & Ludwigs 2004; BirdLife International 2018). In the Netherlands, the species breeds mainly in coastal and inland colonies, with an estimated 17,000–19,000 breeding pairs recorded in 2023 (SOVON 2023). Breeding sites are concentrated along the Wadden Sea, IJsselmeer, and Delta regions, as well as further inland (SOVON 2023). After the breeding season, common terns migrate to wintering grounds along the west coast of Africa to South Africa (summarised in Stienen & Brenninkmeijer 1992). They are predominantly present in the Netherlands from April to September during the breeding season (SOVON 2023).

Globally, the common tern is classified as Least Concern on the IUCN Red List due to its broad distribution and relatively large population (BirdLife International 2019a). Nationally, it is listed as Quite Unfavourable in the Netherlands with a declining breeding bird trend over the last 35 years (SOVON 2023, 2024b). From 1990-2020, the breeding population showed a decline, while short-term data from 2009-2020 indicate a stronger decline compared to the long-term trend (SOVON 2024c).

Foraging range describes the distance from breeding colony to foraging area, which has been reported with maximum ranges up to 10 km, with a mean of 6.3±2.4 km in the German Wadden Sea for the common tern

(Becker et al. 1993; Becker & Ludwigs 2004; Eglington & Perrow 2014). Common terns are reported to feed in different habitats, from freshwater lakes and ponds to brackish and marine areas in the Wadden Sea (e.g., Becker et al. 1997; Eglington & Perrow 2014; Maathuis et al. 2025; Manche et al. 2022b).

3.9.1 Diet during the breeding season

The following sections first address adult diet, followed by the diet of common tern chicks. The results of the literature review are presented first for Dutch colonies, followed by German and other colonies.

3.9.1.1 Adult diet

Little is known about diet of adult common terns in Dutch colonies, particularly in recent years. However, Becker & Ludwigs (2004) provided a comprehensive overview of the species' ecology across Europe, noting that common terns can switch between marine and freshwater foraging areas and predominantly feed on small fish <15 cm in length. Their diet can also include crustaceans and insects. Becker & Ludwigs (2004) emphasised that adult diet can vary considerably between locations. In general, over 30 marine fish species are reported to comprise the marine diet of common terns. This includes clupeids, Ammodytidae, sticklebacks, whiting, cod, and flatfish (*Pleuronectiformes*). Additionally, European eel (*Anguilla anguilla*), *Gobiidae*, fish larvae, but also shrimp such as *Crangon crangon*, other crustaceans, polychaete worms, and fish from brackish and freshwater habitats (e.g., perch, pike-perch, ruffe) can be found in the diet of common terns (Becker & Ludwigs 2004).

This dietary variability, combined with the species' generalist foraging behaviour and widespread breeding distribution in the Netherlands, from Zeeland to colonies in Eemshaven and the Wadden Sea, both inland and coastal (SOVON 2023, 2024a), makes it challenging to characterise a representative or consistent adult diet for the Dutch breeding population as a whole. Due to the limited availability of studies on common tern colonies in the Netherlands, most of the available dietary information is derived from research conducted at German colonies, particularly those in and around Jade Bay, which have been studied extensively since the 1980s.

In June 1991, a limited number of regurgitated pellets (n = 40) were collected over the course of two weeks in a colony located at the freshwater site Wolderwijde in Zeewolde, NL (Noordhuis et al. 1993). Thirty-nine of these pellets contained fish remains, making it the most common prey item. The fish species identified to species-level were ruffe, which was present in about 75% of all pellets, perch and smelt which both were present in 25% of the pellets. Additionally, half of the regurgitated pellets contained *Cyprinidae*. The observed prey composition suggests that common terns had been foraging in the vicinity of fishing vessels, which likely made bottom-dwelling species such as ruffe accessible to them (Noordhuis et al. 1993). In early May 1993, Noordhuis et al. (1993) observed hundreds of terns performing repeated contact dips at the water surface, leading the authors to propose that the birds were feeding on mosquito larvae.

During the courtship period starting in early May, male common terns will start presenting prey to and feeding their partners and continue providing for them until egg-laying is complete (Nisbet 1973). During this period, observed on 21 May and 16/23 July 2009, males at the IJsselmeer colony De Kreupel were seen provisioning their female partners with adult *Ammodytidae* as well as larger freshwater species such as perch and pike-perch (van der Winden et al, 2009). It is, however, not clear how representative courtship prey is for general adult diet (Barrett et al. 2007).

Manche et al. (2022) analysed environmental DNA (eDNA) from common tern faeces collected on the island Stern at the Eems–Dollard estuary in 2020. Over 60% of the identified prey species in the adult diet were shrimp, followed by herring (>25%), with *Gobiidae* making up a minor proportion (<5%). However, the representativeness of these results is uncertain, as the analysis was based on only five samples. The results from De Kreupel and Stern suggest that birds breeding at freshwater colonies are not exclusively feeding on freshwater fish but can also use marine habitats for foraging.

In the Westerschelde estuary (Netherlands), visual observations in 2002 revealed a strong seasonal variation in adult diets (Brenninkmeijer et al. 2002). In May and June, diets were dominated by shrimp and fish larvae, together accounting for around half of all prey items, while clupeids only became prominent in July. Ammodytidae occurred mostly in May and June but were far less important than clupeids (by a factor of ten).

Studies on adult diets in common terns across German colonies offer valuable insights into diet composition, especially during courtship and early chick-rearing. Particularly detailed data are available from Minsener Oog in the Wadden Sea and the Banter See colony near Wilhelmshaven, Germany. Together, these studies reveal interannual and intercolonial differences in diet composition.

At the marine colony of Minsener Oog, Dänhardt et al. (2011) documented clear shifts in diet across three phases of the breeding season in 2007. During the first courtship and self-feeding period (3 May–13 June), adult terns consumed primarily clupeids (44%), and low-quality food items, namely pipefish (*Syngnathus* spec., 32%) and brown shrimp (*C. crangon*, 16%), while fish carried from the foraging area, likely intended for their partners, were of higher energetic quality. The prey brought from the foraging area was dominated by clupeids (49%) and followed by *Gadidae* (11%) and *Gobiidae* (9%). Note that prey provisioned and presented to the partners during courtship might not be representative of the general adult diet (Barrett et al. 2007). During early chick-rearing (14–27 June), foraging adults consumed more pipefish (57%) and shrimp (11%), and a relatively lower proportion of clupeids than in the weeks before (20%), indicating a shift to lower-energy prey. However, clupeids (50%) and *Gadidae* (17%) remained dominant among the prey carried away, suggesting preferential delivery of high-quality prey to chicks or mates. A second breeding attempt following flooding-induced chick loss (28 June–28 July) showed a further dietary shift: brown shrimp dominated the diet (65%), while the prey carried away consisted mainly of *Gadidae* (67%). This coincided with a whiting invasion in the Wadden Sea, highlighting how prey availability can rapidly reshape diet composition. Overall, the study on Minsener Oog indicated that adults often consumed lower-quality prey themselves while allocating higher-energy prey to provisioning, possibly due to limited availability of energy-rich fish.

At the freshwater-influenced Banter See colony at the Jade Bay (that is part of the Wadden Sea) in Germany, visual observations of courtship feeding from 1991 to 1994 revealed high interannual variability in diet (Wendeln 1997). Sticklebacks dominated the female diet in 1991 and 1993, while marine species such as clupeids and smelt varied in importance. Clupeids accounted for around 30% of the diet in 1991 but declined to <15% in other years; conversely, smelt increased from <15% in 1991 to up to 40% in later years. Flatfish (*Pleuronectiformes*) appeared in small but notable proportions (around 10%).

Another Banter See study observed 13 common tern pairs during courtship in 1992 (Wendeln et al. 1994). It showed individual variation in diet composition among females, with some receiving >50% sticklebacks and others relying more on marine species such as smelt and clupeids, suggesting different feeding strategies between pairs. Pairs with a higher stickleback diet had significantly higher feeding rates ($p < 0.05$). Notably, the diets of male and female partners were highly similar within pairs (based on seven pairs). The authors concluded that prey choice was not solely driven by prey availability but could also reflect individual or pair-level preferences.

Later observations from the same colony (Dänhardt et al. 2018) reinforced some earlier patterns but also highlighted longer-term trends. During courtship feeding (2006–2011, 2014–2015), smelt and clupeids together consistently comprised over 50% of prey, confirming their importance as high-energy resources during courtship. In 2007, 2008, and 2014, smelt was the dominant species, while other years showed a more balanced contribution of clupeids and smelt. Flatfish, pipefish (*Syngnathidae*), and shrimp appeared more frequently from 2008 to 2011, with shrimp contributing over 10% of the diet between 2008-2010 despite their lower energy content. In 2008, almost 10% of the adult diet consisted of fish larvae.

At the colony in Zeebrugge (Belgium), diet analysis based on food-containing stomachs of dead birds collected between 2004 and 2008 revealed that 72% contained clupeids (Vanaverbeke et al. 2011). *Gobiidae* were present in 45.3% of stomachs, and 30.7% contained polychaetes, indicating some foraging flexibility and inclusion of benthic prey.

3.9.1.2 Chick diet

Chick diet data is commonly obtained through direct observations, camera recordings or photographs of prey items delivered to chicks at the nest. In addition, prey remains in regurgitated pellets are often analysed, which is biased towards hard and easy to regurgitate prey parts. More recently, efforts have been made to analyse chick diet using eDNA analysis or DNA metabarcoding of chick faeces (Maathuis et al. 2025; Manche et al. 2022b).

As for adult common terns, the diet of common tern chicks has been studied at a few Dutch colonies in the Wadden Sea, in the IJsselmeer and Markermeer area, and in the Delta area. However, in the Dutch Wadden Sea area, there have been study gaps from the 1990s to the 2020s. For the Dutch freshwater colonies, data are even more scarce. This makes it difficult to compare chick diet between Dutch marine and freshwater sites. Fortunately, thanks to extensive monitoring in and around Jade Bay (that is part of the Wadden Sea) in Germany starting in the 1980s, data on chick diet from German North Sea colonies are available until the 2020s.

Information on chick diet in Dutch colonies comes from a limited number of studies, with data collected at both marine and freshwater sites. Becker & Ludwigs (2004) summarised that chick diet composition differs between areas in the Netherlands and typically consists of over 60% *Ammodytidae* and clupeids. As for Sandwich tern chicks, prey item size is reported to increase with chick age (Becker & Ludwigs 2004). In the beginning of their lives, predominantly *Ammodytidae* and small clupeids are fed, while with increasing age diet composition switches more towards larger clupeids (Becker & Ludwigs 2004). This reported dominance of clupeids in common tern chick diet has also been described on Griend in the Dutch Wadden Sea. Here, chicks received a diet consisting of about 53% herring in 1989 and 1990 (Stienen & van Tienen 1991). However, their diet was relatively high in low-quality prey such as shrimp and crabs (about 33%), as well as *Pleuronectiformes* (7%) and other prey items (7%). While the authors mention that chicks received more energy-rich prey with increasing age, no detailed diet composition was provided for different chick ages.

Visual observation at five colonies in the Dutch Wadden Sea further highlight the importance of clupeids in chick diet, accounting for mostly over 75% of the diet in 2021 (Manche et al. 2022a). In contrast, the importance of *Ammodytidae* suggested by Becker & Ludwigs (2004) could not be confirmed for these marine sites where *Ammodytidae* accounted for a maximum of 10% in the chick diet. This study found variation in diet composition between the different studied colonies in and around the Dutch Wadden Sea. Flatfish contribution was found to be highest on Griend, while the overall diet was most diverse at the inland site De Westereen where the freshwater species stickleback and roach contributed to identified prey items (Manche et al. 2022a). Differences between colonies are likely to reflect different foraging habitats. Tracking data from two birds from De Westereen showed that they used inland waters relatively often compared to birds from other colonies which were mainly foraging at the Wadden Sea or North Sea, suggesting different foraging habitats explaining the differing prey compositions for chicks at those sites.

Using DNA metabarcoding of faecal samples, Maathuis et al. (2025) described changing proportions in diet items for chicks with increasing age across different marine colonies in the Dutch Wadden Sea in 2022. Clupeids (primarily herring) were highly dominant, accounting for about 75% of the diet in chicks aged 5–12 days, and about 85% at age >12 days. The remaining diet consisted of *Ammodytidae* which increased from under 5% to about 8%, *Gobidae*, and freshwater fish (perch and bream).

In the Eems/Dollard region, herring was also identified as the dominant prey item by weight provisioned to chicks in 2021 and 2022, with over 75% and about 50%, respectively (Manche et al. 2022b). Proportions of *Ammodytidae* were in the same order of magnitude between years, just under 25% in each year. However, in 2022, chick diet was overall more diverse compared to the year before, with chick diet containing more freshwater fish such as ruffe and stickleback, but also crab and flatfish (Manche et al. 2022b).

Between 2020 and 2022, eDNA was used on faecal samples of medium-sized chicks and near fledging to analyse differences in diet composition at different ages (Manche et al. 2022b). For medium-sized chicks, diet was consistently dominated by clupeids in 2020 and 2021, accounting for around 70% of prey, with herring accounting for at least 75% in both years. Shrimp comprised nearly a third of the entire diet in 2020, while additional non-fish prey was detected in 2021, reducing the proportion of shrimp in the diet to around

20% (Manche et al. 2022b). In 2022, the analysis focussed exclusively on fish, ignoring other non-fish prey. Herring accounted for roughly 37% of the diet of medium-sized chicks, with smaller contributions from sprat (20%) and Ammodytidae (8%). Freshwater and brackish species such as *Blicca* sp. or *Vimba vimba* (~15%), and flatfish (~8%) were only recorded in 2022 (Manche et al. 2022b).

Older chicks close to fledging also showed a clupeid-based diet, although patterns of prey diversity varied between years (Manche et al. 2022b). In 2020, herring comprised 60% of the overall diet, with sprat making up only a small proportion (~3%), and shrimp accounting for the remainder. Fish-specific analysis for that year highlighted the importance of herring as dominant prey fish, with 97% of the fish identified as herring. In 2021, fish composition shifted slightly: herring still dominated (~70%), but sprat and *Ammodytidae* each accounted for roughly 15%. The diet of older chicks further comprised non-fish prey like shrimp (15%) and *Alitta virens* (7%) in 2021. In 2022, herring remained the most abundant prey species (~70%), followed by sprat (Manche et al. 2022b).

The results from Maathuis et al. (2025) and Manche et al. (2022b) demonstrate a consistent reliance on herring across chick age classes, years, and colony sites in the Netherlands. At the same time, both the diversity and composition of prey varied between years and chick developmental stages. These patterns likely reflect not only age-specific foraging by adults but also differences in local prey availability across colony locations and years.

Already in the early 1960s, studies from the Wadden Sea island Wangerooge in Germany (1962–1964; Boecker 1967) reported a fish-dominated chick diet, with clupeids as the main prey group (~53% by number, ~61% by weight), followed by *Ammodytidae* (combined sandeel and eel *Anguilla anguilla*), *Gasterosteidae*, and flatfish (all below 10% by number). Other fish species such as *Syngnathidae, Gobiidae*, *Gadidae*, and others accounted for under 2% each. Crustaceans accounted for around 18% and polychaetes for around 7%. These findings suggest a marine-based diet composition relatively similar to island colonies in the Dutch Wadden Sea.

During the 1980s, multiple studies around Jade Bay (that is part of the Wadden Sea), Germany, namely Minsener Oog, Augustgroden, and Banter See in Wilhelmshaven, revealed strong interannual and inter-colonial variation in diet. From 1982-1984, Becker et al. (1987) collected dropped prey items and regurgitated pellets at all three colonies, showing that chicks raised in the inland colonies were fed with higher amounts of sticklebacks which were predominantly caught at inland sites. At the more marine colony Minsener Oog, higher amounts of pellets contained crabs, insects, polychaetes, and molluscs. *Ammodytidae* were found in only very low numbers (Becker et al. 1987), comparable to the most recent findings from the Dutch Wadden Sea (Maathuis et al. 2025; Manche et al. 2022b). Becker et al. (1987) concluded that food availability at the locations reflected the prey provisioned to the chicks, and that diet composition varied significantly between study years and sites.

Follow-up studies in the German colonies (Frank 1992; Massias & Becker 1990) showed a consistent dominance of marine fish such as clupeids and *Ammodytidae* on Minsener Oog, versus dominance of sticklebacks at inland sites that was already described in the 1980s. Pellets and dropped prey items suggested that sticklebacks served as a fallback diet at mainland sites during times of reduced availability of more energy-rich prey. Significant differences in diet between island and mainland colonies were found in all years ($p<0.001$; Frank 1992).

In 1991 and 1992, visual observations at Minsener Oog, a German island in the Wadden Sea, documented substantial interannual variation in prey composition ($p<0.001$) (Frick & Becker 1995). In 1991, clupeids made up 31.5% of chick diet, with fish larvae (26%) and shrimp (~11%) also contributing significantly. By 1992, clupeid proportions had risen to 54.3%, while *Ammodytidae* (~13%) and Syngnathidae (~12%) also increased. These shifts were likely attributed to changes in the age composition of prey (e.g., more clupeid larvae in 1991), suggesting plasticity in diet depending on local prey availability.

Adult common terns were observed carrying prey items away from their foraging areas, likely to feed their offspring at Minsener Oog from mid to late June 2007 (Dänhardt et al. 2011). Energy-rich clupeids made up 50% of these items, followed by gadids (17%), the rest remained unidentified. However, a storm flood at the end of June led to the death of all chicks, precluding further analysis of seasonal diet shifts. Nonetheless, the dominance of clupeids early in the season aligns with earlier findings from this site (Frank, 1992; Frick & Becker, 1995; Massias & Becker, 1990) and from recent findings in the Dutch Wadden Sea described above (Maathuis et al. 2025; Manche et al. 2022b).

Additional long-term data from the Banter See colony in Wilhelmshaven (2006–2015; Dänhardt et al. 2011) showed considerable inter-annual variation in diet composition. In most years, clupeids and smelt dominated (>70%), but in the years 2006–2009 and 2015, their proportion dropped below 50%, with Syngnathidae and shrimp increasing. Cod contributed about 10% in 2007–2008 but disappeared in subsequent years. Flatfish were generally rare but increased in 2010 and 2015 and accounted for about 10% in each year. Notably, an unusually high proportion of fish larvae (>30%) which were otherwise found in low numbers was recorded in 2015. Seasonal shifts were not consistently described across years, but interannual diet fluctuations were pronounced, likely reflecting variable prey availability and possibly energy intake consequences for the chicks when energy-rich prey such as clupeids declined. Overall, clupeids and in some years also sprat, were the most important prey species for common tern chicks on Minsener Oog, although yearly proportions of all prey species were highly variable between study years. *Ammodytidae* did not play a central role in chick diet for this colony (Dänhardt et al. 2011).

Observations from the German islands Neufeld and Neuwerk (Hennig et al. 2016) provided insights into spatial diet variation across sites in 2015. Between 9 June and 11 August, the diet in Neufeld was dominated by smelt (98.2%). Meanwhile on Neuwerk, smelt and clupeids each accounted for about 40.5%, while *Ammodytidae* and shrimps accounted for about 10% and 5%, respectively. This underscores how local habitat differences can shape chick diet composition, even over short spatial scales.

In both Dutch and German studies, chick diet composition showed varying dynamics between prey types depending on colony location and consequent foraging habitat and also revealed inter-annual variation in the German colonies. Key differences between German and Dutch colonies were the greater contribution of smelt and stickleback in German inland or coastal colonies, and the higher occurrence of low-energy prey items such as shrimp, Syngnathidae, and polychaetes in German colonies, especially in years or regions where high-energy prey was less available.

In the Belgian colony at Zeebrugge, chick diet was consistently dominated by clupeids, particularly herring. In 2007, observations indicated that a substantial surplus of small herring was provisioned, more than chicks could consume (Courtens et al. 2007). Other prey species like sandeel and sprat were present but made up a minor proportion of the diet. Across the breeding seasons of 2007, 2008, and 2010, food remains found in the colony (2007-2008) and visual observations of provisioning adults (2010) further supported the predominant role of clupeids in chick diet, with, on average, 92.1% of all prey items identified as clupeids (Vanaverbeke et al. 2011). While prey composition varied slightly between years, herring remained the dominant species. In 2010, the recorded diet appeared more diverse than in the two years studied before, with additional records of *Gobiidae*, polychaetes (*Nereis* spp.), and higher numbers of *Ammodytidae* compared to 2007-2008.

3.9.2 Diet outside the breeding season

The overall focus of diet research in the Netherlands lies on the breeding season (May–June/July) when birds are present in the Dutch colonies, as information on diet during migration or in their wintering habitat is scarce or completely lacking.

3.9.3 Selection in size and/or quality

Little information is available regarding prey length. Common terns are generally described as feeding on small fish with lengths <15 cm (Becker & Ludwigs 2004). In the Belgian Zeebrugge colony, adult common terns were reported to dominantly feed on fish in the category 4-4.5 cm length, with about two thirds of their fish diet comprising of individuals of this length class (Vanaverbeke et al. 2011). The freshwater colony De Kreupel in the IJsselmeer is, to our knowledge, the only one for which courtship prey length changes are described (van der Winden et al. 2009). The mean length of courtship prey brought into the colony was reported as more uniform in late July compared to earlier in the same month. Furthermore, the courtship prey observed consisted mainly of *Ammodytidae* with a mean length of 6.3 cm (11 July 2009). Two weeks later, mean length across the more diverse prey species was reported at about 7.0 cm (van der Winden et al. 2009).

As for adult prey sizes, information on prey lengths fed to common tern chicks is limited. Generally, chicks are reported to be fed with prey items between 3-9 cm in length (Becker & Ludwigs 2004), increasing with chick age at both freshwater and marine sites (Becker & Ludwigs 2004; Manche et al. 2022b, 2022a; van der Winden et al. 2009), therefore being larger than the reported prey sizes for adults (e.g., Vanaverbeke et al., 2011). The few studies available differ with regard to reported intra-annual differences. However, none of the studies statistically analysed the potential differences. While Manche et al. (2022b) did not report any differences in prey lengths at the Eems/Dollard estuary between 2021 and 2022, Frick & Becker (1995) reported significant differences in average prey lengths provisioned to chicks on Minsener Oog in 1991 and 1992 (4.4 cm and 6.2 cm, respectively; $p<0.001$). At the Zeebrugge colony, over two thirds of the clupeids presented to chicks ranged between 5.5-6.5 cm in length in 2010 (Vanaverbeke et al. 2011).

Prey size increase with chick age was reported for instance by Manche et al. (2022a) in the Dutch Wadden Sea in 2021. They compared chicks aged 14 days to chicks that were (almost) fledged and found an increase of prey length of at least 2 cm (~5 cm to >7 cm prey length). This increase was found at all five Wadden Sea colonies monitored (Manche et al. 2022a). Hennig et al. (2016) described changes in prey length from mid-June to about 10 August 2016 for the German Wadden Sea islands Neufelderkoog and Neuwerk. Mid-June, mean prey item size was recorded at 7.5±2.4 cm. Between the end of June and the first week of July, mean length increased from 6.8±1.7 cm to 9.3±2.6 cm. Mean length of prey delivered to the chicks reached levels comparable to late June around and after 10 August (7.0±2.5 cm and 7.1±2.4 cm, respectively). The differences between the end of June and the first week of July, as well as between the second week of July and 10 August were both found to be significant (Hennig et al. 2016). The increase in size is likely to go along with an increase in energetic value of the prey items as chicks are reported to receive more energy-rich prey with increasing age (Stienen & van Tienen 1991).

Prey size was considerably lower at freshwater site De Kreupel in the IJsselmeer (van der Winden et al. 2009). Observations were made on 16 and 23 July 2009, showing an increase in prey size over the course of two weeks. Chicks received an *Ammodytidae*-dominant diet during the first observation with a recorded mean length of 4.2 cm. Of the 39 observations, circa three individuals were between six and eight centimetres long. *Ammodytidae* provisioned on 23 July 2009 mainly fell in the 6 cm category. The overall mean length of prey provisioned was reported at 6.5 cm.

3.9.4 Other variables affecting diet choice

A single study reported kleptoparasitism by other adult terns or older chicks because of adult common terns provisioning prey items that were larger than their young chicks were able to consume. This study was conducted at freshwater site De Kreupel in the IJsselmeer in July 2009 (van der Winden et al. 2009). Brenninkmeijer et al. (2002) applied a Generalised Linear Model (GLM) to examine the relationship between foraging common terns and several abiotic factors in the Dutch Westerschelde. Their analysis did not reveal any significant associations between the spatial distribution of foraging terns and the environmental variables considered. The authors suggested that, as opportunistic feeders, common terns are highly adaptable to changes in prey availability and therefore may not rely strongly on specific abiotic conditions. However, they noted that the spatial resolution of their dataset might have been too coarse to detect localised responses to environmental variability. Nevertheless, other studies conducted in different areas in the Dutch Wadden Sea and German colonies have found effects of abiotic factors such as wind speed, tidal stage, or prey availability on the foraging behaviour and distribution of common terns (e.g., Becker & Ludwigs 2004).

Studies from the German and Dutch Wadden Sea show that wind speed can significantly influence the diet and foraging efficiency of common terns. At the German inland colony in Augustgroden higher wind speeds were associated with a shift in chick diet from clupeids to *Ammodytidae* (Frank 1992). Similarly, on Griend in the Dutch Wadden Sea, significantly more herrings were fed to chicks on days with wind speeds below 40 km/h, while shrimp consumption and the total number of prey items delivered per hour dropped sharply at wind speeds above 50 km/h in both 1989 and 1990. Energy intake per hour declined with increasing wind speed from around 35–45 km/h onwards, suggesting that under high wind conditions, chicks may not meet their energetic needs (Stienen & van Tienen 1991). On the German island Minsener Oog, diet composition was only significantly influenced by wind speed in 1986 ($p<0.05$), but not in 1984 and 1985 (Frank 1992). In 1985, however, increasing wind speeds were linked to longer foraging trips and reduced body mass after feeding (Frank & Becker 1992). A strong negative correlation between wind speed and body mass after feeding was found for both 1985 and 1986 ($p<0.001$), while a weaker negative relationship between wind speed and foraging duration was observed at Augustgroden in 1986 ($p<0.05$; Frank & Becker 1992).

The influence of tidal stage on diet composition and foraging patterns of common terns, with effects observed in both chick and adult diets has been described across multiple Wadden Sea locations. At Minsener Oog and Augustgroden, Germany, clupeids were more frequently fed to chicks around high water, while Ammodytidae dominated chick diet during low water in 1984-1986 (Frank 1992). Stickleback proportions in the diet increased during incoming tides, and diet composition overall varied significantly with tidal stage at Augustgroden in 1985 ($p<0.01$; Frank 1992). Furthermore, Frank & Becker (1992) found that adult body mass after foraging was also influenced by tidal stage, with birds found to be heavier after foraging during ebb compared to flood and high water ($p<0.05$) on Minsener Oog. At Augustgroden, the tidal effect was less pronounced and without a clear pattern. However, body weight after feeding differed significantly between feeding during incoming tide and around high water in 1986 ($p<0.01$; Frank & Becker 1992).
In 1991 and 1992, Frick & Becker (1995) reported significant tidal differences in prey composition ($p<0.001$), with flatfish and *Crangonidae* especially abundant during outgoing tides (Figure 3-28). During this time, these species are gathered in the tidal creeks, making them easily accessible to common terns. Clupeids were consistently the main prey in all tide stages for birds from Minsener Oog in 1991, but their proportion was lowest during incoming tide, which instead saw the highest share of fish larvae (Frick & Becker 1995). Becker et al. (1993, 1997) further reported an influence of the tidal cycle on the use of foraging areas, suggesting that adult terns remember spatial-temporal patterns in prey availability.
At the Banter See colony, adult courtship feeding observations revealed that smelt and clupeids were more common during outgoing tide, while sticklebacks increased during and around high tide in 1992 (Wendeln et al., 1994). It is important to note that courtship prey might not be representative for general adult diet (Barrett et al. 2007). Differences in prey proportions were significant between high and outgoing tide ($p<0.05$), with marine prey (smelt and clupeids) dominant during outgoing and high tide, and sticklebacks consumed in significantly higher numbers during and around high tide compared to outgoing tide ($p<0.05$; Wendeln et al. 1994).

Tide dependency further differs between marine and stickleback feeding adults. Diet composition of stickleback feeders is weakly tide-dependent, while marine feeders will switch to preying on sticklebacks when marine prey is less available (Wendeln et al. 1994). Hennig et al. (2016) observed that most prey items were delivered to chicks during outgoing tide (45.3%), followed by low tide (22.1%), suggesting a preference for feeding during ebbing conditions in the northern area of the German Wadden Sea. On Griend in the Dutch Wadden Sea, chick diet was also affected by tide. Significantly more herring and less shrimp and flatfish were delivered during incoming tide compared to outgoing tide (Stienen & van Tienen 1991). Overall energy intake was slightly lower during incoming tide, while outgoing tide was associated with higher energetic gain.

Overall, these findings indicate that tidal stage plays a crucial role in shaping the foraging behaviour and diet composition of common terns, likely by impacting the accessibility and availability of different prey types across the tidal cycle.

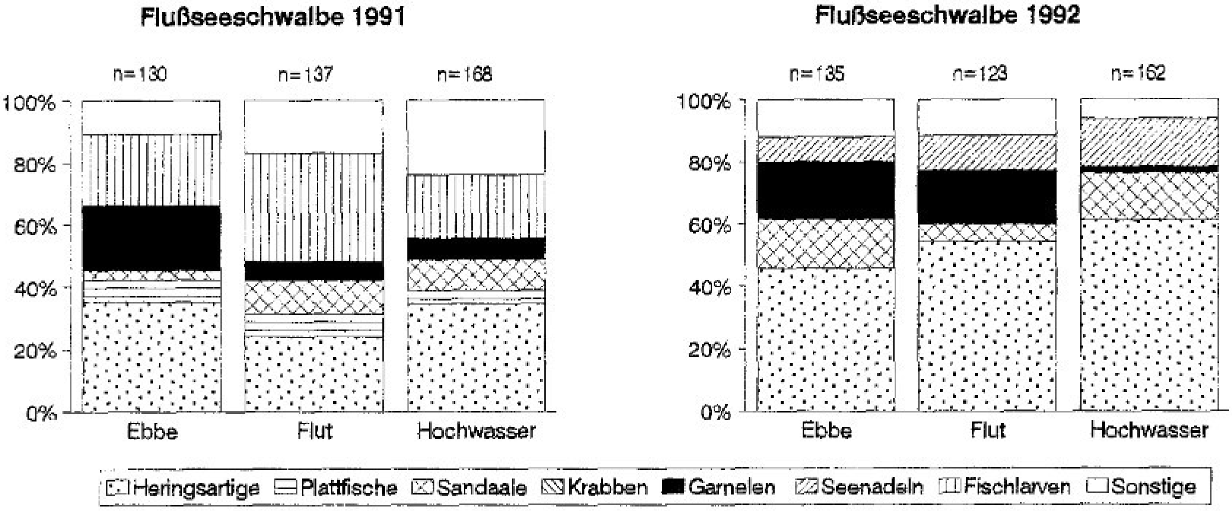


Figure 3-28 *Changes in diet composition for common terns at different tidal stages (outgoing tide, incoming tide, high tide) at Minsener Oog, Germany, in 1991 and 1992. Number of total food items, year, and tidal stage is provided (n). Prey species listed are clupeids, flatfish, Ammodytidae, crabs, shrimps, Syngnathidae, fish larvae, others. Figure modified from Frick & Becker (1995).*

Diurnal variation had a clear influence on foraging in common terns on Griend, with peak prey intake between 5–8 a.m., largely driven by high shrimp and flatfish consumption, while herring was more commonly taken between 2–8 p.m., coinciding with the highest energy intake in chicks (Stienen & van Tienen 1991).

Temperature also affected chick diet composition and energy provisioning. On Griend, shrimp dominated common tern chick diet at 15–19°C, while herring intake significantly increased above 19°C. Overall energy consumption was lower at temperatures below 15°C, likely no longer meeting the chicks' energy demands (Stienen & van Tienen 1991).

Foraging can further be spatially constrained by bathymetry, as shown for common terns in Zeebrugge, (1992–2010) that were restricted to nearshore transition zones where depth gradients were steep (Vanaverbeke et al. 2011).

Three studies addressed the combined effects of environmental factors on diet and chick condition. In the German colonies around the Jade Bay, chick mortality was positively correlated with wind speed, rain at the coast, and negatively with minimum temperature (Becker & Specht 1991). The singular effects of each of these factors were suggested to amplify when all three were at play, particularly in combination with limited food availability and tides restricting foraging and provisioning (Becker & Specht 1991). Similarly, at the River Ythan, Scotland, wind and tide interacted to affect capture rate and success, with strong winds reducing both at low tide, and altering dive types at high tide (Taylor 1983)

Two recent studies in the Dutch Wadden Sea confirmed that common terns forage in areas with high densities of small pelagic fish, especially in deeper gullies near breeding colonies, reinforcing the importance of prey availability in shaping foraging behaviour (Maathuis et al. 2025; Manche et al. 2023).

3.10 European herring gull

The European herring gull is a large gull that is considered a generalist species that has, at species level, a broad diet. The herring gull is a Dutch breeding bird, that particularly can be found along the coast and on (Wadden) islands (Photo 3-29). They have a wide distribution throughout northwest Europe and Russia. In more northern breeding populations herring gulls are migratory, while the southern populations are partly or completely migratory (del Hoyo et al. 1996). Herring gulls can be found in the Netherlands year-round. The breeding population here is estimated on 26,750-29,000 (2024) but breeding pairs are decreasing since the start of monitoring (Sovon.nl). Herring gulls are also present in winter and estimated winter maxima are 130,000-240,000 (Sovon.nl). European herring gulls were classified as Least Concern by the IUCN Red List due to its extensive range and large population size (Birdlife International, 2025. However, populations including the Dutch breeding population are decreasing. Within the Netherlands, its conservation status is therefore listed as unfavourable for both the breeding population as the non-breeding population (Sovon.nl). The Herring Gull is a mostly coastal oriented bird feeding along the coast on marine prey like shellfish and crustaceans and often to a lesser extent also fish and other marine prey like ragworms (Camphuysen 2013; Kubetzki & Garthe 2003; Löhmer & Vauk 1969; Pennycott et al. 2020a, 2020b; Van Donk et al., 2017). However, herring gulls can exploit many other habitats and prey types, several of these opportunities created by humans. For instance, they forage at sea following fishing vessels and eating discards (Garthe & Scherp, 2003; Sotillo et al., 2014), but they also forage at refuse dumps (Pons, 1992; Verbeek, 1977) or in cities profiting from urban foods (Huig et al. 2016). Besides, they can be seen using several foraging methods, for instance trampling in the grass to forage on earthworms , dropping large shellfish from the sky on hard surfaces (Cristol et al. 2017) and foraging on large feeding events such as washed ashore marine life (Cadée 2001). Diet can differ greatly depending on the location, in some environments herring gulls were reported to have a diet that primarily contained berries and terrestrial animals (Spaans 1971).

Photo 3-29 *Herring gull in the dunes of Texel, the Netherlands. Photo: S. van Donk.*

3.10.1 Diet during the breeding season

3.10.1.1 Adult diet

The diet of Herring Gulls in the Netherlands during breeding has been mainly studied extensively in two bigger studies. Diet during the breeding season can be studied relatively easily, as prey remains such as regurgitates, boluses and prey provisioned for chicks can be gathered around the breeding sites (Camphuysen 2013; Van Donk et al. 2017). However, shortcomings and biases in these methods must always be considered in interpreting the results (Barrett 2007). We focus on two larger studies, the first took place on the island of Terschelling/Vlieland (1966-1969) (Spaans 1971) and the second still ongoing study on Texel since 2006 (Camphuysen 2013; Van Donk et al. 2017).

The two larger studies both used an analysis of prey remains as the main source of diet information. They gathered diet data on pellets, faeces, lumps of food regurgitated by chicks while handling them. In Spaans et al. most of the pellets were examined in the field, which is an advantage in the speed of examination, but details can be missed e.g. parts of earthworms that can only be determined using a microscope, the reason why Camphuysen (2013) analyzed most pellets in the lab. In Spaans et al. (1971) additional information was gathered through observations of adults feeding chicks and some stomach and oesophagus contents of adult birds and chicks.

The diet of gulls in the colonies of Vlieland and Terschelling were comparable with other studies from the same period in the sense that the majority of pellets found contained prey from the coastal/intertidal marine area (Spaans 1971). Based on ~27,000 food samples, the most common prey in more or less comparable occurrence were shellfish species (blue mussel (*Mytillus edulis);* common cockle (*Cerastoderma edule)*; sand gaper (*Mya arenaria*)), common starfish (*Asterias rubens*) and European green crab (*Carcinus maenas*), and also present in reasonable amounts were marine fish which came mostly from discards, and brown shrimp (*Crangon crangon*). Besides prey, items from terrestrial sources and refuse dumps were also part of the diet. Prey types that were only found on a few occasions were marine worms such as *Nerius virens*, non-marine food items like rabbits, moles, some small rodents, songbirds or chicks of several bird species, eggshell remains of herring gulls, and some insects.

A study on Terschelling in 1992 examined diet in relation to reproductive success in a small subsample of a colony (26 pairs) (Bukacińska et al. 1996). The pairs were split into successful and unsuccessful pairs, but their diet (based on gathered pellets, frequency of occurrence) consisted mainly of marine invertebrates (~70%) of which most were bivalves (52-55%) and crabs (25-33%), followed by fish (24-32%), both marine and freshwater fish. Other prey items were grass (6-7%), chicks (4-12%), refuse (2-5%) and berries (0-2%). Diet of successful pairs contained more fish and chicks while the diet of unsuccessful pairs contained more crabs and starfish.

The diet of a more recent study on Texel was comparable as the diet also contained mostly prey from the coastal/intertidal marine area(Camphuysen 2013; Van Donk et al. 2017). Based on ~10,000 food samples, the most common prey were shellfish species, mainly blue mussel (55-77%) and to a lesser extent cockles (<1-5%) and a species that was introduced in the Wadden Sea in the beginning of the eighties, the razor clam (*Ensis Leei)* (4-9%). Other common intertidal/marine prey during the breeding season were European green crab (8-12%) and swimming crab (*Liocarcinus holsatus)* (<1-8%), whiting (3-9%) and flatfish (*Pleuron/Limanda)* (4-12%). Other prey were fresh water fish common roach (~2%), beetles (~2%), cannibalistic prey (large gull egg and chicks; 2-11%) and garbage (~4%) (Camphuysen 2013). Adult birds that were caught and regurgitated the meal they brought to the colony had a slightly different composition compared to the pellets. Boluses of adult birds still contained mostly blue mussels but a lower percentage compared to pellets (28%). Higher than in the pellets is the percentage of flatfish (*Pleuron./Limanda*, 28%), bread (19%), brown shrimp (17%) and European sprat (13%).

Just over the border on Helgoland, an island in the German Wadden Sea, pellets (n=~15,000) of herring gulls and great black-backed gulls were gathered from roosting piers throughout the year (1999) in research into the effect of large gulls on passerine predation (Dierschke 2001). Unfortunately, no difference could be made between pellets of the two species. Twice as many herring gulls were counted compared to great black-backed gulls over the year, but relative abundance of herring gulls was especially high between

February and April (87-91% of total). In these months, the diet consisted mainly of fish (20-69% of pellets), crustaceans (7-45%), molluscs (10-16%) and to a lesser extent non-passerine birds (1-11%), passerines (0-7%), algae (0-7%), garbage (<2%) and kelp flies (<1%) (Dierschke 2001).

Another German study, examined the difference in diet between breeding gull species on the island of Juist and Amrum in the German Wadden Sea during incubation and chick-rearing on Juist and only during incubation for Amrum (Kubetzki & Garthe 2003). Herring gull main prey were bivalves on both islands during incubation (frequency of occurrence: 88% and 68% resp.) and also during the chick phase on Juist (78%). The other more common prey were crustaceans (Juist egg: 11%, Juist chick: 24%, Amrum egg: 36%). Other prey were insects (1-8%), birds (0-4%), mammals (0-7%), eggs (0-2%), grass (0-3%), cereals (1-4%), refuse (1-4%) polychaete (0-2%) and fish (1-3%). Prey that only occurred in 1% of the pellets were: gastropods and starfish.

Discards in the diet during the breeding season can be exploited in the Wadden Sea. A study between March and August 1994 studied the occurrence and consumption of discards originating from shrimp trawlers in the German part of the Wadden Sea near Spiekeroog (Walter & Becker 1997). Herring gulls were, together with black-headed gulls, the most common scavengers and herring gulls were also the most successful. They represented 45% of all birds counted but they took 82% of the total number of prey consumed. As found in earlier studies, birds consumed roundfish (79%) in a higher rate than flatfish (41%), and discarded invertebrate species were consumed even less (23%).

In the breeding season (1987-1993 May-August), the distribution and feeding range at sea of herring gulls and lesser black-backed gulls were investigated using ship-based surveys in the southern North Sea. Herring gulls were found in much lower numbers further out at sea compared to lesser black-backed gulls; they were mainly restricted to a zone of 25 km from the nearest coast and most of them were also found closer to their breeding sites (95% within 54 km compared to 95% within 135 km for lesser black-backed gulls). Most of the observations were dominated by adult gulls, but immatures were relatively frequent further at sea (>100 km from the coast; 33% adult birds) (Camphuysen 1995). Most of the associations with fishing vessels occurred close to the coast; 80% of flocks of herring gulls were counted <10 km from the coast. Adults predominated (93%) in all associations with vessels, independent of distance to the coast (Camphuysen 1995). There was more competition and the percentage of discards consumed was higher between 06:00-15:00 compared to early mornings and the afternoon, possibly because gulls had to arrive from roosting ashore.

Some more recent studies have been published in the last 20 years, studying behaviour around fishing vessels, but in waters outside the NCP. In the Belgian North Sea, similar discard experiments were done between May-August of 2011. Again, discards were eaten depending on the discarded species, but selectivity by birds decreased during the chick rearing stage (Sotillo et al. 2014). Also in the Belgian waters, herring gulls were relatively more abundant closer to the coast and herring gulls were more dominant in the flocks of scavengers than predicted by the relative abundance of local counts (Sotillo et al. 2014). Preferred discarded species were roundfish, followed by sole, but plaice and dab were avoided. Interestingly, more flatfish was consumed when the proportion of immature birds was larger. Besides this, immatures were less successful in capturing prey compared to adults and they were more often robbed of their prey (Sotillo et al. 2014).

A smaller study conducted in the southern North Sea to on the foraging behaviour of birds around beam trawlers just above the Wadden islands in the Netherlands and Germany the end of June in 1993, showed that lesser black-backed gulls and herring gulls were common around fishing vessels (Camphuysen 1993). Of the herring gulls that were seen, most were adults. Species-specific characteristics were observed; the herring gull consumed more offal than expected based on the numbers around the vessel, but they were less successful, compared to the other species, in picking up gurnards. However, they were more successful in picking up cod and whiting compared to lesser black-backed gulls, although great black-backed gulls were even more successful. Overall, the percentage of discarded offal (94%) and roundfish (85%) was far higher than the consumed flatfish (34%) and benthic species (0,3%) (Camphuysen 1993).

In competition behind fishing vessels, herring gulls are more successful than lesser black-backed gulls but less successful than great black-backed gulls. Herring gulls lost less prey based on relative abundance present to lesser black-backed gulls, but more to great black-backed gulls. Lesser black-backed gulls dropped the fish that they took more often and the fish was stolen more often by great black-backed gulls and herring gulls, while they stole less often from the other species (Camphuysen 1994). Competitive success also differed per species. Overall herring gulls were more successful when fish offal and gadoids (a roundfish) was offered, compared to lesser and great black-backed gulls, compared to their relative abundance. However, the latter two outcompeted the herring gull again on other roundfish, (Camphuysen 1993). The research suggest that herring gulls were slightly better in picking up prey with a higher caloric value (Camphuysen 1993).

Besides foraging for discards, herring gulls can catch prey themselves by plunge diving. Spaans et al (1971) assumed that pelagic fish like *Clupidae*, sandeels and mackerel could be caught by herring gulls. A more recent diet study on herring gulls in the breeding season, showed that the proportion of such fatty fish is very low, most fish originate from fishery discards (like flatfish, whiting). However, some of the fish that is more frequently found in chick boluses could have been caught by herring gulls themselves, like sandeel and European sprat.

3.10.1.2 Chick diet

Chick diet appears to differ from that of adults during the breeding season. In Spaans et al. (1971), the food that was brought to chicks was studied by both observations from a hide, as well as boluses of chicks (thrown up food during handling). The food of chicks consisted mainly of fish; marine fish was the most frequently found prey type (53% of the observed prey and in about 75% of the boluses). The fish that chicks regurgitated while being handled were mostly part of the *Clupidae* family (like sprat and herring) followed by fish of the *Gadidae* family (like whiting, haddock and cod) and flat-fish (like plaice and dab), but also contained *Ammoditydae* -sandeel species and some other species like mackerel and horse-mackerel. In the regurgitates, also garbage was also found relatively often (~25% of regurgitates), while in both cases marine invertebrates were far less common than in the pellets of adult birds (Spaans 1971). The researchers concluded that about 50% of the food was obtained through man via garbage and discards.

Similarly, the species composition of boluses of chicks also differed in the Texel colony (Camphuysen 2013). The percentage of fish was much higher than in the pellets of adults; flatfish (33% compared to 12%), whiting (16%), European sprat (*Sprattus sprattus)* (12%) and *Ammodytidae* (8%) were all found in higher occurrence compared to pellets. brown shrimps (29%) also occurred often in boluses. Interestingly, blue mussels were only found in 16% of cases. The amount of bread found in boluses was also very high, compared to what was found in pellets (12%), suggesting a bias towards prey with indigestible parts while looking at pellets.

There are several theories about the difference in diet between adults and chicks. Parents could feed fish to chicks because of the higher nutritional value as they are constrained in the amount of food they can bring back to the nest; molluscs contain many indigestible parts that are usually regurgitated. Besides this, it is possible that the chicks, especially when they are young, require soft prey. The switch might also be a consequence of the shift in the foraging pattern of the parents, from following the tidal rhythm to a diurnal pattern (Spaans 1971). Note that the diet composition in adults differs depending on the method of gathering the prey remains. Pellets have a bias towards hard prey remains, and also boluses of adult birds have a higher percentage of fish.

3.10.2 Diet outside the breeding season

During the winter period, diet studies are more difficult to conduct, due to the low accessibility of birds outside their breeding colony. The studies that are done are often based on observations of (groups of) gulls. It is therefore harder to study the complete diet of herring gulls outside the breeding season. Only some studies gather for instance pellets at roosting areas which can provide a better indication of the diet of such a local winter population. Furthermore, observations and selectivity tests are done from ships to study foraging behaviour at sea.

Herring gulls on Terschelling in winter also mainly fed on cockles and occasionally starfish. In Vlieland, cockles were also most common, but here also blue mussels were eaten from the local breakwaters. Besides this, crab and fish remains were found but in low quantities. However, it is expected that in this period of time, a large number of gulls fed on refuse and fishery discards. In the northern part of the Netherlands, estimates were made that suggested that in the autumn and winter of 1967-1968 at least 32% of the population were constantly feeding on the mainland, mainly food provided by humans (garbage and other human waste). This could increase to 77-82% when foraging conditions at sea were unfavorable (Spaans 1971). During this period, the amount of open dump sites was very high.

During the breeding season until autumn, herring gulls are clearly bound to the coast, and almost absent further offshore sea until October. In the winter months (November-February), herring gull numbers increase but densities are still higher in the coastal zone, probably foraging on intertidal prey (Camphuysen 2013; Waggitt et al. 2020).

When at sea, herring gulls are strongly attracted to fishing vessels (Camphuysen 2013) that provide discards, an important marine prey component. Discards are even considered to be partly responsible for the growth in populations of herring gull populations in the last decades of the 20th century (Catchpole et al. 2006). Although the amount of discards has decreased since then due to stricter regulations, estimations of the number of (all) seabirds that are supported by discards in the North Sea are still around 2 million individuals, which is 3 million less than estimates from 1990 (Sherley et al. 2020). Several research projects at sea were done, to investigate the presence, success-rate and prey selection of seabirds following fishing vessels.

In a study on the effect of trawling around Helgoland, the diet of herring gulls and great black-backed gulls was studied (Hüppop & Wurm 2000). Pellets (n=233) were gathered in the winter of 1997-1998 on piers where the gulls were resting at night. It was not possible to distinguish between the two species unfortunately, as they rest together at roosting sites. Pellets were gathered during periods with active cod fishery and without. When fishery discards were available in the proximity of the island, 83-87% of the pellets contained discarded fish remains and 70-73% contained these types of discards exclusively. Cod was the most common species found, in a few pellets whiting, scad and some other species occurred. Other prey types during this period were discarded invertebrates, non-discarded fish, non-discarded invertebrates and terrestrial prey or marine invertebrates (all <12%). When discards were not available nearby, gulls foraged in rocky intertidal areas, mostly foraging on the hooknose fish eggs (*Agonus cataphractus)* that are spawning in the shallow waters (~30-65% of the pellets) and invertebrate prey (~15-30%) like Blue mussels *Mytilus edulis* and shore crab (*Carcinus meanas)*. Besides this, terrestrial prey/garbage was found in ~20-30% of the pellets. Nevertheless, discard remains were still present in 12-32% of the pellets even when no fisheries were near, suggesting a wider foraging range than the observers of trawlers in the area could spot. Besides the change in diet, also body condition was measured by catching gulls at night. The body condition of both the herring gull and great black-backed gull was lower in periods without fishing activity nearby, although the sample size was low (11 great black-backed gulls and 17 herring gulls). Without trawling activity, herring gulls had a 13% lower body condition compared to with trawling activity and great black-backed gulls showed a mean decline of 24%. This effect was only seen in adult gulls. Three gulls were caught twice, and they showed the same trend. Besides the decrease in body condition, there were far fewer gulls present at the island when fisheries declined. Herring gull presence dropped to more than half of the numbers but increased again to levels comparable to times with fishing activity when hooknose eggs were available in the area. Great black-backed numbers fell even more to ~25% of the numbers when no fishing was available. Numbers did not increase in periods with hooknose eggs, but they might have already left to breeding areas up north (Hüppop & Wurm 2000).

A study on the east coast of Scotland observed several multi-species feeding associations formed near fishing vessels, above schools of fish or because birds were attracted to attracted by cetaceans (Camphuysen & Webb 1999). Herring gulls, as well as lesser black-backed gulls, profit in these multi-species feeding associations from so called ‘producers’; common guillemots, razorbills or cetaceans driving up fish towards the surface. However, when herring gulls participated, the multi-species feeding associations was often ended quite quickly afterwards. Small and short-lived MSFAs were the most common type of associations, and mostly formed over natural prey like sandeels and small *Clupeoids* which are energy-rich and fatty prey species (Camphuysen & Webb 1999). Herring gulls and lesser black-backed gulls in this area were often aiming for MSFAs while foraging (>80% of recorded offshore feeding activities in summer). During ship-based surveys in the Dutch part of the sea (2002-2009), these associations were far less common; only 1% of herring gulls and 3% of lesser black-backed gulls were observed joining feeding associations (Camphuysen 2013).

3.10.3 Temporal and spatial patterns

Diet often differs in composition between years and months. On Terschelling in the 1960s, some prey types peaked in occurrence in pellets early in the season like common cockles (~20%), sand gaper (10-20% but almost absent in Vlieland colony). The common seastar peaked early in the season on Terschelling and was consumed less overall in this colony, but on Vlieland peaked usually late and was found more frequently in the diet (resp. ~40% and 20-40% of occurrence). On both islands crabs formed a larger part of the diet from May onwards (~20-40%) and fish usually also increased in occurrence in the diet (~20% May onwards Terschelling, ~10% June onwards on Vlieland). Mussels were very common in the diet of Vlieland herring gulls and were almost always present in >40% of occurrence in the diet peaking to >70% of occurrence. Mussels were less part of the diet in Terschelling (although still <35%). The proportion of mussels over the season also seemed to differ between the islands; occurrence on Terschelling was highest in May and June, while on Vlieland occurrence was sometimes higher early in the season and sometimes higher later in the season. Brown shrimp was not found often but increased slightly over the breeding season (~max 4% of occurrence) (Spaans 1971).

A later study on Terschelling (1992), also showed a change in diet between the incubation period and the first days of chick-rearing (Bukacińska et al. 1996). Gulls ate slightly fewer marine invertebrates during chick-rearing compared to the incubation period (especially fewer bivalves). This change in diet was larger in successful pairs, which also consumed fewer freshwater fish, more crabs and chicks.

In the Texel colony, a difference was found between the pre-hatching and chick-rearing period. Similar to the study on Terschelling, the occurrence of fish in the diet increased and shellfish decreased during the chick-rearing period (Camphuysen 2013; Van Donk et al. 2017). The difference in diet could partly be attributed to differences in the surrounding of the colonies. The Vlieland colony was situated close to hard substrate breakwaters where a lot of blue mussels as well as young common starfish are growing, while there was no such hard substrate near the Terschelling colony. Such seasonal patterns might be explained by patterns of occurrence in the environment or size selection and growth of prey to the 'right size'. Crabs probably return to sublittoral and littoral zone from the channels and tidal inlets when it gets warmer, and are then more reachable accessible to gulls (Spaans 1971). The Texel colony is also situated close to breakwaters along the coast of Texel and mainland Noord-Holland, where many herring gulls from this colony foraged (van Donk et al. 2018). Besides that, shrimp fishery is also common around the islands, both in the North Sea near the coast as the Wadden Sea and these fisheries produce discards like small flatfish.

3.10.4 Selection in size and/or quality

Both during the breeding season as outside the breeding season, herring gulls can be associated with fishing vessels, profiting from discards (Garthe et al. 1996). Different types of fishing vessels produce different discards and this affects profitability for seabirds. Most seabirds prefer a certain shape and length depending on their own body size (Garthe & Huppop 1994). Gulls select discards with a preference for certain species: in experiments with discarded fish north of the Dutch and German islands between June and August, herring gulls and lesser black-backed gulls had a higher consumption rate of roundfish (70.7% consumed) and fish offal (65,9% consumed), compared to flatfish (30.5% consumed) and benthic invertebrates (0.3% consumed). Discarded flatfish are not ideal, because of their wide shape. During the experiments there was a clear size selection of smaller flatfish based on the size distribution provided, and fish of a width >8 cm were barely eaten (Camphuysen 1994). The median size of roundfish was slightly higher for herring gulls compared to lesser black-backed gulls (19 cm versus 18 cm), but these sizes were more comparable to what was offered. Depending on the roundfish, the average length of eaten fish fell between 12-23 cm but fish up to 30 cm were sometimes consumed as well. (Garthe & Huppop 1994).

3.11 Lesser black-backed gull

The lesser black-backed gull is a generalist species that has, at species level, a broad diet (Photo 3-30). The species was not common and its numbers have only increased significantly since the 1970s (Spaans, 1998), and since then is a common Dutch breeding bird (Sovon.nl). The species is now a widespread breeding bird from the central-north of Russia, northwest Europe, but also on the coast of Portugal and southern Ireland (del Hoyo et al. 1996). The lesser black-backed gull migrates in autumn to their overwinter areas in southern Europe, west Africa but also England. The breeding population here is estimated on 82.500-86.000 (2024) but breeding pairs are decreasing since ~2010 (Sovon.nl). Lesser black-backed gulls are only present in very low numbers in winter (~1000) (Sovon.nl). Lesser black-backed gulls were classified as Least Concern by the IUCN Red List due to its extensive range and large population size (Birdlife International, 2025. Within the Netherlands, its conservation status is listed as favourable for both the breeding population as the non-breeding population (Sovon.nl). This gull species is, compared to the herring gull, more often found further out at sea but also forages along the coast and inland. Prey choice can be wide and include marine oriented prey like fish and swimming crabs (Camphuysen 2013; Isaksson et al. 2015; Schwemmer et al. 2013). Similar to other large gulls, they can exploit many habitats and prey types, several of these opportunities being created by humans, for instance foraging at sea following fishing vessels and eating discards (Garthe & Scherp 2003; Sotillo et al. 2014), but they also forage at refuse dumps, in cities profiting from urban foods and agricultural land (Camphuysen 2013; Huig et al. 2016). Lesser black-backed gulls are migratory and do not spend the winter in the Netherlands. Most studies on the diet of this species are conducted in a large breeding colony on Texel, but there are also several foraging studies.

Photo 3-30 *A lesser black-backed gull on Texel, the Netherlands. Photo: M. Leopold.*

3.11.1 Diet during the breeding season

3.11.1.1 adult diet

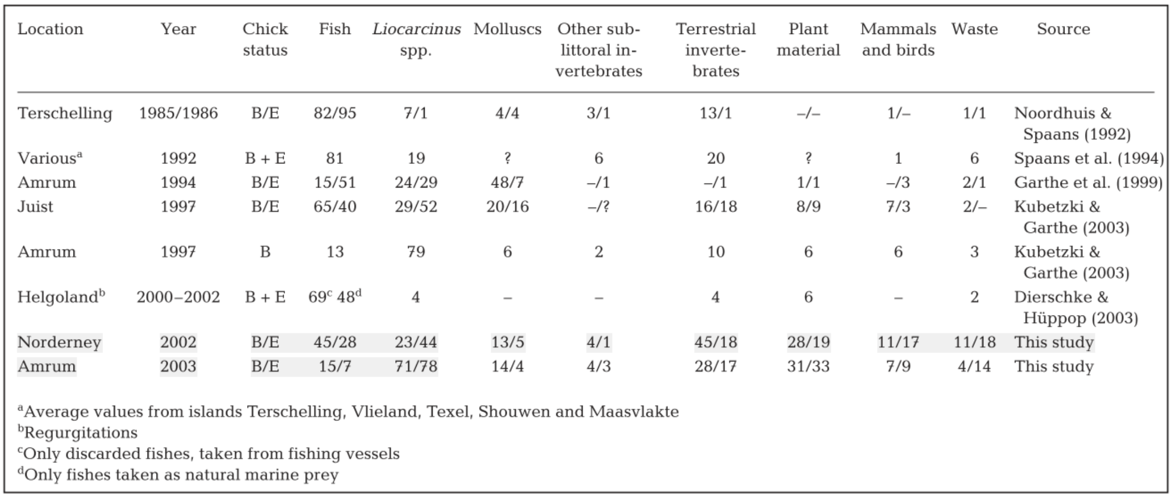
As described earlier for the herring gull, the lesser black-backed gull has been studied extensively on Texel since the beginning of 2006 and this remains ongoing (Camphuysen 2013; Camphuysen et al. 2024). The authors analysed prey remains as the main source of diet information. They gathered diet data on pellets, faeces, and lumps of food regurgitated by chicks while being handled. Prey remains were studied in the lab, so that very small prey items like parts of earthworms and small otoliths can be determined using a microscope.

Lesser black-backed gulls had a wide dietary spectrum on the island. There were 307 different types of food found, which differed between season and individual. Of all prey samples collected (8,203 samples, gathered between 2006-2021), 82.2% contained marine prey. This result is similar to older research to breeding colonies around on Dutch Wadden Islands, in which they found that most of the prey remains were (marine) fish and to a lesser extent terrestrial invertebrates (Noordhuis & Spaans 1992, Spaans et al. 1994;Table 3-12). The majority of marine prey on the Texel colony were roundfish like whiting, horse mackerel and grey gurnard (67.7%) and flatfish (52.5%) like plaice, dab and Dover sole. Most of these fish species are demersal, that mainly become available as discards from large beam trawlers. Marine crustaceans were also relatively common and represented 27.2% of all prey samples holding marine prey (typically swimming crabs like *Liocarcinus holsatus*), while marine polychaetes (14.7%) formed a smaller group, mostly represented by *Eunereis longissimi*. Other common prey were terrestrial prey (31.0% of all prey samples), mostly insects and spiders (50%), followed by plants, mostly livestock food from farms and sometimes berries (30%), earthworms (14%) and to a lesser extent mammals and birds (among them gull eggs and small rodents). Food samples that contained parts of anthropogenic origin were found in 7.3% of all prey samples, and were waste materials like plastic fragments, bread seeds, chicken, plastic pellets and paper, probably originating from garbage in cities and holiday resorts or a waste processing plant. A very common prey type for herring gulls (intertidal prey found along the coast like mussels or cockles) are very uncommon for the lesser black-backed gull and are only found in 3% of prey samples. Also freshwater prey are very rarely found (1.4%) (Camphuysen et al. 2024).

Ultimately, colony location determines in what can be found in the diet. Another study executed in the Netherlands, studied foraging behaviour of a colony 30 km from the coast (Gyimesi et al. 2016). These birds almost exclusively foraged in terrestrial habitats (confirmed through GPS loggers) and had no food samples containing marine prey. The results of gathered pellets (67) of one breeding season during chick-rearing care showed the following prey types: 69% of the pellets were of terrestrial source, 19% of mixed and 12% of aquatic source. The occurrence of prey types within all pellets showed that beetles were the most common prey (84%) followed by shell remains (40%). Other common prey were moles, refuse, ants, seeds, and freshwater fish (27-36% of occurrence). Less common were bird remains, larvae, crustacea and the zebra mussel (*Dreissena polymorpha)* (6-10%) (Gyimesi et al. 2016).

The diet of another colony of lesser black-backed gulls that is situated 15 km from the coast, also showed a mostly terrestrial diet, the total amount of food from a marine origin was probably only ~15% (Camphuysen et al. 2005). The colony was sampled twice, during egg hatching in June 2005 (n=133). Diet contained mostly the remains of mammals (~40%, frequency of occurrence) mainly moles and mice, birds, mainly meadow birds and young birds of ducks and starlings (22-29%) and fish, both marine as freshwater fish (13-22%) and to a lesser extent refuse (0-7%), insects (~4%), crustaceans (~2%), bivalves (~1%) and plants (~2%). Some pellets did not contain prey remains and consisted only of grass or hair (19-30%).

Table 3-12 *Table copied from Schwemmer & Garthe (2005), showing a comparison of different studies on diet of lesser black-backed gulls along the coast of the Netherlands and Germany in the Wadden Sea region. Values are frequency of occurrence (%). Breeding status of chicks: breeding stage (B), egg stage (E).*



Location	Year	Chick status	Fish	*Liocarcinus* spp.	Molluscs	Other sub-littoral invertebrates	Terrestrial invertebrates	Plant material	Mammals and birds	Waste	Source
Terschelling	1985/1986	B/E	82/95	7/1	4/4	3/1	13/1	–/–	1/–	1/1	Noordhuis & Spaans (1992)
Various[a]	1992	B + E	81	19	?	6	20	?	1	6	Spaans et al. (1994)
Amrum	1994	B/E	15/51	24/29	48/7	–/1	–/1	1/1	–/3	2/1	Garthe et al. (1999)
Juist	1997	B/E	65/40	29/52	20/16	–/?	16/18	8/9	7/3	2/–	Kubetzki & Garthe (2003)
Amrum	1997	B	13	79	6	2	10	6	6	3	Kubetzki & Garthe (2003)
Helgoland[b]	2000–2002	B + E	69[c] 48[d]	4	–	–	4	6	–	2	Dierschke & Hüppop (2003)
Norderney	2002	B/E	45/28	23/44	13/5	4/1	45/18	28/19	11/17	11/18	This study
Amrum	2003	B/E	15/7	71/78	14/4	4/3	28/17	31/33	7/9	4/14	This study

[a] Average values from islands Terschelling, Vlieland, Texel, Shouwen and Maasvlakte
[b] Regurgitations
[c] Only discarded fishes, taken from fishing vessels
[d] Only fishes taken as natural marine prey

Besides the study on Texel, the diets of lesser black-backed gulls were studied in nearby countries like Belgium and Germany, that have comparable foraging conditions. In Germany, two other colonies on Wadden Sea islands that are close by (SE North Sea; Norderney & Amrum) were studied in 2002 (Schwemmer & Garthe 2005). Here, pellets were gathered in both the incubation and chick-rearing phase but were studied in less in detail compared to the Campuysen et al. studies. In the Norderney colony, the most common prey types during the incubation phase were fishes and terrestrial invertebrates (both in 45% of the pellets) and swimming crabs - *Liocarcinus spp*. (23% presence in all pellets). During chick-rearing this changed to *Liocarcinus spp*. being the most frequent prey (44% of all pellets), followed by fish (28%) and terrestrial invertebrates (18%). In the colony of Amrum, *Liocarcinus spp*. were the most frequent prey during the egg phase (71%), followed by terrestrial invertebrates (28%) and fishes (15%). During the chick-rearing phase, *Liocarcinus spp*. increased slightly in the diet (78% *Liocarcinus spp*., 17% terrestrial invertebrates, 7% fishes). The last colony was studied again later in 2006, and then still swimming crabs were the most common prey (69% of the pellets during incubation and 75% during chick-rearing). Analysis suggested that the diet consisted of 52-57% swimming crabs in this colony (Schwemmer et al. 2013). In both colonies, molluscs, other sublittoral invertebrates, mammals and birds and waste was also to a lesser extent part of the diet (Schwemmer & Garthe 2005).

Another study in a Wadden island colony in Germany (Spiekeroog) studied diet and behaviour in relation to habitat use (marine oriented or inland), using isotopes and pellets (Garthe et al. 2016). Isotopes are interesting for studying what chicks have eaten, but the method can only show the difference between larger categories e.g. distinguish between a marine and terrestrial-based food source. The number of pellets gathered were limited (n = 50) but showed the dual use of both marine and agricultural habitats. Most common items (besides grass 48%) in pellets were insects (38%) mainly *Coleoptera*, fish (28%) mainly of the following species (in decreasing order of abundance) grey gurnards, cod, unidentified gurnards, unidentified gadids, scad and unidentified flatfish, litter (26%), earthworms (20%), crustaceans (16%) exclusively swimming crab, mammals (12%) like northern moles and common voles, bivalves (8%), seeds (8%), polychaetes (6%) and eggs (4%). The origin of fish was likely all from discards.

In Belgium, chick diet was studied using stable isotope analysis (Sotillo et al. 2019). The colony, that was traditionally foraging in the marine and intertidal, is now increasingly using foraging opportunities created by human activities on land like agricultural fields and urban environments, and the amount of chicks that had eaten terrestrial based food ranged from 4-80%, but the data implied that most chicks were raised predominantly on a marine diet (terrestrial component was mean 30%, median 24%). The diet did not change significantly during the breeding season (Sotillo et al. 2019).

On Texel, the origin of prey remained relatively stable over the breeding season from pre-laying to egg to chick-rearing (marine or terrestrial origin), however, prey species differed over time. For marine prey for instance, the type of fish changed over time. The frequency of occurrence of lean fish *(Gadidae, Syngnathidae, Trachinidae)* and/or difficult to handle *(Belonidae, Bothidae, Pleuronectidae)* or bony fish *(Callionynidae, Cottidae, Triglidae)* decreased while fatty, small pelagic fish doubled in the diet towards the chick-rearing phase. These are for instance fish from the *Ammodytidae* and *Clypeidae* family (sandeel, herring, sprat) (Camphuysen et al. 2024). Prey species like swimming crabs and marine polychaetes were found in peaks throughout the breeding season, suggesting that these are sometimes available in larger quantities for foraging gulls at sea.

Besides the different diets between colonies, diets can also change over time. Over the measured years (2006–2021) terrestrial prey stayed in the diet in similar amounts on Texel, while marine prey declined substantially from 80-95% in all food samples to only around two-thirds or even less. Food samples of anthropogenic origin increased in frequency (Camphuysen et al. 2024). This is a trend that is also seen in other colonies, suggesting a change in supplies.

Within the same year, food availability can change, and gulls seem to be able to respond partly to unpredictable events. Lesser black-backed gulls are generalists on species level, but GPS tracking data shows that individuals often only use two or three different feeding areas that are visited repeatedly. Nevertheless, individuals could also respond to special events, for instance in a year of many common voles or other prey types that were shortly available, like swimming crabs, marine polychaetes (only available during spawning bouts), ripening berries or insects. Also birds that specialised on beam trawlers, switched to foraging on terrestrial habitats in the weekends, when the trawlers returned to the harbours (Tyson et al. 2015).

When at sea, lesser black-backed gulls are strongly attracted to fishing vessels (Camphuysen 2013), which are a source for discards, an important prey at sea, as already described from diet research in breeding colonies. Discards are even considered to be partly responsible for the growth in populations of herring gulls and lesser black-backed gulls at the end of the 20th century (Catchpole et al. 2006). Although the amount of discards has decreased since then due to stricter regulations and potentially decreases in fishing effort, estimations of the number of all seabirds that are supported by discards in the North Sea are still around 2 million birds, which is 3 million less than estimations for 1990 (Sherley et al. 2020). Several research projects at sea were done, to investigate the presence, success-rate and prey selection of seabirds following fishing vessels.

In a German study, gulls were studied while foraging in the Southeast North Sea and Wadden Sea (mostly near Germany and Denmark) (Schwemmer & Garthe 2005). Gulls were counted and their behaviour classified from a ship in May-August 2002. Lesser black-backed gulls foraged both in coastal areas as further at sea >100 km from the coast. More than half of the observed lesser black-backed gulls could be classified to a behavioural class and most of them (25.4%) were associated with fishing vessels. High numbers were observed in coastal waters (mostly shrimp trawlers) and the highest numbers were found at 40-60 km distance from the coast, mostly associated with beam trawlers (15.9% of the gulls were resting at sea and 44.7% could not be classified to a behavioural category). Associations with fishing vessels differed over the breeding season. In July and August, highest densities were associated with highest fishing effort, but this was not the case for May and June when most gulls were constrained to their breeding colony (Schwemmer & Garthe 2005).

Other studies also showed that large groups of lesser black-backed gulls were seen following beam trawlers. For instance 25-80 km north of the Wadden Sea islands (1997 June-July), flying to colonies after a successful forage trip (Flore 1997). Also gulls breeding on the Dutch Wadden Sea were observed while associated with fishing vessels. In the breeding season (1987-1993 May-August), the distribution and feeding range of herring gulls and lesser black-backed gulls was investigated using ship-based surveys in the southern North Sea. Lesser black-backed gulls were further at sea; 95% of the gulls were observed within 135 km of the coast (compared to 54 km for herring gulls). Lesser black-backed gulls were not found in high numbers along the coast in association with fishing vessels, higher numbers were found further at sea (>25km). Most observations were dominated by adult gulls (90%), but immatures were relatively frequent further out at sea (>100 km from the coast; 57% adult birds) (Camphuysen 1995).

In competition behind fishing vessels, herring gulls are more successful than lesser black-backed gulls but less than great black-backed gulls. Herring gulls lost less prey based on relative abundance present to lesser black-backed gulls, but more to great black-backed gulls. Lesser black-backed gulls dropped the fish that they took more often and the fish was more often stolen by great black-backed gulls and herring gulls, while they stole less often from the others (Camphuysen 1994). The competitive success differed per species. Overall herring gulls were more successful when fish offal and gadoids (a roundfish) was offered, compared to lesser and great black-backed gulls, compared to their relative abundance. However, the latter outcompeted the herring gull on other types of roundfish (Camphuysen 1993).

In the Belgian part of the North Sea, similar discard experiments were done between May-August of 2011. Again, discards were eaten depending on the discarded species, but selectivity by birds decreased during the chick-rearing stage (Sotillo et al. 2014). Also in the Belgian waters, lesser black-backed gulls were found further at sea compared to herring gulls. Flocks of scavengers were dominated by lesser black-backed gulls >10-20 km from the coast and further (Sotillo et al. 2014). Preferred discarded species were roundfish, followed by sole, but plaice and dab were avoided. Interestingly, more flatfish was consumed when the proportion of immature birds was larger. Besides, immatures were less successful in capturing prey compared to adults and they were more often robbed of their prey (Sotillo et al. 2014).

A smaller study that was conducted in the southern North Sea to foraging behaviour of birds around beam trawlers just above the Wadden islands in the Netherlands and Germany the end of June in 1993, showed lesser black-backed gulls and herring gulls were common around fishing vessels (Camphuysen 1993). The lesser black-backed gulls that were seen, were mostly adult. There were species-specific characteristics observed; lesser black-backed gulls consumed less offal than could be expected based on the numbers around the vessel, but they were more successful, compared to the other species around, in picking up gurnards. However, they were less successful in picking up cod and whiting compared to herring gulls and great black-backed gulls. Overall, the percentage of discarded offal (94%) and roundfish (85%) was far higher than the consumed flatfish (34%) and benthic species (0.3%) (Camphuysen 1993).

Lesser black-backed gulls were also observed to forage ‘naturally’ at sea (defined here as not foraging on discards behind fishing vessels). Lesser black-backed gulls can forage in the surface <0.6m of the sea surface for pelagic fishes and crabs.(Baptist et al. 2019). As these studies are rare in the Dutch part of the sea, we also used some studies of neighbouring countries.

In a German study by Schwemmer & Garthe (2005), 14% of the observed birds were actively searching for natural food (compared to 15.9% of the gulls were resting at sea and 44.7% of birds could not be classified to a behavioural category) and these birds were more widespread than birds following fishing vessels. The naturally foraging birds were found in highest numbers close to the shore and 60-100 km away from the coast. Interestingly, the proportion of individuals searching for natural food was highest during the morning and evening and decreased in between. This was also seen in another study, possibly because swimming crabs migrate vertically in the water column (Schwemmer et al. 2013). The amount of gulls associated with fishing vessels showed the opposite pattern, which was also seen in another study where the percentage of eaten discards and level of competition was higher between 06:00 and 15:00 compared to early mornings or afternoons/evenings (Camphuysen 1994). When lesser black-backed gulls were naturally foraging, their most common prey were crustaceans (85 times) (of which ~40% were *Liocarcinus* spp.; swimming carbs), followed by 39 fishes, 3 birds, 1 starfish and 1 bivalve. Most crustacean prey were recorded at distances up to 30km (Schwemmer & Garthe 2005). A longer study to the importance for lesser black-backed gulls to this prey *Liocarcinus* spp. showed that it can be quite determining in the diet of some colonies (Schwemmer et al. 2013). As swimming crabs have increased substantially, they can thus form an interesting prey for gulls in the North Sea. Swimming crabs were mainly caught closer to the colony (<30km) although swimming crabs were most abundant at distances of 20-70 km from the coast. Furthermore, gulls selected larger crabs than expected based on sizes of swimming crabs that were available (Schwemmer et al. 2013).

Also in other studies, observations of natural feeding lesser black-backed gulls were conducted. For instance, in June and July 1997 in the German Bight, large flocks of naturally feeding gulls were encountered while observing from ships, foraging in waters of 10-20m depth and 6-30km off the nearest colonies in areas without fishing fleet (Flore 1997).

A study on the east coast of Scotland studied MSFAs in the North Sea along the coast of Scotland (Camphuysen & Webb 1999). Herring gulls, as well as lesser black-backed gulls, profit in these situations from so called 'producers' in multi-species feeding associations; common guillemots and razorbills driving up fish towards the surface. Small and short-lived MSFAs were the most common type of associations, and mostly formed over natural prey like sandeels and small *Clupeoids* which are energy rich and fatty prey species (Camphuysen & Webb 1999). Herring gulls and lesser black-backed gulls in this area were often aiming for MSFAs while foraging (>80% of recorded offshore feeding activities in summer). During ship-based surveys in the Dutch part of the sea (2002-2009), these associations were way less common; only 1% of herring gulls and 3% of lesser black-backed gulls were observed joining feeding associations (Camphuysen 2013).

Around the Frisian Front area in the southern North Sea, lesser black-backed gulls were also observed exhibiting naturally foraging behaviour. However, gulls were mainly observed to use 'facilitated foraging' in multispecies feeding associations with common guillemots or foraging on discarded bycatch (Baptist et al. 2019).

The amount of foraging in MSFAs differed; in a year with high common guillemot densities (2006) this was seen relatively often; in this year individual gulls were associated with feeding associations or self-feeding in ~20% of the cases when no fishing vessel was near, compared to ~45% associated with an offshore platform and ~35% no association or flying (this decreased to ~10 when there was a near fishing vessel, then about 80% of the gulls were associated with fishing vessels). In a year with less common guillemots (2009) this decreased to a couple percentages. In this study, no observations were done on the prey eaten by gull, but the availability of fish in the upper 3 meters was sampled which could give an indication of prey caught. The most abundant species were sprat followed by scad, mackerel and whiting. Swimming crabs were also available, but in way lower abundance than these fish species (sprat ~20.000 versus 60 swimming crabs) (Baptist et al. 2019).

3.11.1.1 Chick diet

Some studies looked at the differences found in pellets (prey remains) and boluses (food that was thrown up by birds while handling). On Texel, the species composition of adult boluses (n=84) differed slightly with the prey remains that were found in the colony as pellets. Boluses contained more European sprat (14%) and brown shrimp (11%). Very common species in the pellets like Whiting and flatfish species were also commonly found in boluses (33% and 30% resp.). Chick boluses (n=340) also contained mostly flatfish (36%), but besides contained a relatively high percentage of the fatty pelagic fish European Sprat (25%) and sand lances (14%) (Camphuysen 2013).

In a more inland colony, where the gulls mostly fed on prey with a terrestrial origin, boluses of chicks also contained a slightly different diet composition. However, the sample size was limited to 18 boluses. The boluses also mainly had a terrestrial origin (83%), but most of the prey contained domestic waste like bread or waste meat, while in pellets from the same colony beetles were the most commonly encountered prey type. This could have been caused by the bias of pellets towards hard prey remains. Furthermore, earthworms, larvae and beetle species were identified in the boluses but less often (Gyimesi et al. 2016).

3.11.2 Diet outside the breeding season

As lesser black-backed gulls migrate, the diet is focused on and around the breeding season and of lesser black-backed gulls at sea. It is unknown whether diet between breeding and non-breeding adults differs.

3.11.3 Selection in size and/or quality

Different types of fishing vessels have different discards and this affects profitability for seabirds. Most seabirds prefer a certain shape and length depending on their own body size (Garthe & Huppop 1994). Gulls select discards with a preference for certain species: in experiments with discarded fish north of the Dutch and German islands between June and August, herring gulls and lesser black-backed gulls had a higher consumption rate of roundfish (70.7% consumed) and fish offal (65.9% consumed), compared to flatfish (30,5% consumed) and benthic invertebrates (0.3% consumed). Discarded flatfish are not ideal, because of their wide shape. During the experiments there was a clear size selection of smaller flatfish based on the size distribution provided, and fish of a width >8 cm were barely eaten (Camphuysen 1994). Garthe & Hüppop (1994) showed that lesser black-backed gulls eat, depending on the species of roundfish, an average length between 13-24 cm but can also eat fish up to ~30 cm.

3.11.4 Other variables affecting diet choice

Another interesting finding is the different habitat use (and potentially diet) between males and females in the Texel colony. Males travelled further from the colony and spent more time at sea while females foraged more on land and nearshore following shrimpers (Camphuysen et al. 2015; Tyson et al. 2015). This is, obviously, reflected in their diet, although this was not specifically reported.

3.12 Great black-backed Gull

Great black-backed gulls can mainly be seen in winter and is only since ~1995 increasing as a breeding bird but still scarce (Sovon.nl; Photo 3-31). Larger breeding numbers can be found more north from the Netherlands like Scandinavia, Russia, Iceland but also the east coast of the USA and Canada (del Hoyo et al. 1996). The breeding population here is estimated on 118-120 pairs (2024) and breeding pairs are increasing (Sovon.nl). Wintering great black-backed gulls are more common and numbers are estimated on 25.800-66.700 (2016/17-2020/21) (Sovon.nl). Great black-backed gulls were classified as Least Concern by the IUCN Red List (Birdlife International, 2025. Within the Netherlands, its conservation status is listed as favourable for the breeding population but as unfavourable as non-breeding population (Sovon.nl). The species is, just as the other gull species, a generalist species but is also described as an opportunistic predator. Its diet can consist of marine prey like fishes and invertebrates, but they can also exploit other prey like refuse, mammals and other (sea-)birds (Farmer & Leonard 2011; Rome & Ellis 2004; Washburn et al. 2013; Westerberg et al. 2019). Great black-backed gulls are also known to exploit other birds as a food source (Veitch et al., 2016; Westerberg et al., 2019). The species breeds mostly in coastal areas in the North Atlantic and the Baltic mainly on islands. In the Netherland they breed since 1993, mostly around the Wadden Sea and in the Delta estuary (Koks & Jongelen, 1998). As there are no large breeding colonies, it is harder to study the diet of this species. This affects the amount of information that is available and therefore we used some information of other countries as well.

Photo 3-31 *A great black-backed gull and lesser black-backed gull at the North Sea. Photo: S. Kühn.*

3.12.1 Diet during the breeding season

Since great black-backed gulls only recently started breeding in the Netherlands and Germany, diet studies nearby are lacking. However, the closest breeding great black-backed gulls that have been studied are found along the coast of Germany. The species is also in Germany a more recent breeding bird, and can be found in small colonies, of which the biggest is 25-30 pairs on Föhr island. On this island that is situated in the Wadden Sea, a small tracking study was done in they showed that most great black-backed gulls spent their time foraging in intertidal area (>~75% of their time) and to a lesser extent in aquatic and terrestrial habitat (Borrmann et al. 2019). However, no pellets or other food items were gathered to investigate diet.

A review study discussed the food and foraging behaviour of the great black-backed gull in north-west Europe (Gotmark 1984). Most of the studies were situated on the west coast of the United Kingdom and around the Baltic Sea. The diet of the great black-backed gull varies widely per colony and location. For instance, some studies report a complete diet of seabirds, for instance 40 breeding pairs on St. Kilda (west of Scotland) (Harris 1980) while other colonies in Scotland foraged mostly on shoals of sandeels that they caught by plunge-diving, and to a lesser extent on fish offal (Gotmark 1984). A colony in Sweden at the Baltic Sea was monitored over two years, and fish was found to be a major prey (73-82%), and to a lesser extent eggs (4-11%) and birds (6-7%). Studies executed further away (Finland, Iceland) found similar prey as mentioned above, although composition could differ. Diet could compose of fish (like fish offal, sandeels, capelins), birds and mussels (Gotmark 1984).

Another study was conducted at Skomer and Skokholm island, two islands near Wales, UK (Harris 1965). In this study, the diet was studies by stomach analysis, pellets and direct observations between March and July. The food remains showed that diet consisted mostly of birds (53%, mainly shearwaters), fish (21%, probably obtained through human activities), rabbits (15%) and refuse (7%). Stomach contents confirmed these preys, although beetles were also found in 11% of the stomachs.

Besides the above-mentioned prey, great black-backed gulls were also observed using dump sites to forage. A study on the foraging behaviour of great black-backed gulls in Northwestern Europe, described that great black-backed gulls mostly foraged on refuse dumps (33%), followed by effluent; a liquid waste discharge from for instance sewers or fish processing plants (32%), mud (17%), and water (15%) and were often seen eating carrion ranging from fish to seal carcasses (Hunt & Hunt 1973)

A more recent study on the isle of May, an island on the east coast of Scotland, investigated the diet of the great black-backed gull during the breeding season using stable isotopes (Lopez 2023). This method can detect the diet of individual gulls in rough categories. While breeding, roughly 75% of the diet contained marine prey, followed by anthropogenic prey of terrestrial origin (~23%) and natural terrestrial prey (~5%). Outside the breeding period, the percentage of marine prey in the diet was higher, especially in autumn (~95%). In the early non-breeding period (January-February), the percentage of anthropogenic terrestrial prey was still relatively high (~23%). Although the type of prey cannot be distinguished, regurgitated prey was gathered while handling the birds. Marine prey could be shoaling fish like *Clupeidae sp, Gadidae sp* and *Ammodytidae sp.*, demersal fish like whiting, plaice and haddock, intertidal prey like swimming crabs or cephalopods and seabirds like eider ducklings (*Somateria mollissima)* or Atlantic puffin (*Fratercula arctica)*. Anthropogenic prey of terrestrial origin could contain grain, invertebrates or refuse and natural prey were European rabbits (*Oryctolagus cuniculus)*.

3.12.2 Diet outside the breeding season

Again, there is very little information on the diet of great black-backed gulls in the Netherlands outside the breeding season. There is only some anecdotal information. For instance some observations of great black-backed gulls eating other birds like great crested grebe (*Podiceps cristatus)*, young pied avocets (*Recurvirostra avosetta)* (late summer), or trying to eat common mergansers (*Mergus merganser)* (Heg 1991; Shillcock 1991). Other diet information is taken from neighbouring countries.

In Helgoland, an island in the German Wadden Sea, pellets (n=~15,000) of herring gulls and great black-backed gulls were gathered on roosting piers throughout the year (1999) in research to the effect of large gulls on passerine predation (Dierschke 2001). Unfortunately, no difference could be made between pellets of the two species. There were about twice the amounts of herring gulls counted compared to great black-backed gulls over the year, but relative abundance great black-backed gulls was slightly higher in July-September (47-62% out of total). The main prey were fish and crustaceans, but during migratory seasons of passerines (March to May & August to November) up to 7% of the pellets contained remains of passerines. Other prey were kelp fly larvae that came available during storms (October-December), seabird remains (mainly in winter months) and non-passerine birds (mostly chicks of kittiwakes and guillemots). Diet in the period of higher abundance of great black-backed gull (July-September) contained mostly of fish (~48-72%), crustaceans (18-37%) and to a lesser extent molluscs (<3%), algae (<2%), garbage (<1%), kelp (<2%) and passerine birds (<1%). Non-passerine birds (mainly seabird chicks) varied from zero to 9% of the diet.

In a study on the effect of trawling around the German island of Helgoland, diet of herring gulls and great black-backed gulls was studied (Hüppop & Wurm 2000). Pellets (n=233) were gathered in the winter of 1997-1998 on piers where the gulls were resting at night. It was not possible to distinguish between the two species, as they roost together. Pellets were gathered during periods with cod fishery and without. When fishery discards were available in the proximity of the island, 83-87% of the pellets contained discarded fish remains and 70-73% contained these types of discards exclusively. Cod was the most common species found, in a few pellets whiting, scad and some other species occurred. Other prey types during this period were discarded invertebrates, non-discarded fish, non-discarded invertebrates and terrestrial prey or marine invertebrates (all <12%). When discards were not available nearby, gulls foraged at rocky intertidal areas, mostly foraging on hooknose fish eggs *Agonus cataphractus* that are spawning in the shallow waters (~30-65% of the pellets) and invertebrate prey (~15-30%) like blue mussels (*Mytilus edulis)* and shore crab (*Carcinus meanas)*. Besides, terrestrial prey/garbage was found in ~20-30% of the pellets. Nevertheless, discard remains were still present in 12-32% of the pellets when no fisheries were near, suggesting a wider foraging range than the observers of trawlers in the area could spot. Besides the change in diet, also the numbers gulls and the body condition (relation between body mass and head+bill length) was measured by catching gulls in the night. Both body condition of the herring gull as of the great black-backed gull was lower in periods without fishing activity nearby, although the sample size was low (11 great black-backed gulls and 17 herring gulls). Without trawling activity, herring gulls had a 13% lower body condition compared to trawling activity and great black-backed gulls showed a mean decline of 24%. This effect was only seen in adult gulls. Three gulls were caught twice, and they showed the same trend. Besides the drop in body condition, there were way less gulls present at the island when fisheries dropped. Herring gull presence dropped to more than half of the numbers but increased again comparable to times with fishing activity when hooknose eggs were available in the area. Great black-backed numbers fell even more to ~25% of the numbers when no fishing was available. Numbers did not increase in periods with hooknose eggs, but they might have already left to breeding areas up north (Hüppop & Wurm 2000).

Great black-backed gulls are also strongly attracted to fishing vessels. Although the amount of discards decreased since then due to stricter regulations and potentially decreases in fishing effort, estimations of the number of birds that are supported by discards in the North Sea are still around 2 million birds, which is 3 million less than estimations for 1990 (Sherley et al. 2020). Several research projects at sea were done, to investigate the presence, success-rate and prey selection of seabirds following fishing vessels. Great black-backed gulls seem to target slightly different prey types compared to the other large gull species.

In competition behind fishing vessels, great black-backed gulls are often more successful than lesser black-backed gulls and herring gulls. Besides, great black-backed gulls and herring gulls took fish from lesser black-backed gulls more often (Camphuysen 1994). A smaller study that was conducted in the Southern North Sea to foraging behaviour of birds around beam trawlers just above the Wadden islands in the Netherlands and Germany the end of June in 1993, showed that great black-backed gulls were common birds around the vessels (but lesser black-backed gulls and herring gulls were more common) (Camphuysen 1993). The great black-backed gulls that were seen, were mostly subadult. There were species-specific characteristics observed; the great black-backed gull consumed less offal then could be expected based on the numbers around the vessel, but they were most successful, compared to the other species around, in picking up roundfish, especially cod and whiting (and slightly less in gurnard sp.).

A discard study in the Baltic Sea Between June and December 1998 showed that the great black-backed gull was the second most common gull in their utilization of discards and offal at sea after the herring gull (Garthe & Scherp 2003). During experimental discarding, gadoids (cod and whiting), clupeids (herring and sprat), scad, rockling and offal was consumed in high proportions (78-90%) by seabirds, but the proportion of flatfish consumed was extremely low (0-9%).

Another study looked specifically into multi-species feeding associations off the British east coast (Camphuysen & Webb 1999). Great black-backed gulls were especially numerous in small, short-lived flocks over tightly clumped prey around fishing vessels and they were present in ~60% of these type of feeding associations. Great black-backed gulls were not common in feeding associations around cetaceans and self-sustained (‘natural’) MSFAs. Furthermore, great black-backed gulls were observed feeding jointly on seal, whale and bird carcasses (Camphuysen & Webb 1999).

3.12.3 Selection in size and/or quality

Great black-backed gulls selected slightly bigger fish compared to what herring gulls and lesser black-backed gulls picked up, but the difference was minimal (~3 cm bigger for gurnards and 1-2 cm bigger for cod/whiting). Overall, the percentage of discarded offal (94%) and roundfish (85%) was way higher than the consumed flatfish (34%) and benthic species (0,3%) (Camphuysen 1993).

In a discard study in the Baltic Sea Between June and December 1998 consumption rate was dependent on fish size in cod and whiting, but not so much for clupeids and dab. Cod was taken in a high rate <26cm and mostly by herring gulls, when larger cod was consumed, this was more often or exclusively (in fish >35cm) done by great black-backed gulls (Garthe & Scherp 2003).

4 Conclusion & recommendations

In this section, the findings described in the previous sections are summarised and some knowledge gaps are described. We discuss the findings per foraging group as described in Table 1-1; coastal diving species, pelagic species and surface feeders.

4.1.1 Coastal diving species

4.1.1.1 Conclusion diet coastal diving species

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

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

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

4.1.1.2 Knowledge gaps coastal diving species

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

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

4.1.2 Pelagic species

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

4.1.2.1 Diet of pelagic divers

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

4.1.2.2 Diet of pelagic surface species

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

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

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

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

4.1.2.3 Knowledge gaps pelagic species

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

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

4.1.2.4 Knowledge gaps pelagic surface species

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

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

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

4.1.3 Surface feeders

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

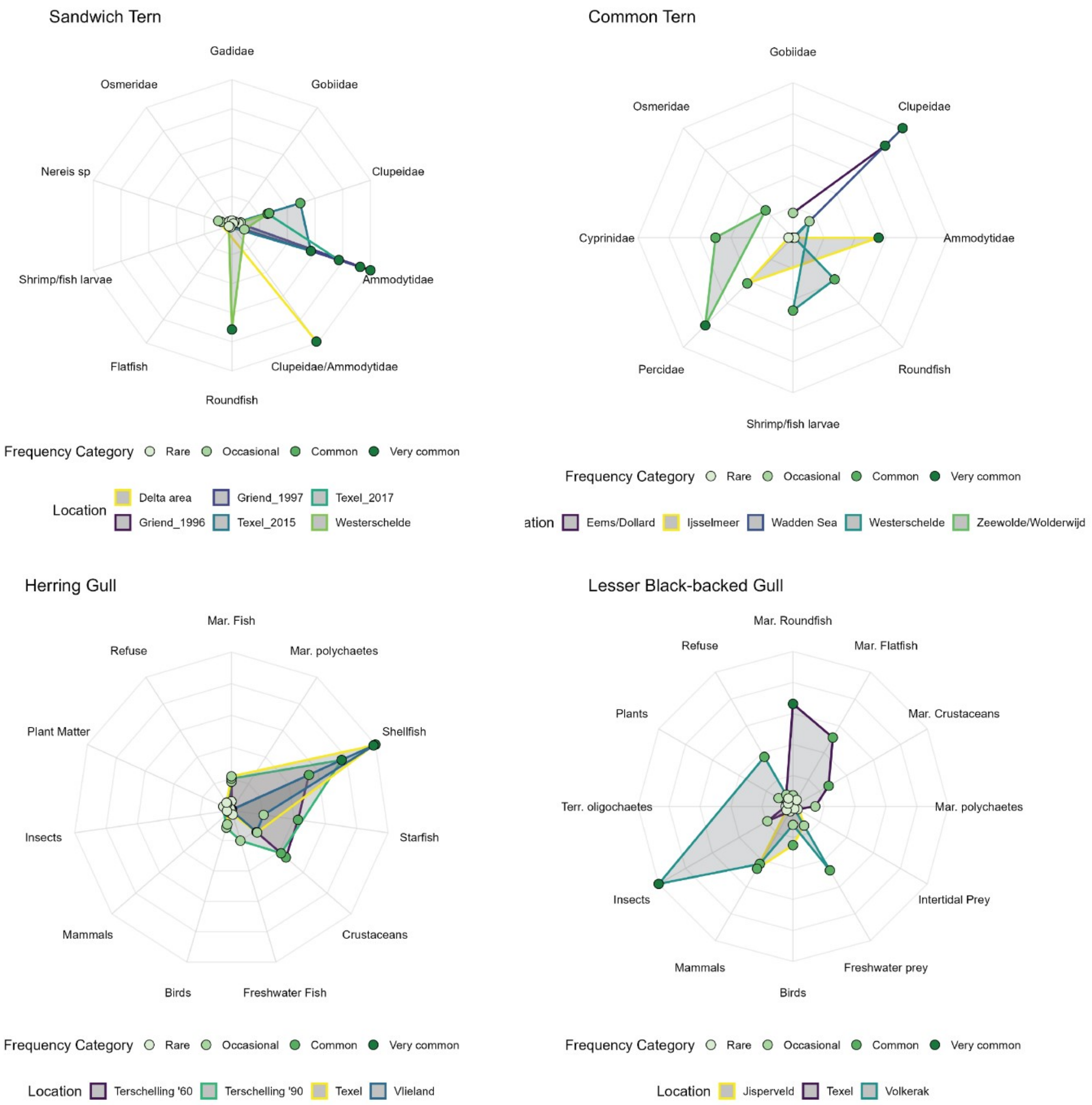


Figure 4-1 *Summary of the literature of diet of surface feeding breeding birds of the Netherlands. Only Dutch studies were used for these figures.*

4.1.3.1 Diet of surface feeders

Both Sandwich tern and common tern breed in the Netherlands in large numbers. Although the diet of both species contains small pelagic marine fish such as Clupeidae (herring, sprat), their dietary preferences differ (Figure 4-1). For Sandwich terns, the importance of Clupeidae and Ammodytidae (sandeel spp.) throughout the chick-rearing period is evident, both for adults and chicks (van Bemmelen et al., 2022). Particularly for adult Sandwich terns, other prey species such as ragworms (Nerediidae), and different flatfish and round fish species can supplement their diet (Brabant 2004; Brenninkmeijer et al. 2002; Courtens et al. 2017; Hoffmann 2000; Stienen 2006; van Bemmelen et al. 2022; van der Beek 2017). However, the respective importance of the different prey groups is likely influenced by chick age, variability in food availability due to daily and seasonal effects, variability between years and colony location, and different environmental factors at the foraging location. Sandwich terns eat mainly small fish (ranging from 5-14 cm), but prey length increases with growing chicks (Engels 2015; Stienen & Brenninkmeijer 1994, 2002; van Bemmelen et al. 2022; van der Meer 2018). New results of stomach contents from individuals that died from avian influenza in the Dutch Delta area and Wadden Sea showed that sandeels and clupeids were the most abundant prey, followed by gadoids, gobies and estuarine roundfish. Prey ranged from 5-23 cm.

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

All large gulls are generalist species; they utilise a variety of resources and/or foraging areas although they often exhibit individual specialisation. Gulls make use of a variety of habitats, including land-based resources like landfills and agricultural land (Isaksson et al. 2015). Although the three focal gull species selected for this work package show similarities, there are also differences in their feeding patterns (Figure 4-1, Figure 4-2). For the herring gull and lesser black-backed gull, diet studies that were (mainly) executed in the Netherlands are highlighted, while for the great black-backed gull, most of the literature originated from outside the Netherlands.

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

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

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

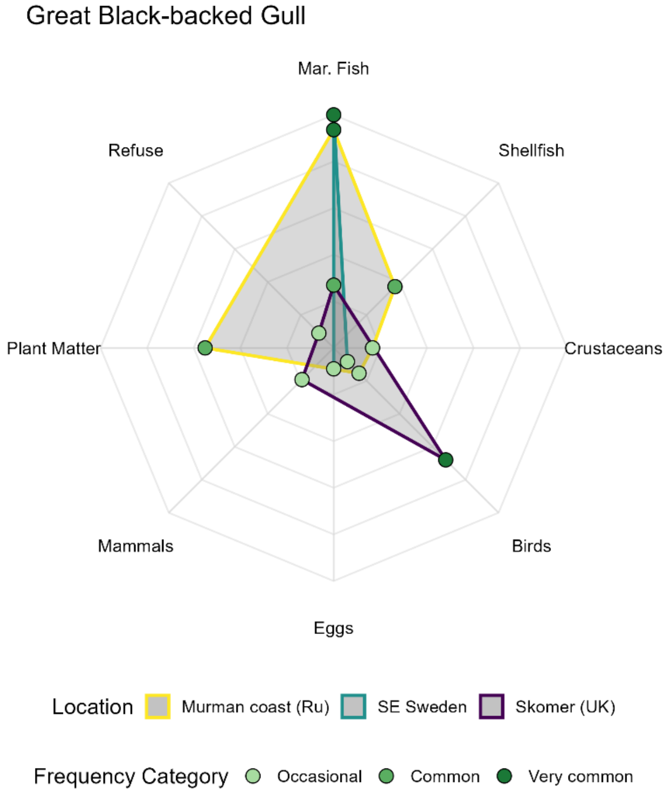


Figure 4-2 *Summary of the diet of the surface feeder Great Black-backed Gull breeding mainly outside the Netherlands. Only European studies were used for these figures, no Dutch data was available.*

4.1.3.2 Knowledge gaps coastal surface feeders

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

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

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

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

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

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

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

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

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

References

Amundsen P.A., Gabler H.M. & Staldvik F.J. 1996. A new approach to graphical analysis of feeding strategy from stomach contents data-modification of the Costello (1990) method. J. Fish Biol. 48: 607-614. https://doi.org/10.1111/j.1095-8649.1996.tb01455.x

Anker-Nilssen, T, Barrett, R, Christensen-Dalsgaard, S, Dehnhard, N, Descamps, S, Systad, GH, Moe, B, Reiertsen, TK, Bustnes, JO, Erikstad, K-E (2021) Key-site monitoring in Norway 2020, including Svalbard and Jan Mayen, Trondheim, Norway, pp 15. https://seapop.no/wp-content/uploads/2021/06/seapop-short-report-1-2021.pdf

Arnott, SA, Ruxton, GD (2002) Sandeel recruitment in the North Sea: demographic, climatic and trophic effects. Marine Ecology Progress Series 238: 199-210. https://doi.org/10.3354/meps238199

Baptist, M.J., Van Bemmelen, R.S.A., Leopold, M.F., De Haan, D., Flores, H., Couperus, B., Fassler, S., Geelhoed, S.C.V., 2019. Self-foraging vs facilitated foraging by Lesser Black-backed Gull (Larus fuscus) at the Frisian Front, the Netherlands. Bull. Mar. Sci. 95, 29–43. https://doi.org/10.5343/bms.2017.1179

Barrett, R (2003) The food of razorbill *Alca torda* chicks on Hornoya, North Norway. Ornis Norvegica 26: 48-54. doi https://www.researchgate.net/profile/Robert-Barrett/publication/286884641

Barrett, RT (2007) Food web interactions in the southwestern Barents Sea: black-legged kittiwakes *Rissa tridactyla* respond negatively to an increase in herring *Clupea harengus*. Marine Ecology Progress Series 349: 269-276. https://doi.org/10.3354/meps07116

Barrett, RT, Camphuysen, K, Anker-Nilssen, T, Chardine, JW, Furness, RW, Garthe, S, Hüppop, O, Leopold, MF, Montevecchi, WA, Veit, RR (2007) Diet studies of seabirds: a review and recommendations. ICES Journal of Marine Science 64: 1675-1691. https://doi.org/10.1093/icesjms/fsm152

Becker, P. H., & Specht, R. (1991). Body mass fluctuations and mortality in common tern *Sterna hirundo* chicks dependent on weather and tide in the Wadden Sea. *Ardea*, *79*, 45–56.

Becker, P. H., Frank, D., & Sudmann, S. R. (1993). Temporal and spatial pattern of common tern (*Sterna hirundo*) foraging in the Wadden Sea. *Oecologia*, *93*(3), 389–393. https://doi.org/10.1007/BF00317883

Becker, P. H., & Ludwigs, J.-D. (2004). *Sterna hirundo* Common Tern. *BWP Update*, *6*(1 and 2), 91–137.

Becker, P. H., Frank, D., & Wagener, M. (1997). Luxury in freshwater and stress at sea? The foraging of the Common Tern *Sterna hirundo*. *Ibis*, *139*(2), 264–269. https://doi.org/10.1111/j.1474-919X.1997.tb04624.x

Becker, P. H., Frank, D., & Walter, U. (1987). Geographische und jährliche Variation der Ernägrung der Flußseeschwalbe (*Sterna hirundo*) an der Nordseeküste. *Journal of Ornithology*, *128*(4).

Bergman R.D. & Derksen D.V. 1977. Observations on Arctic and Red-throated Loons at Storkersen Point, Alaska. Arctic 30: 41-51.

Bicknell, A.W.J., Oro, D., Camphuysen, K.C.J., Votier, S.C., 2013. Potential consequences of discard reform for seabird communities. J. Appl. Ecol. 50, 649–658. https://doi.org/10.1111/1365-2664.12072

BirdLife International (2018) Species factsheet: Common Murre *Uria aalge*. Downloaded from https://datazone.birdlife.org/species/factsheet/common-murre-uria-aalge (Accessed: 18/05/2025)

BirdLife International (2021) Species factsheet: Razorbill *Alca torda*. Downloaded from https://datazone.birdlife.org/species/factsheet/razorbill-alca-torda (Accessed: 03/06/2025)

BirdLife International (2025) IUCN Red List for birds. Downloaded from https://www.birdlife.org/projects/iucn-red-list/ on 28/08/2025

BirdLife International. (*Sterna hirundo (amended version of 2018 assessment)* (The IUCN Red List of Threatened Species 2019 No. e. T22694623A155537726). https://www.iucnredlist.org/species/22694623/155537726

BirdLife International. (2018). Species Factsheet: Common Tern *Sterna Hirundo*. BirdLife DataZone. https://datazone.birdlife.org/species/factsheet/common-tern-sterna-hirundo#Citations

BirdLife International. (2024, 2025). Species factsheet: *Sandwich Tern Thalasseus sandvicensis.* BirdLife DataZone. https://datazone.birdlife.org/species/factsheet/sandwich-tern-thalasseus-sandvicensis?utm_source=chatgpt.com

BirdLife International (2018) *Morus bassanus* The IUCN Red List of Threatened Species

Blake, BF (1984) Diet and fish stock availability as possible factors in the mass death of auks in the North Sea. Journal of Experimental Marine Biology and Ecology 76: 89-103. https://doi.org/10.1016/0022-0981(84)90058-3

Blake, BF, Dixon, TJ, Jones, PH, Tasker, ML (1985) Seasonal changes in the feeding ecology of guillemots (*Uria aalge*) off north and east Scotland. Estuarine, Coastal and Shelf Science 20: 559-568. https://doi.org/10.1016/0272-7714(85)90107-6

Bodey TW, Cleasby IR, Votier SC, Hamer KC and others (2018) Frequency and consequences of individual dietary specialisation in a wide-ranging marine predator, the northern gannet. Marine Ecology Progress Series 604:251-262. https://doi.org/10.3354/meps12729

Boecker, M. (1967). Vergleichende Untersuchungen zur Nahrungs- und Nistökologie der Flußseeschwalbe (*Sterna hirundo L.*) und der Küstenseeschwalbe (Sterna paradisaea Pont.). *Bonner zoologische Beiträge*, *18*(1/2), 15–126.

Bolnick, D.I., Yang, L.H., Fordyce, J.A., Davis, J.M., Ecology, S., Oct, N., 2002. Measuring Individual-Level Resource Specialization. Ecology 83, 2936–2941.

Borrmann, R.M., Phillips, R.A., Clay, T.A., Garthe, S., 2019. High foraging site fidelity and spatial segregation among individual great black-backed gulls. J. Avian Biol. 50, 1–10. https://doi.org/10.1111/jav.02156

Brabant, R. (2004). Vergelijkende studie van het dieet van de grote stern *Sterna sandvicensis*. Universiteit Gent.

Brenninkmeijer, A., Fouw, J. D., & Doeglas, G. (2002). Foerageergedrag van sterns in de westelijke Westerschelde in 2002*.* (A&W-rapport No. 346). Altenburg & Wymenga Ecologisch oderzoek. http://rgdoi.net/10.13140/RG.2.1.5082.3207

Bull, J, Wanless, S, Elston, D, Daunt, F, Lewis, S, Harris, M (2004) Local-scale variability in the diet of black-legged kittiwakes *Rissa tridactyla*. Ardea 92: 43-52.

Bukacińska, M., Bukaciński, D., Spaans, A.L., 1996. Attendance and diet in relation to breeding success in Herring Gulls (*Larus argentatus*). Auk 113, 300–309.

Burnell, D (2023) Northern Fulmar *Fulmarus glacialis*. In: Burnell, D, Perkins, AJ, Newton, SF, Bolton, M, Tierney, TD, Dunn, TE (eds) Seabirds count. A census of breeding seabirds in Britain and Ireland (2015-2021). Lynx Nature Books, Barcelona, pp 43-58.

Cadée, G.C., 2001. Zilvermeeuwen profiteren van sterven van *Ensis Directus*. Het zeepaard 61, 133–140.

Caliendo, V, Kleyheeg, E, Beerens, N, Camphuysen, KCJ, Cazemier, R, Elbers, ARW, Fouchier, RAM, Kelder, L, Kuiken, T, Leopold, M, Slaterus, R, Spierenburg, MAH, van der Jeugd, H, Verdaat, H, Rijks, JM (2024) Effect of 2020-21 and 2021-22 Highly Pathogenic Avian Influenza H5 Epidemics on Wild Birds, the Netherlands. Emerging Infectious Diseases 30: 50-57. https://doi.org/10.3201/eid3001.230970

Camphuysen CJ, van Dijk J (1983) Zee- en kustvogels langs de Nederlandse kust, 1974-79. Limosa 56:81-230

Camphuysen, CJ (1989) Crash van pas uitgevlogen Drieteenmeeuwen (*Rissa tridactyla*) op de Nederlandse kust, Augustus 1987. De Graspieper 9: 11-17.

Camphuysen, CJ (1990) Dieet, leeftijd en geslacht van de Zeekoet *Uria aalge* in de Nederlandse Noordzee in het voorjaar. Sula 4: 41-54.

Camphuysen, C.J. (19930 Fourageermogelijkheden voor zeevogels in de boomkorvisserij: een verkennend onderzoek. Sula 7, 81–104.

Camphuysen, K, Keijl, G (1994) Leeftijd, geslacht, conditie en voedsel van Zeekoeten *Uria aalge* betrokken bij de massastranding op de Hollandse kust, november 1990. Sula 8: 257-267.

Camphuysen C.J. & Leopold M.F. (1994). Atlas of seabirds in the southern North Sea. IBN Research report 94/6, NIOZ Report 1994-8, Institute for Forestry and Nature Research, Netherlands Institute for Sea Research and Dutch Seabird Group, Texel.

Camphuysen, KC (1994) Scavenging seabirds at beamtrawlers in the southern North Sea: distribution, relative abundance, behaviour, prey selection, feeding efficiency, kleptoparasitism and the possible effects of the establishment of 'protected areas' Royal Netherlands Institute for Sea Research (NIOZ), pp 47.

Camphuysen, C.J. (19940 Flatfish selection by herring gulls *Larus argentatus* and lesser black- backed gulls *Larus fuscus* scavenging at commercial beamtrawlers in the southern North Sea. Netherlands J. Sea Res. 32, 91–98. https://doi.org/10.1016/0077-7579(94)90031-0

Camphuysen, CJ (1995) Het voedsel van Zeekoeten *Uria aalge* voor de Zeeuwse kust, december 1991. Sula 9: 164-166.

Camphuysen, C.J. (1995) Herring gull Larus argentatus and Lesser Black-backed Gull L fuscus feeding at fishing vessels in the breeding season: Competitive scavenging versus efficient flying. ARDEA 83, 365–380.

Camphuysen, C. J., Calvo, B., Durinck, J., Ensor, K., Follestad, A. W. F. R., Furness, R.W.; Garthe, S.; Leaper, G.; Skov, H.; Tasker, M.L.; Winter, C.J. N. (1995). Consumption of discards by seabirds in the North Sea. *NIOZ-rapport*, (5).

Camphuysen, K, Garthe, S (1997) An evaluation of the distribution and scavenging habits of northern fulmars (*Fulmarus glacialis*) in the North Sea. ICES Journal of Marine Science 54: 654-683. https://doi.org/10.1006/jmsc.1997.0247

Camphuysen, K (1998) Het voorkomen van de Alk *Alca torda* in Nederlandse wateren. Limosa 71: 69-77. doi

Camphuysen K.C.J., Barreveld H., Dahlmann G. & van Franeker J.A. (1999). Seabirds in the North Sea demobilized and killed by Polyisobutylene (C4H8)n (PIB). Mar. Poll. Bull. 38: 1171-1176. https://doi.org/10.1016/S0025-326X(99)00152-6

Camphuysen, CJ, Wright, P, Leopold, M, Hüppop, O, Reid, J (1999) A review of the causes, and consequences at the population level, of mass mortalities of seabirds, Copenhagen, Denmark, pp 51-66.

Camphuysen, K.C.J., Webb, A. (1999) Multi-species feeding associations in North Sea seabirds: Jointly expoiting a patchy environment. Ardea 87, 177–198.

Camphuysen, C, Garthe, S (2000) Seabirds and commercial fisheries: population trends of piscivorous seabirds explained. In: Kaiser, MJ, De Groot, SJ (eds) The effects of fishing on non-target species and habitats: Biological, conservation and socio-economic issues. Blackwell, Oxford, UK, pp 163-184.

Camphuysen CJ (2001) Northern gannets *Morus bassanus* found dead in The Netherlands, 1970-2000. Atl Seabirds 3:15-30

Camphuysen C.J. & Leopold M.F. (2004). The Tricolor oil spill: characteristics of seabirds found oiled in The Netherlands. Atlantic Seabirds (special issue) 6: 109-128.

Camphuysen, K, de Vreeze, F (2005) De Drieteenmeeuw als broedvogel in Nederland. Limosa 78: 65-74. doi

Camphuysen, K, Leopold, M (2005) Aangespoeld: Het voedsel van roodkeelduikers, zeekoeten en alken voor de Noord-Hollandse kust in de winter van 2004/2005. Nieuwsbrief NZG 6: 8-9. doi https://natuurtijdschriften.nl/pub/557480/NNZG2005006003006.pdf

Camphuysen, K., Camphuijsen, D.C., Van Spanje, T.M. (2005) Het voedsel van de kleine mantelmeeuwen van het wormer- en jisperveld. Limosa 78, 145–154.

Camphuysen, CJ (2006) Wat een jonge zeekoet al niet uit een eikenbos kan halen. Nieuwsbrief NZG 7: 5-5. doi

Camphuysen C.J. (2007a). Gaviidae: Divers or loons. Technical documents 4.1, Handbook on Oil Impact Assessment, version 1.0. (living document, available via ResearchGate).

Camphuysen CJ (2007b) Massastranding jan van genten op Texel, april 2006. Nieuwsbrief NZG 3-5

Camphuysen, K, Leopold, M (2007) Drieteenmeeuw vestigt zich op meerdere platforms in Nederlandse wateren. Limosa 80: 153-156.

Camphuysen, CJ, Bao, R, Nijkamp, H, Heubeck, M (2007) Handbook on oil impact assessment. European Commission / NIOZ / Sea Alarm Foundation, Texel, The Netherlands, pp 195. https://eurowa.eu/resource/handbook-on-oil-impact-assessment-for-seabirds/

Camphuysen, C, Schouten, S, Gronert, A (2010) Mystery spill of Polyisobutylene (C4H8) n off the Dutch coast affecting seabirds in March 2010. Seabird 23: 143-145.

Camphuysen K (2011) Northern gannets in the North Sea: foraging distribution and feeding techniques around the Bass Rock. Br Birds 104:60

Camphuysen, C.J. (2013) A historical ecology of two closely related gull species (*Laridae*): multiple adaptations to a man-made environment. Ph.D. Thesis, University of Groningen.

Camphuysen, C.J., Shamoun-Baranes, J., Van Loon, E.E., Bouten, W. (2015) Sexually distinct foraging strategies in an omnivorous seabird. Mar. Biol. 162, 1417–1428. https://doi.org/10.1007/s00227-015-2678-9

Camphuysen, CJ, Henderson, JR, with major contribution from, Velilla, E, Kühn, S, Leopold, MF, Somes, R (2017) North Sea Fish and their remains. Royal Netherlands Institute of Sea Research & Pisces Conservation Ltd, Texel, The Netherlands.

Camphuysen C.J. (2022). Mission accomplished: chronic marine oil pollution now at acceptable levels, with North Sea Guillemots as sentinels. Seabird 34: 1-32.

Camphuysen, C (2024) Beached bird surveys in The Netherlands, summer 2023 and winter 2023/24. Royal Netherlands Institute for Sea Research, Texel, The Netherlands, pp 57.

Camphuysen, K., van Donk, S.C., Shamoun-Baranes, J., Kentie, R. (2024) The annual cycle, breeding biology and feeding ecology of the Lesser Black-backed Gull *Larus fuscus*. Ardea 112, 31–65. https://doi.org/10.5253/arde.2023.a7

Camphuysen, C.J., Lieshout, S., (2024). Zwarte Zee-eenden in Nederland - foerageergebieden, dagritmes en ruimtegebruik in de Noordzeekustzone. Limosa 97, 145–161.

Carboneras, C. and G. M. Kirwan (2020). Common Scoter (*Melanitta nigra*), version 1.0. In Birds of the World (J. del Hoyo, A. Elliott, J. Sargatal, D. A. Christie, and E. de Juana, Editors). Cornell Lab of Ornithology, Ithaca, NY, USA.

Catchpole, T.L., Frid, C.L.J., Gray, T.S. (2006) Importance of discards from the English Nephrops norvegicus fishery in the North Sea to marine scavengers. Mar. Ecol. Prog. Ser. 313, 215–226.

Ceia, F.R., Ramos, J.A. (2015) Individual specialization in the foraging and feeding strategies of seabirds: a review. Mar. Biol. 162, 1923–1938. https://doi.org/10.1007/s00227-015-2735-4

Clarke K.R. & Warwick R.M. (2001). Change in marine communities: an approach to statistical analysis and interpretation. PRIMER-E Limited, Plymouth.

Coulson, J (2011) The Kittiwake. T & AD Poyser, London.

Courtens, W., Stienen, E. W. M., & van der Walle, M. (2007). Het broedseizoen 2007 te Zeebrugge: Een eerste impressie (No. 8; Vogelnieuws: ornithologische nieuwsbrief van het Instituut voor Natuur-en Bosonderzoek, pp. 16–18).

Courtens, W., Verstraete, H., Vanermen, N., Van De Walle, M., & Stienen, E. W. M. (2017). Faecal samples reveal the diet of breeding adult Sandwich terns *Thalasseus sandvicensis* in Belgium and the southern part of the Netherlands. Journal of Sea Research, 127, 182–193. https://doi.org/10.1016/j.seares.2017.03.014

Craeymeersch, J.A., Engelberts A. & Buus J. (1991). Evaluatie-onderzoek grootschalige locatie: onderzoek naar de effecten op bodemdieren: voortgangsreportage september 1990. Rapport 1991-01 Delta Instituut

Cramp S. & Simmons K.E.L. (1977). The Birds of the Western Palearctic, Vol 1. Oxford Univ. Press, Oxford: 43-49.

Cristol, D.A., Akst, J.G., Curatola, M.K., Dunlavey, E.G., Fisk, K.A., Moody, K.E. (2017) Age-Related Differences In Foraging Ability Among Clam-Dropping Herring Gulls (*Larus argentatus*). Wilson J. Ornithol. 129, 301–310. https://doi.org/10.1676/15-024.1

d'Entremont KJ, Guzzwell LM, Wilhelm SI, Friesen VL, Davoren GK, Walsh CJ, Montevecchi WA (2022) Northern Gannets (*Morus bassanus*) breeding at their southern limit struggle with prey shortages as a result of warming waters. ICES Journal of Marine Science 79:50-60. https://doi.org/10.1093/icesjms/fsab240

Daunt F, Wanless S, Greenstreet SP, Jensen H, Hamer KC, Harris MP (2008) The impact of the sandeel fishery closure on seabird food consumption, distribution, and productivity in the northwestern North Sea. Canadian journal of fisheries and aquatic sciences 65:362-381. https://doi.org/10.1139/f07-164

Davies RD (2012) Foraging behaviour and population dynamics of northern gannets over a period of environmental change, Vol. University of Leeds

Davies, JG, Humphreys, EM, Evans, T, Howells, RJ, O'Hara-Murray, R, Pearce-Higgins, JW (2023) Seabird abundances projected to decline in response to climate change in Britain and Ireland. Marine Ecology Progress Series 725: 121-140. doi https://doi.org/10.3354/meps14462

Davis R.A (1972) A comparative study of the use of habitat by Arctic loons and red-throated loons. PhD Dissertation, University of Western Ontario, Digitized Theses 575. https://ir.lib.uwo.ca/digitizedtheses/575

De Gee, A, Baars, M, Van der Veer, H (1991) De ecologie van het Friese Front - waarnemingen aan een biologisch-rijke zone in de noordzee, gelegen tussen de zuidelijke bocht en de oestergronden. NIOZ 1991-2, Texel, Netherlands, pp 96.

de Graaf, J. (2016). Food provisioning and foraging conditions of breeding Sandwich terns *(Thalasseus sandvicensis)* in the Dutch Wadden Sea. Wageningen Univeristy Research.

del Hoyo, J., Elliott, A., Sargatal, J. (1996) Handbook of the birds of the world. Volume 3.

DePooter, D (2010) Comparative study of the diet of common guillemots *Uria aalge* and razorbills *Alca torda*, collected during beached bird surveys along the Belgian coast between 2002 and 2010. MSc Thesis. Faculty of Science, University Gent/INBO, Gent, Belgium.

Den Hollander N. (1993). Zwarte Zeeeenden (*Melanitta nigra*) en schelpdiervisserij. Studentenverslag NIOZ en DLO-IBN, Texel

Dias, MP, Martin, R, Pearmain, EJ, Burfield, IJ, Small, C, Phillips, RA, Yates, O, Lascelles, B, Borboroglu, PG, Croxall, JP (2019) Threats to seabirds: A global assessment. Biological Conservation 237: 525-537. doi https://doi.org/10.1016/j.biocon.2019.06.033

Dierschke, A.-K., Hüppop, O. (2003) Langfristige Veränderungen in der Ernährung von Silbermöwen (*Larus argentatus*) auf Helgoland unter dem Einfluss der Fischerei mit Vergleichen zur Heringsmöwe (*Larus fuscus*). Seevögel 24, 1–11.

Dierschke, V. (2001) Large gulls as predators of passerine landbirds migrating across the southeastern North Sea. Ornis Svecica 11, 171–180.

Dierschke, V, Garthe, S (2022) Bestandsentwicklung und Gefährdungsfaktoren des Eissturmvogels *Fulmarus glacialis* im Nordost-Atlantik. Seevögel (Sonderheft, Dez. 2022; in German with English summary) 43: 65-71. doi https://www.jordsand.de/2023/01/25/sonderheft-%C3%BCber-eissturmvogel-ver%C3%B6ffentlicht/

Dirksen S., R.H. Witte & M.F. Leopold (2005). Nocturnal movements and flight altitudes of Common Scoters *Melanitta nigra*. Research north of Ameland and Terschelling, February 2004, for the Baseline study Near Shore Windfarm. Report 05-062. Bureau Waardenburg, Culemborg.

Durinck, J., Christensen, K.D., Skov, H., Danielsen, F., Scoter, V., (1993). Diet of the Common Scoter *Melanitta nigra* and Velvet Scoter *Melanitta fusca* wintering in the North Sea. Ornis Fenn. 215–218.

Durinck J., Skov H., Jensen F.P. & Pihl S. (1994a). Important marine areas for wintering birds in the Baltic Sea. EU DG XI research contract no. 224/90-09-01, Ornis Consult Report 1994: 1-110, Copenhagen, pp 48-49.

Durinck J., Skov H., Danielsen F. & Christensen K.D. (1994b). Vinterføden hos Røkstrubet Lom Gavia stellata i Skagerrak [Winter food of Red-throated Divers *Gavia stellata* from the North Sea coast of Jutland]. Dansk Orn. Foren. Tidsskr. 88: 39-41.

Dänhardt, A., Fresemann, T., & Becker, P. H. (2011). To eat or to feed? Prey utilization of Common Terns *Sterna hirundo* in the Wadden Sea. Journal of Ornithology, 152(2), 347–357. https://doi.org/10.1007/s10336-010-0590-0

Dänhardt, A., Riechert, J., Bouwhuis, S., Millat, G., Abel, C., & Becker, P. H. (2018). Nahrungsnetzbeziehungen zwischen Flussseeschwalben und Fischen an der Jade. Forschungsergebnisse 2006 – 2015 (No. 16). Nationalparkverwaltung „Niedersächsisches Wattenmeer".

Eglington, S. M., & Perrow, M. R. (2014). Literature review of tern (*Sterna & Sternula spp.*) foraging ecology. ECON Ecological Consultancy Ltd.

Einarsson A. & A. Gardarsson (2004) Moulting diving ducks and their food supply. Aquatic Ecology 38: 297-307.

Engels, B. W. R. (2015). Utopia of utopie? De grote stern op Texel: Wat zijn de ecologische knelpunten van het broedgebied Utopia? [Onderzoeksrapport]. IMARES Wageningen UR Texel.

Eriksson M.O.G (1994) Susceptibility to freshwater acidification by two species of loon - red-throated loon (*Gavia stellata*) and Arctic loon (*Gavia arctica*) in southwest Sweden. Hydrobiologia 280: 439-444.

Eriksson M.O.G., Blomqvist D., Hake M. & Johansson O.C. (1990). Parental feeding in the Red-throated Diver *Gavia stellata*. Ibis 132: 1-13.

Farmer, R.G., Leonard, M.L. (2011) Long-term feeding ecology of Great Black-backed Gulls (*Larus marinus*) in the northwest Atlantic: 110 years of feather isotope data. Can. J. Zool. 89, 123–133. https://doi.org/10.1139/Z10-102

Fijn, R. C., Wolf, P., Courtens, W., Verstraete, H., Stienen, E. W. M., Iliszko, L., & Poot, M. J. M. (2014). Post-breeding prospecting trips of adult Sandwich Terns *Thalasseus sandvicensis*. Bird Study, 61(4), Article 4. https://doi.org/10.1080/00063657.2014.950942

Fijn, R., Leopold, M., Dirksen, S., Arts, F., van Asch, M., Baptist, M., Craeymeersch, J., Engels, B., van Horssen, P., de Jong, J., Perdon, J., van der Zee, E., van der Ham, N., (2017a). Een onverwachte concentratie van Zwarte Zee-eenden in de Hollandse kustzone in een gebied met hoge dichtheden van geschikte schelpdieren. Limosa 90, 97–117.

Fijn, R. C., De Jong, J., Courtens, W., Verstraete, H., Stienen, E. W. M., & Poot, M. J. M. (2017b). GPS-tracking and colony observations reveal variation in offshore habitat use and foraging ecology of breeding Sandwich Terns. Journal of Sea Research, 127, 203–211. https://doi.org/10.1016/j.seares.2016.11.005

Fijn, R. C., Courtens, W., Engels, B. W. R., Van Loon, E. E., & Shamoun-Baranes, J. (2024). Combining video and GPS-tracking to study the spatial foraging distribution of a single-prey loading seabird. Avian Research, 15, 100196. https://doi.org/10.1016/j.avrs.2024.100196

Finney, SK, Wanless, S, Harris, MP (1999) The effect of weather conditions on the feeding behaviour of a diving bird, the Common Guillemot *Uria aalge*. Journal of Avian Biology: 23-30. https://doi.org/10.2307/3677239

Fliessbach, K.L., Borkenhagen, K., Guse, N., Markones, N., Schwemmer, P., Garthe, S. (2019) A ship traffic disturbance vulnerability index for Northwest European Seabirds as a tool for marine spatial planning. Front. Mar. Sci. 6, 1–15. https://doi.org/10.3389/fmars.2019.00192

Flore, B.-O. (1997) High numbers of lesser black-backed gulls *Larus fuscus* foraging at trawlers and in natural feeding flocks in the Southeastern North Sea. Atl. Seabirds 1, 182–186.

Fox, A.D., (2003). Diet and habitat use of scoters *Melanitta* in the Western Palearctic - a brief overview. Wildfowl 54, 163–182.

Franci CD, Vézina F, Grégoire F, Rail J-F, Verreault J (2015) Nutritional stress in Northern gannets during an unprecedented low reproductive success year: Can extreme sea surface temperature event and dietary change be the cause? Comparative Biochemistry and Physiology Part A: Molecular & Integrative Physiology 181:1-8. https://doi.org/10.1016/j.cbpa.2014.11.017

Frank, D. (1992). The influence of feeding conditions on food provisioning of chicks in common terns *Sterna hirundo* nesting in the German Wadden Sea. Ardea, 80, 45–55.

Frank, D., & Becker, P. H. (1992). Body mass and nest reliefs in common terns *Sterna hirundo* exposed to different feeding conditions. Ardea, 80, 57–69.

Frederiksen, M, Wanless, S, Harris, MP, Rothery, P, Wilson, LJ (2004) The role of industrial fisheries and oceanographic change in the decline of North Sea black-legged kittiwakes. Journal of Applied Ecology 41: 1129-1139. https://doi.org/10.1111/j.0021-8901.2004.00966.x

Frick, S., & Becker, P. H. (1995). Unterschiedliche Ernährungsstrategien von FIuß- und Küstenseeschwalbe (*Sterna hirundo und S. paradisaea*) im Wattenmeer. Journal of Ornithology, *136*, 47–63.

Furness, RW, Todd, CM (1984) Diets and feeding of fulmars *Fulmarus glacialis* during the breeding season: a comparison between St Kilda and Shetland colonies. Ibis 126: 379-387. https://doi.org/10.1111/j.1474-919X.1984.tb00259.x

Furness R, Ensor K, Hudson A (1992) The use of fishery waste by gull populations around the British Isles. Ardea 80:105-113

Garðarsson, A, Guðmundsson, GA, Lilliendahl, K (2011) Fýlabyggðir fyrr og nú [Fulmar colonies past and present]. Bliki 31: 1-10. doi http://utgafa.ni.is/Bliki/Bliki-31.pdf

Garthe, S, Hüppop, O (1994) Distribution of ship-following seabirds and their utilization of discards in the North Sea in summer. Marine Ecology Progress Series 106: 1-9.

Garthe, S., Camphuysen, C.J., Furness, R.W. (1996) Amounts of discards by commercial fisheries and their significance as food for seabirds in the North Sea. Mar. Ecol. Prog. Ser. 136, 1–11.

Garthe, S., Scherp, B. (2003) Utilization of discards and offal from commercial fisheries by seabirds in the Baltic Sea. ICES J. Mar. Sci. 60, 980–989. https://doi.org/10.1016/S1054-3139(03)00099-7

Garthe S, Montevecchi WA, Davoren GK (2011) Inter-annual changes in prey fields trigger different foraging tactics in a large marine predator. Limnology and Oceanography 56:802-812. https://doi.org/10.4319/lo.2011.56.3.0802

Garthe, S., Schwemmer, P., Paiva, V.H., Corman, A.-M., Fock, H.O., Voigt, C.C., Adler, S. (2016) Terrestrial and Marine Foraging Strategies of an Opportunistic Seabird Species Breeding in the Wadden Sea. PLoS One 11, 1–19. https://doi.org/10.1371/journal.pone.0159630

Gaston, AJ, Woo, K (2008) Razorbills (*Alca torda*) Follow Subarctic Prey into the Canadian Arctic: Colonization Results from Climate Change? The Auk 125: 939-942. https://doi.org/10.1525/auk.2008.07195

Gayk Z.G., Le Duc D., Horn J. & Lindsay A.R. 2018. Genomic insights into natural selection in the Common Loon (*Gavia immer*): evidence for aquatic adaptation. BMC Evolutionary Biology 18:64. doi:10.1186/s12862-018-1181-6

Geelhoed, S, van Bemmelen, R, Keijl, G, Leopold, M, Verdaat, H (2011) Nieuwe kolonie Drieteenmeeuwen *Rissa tridactyla* in de zuidelijke Noordzee. Sula 24: 27-30.

Geertsma, M (1992) Dieet van de Zeekoet *Uria aalge* op het Friese Front in het najaar van 1989: een vergelijkend voedselonderzoek. PhD Thesis. Faculty of Science and Engineering, Groningen University, Groningen, The Netherlands, pp 45.

Glutz von Blotzheim, U. N. & Bauer, K. M. (Hrsg.) (1982). Handbuch der Vögel Mitteleuropas, Band 4,. Wiesbaden: Aula-Verlag.

Gotmark, F. (1984) Food and foraging in five European *Larus* gulls in the breeding season: a comparative review. Ornis Fenn. 61, 9–18.

Gray C.E., Gilbert A.T., Tash J. & Anderson C. 2015. Wintering movements and habitat use of Red-throated Loons (*Gavia stellata*) in the mid-Atlantic U.S. In: Williams K.A., Connelly E.E., Johnson S.M. & Stenhouse I.J. (eds.). Wildlife densities and habitat use across temporal and spatial scales on the mid-Atlantic outer continental shelf. Final Report to the Department of Energy EERE Wind & Water Power Technologies Office. Report BRI 2015-11, Biodiversity Research Institute, Portland, Maine, USA, 26 pp.

Grecian WJ, Williams HJ, Votier SC, Bearhop S and others (2019) Individual Spatial Consistency and Dietary Flexibility in the Migratory Behavior of Northern Gannets Wintering in the Northeast Atlantic. Frontiers in Ecology and Evolution Volume 7 – 2019. 10.3389/fevo.2019.00214

Grémillet D, Pichegru L, Kuntz G, Woakes AG, Wilkinson S, Crawford RJ, Ryan PG (2008) A junk-food hypothesis for gannets feeding on fishery waste. Proceedings of the Royal Society B: Biological Sciences 275:1149-1156. 10.1098/rspb.2007.1763

Guillemette M, Grégoire F, Bouillet D, Rail J-F, Bolduc F, Caron A, Pelletier D (2018) Breeding failure of seabirds in relation to fish depletion: Is there one universal threshold of food abundance? Marine Ecology Progress Series 587:235-245. https://doi.org/10.3354/meps12442

Guse N., Garthe S. & Schirmeister B. 2009. Diet of Red-throated Divers Gavia stellata reflects the seasonal availability of Atlantic herring *Clupea harengus* in the southwestern Baltic Sea. J. Sea Res. 62: 268-275. doi: 10.1016/j.seares.2009.06.006

Gwiazda R., Flis A., Szarek-Gwiazda E. & Pszczeliński L. 2020. Prey composition of Great Crested Grebe (*Podiceps cristatus*) and Red-throated Diver (*Gavia stellata*) in freshwater reservoirs during migration. Waterbirds 43: 321-325. doi:10.1675/063.043.0311

Gyimesi, A., Boudewijn, T.J., Buijs, R.J., Shamoun-Baranes, J.Z., de Jong, J.W., Fijn, R.C., van Horssen, P.W., Poot, M.J.M. (2016) Lesser Black-backed Gulls *Larus fuscus* thriving on a non-marine diet. Bird Study 63, 241–249. https://doi.org/10.1080/00063657.2016.1180341

Halley, D, Harrison, N, Webb, A, Thompson, D (1995) Seasonal and geographical variations in the diet of common guillemots *Uria aalge* off a western Scotland. Seabird 17: 12-20.

Hamer, KC, Thompson, DR, Gray, CM (1997) Spatial variation in the feeding ecology, foraging ranges, and breeding energetics of northern fulmars in the north-east Atlantic Ocean. ICES Journal of Marine Science 54: 645-653. doi: 10.1006/jmsc.1996.0218

Hamer K, Phillips R, Wanless S, Harris M, Wood A (2000) Foraging ranges, diets and feeding locations of gannets *Morus bassanus* in the North Sea: evidence from satellite telemetry. Marine ecology progress series 200:257-264. doi: 10.3354/meps200257

Hamer K, Humphreys E, Garthe S, Hennicke J and others (2007) Annual variation in diets, feeding locations and foraging behaviour of gannets in the North Sea: flexibility, consistency and constraint. Marine Ecology Progress Series 338:295-305. doi: 10.3354/meps338295

Hammer, S, Madsen, J, Jensen, JK, Pedersen, K, Bloch, D, Thorup, K (2014) Færøsk Trækfugleatlas. Faroe University Press, Tórshavn.

Härkönen, T (1986) Guide to the otoliths of the bony fishes of the Northeast Atlantic. Danbiu ApS. Biological Consultants, Hellerup, Denmark.

Harris, M.P. (1965) The food of some Larus gulls. Ibis (Lond. 1859). 107, 43–53.

Harris, M.P. (1980) Breeding performance of puffins *Fratercula Arctica* in relation to nest density, laying date and year. Ibis (Lond. 1859). 122, 193–209.

Harris, MP, Wanless, S (1986) The Food of Young Razorbills on the Isle of May and a Comparison with That of Young Guillemots and Puffins. Ornis Scandinavica (Scandinavian Journal of Ornithology) 17: 41-46. doi: 10.1006/jmsc.1996.0216

Harris, MP, Wanless, S (1997) Breeding success, diet, and brood neglect in the kittiwake (*Rissa tridactyla*) over an 11-year period. ICES Journal of Marine Science 54: 615-623. doi: 10.1006/jmsc.1996.0216

Harris, MP, Beare, D, Toresen, R, Nøttestad, L, Kloppmann, M, Dörner, H, Peach, K, Rushton, DRA, Foster-Smith, J, Wanless, S (2007) A major increase in snake pipefish (*Entelurus aequoreus*) in northern European seas since 2003: potential implications for seabird breeding success. Marine Biology 151: 973-983. doi: 10.1007/s00227-006-0564-7

Harris, MP, Albon, SD, Newell, MA, Gunn, C, Daunt, F, Wanless, S (2022) Long-term within-season changes in the diet of Common Guillemot (*Uria aalge*) chicks at a North Sea colony: implications for dietary monitoring. Ibis 164: 1243-1251. doi: 10.1111/ibi.13004

Heg, D., 1991. Adulte Grote Mantelmeeuw Larus marinus pakt juveniele Kluut Recurvirostra avosetta. Limosa 64, 26–27.

Hennig, V., Heining, R., Mendel, L.-C., & Tilse, E. (2016). Flussseeschwalben (*Sterna hirundo L.*) und Stinte (*Osmerus eperlanus L.*) in der Elbmündung – Die einzigartige Bestandsentwicklung und Nahrungsöko- logie der größten deutschen Flussseeschwalbenkolonie. *Corax*, *23*, 87–113.

Hoffmann, F. (2000). Een volwassen benadering van het opvoeden van kuikens bij de Grote Stern (*Sterna sandvicensis*) [PhD dissertation]. Rijksuniversiteit Groningen.

Hope Jones P., Blake B.F. & Anker-Nilssen T. (1982). The examination of birds killed in oilspills and other incidents. A manual of suggested methods. Unpublished Report, Aberdeen.

Huig, N., Buijs, R.-J., Kleyheeg, E. (2016) Summer in the city: behaviour of large gulls visiting an urban area during the breeding season. Bird Study 3657, 1–9. https://doi.org/10.1080/00063657.2016.1159179

Hunt, G.L., Hunt, M.W. (1973) Habitat partitioning by foraging gulls in Maine and Northwestern Europe. Auk 90, 827–839.

Hüppop, O., Wurm, S. (2000) Effects of winter fishery activities on resting numbers, food and body condition of large gulls *Larus argentatus* and *L. marinus* in the south-eastern North Sea. Mar. Ecol. Prog. Ser. 194, 241–247. https://doi.org/10.3354/meps194241

Isaksson, N., Evans, T.J., Shamoun-Baranes, J., Åkesson, S. (2015) Land or sea? Foraging area choice during breeding by an omnivorous gull. Mov. Ecol. 4, 1–14. https://doi.org/10.1186/s40462-016-0078-5

Kaiser, M.J., Galanidi, M., Showler, D.A., Elliott, A.J., Caldow, R.W.G., Rees, E.I.S., Stillman, R.A., Sutherland, W.J. (2006). Distribution and behaviour of Common Scoter *Melanitta nigra* relative to prey resources and environmental. Ibis (Lond. 1859). 148, 110–128. https://doi.org/10.1111/j.1474-919X.2006.00517.x

Kleinschmidt B., Burger C., Dorsch M., Nehls G., Heinänen S., Žydelis R., Moorhouse-Gann R.J., Hipperson H., Symondson W.O.C. & Quillfeldt P. (2019) The diet of Red-throated Divers (*Gavia stellata*) overwintering in the German Bight (North Sea) analysed using molecular diagnostics. Marine Biology 166:77. doi:10.1007/s00227-019-3523-3

Kleinschmidt B., Burger C., Bustamante P., Dorsch M., Heinänen S., Morkūnas J., Žydelis R., Nehls G. & Quillfeldt P. (2022). Annual movements of a migratory seabird-the NW European red-throated diver (*Gavia stellata*)-reveals high individual repeatability but low migratory connectivity. Marine Biology 169:114. doi:10.1007/s00227-022-04096-x

Kloppmann, MH, Ehrich, S, Karl, H (2007) Die grosse Schlangennadel als Nahrung für Seevögel. Seevögel 28: 18 24.

Koks, B.J., M, J.M.G. (1998) Great Black-backed Gull Larus marinus latest newcomer as breeding bird in The Netherlands. Sula 12, 203–208.

Kottsieper, J., Schückel, U., Schwemmer, P., Fox, A.D., Garthe, S., (2019). Comparison of bivalve communities between moulting and wintering areas used by Common Scoter *Melanitta nigra* in the German North Sea. Estuar. Coast. Shelf Sci. 229, 106398. https://doi.org/10.1016/j.ecss.2019.106398

Kottsieper, J., (2020). Distribution and habitat selection of the Common Scoter *Melanitta nigra* in the eastern German North Sea.

Krijgsveld KL, B Klaassen & J van der Winden (2022). Verstoring van vogels door recreatie. Literatuurstudie van verstoringsgevoeligheid en overzicht van maatregelen. Deel 1 hoofdrapport & deel 2 soortbesprekingen. Uitgave Vogelbescherming Nederland, Zeist.

Kruskal J.B. (1964). Nonmetric multidimensional scaling: a numerical method. Psychometrika 29: 115–129. doi:10.1007/bf02289694

Kubetzki, U., Garthe, S. (2003) Distribution, diet and habitat selection by four sympatrically breeding gull species in the south-eastern North Sea. Mar. Biol. 143, 199–207. https://doi.org/10.1007/s00227-003-1036-5

Kubetzki U, Garthe S, Fifield D, Mendel B, Furness RW (2009) Individual migratory schedules and wintering areas of northern gannets. Marine Ecology Progress Series 391:257-265. https://doi.org/10.3354/meps08254

Käkelä A, Furness RW, Kelly A, Strandberg U, Waldron S, Käkelä R (2007) Fatty acid signatures and stable isotopes as dietary indicators in North Sea seabirds. Marine Ecology Progress Series 342:291-301. https://doi.org/10.3354/meps342291

Kühn, S, Meijboom, A, Bittner, O, Van Franeker, JA (2024) Fulmar Litter Monitoring in the Netherlands – Update 2023 Wageningen Marine Research Report C042/24 and RWS Centrale Informatievoorziening Report BM 24.15, Den Helder, The Netherlands, pp 54.

Kühn, S, van Franeker, JA, Jensen, J-K, Olsen, B, Danielsen, J, Simonsen, P-J (2025) Increased longline bait predation by northern fulmars (*Fulmarus glacialis*) around the Faroe Islands during the breeding season. ICES Journal of Marine Science 82: fsae175. doi https://doi.org/10.1093/icesjms/fsae175

Lane, JV, Jeglinski, JW, Avery-Gomm, S, Ballstaedt, E, Banyard, AC, Barychka, T, Brown, I, Brugger, B, Burt, TV, Careen, N (2023) High pathogenicity avian influenza (H5N1) in Northern Gannets: Global spread, clinical signs, and demographic consequences. IBIS 166: 633-650.

Lavers, JL, Jones, IL (2007) Impacts of intraspecific kleptoparasitism and diet shifts on Razorbill *Alca torda* productivity at the Gannet Islands, Labrador. Marine Ornithology 35: 1-7.

Leopold MF, Platteeuw M (1987) Talrijk voorkomen van Jan van Genten *Sula Bassana* bij Texel in de herfst: reactie op lokale voedselsituatie. LIMOSA 60:105-110

Leopold M.F. (1988) De zeeeenden-survey van januari 1988. Sula 2: 23-24.

Leopold, M, Camphuysen, C (1992) Olievogels op het Texelse strand, februari 1992. Oiled seabirds on Texel, February 1992. NIOZ - RAPPORT 1992 - 5, Texel, The Netherlands, pp 33.

Leopold, M.F., Baptist, H.J.B., Wolf, P.A., Offringa, H.R., (1995). De Zwarte Zeeeend *Melanitta nigra* in Nederland. Limosa 68, 49–64.

Leopold M.F., Skov H. & Durinck J. (1995). The distribution and numbers of Red-throated Divers *Gavia stellata* and Black-throated Divers *Gavia arctica* in the North Sea in relation to habitat characteristics. Limosa 68: 125.

Leopold, M.F., van der Land, M.A., Welleman, H.C., (1998). Spisula en zee-eenden in de strenge winter van 1995/96 in Nederland. Beon-rapport 98-6.

Leopold, MF, van Damme, CJG, Philippart, CJM, Winter, CJN (2001). Otoliths of North Sea Fish - Fish Identification key by means of otoliths and other hard parts. ETI/NIOZ/Alterra, Amsterdam.

Leopold, M.F., Wolf, P., (2003). Zee-eenden eten ook *Ensis*. Nieuwsbr. Ned. Zeevogelgroep 4, 5.

Leopold, M., (2010). Zwarte Zee-eenden: nomaden op zee. Tussen Duin Dijk 10, 10–13.

Leopold, M, van Bemmelen, R, Geelhoed, S, Witte, R (2011) Alken *Alca torda* als fanatieke scheepsvolgers in januari 2012. Sula 24: 109-120.

Leopold, M.F., Bemmelen, R. Van, Perdon, J., Poot, M., Heunks, C., Beuker, D., Jonkvorst, R.J., Jong, J. De, (2013). Zwarte Zee-eenden in de Noordzeekustzone benoorden de Wadden: verspreiding en aantallen in relatie tot voedsel en verstoring. IMARES Rep. C023/13 1–47.

Leopold M.F., Begeman L., Heße E., van der Hiele J., Hiemstra S., Keijl G., Meesters E., Mielke L., Verheyen D. & Gröne A. (2015). Porpoises: from predators to prey. Journal of Sea Research 97: 14-23. https://doi.org/10.1016/j.seares.2014.12.005

Leopold, M (2016) Mogelijke effecten van de discardban op Jan–van-Gent en Drieteenmeeuw in het Bruine Bank-gebied. IMARES, Texel, The Netherlands, pp 18.

Leopold, MF, Kik, M, van Tulden, P, van Franeker, JA, Kühn, S, Rijks, J (2019) De Zoe en de zeekoet. Een onderzoek naar de doodsoorzaak en de herkomst van de zeekoeten die massaal strandden op de Nederlandse kust in januari en februari 2019. Wageningen Marine Research, Den Helder, The Netherlands, pp 59.

Leopold M.F. & Overmaat W. (2023). Zeekoeten verdrinken in staand want: nieuwe kansen voor dieetonderzoek? Limosa 96: 174-187.

Leopold, M., Poot, M., Tamis, J., Schekkerman, H., Goutbeek, A., van Oijen, T., Jongbloed, R., (2025). Seabirds in the Dutch North Sea. Wageningen University & Research, Report C047/25

Leopold, M. F. (n.d.). Zandspiering lengtes Wagejot.

Leopold, M.F., Spannenburg, P.C., Verdaat, H.J.P., Kats, R.K.H., (n.d.) Identification and size estimation of *Spisula subtruncata* and *Ensis americanus* from shell fragments in stomachs and faeces of Common Eiders *Somateria mollissima* and Common Scoters *Melanitta nigra*. In: Kats, R.K.H., 2007. Common eiders *Somateria mollissima* in the Netherlands: the rise and fall of breeding and wintering populations in relation to stocks of shellfish. Proefschrift Alterra, Wageningen.

Lewis S, Sherratt T, Hamer K, Wanless S (2001) Evidence of intra-specific competition for food in a pelagic seabird. Nature 412:816-819

Lewis S, Benvenuti S, Dall–Antonia L, Griffiths R and others (2002) Sex-specific foraging behaviour in a monomorphic seabird. Proceedings of the Royal Society of London Series B: Biological Sciences 269:1687-1693

Lewis S, Sherratt TN, Hamer KC, Harris MP, Wanless S (2003) Contrasting diet quality of northern gannets *Morus bassanus* at two colonies. Ardea 91:167-176

Liao H., Pierce C. & Larscheid J. (2001). Empirical assessment of indices of prey importance in the diets of predacious fish. Transactions of the American Fisheries Society 130: 583-591. doi:10.1577/1548-8659(2001)130<0583:EAOIOP>2.0.CO;2

Löhmer, K., Vauk, G. (1969) Nahrungsökologische Untersuchungen an übersommernden Silbermöwen (*Larus argentatus*) auf Helgoland im August/September 1967 1–23.

Lopez, S.L. (2023) The foraging ecology and conservation of the Great Black-backed Gull *Larus marinus*. Thesis.

Maathuis, M. A. M., Manche, P., Couperus, B., Parmentier, B., Poos, J. J., Poot, M., Schekkerman, H., Sakinan, S., & Tulp, I. (2025). The small pelagic fish food landscape and its use by common terns *Sterna hirundo* in the Wadden Sea. Marine Biology, 172(6), 87. https://doi.org/10.1007/s00227-025-04640-5

Madden, H.M., R.S.A. van Bemmelen, T.M. van der Have & R.C. Fijn. 2025. Foraging areas of coastal and offshore seabirds in the Dutch North Sea. An analysis of survey and tracking data. Report 25-134. Waardenburg Ecology, Culemborg.

Madsen F.J. (1957). On the food habits of some fish-eating birds in Denmark. Dan. Rev. Game Biol. 3(2): 19–83.

Mallory, ML, Hatch, SA, Nettleship, DN (2012) Northern Fulmar (*Fulmarus glacialis*), version 2.0. In: Poole, AF (ed) The Birds of North America Cornell Lab of Ornithology, Ithaca, NY, USA. https://doi.org/10.2173/bna.361

Mallory, ML, Dey, CJ, McIntyre, J, Pratte, I, Mallory, CL, Francis, CM, Black, AL, Geoffroy, C, Dickson, R, Provencher, JF (2020). Long-term Declines in the Size of Northern Fulmar (*Fulmarus glacialis*) Colonies on Eastern Baffin Island, Canada. Arctic 73: 187-194. https://doi.org/10.14430/arctic70290

Manche, P., Poot, M., Kleefstra, R., Koffijberg, K., Maathuis, M., Schekkerman, H., & van Roomen, M. (2023). Aantallen en verspreiding van visetende broedvogels in het Nederlandse Waddengebied in mei-juni 2022 (Sovon-rapport No. 2023/33). Sovon Vogelonderzoek Nederland.

Manche, P., Schekkerman, H., & van Roomen, M. (2022a). Verdiepende monitoring van kustbroedvogels in Wij & Wadvogels: Jaarrapportage 2021 (Sovon-rapport No. 2022/25). Sovon Vogelonderzoek Nederland.

Manche, P., Schekkerman, H., & van Roomen, M. (2022b). Zenderonderzoek aan Visdieven en Noordse Sterns op broedeiland Stern in 2022 (Sovon-rapport No. 2022/24). Sovon Vogelonderzoek Nederland.

Markones, N, Guse, N (2009) Eignung von Strandfunden zum Studium der Ernährungsökologie von Basstölpeln (*Sula bassana*) und Dreizehenmöwen (*Rissa tridactyla*). Corax 21: 5-12.

Markones, N, Guse, N, Hüppop, O, Garthe, S (2009) Unchanging diet in a stable colony: contemporary and past diet composition of black-legged kittiwakes *Rissa tridactyla* at Helgoland, south-eastern North Sea. Helgoland Marine Research 63: 199-206. https://doi.org/10.1007/s10152-009-0149-8

Martin A (1989) The diet of Atlantic Puffin *Fratercula arctica* and Northern Gannet *Sula bassana* chicks at a Shetland colony during a period of changing prey availability. Bird Study 36:170-180

Massias, A., & Becker, P. H. (1990). Nutritive Value of Food and Growth in Common Tern *Sterna hirundo* Chicks. Ornis Scandinavica, 21(3), 187. https://doi.org/10.2307/3676778

Maul, AM (1994) Ernährungsweisen und Brutbiologie der Dreizehenmöwe *Rissa tridactyla* (Linnaeus, 1758) auf Helgoland. Diplom Thesis. Natural Science Faculty, Karl-Franzens University Graz, Graz, Austria, pp 90.

Meissner, J., Brager, S., (1990). The Feeding Ecology of Wintering Eiders *Somateria Mollissia* and Common Scoters *Melanitta Nigra* on the Baltic Sea Coast of Schleswlg-holstein, Frg. Wader Study Gr. Bull. 58, 1–4.

Montevecchi WA (2007) Binary dietary responses of northern gannets *Sula bassana* indicate changing food web and oceanographic conditions. Marine Ecology Progress Series 352:213-220

Morkūnė R., Lesutiene J., Bariseviciute R., Morkūnas J. & Gasiunaite Z.R. 2016. Food sources of wintering piscivorous waterbirds in coastal waters: a triple stable isotope approach for the southeastern Baltic Sea. Estuarine, Coastal and Shelf Science 171:41-50. doi:10.1016/j.ecss.2016.01.032

Murray S, Wanless S, Harris M (2014) The Bass Rock-now the world's largest Northern Gannet colony. Br Birds 107:769-770

Nelson B (2002) The Atlantic Gannet, Vol. Originator Publishing Services, Norfolk

Nisbet, I. C. T. (1973). Courtship-feeding, Egg-size and Breeding Success in Common Terns. Nature, 241(5385), 141–142. https://doi.org/10.1038/241141a0

Noordhuis, R., Spaans, A.L. (1987) Interspecific competition for food between Herring Gulls (*Larus Argentatus*) and Lesser Black-backed Gulls (*Larus Fuscus*) in the Dutch Wadden Sea area. Ardea 80, 115–132.

Noordhuis, R., Marteijn, E. C. L., Boudewijn, T. J., & Dirksen, S. (1993). Voedseltekort voor de Visdieven van Zeewolde in 1991? *Limosa*, *66*, 61–65.

Norberg R.A. & Norberg U.M. 1976. Size of fish carried by flying Red-throated Divers (*Gavia stellata*) to nearly fledged young in a nesting tarn. Ornis Fennica 53: 92-95.

O'Brien S.H., Wilson L.J., Webb A. & Cranswick P.A. (2008). Revised estimate of numbers of wintering Red-throated Divers *Gavia stellata* in Great Britain. Bird Study 55: 152-160. https://doi.org/10.1080/00063650809461517

Offringa H. (1991). Verspreiding en voedselecologie van de Zwarte Zeeeend (*Melanitta nigra*) in Nederland. NIOZRapport 1991-13

Ojowski, U, Eidtmann, C, Furness, R, Garthe, S (2001) Diet and nest attendance of incubating and chick-rearing northern fulmars (*Fulmarus glacialis*) in Shetland. Marine Biology 139: 1193-1200. https://doi.org/10.1007/s002270100655

OSPAR (2015) Guidelines for Monitoring of plastic particles in stomachs of fulmars in the North Sea area, pp 26.

Ouwehand, J, Leopold, M, Camphuysen, CJ (2004) A comparative study of the diet of guillemots *Uria aalge* and razorbills *Alca torda* killed during the TRICOLOR oil incident in the south-eastern North Sea in January 2003. Atlantic Seabirds 6: 147-164.

Pearson, TH (1968) The Feeding Biology of Sea-Bird Species Breeding on the Farne Islands, Northumberland. Journal of Animal Ecology 37: 521-552. https://doi.org/10.2307/3073

Pedersen J. & Hislop J.R.G. 2001. Seasonal variations in the energy density of fishes in the North Sea. J. Fish Biol. 59: 380-389. https://doi.org/10.1111/j.1095-8649.2001.tb00137.x

Pennycott, T.W., Grant, D., Leopold, M.F., Nager, R.G. (2020a) Ragworms and other marine food items in the diet of Herring Gulls *Larus argentatus* breeding on Lady Isle, Firth of Clyde, Scotland. Bird Study 67, 402–408. https://doi.org/10.1080/00063657.2020.1869697

Pennycott, T.W., Grant, D., Nager, R.G. (2020b) Earthworms in the diet of Herring Gulls *Larus argentatus* breeding on an off-shore island. Bird Study 67, 131–134. https://doi.org/10.1080/00063657.2020.1743232

Pettex E, Barrett RT, Lorentsen S-H, Bonadonna F, Pichegru L, Pons J-B, Grémillet D (2015) Contrasting population trends at seabirds colonies: is food limitation a factor in Norway? Journal of Ornithology 156:397-406. https://doi.org/10.1007/s10336-014-1137-6

Pettex E, Lambert C, Fort J, Dorémus G, Ridoux V (2019) Spatial segregation between immatures and adults in a pelagic seabird suggests age-related competition. J Avian Biol 50. https://doi.org/10.1111/jav.01935

Philippart, C.J.M., M.F. Leopold, R. Mulder & A. Seinen (2023) Ruimte voor vissers en vogels. Handelingsperspectief voor een duurzame visserij op *Spisula subtruncata* in de Nederlandse kustwateren. Eindrapport EFMZV-RVO project 17684000005, 31 pp

Phillips, R, Petersen, M, Lilliendahl, K, Solmundsson, J, Hamer, K, Camphuysen, C, Zonfrillo, B (1999) Diet of the northern fulmar *Fulmarus glacialis*: reliance on commercial fisheries? Marine Biology 135: 159-170. https://doi.org/10.1007/s002270050613

Pichegru L, Ryan PG, van der Lingen CD, Coetzee J, Ropert-Coudert Y, Grémillet D (2007) Foraging behaviour and energetics of Cape gannets *Morus capensis* feeding on live prey and fishery discards in the Benguela upwelling system. Marine Ecology Progress Series 350:127-136. https://doi.org/10.3354/meps

Platteeuw, M., F van der Ham, N. and E den Ouden, J., (1994). Zeetrektellingen in Nederland in de jaren tachtig. *Sula*, *8*(1/2), pp.1-206.

Pons, J. (1992) Effects of changes in the availability of human refuse on breeding parameters in a Herring gull *Larus argentatus* population in Brittany, France. Ardea 80, 143–150.

Poot M.J.M., C. Heunks, T.J. Boudewijn, J. de Jong, P.W. van Horssen, M. Japink, W. Lengkeek, S. Bouma, M.F. Leopold, R. Van Bemmelen, P. Pruisscher, K. Buijtelaar, P.A. Wolf, S.J. Lilipaly & A.F. Zuur (2014). Perceel Vogels – Zee-eenden. In: Prins, T.C. & van der Kolff, G.H. (eds). PMR Monitoring natuurcompensatie Voordelta: eindrapport 1e fase 2009-2013 deel B. Deltares rapport 1200672-000-ZKS-0043. Deltares, Delft

Prüter, J (1986) Untersuchungen zum Bestandsaufbau und zur Ökologie der Möwen (*Laridae*) im Seegebiet der Deutschen Bucht. PhD Thesis. Biology Department, University of Hannover, Hannover, Germany, pp 143.

Reimchen T.E. & Douglas S (1984) Feeding schedule and daily food consumption in red-throated loons (*Gavia stellata*) over the prefledging period. Auk 101: 593-599.

Rome, M.S., Ellis, J.C. (2004) Foraging Ecology and Interactions between Herring Gulls and Great Black-Backed Gulls in New England. Waterbirds 27, 200–210.

Ruggles A.K (1994) Habitat selection by loons in southcentral Alaska. Hydrobiologia 279/280: 421-430.

Schekkerman H. (2018). Roodkeelduiker *Gavia stellata*. pp. 154-155 in: SOVON Vogelonderzoek Nederland. Vogelatlas van Nederland. Broedvogels, wintervogels en 40 jaar verandering. Kosmos Uitgevers, Utrecht/Antwerpen.

Schekkerman H., Manche, P & van Kleunen, A (2025) Review of demographic studies on seabirds of the Dutch North Sea. Sovon-rapport. Sovon Vogelonderzoek Nederland, Nijmegen.

Schoener T.W. (1970). Nonsynchronous spatial overlap of lizards in patchy habitats. Ecology 51: 408-418. doi:10.2307/1935376

Schreckenbach K., Knösche R. & Ebert K. (2001). Nutrients and energy contents of freshwater fishes. J. Appl. Ichthyol. 17: 142-144. https://doi.org/10.1111/j.1439-0426.2001.00295.x

Schwemmer, P., Garthe, S. (2005) At-sea distribution and behaviour of a surface-feeding seabird, the lesser black-backed gull *Larus fuscus*, and its association with different prey. Mar. Ecol. Prog. Ser. 285, 245–258. https://doi.org/10.3354/meps285245

Schwemmer, H., Schwemmer, P., Ehrich, S., Garthe, S. (2013) Lesser black-backed gulls (*Larus fuscus*) consuming swimming crabs: An important link in the food web of the southern North Sea. Estuar. Coast. Shelf Sci. 119, 71–78. https://doi.org/10.1016/j.ecss.2012.12.021

Schwemmer, P., Volmer, H., Enners, L., Reimers, H., Binder, K., Horn, S., Adler, S., Fox, A.D., Garthe, S., (2019). Estuarine , Coastal and Shelf Science Modelling distribution of common scoter (*Melanitta nigra*) by its predominant prey , the American razor clam (*Ensis leei*) and hydrodynamic parameters. Estuar. Coast. Shelf Sci. 225, 106260. https://doi.org/10.1016/j.ecss.2019.106260

Seip P. A. & Brand R. (1987). Inventarisatie van macrozoobenthos in de Voordelta. NIOZ rapport 1987-1

Sherley, R.B., Ladd-Jones, H., Garthe, S., Stevenson, O., Votier, S.C. (2020) Scavenger communities and fisheries waste: North Sea discards support 3 million seabirds, 2 million fewer than in 1990. Fish Fish. 21, 132–145. https://doi.org/10.1111/faf.12422

Shillcock, N.H. (1991) Grote Mantelmeeuwen *Larus marinus* vallen Grote Zaagbekken *Mergus merganser* lastig. Limosa 64, 26.

Skov H., Durinck J., Leopold M.F. & Tasker M.L. (1995). Important bird areas in the North Sea, including the Channel and the Kattegat. BirdLife International, Cambridge: 26-29.

Sluijter M, Arts F.A., Lilipaly S.J., Wolf P.A (2021) Midwintertelling van zee-eenden in de Waddenzee en Nederlandse kustwateren in november 2020, januari en maart 2021. Rapport RWS – Centrale Informatievoorziening. Rapport BM 21.22 / Deltamilieu Projecten rapport 2021-09 Vlissingen.

Sonntag, N, Hüppop, O (2005) Snacks from the depth: summer and winter diet of common guillemots *Uria aalge* around the Island of Helgoland. Atlantic Seabirds 7: 1-14.

Sotillo, A., Depestele, J., Courtens, W., Vincx, M., Stienen, E.W.M. (2014) Consumption of discards by herring gulls *larus argentatus* and lesser black-backed gulls *larus fuscus* off the belgian coast in the breeding season. Ardea 102, 195–205. https://doi.org/10.5253/arde.v102i2.a9

Sotillo, A., Baert, J.M., Müller, W., Stienen, E.W.M., Soares, A.M.V.M., Lens, L. (2019) Recently-adopted foraging strategies constrain early chick development in a coastal breeding gull. PeerJ 7, 1–21. https://doi.org/10.7717/peerj.7250

SOVON. (2023). Common Tern. Sovon Vogelonderzoek Nederland. https://stats.sovon.nl/stats/soort/6150

SOVON (2024a) Bouwsteen ten behoeve van de VHR-opgave A016 Jan-van-gent *Morus bassanus,* niet-broedvogel

SOVON. (2024b). Bouwsteen ten behoeve van de VHR-opgave. Grote stern *(Thallasseus sandvicensis)*.

SOVON. (2024c, October). Bouwsteen ten behoeve van de VHR-opgave. Visdief *(Sterna hirundo)*. Sovon Vogelonderzoek Nederland.

SOVON (2025) Black-legged Kittiwake (*Rissa tridactyla*) - Factsheet. (Accessed: 28-Apr-2025)

Sovon Vogelonderzoek Nederland. (n.d.). Noordse Stormvogel | Sovon Vogelonderzoek. Sovon Vogelonderzoek. https://stats.sovon.nl/stats/soort/220

Spaans AL, Bukacinska M, Bukacinski D, van Swelm ND (1994) The relationship between food supply, reproductive parameters and population dynamics in Dutch lesser black-backed gulls (*Larus fuscus*): a pilot study. BEON Report 94–15. Institute for Forestry and Nature Research, Wageningen

Spaans, A.L. (1998) Breeding lesser black-backed gulls *Larus graellsii* in The Netherlands during the 20th century. Sula 12, 175–184.

Spaans, A.L. (1971) On the feeding ecology of the Herring gull *Larus argentatus Pont.* in the Northern part of the Netherlands. Ardea 59, 73–188. https://doi.org/10.5253/arde.v59.p73

Sprengelmeyer Q.D. (2014). A phylogenetic reevaluation of the genus *Gavia* using next-generation sequencing. Master's Theses, Northern Michican University. https://commons.nmu.edu/theses/1

Stauss C, Bearhop S, Bodey TW, Garthe S and others (2012) Sex-specific foraging behaviour in northern gannets *Morus bassanus*: incidence and implications. Marine Ecology Progress Series 457:151-162. https://doi.org/10.3354/meps09734

Stavenow J., Roos A.M., Ågren E.O., Kinze C., Englund W.F. & Neimanis A (2022) Sowerby's beaked whales (*Mesoplodon bidens*) in the Skagerrak and adjacent waters: Historical records and recent post-mortem findings. Oceans 3: 250-268. doi:10.3390/oceans3030018

Stienen, E. W. M., & van Tienen, P. G. M. (1991). *Prooi- en energiecomsumptie door kuikens van noordse stern Sterna paradisaea en visdief S. hirundo in relatie tot enkele abiotische factoren* (Internal Report No. 91/32). Rijksinstituut voor Natuurbeheer.

Stienen, E. W. M., & Brenninkmeijer, A. (1992). Ecologisch profiel van de visdief *(Sterna hirundo)* (RIN-rapport No. 92/18). DLO Instituut voor Bos- en Natuuronderzoek.

Stienen, E. W. M., & Brenninkmeijer, A. (1994). Voedselecologie van der grote stern *(Sterna sandvicensis):* Onderzoek ter ondersteuning van een populatie-dynamisch model (IBN-rapport 120). Instituut voor Bos- en Natuuronderzoek.

Stienen, E. W. M., & Brenninkmeijer, A. (2002). Foraging decisions of sandwich terns in the presence of kleptoparasitising gulls. The Auk, 119(2), 473–486.

Stienen, E. W. M. (2006). Living with the gulls: Trading off food and predation in the Sandwich Tern *Sterna sandvicensis* [Wageningen Univeristy Research]. http://www2.alterra.wur.nl/webdocs/pdffiles/alterrarapporten/SciContrib15.pdf

Swennen, C, Duiven, P (1977) Size of food objects of three fish-eating seabird species: *Uria aalge, Alca torda*, and *Fratercula arctica* (Aves, Alcidae). Netherlands Journal of Sea Research 11: 92-98. https://doi.org/10.1016/0077-7579(77)90022-9

Tasker, M, Camphuysen, C, Fossum, P (1999) Variation in prey taken by seabirds. In: Furness, RW, Tasker, ML (eds) Diets of seabirds and consequences of changes in food supply. International Council for the Exploration of the Sea (ICES), Copenhagen, Denmark, pp 18-28.

Taylor, I. R. (1983). Effect of wind on the foraging behaviour of Common and Sandwich terns. Ornis Scandinavica, 14, 90–96. https://doi.org/10.2307/3676011

Temming A. & Herrmann J.-P. 2003. Gastric evacuation in cod. Prey-specific evacuation rates for use in North Sea, Baltic Sea and Barents Sea multi-species models. Fisheries Research 63: 21-41. https://doi.org/10.1016/S0165-7836(03)00041-9

Tree, A. J. (2011). Origins, occurrence and movements of Sandwich Tern *Thalasseus sandvicensis* in southern Africa. Marine Ornithology, *39*, 137–181.

Tulp, I., Craeymeersch, J., Leopold, M., Damme, C. Van, Fey, F., Verdaat, H., (2010). Estuarine , Coastal and Shelf Science The role of the invasive bivalve *Ensis directus* as food source for fish and birds in the Dutch coastal zone. Estuar. Coast. Shelf Sci. 90, 116–128. https://doi.org/10.1016/j.ecss.2010.07.008

Turner, D (2010) Counts and breeding success of Black-legged Kittiwakes *Rissa tridactyla* nesting on man-made structures along the River Tyne, northeast England, 1994-2009. Seabird 23: 111-126. doi

Tyson, C., Shamoun-baranes, J., Loon, E.E. Van, Camphuysen, K.C.J., Hintzen, N.T. (2015) Individual specialization on fishery discards by lesser black-backed gulls (*Larus fuscus*). ICES J. Mar. Sci. 72, 1882–1891.

Van Bemmelen, R.S.A., Courtens, W., Collier, M. P., & Fijn, R. C. (2022). Sandwich Terns in the Netherlands in 2019-2021. Distribution, behaviour, survival and diet in light of (future) offshore wind farms (Bureau Waardenburg. https://purews.inbo.be/ws/portalfiles/portal/87746292/2022_Van_Bemmelen_et_al._Sandwich_Terns_in_the_Netherlands_in_2019_2021..pdf

Van Bemmelen, R.S.A., de Jong JW, Arts FA, Beuker D and others (2024) Verspreiding, abundantie en trends van zeevogels en zeezoogdieren op het Nederlands Continentaal Plat in 2023-2024. Report No. 24-433, Waardenburg Ecology & Deltamilieu Projecten, Culemborg

Van Bemmelen, R.S.A., Schekkerman, H, Fijn, R (2025) Tracking of Black-legged Kittiwakes from an offshore platform in the Dutch North Sea during summer. Seabirds 37. https://doi.org/10.61350/sbj.37.1

Van de Wolfshaar, K.E., Brinkman, A.G., Benden, D.L.P., Craeymeersch, J.A., Glorius, S., Leopold, M.F., (2023). Impact of disturbance on common scoter carrying capacity based on an energetic model. Journal of Environmental Management 342, 118255. https://doi.org/10.1016/j.jenvman.2023.118255

Van der Beek, I. (2017). De voedselecologie en verspreiding van der grote sterns *(Thalasseus sandvicensis)* van Texel (Wageningen Marine Research rapport Wageningen Marine Research.

Van der Meer, R. (2018). Sandwich Tern *(Thalasseus sandvicensis).* Prey preferences and spatial distribution in north-western Europe (pp. 1–23). Wageningen Marine Research.

Van der Winden, J., Dirksen, S., & Poot, M. J. M. (2009). Laag broedsucces visdieven op de Kreupel in 2009. Voedseltekort in de grosste kolonie van West-Europa (Nos. 09–202). Bureau Waardenburg.

Van Donk, S., Camphuysen, C.J., Shamoun-Baranes, J., van der Meer, J (2017) The most common diet results in low reproduction in a generalist seabird. Ecol. Evol. 7, 4620–4629. https://doi.org/10.1002/ece3.3018

van Donk, S., Shamoun-baranes, J., Bouten, W., van der Meer, J., Camphuysen, K.C.J. (2018) Individual differences in foraging site fidelity are not related to time-activity budgets in Herring Gulls. Ibis (Lond. 1859). 1–17. https://doi.org/10.1111/ibi.12697

van Donk, S., Shamoun-Baranes, J., van der Meer, J., Camphuysen, K.C.J. (2019) Foraging for high caloric anthropogenic prey is energetically costly. Mov. Ecol. 7, 17. https://doi.org/10.1186/s40462-019-0159-3

van Donk S., van Bemmelen, R., Fijn, R., van der Have, T., Hesse, E., Kühn, S., Leopold, M., Madden, H., Melis, E., Poot, M., Schekkerman, H. (2025) Knowledge gaps and research options for coastal birds and seabirds of the Dutch North Sea, Wageningen University & Research Report C093/25, https://doi.org/10.18174/704511

Van Franeker J.A. (2004). Save the North Sea Fulmar-Litter-EcoQO Manual Part 1: Collection and dissection procedures. Alterra-rapport 672, Wageningen, pp 38.

van Franeker J.A. & Camphuysen C.J. (2007). Condition manual: the physical condition of stranded seabirds & ageing and sexing manual for stranded seabirds. Handbook on Oil Impact Assessment version 1.0. (living document, available via ResearchGate).

Van Franeker J.A., Blaize C., Danielsen J., Fairclough K., Gollan J., Guse N., Hansen P.L., Heubeck M., Jensen J.K., Le Guillou G., Olsen B., Olsen K.O., Pedersen J., Stienen E.W. & Turner D.M. (2011). Monitoring plastic ingestion by the Northern Fulmar *Fulmarus glacialis* in the North Sea. Env. Poll. 159: 2609-2615. https://doi.org/10.1016/j.envpol.2011.06.008Get rights and content

Van Franeker, JA, Kühn, S (2020) Onderzoek naar plastic in magen van noordse stormvogels en andere zeevogels in relatie tot het verlies van MSC-ZOE containers in begin januari 2019. Wageningen Marine Research, Den Helder, The Netherlands, pp 19.

Van Franeker, Jan & Kühn, Susanne & Anker-Nilssen, Tycho & Edwards, Ewan & Gallien, Fabrice & Guse, Nils & Kakkonen, Jenni & Mallory, Mark & Miles, Will & Olsen, Kåre & Pedersen, John & Provencher, Jennifer & Roos, Mervyn & Stienen, Eric & Turner, Daniel & Loon, Willem M.G.M.. (2021). New tools to evaluate plastic ingestion by northern fulmars applied to North Sea monitoring data 2002–2018. Marine Pollution Bulletin. 166. 112246. 10.1016/j.marpolbul.2021.112246.

Van Franeker, JA, Kühn, S. (in review) Sex and age characteristics of northern fulmars *Fulmarus glacialis* used in programs to monitor plastic ingestion. Marine Ornithology.

Van Scheppingen Y. & Groenewold A. 1990. De ruimtelijke verspreiding van het benthos in de zuidelijke Noordzee. De Nederlandse kustzone - overzicht 1988-1989. Rapport Rijkswaterstaat Milzon 90- 003.

Vanaverbeke, J., Braarup Cuykens, A., Braeckmann, U., Courtens, W., Cuveliers, E., Goffin, A., Hellemans, B., Huyse, T., Lacroix, G., Larmuseau, M., Mees, J., Provoost, P., Rabaut, M., Remerie, T., Savina, M., Soetaert, K., Stienen, E. W. M., Verstraete, H., Volckaert, F., & Vincx, M. (2011). *U*nderstanding benthic, pelagic and airborne ecosystem interactions in shallow coastal seas 'WestBanks' (Final Report No. SD/BN/01). Belgian Science Policy Office.

Vauk-Hentzelt, E, Bachmann, L (1983) Zur Ernährung nestjunger Dreizehenmöwen (*Rissa tridactyla*) aus der Kolonie des Helgoländer Lummenfelsens. Seevögel 4: 42-45.

Veen, J. (1977). Functional and Causal Aspects of Nest Distribution in Colonies of the Sandwich Tern (*Sterna S. Sandvicencis Lath.*). Behaviour. Supplement, 20, I–201.

Veitch, B.G., Robertson, G.J., Jones, I.L., Bond, A.L. (2016) Great Black-Backed Gull (*Larus marinus*) Predation on Seabird Populations at Two Colonies in Eastern Canada. Waterbirds 39, 235–245. https://doi.org/10.1675/063.039.sp121

Verbeek, N.A.M. (1977) Interactions between Herring and Lesser Black-Backed Gulls Feeding on Refuse. Auk 94, 726–735.

Voous K.H. (1960). Atlas of European birds. Nelson and sons Ltd, London, 284p.

Voss, M, Hartwig, E, Vauk, G (1987) Untersuchungen zum Nahrungsverbrauch der Dreizehenmöwe (*Rissa tridactyla*) auf Helgoland an handaufgezogenen Jungtieren. Seevögel 8: 5-13.

Votier SC, Grecian WJ, Patrick S, Newton J (2011) Inter-colony movements, at-sea behaviour and foraging in an immature seabird: results from GPS-PPT tracking, radio-tracking and stable isotope analysis. Marine Biology 158:355-362. https://doi.org/10.1007/s00227-010-1563-9

Waggitt, J.J., Evans, P.G.H., Andrade, J., Banks, A.N., Boisseau, O., Bolton, M., Bradbury, G., Brereton, T., Camphuysen, C.J., Durinck, J., Felce, T., Fijn, R.C., Garcia-Baron, I., Garthe, S., Geelhoed, S.C.V., Gilles, A., Goodall, M., Haelters, J., Hamilton, S., Hartny-Mills, L., Hodgins, N., James, K., Jessopp, M., Kavanagh, A.S., Leopold, M., Lohrengel, K., Louzao, M., Markones, N., Martínez-Cedeira, J., Ó Cadhla, O., Perry, S.L., Pierce, G.J., Ridoux, V., Robinson, K.P., Santos, M.B., Saavedra, C., Skov, H., Stienen, E.W.M., Sveegaard, S., Thompson, P., Vanermen, N., Wall, D., Webb, A., Wilson, J., Wanless, S., Hiddink, J.G. (2020) Distribution maps of cetacean and seabird populations in the North-East Atlantic. J. Appl. Ecol. 57, 253–269. https://doi.org/10.1111/1365-2664.13525

Wagner, R (1997) Differences in prey species delivered to nestlings by male and female Razorbills *Alca torda*. Seabird: 58-59.

Wallace R.K. (1981). An assessment of diet-overlap indexes. Trans. Am. Fish. Soc. 110: 72–76. doi:10.1577/1548-8659(1981)110<72:AAODI>2.0.CO;2

Walter, U., Becker, P.H. (1997) Occurrence and consumption of seabirds scavenging on shrimp trawler discards in the Wadden Sea. ICES J. Mar. Sci. 54, 684–694. https://doi.org/10.1006/jmsc.1997.0239

Wanless S, Harris M, Redman P, Speakman J (2005) Low energy values of fish as a probable cause of a major seabird breeding failure in the North Sea. Marine Ecology Progress Series 294:1-8. https://doi.org/10.3354/meps294001

Wanless, S, Harris, MP, Newell, MA, Speakman, JR, Daunt, F (2018) Community-wide decline in the occurrence of lesser sandeels *Ammodytes marinus* in seabird chick diets at a North Sea colony. Marine Ecology Progress Series 600: 193-206. https://doi.org/10.3354/meps12679

Washburn, B.E., Bernhardt, G.E., Kutschbach-Brohl, L., Chipman, R.B., Francoeur, L.C. (2013) Foraging Ecology of Four Gull Species at a Coastal–Urban Interface. Condor 115, 67–76. https://doi.org/10.1525/cond.2013.110185

Weir D.N., Kitchener A.C., McGowan R.Y., Kinder A. & Zonfrillo B. (1997). Origins, population structure, pathology and diet samples of diver and auk casualties of the Sea Empress oil spill. Final report by the National Museums of Scotland and University of Edinburgh to the Sea Empress Environmental Evaluation Committee, CCW Contract No. FC 73-02-69.

Wendeln, H., Mickstein, S., & Becker, P. H. (1994). Auswirkungen individueller Ernährungsstrategien von Flußseeschwalben (Sterna hirundo) auf die Anwesenheit am Koloniestandort. *Die Vogelwarte*, *37*, 290–303.

Wendeln, H. (1997). Body Mass of Female Common Terns (*Sterna hirundo*) during Courtship: Relationships to Male Quality, Egg Mass, Diet, Laying Date and Age. Colonial Waterbirds, 20(2), 235–243. https://doi.org/10.2307/1521689

Westerberg, K., Brown, R., Eagle, G., Votier, S.C. (2019) Intra-population variation in the diet of an avian top predator: generalist and specialist foraging in Great Black-backed Gulls *Larus marinus*. Bird Study 66, 390–397. https://doi.org/10.1080/00063657.2019.1693961

Winkler D.W., Billerman S.M. & Lovette I.J. (2020). Loons (*Gaviidae*), version 1.0. In: S.M. Billerman, B.K. Keeney, P.G. Rodewald & T.S. Schulenberg (Eds). Birds of the World. Cornell Lab of Ornithology, Ithaca, NY, USA. doi:10.2173/bow.gaviid1.01

Woehler EJ, Hobday AJ (2024) Impacts of marine heatwaves may be mediated by seabird life history strategies. Mar Ecol Prog Ser 737:9-23 . https://doi.org/10.3354/meps14333

Wolf, P.A., Meininger, P.L., (2004). Zeeën van zee-eenden bij de Brouwersdam. Nieuwsbr. Ned. Zeevogelgroep 5, 1e2. 5, 8–9.

Zuur A.F., P.W. van Horssen, E.N. Ieno, A.A. Saveliev & M.J.M. Poot (2014). Zero-inflated and spatial correlated Common Scoter data. In: A.F. Zuur, A.A. Saveliev & E.N. Ieno (eds). A Beginner’s Guide to Generalised Additive Mixed Models with R. Highland Statistics Ltd, Newburgh.

Zydelis R. (2002). Habitat selection of waterbirds wintering in Lithuanian coastal zone of the Baltic Sea. PhD-thesis, University of Vilnius, Biomedical Sciences: Ecology & Environmental Sciences.

Justification

Report: C092/25
Project Number: 4315100243

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

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