Sandwich Terns in the Netherlands in 2019-2021

Distribution, behaviour, survival and diet in light of (future) offshore wind farms

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List of co-authors and affiliations in this report

The chapters of this report are set up as manuscripts, aimed at submitting them to peer-reviewed journals since this is one of the aims of the Wozep programme. Especially, chapter 4 – 8 are ready for submission. This setup explains why authors are listed per individual chapter rather than for the entire report (only first authors included). A full list of all authors are:

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Summary

Renewable energy, and in particular the development of offshore wind farms (OWF), is one of the key strategies of the Dutch government to fulfill the requirements of the various agreements to combat global climate change. Seabirds can however be negatively impacted by the development of Offshore Wind Farms (OWF) through the risk of direct mortality due to collisions and the risk of indirect mortality due to either displacement leading to habitat loss, or barrier effects leading to avoidance and increased energy expenditure. The Sandwich Tern Thalasseus sandvicensis is one of the species that was identified as particularly vulnerable to the direct effects of OWFs. However, assessing the potential negative effects of OWF development on Sandwich Terns is hampered by a variety of knowledge gaps mainly related to disturbance effects of operational OWFs, leading effectively to habitat loss, but also to some specific parameters that are part of Collision Rate Models (CRM) that are used in assessment procedures. Furthermore, some demographic and life-history parameters of Sandwich Terns are unknown too, leading to a reduced ability to calculate population-level effects.

In this study, the at-sea distribution, and the macro-avoidance of OWFs by Sandwich Terns were thus of primary interest, as these will together determine how often birds encounter an OWF (also related to collision rates) and how much habitat could be lost after construction of OWFs. GPS-tracking allows to study behavioural responses to the presence of OWFs in detail, including macro-scale avoidance as well as many aspects of the actual flight behaviour, such as speed, flight altitude and behaviour. Therefore, a main component of the studies reported in this report is based on GPS-tracking of individual Sandwich Terns. Avoidance of OWFs may also mean that movements of individual birds are compromised, which could lead to higher energy expenditure or less profitable prey availability. Habitat loss may thereby affect diet, which in turn may affect reproductive success through so-called carry-over effects. Therefore, baseline data on Sandwich Tern diets has been collected in this study. Furthermore, annual survival of Sandwich Terns is a primary parameter in population modelling, which was studied with colourrings. It is also important to estimate how many individual Sandwich Terns can interact with an OWF over longer time spans than just a single breeding season. Therefor, immi- and emigration rates of different populations were studied.

In total 117 Sandwich Terns were tagged with GPS-loggers. These birds had a mean foraging range of up to 25 km from the colony and mean trip durations were between 1.4 and 3.2 hours. Within the different foraging ranges of terns from different colonies, a maximum of 0.6% overlap with Offshore Wind Farms was recorded (**Chapter 3**). Integrated Step-Selection Models (iSSMs) considering habitat characteristics (land, water depth and sediment grain size) and movement characteristics, indicate a macro-avoidance rate of 0.05 for Scolt Head and 0.22 for De Putten. These avoidance rates imply that Sandwich Terns experience habitat loss when OWFs are constructed within their foraging ranges but also that avoidance rates vary substantially per geographic location (**Chapter 4**). Hidden Markov Models showed that the probability to switch between transit and foraging was most strongly affected by two static variables (sediment type and water depth), but less strongly

by dynamic variables related to weather (air temperature, wind speed, cloud cover) or varying spatially and seasonally (salinity, water temperature) (**Chapter 5**). Based on the tracking data and colony-counts it is possible to predict the at-sea distribution of Sandwich Terns using Resource Selection Functions for southern North Sea colonies. This approach can be used in future impact assessments to predict overlap of breeding Sandwich Terns with proposed offshore wind farms (**Chapter 6**). Flight height measurements show that over 87% of all Sandwich Terns were flying below 20m, with half of these between 11-20m. Numbers above 20m decreased rapidly with decreasing height with fewer than 1.5% being recorded above 40m. This has important consequences for CRM (**Chapter 7**). Sandwich terns are long-lived animals (annual survival of 0.92 for adult birds) and show a low breeding site fidelity among years (**Chapter 8**). To gather reference data for future comparison, we further collected data on breeding numbers and success by direct observation and using Unmanned Aerial Vehicle (UAV or ‘drone’) surveys (**Chapter 9**), and comperative data on diet in different colonies along the coast (**Chapter 10**).

In summary, Sandwich Terns 1) avoid entering OWFs for 5-22%, 2) show distributional overlap of up to 0.6% during breeding with OWFs that are nearshore and close to colonies, 3) generally fly at low altitudes although 4.1% of the flux flies at rotor height, 4) are long-lived (annual survival rate of 0.92 for adults) and show 5) low year-to-year fidelity to breeding colonies.

This indicates that OWFs that are nearshore and close to colonies pose a potential threat to Sandwich Terns in a given year: they regularly encounter OWFs and avoid entering OWFs only in a minority of instances. Furthermore, because Sandwich Terns are long-lived and regularly switch between breeding colonies between years, the number of individual birds breeding in a colony is much greater across years than in any given year. Hence, also the number of individual terns that will interact with any given OWF will be very large over the life span of an OWF. On the other hand, Sandwich Terns’ collision rates with offshore wind turbines may be relatively low considering some macro-avoidance takes place, and they normally stay below rotor heights. On the other hand, in previous CRMs a smaller proportion of birds flying at rotor height has been used, so mortality rates may have been underestimated.

Finally, if future OWFs are built outside the foraging ranges of breeding Sandwich Terns, the exposure of them to OWFs during the breeding season will be much reduced and potentially negligible in that period. That said, aerial surveys show that outside the breeding season Sandwich Terns do spend time far offshore, so in another part of the season interaction between OWFs and these birds might still occur.

Nederlandse samenvatting

Hernieuwbare energie, en in het bijzonder de ontwikkeling van offshore windparken, is één van de belangrijkste strategieën van de Nederlandse overheid om te voldoen aan de eisen van het Klimaatakkoord. Offshore windparken kunnen gevolgen hebben voor zeevogels door het risico op directe sterfte als gevolg van aanvaringen en het risico van indirecte sterfte als gevolg van het verlies van leefgebied, of barrière-effecten die leiden tot een verhoogde energie uitgave. De grote stern *Thalasseus sandvicensis* is één van de soorten waarvan gedacht wordt dat deze kwetsbaar zijn voor de effecten van offshore windturbines. Het beoordelen van de mogelijke negatieve effecten op grote sterns wordt echter belemmerd door een aantal kennisleemten die met name te maken hebben met de verstoringseffecten van operationele windparken, die leiden tot habitatverlies, maar ook met enkele specifieke parameters die deel uitmaken van aanvaringsmodellen die worden gebruikt in beoordelingsprocedures. Daarnaast zijn enkele demographische paramaters van grote sterns onbekend, waardoor het moeilijk is om in detail effecten op populatieniveau door te rekenen.

In deze studie ligt de focus op de verspreiding op zee en de macro-uitwijking van grote sterns op offshore windturbines, omdat deze samen bepalen hoe vaak vogels een windpark tegenkomt en hoeveel leefgebied verloren kan gaan na de bouw van windparken. GPS-tracking maakt het mogelijk om effecten van de aanwezigheid van offshore windturbines in detail te bestuderen, inclusief macro-uitwijking en vele aspecten van het vlieggedrag, zoals snelheid en gedrag. Daarom is een belangrijk onderdeel van de onderzoeken die in dit rapport worden gerapporteerd gebaseerd op GPS-tracking van individuele grote sterns. Uitwijking van offshore windparken kan ook gevolgen hebben voor de bewegingen van individuele vogels wat kan leiden tot een hoger energieverbruik of een minder beschikbaarheid van prooien. Habitatverlies kan daarmee ook het dieet beïnvloeden dat op haar beurt het reproductieve succes kan beïnvloeden door zogenaamde carry-over effecten. Daarom wordt in deze studie ook baseline data verzameld van het dieet van grote sterns. Bovendien is de jaarlijkse overleving van grote sterns een primaire parameter in populatiemodellering. Dit laatste is bestudeerd door het analyseren van (kleur)ringbestanden. Verder zijn nauwkeurige schattingen van de verplaatsingssnelheid van vogels tussen kolonies, evenals nauwkeurige schattingen van individuele jaarlijkse overlevingspercentages van cruciaal belang voor de beoordeling van mogelijke effecten van OWF's. Ook deze werden bepaald aan de hand van kleurringbestanden.

In totaal werden in deze studie 117 grote sterns van een GPS-logger voorzien. Deze vogels hadden een gemiddeld foerageerbereik van 25 km van de kolonie en de gemiddelde tripduur was tussen 1,4 en 3,2 uur. Binnen de foerageergebieden van sterns uit verschillende kolonies is maximaal 0,6% overlap met offshore windparken vastgesteld (**hoofdstuk 3**). Geïntegreerde Stap-Selectie Modellen die rekening houden met habitatkenmerken (land, waterdiepte en sedimentkorrelgrootte) en bewegingskenmerken, geven een macro-uitwijking aan van 0,05 voor Scolt Head en 0,22 voor De Putten. Deze vermijdingspercentages impliceren dat grote sterns habitatverlies ervaren wanneer offshore windparken worden gebouwd binnen hun foerageerbereik, maar ook dat uitwijkingsgetallen sterk wisselen tussen verschillende locaties (**hoofdstuk 4**). Hidden Markov Models lieten zien dat grote sterns op foerageren overgaan bij specifieke sedimenttypes en waterdiepten, en in mindere mate door dynamische variabelen gerelateerd aan het weer (luchttemperatuur, windsnelheid, bewolking) of ruimtelijk en seizoensgebonden variabelen (zoutgehalte, watertemperatuur) (**hoofdstuk 5**). Op basis van de GPS-gegevens en jaarlijkse kolonie-tellingen is het mogelijk om de verspreiding van grote sterns op zee te voorspellen voor kolonies in de zuidelijke Noordzee. Deze benadering kan worden gebruikt in toekomstige effectbeoordelingen om overlap van broedende grote sterns met voorgestelde offshore windparken te voorspellen (**hoofdstuk 6**). Uit vlieghoogtemetingen bleek dat meer dan 87% van alle grote sterns onder de 20 meter vloog, waarvan de helft tussen 11 en 20 meter. Aantallen sterns boven de 20 m namen snel af met afnemende hoogte, waarbij minder dan 1,5% werd geregistreerd boven de 40 m. Dit heeft belangrijke consequenties voor CRM (**hoofdstuk 7**). Grote sterns hebben een lange levensduur (jaarlijks overlevingspercentage van 0,92 voor volwassen vogels) en een lage jaarlijkse trouw aan broedkolonies vertonen (**hoofdstuk 8**). Om referentiegegevens te verzamelen voor toekomstige vergelijking, gegevens over broedaantallen en broedsucces verzameld door directe observatie en het gebruik van Unmanned Aerial Vehicle (UAV of 'drone') onderzoeken (**hoofdstuk 9**) en gegevens over het dieet in verschillende kolonies langs de kust (**hoofdstuk 10**).

Samengevat bleek dat grote sterns 1) offshore windparken vermijden met 5-22%, 2) tijdens het broedseizoen een overlap met offshore windparken dichtbij de kust en dicht bij kolonies vertonen van maximaal 0,6%, 3) over het algemeen op lage hoogte vliegen, hoewel 4,1% van de flux op rotorhoogte vliegt, 4) een lange levensduur (jaarlijks overlevingspercentage van 0,92 voor volwassenen) hebben en 5) een lage jaarlijkse trouw aan broedkolonies vertonen.

Dit alles leidt tot de conclusie dat offshore windparken dichtbij kolonies in sommige jaren een potentiële bedreiging vormen voor grote sterns omdat ze deze regelmatig tegenkomen en maar in een beperkt aantal gevallen vermijden. Aangezien grote sterns een lange levensduur hebben en regelmatig tussen broedkolonies wisselen tussen de jaren, is het aantal individuele vogels dat met een bepaald offshore windpark te maken krijgt groot zijn gedurende de levensduur van een windpark. Aan de andere kant aanvaringspercentages van grote sterns met offshore windturbines relatief laag door het optreden van enige macro-uitwijking en een groot aantal vogels dat niet op rotorhoogte vliegt. Aan de andere kant is in eerdere CRM's een kleiner percentage van de flux op rotorhoogte gebruikt, waardoor de sterftecijfers mogelijk zijn onderschat.

Ten slotte, als toekomstige offshore windparken buiten de foerageergebieden van broedende grote sterns worden gebouwd, zal de blootstelling van deze vogels aan parken tijdens het broedseizoen laag zijn. Dat gezegd hebbende, tonen tellingen aan dat grote sterns buiten het broedseizoen ook ver uit de kust tijd doorbrengen. In een ander deel van het jaar kan de interactie tussen offshore windparken en grote sterns dus weer veel groter zijn.

1 Introduction

1.1 Background

Renewable energy, and in particular the development of offshore wind farms (OWF), is one of the key strategies of the Dutch government to fulfill the requirements of the various agreements to combat global climate change (Klimaatakkoord 2019). Upscaling of the capacity of OWFs in the Dutch North Sea is currently ongoing (Structuurvisie Wind op Zee, routekaart 2030) but given the potential negative effects of OWFs on physical and biological parameters, a detailed insight in these consequences is urgently needed (Fox *et al.* 2006, Bailey *et al.* 2014, Goodale & Milman 2016, Nazir *et al.* 2020).

Seabirds can be negatively impacted by the development of Offshore Wind Farms (OWF) through the risk of direct mortality due to collisions and the risk of indirect mortality due to either displacement leading to habitat loss, or barrier effects leading to avoidance and increased energy expenditure (Desholm & Kahlert 2005, Hüppop *et al.* 2006, Masden *et al.* 2010). In addition, OWFs may impact seabirds indirectly if OWFs indeed cause changes in seasonal spatial stratification patterns, with ultimately may affect the suitability of foraging areas of seabirds (van Duuren *et al.* 2021).

The Sandwich Tern *Thalasseus sandvicensis* is one of the species that was identified as particularly vulnerable to the direct effects of OWFs (e.g. Dierschke *et al.* 2016). As the species is also of high conservation concern, being classified as Vulnerable on the Dutch Red List (Sovon 2021), and protected under several laws and treaties, assessment of the potential effects of OWFs on the species is required. However, assessing the potential negative effects of OWF development on Sandwich Terns is hampered by a variety of knowledge gaps which were summarized by van Kooten *et al.* (2019). These knowledge gaps mainly relate to disturbance effects of operational OWFs, leading effectively to habitat loss, but also to some specific parameters that are part of Collision Rate Models (CRM) that are used in assessment procedures.

To fill in these knowledge gaps amongst many others, the Dutch Government initiated a strategic monitoring programme to study the effects of offshore wind developments on wildlife, which is known as the Offshore Wind Ecological Programme (Wozep; Rijkswaterstaat 2021). Particularly in response to the development of the OWFs Hollandse Kust Noord and Borssele, the Sandwich Tern became one of the focal species.

The at-sea distribution and the macro-avoidance of OWFs by Sandwich Terns are thus of primary interest, as these will together determine how often birds encounter an OWF (also related to collision rates) and how much habitat could be lost after construction of OWFs. This latter might influence inter-specific competition for resources (Busch & Garthe 2016, Heinänen *et al.* 2020). The at-sea distribution can be recorded effectively and across a long and continuous time frame by tracking movements of individual birds with GPS-loggers (e.g. Ropert-Coudert & Wilson 2005, Burger & Shaffer 2008). GPS-tracking also allows to study behavioural responses to the presence of OWFs in detail, including macro-scale avoidance (Cook *et al.* 2018, Peschko *et al.* 2020). Furthermore, many aspects of the actual flight behaviour, such as speed and behaviour, can be recorded using GPS-loggers, that can be used and have particular consequences on the outcomes of CRMs (Fijn & Gyimesi 2018). Therefore, a main component of the studies reported in this report is based on GPS-tracking of individual Sandwich Terns.

Avoidance of OWFs may also mean that movements of individual birds are compromised, which could lead to higher energy expenditure or less profitable prey availability. Habitat loss may thereby affect diet, which in turn may affect reproductive success through so-called carry-over effects (Betini *et al.* 2013). These latter aspects have been studied in a subset of colonies.

It is also important to estimate how many individual Sandwich Terns can interact with an OWF over longer time spans than just a single breeding season. This is all the more relevant in Sandwich Terns, as their low breeding site fidelity means that a single colony in proximity to an OWF can harbour many more individuals than the individuals present in a single year. Therefore, accurate estimates of the rate of movements of birds between colonies, as well as accurate estimates of individual annual survival rates are critical for the assessment of potential effects of OWFs.

All in all, the above-mentioned potential consequences of OWFs on Sandwich Terns and the various parameters that play a role in these consequences, call for an integrated approach to study different aspects of the breeding and feeding ecology of the species in the Dutch North Sea. To do so, two large-scale research projects were designed within the Wozep programme, that are targeted on Sandwich Terns.

1.2 Research questions

The initial research questions defined in the tenders for these two projects targeted at Sandwich Terns were

1. How do Sandwich Terns breeding in the Dutch Delta use the adjacent marine habitat for foraging?
2. What is the influence of existing wind farms on the distribution and foraging behaviour of Sandwich Terns?
3. What is the relationship between foraging habitat, prey choice and breeding success?
4.

These broad questions were translated into specific research questions which are addressed in the report at hand. These specific questions are given below with references to the chapters in which they are treated:

- To what degree does at-sea distribution of Sandwich Terns overlap with (planned) OWFs and with Natura 2000 areas, and how does this differ between colonies? (**Chapter 3**)
- To what degree do Sandwich Terns avoid OWFs at the macro-scale? (**Chapter 4**)
- What environmental conditions drive foraging behaviour at sea? (**Chapter 5**)

- To what degree do overlaps with OWFs change between years as a function of location and size of Sandwich Tern colonies around the North Sea? (**Chapter 6**)
- To what degree do flight altitudes of Sandwich Terns overlap with rotor zones of offshore wind turbines? (**Chapter 7**)
- What is the annual survival rate of adult and immature Sandwich Terns? (**Chapter 8**)
- What are the emigration/immigration rates of adult Sandwich Terns among colonies? (**Chapter 9**)
- What is the diet of chicks and adult Sandwich Terns (**Chapter 10**)

1.3 Report setup

We used data from studies carried out in multiple colonies in the Netherlands and the United Kingdom during 2012-2021 to increase sample sizes, the generality of the conclusions and to maximize multi-use of data. Work at the Scheelhoek and the Slijkplaat started under the umbrella of the PMR-NCV project from 2009 onwards and was continued under Wozep in the ‘GPS tagging coastal birds project 31154272’ during 2020-2021. Work at De Putten (Camperduin, Noord-Holland) started in 2019-2021 as part of the Wozep (‘Onderzoek Grote Stern 2019-2021 project 31147211’). Sandwich Terns were also studied at Scolt Head (United Kingdom), in collaboration with the British Trust for Ornithology (BTO), during 2016-2019 as part of a project funded by Equinor ASA in relation to the ecological effect monitoring of Dudgeon Offshore Wind Farm. Finally, Sandwich Terns were tracked from Texel in 2018 and 2020 by Wageningen Marine Research (WMR) in a project commissioned by Rijkswaterstaat (RWS) to study effects of foreshore coastal nourishment (Baptist & Leopold 2018).

The chapters of this report are set up as manuscripts, aimed at submitting them to peer-reviewed journals since this is one of the aims of the Wozep programme. This setup explains why authors are listed per individual chapter rather than for the entire report. Publishing these chapters in the scientific literature will further improve the studies and the support for the inferences made. In addition, it should help to disseminate the results of the Wozep programme to a wider audience than Dutch stakeholders only and will hopefully help future assessments of effects of OWFs in other countries and/or on other species.

2 Methods

2.1 Tracking

2.1.1 Field methods

This report relies heavily on tracking data collected in several colonies, by different teams and in different projects. However, chapters in the report differ in which data have been used for particular analyses. As this is a potential cause of confusion, this chapter gives an overview of when, where and how tracking data have been collected and which methods have been used. Inevitably, this caused substantial overlap in information between this chapter and the methods sections of each chapter. To limit this overlap, we focus here only on the main aspects.

Field methods and preliminary results have also been published in several reports, including these:

- Collier, M.P., Taylor, R.C., & R.C. Fijn, 2019. Tracking breeding Sandwich terns on the North Norfolk Coast. Fieldwork report 2019. Bureau Waardenburg report 19-173, Culemborg**.**
- Fijn, R.C., Collier, M.P., 2019. Tracking Sandwich terns *Thalasseus sandvicensis* breeding in De Putten with GPS loggers: Fieldwork Report 2019. Bureau Waardenburg Report 19-085. Bureau Waardenburg, Culemborg.
- Fijn, R.C., R.S.A. van Bemmelen & M.P. Collier 2020. Tracking Sandwich terns *Thalasseus sandvicensis* with GPS-loggers in De Putten. Fieldwork report 2020. Bureau Waardenburg report 20-156. Bureau Waardenburg, Culemborg.
- Fijn, R.C., W. Courtens, R.S.A. van Bemmelen, R.P. Middelveld, T. van Daele, P. Verschelde, E.W.M. Stienen, M.P. Collier 2020. Tracking Sandwich terns *Thalasseus sandvicensis* breeding in De Putten and survival analysis of ringing data. Annual report 2020. Bureau Waardenburg report 20-308. Bureau Waardenburg,Culemborg.
- Fijn, R.C., van Bemmelen, R.S.A. & M.P. Collier, 2021a. Tracking Sandwich terns *Thalasseus sandvicensis* breeding in De Putten with GPS-loggers. Fieldwork report 2021. Bureau Waardenburg report 21-181, Culemborg.
- Fijn, R.C., Middelveld R.P. & N. Vanermen, 2021b. Tracking Sandwich terns in the Dutch Delta and data on breeding success and foraging ecology. Progress Report 2021. Bureau Waardenburg report 21-246, Culemborg.

2.1.2 Study colonies

Adult Sandwich Terns were captured in seven colonies, of which one in the United Kingdom and the others in the Netherlands (Figure 2.1). These colonies are Scolt Head, Norfolk, United Kingdom (N52° 59’ E0° 40’), and Scheelhoek, Zuid-Holland (N51° 49’ E4° 04’), Slijkplaat, Zuid-Holland (N51° 48’ E4° 09’), De Putten, Camperduin, Noord-Holland (N52° 44’ E4° 39’), Wagejot, Texel, Noord-Holland (N53° 05’ E4° 54’), Utopia, Texel, Noord-Holland (N53° 07’ E4° 54’), Griend, Friesland (N53° 15’ E5° 15’).

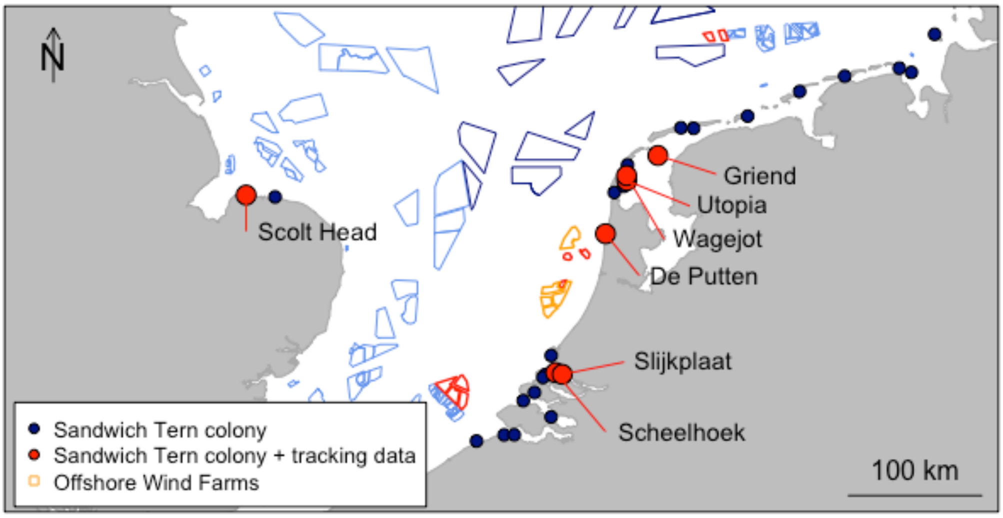

Figure 2.1 *Locations of colonies of Sandwich Terns that have been occupied in any of the years between 2002 and 2021 (blue and red dots). Colonies with tracking data are highlighted as larger, red dots. Polygons show (planned) offshore wind farms, based on KEC 4.0 (Potiek et al. in prep). For Dutch OWFs, operational OWFs are outlined in red, under construction in orange, licensed in yellow and search areas in dark blue.*

2.1.3 Catching & tagging

Pre-fieldwork site visits were carried out to determine laying dates and identify suitable parts of the colony for catching. The fieldwork team consisted of one or two teams, with each team consisting of two ringers. Individual Sandwich Terns were captured on the nest using walk-in traps. The traps used were specifically built for Sandwich Terns. To maximize the capture success rate and reduce the risk of nest desertion, nests were targeted that were in their second or third week of incubation. Trapping was carried out using four to eight traps at any one time. Terns that entered the trap usually started incubating. In some cases, they walked around the trap searching for an exit. After deployment of traps, capture attempts were abandoned whenever the birds took off in alarm; or after about 20-25 minutes.

After capture, each individual was ringed with a steel ring (Vogeltrekstation Arnhem, Holland or BTO ring, United Kingdom) and a darvic ring with readable three-alpha-numeric code. Darvic rings were either white (Scheelhoek/Slijkplaat), blue (Scheelhoek, De Putten, Scolt Head, Texel), lime (Slijkplaat), orange (Griend) or yellow (Scheelhoek, Slijkplaat). Subsequently, the following biometrics were taken: tarsus length, wing length, bill length to feathers, bill plus head, and bill depth at the gonys. Also, body mass was measured. Individuals with a body mass of at least 220g were fitted with a GPS-logger.

2.1.4 Attachment method

The method of attachment of the loggers to the birds evolved over the years from methods that allow temporary deployments to permanent harnesses. We started at Scheelhoek in 2012 using TESA tape (No. 4651; Beiersdorf AG) on seven birds following the methods of Wilson *et al.* (1997). This deployment method was not a success, and a high rate of tag loss was found. In 2012 we experimented with the first temporary harness on three birds. In the following years we used a backpack loop harness (Kenward 1985) from natural latex slip elastic (Preston Innovations Slip Elastic, diameter 1.4 – 2.2 mm), which allows loggers to fall off after a few weeks when the harness material degrades. In 2017 we started experimenting with glue attachments using Loctite Superglue (Henkel) following license restrictions in the UK (see for methodology Collier *et al.* 2017, Seward *et al.* 2021). Using glue (or tape) instead of harnesses increased handling time (capture to release) from approximately 10 min to 15/20 min, but there are indications that return rates are higher when using glue. Finally, permanent backpack loop harnesses constructed from 2 mm teflon were used for birds at De Putten and at Slijkplaat (see for a complete overview in Table 2.1).

Table 2.1 Attachment method per colony and per research program.

Colony	Tape	Temporary harness	Glue	Permanent harness	Total
Scheelhoek	7	53	4		64
• Wozep projects		27			
• Previous projects	7	26	4		
Slijkplaat		9		27	36
• Wozep projects				27	
• Previous projects		9			
De Putten (Wozep)		26		38	64
Griend (previous)		6			6
Utopia (previous)				5	5
Scolt Head (previous)		24	19		43
Wagejot (previous)				15	15
Total	7	118	23	85	233

2.1.5 Logger specifications and settings

At all locations except Texel, loggers were Ecotone GPS-UHF loggers, weighing ~4g and measuring 35 x 15 x 10 mm). Loggers used in 2012-2017 had a single-use battery, allowing up to ~400 GPS-fixes on one battery load depending on environmental conditions and sampling interval. From 2013 onward, loggers (3 in 2013, 2 in 2014, 3 in 2017, and from 2019 on all loggers) were powered by solar panels. The weight of the loggers, rings and harness material (5.8 g) is within the generally accepted limit of 3% of the body mass (Phillips *et al.* 2003, Vandenabeele *et al.* 2011) of the Sandwich Terns in our study (average weight of 241 ± 13.4 g; range 210–270 g; ~2.4 %).

The Ecotone loggers recorded date, time, GPS position and speed at 5-15 minutes intervals, but differed in power supply. To save battery power or maintain a high voltage in solar-powered loggers, loggers were programmed to collect data during 6 hours per day in 2012-2013 to cycles of 12 – 16 hr in later years. Data from GPS-UHF loggers were automatically transferred via UHF to base stations placed in the colony; data were transferred when birds were within 200 to 500 m from the base station. During weekly or bi-weekly visits to the base station, data were downloaded and inspected for anomalies. Of particular interest was the voltage of loggers, which should remain >3.7 V to ensure steady collection of data. In case of low battery voltage, loggers were re-programmed with shorter activity cycles or with longer time intervals between positions.

At Utopia, UvA-BiTS loggers were used (~7.5g, L:52 x W:22 x H:9 mm), whereas at all other sites Ecotone GPS-UHF loggers were used (~4g, L:30 x W:14 x H:9 mm). UvA-BiTS loggers were equipped with solar panels and collected data in 5 min intervals at daytime and 15 min intervals in the evening and at nighttime, as well as high frequency data inside a geofence (i.e. GPS positions in 4 s, 13 s or 32 s intervals; not used in this study).

2.2 Boat-based surveys

The methodology of the boat-based surveys is described in Chapter 7.

2.3 Colour-ringing

The methodology of the colour-ringing activities and the analysis thereof is described in Chapter 8.

2.4 Breeding success

The methodology of the breeding biology programme is described in Chapter 9.

2.5 Diet

The methodology of the diet sampling and analysis is described in Chapter 10.

3 Habitat use of breeding Sandwich Terns along the Dutch coast: spatial overlap with offshore wind farms and Natura 2000 areas.

R.S.A. van Bemmelen, R.P. Middelveld

Abstract

Mobile species such as seabirds often use areas that pose threats as well as conservation areas that should offer benign conditions. Sandwich Terns are among the species potentially impacted by the development of Offshore Wind Farms (OWFs), but for which also conservation areas have been designated. Based on a multi-year GPS-tracking study, we estimate the at-sea distribution of Sandwich Terns during the breeding season and its spatial overlap with both OWFs and marine Natura-2000 areas.

3.1 Introduction

Seabirds are among the most threatened groups of birds (Croxall *et al.* 2012). Threats to seabirds include mortality due to by-catch in fisheries, overfishing, oil pollution, but also the increasing development of anthropogenic infrastructure at sea, such as Offshore Wind Farms (OWFs). To counter threats to seabirds, many measures to protect them are developed, including the designation of marine protected areas. However, marine protected areas may be designated for habitats or other taxa than seabirds and may therefore not be tailored to fit the distribution of seabirds. Knowing to what degree the distribution of seabird species overlaps with areas with intensive anthropogenic use and marine protected areas (MPAs) is therefore critical to effective conservation.

Mapping the at-sea distribution of seabirds can be done using ship-based or aerial wildlife surveys (Leopold *et al.* 2013, Bradbury *et al.* 2014, Welcker & Nehls 2016), or tracking of individual seabirds (Davies *et al.* 2021). The latter method has seen rapid development over the past decades, enabling researchers now to track even relatively small birds (Bridge *et al.* 2011). Tracking individual birds has the advantage over wildlife surveys that it is continuous over time (rather than a snapshot) and that the colony of origin of birds is known.

Here, we quantify the overlap of the at-sea distribution of Sandwich Terns *Thalasseus sandvicensis* breeding in a few colonies along the coasts of the southern North Sea. Sandwich Terns tend to avoid OWFs (Dierschke *et al.* 2016) and their foraging range overlaps with OWFs that have already been built or are planned to be built over the coming decades. At the same time, the Dutch government has designated several MPAs in the southern North Sea. In this study, we show the area-use of Sandwich Terns tracked from multiple colonies around the southern North Sea and quantify their 1) foraging trip duration and distance, 2) at-sea distribution, 3) overlap with both existing and planned OWFs 4) overlap with existing protected areas. Overlap can be quantified at individual and colony levels.

3.2 Methods

3.2.1 Fieldwork

During 2020-2021, adult Sandwich Terns were captured on the nest in colonies at the Scheelhoek (2020), Slijkplaat (2021) and De Putten (2019-2021). See Chapter 2 for further details.

3.2.2 Analysis

Tracking data were regularized to intervals of 10 min. Positions were classified as in the colony when they were within 2 km from the center of a colony that was occupied that year (not necessarily the colony in which the bird was tagged). Then, foraging trips were defined as periods between departing and arrival from colonies. Foraging trips were split into two trips whenever 1) time gaps were greater than 35 minutes or 2) when the bird could have returned to the colony and back within two positions outside the colony, assuming a speed of 44.4 km h^{-1} (Fijn & Gyimesi 2018). Trip statistics across individuals (mean and maximum range, i.e., the distance from the colony, and mean duration) were calculated per colony per year, and for complete trips only (trips that started and ended in the colony, and that did not have time gaps larger than 25 minutes).

The ‘home’ colony, i.e., the colony to which a bird regularly returned, was determined using a changepoint analysis on the longitudes and latitudes recorded in colonies. Subsequently, only data where the home colony was determined to be Slijkplaat, Scheelhoek or De Putten colonies were retained in further data analyses.

Utilization Density (UD) kernels were estimated per home colony, year and individual. UD kernels were estimated using a smoothing factor of 2 km and a grid cell size of 1 km, using the adehabitatHR package version 0.4.19 in R (Calenge 2006). Shapefiles for OWF on the Dutch Continental Shelf were obtained from the recent KEC update project (Figure 3.1, Potiek *et al.* in prep.). OWFs were categorized as operational (n = 10), under construction (n = 5) or awaiting licensing (n = 7). This excludes areas assigned as areas where future OWFs might be built, but where the licensing and exact delineation has not yet been determined. Shapefiles of the Dutch Natura 2000 areas (N2000 hereafter) were obtained from the www.eea.europa.eu website (accessed 15 October 2021) and supplemented with a polygon of the recently assigned N2000 area ‘Bruine Bank.’ N2000 areas were selected that were either marine or large fresh or brackish water bodies. Then, per home colony, year and individual, the size of the overlapping area was calculated between UD kernels, and both OWFs and N2000 areas.

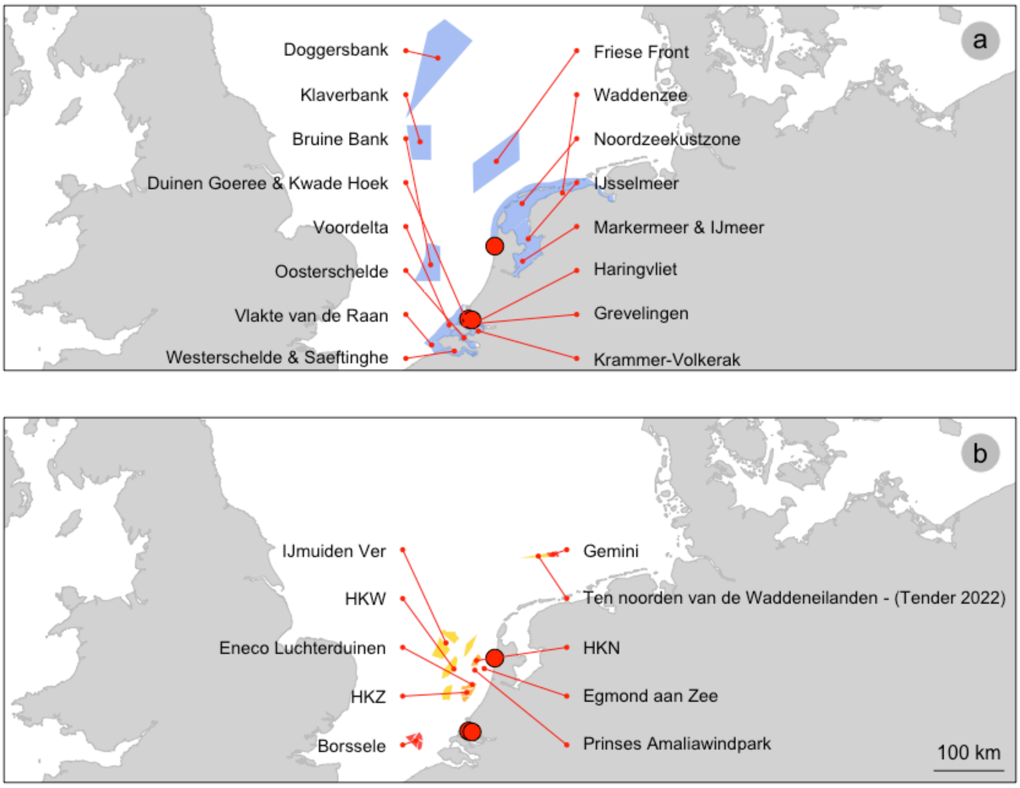

Figure 3.1 *Map of the Dutch North Sea, showing a) Natura 2000 areas relevant to Sandwich Terns and b) OWFs that are operational (red), under construction (orange) and not yet licensed (yellow). Red dots indicate De Putten in the north and the Scheelhoek and Slijkplaat colony locations in the south. OWF data are from KEC 4.0 (Potiek et al. 2021)*

3.3 Results

3.3.1 Sample size

Overall, data from 117 individuals-year combinations were retained in the final data set. Sample sizes vary per year and per colony (Table 3.1). Two individuals were captured and tagged at Scheelhoek but lost their broods shortly after tagging. These birds then moved to De Putten to start another breeding attempt. These two individuals have been included in both the Scheelhoek and De Putten data analyses, but only those parts in which they were based at either colony.

Mean trip durations varied among years and colonies between 1.4 and 3.2 hours. Mean maximum ranges from the colonies differed markedly between the colonies in De Putten and in Haringvliet (Scheelhoek and Slijkplaat). Birds from De Putten travelled over ranges between a maximum of 12 and 18 km, compared to 22 and 25 km for bird from Haringvliet. This clearly reflects the location of the colony with De Putten bordering the sea and the Haringvliet colonies being located approximately 5 to 11 km inland (Table 3.2).

Table 3.1 *Sample size per colony per year*

colony	year	n individuals	n bird*days	n foraging trips	n positions
De Putten	2019	14	171	531	4,075
De Putten	2020	25	651	2,879	17,254
De Putten	2021	27	1,042	3,453	27,579
Scheelhoek	2020	27	576	1,726	16,104
Slijkplaat	2021	24	563	2,711	13,742

Table 3.2 *Trip statistics for colonies and years across individuals. Range refers to the maximum distance from the colony within a trip.*

colony	year	mean trip duration (hr)	maximum trip duration (hr)	mean range (km)	maximum range (km)
De Putten	2019	3.2	23.0	12	127
De Putten	2020	2.0	27.3	18	217
De Putten	2021	2.2	43.8	16	121
Scheelhoek	2020	2.5	37.0	25	292
Slijkplaat	2021	1.4	113.0	22	227

The homerange of Sandwich Terns breeding in De Putten is basically a ‘flattened half circle with extensions along the coast’ (Figure 3.2 - Figure 3.4), whereas the homerange of Sandwich Terns breeding in Haringvliet is more ‘cone shaped’ with its tip in Haringvliet (Figure 3.5 - Figure 3.6). Birds from De Putten had a core foraging area between roughly Texel and IJmuiden within some years (2019) a slightly smaller core foraging area (Figure 3.2) than in other years (Figure 3.3 - Figure 3.4). Birds from Haringvliet (Slijkplaat/Scheelhoek colonies) mainly foraged in a northwestern direction from the Haringvliet. In 2020 Sandwich Terns from Scheelhoek ranged slightly further offshore (Figure 3.5) than in 2021 when the colony was located at Slijkplaat (Figure 3.6).

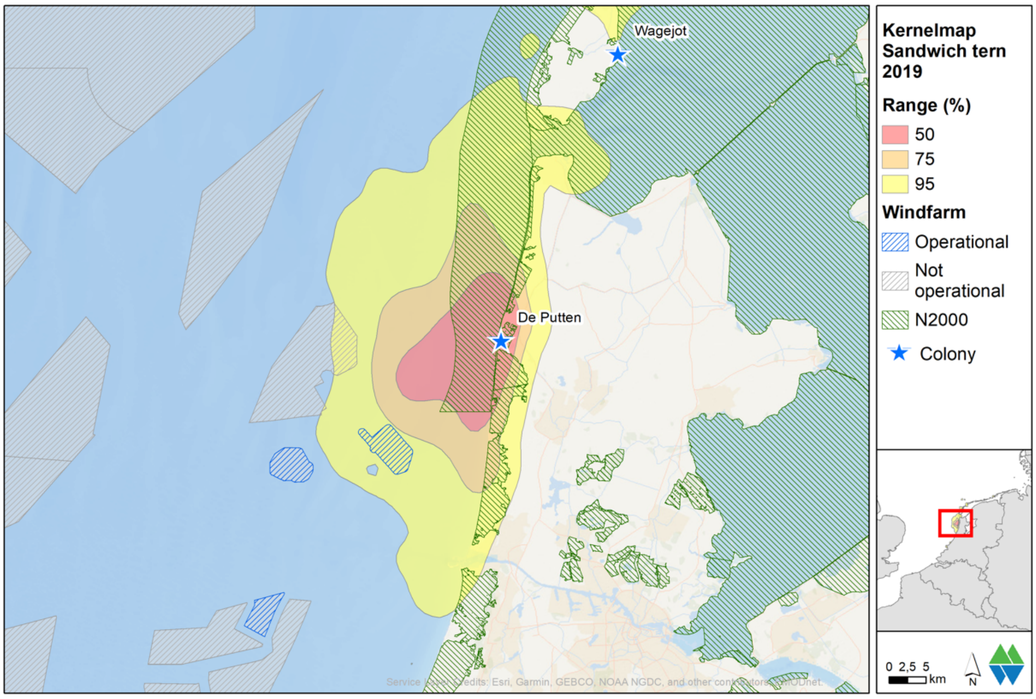

Figure 3.2 UD kernels for De Putten in 2019 for all individuals combined.

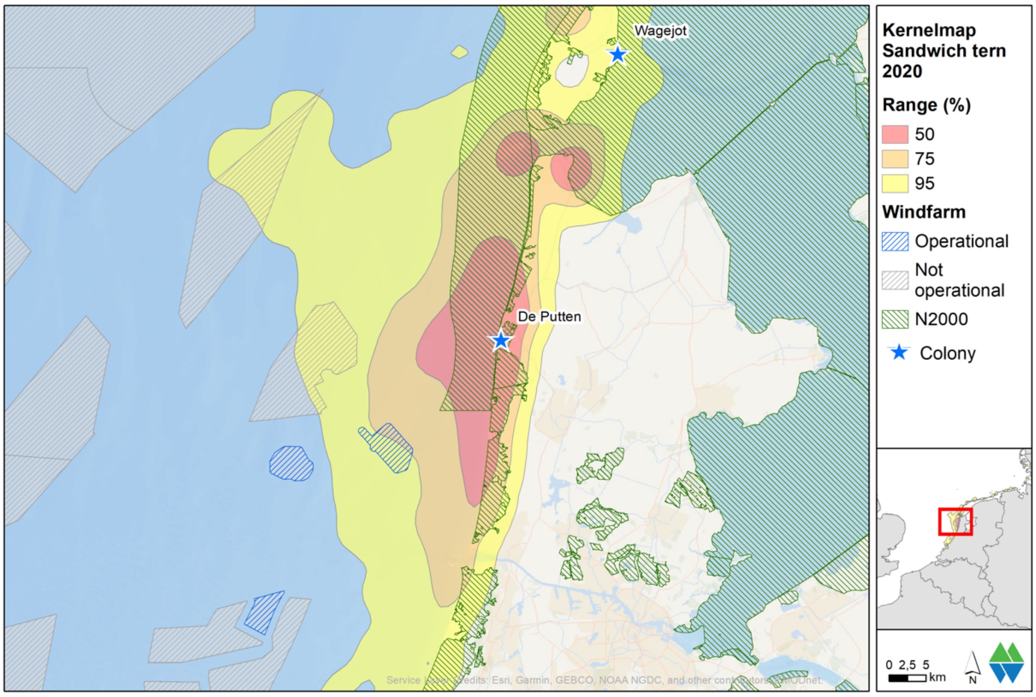

Figure 3.3 UD kernels for De Putten in 2020 for all individuals combined.

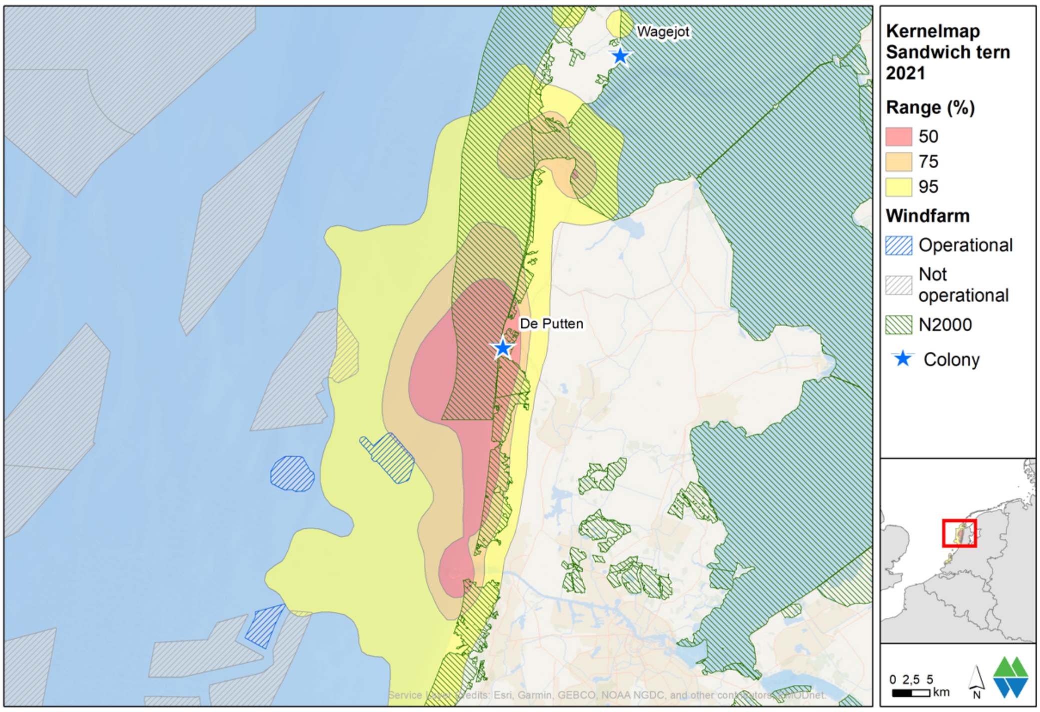

Figure 3.4 *UD kernels for De Putten in 2021 for all individuals combined.*

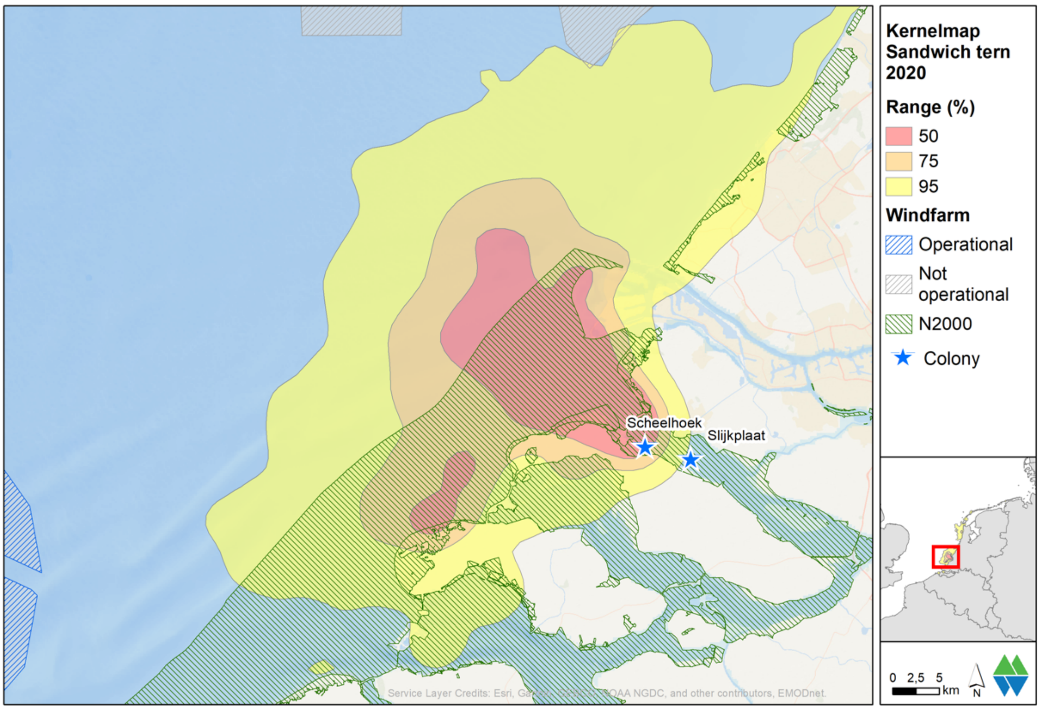

Figure 3.5 *UD kernels for the Scheelhoek in 2020 for all individuals combined.*

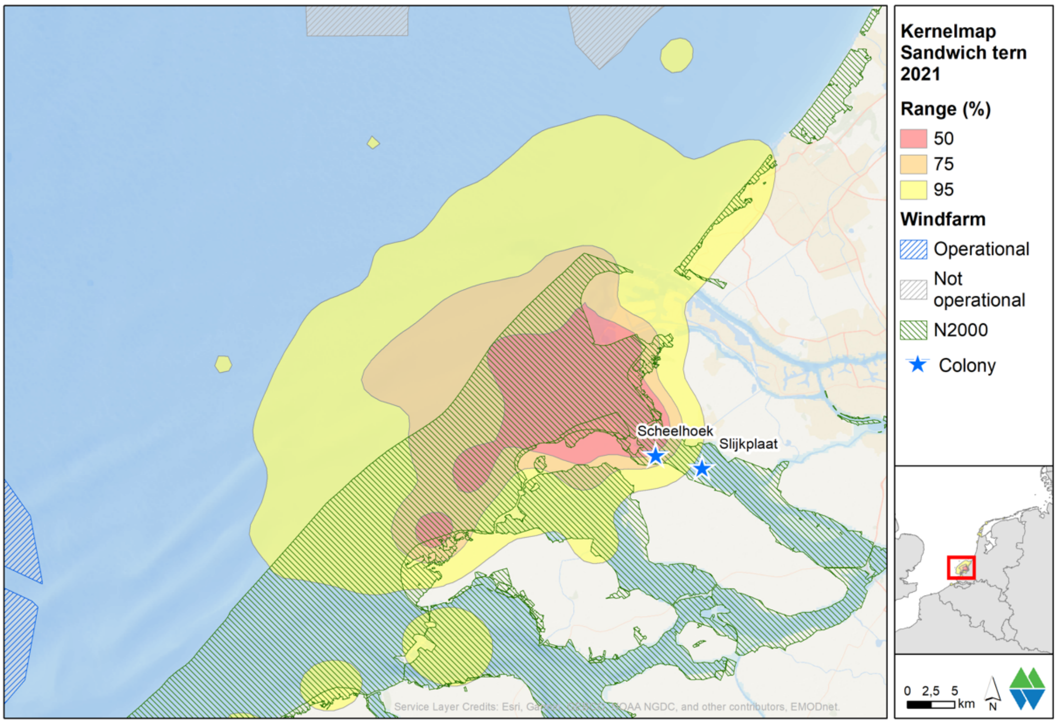

Figure 3.6 UD kernels for the Slijkplaat in 2021 for all individuals combined.

3.3.2 Overlap with N2000 and OWFs areas

The percentage of individuals showing overlap between their kernels and OWFs was much larger for birds from De Putten than for those from the Scheelhoek/Slijkplaat colonies. A large proportion of the birds from De Putten showed overlap with Egmond aan Zee offshore windfarm (OWEZ) in all three years, followed by Hollandse Kust Noord (HKN). Other OWF areas overlapped with less than 20% of individuals from De Putten. Birds from the Slijkplaat almost never showed overlaps between their UD kernels and N2000 areas; only OWEZ and Hollandse Kust Zuid (HKZ) were within the UD kernels of single individuals (Figure 3.7).

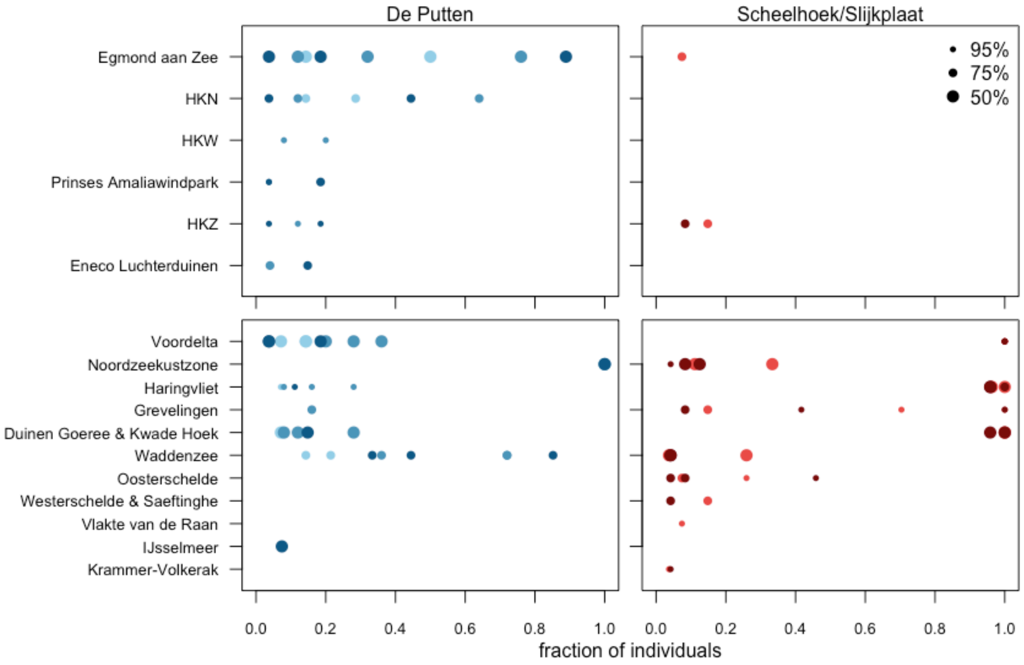

Figure 3.7 *Percentage of individuals showing overlap between their UD kernels and operational or planned OWFs (top panels) and selected N2000 areas (lower panels). Dot sizes correspond to UD kernel size and colour to year, with later years in darker shades.*

For birds from De Putten, mean percentage overlap of individual 95% UD kernels with any of the operational OWFs was largest for the OWEZ, with 1.04%, followed by Eneco Luchterduinen (LUD) with 0.7% and Prinses Amalia windfarm (PAWP) with 0.19%. For planned offshore wind areas, this was 0.14% for HKN and 0.01% or less for HKW and HKZ. For 75% UD kernels, some overlap was observed for the three operational wind farms, but not for the planned areas. Finally, 50% UD kernels only overlapped with OWEZ (0.15%) (Figure 3.8a). For birds from the Scheelhoek/Slijkplaat, mean percentage overlap of individual 95% UD kernels with any of the operational OWFs was largest for the KHZ, with 0.06%, followed by OWEZ with 0.01%. Mean overlap was 0 for other (planned) OWFs, and also for smaller UD kernels (50 and 75%) (Figure 3.8b).

Overlap of individual UD kernels with N2000 areas was much larger in both colonies. Also, while overlap with OWFs was smaller for 50% and 75% UD kernels than for 95% UD kernels, the opposite was true for some N2000 areas. For example, the mean overlap of individual 50% UD kernels amounted to almost 30% in the Noordzeekustzone, whereas the 95% UD kernels overlapped about 15%. Three N2000 stood out in this analysis: Voordelta, Noordzeekustzone and Haringvliet. Whereas the Noordzeekustzone was used extensively by Sandwich Terns from De Putten, the two other areas are important for those breeding in the two Haringvliet colonies: Slijkplaat and Scheelhoek (Figure 3.8c, d).

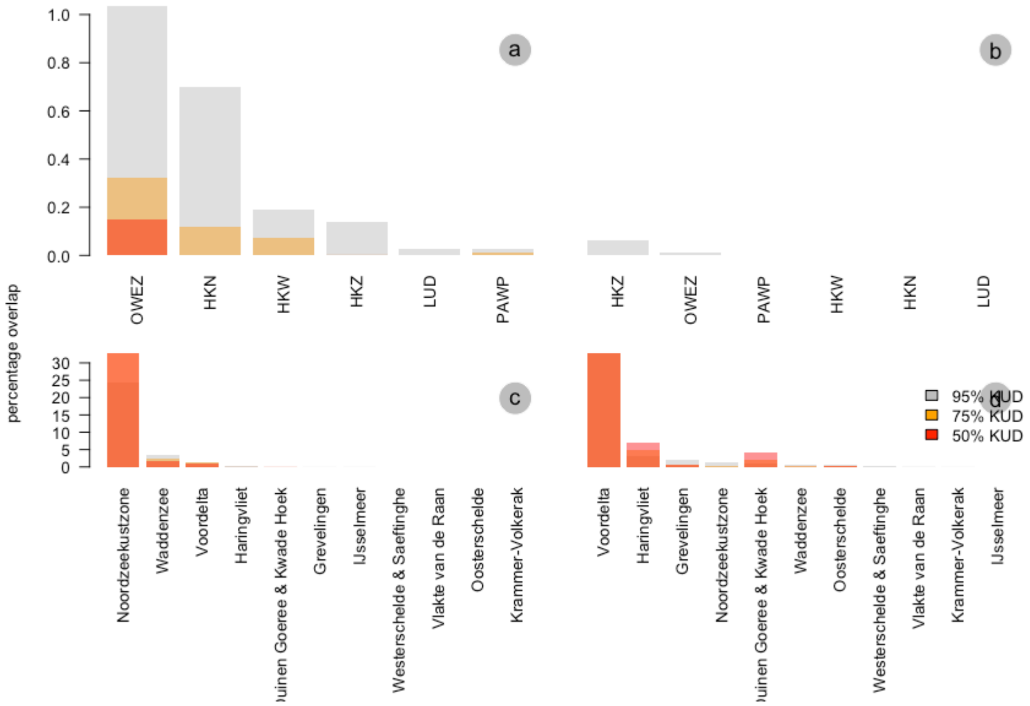

Figure 3.8 *Mean percentage overlap across individuals between individual UD kernels and (a) OWFs and (b) N2000 areas. Note the different y-axis scales.*

3.4 Discussion

Sandwich Terns from De Putten usually ranged to 12-18 km from the colony, whereas birds from the Scheelhoek/Slijkplaat ranged somewhat further, to 22-25 km. However, much longer trips were observed among individuals from both colonies. Several OWFs are thus within reach of these colonies, but only Offshore Windfarm Egmond aan Zee (OWEZ) had a spatial overlap with a substantial part of the UD kernels of individual Sandwich Terns from the De Putten colony. Even though a majority of individuals had kernels overlapping with this OWF, it only concerned a tiny proportion of the surface area of their kernels: less than 1% of the 95% UD kernels to less than 0.01% of the 50% UD kernels.

In contrast, overlap with N2000 areas was much more pronounced, which was no surprise given that both studied colonies are within or bordering N2000 areas. Foraging trips from both colonies will therefore always start within a N2000 area. Still, the larger part of the kernels was outside these areas. This is largely because the western borders of the N2000 areas Voordelta and Noordzeekustzone are at *ca.* 6-8 km from the coast, whereas many foraging trips venture much further offshore. Remarkably, conservation goals for Sandwich Terns have been formulated only for the N2000 areas Wadden Sea, Voordelta, Haringvliet, Grevelingen en Westerschelde, but not for the Noordzeekustzone, although this is obviously an important area for them.

Some overlap was also detected with coastal, terrestrial areas. This results from some ‘spill-over’ effect when estimating UD kernels, resulting in part of the kernels being estimated on land. This highlights that UD kernels show the general distribution of positions, and that especially the edges of these kernels (described here by the 95% UD kernels) should be interpreted with caution.

Our results indicate that a large proportion of individual Sandwich Terns from the De Putten colony will have repeatedly visited (the vicinity of) the OWEZ windfarm, but that this area only represents a small portion of their total home range.

3.5 Appendix I

Digital aerial seabird surveys show Sandwich Tern occurrence in and around Borsele OWFs

In the first half of 2022, digital aerial surveys of seabirds and marine mammals were carried out in two areas in the southern Dutch North Sea, covering the Borsele offshore wind farms (OWFs), by Bureau Waardenburg and HiDef/BioConsult SH. Preliminary results of these monthly surveys are presented in Collier *et al.* (2021) and repeated here, showing the distribution of Sandwich Terns in and around the Borsele OWFs for February-July (Figure 3.9).

During these surveys, between 65 (July) and 739 (April) Sandwich Terns were recorded. The results clearly demonstrate that Sandich Terns regularly venture close to and inside the Borsele OWFs. During May-July, Sandwich Terns observed in and around the Borsele OWFs likely mainly originate from the nearby large colony at Waterdunen, Zeeland. Note that the distribution in April was more offshore than in other months, suggesting these individuals were mainly migrating rather than commuting from the Waterdunen.

Figure 3.9 *Density of Sandwich Terns during monthly digital surveys starting in February.*

4 Avoidance of offshore wind farms by Sandwich Terns in the North Sea.

R.S.A. van Bemmelen, J.J. Leemans, M.P. Collier, R.P. Middelveld, R.C. Fijn

Abstract

A prerequisite for adequate assessment of the potential impact of Offshore Wind Farms (OWFs) on seabirds is the quantification of avoidance of OWFs by seabirds. Here, we used integrated Step-Selection Models (iSSMs) and GPS-tracking data to estimate avoidance of OWFs by Sandwich Terns *Thalasseus sandvicensis* during the breeding season, from two colonies: Scolt Head (United Kingdom) and De Putten (the Netherlands). The foraging ranges of birds from each colony overlap with multiple OWFs. iSMMs taking into account habitat characteristics (land, water depth and sediment grain size) and movement characteristics, indicate a macro-avoidance rate of 0.05 for Scolt Head and 0.22 for De Putten. These avoidance rates imply that Sandwich Terns experience habitat loss when OWFs are constructed within their foraging ranges.

4.1 Introduction

To reduce greenhouse gas emissions, ambitious plans have been laid out to develop offshore wind energy farms (OWFs) in the Dutch sector of the North Sea (Economic Affairs 2018 2013). OWFs can impact seabird populations through increased collision risks and through habitat loss if birds are avoiding OWFs (Stienen *et al.* 2007, Furness *et al.* 2013, Dierschke *et al.* 2016, Welcker & Nehls 2016). With the expansion of OWFs, also the potential for conflicts between OWFs and wildlife increases, and could lead to unfavourable conservation status of populations of seabirds that fall under the EU Birds Directive and Habitats Directive (Commission 2009). Since the construction of the first OWFs, efforts have been made to estimate avoidance and attraction, as such behaviours are important determinants of both collision rates and habitat loss (Dierschke *et al.* 2016).

Avoidance behaviour is usually characterized at three spatial levels: macro- (avoidance of the entire OWF), meso- (avoidance of the turbines, once a bird has entered the OWF) and micro-scales (avoidance of individual rotor blades once the bird is approaching the rotor area) (Cook *et al.* 2018, Thaxter *et al.* 2018), but attraction could be conceptualized at the same spatial scales (Vanermen *et al.* 2019). Although coarser spatial scales require less high temporal and spatial resolution of bird tracking data, robust estimates of avoidance and attraction are lacking even at the course (macro-) scale for many species, including species of high conservation concern. This lack hampers the assessment of potential impacts from OWFs.

Macro-avoidance or attraction rates can be estimated from seabird densities within and outside the OWF, for example using ship-based seabird surveys (Leopold *et al.* 2013, Welcker & Nehls 2016), aerial surveys (Bradbury *et al.* 2014) or radar data (Krijgsveld *et* *al.* 2011, Skov *et al.* 2018). Such data typically show the densitiy of animals. Alternatively, avoidance or attraction can be estimated from tracking data of individual seabirds (Peschko *et al.* 2020). However, tracking data are presence-only data and therefore provide no direct information on which areas birds did not use. Therefore, habitat-selection models compare conditions (e.g. the presence of an OWF) at positions visited by the animal ('used' positions, i.e., the tracking data) with those at positions that were available to the animal, but not used at that time ('available' positions) (Boyce & McDonald 1999). The relation between used and available positions can be modelled as a function of environmental characteristics, such as distance from the colony, water depth, but also the presence of an OWF. Slope estimates indicate the preferential use or avoidance of covariates. By including environmental covariates, such models can be used to account for differences in habitat suitability when estimating the avoidance or attraction of an OWF. From the several types of habitat-selection models, integrated Step Selection Functions (iSSFs) model both the habitat selection process and the movement process by comparing used locations against locations that were available to the individual from its previous location and taking into account step lengths and turning angles between subsequent positions (Avgar et al. 2016). iSSFs are also suitable for estimating macro-avoidance and attraction because they provide unbiased and robust parameter estimates and can be fitted using freely available and open-source software (Avgar *et al.* 2016, Fieberg *et al.* 2021, Mercker *et al.* 2021).

One of the species for which current estimates of macro-avoidance rates could be improved is the Sandwich Tern *Thalasseus sandvicensis*, a species that has been identified as a species potentially sensitive to OWFs (Dierschke *et al.* 2016, Harwood *et al.* 2017). The Sandwich Tern is a colony-breeding seabird, usually foraging exclusively at sea, targeting pelagic fish. Foraging trips from the colony are mostly restricted to ~40 km from the colony, but longer trips are occasionally made either for foraging, or to prospect other colonies (Fijn *et al.* 2017). Since foraging ranges overlap with (planned) OWFs (chapter 3), the species is potentially affected by OWFs through avoidance behaviour and subsequent displacement from OWFs. However, also attraction has been suggested to occur at (the outer ring of) turbines, where turbulence potentially creates foraging opportunities (Vanermen *et al.* 2013). In this study, we estimate the macro-scale response of breeding Sandwich Terns to environmental conditions (distance from the colony, water depth and sediment type) and operational OWFs, as well as their direct surroundings, using iSSFs and GPS-tracking data collected at colonies in the Netherlands and the United Kingdom.

4.2 Methods

4.2.1 Fieldwork

Adult Sandwich Terns were captured on the nest in the colonies of De Putten, Camperduin, the Netherlands (N52° 44' E4° 39) and at Scolt Head, Norfolk, United Kingdom (N52° 59' E0° 40), during the second or third week of incubation. Individuals weighing >220g were selected for GPS-logger deployment, using Ecotone GPS-UHF logger with solar panels and a full body harness. See Chapter 2 for further details on tagging methods. A total of 63 individuals were tagged at De Putten in 2019, 2020 and 2021 and 43 at Scolt Head during

2016, 2017, 2018 and 2019. Furthermore, additional data were included from two individuals GPS-tagged at Slijkplaat in 2021 that relocated for a second breeding attempt in De Putten that year.

GPS loggers automatically transferred the tracking data to base stations positioned at each colony. GPS loggers were pre-set to record positions between 5AM and 21PM local time, taking positions at intervals of 5, 10 or 15 min, depending on year, location and the voltage of the battery. If voltage dropped below 3.7V, loggers switched to take positions at hourly intervals.

4.2.2 Analysis

Step-selection Functions require positional data at regular time intervals, but considering the different recording regimes, tracking data needed to be regularized (and interpolated) to a single time interval. Selecting an appropriate time interval involves balancing the handling of many interpolated positions (when selecting short intervals) with coping with the loss of spatial and temporal resolution (when selecting long intervals). Here, we regularized tracking data to time intervals of 10 min, considering most data were collected at intervals of 5 or 10 min (15 min data concerned only some loggers in De Putten in 2019), with linear interpolation of positions across time gaps no longer than 35 min (thus, a maximum of 2 positions). For each set of subsequent positions (a ‘step’), ten random positions were generated from the distribution of step length and turning angles, using the amt package (Signer *et al.* 2019). At each endpoint of each step, the water depth (EMODnet, 2018), median grain size of the bottom sediment (hereafter referred to as ‘sediment’, data Deltares) and the distance to the colony (avoiding overland routes) were extracted. Fijn *et al.* (Chapter 5) and van Bemmelen *et al.* (Chapter 6), studies that are partly based on the same data as this paper, indicate that water depth and sediment are the most important factors in explaining the switch to foraging behaviour and in habitat selection, respectively. To avoid overfitting of models, no additional environmental variables were added other than our primary interest, the presence in or proximity to OWF. Wind turbine positions were obtained from Zhang et al. (2021) and turbines from Lincs, Lynn and Inner Dowsing OWFs were combined as theses OWFs border each other and buffers would overlap. Around the turbines of each OWF, a convex hull was drawn, as well as a ring of 0-1500m around the convex hull. Only OWFs overlapping with the foraging ranges of the two colonies were considered (Figure 4.1). These were Eneco Luchterduinen, Prinses Amaliawindpark and Egmond aan Zee near De Putten and Sheringham Shoal, Race Bank, Inner Dowsing, Lynn, Dudgeon, Lincs and Lincs-Lynn-Inner Dowsing wind farms near Scolt Head. Other operational OWFs were not considered as they were far outside the foraging ranges of the two colonies (>100km) and no bird positions were recorded within these OWFs.

Five iSMMs were fitted per colony: 1) OWF not included, 2) OWF as a fixed, binary effect, indicating whether a position was either inside or outside any of the OWF perimeters, 3) as model 2 but also with a parameter for the 0-1500m ring around OWFs, 4) OWF as a fixed effect with a parameter for each individual OWF or 5) as model 4 but also with parameters for each OWFs’ 0-1500m ring. All iSSFs included the available (coded as 0) and used (coded as 1) steps as the binomial response variable, and distance to the colony, water depth and sediment as fixed effects. Step ID was included as a random intercept, with the θ of the random effect of step ID fixed at 10^3 (Muff *et al.* 2019). For each environmental variable, random slopes were included per individual. For the effect of OWFs, no random slopes per individual could be included, due to the small number of positions within OWFs. Availability points were assigned a weight of 10^3 (Aarts *et al.* 2012, Fithian & Hastie 2013).

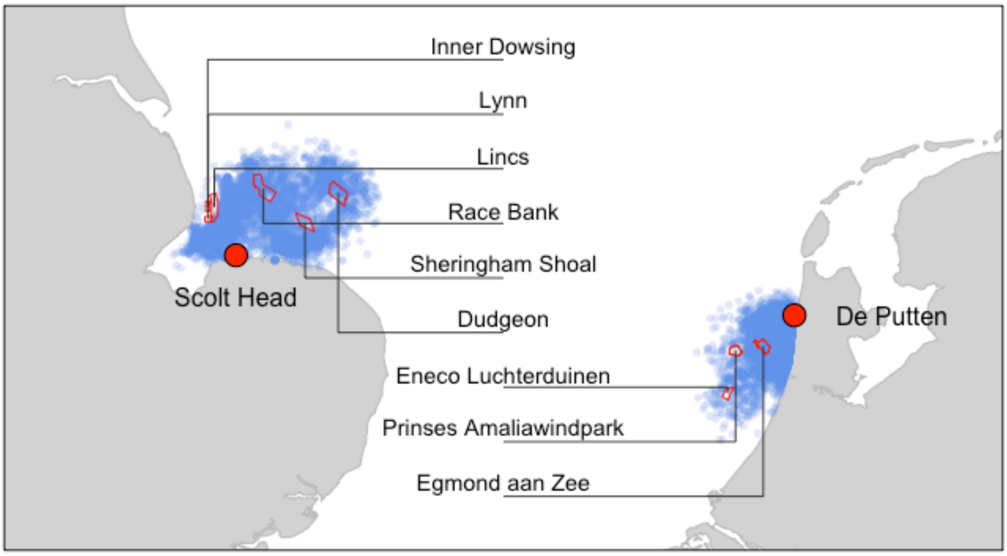

Figure 4.1 *Distribution of tracking data of Sandwich Terns breeding in the Scolt Head (United Kingdom) and De Putten (the Netherlands; colonies indicated by red-filled dots) and relevant operational OWFs (red outlined polygons): five near Scolt Head and three near De Putten. Note that in the iSSFs, only steps have been included in which at least one of the used or available positions were within 10 km of an OWF. This causes the rather sharp cut-off of positions north of De Putten.*

Only steps were selected in which at least one of the used or available positions was within 10 km from an OWF. This restriction reduces data size and therefore computation time and will also make the relations with environmental variables more tailored towards the area around the OWFs, reducing the effect of measurements in distant areas. Moreover, because the environment (e.g., bathymetry) is rather different between the two colonies, and therefore the habitat selected by Sandwich Terns potentially as well, separate models were fitted for each colony. Within each colony, the effect on model fit of the addition of OWFs as a fixed effect, either as single or multiple parameters, relative to the model with no OWF effect, was assessed using the Deviance Information Criterion (DIC). Models with lower DICs are considered to better fit the data. Models with ΔDIC < 5 relative to the model with the lowest DIC are considered to have a similar fit. Reduction in the relative use of OWFs was calculated following instructions by Fieberg *et al.* (2021), to calculate the relative selection strength (RSS) of OWFs by the ratio of exponentiated regression coefficients for OWFs. RSSs of OWF effects represent relative intensities within OWFs versus outside OWFs when availability of locations inside and outside OWFs, as well as habitat characteristics, are equal. Avoidance rate was calculated from parametere estimates β as $1-\left(exp(\beta)/(1+exp(\beta))\right)/0.5$. Models were fitted using Integrated Nested Laplace

Approximation as implemented in the R-INLA package version 21.02.23 in R version 4.0.2 (Lindgren & Rue 2015, R Core Team 2020).

4.3 Results

4.3.1 Sample size

The final dataset comprised 18087 positions of 90 individuals (Figure 4.1). The number of positions per individual ranged from 9 to 588 for Scolt Head and from 14 to 1418 for De Putten (Table 4.1Table 4.1). Bird positions within OWFs comprised *ca.* 1% for both colonies, and within the 1.5 wide rings around the OWFs comprised <1% of the positions for Scolt Head and <1% for De Putten (see examples in Figure 4.2).

Table 4.1 Sample size of tracking data for each colony, within 10 km from OWFs.

colony	N ind	N positions	N pos in OWFs	N pos in rings
De Putten	58	13,358	93	361
Scolt Head	32	4,729	150	269

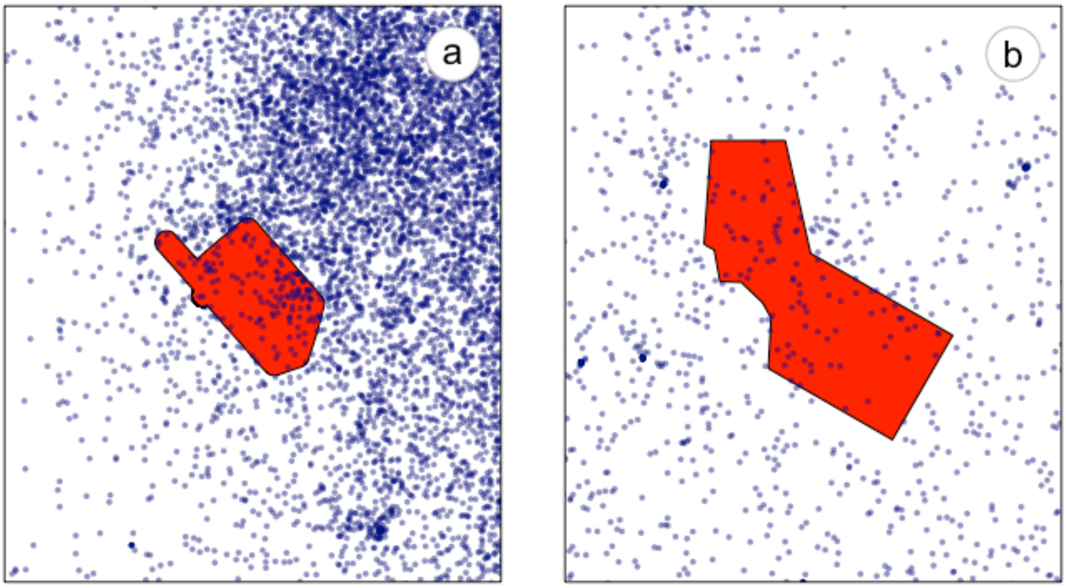

Figure 4.2 Enlarged examples of two OWFs, a) Egmond aan Zee OWF (OWEZ, the Netherlands) and b) Race Bank OWF (United Kingdom), with recorded positions of GPS-tracked Sandwich Terns (blue dots).

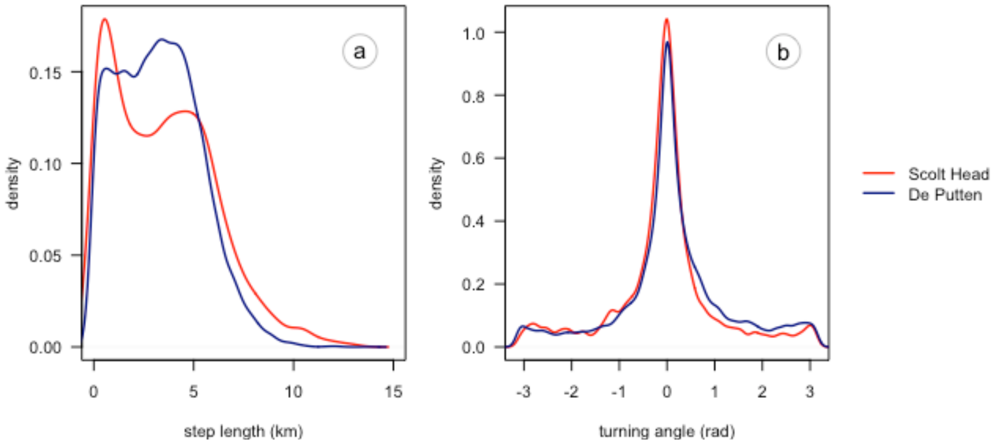

Figure 4.3 *Distribution density curves of a) step lengths and b) turning angles for GPS-tracking data regularized to 10 min intervals, for Scolt Head and De Putten. Random steps were generated by sampling from these distributions. The distributions show strong directionality (turning angles strongly peak around 0) and step lengths of mostly less than 5 km.*

4.3.2 iSSMs

Median step length was 3.12 km (95% CI: 0.008-8.87) for Scolt Head and 3.11 km (95% CI: 0.038-7.439) for De Putten (Figure 4.3a). Flights were strongly directional (Figure 4.3b). Both step length and turning angle distributions were very similar between Scolt Head and De Putten.

In line with other studies of partially the same data set (chapter 5 and 6), distance from the colony, land/sea, water depth and sediment had strong effects on the movements of Sandwich Terns, which preferentially selected marine areas close to the colony and coarser sediments. However, whereas birds at De Putten preferred shallower waters, birds at Scolt Head appeared to select deeper waters.

Compared to models with only the environmental covariates, models including OWF as a fixed effect (either as a single parameter or parameter per individual OWF) had substantially lower DIC values for Scolt Head, but not for De Putten (Figure 4.4Figure 4.4), suggesting that the presence of OWFs had a significant influence on the relative space use of Sandwich Terns on in the former area. For Scolt Head, the best model contained parameters for each OWF as well as parameters for rings around each OWFs; this model outcompeted all other models based on DIC (Figure 4.4). For De Putten, the model with a single parameter for all OWFs performed best, but several more complex models were competitive, with $\Delta DIC < 5$, suggesting that differences between the effects of OWFs as well as the effect of rings were small.

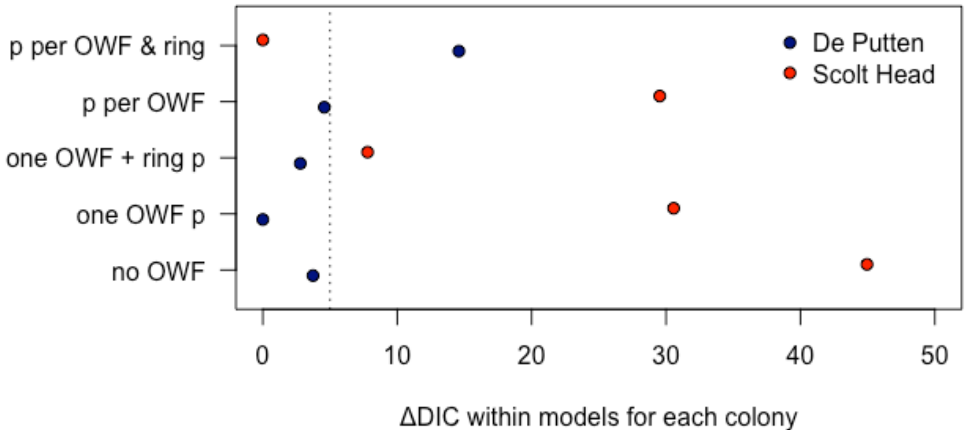

Figure 4.4 Comparison of model fit by ΔDICs of iSMMs of the effect of OWFs on the movement characteristics and habitat selection of Sandwich Terns in two colonies: Scolt Head and De Putten. Models with ΔDIC values >5 (dotted line) are considered to have a substantially less support.

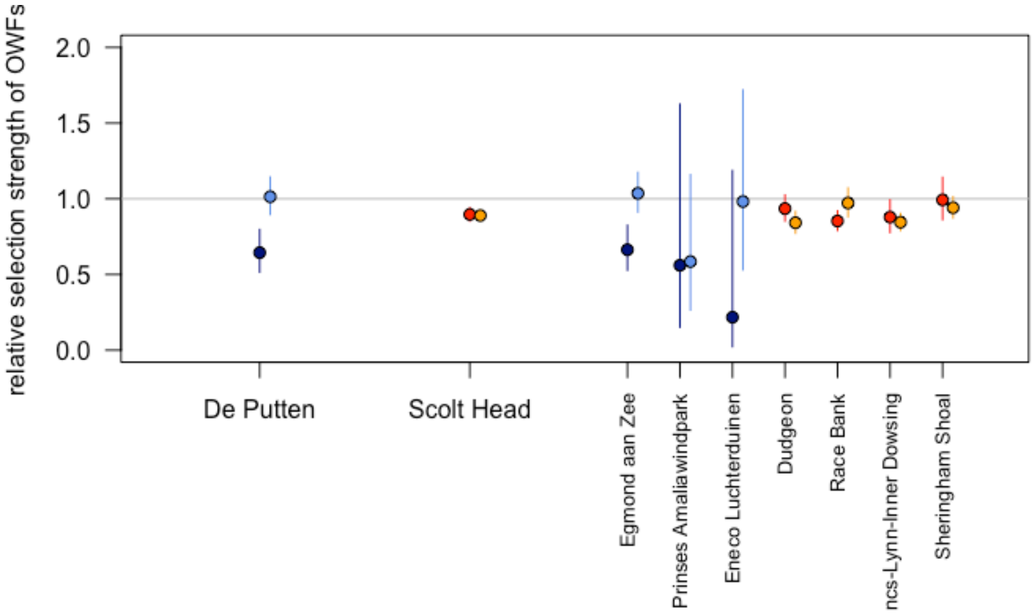

Figure 4.5 Relative Selection Strength (RSS) of OWFs and rings around OWFs by Sandwich Terns from two colonies (De Putten, blue/light blue, and Scolt Head, red/orange), estimated by iSMMs from GPS-tracking data. Values close to 1 indicate indifference, values lower than 1 indicate avoidance, and values higher than 1 indicate attraction. The estimates for De Putten and Scolt Head on the left correspond to models with a single parameter for the effect of each OWFs and its ring that are separately shown on the right, in the same colours. Thus, Egmond aan Zee, Prinses Amaliawindpark and Eneco Luchterduinen are close to the De Putten. Error bars show 95% credible.

In models with parameters for each OWF, all parameters indicated macro-avoidance. Only the parameters for Dudgeon, Sheringham Shoal and Lincs OWFs had exponentiated parameters overlapping and close to 0, indicating indifference to the OWFs can not be excluded (Figure 4.5, Table 4.2). For De Putten, the smallest avoidance was estimated for

Egmond aan Zee (the OWF closest to the De Putten colony), whereas the two OWFs further away were associated with larger avoidance estimates, but also with very wide credible intervals. This pattern was reversed for Scolt Head, where the smallest avoidance rate was estimated for Dudgeon OWF (the farthest OWF) and the highest avoidance rate for Lincs OWF (the second closest OWF, after Lynn OWF).

Interestingly, the relative selection of rings appears to differ between colonies and OWFs. There was no evidence of avoidance or attraction for OWFs near De Putten, although OWF-level parameters suggest avoidance of the ring around Prinses Amaliawindpark to the same degree as the OWF itself. For OWFs near Scolt Head, overall, rings appeared to be avoided to similar degrees as OWFs. However, OWF-level parameters show inconsistent patterns, with in some cases indifference to rings, and in other cases avoidance.

Table 4.2 *Mean and 95% credible intervals of raw parameter estimates and of avoidance rates of OWFs by Sandwich Terns, and the approximate distance from each OWF to the corresponding Sandwich Tern colony. The estimates for the overall effect of OWFs (from models with a single parameter for all OWFs) for each of the two colonies are printed in bold. Negative values for (CI boundaries of) avoidance indicate attraction.*

colony/OWF	estimate	avoidance rate	distance to colony (km)
OWFs near De Putten	**-0.44 (-0.66 - -0.23)**	**0.22 (0.32 - 0.11)**	
Egmond aan Zee	-0.41 (-0.64 - -0.19)	0.2 (0.31 - 0.1)	21
Prinses Amaliawindpark	-0.58 (-1.89 - 0.49)	0.28 (0.74 - -0.24)	33
Eneco Luchterduinen	-1.53 (-3.79 - 0.17)	0.64 (0.96 - -0.09)	49
OWFs near Scolt Head	**-0.11 (-0.16 - -0.06)**	**0.05 (0.08 - 0.03)**	
Dudgeon	-0.07 (-0.16 - 0.02)	0.03 (0.08 - -0.01)	58
Race Bank	-0.16 (-0.24 - -0.08)	0.08 (0.12 - 0.04)	35
Lincs-Lynn-Inner Dowsing	-0.13 (-0.25 - -0.01)	0.06 (0.13 - 0)	24
Sheringham Shoal	-0.01 (-0.15 - 0.13)	0 (0.07 - -0.07)	37

4.4 Discussion

Using integrated Step-Selection Functions (iSSFs) to model GPS-tracking data of Sandwich Terns from two colonies, we show macro-avoidance of Offshore Wind Farms (OWFs) by Sandwich Terns during the breeding season. Our estimates indicated macro-avoidance of 0.05 for the Scolt Head colony and 0.22 for the De Putten colony, at the scale of the step lengths of *ca.* 2 km. Avoidance estimates for single OWFs ranged from 0.20 to

0.64 for De Putten and 0.08 to 0.37 for Scolt Head, but some of these were associated with substantial uncertainty. Furthermore, our results suggest that Sandwich Terns are generally indifferent to the areas directly surrounding OWFs.

Whereas our results indicate consistent avoidance by Sandwich Terns of OWFs, previous studies showed mixed results. Sandwich Tern was classified as weakly avoiding OWFs in the literature review by Dierschke *et al.* (2016), with “continued use of a marine area after the construction of the OWF, but to a lesser degree or at a lower abundance.” Indeed, tern densities were often reduced by *ca.* 30% inside the Horns Rev II OWF, but this was statistically not significant (Petersen *et al.* 2006). Studying the response of Sandwich Terns from Scolt Head to the Sheringham Shoal OWF, Harwood *et al.* (2017) reported a decrease of 36%, 37% and 45% in three study years within the OWF relative to pre-construction densities. These estimates are considerably higher than our estimate of 1% avoidance of Sheringham Shoal, based on different data. In contrast to studies reporting avoidance, Vanermen *et al.* (2013) reported attraction to a single row of six turbines, similar to the high percentage of foraging individuals at the edge of the Egmond aan Zee OWF reported by Krijgsveld *et al.* (2011). Some studies were unable to detect an effect of OWFs on Sandwich Terns, due to low bird densities (Petersen et al. 2006, Leopold et al. 2013). Note that the study by Leopold et al. (2013) focused on the same OWFs as in our study (OWEZ and PAWP, near De Putten; LUD was not yet built at that time). During the study of Leopold *et al.* (2013), however, the closest breeding colony was located at a distance of *ca.* 55 km (*ca.* 25 km during our study), and the observed numbers of Sandwich Terns were accordingly low. According to Dierschke *et al.* (2016), the observed variation in responses between OWFs may be related to changes in food supplies, i.e., lower avoidance rates would be triggered by better foraging conditions inside the OWF. However, none of the earlier estimates of avoidance behaviour in Sandwich Tern considered food availability or habitat characteristics. In our models, habitat characteristics were considered but are probably only a rough proxy of food availability and/or food attainability.

How robust are our avoidance estimates? The uncertainty in our estimates of avoidance is relatively low for estimates for the overall effect of OWFs per colony, but larger for some OWF-specific estimates. Obviously, part of this uncertainty is due to few GPS positions in and directly around the OWFs, which is partly because some OWFs are relatively far from the studied tern colonies. This uncertainty would be reduced if larger sample sizes were available.

Our study follows a series of other publications that use habitat-selection analyses to estimate macro-avoidance rates by seabirds (Peschko *et al.* 2020, 2021). Although this approach is currently the state-of-art method, constructing such models is not always straightforward and needs to balance model complexity, computational feasibility, interpretability and generalizability. The use of random slopes per individual has been advocated by several authors to reduce bias in parameter estimate and error margins (Gillies *et al.* 2006, Duchesne *et al.* 2010) but its merits have also been questioned (Fieberg *et al.* 2021) and including random slopes greatly increased computation time. Here, we included random slopes because we had a rather large number of potentially differently behaving individuals, while having a sufficiently large sample size per individual to estimate random slopes. Other options that may improve model fit is to relax the linear relation between environmental covariates and the response variable.

Our macro-avoidance estimates fill an important knowledge gap in assessing the avoidance rate of OWFs by Sandwich Terns. The avoidance behaviour indicates that OWFs within foraging ranges of colonies will lead to habitat loss, but also to less collisions compared to a situation with no avoidance behaviour. A next step is to estimate avoidance at the meso- and micro-scales, but this requires tracking data at high temporal resolutions. Higher temporal sampling rates are already possible for larger and heavier GPS-loggers than the model we used in our study, and with further miniaturization of loggers, collecting more high-resolution data will eventually be possible also for Sandwich Terns.

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5 Relative roles of static and dynamic abiotic conditions as drivers of foraging behaviour in breeding Sandwich Terns

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Abstract

Where and when animals forage depends on the spatio-temporal distribution of prey. In dynamic environments, animals could repeatedly target areas that provide predictable availability of prey or may search for more ephemeral conditions of high prey availability. However, how foraging behaviour is initiated in response to static versus more dynamic environmental conditions is difficult to study as data on abiotic factors are often lacking. In this study, central-place foraging Sandwich Terns were tracked using GPS-loggers while foraging in coastal habitats. Using Hidden Markov Models, the probability of switching between transit and foraging was shown to be most strongly affected by two static variables (sediment type and water depth), but less strongly by dynamic variables related to weather (air temperature, wind speed, cloud cover) or varying spatially and seasonally (salinity, water temperature). We suggest that Sandwich Terns target broad areas with coarser sediments where sandeel (*Ammodytidae spp.*) are more common, and that weather variables may be related to prey visibility. Our study suggests that, even in highly dynamic environments, static environmental variables may more strongly affect foraging behaviour than dynamic variables.

5.1 Introduction

How animals move to obtain food for survival and reproduction is a central topic in ecology (Hays *et al.* 2016, Joo *et al.* 2020). Foraging animals are generally expected to match their distribution to the distribution of their prey to maximize energy gain (Stephens & Krebs 1986). Many animals also act as ‘central place foragers’, making repeated trips to and from a central place (Orians & Pearson 1979). For example, breeding marine birds need to return to their terrestrial nesting site after each foraging trip (Buckley & Buckley 1980). This central place foraging represents an additional energetic burden while traveling between breeding and foraging areas to adequately provision offspring as well as themselves (Burke & Montevecchi 2009). Each foraging trip, they need to relocate their prey in a highly dynamic three-dimensional fluid environment. Species have therefore evolved specific foraging strategies and patch choice rules, that are often driven by the occurrence of favourable biotic and/or abiotic conditions that lead them to available food resources (Weimerskirch *et al.* 1993, Hamer *et al.* 2001, Watanuki *et al.* 2008, Ventura *et al.* 2020). The aforementioned studies, however, almost exclusively focus on describing foraging cues of larger seabirds in oceanic environments. Yet, how smaller species in coastal ecosystems choose their foraging grounds is less known.

In such dynamic environments, where the distribution of prey availability may change quickly, foragers need to adapt their foraging movement accordingly (Weimerskirch *et al.* 2005). Due to varying water depths and sediment types, the tidal cycle, currents, fronts and high local turbidity at the discharges of rivers, the coastal waters of the North Sea are inherently dynamic (Smout *et al.* 2013, Thaxter *et al.* 2013, Goyert 2015, Robertson *et al.* 2016, Marinao *et al.* 2019). When both prey and predator species rely on dynamic habitats, predators are expected to show a strong behavioural response to ephemeral environmental conditions that may indicate prey availability and vary their at-sea area use according to the spatial and temporal scales at which environmental conditions change. For example, seabird foraging congregations (Embling *et al.* 2012, Cox *et al.* 2013), chick-provisioning rates at the colonies (Stienen *et al.* 2000) and individual seabirds' foraging site selection (Trevail *et al.* 2019) have been linked to tidal cycles. In addition, foraging of seabirds is also driven by windscape (De Pascalis *et al.* 2020, Ventura *et al.* 2020), turbidity (Kowalczyk *et al.* 2015, Baptist & Leopold 2010) and currents/eddies (Hyrenbach *et al.* 2006, Scales *et al.* 2014). Studying the response of individual seabird movements to dynamic environmental covariates is challenging as it requires concurrent data on individual movement data and environmental covariates (Ogburn *et al.* 2017).

The piscivorous Sandwich Tern *Thalasseus sandvicensis* [Latham, 1787] is a species with a mean maximum foraging range of 25 - 30 km during the breeding season (Fijn *et al.* 2017). In the North Sea, Sandwich Terns specialize in feeding on a few pelagic fish prey species (sandeel *Ammodytidae spp*., Atlantic Herring *Clupea harengus* and European Sprat *Sprattus sprattus*; Veen 1977, Stienen *et al.* 2000) particularly during chick rearing (Courtens *et al.* 2017). Sandwich Terns generally only bring one prey item back to the chick per foraging trip, a strategy called 'single-prey loading' (Stienen *et al.* 2015, Gaglio *et al.* 2018). Despite this diet specialization, substantial variation in foraging site selection within and between individual Sandwich Terns (Perrow *et al.* 2017, Fijn *et al.* 2017) suggests that prey become available unpredictably in space and time or occur at predictable combinations of environmental factors but at varying locations at different times. If and how Sandwich Terns respond to static and dynamic environmental conditions, and how they adjust their foraging movements in response to tidal, diurnal and seasonal cycles has not been studied in detail before.

In this study, we used the Sandwich Tern as a model species to study how breeding seabirds foraging in dynamic coastal ecosystems initiate and stop foraging in response to static and dynamic environmental variables. For this, we studied the foraging trips of Sandwich Terns breeding along the Dutch North Sea coast during late incubation and chick-rearing using GPS-logger data and information on environmental variables. The foraging area of these birds covers the south-western part off the Dutch coastal zone, which is a large river delta that has a variety of water depths and sediment types, where river discharge causes frontal zones and the tidal cycles have a large influence on currents (Fijn *et al.* 2017). We aimed to quantify the relative importance of static variables (e.g. sediment type) and dynamic variables linked to the tidal cycle (water level, water current speed) and weather (wind speed, cloud cover) on the probability of Sandwich Terns to switch from transit flights to foraging and back. Considering the strong effect of the tidal cycle on chick provisioning rates and lengths of sandeel brought to the chicks (Stienen *et al.* 2000), and the importance of sediment grain size for sandeels (Holland *et al.* 2005a, Kooij *et al.* 2008, Tien *et al.* 2017), we hypothesize that predictors of prey availability such as sediment type, water depth, tidal currents and turbidity will mainly predict the start of foraging behaviour in Sandwich Terns. We expected dynamic factors such as weather conditions to affect foraging behaviour less, since these will be more of influence on the foraging efficiency of terns rather than patch choice.

5.2 Methods

5.2.1 Deployment of tracking devices

In May and June 2012-2015 and 2017, 48 adult Sandwich Terns were captured in the Natura 2000-Special Protection Area (SPA) Haringvliet located in the south-western part of the Netherlands. In 2012, 2013, 2015 and 2017 the breeding colony was located at the Scheelhoek (N51°49’ E04°04’) whereas in 2014 the colony was located at the Slijkplaat (N51°48’ E04°09’), 5 km to the east. Both colonies were located in freshwater respectively 2.5 and 7.5 km away from the sea and combinedly held between 1,500 and 3,300 pairs annually between 2012 and 2017. Breeding birds were captured on the nest with walk-in traps during the last week of incubation, or with spring traps during chick-rearing. Birds were ringed with a uniquely numbered metal ring and a field-readable darvic colour-ring.
All birds were equipped with a GPS-logger (Ecotone GPS-UHF loggers, ~4g, L:35 x W:15 x H:10 mm) that recorded date, time, GPS position and speed at 5 minutes intervals, but that differed in power supply. Most loggers had a single-use battery allowing up to ~400 GPS-fixes on one battery load, depending on environmental conditions and sampling interval. Eight loggers (3 in 2013, 2 in 2014, 3 in 2017) were equipped with solar panels allowing data recording until the loggers fell off due to the degradation of the harness material. Data were automatically transferred via UHF to base stations placed in the colony from a distance up to ~100 m. In 2012-2013 loggers were programmed to collect data during 6 hours per day to save battery power and increase longevity of the logger, while in later seasons devices were programmed with cycles of 12 – 16 hr to allow data collection over the entire day.

In 2012, seven of these loggers were attached to feathers on the back with TESA tape (No. 4651; Beiersdorf AG) following Wilson *et al.* (1997). Sandwich Terns were aggressive towards the tape deployments and some removed their logger by plucking and biting the taped feathers, resulting in premature loss of 4 out of 7 tags. In 2017, we deployed four tags with super glue (Loctite Superglue, Henkel) following successful deployments in the UK with this methodology (Collier *et al.* 2017), but again tag loss occurred within a week. The remaining 37 loggers were attached with a backpack loop harness following Kenward (1985). The harness was constructed from fishing elastic (Preston Innovations Slip Elastic, diameter 1.4 – 2.2 mm), which made the harness strong and flexible but also ensured that the harness was shed after 2 to 3 months due to degradation by sunlight and salt water (Fijn *et al.* in prep). Using the harness instead of taping or glueing reduced handling time (capture to release) from approximately 15 min to 10 min. In a follow-up project on Sandwich Terns with the same tagging methods, Green *et al.* (under review) showed long-term tag effects where loggers were deployed with a harness (lower return-rates in subsequent years), whereas foraging behaviour of birds with glue and harness deployments did not differ. The weight of the loggers, rings and harness material (5.8 g) is within the generally accepted limit of 3% of the body mass (Phillips *et al.* 2003, Vandenabeele *et al.* 2011) of the Sandwich Terns in our study (average weight of 241 ± 13.4 g; range 210–270 g; ~2.4 %).

5.2.2 GPS-data, trip definition and home range

All analyses were carried out in R version 4.1.2 (R Core Team 2021).

A total of 34 out of 48 loggers successfully transferred positional data to the base station placed in the colony. Nine loggers were lost before they transferred any data and the fate of the remaining five loggers is unknown. These loggers may have encountered technical failures or may have been lost on the first trip. Alternatively, birds may have deserted the colony after deployment.

The resulting data was classified into ‘trips’ based on two criteria: 1) The bird was ≥ 2.5 km from the colony centre (which is where outbound terns enter the North Sea by crossing the Haringvlietsluizen) or 2) There was a time gap of >30 minutes between locations. Trips were considered completely recorded when they started and ended at the colony.
Utilization Density (UD) Kernels were estimated to define a combined home range for all tracked individuals. UD kernels were estimated using a smoothing factor of 2 km and a grid cell size of 1 km, using the adehabitatHR package version 0.4.19 in R (Calenge 2006).

5.2.3 Hidden Markov Models for behavioural classification

Behavioural states and the probabilities of switching between states were determined using a Hidden Markov Model (HMM), which classifies track segments based on speed and relative turning angle (Langrock *et al.* 2012, McClintock & Michelot 2018). As this requires a constant sampling rate, tracking data was selected from loggers that were pre-set to sample at 5-minute intervals and in which the resulting intervals were not longer than 6 minutes. As timestamps in the original tracking data were rounded to minutes, selected data included intervals up to 6.5 min. In total, 6-minute intervals accounted for 13% of the data. HMM generally assume regular time intervals between subsequent positions, as variability introduces noise in derived track characteristics - in particular in step lengths. Variability in time intervals resulted in on average 114 m longer step length in 6-minute interval data (β_{6-min} = 0.07, t = 3.2, p = 0.001) and fitting a 3-state HMM using data with only 5-minute intervals led to very similar distributions of step length and turning angles, and the same classifications of behavioural states in 100% ($n_{positions}$ = 13918) of all positions and 100% ($n_{positions}$ = 11554) of positions with 5-minute intervals. However, we did not resample data to regular intervals because we were mainly interested in environmental covariates at specific locations and times. The R package ‘momentuHMM’ version 1.5.4 in R (McClintock & Michelot 2018) was used to fit a three-state HMM using a gamma distribution for step lengths and a von Mises distribution for turning angles. In HMMs, the number of states must be defined a priori, as well as starting values. We used the following starting values for the mean step size: μ_{step} = 5, 250 and 1500 m; and for the concentration parameter of the turning angles: φ_{angle} = 0.7, 0.9 and 2. We varied these initial parameters to test the sensitivity of the model results to starting value selection. A three-state model was specified because foraging trips of seabirds typically consists of 1. outbound and inbound flights between foraging areas and the colony (commuting), 2. searching and foraging (foraging), and 3. resting at the colony or elsewhere (resting). We predicted commuting to be characterized by high travel speeds and strongly directional flight paths, foraging to be characterized by slower travel speeds and sinuous turning angles, and resting to be characterized by travel speeds of (nearly) zero and random turning angles. After fitting the model, the Viterbi algorithm was used to assign the most likely state to each step (Morales *et al.* 2004, McClintock & Michelot 2018).

5.2.4 Environmental covariates

For each position, the following covariates were retrieved. Median grain size of the sediment ($\boldsymbol{\mu m}$) was extracted from the Deltares website (http://opendap.deltares.nl/thredds/fileServer/opendap/tno/ncp/) for the Dutch Continental Shelf, and from the VLIZ website (https://www.vliz.be; Verfaillie *et al.* 2006) for the Belgian Continental Shelf. The following modelled abiotic data were generated by the TRIWAQ model, which simulates hydrostatic water movement in 3D (Adema 2019): water depth ($\boldsymbol{m}$), water current speed at the surface ($\boldsymbol{N/m^2}$), salinity at the surface ($\boldsymbol{PSU}$), water temperature at the surface ($°\boldsymbol{C}$), wave height ($\boldsymbol{m}$), wave direction ($^{\boldsymbol{o}}$), wave period ($\boldsymbol{s}$), wind speed ($\boldsymbol{ms^{-1}}$), air temperature ($^{\boldsymbol{o}}\boldsymbol{C}$) and cloud cover (%). The TRIWAQ model has a temporal (output) resolution of 1 hour and a spatial resolution of 300-500 m (thus much smaller than most foraging or transit step sizes, see results). TRIWAQ values were intrapolated to GPS-positions and -times. All covariates were standardized using the standardize package in R, so that all have a mean of 0 and a standard deviation of 1 (Eager 2017). To aid interpretation of the results, we plotted the values for six sample locations (Figure 5.1 - Figure 5.3), and categorized the spatial variability and the temporal variability at three temporal scales (Table 5.2). These six locations were selected at positions where Sandwich Terns either regularly foraged (locations 1-4) or where only very few tracks of Sandwich Terns occurred (locations 5-6). Variance Inflation Factors (VIF) indicated strong multicollinearity for wave height (VIF = 2.5) and was therefore removed. Among the remaining covariates, VIFs ranged from 1 for sediment median grain size to 2.1 for water depth, thus below what is generally considered 'severe' multicollinearity (VIF > 3, Zuur *et al.* 2010).

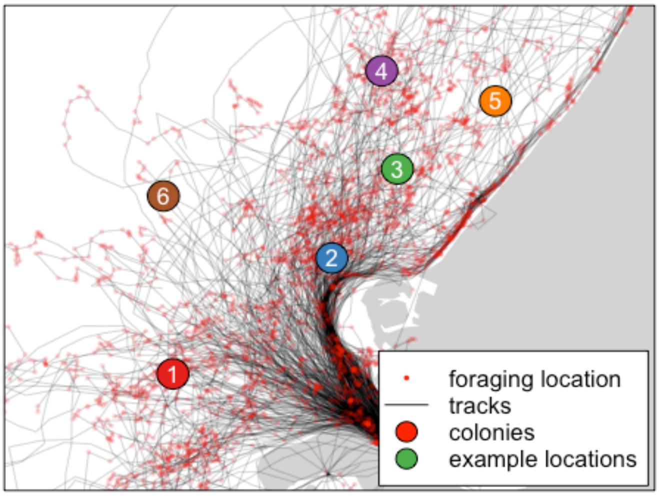

Figure 5.1 *Six example locations where TRIWAQ predictions have been extracted to illustrate the temporal variability of environmental conditions.*

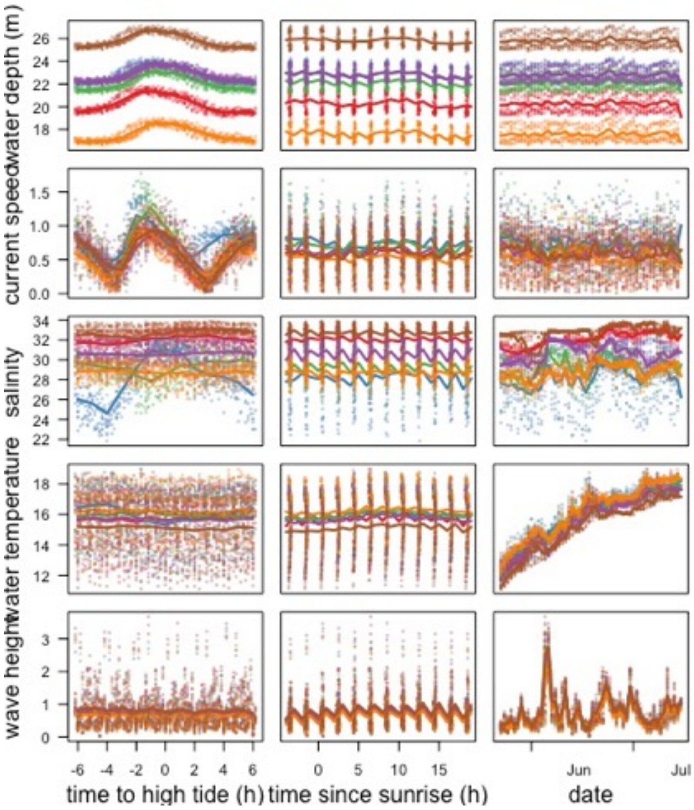

Figure 5.2 *Variability of environmental variables from the TRIWAQ model at six example locations. Colours correspond to the colours in Figure 5.1.*

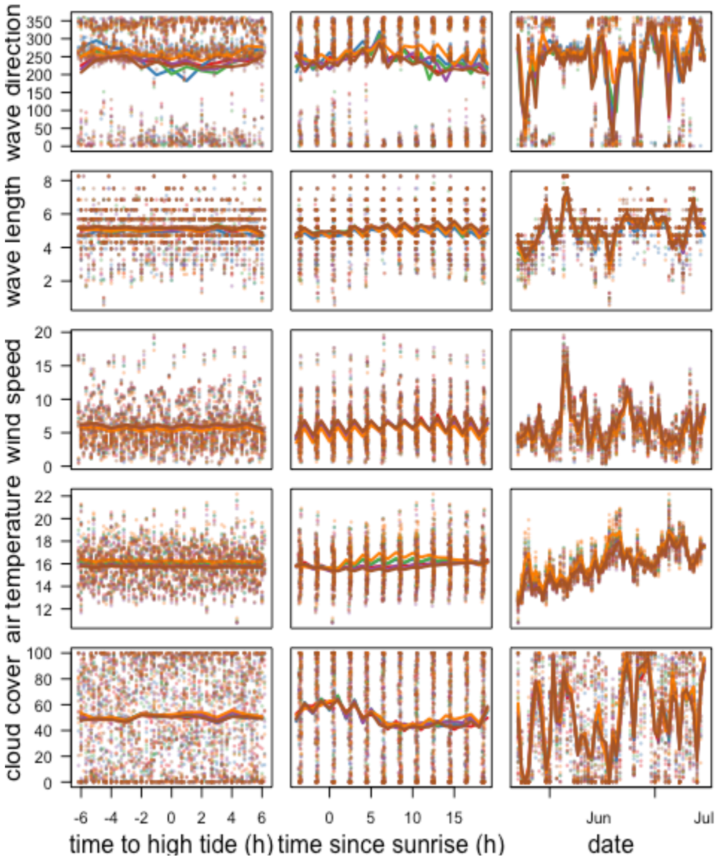

Figure 5.3 *Variability of environmental variables from the TRIWAQ model at six example locations. Colours correspond to the colours in Figure 5.1.*

5.2.5 Model setup and comparison

Using tracking data for which all covariates were available, a three-state model without covariate-effects on the transition probabilities was fitted. Exploration of this first model showed that almost all positions classified by this model as resting were in the colony or on land. As we were interested in foraging at sea and not near the colony (where short, undirected movements may also occur), we constrained the model to prevent switching from the resting to the foraging state; a commuting flight was thus always required before foraging. To include this constraint, we refitted the three-state model while fixing the transition probabilities between resting and foraging to (virtually) zero (the 'null' model). Next, we added covariate effects on the switching probability. Since we were only interested in what environmental covariates affected foraging behaviour, only covariate effects on transition probabilities between transit and foraging were estimated; others were fixed to zero. The effect of covariates (without interactions) on transition probabilities was modelled via a multinomial logit link function, following Michelot *et al.* (2016). We subsequently performed forward model selection based on AIC. The model with ΔAIC < 2 compared to the highest ranked model and the least number of covariates was selected as the final model.

Individuals can differ in their response to the environment and therefore, repeated observations of the same individual represent a source of non-independence in the data. In momentuHMM, individual-level effects on the transition probabilities can be included by estimating two or more ‘mixtures’ - sets of transition probabilities - and a probability for each individual to being in a particular mixture (McClintock & Michelot 2018). Here, we allow for two and three mixtures in the final model and evaluated whether adding mixtures improved model fits using AIC.

5.3 Results

5.3.1 Sample size and behavioural classification

In 2017, a substantially higher number of trips were recorded compared to previous years due to the use of solar-panel loggers with a much longer battery-life (table 5.1).

Table 5.1 Sample size per year, split for data used for the HMM (all data, but excluding parts venturing north of TRIWAQ area) and for the consistency analysis (only complete trips).

year	n individuals	n trips	n positions
2012	5	18	386
2013	3	23	1,120
2014	7	31	690
2015	5	35	1,234
2017	8	181	10,488
Totals	28	288	13918

The 3-state HMM distinguished a state with very small step lengths (mean=75.9 m, sd=111.3 m) and no directionality (h=0), a state with intermediate step lengths (mean=944.7 m, sd=758.4 m) and weak directionality (h=0.43) and a state with long step lengths (mean=2746.1 m, sd=993.1 m) and strong directionality (h=5.71, Figure 5.4). We interpret these as resting/stationary, foraging and in transit, respectively. Overall, 21% of the locations were categorized as resting, 32% as foraging and 47% as in transit.

Tagged Sandwich Terns foraged in a large home range during the breeding season. High numbers of foraging locations were located north of the colony, both nearshore as well as more than 30 km offshore (Figure 5.5).

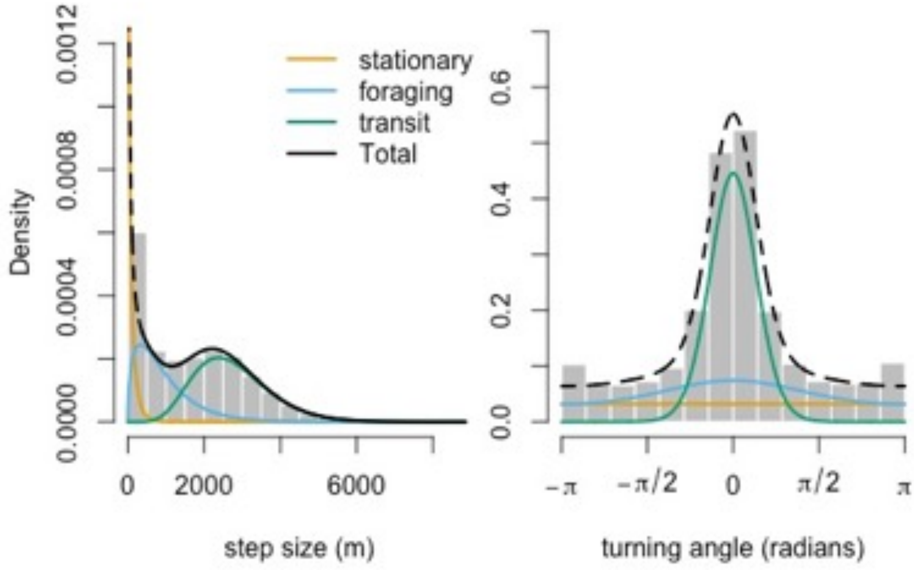

Figure 5.4 *Distribution of step lengths (left) and turning angle (right) per behavioural state.*

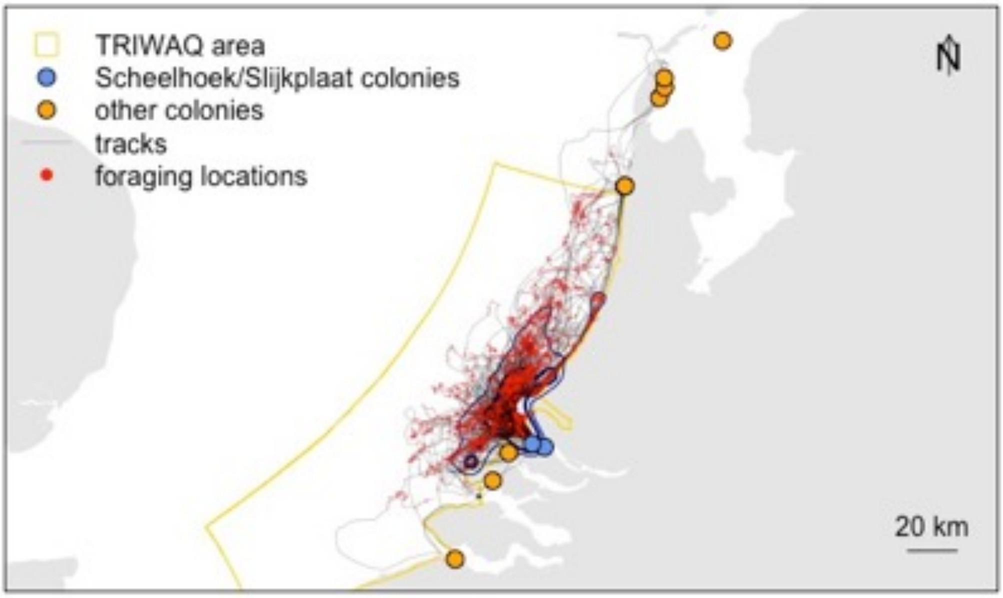

Figure 5.5 *Map showing trips of Sandwich Terns (grey lines) breeding at the Scheelhoek/Slijkplaat colony (blue-filled dots) in 2012-2017, with positions classified as foraging indicated as red dots. The yellow bordered area is the area for which environmental covariates are availabe from the TRIWAQ model. Orange-filled dots show other Sandwich Tern colonies during 2012-2017, which were not necessarily occupied in each year. Blue lines demarcate 50% (thick line) and 75% (thin line) home range kernels estimated across all positions. Note that tracks outside the TRIWAQ model area have been excluded from the HMM as no NAs are allowed in HMMs.*

5.3.2 Covariates affecting transition to/from foraging

The final model contained the following covariates for transition probabilities: median grain size of the sediment, air temperature, cloud cover, salinity, wind speed, water temperature and water depth. Hence, wave height and direction, current speed and slope of the sea floor were not included in the final model. Allowing two or three 'mixtures' of transition probabilities in the selected model reduced model fit (ΔAIC = 2 and 76, respectively). Therefore, we present parameter estimates for the model without additional mixtures.

Sandwich Terns were more likely to switch from transit flight to foraging over coarser sediments, shallower water depths and cooler waters (Figure 5.6, Figure 5.7). The probability of continuing foraging or in the transit flight were nearly constant across different water depths (Figure 5.7). Other covariates on the switch to foraging had 95% confidence intervals of odd ratios overlapping with 1, indicating no or only a weak response. Birds were more likely to stop foraging and switch to transit flights over finer sediments, in lower wind speeds, and with less cloud cover. Again, other covariates had 95% confidence intervals of odd ratios overlapping with 1. The probability of continuing foraging increased whereas the probability of staying in the transit state decreased over coarser sediments (Figure 4). Beside depth and sediment type, resting probabilities were mainly affected by air temperature and wind speed, with birds more likely to continue foraging at higher wind speeds and higher air temperatures (Figure 5.6).

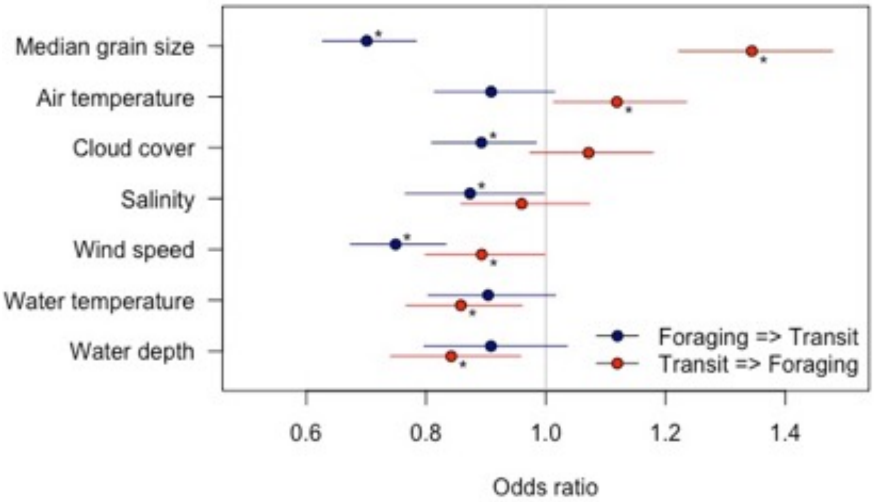

Figure 5.6 *Parameter estimates for probability transitions from the full model, with estimates ranked by their value for the transition from transit to foraging. Note that values further away from 1 have the largest effect size, with positive values indicating a positive relation with the probability to switch behaviour, and that covariates have been standardized. Error bars represent 95% confidence intervals. Asterisks indicate that 95% CIs do not overlap with 1.*

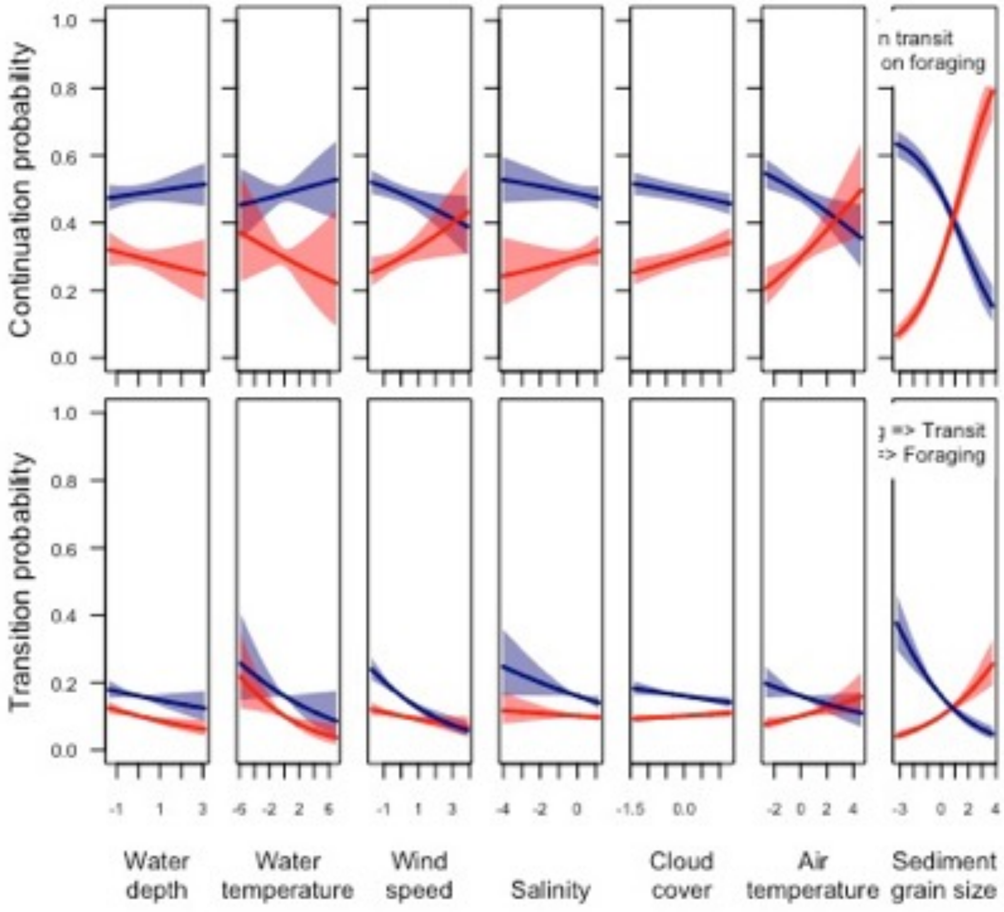

Figure 5.7 *Probability of staying in the same state (continuation probability, upper panels) or switching to another state (transition probabilities, lower panels) in relation to the two most influential variables (water depth and sediment grain size) on transition probabilities. All variables have been standardized.*

5.4 Discussion

The breeding Sandwich Terns in our study foraged in highly dynamic marine habitats of the North Sea, with environmental variables changing over time scales ranging from hours to weeks (Table 2, Supplement Figure S4-6, S8). Despite the dynamics of this coastal system, the terns' switch from transit flights to foraging behaviour and vice versa was most strongly affected by two static variables (on the temporal scales studied here): sediment grain size and water depth. Dynamic factors, such as air and water temperature, that vary over the course of the season or from day-to-day, had smaller effects on the switch to foraging behaviour. As expected, given the stronger effects of static rather than dynamic variables on foraging behaviour, terns were not more consistent or explorative during specific phases of the tidal cycle, the time of day or the season. However, they showed low overall consistency in area use, suggesting terns explore large areas offering potential foraging opportunities.

Table 5.2 *Qualitative variability of environmental conditions at three temporal time scales and spatial, categorized as Y = strong variation, Y/N = some variation, N = no variation. Variables are ordered relative to their effect size, thus when the odds ratio is further from 1.*

variable	seasonal	day-to-day	diurnal	tidal	spatial	transition probability transit -> foraging (odds ratio)
median grain size	N	N	N	N	Y	1.34
water depth	N	N	N	Y	Y	0.84
water temperature	Y	N	N	N	Y/N	0.86
air temperature	Y	Y	N	N	N	1.12
wind speed	N	Y	N	N	N	0.89
cloud cover	N	Y	Y/N	N	N	1.07
salinity	N	N	N	Y/N	Y	0.96

The main drivers of distributions of foraging Sandwich Terns are most likely the availability of forage fish in the first 1.5 – 2.0 m layer of the water column and individual prey-capture efficiency. Unfortunately, simultaneously recording Sandwich Terns' movements and forage fish availability and 'catchability' was not feasible, requiring the use of proxies for prey fish availibility. One of these proxies is sediment grain size, which is linked to the presence of sandeel (Wright *et al.* 2000, Holland *et al.* 2005b, Tien *et al.* 2017, Langton *et al.* 2021), an important prey type for Sandwich Terns throughout the breeding season (Stienen *et al.* 2000, Courtens *et al.* 2017). The sandeels' presence in the water column has a diurnal cycle. Sandeel are visual feeders and therefore feed in the water column during the day and are mostly buried at night (Robards *et al.* 2002a), during which they associate with relatively coarse, sandy sediments (Wright *et al.* 2000, Holland *et al.* 2005b, Tien *et al.* 2017, Langton *et al.* 2021). Beside sandeel, Sandwich Terns also feed on herring and sprat Clupeidae. Whereas sandeel are available throughout the terns' breeding season, the appropriate size of herring and sprat is only available later in the breeding season, with some variation in timing among years (Postuma *et al.* 1965). The seasonal availability pattern of herring and sprat is reflected in the adult and chick-feeding diets found in our study-colony (Courtens *et al.* 2017, Fijn *et al.* 2018). Although herring and sprat may target food sources occurring on or near specific seafloor habitat types, the link is unlikely to be as strong as for sandeel that require specific grain size to bury at night (Holland *et al.* 2005b, Tien *et al.* 2017). Higher abundance of sandeel over coarser sediments therefore likely explains the higher probability of starting Sandwich Terns to forage over coarser sediments.

Why water depth would drive foraging behaviour of Sandwich Terns is less clear. Shallower waters might help small fish to avoid predators such as larger fish, seals and harbour porpoises in deeper water (Munsch *et al.* 2016), thus leading to an increased abundance in shallower water. Shallower waters forces however prey fish closer to the surface, making them easier for Sandwich Terns to capture. Moreover, water transparency is often more reduced in the shallower coastal waters (Fettweis & Van den Eynde 2003), which could potentially lead to a certain optimal level of turbidity for foraging Sandwich Terns, as suggested by Baptist & Leopold (2010). Unfortunately, transparency values were not available in this study, yet we think these could be a strong predictor of Sandwich Tern foraging. Alternatively, shallower waters might be preferred by small fish because higher water temperatures in shallow waters enhance the growth of algae which is the primary food source for several small fish species (Blaxter 1992). In our study water depth and water temperature did not show collinearity, but they are still weakly related with higher temperatures in shallow waters. Higher water temperatures might also be energetically beneficial to small fish and some studies report higher growth rates of juvenile sandeel (Smigelski *et al.* 1984) and sandeel stocks (Robards *et al.* 2002b), and a faster escape response (Domenici *et al.* 2019), with increasing temperature. However, Tien *et al.* (2017) found no evidence for higher temperatures being related to sandeel distribution in the Voordelta. Herring, and probably also sprat, growth rates are higher under increasing temperatures (Høie *et al.* 1999, Brunel & Dickey-Collas 2010) and warmer water are preferred by their larvae (Batty *et al.* 1993). Warmer water may also be preferred by young Herring, which may help explain the the higher probability of foraging over shallower waters.

Terns were more likely to switch to foraging at lower water temperatures, higher air temperatures, and lower wind speeds, although the effects of these factors were less strong than grain size and water depth. Furthermore, terns were more likely to switch from foraging to transit flights with lower cloud cover, lower salinity and lower wind speeds. Water temperature varies mainly seasonally, but also spatially, and foraging may be more profitable at lower water temperatures either because lower temperatures are preferred by fish (e.g. because of higher oxygen levels), or because fish are easier to capture due to slower fish escape response (Domenici *et al.* 2019). Salinity also shows (some) spatial variation, mainly related to river run-off, and higher salinity is known to correlate with sandeel abundance (Tien *et al.* 2017). Other variables retained in the final model are mainly varying on a daily basis, as they are related to weather. Conceivably, cloud cover may increase the depths to which terns can detect prey under the water surface, as direct sunlight may cause reflection at the water surface, whereas higher air temperatures would, on days with partly clouded conditions, be expected when it is less cloudy. The relation between flight behaviour and wind speeds might also be related to visibility of fish. At higher wind speeds, Sandwich Terns were less likely to switch between transit and foraging, less likely to continue in transit flight, but more likely to continue foraging. Seabirds that use only flapping flight modes, but no gliding generally expend more energy in stronger winds (Christensen-Dalsgaard *et al.* 2018, Lane *et al.* 2019, Gabrielsen *et al.* 1987), which may explain why birds would spend more time foraging in stronger winds. In addition, foraging efficiency may be lower in stronger winds (Stienen *et al.* 2000), due to more difficulties in locating and relocating prey fish due to white wave caps and irregularity of the water surface. More detailed study of the response of Sandwich Terns to wind conditions may reveal whether wind conditions affect trip characteristics, such as the total duration and where and when foraging takes places.

In this study, environmental covariates were modelled as linear effects on transition probabilities between transit flights and foraging, with no interactions between variables. However, the relation between behaviour and environmental conditions may be non-linear, which may explain some apparently contradicting results. For example, transition to foraging was more likely over coarser sediment, but also at shallower depths, whereas coarser sediments more commonly occur in deeper waters. Possibly, the linear effects of sediment grain size and water depths capture different parts of the non-linear relation, where Sandwich Terns target a specific grain size at an intermediate water depth.

There was considerable overlap between the step lengths and turning angle distributions of foraging and transit flights, implying uncertainty in our viterbi-based classifications of behaviour. Based on visual inspection of the classifications along tracks, most viterbi-based classifications agreed with our expectations. For example, foraging segments concentrated at the far end of a foraging trip and clustered in particular areas across multiple foraging trips and individuals. In addition, the distribution of flight speed for foraging and transit as inferred by the HMM agreed with flight speeds based on an earlier manual classification using parts of the same data (Fijn & Gyimesi 2018). In some segments that were classified as foraging based on low flight speeds, birds travelled relatively slow but with considerable directionality. Indeed, Sandwich Terns often forage while following a straight flight path (thus with strong directionality), for example when foraging along the surf zone or an oceanic front (Cabot & Nisbet 2013). Behavioural classifications of Sandwich Terns' tracking data using HMMs can be improved by adding auxiliary biotelemetry data, such as dive activity or accelerometer data (McClintock & Michelot 2018).

Acknowledgements

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6 Predicting annual at-sea distribution of Sandwich Terns during breeding across the southern North Sea based on GPS-tracking and colony counts

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Abstract

Mapping the at-sea distribution of seabirds at large scales is critical to marine spatial planning and conservation, but difficult due to logistical constraints. Here, we predict the at-sea area use of breeding Sandwich Terns *Thalasseus sandvicensis* across the southern North Sea, based on GPS-tracking of individual birds, annual colony counts, and environmental variables. Predicting the at-sea distribution is done in two steps: 1) a Resource Selection Function (RSF) approach was used to quantify habitat selection based on the tracking data and 2) the resulting relationships from the RSF were used to predict at-sea (foraging) distribution of all colonies in the study area, for each year. We used annual colony counts for southern North Sea colonies for the years 2003-2020 and GPS-tracking data of 112 individuals from five colonies. The RSF indicated strong negative effects of distance from the colony and water depth on probability of occurrence of Sandwich Terns, and small effects of seabed slope and median grain size of the sediment. RSF parameter estimates were very similar for all data and for foraging locations only. Predicted annual at-sea distribution shows high densities in coastal areas near colonies, but also low densities in areas further offshore. Our study demonstrates the use and utility of this approach to map seabird distribution at a large scale, which may prove a powerful instrument to predict potential overlap with offshore anthropogenic development.

6.1 Introduction

With increasing anthropogenic exploitation of the sea, mapping the distribution of marine animals and identifying potential conflicts with human activities is important for wildlife conservation issues. However, estimating the distribution of highly mobile animals such as seabirds is challenging, in particular at the large scales required in marine spatial planning. Methods to estimate the spatial distribution of seabirds include aerial and ship-based surveys, which are expensive, provide only a snapshot in time, and are unable to link individuals to specific breeding sites. GPS-tracking provides highly detailed data on area use at the individual level, but is usually restricted to small sample sizes and few study sites. Hence, how can the at-sea distribution of seabirds be estimated at large scales from only a small number of tracked individuals? In parallel with the proliferation of tracking devices, analysis methods of movement data have seen a rapid development in recent years. By combining fine-scale GPS-tracking with habitat selection analyses and colony counts, at-sea distribution of seabirds can be modelled (Wakefield *et al.* 2017).

The at-sea distribution during the breeding season of the Sandwich Tern *Thalasseus sandvicensis*, a seabird with key colonies around the southern North Sea. The species has been identified as potentially sensitive to the development of offshore wind farms (Everaert & Stienen 2006, Krijgsveld 2014, Dierschke *et al.* 2016), and with foraging flights during breeding usually restricted to within 40 km from the colony (Fijn *et al.* 2017), many currently operational as well as planned offshore wind farms in the southern North Sea are within the regular flight range of breeding Sandwich Terns. Given the regular appearance, disappearance and re-appearence of Sandwich Tern colonies from year to year, the at-sea distribution of breeding individuals will inevitably also change annually, leading to different overlap with (planned) offshore wind farms.

In this study, the annual at-sea foraging distribution across the southern North Sea of Sandwich Terns is modeled using individual tracking data from British and Dutch colonies in combination with colony counts from French, British, Belgian, Dutch, German and Danish colonies. In a first step, foraging habitat selection is modeled as a function of environmental covariates (water depth, slope and median grain size of the sediment) and distance from/to the colony. Finally, modeled foraging habitat selection is used to predict the annual at-sea distribution for all colonies, taking into account the number of breeding pairs in each year.

6.2 Methods

6.2.1 Colony counts

Annual counts of the number of breeding pairs per colony were collected for colonies around the southern North Sea in between the Strait of Dover in the south, the Scottish border in the northwest and the Kattegat in the northeast. Colony counts were obtained from own data and supplemented by local researchers (see acknowledgements). Colony counts were conducted during the incubation period and usually performed by observers, except for De Putten (the Netherlands), Utopia and Wagejot (Texel, the Netherlands) where counts were based on imagery obtained by drones. In total, annual colony counts were collected for the period 2003-2020 across 43 colonies along southern North Sea coasts of the northern tip of France, the east coast of England, Belgium, the Netherlands, Germany and the west coast of Denmark.

6.2.2 GPS-tracking

Between 2012 and 2020, adult Sandwich Terns were captured at five locations: 1) Scolt Head, Norfolk, United Kingdom (N52° 59’ E0° 40), 2) Haringvliet, with colonies either at the Scheelhoek (N51° 49’ E4° 04) or, in 2014, 5 km to the east at the Slijkplaat, the Netherlands (N51°48’ E04°09’), 3) De Putten, Camperduin, the Netherlands (N52° 44’ E4° 39), 4) Utopia, Texel, the Netherlands (N53° 07’ E4° 54) and Griend, Wadden Sea, the Netherlands (N53° 15’ E5° 15). Birds were captured with walk-in traps on the nest during the last week of incubation, or with spring traps in the colony during chick-rearing. Birds were ringed with a uniquely numbered metal ring and a field-readable darvic colour-ring (see for detailed methodology on tagging Fijn *et al.* 2017).

Two types of GPS-loggers were used. At Utopia, UvA Bits loggers were used (~7.5g, L:52 x W:22 x H:9 mm), whereas at all other sites Ecotone GPS-UHF loggers were used (~4g, L:30 x W:14 x H:9 mm). Ecotone loggers recorded date and time, GPS position and speed at pre-set sampling intervals, ranging from 5 to 15 minutes. However, whether this pre-set interval was attained depended on power supply. Most loggers had a single battery allowing up to ~400 GPS-fixes on one battery load, depending on environmental conditions (temperature, duration and intensity of sunlight) and sampling interval. Eight Ecotone loggers in 2013-2017 (3 in 2013, 2 in 2014, 3 in 201) and all loggers in the UK in 2018-2019, as well as the loggers in De Putten in 2019 were equipped with solar panels allowing data recording until the loggers fell off due to the degradation of the harness material. UvA-Bits loggers collected very detailed information (e.g., bursts of accelerometer data, altitude data), which were downsampled to match the Ecotone data (see below). Data from loggers were automatically transferred via UHF to base stations placed in the colony from a distance up to ~100 m. In 2012-2013, Ecotone loggers were programmed to collect data during 6 hours per day to save battery power and increase longevity of the logger, while in later seasons devices were programmed with cycles of 12 – 16 hr to allow data collection over the entire day.

Data were resampled to 30-min intervals, as this allowed us to use data with intervals of 5, 10 and 15 min without the need to interpolate. Subsequently, positions were selected that were recorded a) at sea, b) at least 2000 m of the colony, c) within the first 30 days counting from the day after each individuals was captured, d) when individuals were commuting to and from the original colony (commuting to and from other colonies suggests fledged chicks or failed breeding). Finally, individuals with less than 20 positions were removed.

6.2.3 Resource Selection Function

The Resource-Selection Function [RSF; Manly *et al.* (2002)] framework was used to model the habitat selection of Sandwich Terns as a function of environmental covariates. In RSFs, the animals' locations are compared to random locations within the potential flight range of the animal, thus reflecting areas that are 'available' to the individual when departing from the colony. We created 10 times as many random locations as animal locations, which were sampled regularly across the area encompassed by the tracking data plus a buffer of 80 km but without area on land. Subsequently, these random locations were randomly assigned to individuals. Habitat selection was inferred from a conditional regression model with a logit link function and fitted using the `R-INLA` package (Lindgren & Rue 2015), where the locations and random locations were treated as Bernoulli response variable. By assigning a weight of 1000 to random locations while keeping the weight of animal locations at 1, the likelihood converges to an Inhomogeneous Poisson Process (IPP) likelihood. As such, the parameters describe the relationships between covariates and the relative density of animal locations (Fithian & Hastie 2013, Fieberg *et al.* 2021).

For each real or random location, water depth relative to mean sea level (hereafter: 'water depth'), slope of the sea bottom (hereafter: 'slope') and median grain size of the sediment (hereafter: 'sediment') were retrieved to use as covariates in the RSFs. Bathymetry was extracted from the EMODnet database (www.emodnet.eu). Sediment data with a spatial resolution of 0.25° was obtained from Mason (2018). As sediment data were heavily left-skewed were log-transformed. For each position, distance from/to the colony was calculated taking routes only over sea. The range of all variables was clipped to the range of values observed for used positions. All variables were standardized. Then, to allow non-linear relations between use and variables, five base functions were calculated per variable using the `mgcv` package. Each base function was included as a linear effect in the model. Variance Inflation Factors (VIF) of the original, non-standardized data varied between 1.01 and 1.29, thus staying below levels which are generally regarded as 'severe' amounts that can impact model inferences (VIF > 3, Zuur *et al.* 2010).

Besides the fixed effects (distance to the colony, water depth and sediment), random slopes were added for each colony (Aarts *et al.* 2008). Recognizing that available habitat within a reasonable foraging distance may differ between colonies, we included random slopes for water depth and sediment, but not for distance to the colony. The prior for α_σ^2 for the random intercept of colony was fixed at a large value (10^6) to avoid shrinkage, which may bias the results (Muff *et al.* 2019).

6.2.4 Predicting at-sea distribution and overlap with OWFs

In the final step, RSF fixed effect parameters were used to predict the at-sea distribution of Sandwich Terns for all colonies around the southern North Sea. After calculating the linear predictor per colony, these were exponentiated to reflect relative densities, rescaled to sum to 1 across the prediction area, and multiplied by twice the number of breeding pairs (to arrive at the number of breeding individuals) for each year between 2012 and 2020. Finally, annual predicted densities per grid cell were were summed across colonies to arrive at general densities of breeding adult Sandwich Terns across the southern North Sea.

It should be noted that predicted densities are not absolute densities, considering that only complete foraging trips were taken into account, meaning positions at land, i.e., when in the colony, where not taken into account. Therefore, the positions used in the RSFs represent the time spent at sea, and the predicted relative densities represent the proportional use of areas at any point in time if all individuals were away from land.

OWF areas were obtained from the KEC 4.0 study (Potiek *et al.* in prep). These areas include operational OWFs, as well as OWFs under construction. For each year, grid cells within the each OWF were selected and predicted densities were summed for each colony. All statistical analyses were carried out in R version 4.0 (R Core Team 2020).

6.3 Results

6.3.1 Colony counts

Total annual counts show that annual totals in the study area are in the order of 25 000-30 000 breeding pairs, with the largest share breeding in the Netherlands (Figure 6.1).

Colonies were concentrated in southwest of the Netherlands, as well as across the Wadden Sea, with most pairs breeding in the Netherlands. Across all colonies, 86% were not occupied in one or more years. Colonies were occupied for on average 8.8 years, ranging from 2 to 18 years. Overall, colonies with larger maximum sizes were occupied in more years (β = 0.0013, df = 35, p = 0, R^2 = 0.3).

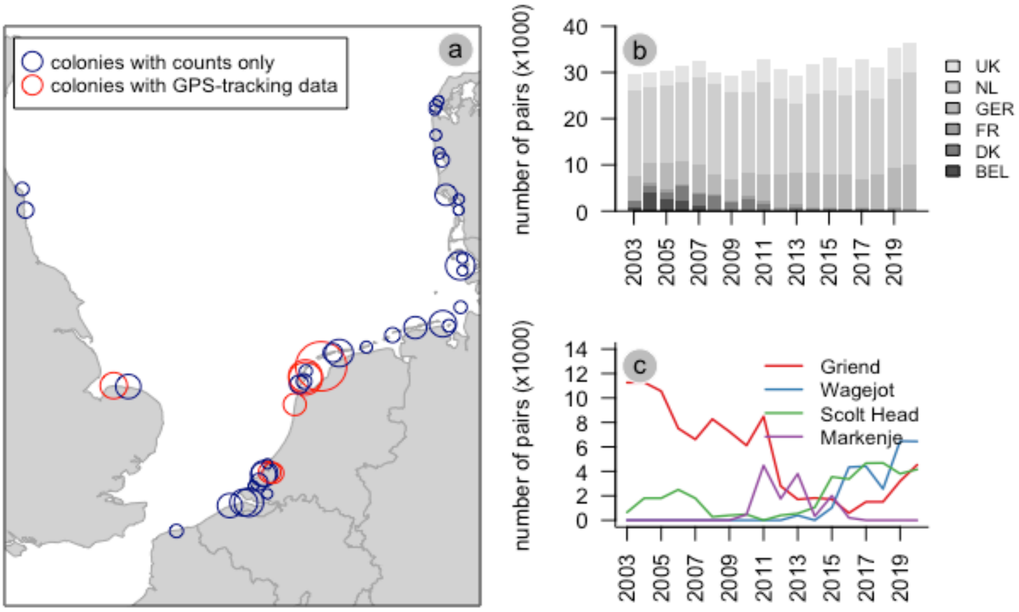

Figure 6.1 *a) The southern North Sea, with Sandwich Tern colonies for which counts were obtained (blue circles) and colonies for which GPS-tracking data was obtained (red stars). Circle size is proportional to the maximum count during 2003-2020. b) Number of breeding pairs in the southern North Sea per country. c) Temporal changes in five example colonies that hosted ca. 5000 breeding pairs during one or more of the study years.*

6.3.2 Tracking data: sample size

GPS-tracking data included 5 colonies, 10 years (2012-2021), 179 individuals, and 28.738 positions (Figure 6.2). The total number of individual-colony-year combinations was slightly higher than the number of tracked individuals (Table 6.1), due to two individuals that switched from the Slijkplaat/Scheelhoek colony to De Putten within the same year and two individuals that were tracked over two breeding seasons. Data were not evenly spread over years, colonies and individuals. Due to the development and application of solar panels, more data could be collected in later years.

Table 6.1 *Annual number of birds with GPS-tracking data per colony, after data selection, used in the RSFs. Two birds tagged in 2020 have also been tracked (from De Putten) in 2021.*

colonies	2012	2013	2014	2015	2016	2017	2018	2019	2020	2021	total
Scheelhoek/Slijkplaat, NL	5	3	6	5		5			26	20	70
De Putten, NL						3		13	20	26	62
Griend, NL						5					5
Wagejot/Utopia, NL							3		15		18
Scolt Head, UK					5	2	15	6			28
all colonies	5	3	6	5	5	15	18	19	61	46	183

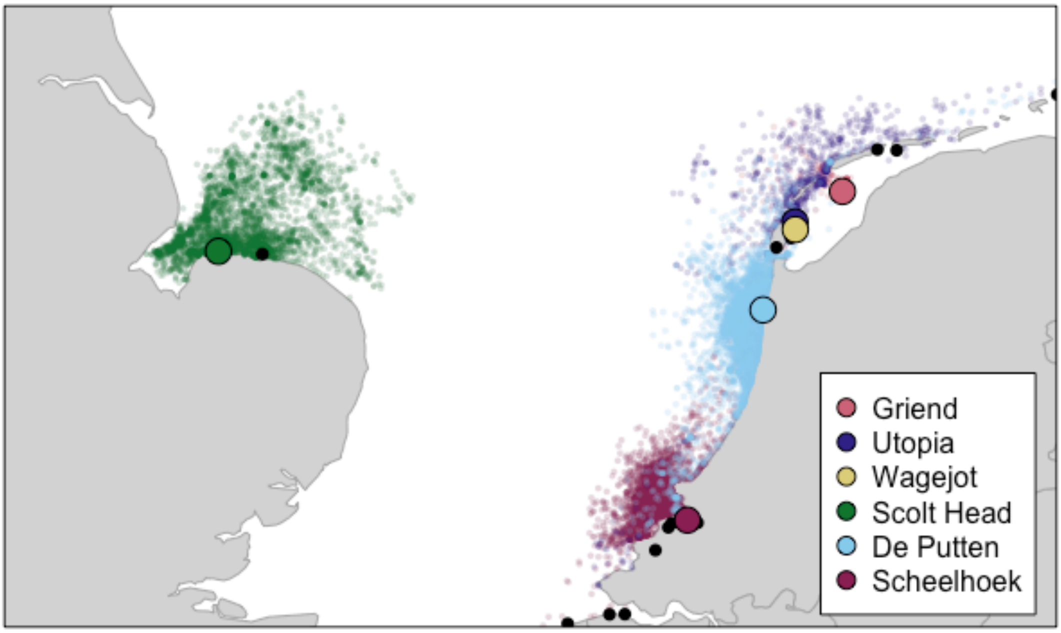

Figure 6.2 *Map showing regularized tracking data from all colonies, each colony represented by a colour. Note that data from the Slijkplaat have been included in the Scheelhoek data. Black dots indicate colony locations with a maximum count of at least 1000 breeding pairs during 2003-2019.*

6.3.3 Habitat selection

Sample size for the RSF included 28.738 positions. Distance to the colony had by far the largest effect on use by Sandwich Terns (Figure 6.3a). Overall, shallow waters were preferred over deeper waters (Figure 6.3b) and finer sediments (Figure 6.3c).

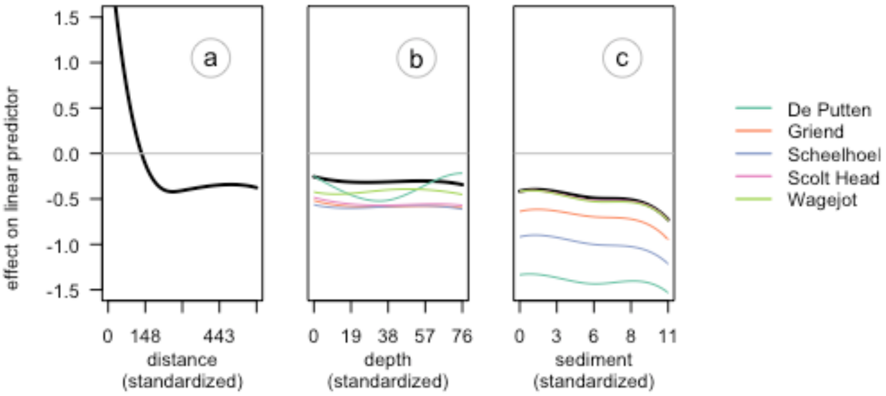

Figure 6.3 *Effects of distance to the colony, water depth, roughness of the seafloor and sediment grain size on the use by Sandwich Terns. Coloured lines show colony-specific effects estimated through random intercepts and slopes.*

6.3.4 Annual predictions of at-sea distributions

Predicted densities based on the mean parameters of the RSF for Scolt Head and De Putten correlated with the number of positions per grid cell (Figure 6.4), suggesting reasonable fit. Note that these model predictions are based on the mean parameter estimates - ignoring the colony-level random intercepts and slopes.

Predicted distributions based on the RSF are shown in Figure 6.5. As an example, we enlarged the resulting map for 2020 - one of the two years in which tracking data were obtained from three colonies, and the one with most data collected (Figure 6.6). In all years, highest densities occurred along almost the entire a coastline but differed slightly between years according to position and size of colonies.

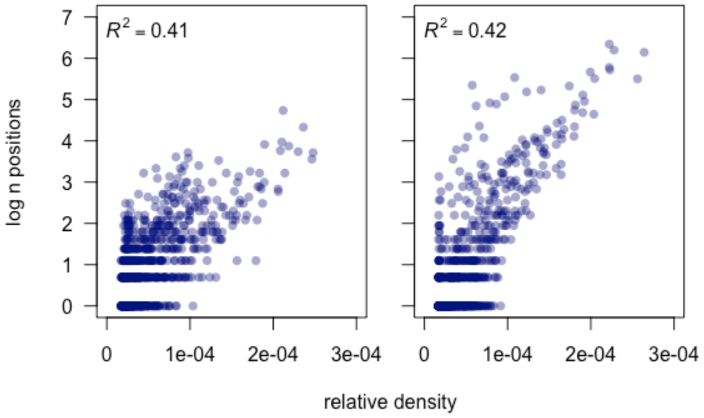

Figure 6.4 *Comparison between relative densities predicted from the RSF, scaled to sum to 1 for the colony, and the number of positions in each 2.5 x 2.5 km grid cell.*

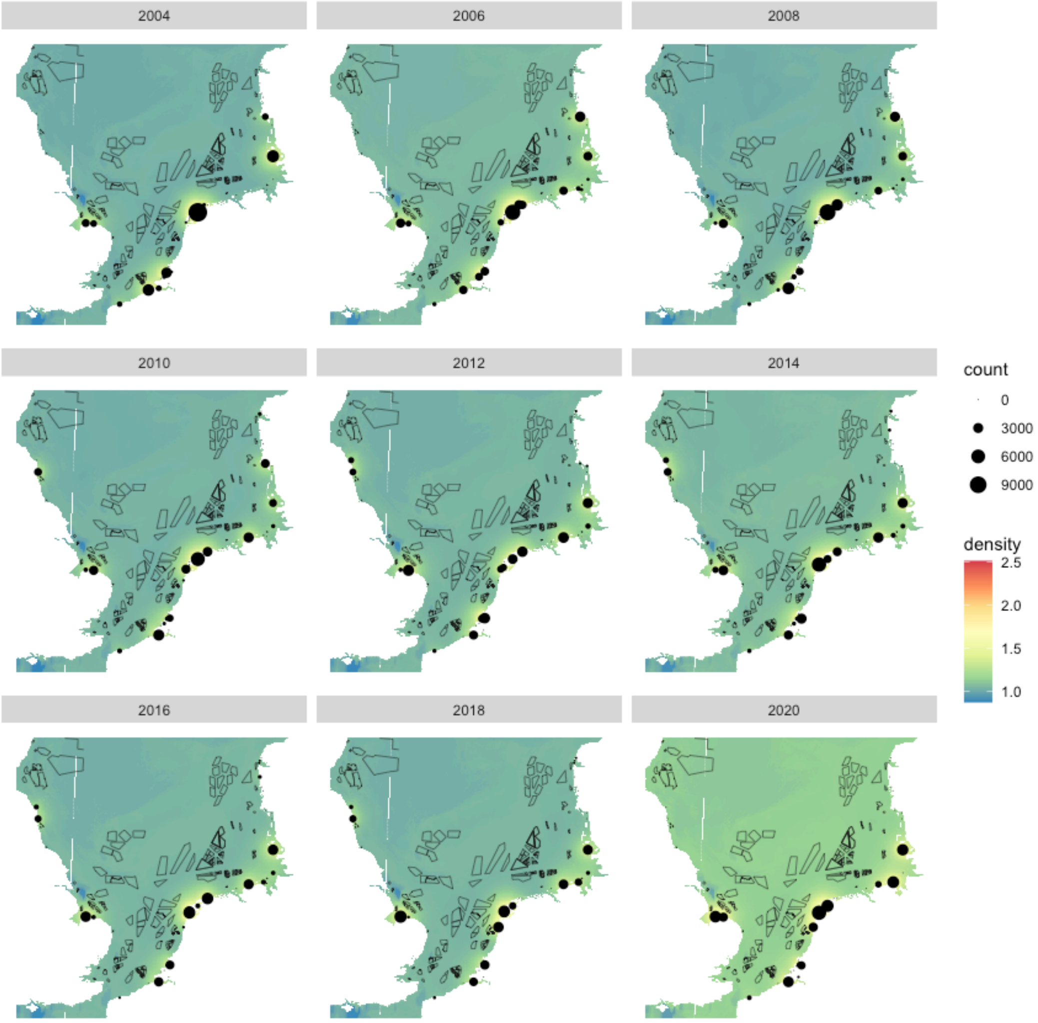

Figure 6.5 *Predicted density of Sandwich Terns for the years 2012-2020. To limit the number of figures, only even-numbered years are shown. Red dots show colony locations and are proportional to the maximum number of breeding pairs in 2003-2020. Note that German data for 2017-2020 is incomplete. Grey polygons show planned or realized offshore wind farms.*

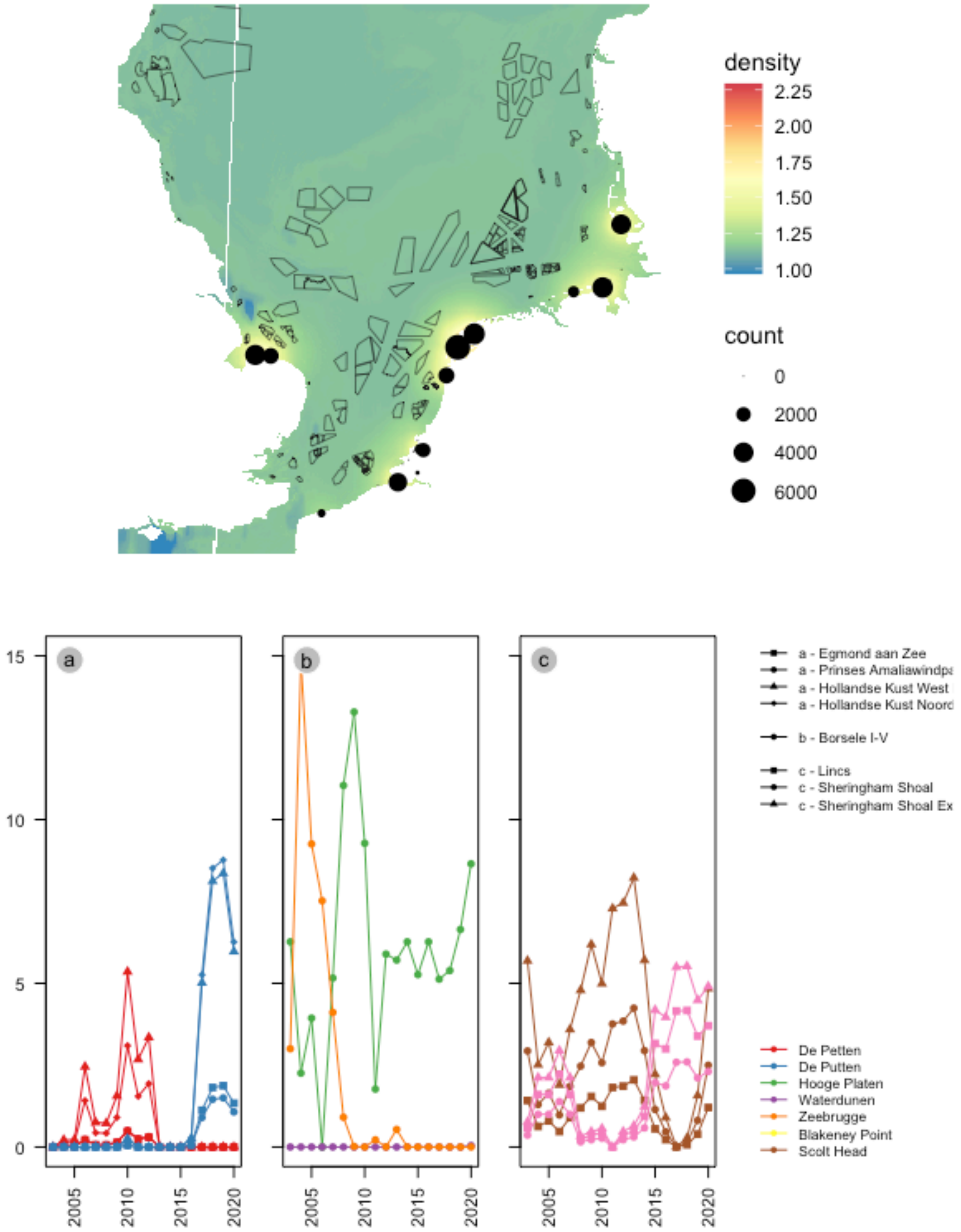

Figure 6.6 *Predicted use (the predicted number of individuals present in each area at any time) of (planned) OWF areas, for example OWFs in the Netherlands (left) and the United Kingdom (right). Colonies are included that were within 50 km of the example OWF areas.*

6.4 Discussion

We mapped the at-sea foraging distribution of Sandwich Terns across the southern North Sea by combining detailed individual movement data from five colonies, a resource selection function to infer habitat selection and colony counts from coasts around the southern North Sea. The resulting foraging distribution maps provide important information to assess potential conflicts with marine spatial planning, such as offshore wind farm developments.

The predicted annual distributions show a largely pattern that was expected based on known foraging ranges (Fijn *et al.* 2017), preferred depths (Bemmelen *et al.* 2019) and aerial surveys (Fijn *et al.* 2020) and ship-based surveys (Camphuysen & Leopold 1994), with highest densities in the coastal zones around the larger colonies along the Dutch coast and north of the Norfolk area. Although predicted relative usage of areas much further offshore are close to zero, they follow the total population size because colony-level colony counts are distributed across the entire study area, which may not be realistic. However, the use of offshore area fits with observations from aerial surveys (Fijn *et al.* 2020) and ship-based surveys (Camphuysen & Leopold 1994), showing that Sandwich Terns regularly occur in low densities in offshore areas during the breeding season. Of course, the breeding status of these individuals is unclear: they may be non- or failed breeders or immatures.

Our study highlights how the usage of a particular area can rapidly change, following the size of nearby colonies (Figure 6.6), which can greatly affect the assessment of potential impacts of OWF developement on Sandwich Terns. For example, the area nowadays occupied by the Borssele OWFs was likely to be intensely used prior to its construction by the colony at Zeebrugge in the early 2000s. If Zeebrugge will harbour a Sandwich Tern colony again in the future, the Borssele OWFs may incur substantially higher colission rates than what is assumed based on the current distribution and size of Sandwich Tern colonies. Of particular concern in this respect, is that the Waterdunen colony, which is close to the Borssele OWFs, expanded from 15 breeding pairs in 2020 to 4850 pairs in 2021. Although such shifts may be difficult to predict, it highlights that proximity to (planned) OWFs should be considered when creation new breeding habitat for Sandwich Terns, and *vice versa*, that potential settlement of larger numbers of Sandwich Terns are considered when assessing the potential impact of planned OWFs. In that respect, it is of note that the predictions for two planned OWFs off the De Putten colony (Hollandse Kust West Noord and Hollandse Kust Noord) indicate substantial overlap with the area used by Sandwich Terns breeding here. When built, these OWFs are therefore likely to lead to habitat loss and/or increased collision rates unless the De Putten colony shrinks.

By using only tracking data of adults during the incubation phase and early chick period, and using only colony counts of breeding adults, our results preclude a) other periods of the year and b) other age-classes and birds that skipped of failed breeding. During the incubation phase and early chick period, adults regularly return to the colony, thus behaving as central place foragers (CPF). Considering CPFs must balance travel costs and foraging success, adults generally forage near the colony, which was reflected in a strongly negative parameter in the RSF. However, other age-classes (juveniles and immatures) and adults that either skipped or failed breeding (*floaters*) are not constrained by the need to regularly return to a colony. Therefore, the foraging distribution of immatures and floaters may differ considerably from those of breeding adults as assessed in our RSF. Floaters potentially comprise a considerable proportion of the population, but their abundance is difficult to assess.

At-sea distribution of seabirds depends on individual habitat preferences and the spatial distribution of available habitats. Therefore, habitat selection may differ between colonies. For example, in accordance with an earlier analysis of the GPS-tracking data from the Scheelhoek and Slijkplaat colonies (Bemmelen *et al.* 2019), Sandwich Terns selected nearshore waters as well as water depths of 20-25 m. Subtle differences between colonies in flight distances suggest Sandwich Terns are selecting specific marine habitats for foraging and need to travel different distances according to their colony location. Inclusion of random slopes (in addition to random intercepts) in the RSF should reduce bias in the estimates, but colony-specific adjustments cannot be esimated for colonies with no GPS-tracking data available. A critical future step in evaluating the extent of colony-specific effects, is to cross-validate predicted densities between colonies by sequentially leaving out GPS-tracking data of each colony and assessing the difference. Another possibility to assess the fit of the model, is to compare predicted densities with observed densities during aerial seabird surveys.

With a RSF based on GPS-tracking data of birds from only sandy Dutch and British shores, at-sea distribution can only be predicted for areas with similar environmental characteristics. Coastal waters near British colonies in Northumberland differ from colonies elsewhere in the southern North Sea (including sites from where we have GPS-tracking data), in that they are characterized by much deeper, rockier near shore waters. Therefore, predictions for that area may not be accurate and should be treated with caution.

In this study, foraging habitat selection of Sandwich Terns was modeled as a function of distance to the colony, water depth, slope and median grain size. These covariates may capture only part of the Sandwich Terns habitat selection, as they are known to target dynamic, ephemeral phenomena such as thermal fronts, or waters with a particular transparency (Baptist & Leopold 2010), which are not captured in the static environmental covaraties in our model. Frontal systems may be included using remotely sensed Finite-Time Lyapunov Exponents (FTLE) (Boffetta *et al.* 2001), which provide a proxy for frontal activity such as sub-mesoscale chlorophyll and SST filaments and has been used before in modeling seabird foraging behaviour (Grecian *et al.* 2018). In addition, seabird foraging distributions may be driven by tidal cycles (Trevail *et al.* 2019).

At-sea habitat selection was assumed to be similar within and across years. Conceivably, foraging distributions change in response to 1) prey availability and 2) requirements of adults and chicks. Seasonal changes in Sandwich Tern diet have been shown for several Dutch colonies but concerns mainly a switch from sand lances to clupeids around mid-May (Fijn *et al.* 2018). By selecting GPS-tracking data from late May to late June, our sample should reflect the period in which clupeids remain the most important prey. In addition, although including intra- and inter-annual effects in the RSF is possible, this is problematic given the current small sample sizes, which were also not evenly spread across years, colonies and individuals. Furthermore, inter-annual effects would be confounded by individual effects, as individuals are only tracked within a given year.

Our study highlights the importance of considering changes in abundance of breeding birds when assessing the potential impact of OWFs. In Sandwich Terns, this is all the more critical considering the dramatic changes in the appearance, disappearance and size of colonies, as well as the desire to support this species by artificially increasing availability of nesting habitat.

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Tracking of Sandwich Terns in the Netherlands was performed under project licence for animal procedures AVD401002015102 of the Central Authority for Scientific Procedures on Animals and the appropriate ringing licences issued by the Vogeltrekstation. Tracking of Sandwich Terns in the UK was performed under the appropriate Special Methods Licences, ringing permits and Schedule 1 licences.

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Thanks to all who provided colony counts; C. Redfern (Newcastle University), P. Morrison (RSPB) and A. Wilson (Natural History Society of Northumbria) for the colonies of the

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7 Distribution and flight altitude of foraging Sandwich Terns near newly constructed wind farms in the Dutch Delta

M.P. Collier, R.P. Middelveld, J.W. de Jong, R.C. Fijn

Abstract

During 2020 and 2021, the distribution, activity and flight heights of Sandwich Terns in the area east of the Borssele wind farm area to the Dutch coast were recorded during the breeding season. At-sea data were collected using ship-based survey methods adapted to focus on Sandwich Terns. Flight heights and activity (foraging, searching, in transit or resting) were collected for around 1,500 birds over six day-long surveys. Most observations of Sandwich Terns were of birds in transit, followed by searching and foraging birds. Very few birds were recorded as resting in the survey area, reflecting the species' habit of using structures and beaches for this purpose. Sandwich Terns were recorded throughout the survey area, and this was also true for birds that were foraging and searching. Concentrations of foraging and searching birds were found east of the Borssele wind farm area, some 20 km from the coast, in 2020 and close to shore south of Westkapelle in both years. Birds recorded as in transit were again present throughout the survey area with higher numbers off the coast between Westkapelle and Cadzand. Over 87% of all Sandwich Terns were flying below 20m, with half of these between 11-20m. Numbers above 20m decreased rapidly with decreasing height with fewer than 1.5% being recorded above 40m. A similar pattern was observed for each activity, although for birds in transit, a greater proportion of birds were recorded below 5m than for other activities. This characteristic for birds in transit flying low over the water was accentuated in birds with prey, for which over 37% were recorded in this lowest height category.

7.1 Introduction

Sandwich Terns breed in several coastal colonies around the southern North Sea, including in the Dutch Delta. Birds from these colonies forage along the coast and further offshore. The extent to which Sandwich Terns use offshore areas is being investigated with GPS tagging. In addition, ship-based surveys can provide additional information on Sandwich Tern distribution, abundance, behaviour and flight height, particularly for specific areas. Flight height of the birds at sea is of particular interest in relation to assessing the potential impacts of offshore wind farm developments. The number of collisions at future offshore wind farms are typically assessed using collision rate models and these rely on input parameters such as flight height, but few data for Sandwich Tern, particularly during various activities, are as yet available for offshore areas. In this study, we determined flight height distributions for different behaviours of Sandwich Terns based on observational data from ships.

Survey team aboard the MV Hammen (R. Fijn, Bureau Waardenburg)

One of the survey lines was very close to one of the Belgian wind farms (R. Fijn, Bureau Waardenburg)

7.2 Methods

Ship-based surveys were conducted to collect information on the broad distribution and behaviour of Sandwich Terns offshore and specifically near OWF Borssele. Such surveys provide information on both the offshore distribution of Sandwich Terns west of the Westerschelde colonies and on whether these birds use the areas near OWF Borssele to forage. We used a laser range finder to measure highly accurate flight height information in the vicinity of OWF Borssele.

A total of six surveys were undertaken, with three in 2020 (16 May, and 10 and 25 June) and three in 2021 (18 May, 15 June and 6 July; Table 7.1). During surveys two observers (three on 10 June and 25 June 2020) recorded all species, but prioritised Sandwich Terns, using ESAS methodology (Tasker *et al.* 1984, Camphuysen *et al.* 2004). In addition, flying Sandwich Terns were assigned behaviours of ‘searching’ (bill pointing down), ‘foraging’ (diving) or in ‘transit’ (bill horizontal) and information on prey type and size was collected. Flight heights were recorded visually in the following categories: 0-5; 6-10; 11-20; 21-30; 31-40; 41-50; 51-75; 76-100; and >100m. Where possible, flight heights were measured using laser range finder.

Table 7.1 Dates, times and conditions for ship-based surveys in 2020 and 2021 to determine the distribution and activity of Sandwich terns.

Date	Ship	Start Time	End Time	Seastate	Visibility (km)
16/05/2020	Hammen	07:25	17:50	2	>10
10/06/2020	Hammen	06:58	17:50	2 - 3	>10
25/06/2020	Hammen	07:25	17:25	2	>10
18/05/2021	Scheldestroom	07:21	18:18	2 - 4	>10
15/06/2021	Scheldestroom	06:45	16:30	2 - 4	>10
06/07/2021	Scheldestroom	07:25	20:10	2 - 4	>10

The survey route covered a length of approximately 215 km between the coast of Walcheren and the wind farm area of Borssele. The route transect the Dutch-Belgian border. The actual route varied slightly between surveys due to wind farm construction, other vessels and shallows, although routes remained largely similar within years (Figure 7.1).

7.3 Results

A total of 1551 Sandwich Terns were recorded during the 64 hours and 44 minutes of survey time during the six surveys in 2020 and 2021. Most birds were recorded as ‘in transit’, with slightly fewer as ‘searching’ and fewer still as ‘foraging’ (

Table 7.2). Less than 0.5% of birds were recorded as ‘resting’ reflecting the preference of Sandwich Terns to rest on buoys and similar structures. A total of 184 Sandwich Terns were recorded carrying prey. Almost all prey could be identified and showed similar numbers of Herring/Sprat (*Clupeidae*) and sandeel (*Ammodytidae*) were being taken.

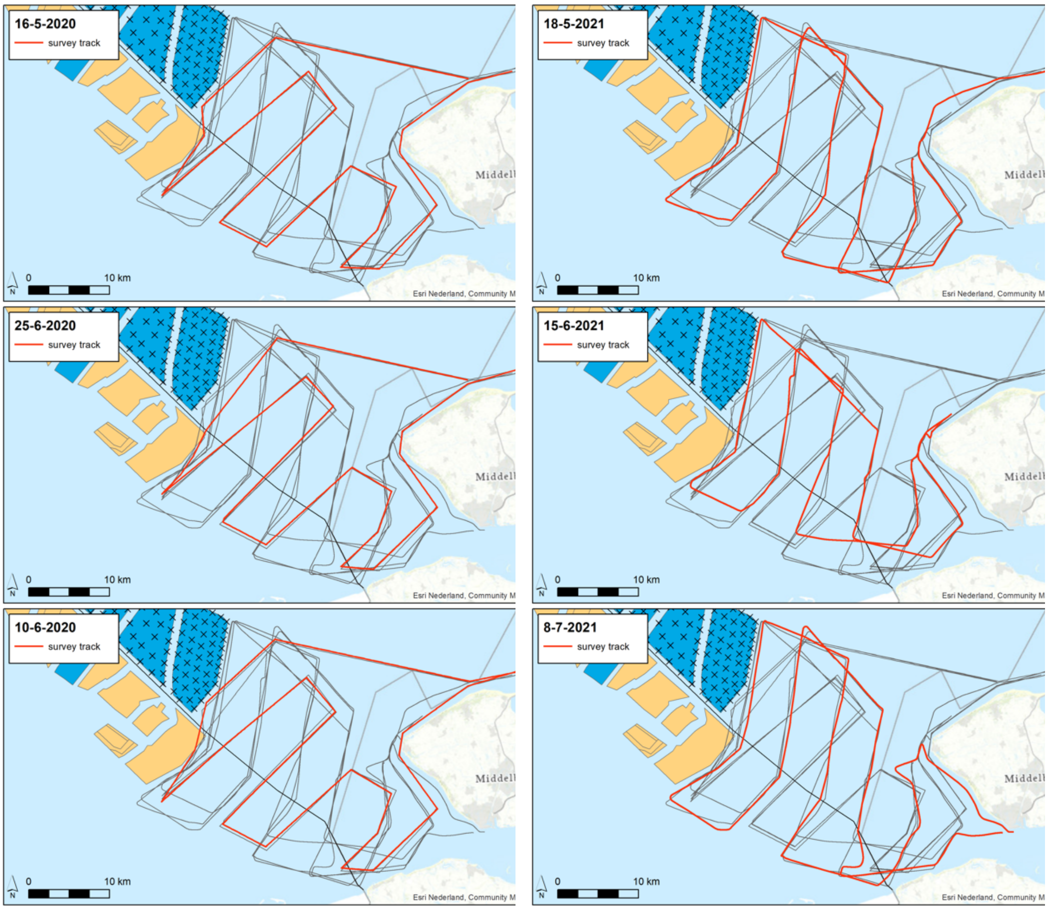

Figure 7.1 *Survey routes for ship-based surveys in 2020 (left) and 2021 (right) to determine the distribution and activity of Sandwich Terns.). Survey routes varied slightly each time due to the wind farm construction, other vessels and shallows, although remained largely similar within years. Each map shows the survey track for the survey in question (red) and for all other surveys (black).*

Table 7.2 *Numbers and behaviour of Sandwich Terns recorded during each of the six ship-based surveys during 2020 and 2021.*

Date	**Foraging**	**Resting**	**Searching**	**Transit**	**Total**
16/05/2020	60	4	39	109	212
10/06/2020	23	1	107	180	311
25/06/2020	13		72	79	164
18/05/2021	24	2	100	71	197
15/06/2021	35		116	189	340
08/07/2021	37		74	216	327
Total	**192**	**7**	**508**	**844**	**1551**

A total of 687 Sandwich Terns were recorded in 2020 and 864 in 2021. In 2020, concentrations of birds were found close to the coast between Westkapelle and Zoutelande and at several locations closer to the wind farms and in the Belgian North Sea (Figure 7.2).

In 2021, concentrations were found close to the coast at Westkapelle and Cadzand with fewer concentrations further offshore, although birds were recorded throughout the route (Figure 7.3).

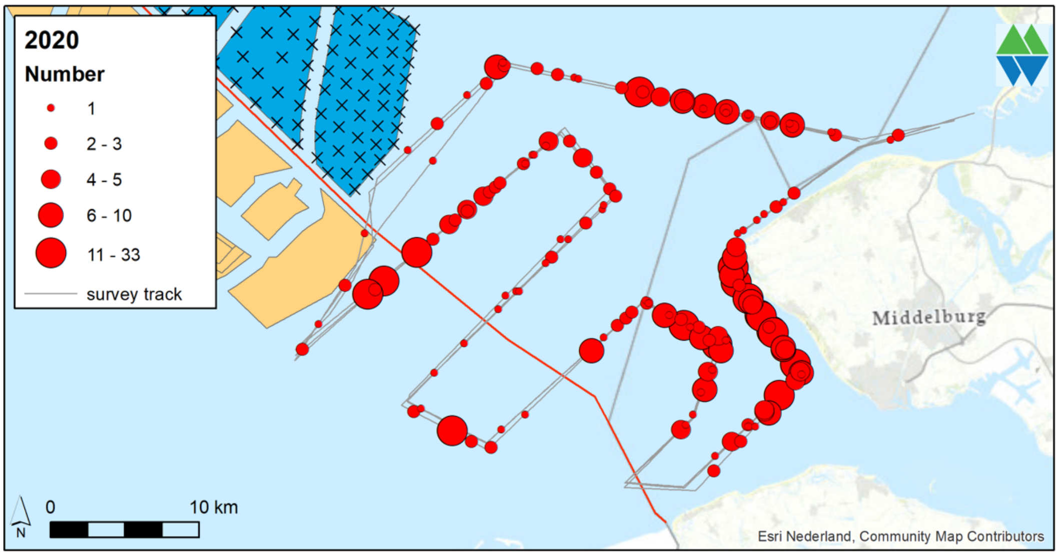

Figure 7.2 Distribution of Sandwich Terns recorded during three ship-based surveys in 2020.

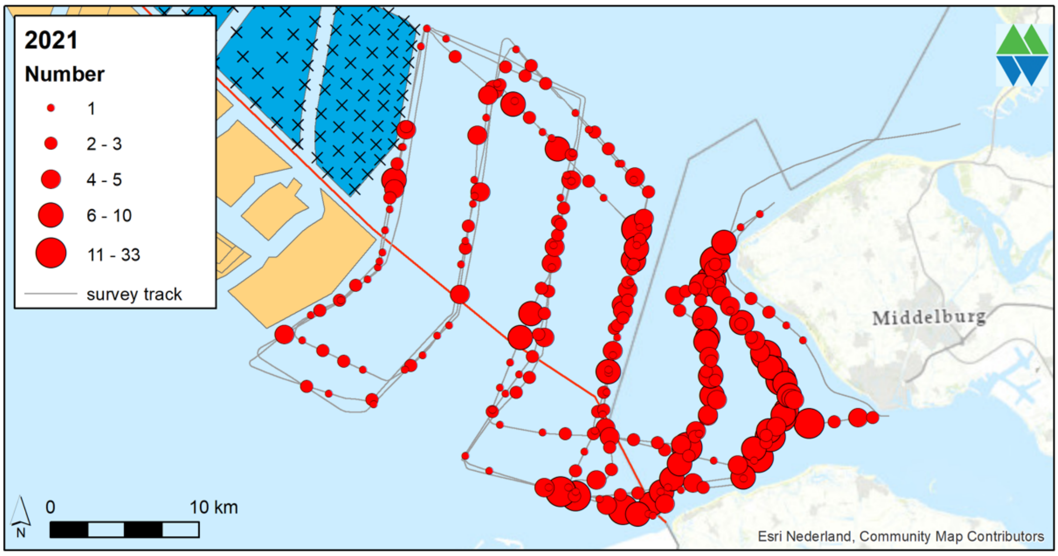

Figure 7.3 Distribution of Sandwich Terns recorded during three ship-based surveys in 2021.

Only five birds in 2020 and two in 2021 were recorded as resting. Sandwich Terns use structures such as buoys or platforms on which to rest and the numbers of resting birds recorded can be influenced by the presence of suitable structures close to the transect route. Based on the distribution of resting birds, it can be assumed that both buoys and wind farm structures were being used.

The distribution of foraging Sandwich Terns differed between years with concentrations in 2020 being found east of the wind farm area, whereas in 2021 concentrations were closer to shore, particularly near the coast at Westkapelle (Figure 7.4). In both years foraging birds were recorded throughout much of the survey area, although notably in 2020 no foraging birds were recorded in the area closest to the wind farms.

In both 2020 and 2021, searching behaviour was recorded throughout the survey area, even very close to the wind farm areas. Concentrations were recorded close to Westkapelle and further off the Belgian coast in 2020, whereas in 2021 searching activity appeared more spread throughout the survey area (Figure 7.5).

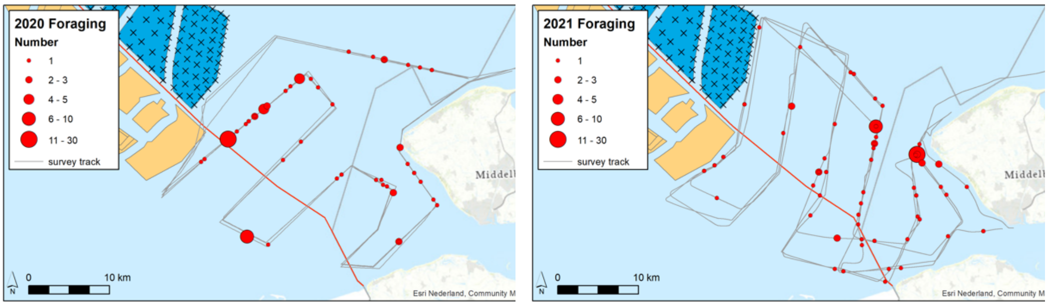

Figure 7.4 *Distribution of Sandwich Terns recorded as foraging during three ship-based surveys in 2020 (left) and 2021 (right).*

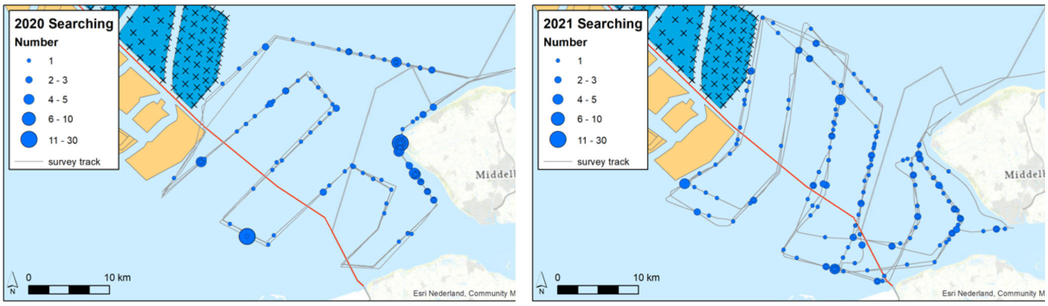

Figure 7.5 *Distribution of Sandwich Terns recorded as searching during three ship-based surveys in 2020 (left) and 2021 (right).*

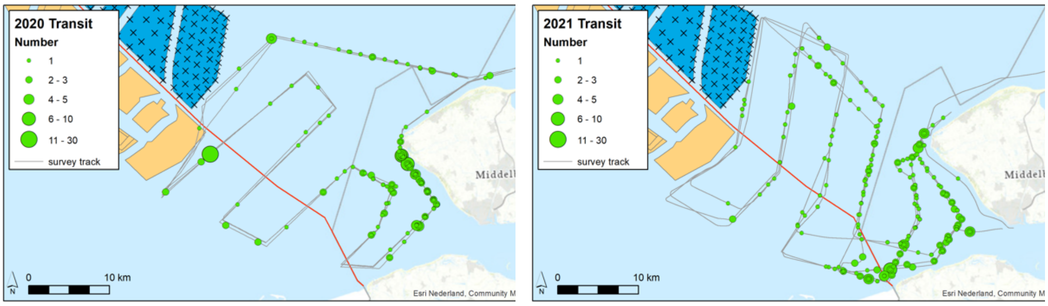

Figure 7.6 *Distribution of Sandwich Terns recorded as in transit during three ship-based surveys in 2020 (left) and 2021 (right).*

The majority of flying Sandwich Terns were recorded as being in transit, and this is evident from the distributions of birds in transit in both 2020 and 2021. In both years, higher numbers of birds in transit were recorded in the eastern part of the survey area, particularly in the area between Westkapelle and Cadzand (Figure 7.6).

Flight heights were recorded for 1460 Sandwich Terns, of which 842 were in transit, 502 searching and 116 foraging. About half the number of birds were recorded between 11-20 m above sea level, with almost 40% of the remaining birds below this height (Figure 7.7). The proportions of Sandwich Terns recorded above 20 m above sea level totalled just over 10% of the total and numbers rapidly decreased with increasing height.

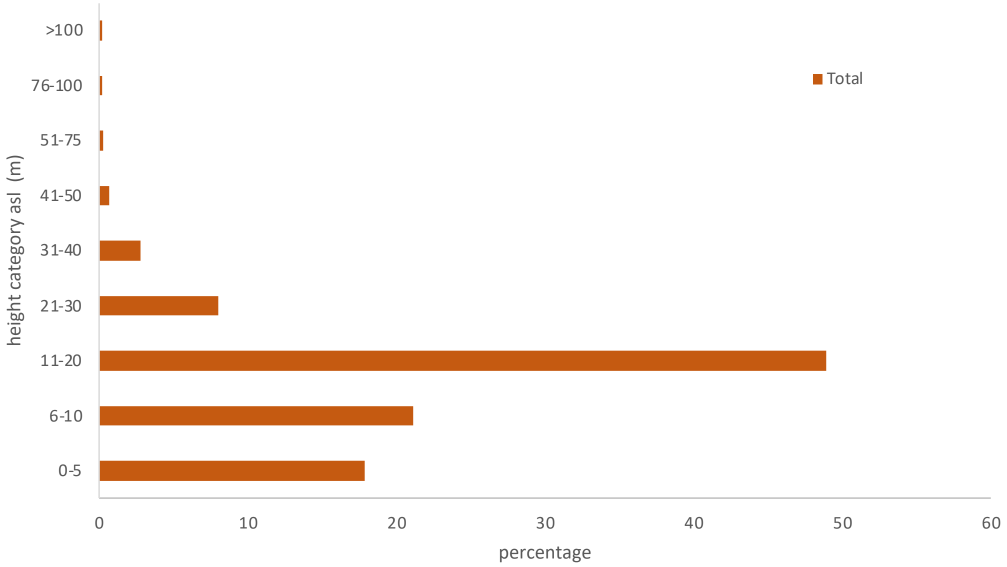

Figure 7.7 *Proportions of flight heights for all flying Sandwich terns recorded surveys during 2020 and 2021.*

Foraging birds were recorded exclusively below 40m, with 60% between 11-20m above sea level. Less than 5% of foraging birds were above this height, with 25% between 6-10m and 10 below this height (Figure 7.8 top). For searching birds, the distribution was less concentrated, with less than 50% between 11-20 m and birds recorded up to 51-75 m. Nevertheless, the general pattern was similar to that of foraging birds with over 40% in the lowest two height categories (Figure 7.8 middle). For birds in transit, again almost 50% were between 11-20m. Unlike for foraging or searching birds, the second-most recorded height was under 5m, with 21% of birds being in this lowest category. Almost 14% of foraging birds were recorded above 21m, the most of any behaviour (Figure 7.8 bottom).

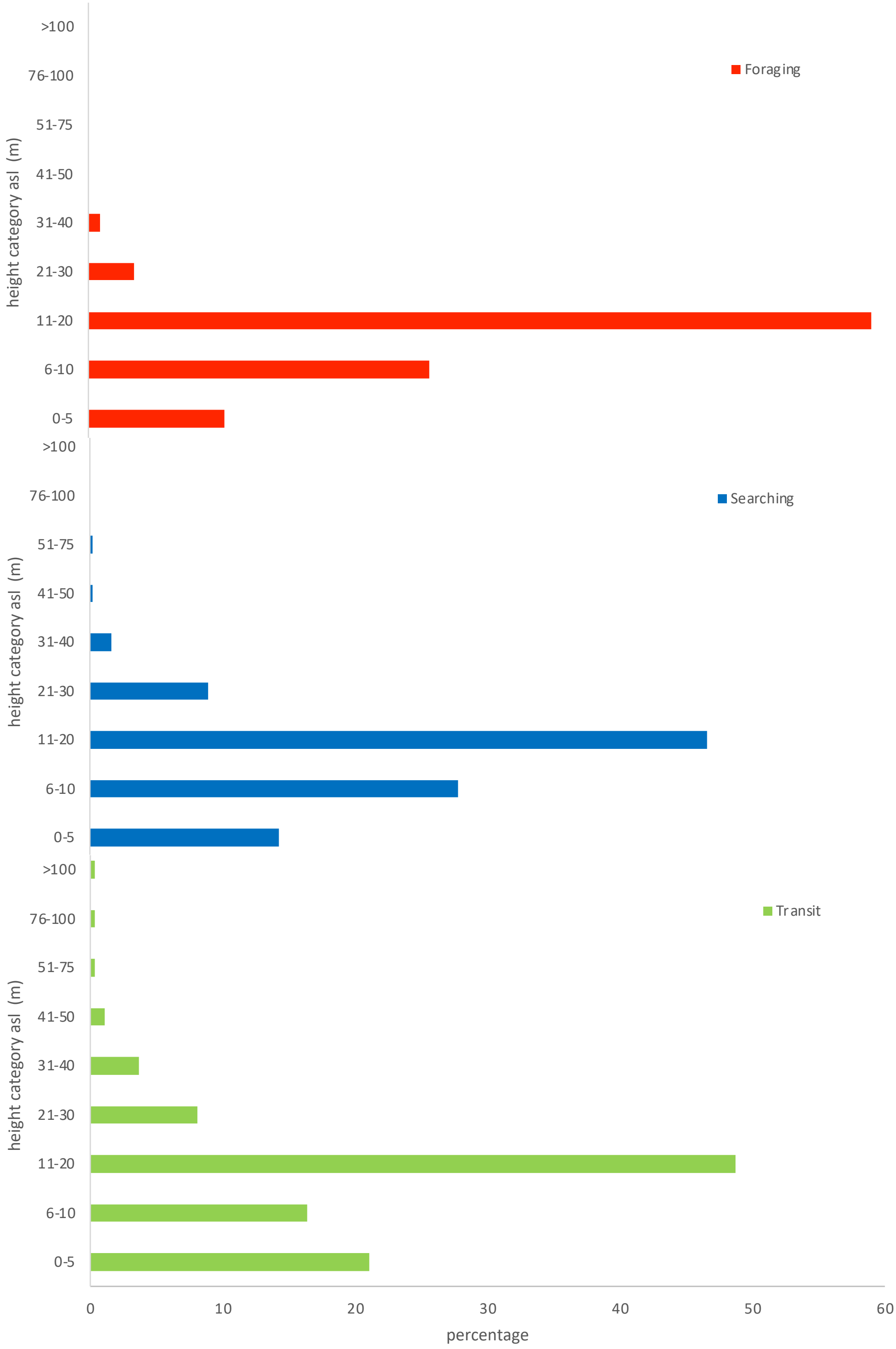

Figure 7.8 *Flight height distributions for Sandwich Terns based on behaviour: foraging (top), searching (middle), and in transit (bottom), recorded during surveys in 2020 and 2021.*

A total of 172 (20%) Sandwich Terns in transit were recorded carrying prey. Flight height distributions differed between birds with and those without prey, with most birds with prey being below 5m (Figure 7.9 top), and most without prey being between 11-20m (Figure 7.9

bottom). With a lower proportion of birds with prey than without prey recorded between 6-10m, flight height distributions for bird with prey show a shift in birds under 10m to the lower category. For both groups, the number of birds decreased with increasing height, particularly above 50m (and for birds without prey above 40).

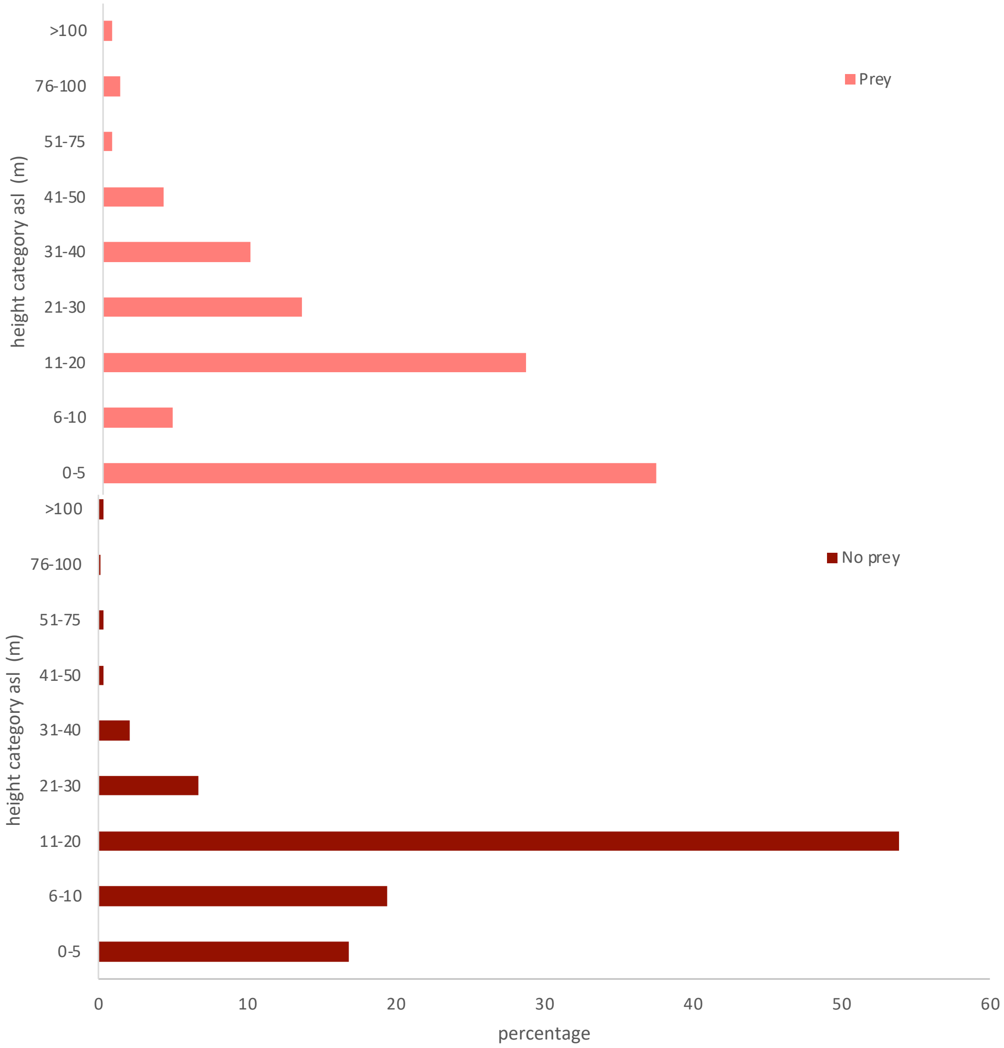

Figure 7.9 *Flight height distributions for Sandwich Terns 'in transit' with (top) and without (bottom) prey, recorded during surveys in 2020 and 2021.*

7.4 Discussion

Sandwich Terns were recorded throughout the area between Westerschelde and the Borssele wind farm area, up to 25 km from the coast of Walcheren showing the potential use of offshore wind farm areas. The higher numbers close to the mouth of Westerschelde were driven by birds in transit, which can be explained by the colonies at Hooge Platen (2020) and Waterdunen (2021). Birds foraged at all distances from the coast and the difference in hotspots between the two years may be explained by food availability or environmental conditions such as wind, tidal state or turbidity.

In general, the flight heights found in this study were similar to those found in England where Perrow *et al.* (2017) found a mean flight height of 22.3 m (2-113 m) using a laser range finder to record flight heights of 70 Sandwich Terns visually into 5 m categories from a boat. Higher birds were more likely to be searching or in transit, with very few birds foraging above 30 m. This may have an influence on assessments of offshore wind farm developments where differences in activities might be expected.

The relative number of collisions calculated using a widely used collision rate model (Band 2012) show the effect of activity on flight height may lead to differences in the numbers of estimated collisions (Table 7.3). Comparing flight height figures from this study with published figures from Johnston *et al.* (2014) shows that collisions may be underestimated with existing figures, although this is ultimately also dependent on the rotor height of the turbine.

Table 7.3 Relative estimates of collision victims in a wind farm with 8 MW turbines for Sandwich Terns and for different flight behaviours. Underlying numbers were calculated using the basic SOSS Band model (Band 2012) using a proportion of birds at rotor height with a minimum rotor height of 30 m. Relative number of casualties compared to using figures in Johnston et al. (2014).

Activity/Source	**Proportion at rotor height**	**Relative number of casualties in wind farm with 8 MW turbines**
Foraging	0.009	0.47
Searching	0.020	1.08
Transit	0.058	3.15
Total	0.041	2.23
Perrow *et al.* 2017	0.301	16.31
Johnston *et al.* 2014	0.018	1

Birds in transit were recorded from sea level to above 100 m, although most birds were recorded between 11-20 m and below this height. However, birds carrying prey were most frequently recorded up to 5 m above sea level. This type of inbound flight activity is also known to have higher flight speeds than other activities (Fijn & Gymesi 2018).

Acknowledgements

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8 Estimates of survival and dispersal of Sandwich Terns in the Netherlands. The added value of colour-ring projects in estimating survival and dispersal of Sandwich Terns in the Netherlands

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Abstract

Models predicting population effects of OWFs on seabirds greatly benefit from the availability of area- and age-specific mortality rates and estimates of the degree of exchange of individuals between (sub-populations, areas or colonies. In this study we provide reliable estimates for survival immature and adult Sandwich Terns and an order of magnitude of dispersal between the southern (S) and northern (N) colonies of the Netherlands. Burnham model estimates for immature (1-3Y) survival for the S and N Netherlands amounted 0.27 and 0.34 respectively, and adult survival 0.92 and 0.91. Analyses of recoveries of colour ringed Sandwich Terns lead to valuable and somewhat different insights in the survival of the different age classes. It yielded remarkably high survival rates in the 3rd year and resulted in a very different pre-breeding survival estimate from the Burnham estimates. Despite the limited time span of the Dutch colour-ring dataset (colour ringing only started in 2012), these figures nevertheless seem reliable as they are comparable for the different colonies in the study area. This study highlights the fact that Sandwich Terns belong to a select group of (sea)birds that show rather low site fidelity and particularly high dispersion rates. Using resightings of colour-ringed individuals we found remarkable differences in the probability of exchange between northern and southern colonies, which strongly determine the current composition of these colonies. Net migration from the S to N was greater than vice versa with older adult birds showing a higher degree of philopatry than younger ones. While northern birds are much more faithful to their part of the study area, they are also more prone to move to another colony within that area. Furthermore, even within a breeding season, Sandwich Terns often visited multiple colonies, thereby potentially passing multiple OWFs which heightens collision hazards. Also, post-breeding visits of various colonies by adults and juveniles seems a common behaviour in this species. This nomadic behaviour (within-years, between-years and post-breeding) makes it very difficult to model collision mortality based on colony-specific features. We expect that such will result in an underestimate of true collision rates.

8.1 Introduction

Sandwich Terns *Thalasseus sandvicensis* breed along the Dutch coast with about 15.000 – 20.000 pairs (Sovon 2018). These are spread over a limited number of large colonies (with usually a few hundred to thousands of pairs) mainly in the Delta area, North Holland

and the Wadden Sea area. After the breeding season, newly fledged birds stay with their parents for a relatively long time, adults sometimes even accompany their young during the southward migration (e.g. Fernandez-Cordeiro & Costas 1991). Between October and March, most European Sandwich Terns reside in the wintering quarters. These are mainly in Africa, but some winter in the Mediterranean, the European coasts between Normandy and Portugal or further north (Vogeltrekatlas 2020). Most juveniles remain in the wintering areas for at least one, but usually two or even three years before returning to the breeding colonies for the first time (e.g. Langham 1971). Sandwich Terns are long-lived seabirds with a typical life expectancy of 12 years but birds of up to 30 years old have been recorded (Robinson 2005, Fransson *et al.* 2010). This longevity and the concentration of breeding pairs in only a small number of coastal locations potentially makes the species especially vulnerable to the impact of human-induced pressures such as the construction and operation of offshore wind farms (further OWFs) within a colony's feeding range.

OWFs may directly increase mortality of seabirds through collision mortality and indirectly by displacing birds from foraging habitat or by creating barriers to movement increasing their energy costs (Drewitt & Langston 2006, Masden *et al.* 2010). Collision is more likely to occur if seabirds fail to avoid wind farms, whereas displacement from foraging habitat typically happens when seabirds do avoid wind farms (Furness *et al.* 2013). Sandwich Terns avoid OWFs not only during the construction phase (Harwood *et al.* 2017). Dierschke *et al.* (2016) – updated by Vanermen & Stienen (2019) – identified Sandwich Tern as one of the seabird species also (weakly) avoiding operational OFWs. As this might lead to habitat loss and collision risks for birds that do enter wind farms, Sandwich Tern was selected as one of the target species for the Dutch 'Wozep'-programme. This scientific programme investigates knowledge gaps in the assessment of ecological effects of installing and operating OWFs in the Dutch part of the North Sea. The setup of this programme strongly relies on an individually based modelling approach of the potential cause-effect chain, thereby translating the potential effects of habitat loss and collision mortality on individual seabirds to the impact on the (sub)population or colonies where they breed. Given the ambitious plans for future OWF development, a reliable model predicting population effects (impact) of OWFs on populations of seabirds protected under the EU Birds and Habitats Directive (European Commission 2009) is necessary. Determining the consequences of additional mortality to a population requires an estimate of population size, an understanding of life history, estimates of demographic rates and how these are regulated by density-dependence and environmental stochasticity (Lande *et al.* 2003). For Sandwich Terns, two of the major knowledge gaps that were identified in the 'Wozep'-programme are age-specific mortality rates (or survival estimates) of the Dutch breeding population and the degree of exchange (dispersal) of individuals between (sub)populations, areas or colonies (van Kooten *et al.* 2018).

Population models for long-lived animals are particularly sensitive to changes in mortality rates, especially to those of adults (e.g. Pfister 1998, Saether & Bakke 2000; Weimerskirch 2001, Doherty *et al.* 2004, Schekkerman *et al.* 2021). Published Sandwich Tern survival estimates, however, show much variation. This might be caused by different time-periods and study locations but may also have a methodological background (Francis & Saurola 2002, Newton *et al.* 2016), urging for reliable estimates for the Dutch population.

Furthermore, reliable survival estimates for Sandwich Terns of different age-classes for the Netherlands would greatly improve the population models and including annual mortality rates (or at least estimates for shorter time periods) would allow to account for environmental stochasticity (Miller *et al.* 2018).

Sandwich Tern populations are characterized by a relatively high degree of exchange between colonies, sometimes over long distances (Stienen 2006, Fijn *et al.* 2014). This is the result of at least two processes. On the one hand, there is a gradual process of 'slow' dispersal in which young birds recruit to a non-natal colony or where a limited number of already established adults move to another breeding location. This slow dispersion appears to take place over long distances (Schekkerman *et al.* 2017). On the other hand, the various Dutch colonies have shown periods of 'rapid' dispersion in which a part of an existing colony (or sometimes even an entire colony) splits off and joins another colony. Sometimes a new colony is formed in an entirely new location. In the past, this was often the result of the deterioration of breeding habitat or changes in the food supply in the original breeding area in combination with nature development which created attractive new breeding areas elsewhere (Stienen 2006, van der Jeugd *et al.* 2014). As far as we know, birds that suddenly move en masse largely do so within clusters of nearby colonies (for example within the Wadden Sea or the Delta area, van der Jeugd *et al.*, 2014) and thus over relatively short distances. It is therefore important to distinguish between these two types of dispersal. The magnitude of both phenomena (that can also be age- and even sex-dependent, cf. Acker *et al.* 2018) has yet to be quantified for Sandwich Tern populations.
The basis of most survival and dispersal studies of birds has long been the extensive scientific ringing programmes with metal rings by national ringing schemes. The Dutch scientific ringing programme for Sandwich Tern is worldwide the most extensive one for this species with many hundreds ringed every year. The main advantages of metal rings are the durability of the rings and the practically unlimited number of combinations possible. The main disadvantage is that they are hard to read in the field and generate relatively few resightings. Therefore, during the last decades, scientific ringing schemes were complemented by colour-ring programmes and more recently also by tracking devices (e.g. Ward 2000, Burger & Shaffer 2008). Colour-rings are much easier to read in the field but are on the other hand less durable (leading to more ring loss, especially in long-lived species) and, particularly for smaller birds such as Sandwich Terns, the number of unique codes is limited. In 2012, a colour-ring programme was initiated in the Dutch Delta area and some years later in other colonies as well.

In this report we combine both scientific (metal ring) and colour-ring databases to 1) calculate age-related survival estimates of Sandwich Terns for the southern and northern part of the Netherlands and 2) estimate the degree of dispersal between regions and colonies.

8.2 Methods

8.2.1 Study area

The Belgian and Dutch coastal areas were combined to one study area. Here, between 1991 and 2021 multiple large Sandwich Tern colonies were present (Figure 8.1, Figure 8.2). In the southern part of the study area (further referred to as ‘S Netherlands’, although including a part of Belgium), the most important colonies were at Zeebrugge (Belgium, 1991-2008), Western Scheldt (Hooge Platen (1991-2020) and Waterdunen (2021)), Flaauwers Inlaag (2004-2015), Grevelingen (Hompelvoet (1991-2004) and Markenje (2010-2016)) and Haringvliet (Scheelhoek and Slijkplaat, 2005-2021). Zeebrugge and the Western Scheldt colonies are grouped as ‘Delta S’, the others are in ‘Delta N’. The main colonies in the northern part of the study area (further ‘N Netherlands’) were at De Putten (2016-2021), Texel (De Petten, Ottersaat, Wagejot and Utopia, 2004-2021), Griend (1991-2021) and Ameland (2000-2017). Between 1995 and 2005, small and occasionally larger colonies were present in other locations (Steenplaat, Terschelling, Rottumerplaat and Schiermonnikoog) in some years.

Overall, the distribution and number of Sandwich Tern colonies in the Netherlands changed substantially during the study period. Until 2005, the largest colonies were found in Zeebrugge and on the Hooge Platen, Hompelvoet and Griend. Predation by Red Fox *Vulpes vulpes* led to the disappearance of the colony of Zeebrugge in 2008. In 2005, a large colony settled at Scheelhoek. This colony is still present, although in some years it moved (partially) to nearby Slijkplaat. One year before, in 2004, Sandwich Terns started breeding in Flaauwers Inlaag. After reaching a maximum size of 2100 breeding pairs (bp) in 2006, this location was abandoned altogether after 2015. Sandwich Terns left Hompelvoet (where they were already breeding in large numbers before the start of the study period) in 2004 due to habitat deterioration. In 2010 a new breeding location emerged in the Grevelingen, on Markenje this time. After reaching a maximum number of 3800 bp in 2013, Grevelingen was abandoned completely in 2016.

Also the numbers and breeding locations in the N Netherlands showed a lot of variation. In 2005, a colony settled on Feugelpolle on Ameland (further ‘Ameland’) reaching a maximum of 5000 bp in 2007. Due to predation, flooding and human disturbance, this colony disappeared in 2017. The thriving colony of Griend was deserted by Sandwich Terns in 2011 after severe predation by Herring Gulls of Black-headed Gulls and Sandwich Terns. In the years that followed this event, the numbers remained relatively low (600-1800 bp) until 2019 (3192 bp) and 2020 (4500 bp). In 2021, only 700 pairs were counted. Driven by several nature development projects (Ottersaat, Utopia and Wagejot), Texel became a hotspot for thousands of breeding Sandwich Terns from 2006 onwards with a maximum of 7440 bp in 2016 (Spaans *et al.*, 2018). While the numbers of pairs differed between the several potential breeding locations, here they are treated as one ‘population’ (‘Texel’). After the finalization of the nature creation project of De Putten in 2015, the first breeding Sandwich Terns settled there in 2016. From 2017 onward this became one of the most important new colonies in the Netherlands with a maximum of 3500 bp in 2019. The last large new colony settled on the newly created Waterdunen in 2021 (4850 bp), this coincided with the disappearance of the nearby Hooge Platen colony.

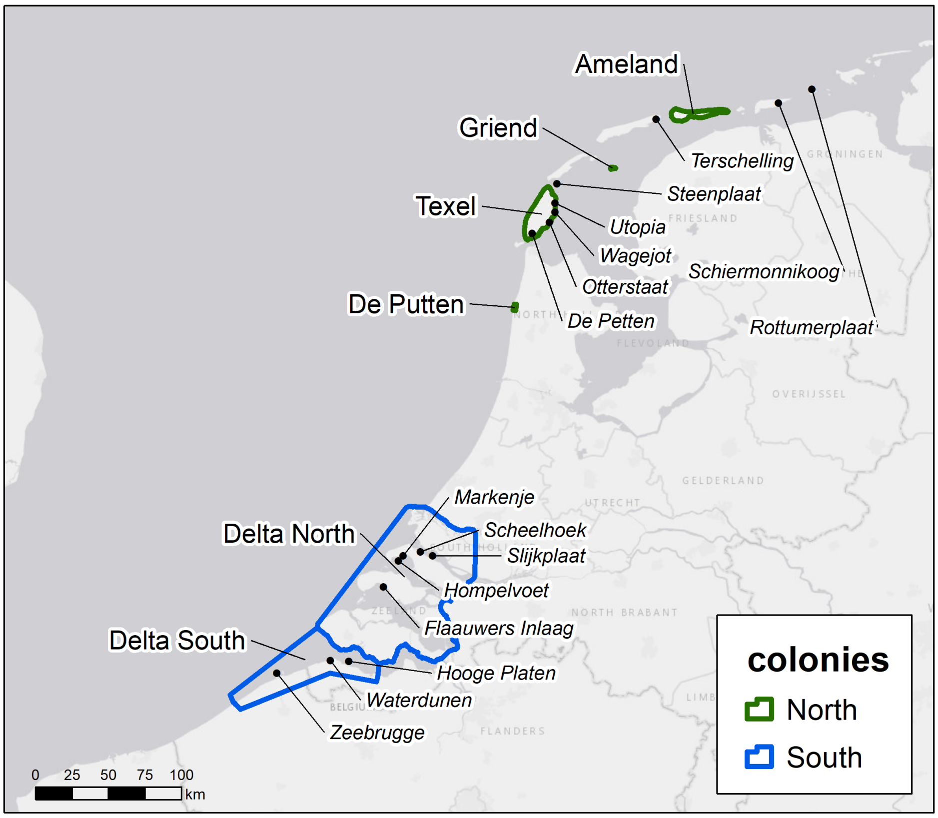

Figure 8.1 *Delineation of the S and N Netherlands with indication of the most important subareas or major colonies.*

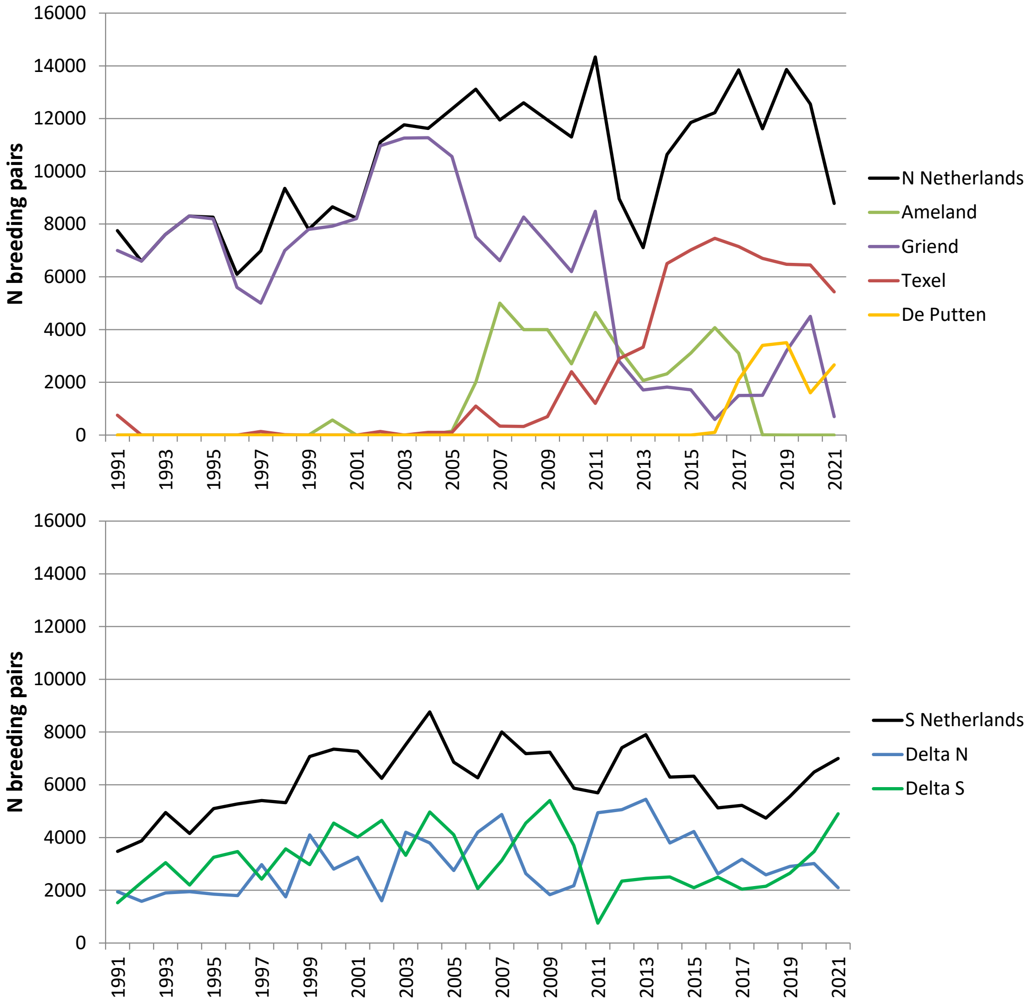

Figure 8.2 *Fluctuations in the number of breeding pairs of Sandwich Tern in the S and N Netherlands for 1991-2021 (black lines). Colored lines show the numbers in subareas or major colonies.*

8.2.2 Survival estimates

Data availability

Data from the national ringing schemes of the Netherlands (Vogeltrekstation) and Belgium (BeBirds) that used metal rings were merged with data from the various Dutch colour-ring projects (CR-birding Submit). Metal rings were applied during the whole study period (1991-2020) but with large differences between years, areas and age-classes (Figure 8.3).

Large numbers of metal rings were applied in Zeebrugge, the Haringvliet colonies and on Griend. To a lesser extent this was also the case in the Grevelingen colonies, on Texel and Ameland while almost no Sandwich Terns were ringed in the Western Scheldt colonies. In 2012 (after a small pilot project in 2010), a colour-ring project was started in the colonies in Delta N. Every year, several 100s of 1CY birds and 10s of breeding adults were fitted with a colour-ring. Several other Dutch colonies followed, with from 2014 onward colour-rings being applied to 1CY and/or adults on Texel, Griend and Ameland (Table 8.1).

Also ring-reading differed between the S and N Netherlands (Figure 8.3). In the S Netherlands, all large colonies were off-limits for amateur ring-readers as they were situated in sensitive nature reserves and not visible from public roads. Only in Zeebrugge and more recently the Haringvliet colonies, ring-reading from mobile or fixed hides placed in the colony itself was allowed. In contrary, the colonies on Texel and De Putten are visible from public roads and attract many avid ring-readers generating large numbers of resightings. Also the colony of Griend is rather well covered as the wardens invest a lot of time in looking for rings.

During migration and in especially in the wintering quarters, the number of resightings is much lower (see Figure 8.4) as the birds are much less concentrated and often occur in places less frequently visited by observers.

The final combined dataset contains all available information (date, location, age, condition of the bird etc.) on the ringing events of 1CY (mainly birds ringed as pullus in the colony) and older birds (2Y+; breeders caught on the nest and birds caught in the wintering areas and on migration) and on all subsequent 'encounters' of these birds between May 1st 1991 and April 30th 2021. An '**encounter**' can be a live resighting/recapture (further '**resighting**') or a dead recovery (further '**recovery**'). All birds colour-ringed in the same year will further be referred to as a '**cohort**'.

Table 8.1 Number of colour-ringed 1CY and adult Sandwich Terns per cohort in different colonies in the Netherlands in 2012-2021.

	1CY					Adult				
	Delta N	De Putten	Texel	Griend	Ameland	Delta N	De Putten	Texel	Griend	Ameland
2012	490					10				
2013	399					25				
2014	324		88		76	28				
2015	188		309	99	86	34				
2016	362		332	59	126	24				
2017	406		295	207		41			13	
2018	347		275	225		23		17	26	
2019	474			280			21		7	
2020	474			367		29	21	23		
2021	730					43	30			
Total	4194	0	1299	1237	288	257	72	40	46	0

Analysis
Two approaches to estimate the chance of survival for different age-classes of Sandwich Terns were followed: a modeling approach and an analysis of the colour-ring dataset.

Burnham model
In the modeling approach, survival estimates were calculated with the joint dead recoveries/live recaptures model of Burnham (1993). Contrary to the Cormack-Jolly-Seber-model (Cormack 1964, Joly 1965, Seber 1965 and 1970) or Brownie (Brownie *et al.* 1985)

models that rely on only one data type (respectively live recaptures and dead recoveries) and estimate ‘apparent survival’, the Burnham model uses both data types and estimates ‘true survival’. Combining data of different encounter types (e.g. recoveries, recaptures, telemetry, occasional resightings etc.) improves the precision of the results, allows the estimation of parameters that cannot be estimated by using only one data source/type and leads to a more ‘robust’ model (Lebreton *et al.* 1995, Cooch & White 2019).

The Burnham model only uses resightings in the study area during the breeding season (here the 1st of May-30th of July) and all recoveries (year-round and regardless of the place of recovery). Multiple resightings in the same year were resampled to one. Birds that died before July 15th in the year of ringing were omitted from the dataset to avoid including chick mortality in post-fledging mortality. The final dataset contained 63.966 ringing events, 16.985 resightings and 387 dead recoveries between May 1st 1991 and April 30th 2021.

We used the package ‘RMark’ (Laake 2013) in R (version 4.1.1; R Core Team 2021). To limit the number of combinations, the model selection was performed parameter per parameter. Model selection was based on the Akaike Informative Criterion corrected for small sample size and overdispersion (QAICc). The model with the lowest QAICc (delta >2) was considered the best-fitting model. The most extensive model was used for the other parameters and included all relevant covariates:

S(~ageCl * time)*p*(~ageCl * time + RingType * time)*r*(~ageCl * Time)*F*(~ageCl * Time)

With:

- *S* = true survival probability
- *p* = detection probability
- *r* = recovery probability
- *F* = site fidelity

And:

- ageCl = age-class (immature or adult)
- RingType = ring type (metal or colour-ring)
- time = year as a factor variable
- Time = year as a linear variable

For the S and N Netherlands, all possible models with *S*, *p*, *r* and *F* age-, time- and age-time dependent and fixed to a single value for both age-classes (~1) were run. RingType (metal/colour-ring) was expected to have a strong influence on the detection probability and was modeled as a covariate for *p*. We performed the parametric bootstrap goodness-of-fit procedure (n = 500 simulations; White & Burnham 1999). To adjust for lack of fit, the overdispersion parameter (ĉ) was calculated as the observed deviance of the global model divided by the mean deviance of 500 bootstrap simulations.

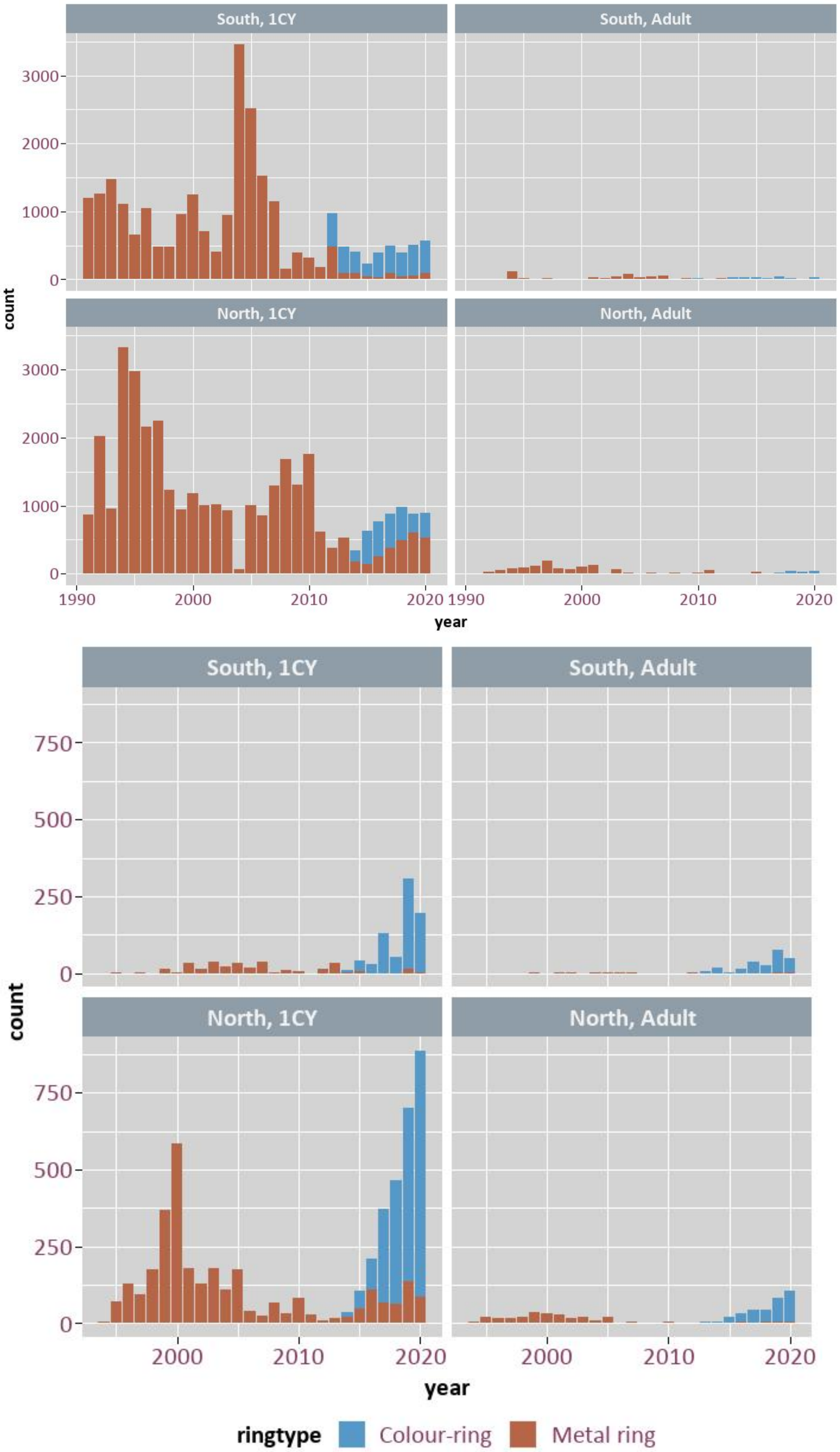

Figure 8.3 *Number of birds ringed by area, ring type and age (upper panels) and resightings thereof (lower panels) during the breeding season in the study area in 1991-2020.*

When ĉ >1, the QAICc tends to increasingly favour models with fewer parameters (Anderson *et al.* 1994, Burnham & Anderson 2002). The standard errors and 95% confidence intervals of the parameter estimates were adjusted accordingly. For parameter estimates close to the boundary (close to 0 or 1), the default confidence intervals from RMark are not always reliable. The final models were re-run with the profiling option to obtain reasonable 95% confidence intervals (given as upper and lower confidence intervals (ucl and lcl), which are not necessarily symmetrical).

Colour-ring data analysis

Given the high detection rate of colour-ringed Sandwich Terns, we used 39.451 resightings (May 1st 2012- August 30th 2021) of 7449 birds to estimate survival probability as an alternative analysis to the Burnham model. Contrary to the Burnham-modeling approach, all resightings (also those outside the study area and the breeding season) were used for this analysis. The chance that a colour-ringed Sandwich Tern is resighted is so high (especially for adults in the breeding season, Figure 8.4) that backfilling of resighting data gives reliable proxies of survival that allow age-specific analyses which could not be performed with the statistical models mentioned before.

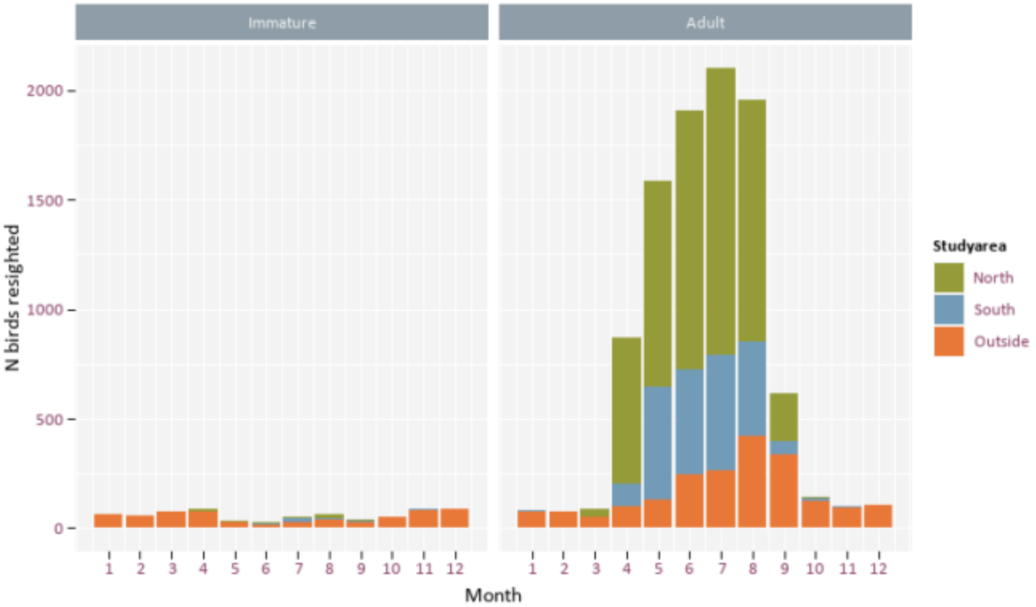

Figure 8.4 *Monthly resightings of immature (1Y and 2Y; note that this differs from the classification used in the Burnham model where 'immature' is defined as 1-3Y) and adult colour-ringed Sandwich Terns in the S and N Netherlands and outside the study area. Every resighted bird is counted only once per month. To avoid the abundant resightings of young birds immediately after fledging creating the impression that young birds frequently return to the breeding areas, resightings for birds ringed as 1CY in June-October of the year of ringing are omitted from these graphs.*

In a first step, the number of resightings was resampled to one record per year (May 1st- April 30th) for each bird: a bird was either seen alive (1) or not (0). From the last year with a resighting of an individual bird, all previous years without sightings were 'backfilled' (1), i.e. coded as being alive (Table 8.2).

Table 8.2 *Example of 'backfilling' of alive birds. Years with resightings of a bird are green, backfilled years without sightings but in which the bird was certainly alive because it was observed later, are red. 'p' is the detection probability for these particular birds (n years with observations/total years alive).*

CR-Code	RingYear	RingLocation	RingAge	2012	2013	2014	2015	2016	2017	2018	2019	2020	2021	p
B-01T	2018	Texel	1CY							1	1	1	1	0.75
B-T05	2018	Texel	Adult							1	1	1		1.00
B-N03	2012	Scheelhoek	1CY	1	1	1	1	1	1	1	1	1	1	0.80
B-N73	2012	Scheelhoek	Adult	1	1	1	1	1	1	1	1			0.38

Because the year of birth is known for all birds ringed as 1CY, **survival probability** could be calculated for the exact age of the birds (instead of using age-classes). Survival of 1Y birds could not be determined because of the very low detection probability in the winter quarters (Figure 8.4). Therefore, survival probability for the first 2 years of life (1Y and 2Y) was calculated by dividing the number of individuals known to be alive two years after ringing by the total number of colour-ringed chicks. For subsequent years of life as well as for adults ringed on the nest (expressed in years after ringing as the age of the birds was only very infrequently known), survival and **detection probability** were calculated by:

- **Survival probability** = n alive birds in year x / n alive birds in year x-1.
- **Detection probability** = n birds seen in year x / n alive birds in year x

A drawback of backfilling is that the young ages of birds ringed as 1CY are more likely to be coded alive than the older ages. Equally, adults caught on the nest are more likely to be coded alive in the years immediately after ringing than in the years towards the end of the observation period. Birds may not have been seen in recent years but may be resighted in the future and only then be backfilled in the previous years. Therefore, a **correction factor** was applied (for an example, see Table 8.3) for the S and N Netherlands, as well as for the different subareas/colonies where birds were colour-ringed (Delta N, Texel, Griend & Ameland).

Table 8.3 *Illustration of the calculation of a correction factor (CF) for the lower chance of a bird to be coded alive in years towards the end of the observation period than in the years before. First, two datasets were created: one with only the resightings up to 30/08/2020 and one with all observations until 30/08/2021. Next, survival probability (SP) was calculated for all cohorts and age-classes for both datasets. Here, birds ringed as 1CY of the 2012 and 2013 cohorts in the S Netherlands are used as an example. SP in year x-2 based on the resightings data until 30/8/2020 was respectively 105/128 = 0.820 for the cohort ringed in 2012 (corresponding with SP in their 8Y) and 162/191 = 0.848 for the 2013-cohort (SP in their 7Y). Based on the data till 30/8/2021 the SP was respectively 118/137 = 0.861 for the 2012 cohort and 186/209 = 0.890 for the 2013 cohort. For these cohorts, the difference between the SPs for year x-2 are 0.861 – 0.820 = 0.041 and 0.890 – 0.848 = 0.042. This was calculated for all cohorts and years. The mean of the difference in SP for all cohorts in year x-2 was used as a correction factor for year x-2 and is 0.029. The corrected SP of birds in their 9Y for the 2012 cohort is consequently calculated as follows: 0.788 + (0.788*0.118) + (0.788*0.029) + (0.788 * 0.016) + (0.788 * 0.06) + (0.788*0.008) + (0.788 * 0.004) = 0.932. For birds of the 2013 cohort in their 6Y, the corrected SP is 0.913 + (0.913*0.016) + (0.913*0.006) + (0.913*0.008) + (0.913*0.004) = 0.945.*

	Bird age	**n ringed**	**2Y**	**3Y**	**4Y**	**5Y**	**6Y**	**7Y**	**8Y**	**9Y**	**10Y**
2012	Year of observation		x-8	x-7	x-6	x-5	x-4	x-3	x-2	x-1	x
	N birds alive (data till 2021)	490	211	208	200	187	171	137	118	93	55
	Survival probability (data till 2021)		0.431	0.986	0.962	0.935	0.914	0.801	0.861	0.788	0.591
	N birds alive (data till 2020)	490	207	204	196	182	164	128	105	67	
	Survival probability (data till 2020)		0.422	0.986	0.961	0.929	0.901	0.780	0.820	0.638	
	Difference in survival probability			0.000	0.001	0.006	0.013	0.021	0.041	0.150	
2013	Year of observation		x-7	x-6	x-5	x-4	x-3	x-2	x-1	x	
	N birds alive (data till 2021)	399	253	250	241	229	209	186	157	113	
	Survival probability (data till 2021)		0.634	0.988	0.964	0.950	0.913	0.890	0.844	0.720	
	N birds alive (data till 2020)	399	249	244	231	218	191	162	112		
	Survival probability (data till 2020)		0.624	0.980	0.947	0.944	0.876	0.848	0.691		
	Difference in survival probability			0.008	0.017	0.006	0.037	0.042	0.153		
	Year of observation			x-6	x-5	x-4	x-4	x-3	x-2	x-1	
	Correction factor			0.000	0.004	0.008	0.006	0.016	0.029	0.118	
	Corrected survival probability 2012		0.431	0.986	0.966	0.947	0.931	0.829	0.916	0.932	
	Corrected survival probability 2013		0.634	0.993	0.976	0.968	0.945	0.947	0.998		

8.2.3 Dispersal and composition of colonies by origin of birds

Data availability

Dispersal between the S and N part of the Netherlands and colony composition according to the origin of the birds was assessed based on data of colour-ringed individuals only. In a first step, **Probable Breeding Locations (PBL)** were assigned to colour-ringed individuals encountered in 2017-2021. When possible (i.e. where the 'Behaviour' and/or 'BreedingCode' was noted in the field) observations were recoded into the following categories of **Breeding Probability (BP):**

- 'Certain' (e.g. ringed adult with chicks in the nest or ringed adult caught on the nest)
- 'Probable' (e.g. probable nest location)
- 'Possible' (e.g. courtship, pair in possible breeding habitat).

For the majority of birds BP was lacking and the PBL was based on the resightings during the breeding season. Records before May 21st were not taken into account to avoid assigning prospecting birds to a breeding location. Also sightings after July 7th were not used because many birds with chicks have left the colony by then and are seen in locations where they did not actually breed. Although breeding in their 3Y is possible, only birds older that 3Y were assigned to a PBL to minimize the chance of young prospectors being assigned as breeders. When all resightings were made in the same area or colony in a particular year, the PBL was allocated to that area or colony for that year and with BP 'Possible'. When birds were resighted in more than one colony within one breeding season, the one with the most resightings was allocated as the PBL. Breeders which failed a nest early in the season and were seen multiple times in another area or colony later in the season were assigned to the effective breeding location based on the BP. The resulting database held a total of 2136 PBLs of birds ringed as 1CY and 715 of adults caught on the nest (Table 8.4). When breeding, birds ringed as 1CY are referred to as '**young adults**' and adults caught on the nest as '**older adults**'.

Table 8.4 *The left part of the table gives the number of Probable Breeding Locations per age-class for each year (2017-2021) with percentage of the total number of alive birds. For adults the percentage presents the fraction of birds ringed in previous years for which the PBL is known (thus excluding birds caught on the nest in the same year for which the PBL is evidently also known). The right part of the table gives the amount of birds for which 1 to 5 PBL's are known in 2017-2021.*

Year	1CY	adult	n PBL	1CY	adult
2017	240 (18 %)	105 (47 %)	1	657	180
2018	263 (18 %)	118 (36 %)	2	273	92
2019	512 (29 %)	147 (62 %)	3	152	62
2020	537 (30 %)	163 (46 %)	4	90	30
2021	584 (34 %)	182 (44 %)	5	29	9

Analysis

Multi-state model

Multi-state models are generalizations of the CJS-model, which allow for the movement of animals between states. Because we were interested in the probability of birds switching between breeding areas, the states were derived from the PBLs (cf. section before). They were resampled to **Probable Breeding Areas (PBAs)**, being S Netherlands (S), N Netherlands (N) and Outside (O). This was done to reduce the number of model parameters. In multi-state modeling, comparable to conventional capture-recapture models, each animal is represented by an individual capture history indicating whether or not it was encountered at each occasion (e.g. a series of 0s and 1s for CJS studies). In this multi-state model, however, the generic 1 used to designate a capture/resighting was replaced by the PBA in which the bird was encountered. For example, the multi-state capture history 'SN0N' describes a Sandwich Tern that was noted as a breeding bird in year 1 in the S Netherlands, was breeding in the N Netherlands in year 2, was not noted in year 3 and was last seen breeding in the N Netherlands in year 4. Each individual life-history starts when the bird was ringed in a colony.

Multi-state models typically estimate three parameters: S (survival probability), p (detection probability) and ψ (Psi, a 'movement parameter'). Psi estimates the transition probability between pairs of sites (here PBAs), allowing to calculate the fidelity of individuals from different colonies to their dispersal area. Survival was modelled separately for two age-classes: immature birds (1-3Y) and adults. Detection probability was made age-class- and area-dependent.

The most parameterized model was:
S(~ageCl * time)p(~ageCl * time * PBA) ψ (~ageCl * PBA)

Colour-ring data analysis

Based on the dataset, the composition of the breeding population according to colony of origin and age-class of the birds was determined for the S and N Netherlands and for birds that bred outside the study area for 2019-2021 (only from 2019 onward there are resightings of colour-ringed adults from multiple colonies available). This was also done for the most important colonies (Delta S and N, De Putten, Texel, Griend and Ameland). The colony of origin is considered as the place of birth for birds ringed as 1CY or the colony where an adult bird was originally caught on the nest. For each year, the number of birds per area or colony of origin was weighted for the total number of alive birds from that area or colony (Table 8.5). The number of alive birds for a cohort in a particular year was derived by applying the corrected survival estimates (see paragraph on the analysis of survival estimates). The mean of the values for the 3 years per age-class expresses the '**origin composition**' of the colonies.

Table 8.5 *Illustration of the method to calculate the composition of colonies according to the origin (colony of birth or previous breeding site) of the birds. The number of birds resighted was weighted by the total number of alive birds per year. 92 Sandwich Terns from Delta N had their Probable Breeding Location in De Putten in 2021. A total of 893 colour-ringed birds of all cohorts was alive in 2021, the weighted number seen in De Putten is consequently 92/893 = 0.10. The percentage of young adults that were born in Delta N and were presumed to be breeding in De Putten in 2021 was: (0.10/(0.10+0.24+0.13+0.15) * 100) = 16.7 %.*

2021		Colony of origin											
		N birds resighted				N birds weighted for n birds alive				Composition by colony of origin			
		Delta N	**Texel**	**Griend**	**Ameland**	**Delta N**	**Texel**	**Griend**	**Ameland**	**Delta N**	**Texel**	**Griend**	**Ameland**
Probable Breeding Location PBL)	Delta S	38	11		3	0.04	0.02	0.00	0.04	40.4	20.6	0.0	39.0
	Delta N	75	4		2	0.08	0.01	0.00	0.03	70.4	6.6	0.0	23.0
	De Putten	92	120	28	11	0.10	0.24	0.13	0.15	16.7	38.5	20.4	24.4
	Texel	36	89	24	4	0.04	0.18	0.11	0.05	10.6	46.5	28.4	14.5
	Griend			2		0.00	0.00	0.01	0.00	0.0	0.0	100.0	0.0
	Ameland					0.00	0.00	0.00	0.00				
	Outside	16	19	6	4	0.02	0.04	0.03	0.05	13.1	27.4	19.6	39.9
	N birds alive	893	506	223	73								

The observed net flux of birds between the S and N Netherlands and the chance of migration was derived as follows:

- **Observed migration** = n birds observed in other area / total n birds
- **Net flux of birds** = observed migration S to N Netherlands - observed migration N to S Netherlands
- **Probability of migration** = observed migration S to N Netherlands / observed migration N to S Netherlands

'True migration' was also calculated from 'observed migration' by taking into account the detection probability in the S and N Netherlands. Detection probability for both areas was derived from the *p*-values per year estimated by the Burnham model (see Figure 8.6). All numbers of birds per area were corrected for the total number of birds ringed in that area and alive at that moment.

8.3 Results: Survival estimates

8.3.1 Burnham model

Due to the very low number of resightings of Sandwich Terns in their 1Y and 2Y (and to a lesser extent 3Y) in the study area during the breeding season (Figure 8.4, Figure 8.9), a survival analysis with three age-classes (1Y, subadult (2-3Y) and adult (3Y+)) or two age-classes (1-2Y and 2Y+) failed to distinguish the survival of 1Y or 1-2Y old birds from that of older birds. Therefore, further analysis was limited to two age-classes: immature (1-3Y) and adult (3Y+). Also, fixing F and/or r to a single value for both age-classes did not produce sensible results. Models with these combinations were therefore omitted. Model selection was performed for time-independent S (one estimate for the whole period, 1991-2020) and for annual estimates of S. The results of a selection of the most parsimonious and/or illustrative models for S and N Netherlands are shown in Table 8.6 (note: the meaning of the abbreviations used below and further in this report can be found in the method section of this chapter and in the header of this table).

The best models were:

- S Netherlands – whole period: S(~ageCl)p(~ageCl * time + RingType * Time)r(~ageCl)F(~ageCl)
- S Netherlands – annual: S(~ageCl*time)p(~ageCl * time + RingType * Time)r(~ageCl)F(~ageCl)
- N Netherlands – whole period: S(~ageCl)p(~ageCl * time + RingType * Time)r(~ageCl*Time)F(~ageCl*Time)
- N Netherlands – annual: S(~ageCl*time)p(~ageCl * time + RingType * Time)r(~ageCl*Time)F(~ageCl*Time)

According to the models above, immature and adult survival of Sandwich Terns for the period 1991-2020 were respectively 0.65 ± 0.01 and 0.92 ± 0.02 for the S Netherlands and 0.70 ± 0.01 and 0.91 ± 0.01 for the N Netherlands (Figure 8.5 and Table 8.7). Figure 8.6 shows the annual estimates for the detection probability *p* for metal and colour-rings in both parts of the study area and both age-classes.

When running models for shorter time periods a strong confounding effect between the *S*, *r* and *F* parameter occurred. This resulted in unusable estimates for *S* of one or both age-classes. Therefore *F* and *r* were fixed to the values obtained by the model for the whole period (*S*(~ageCl)). The survival estimates for the whole period, per decade and per 5-year period, are presented in Figure 8.5 and Table 8.7.

Table 8.6 *Burnham models for Sandwich Tern in the S (upper table) and the N Netherlands (lower table) for estimation of true survival (S), encounter probability (p), recovery probability (r) and site fidelity (F). 'ageCl' – ageclass (immature and adult); RingType = ring type (metal or colour-ring); 'time' – year as a factor variable; 'Time' – year as a linear variable; '~1' – parameter fixed to one value for both age-classes. npar – number of parameters; QAICc – quasi-likelihood adjusted AICc (sample-size corrected AIC); QDeviance – adjusted deviance. The models highlighted in green are the models that were used to calculate the survival estimates.*

S	p	r	F	n parameters	QAICc	Qdeviance
~ageCl	~ageCl * time + RingType * Time	~ageCl	~ageCl	67	5046	657
~ageCl * time	~ageCl * time + RingType * Time	~ageCl	~ageCl	125	5104	598
~ageCl * time	~ageCl * time + RingType * Time	~ageCl	~ageCl * Time	127	5106	596
~ageCl * time	~ageCl * time + RingType * Time	~ageCl * Time	~ageCl * Time	129	5106	592
~ageCl * time	~ageCl * time + RingType * Time	~ageCl * Time	~ageCl * Time	129	5106	592
~ageCl * time	~ageCl * time + RingType * Time	~ageCl * Time	~ageCl * Time	129	5106	592
~ageCl * time	~ageCl * time + RingType * Time	~ageCl * Time	~ageCl	127	5107	597
~ageCl * time	~ageCl * Time + RingType * time	~ageCl * Time	~ageCl * Time	129	5132	617
~ageCl * time	~ageCl * time + RingType * time	~ageCl	~ageCl	151	5141	583
~ageCl * time	~ageCl * time + RingType * time	~ageCl	~ageCl * Time	153	5144	581
~ageCl * time	~ageCl * time + RingType * time	~ageCl * Time	~ageCl * Time	155	5144	577
~ageCl * time	~ageCl * time + RingType * time	~ageCl * Time	~ageCl * Time	155	5144	577
~ageCl * time	~ageCl * time + RingType * time	~ageCl * Time	~ageCl	153	5146	584
~ageCl * time	~ageCl * Time + RingType * Time	~ageCl * Time	~ageCl * Time	74	5230	826
~ageCl * time	~ageCl * Time + RingType	~ageCl * Time	~ageCl * Time	73	5292	891
~ageCl * time	~ageCl * time + RingType * time	~ageCl * time	~ageCl * time	263	5310	523
~ageCl * time	~ageCl * time	~ageCl * Time	~ageCl * Time	126	5396	888
~ageCl * time	~ageCl + Time	~ageCl * Time	~ageCl * Time	71	5682	1285
~ageCl * time	~ageCl * Time	~ageCl * Time	~ageCl * Time	72	5683	1283
~ageCl * time	~ageCl	~ageCl * Time	~ageCl * Time	70	6051	1656
~ageCl * time	~1	~ageCl * Time	~ageCl * Time	69	6566	2173

S	p	r	F	n parameters	QAICc	QDeviance
~ageCl * time	~ageCl * time + RingType * Time	~ageCl * Time	~ageCl * Time	129	17161	1568
~ageCl * time	~ageCl * time + RingType * time	~ageCl * Time	~ageCl * Time	155	17196	1550
~ageCl	~ageCl * time + RingType * Time	~ageCl * Time	~ageCl * Time	71	17197	1721
~ageCl * time	~ageCl * time + RingType * Time	~ageCl	~ageCl * Time	127	17245	1656
~ageCl * time	~ageCl * time + RingType * Time	~ageCl + Time	~ageCl * Time	128	17273	1682
~ageCl * time	~ageCl * time + RingType * time	~ageCl	~ageCl	151	17273	1635
~ageCl * time	~ageCl * time + RingType * Time	~ageCl	~ageCl	125	17375	1790
~ageCl * time	~ageCl * time	~ageCl * Time	~ageCl * Time	126	17444	1857
~ageCl * time	~ageCl * time + RingType * Time	~ageCl	~ageCl * Time	127	17508	1919
~ageCl * time	~ageCl * time + RingType	~ageCl * Time	~ageCl * Time	73	17932	2452
~ageCl * time	~ageCl	~ageCl * Time	~ageCl * Time	70	19374	3899
~ageCl * time	~1	~ageCl * Time	~ageCl * Time	69	20539	5066

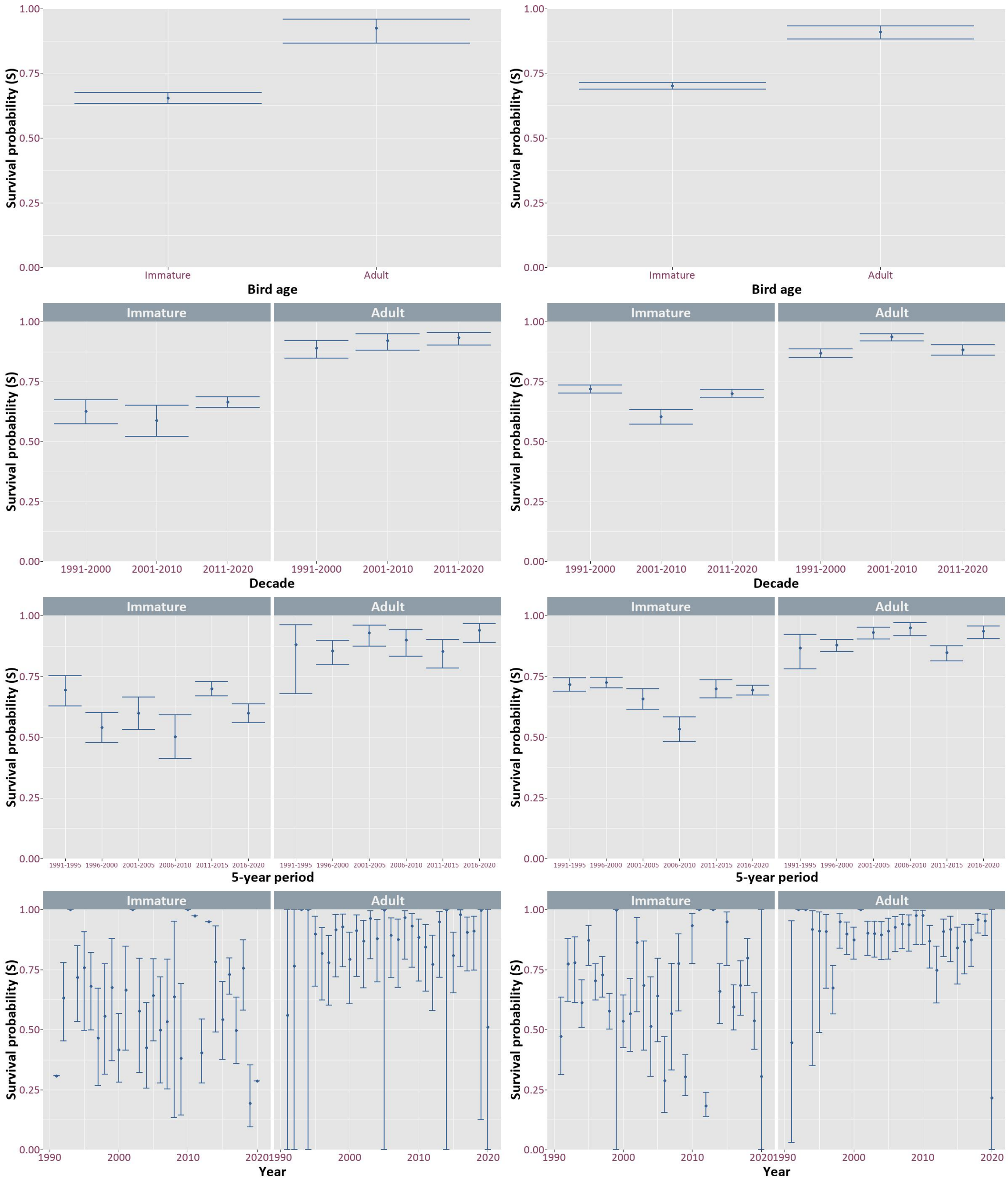

Figure 8.5 *Estimates of true survival probability (S) and 95% confidence intervals for immature and adult Sandwich Terns in the S (left panels) and N Netherlands (right panels) for the whole period (1991-2020), per decade, per 5-year period and per year.*

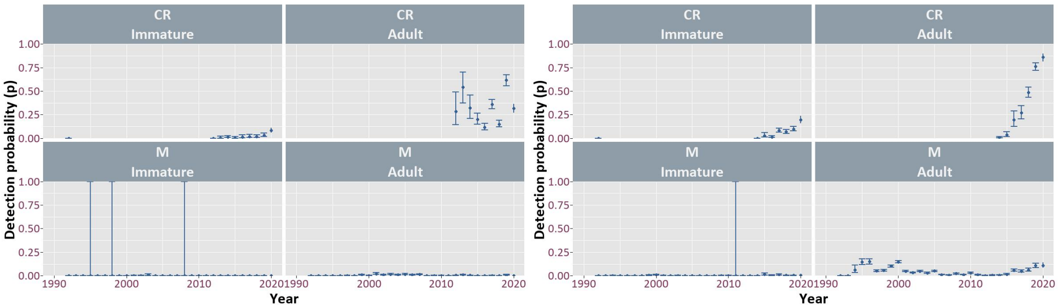

Figure 8.6 *Estimates of detection probability (p) and 95% confidence intervals for immature and adult Sandwich Terns with metal and colour-rings in the S (left panels) and N Netherlands (right panels).*

Table 8.7 *Estimates of true survival (S) and 95% confidence intervals (lower and upper confidence interval, lcl and ucl) for immature and adult Sandwich Terns in the S and N Netherlands.*

		S Netherlands			N Netherlands		
	Age class	**estimate**	**lcl**	**ucl**	**estimate**	**lcl**	**ucl**
Whole period							
1991-2020	Immature	0.65	0.63	0.68	0.70	0.69	0.71
1991-2020	Adult	0.92	0.91	0.94	0.91	0.88	0.93
Decade							
1991-2000	Immature	0.63	0.57	0.68	0.72	0.70	0.74
2001-2010	Immature	0.59	0.52	0.65	0.60	0.57	0.63
2011-2020	Immature	0.67	0.64	0.69	0.70	0.68	0.72
1991-2000	Adult	0.89	0.85	0.92	0.87	0.85	0.89
2001-2010	Adult	0.92	0.88	0.95	0.94	0.92	0.95
2011-2020	Adult	0.93	0.90	0.96	0.88	0.86	0.90
5-year period							
1991-1995	Immature	0.69	0.63	0.75	0.72	0.69	0.74
1996-2000	Immature	0.54	0.48	0.60	0.73	0.70	0.75
2001-2005	Immature	0.60	0.53	0.66	0.66	0.62	0.70
2006-2010	Immature	0.50	0.41	0.59	0.53	0.48	0.58
2011-2015	Immature	0.70	0.67	0.73	0.70	0.66	0.74
2016-2020	Immature	0.60	0.56	0.64	0.69	0.67	0.71
1991-1995	Adult	0.88	0.68	0.96	0.87	0.78	0.92
1996-2000	Adult	0.86	0.80	0.90	0.88	0.85	0.90
2001-2005	Adult	0.93	0.87	0.96	0.93	0.90	0.95
2006-2010	Adult	0.90	0.83	0.94	0.95	0.92	0.97
2011-2015	Adult	0.85	0.78	0.90	0.85	0.81	0.88
2016-2020	Adult	0.94	0.89	0.97	0.94	0.91	0.96

8.3.2 Colour-ring data

Survival probabilities for birds colour-ringed as 1CY and as breeding adults caught on the nest in the S and N Netherlands based on the colour-ring dataset (thus using the back-filling method) are presented in Figure 8.7 and

Table 8.8. Survival of birds ringed as 1CY shows a comparable pattern in both S and N Netherlands. A mean of 41-43% of the birds survived their first 2 years of life, which equals to a survival rate of about 0.65 per year. From their 3Y onward, survival surges up to about 0.98 after which a slow, annual decrease to around 0.90 in their 7Y occurs. As for every year of age fewer and fewer years with data are available, the uncertainty of the survival estimate is higher for older ages. Birds ringed as adults do not show a clear pattern in annual survival probability (between 0.88 and 0.97). The survival probability of young adults (birds ringed as 1CY and between 4Y and 7Y old) is apparently somewhat higher than for older adults. The mean of all survival probabilities (for all cohorts and all ages) for young adults in the S and N Netherlands is 0.94 ± 0.04. For older adults this is respectively 0.91 ± 0.06 and 0.92 ± 0.10.

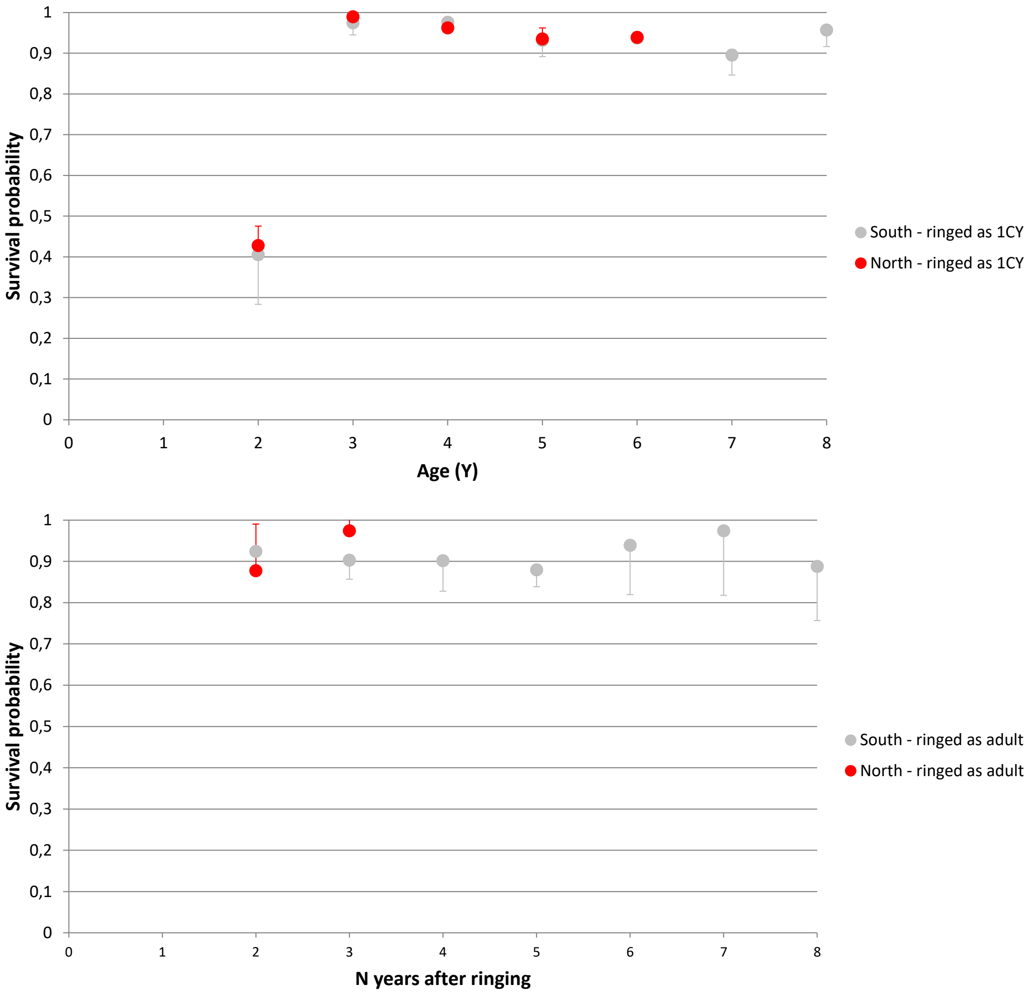

Figure 8.7 *Survival probability (± SD) for birds ringed as 1CY (age in years; left panel) and as adult (in N years after ringing; right panel) in the S and N Netherlands as derived from the colour-ring dataset. For birds ringed as 1CY, the survival probability is calculated for 1 and 2Y together.*

Table 8.8 *Survival probability (± SD) for birds ringed as 1CY (age in years) and as adult (in n years after ringing, YaR) in the S and N Netherlands as derived from the colour-ring dataset. For birds ringed as 1CY, the survival probability is calculated for 1 and 2Y together.*

1CY			**Adult**		
Age (Y)	South	North	YaR	South	North
1Y			0		
2Y	0.41 ± 0.12	0.43 ± 0.05	1	0.92 ± 0.05	0.88 ± 0.11
3Y	0.98 ± 0.03	0.99 ± 0.02	2	0.90 ± 0.05	0.97 ± 0.05
4Y	0.98 ± 0.02	0.96 ± 0.03	3	0.90 ± 0.07	
5Y	0.93 ± 0.04	0.94 ± 0.03	4	0.88 ± 0.04	
6Y	0.94 ± 0.10	0.93 ± 0.01	5	0.94 ± 0.12	
7Y	0.90 ± 0.05		6	0.97 ± 0.16	
8Y	0.96 ± 0.04		7	0.89 ± 0.13	

Age-specific survival shows very comparable patterns for the different colonies, with a mean probability of 0.34-0.46 to survive the first two years, very high survival in their 3 and 4Y and a slight annual decrease in survival probability afterwards (Figure 8.8).

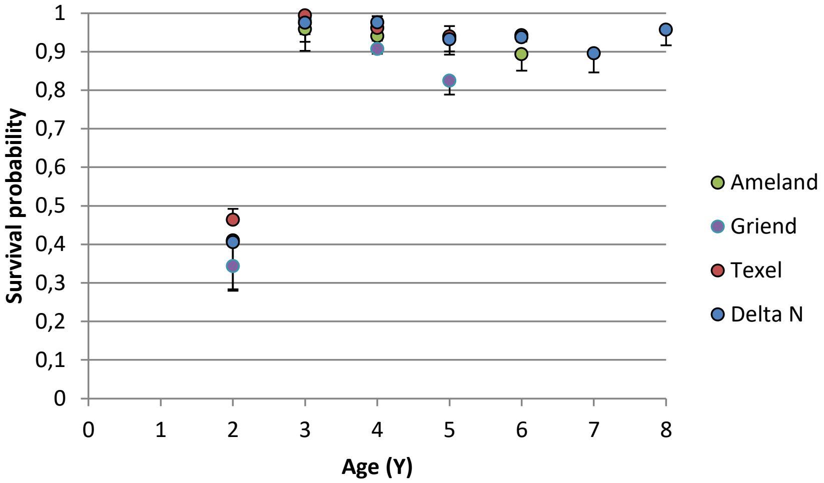

Figure 8.8 *Survival probability (± SD) for birds ringed as 1CY (age in years) in the northern part of the Dutch Delta area, on Texel, Griend and Ameland as derived from the colour-ring dataset.*

The detection probability of birds ringed as 1CY shows a notable increase during the study period (Figure 8.9). Where only 24% of the alive birds of the 2012 cohort were effectively seen in their 3Y, this was 72% for the 2018 cohort. The same pattern is visible for the other ages. Also, an increase in detection probability especially between 2Y and 4Y can be seen.

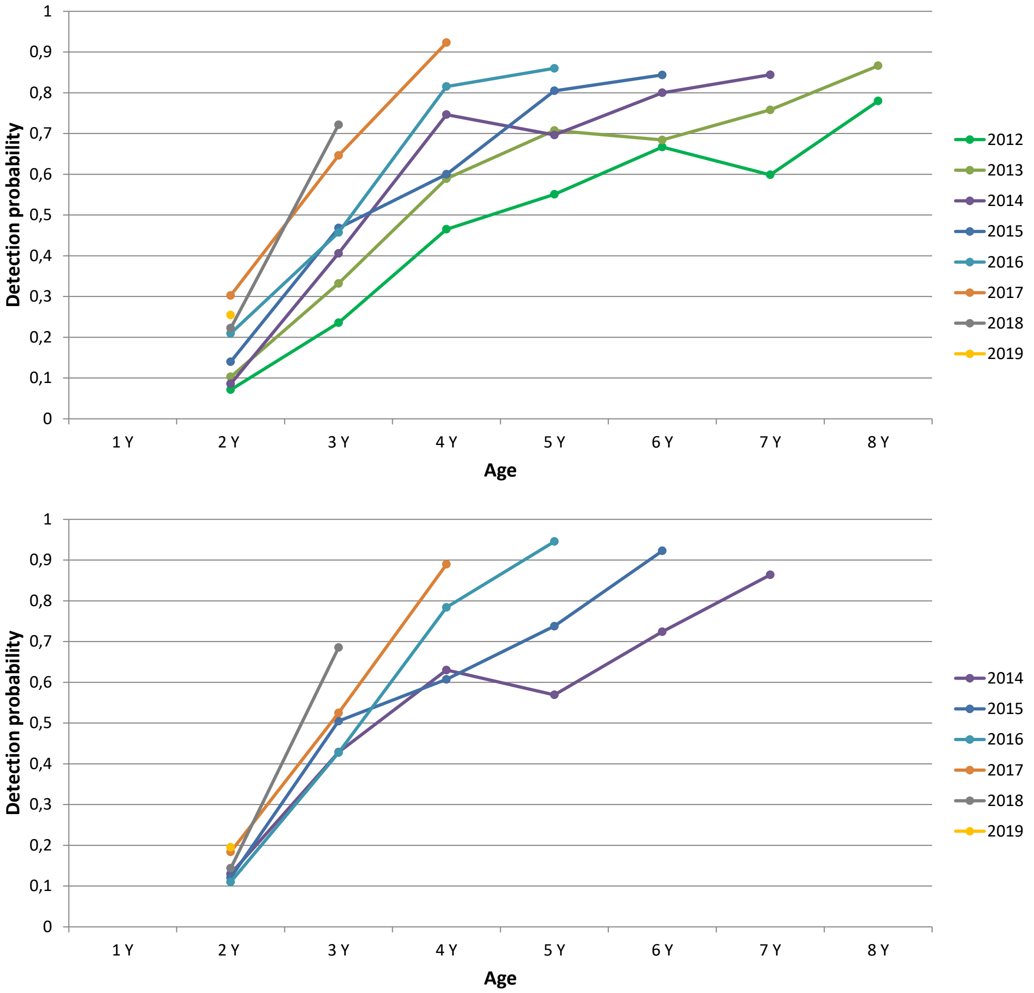

Figure 8.9 *Detection probability per cohort and bird age for Sandwich Terns ringed as 1CY in the S (left panel) and N Netherlands (right panel).*

8.4 Results: Dispersal

8.4.1 Multi-state analysis

A multi-state analysis was conducted but unfortunately the time series available proved too short to produce reliable results. In order to derive figures on the exchange of individuals between areas or colonies we therefore had to fall back on a more conventional method, of which the results are shown in the next paragraphs.

8.4.2 Colour-ring analysis

Composition of colonies by origin of birds

Between 2019 and 2021, the origin of the resighted birds in the breeding colonies in the S Netherlands was markedly different from the N Netherlands and from the composition outside the study area (Figure 8.10). 89% of the resightings in the southern colonies referred to birds that were born there (27% of all resighted birds) or had been caught on the nest as a breeding adult (62%) in one of the southern colonies in earlier years. This pattern was markedly different in the northern colonies, where only 72% originated from a colony in the north (36% young adults and 36% older adults). Sandwich Terns found in colonies outside the study area were 72% young adults (26% from the S and 46% from the N) and 28% older adults (7% from the S and 21% with a northern origin).

Of all young and older adults seen in the southern colonies, respectively 84 and 91% was actually born or had been breeding there previously. In the northern colonies this was respectively 69 and 73%.

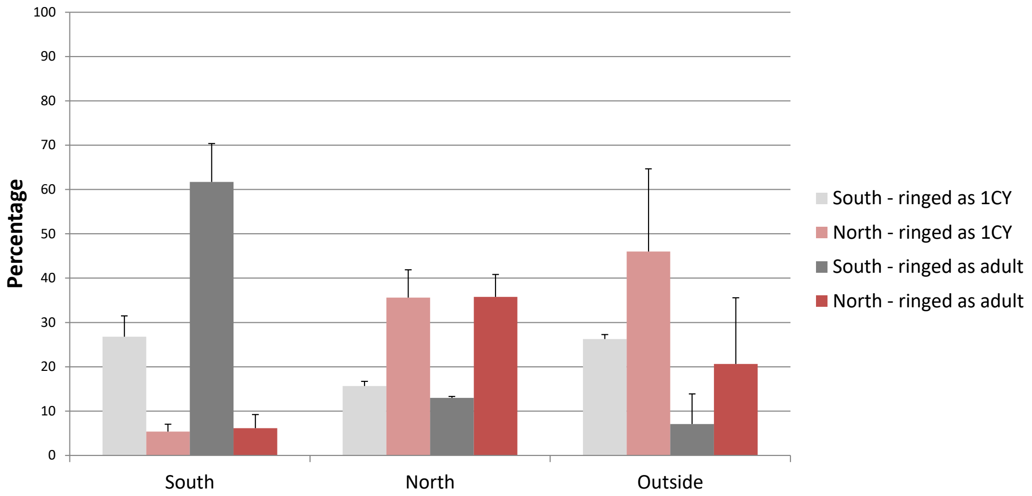

Figure 8.10 *Composition of the of Sandwich Tern breeding population in the S and N Netherlands and outside of the study area (2019-2021) according to origin and age-class. The bars present the mean percentage for the 3 years ± SD. Note that in each year and each category the number of recoveries were weighted for the number of assumed alive birds (see 2.2.2).*

Figure 8.11 shows the composition according to origin and age-class of four Sandwich Terns colonies in 2019-2021. Both the colonies in Delta N and on Griend stand out due to their very high proportion (>88%) of ‘own’ birds, both ringed as 1CY and as breeding adult. In contrary, the more recently settled colonies on Texel and De Putten are characterized by a mixture of own birds and birds from other colonies. The proportion of birds that settled in a new breeding location strongly decreased with the distance from the colony of origin, both for young and older adults (Figure 8.12).

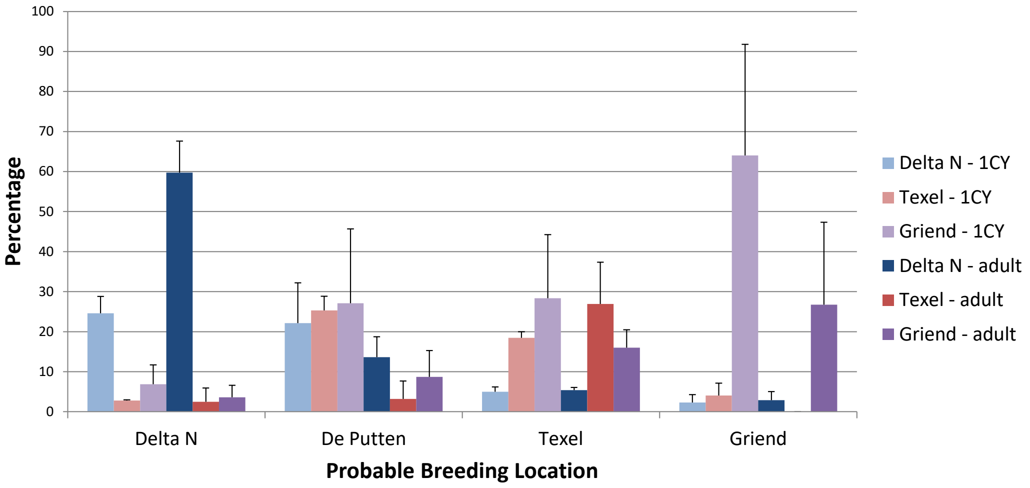

Figure 8.11 *Origin and age-class of Sandwich Terns breeding in 4 large Dutch colonies in 2019-2021. The bars present the mean percentage for the whole period ± SD.*

Net flux between S and N Netherlands

The analysis above clearly shows that the degree of dispersal is rather high. However, because of differences in detection probability between colonies, the exact degree of exchange is not obvious. Based on the number of birds from the S Netherlands effectively seen (and probably breeding) in the N Netherlands and vice versa in the period 2019-2021 (weighted for the expected number of alive birds), there was an observed mean net flux of respectively 17.8 and 15.5% of young and older adults from S to N (Table 8.9, Figure 8.13). Corrected for the differences in detection probability (obtained from the Burnham model, see Figure 8.6), the effective mean net flux was somewhat higher and amounted respectively 20.3 and 16.4%.

Next, these figures can be translated to a probability that a bird migrates from a southern to a northern colony and vice versa. The effective chance (i.e. corrected for differences in resighting probability) of a young adult migrating from S to N was 7.6 times higher than vice versa, for older adults this was 4.9 times higher.

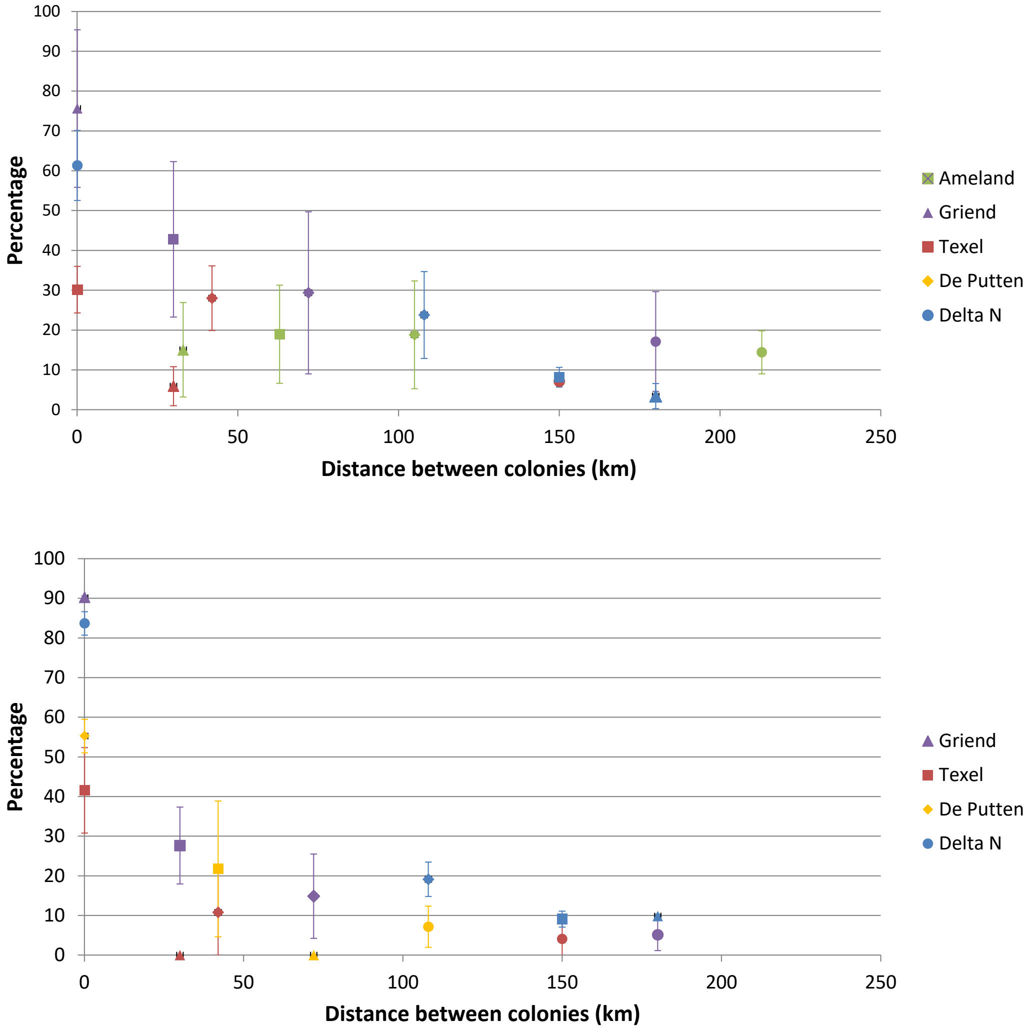

Figure 8.12 *Origin of young (left panel) and older adult (right panel) Sandwich Terns in 4 large Dutch colonies (Delta N, De Putten, Texel and Griend) in 2019-2021 in function of distance between the colonies. No colony was present on Ameland in this period but birds from this colony settled in other locations. Colony of origin is given by the colour, breeding colony is given by the symbol. For example, 69 % of the young adults breeding in Delta N were born there while 7 % was born on Griend (180 km away). Equally, 29 % of the young adults breeding in De Putten were born in Delta N (108 km away) while 36 % was born on Texel (42 km away).*

Table 8.9 *Dispersal of Sandwich Terns ringed as 1CY and adult from the S to N Netherlands and vice versa based on observations in the field (observed migration) and corrected for differences in detection probability between the two areas (corrected migration). The net flux from S to N is the difference in percentage birds from the S Netherlands breeding in the N and birds from the N Netherlands seen in the S. The probability of migration expresses the number of birds migrating from S to N for every bird migrating from N to S. Only in 2021 it was possible to read rings in the Western Scheldt colony, for reasons of comparability the birds observed in Delta S are not included here.*

		Observed migration			Corrected migration			Mean observed	Mean corrected
Age-class		2019	2020	2021	2019	2020	2021	2019-2021	2019-2021
1CY	S to N	22.1	24.7	13.6	27.4	28.1	15.5	20.1	19.0
1CY	N to S	3.9	1.7	1.2	5.4	2.9	2.0	2.3	3.4
Adult	S to N	17.7	19.4	16.5	22.0	22.0	18.9	17.9	20.9
Adult	N to S	3.9	1.4	1.9	5.4	5.4	2.9	2.4	4.6
1CY	Net flux S to N	18.2	22.9	12.4	22.0	25.2	13.6	17.8	20.3
Adult	Net flux S to N	13.8	17.9	14.7	16.6	16.6	15.9	15.5	16.4
1CY	Probability of migration	5.7	14.3	11.1	5.1	9.7	7.9	10.4	7.6
Adult	Probability of migration	4.5	13.7	8.8	4.1	4.1	6.5	9.0	4.9

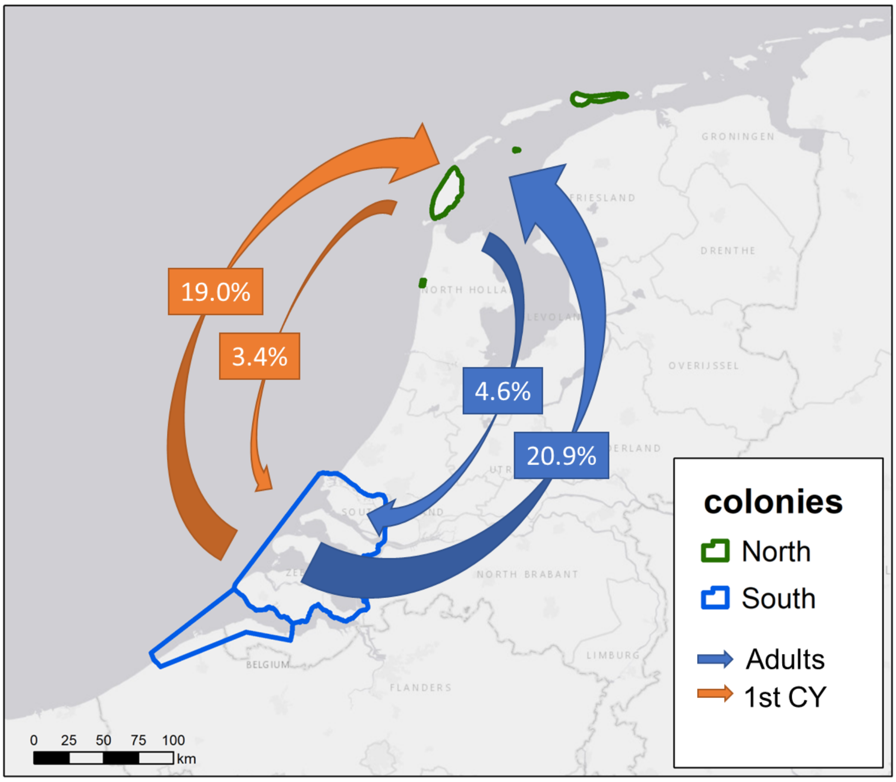

Figure 8.13 *Mean flux of young and older adults between the S and N Netherlands based on the number of birds from the S Netherlands effectively seen (and probably breeding) in the N Netherlands and vice versa in the period 2019-2021.*

While for young and older adults the net flux from the S to the N Netherlands is comparable, the probability of migration is higher for younger birds. To estimate how faithful young adults are to their natal colony and older adults to the colony where they nested before, during the breeding season of 2019, as many colour-rings of birds breeding in the Scheelhoek colony (Delta N) as possible were read from mobile hides in the colony. This permitted to calculate the return rate of each cohort of previously colour-ringed Sandwich Terns. Of the birds born on Scheelhoek, a mean of 23.5 ± 3.3% of each cohort (2012-2016) was resighted as a breeding bird there. The percentage of older adults returning to breed was significantly higher with 45.6 ± 16.9%. Taking into account a detection probability of 62% as calculated by the Burnham model (Figure 8.6), this means that 38% of the young adults and 74% of the older adults returned to the colony where they were ringed before. On Texel, a mean of 19.9 ± 3.4 % of each cohort (2014-2016) was resighted in the breeding colony in 2019. As colour-ringing of adult birds started in 2018, only adults from that cohort could be noted in the colony. 6 out of the 17 (or 35%) colour-ringed older adults from 2018 were resighted in the colony on Texel in 2019. When correcting for detection probability (76% in 2019) a return rate of respectively 26 and 46% for young and older adults can be calculated.

Multiple transitions

While the flux between areas is an estimation of the number of birds that switched between areas, it is in fact a static estimation of the number of birds of one area present in another area at a given moment. In other words, it does not give an indication if birds that move to another area remain faithful to the new area or change several times. To get a grasp of this, the number of birds that stayed faithful to one area or moved once or more to another area was calculated. Of 110 Sandwich Terns colour-ringed as 1CY (26 S and 84 N) in 2017-2018, 2 or 3 PBLs were known for the period 2019-2021. Equally, 2-4 PBLs were known of 138 adults (61 S and 77 N ringed in 2017-2020) for the period 2017-2021. Dispersal from the natal colony to the first PBL in young adults was also counted as a transition, therefore the maximum number of transitions is 3 (considered that birds in their 3Y were omitted as breeders). For older adults, the maximum number of transitions is 4.
Both young and older adults from the S Netherlands seem to be more prone to move to another area than Sandwich Terns from the N Netherlands (Figure 8.14). Only 45-56% of the S older adults did not move to another area compared to 71-90% of the N older adults. Of the young adult Sandwich Terns from the S Netherlands, 47% of the birds with two PBLs did not switch areas compared to 90% of the northern birds. When 3 PBLs were known, the difference is even more remarkable: only 11% of the southern young adults stayed loyal to the natal area compared to 80% of the northern young adults.

Also on colony level, Sandwich Terns often make multiple transitions. Of the S and N young adults only 15 and 26%, respectively, did not switch colonies while most birds did at least move to another colony once. Of the older adults, between 30 to 40% seems to be faithful to the same colony while around 30% changed almost every year.

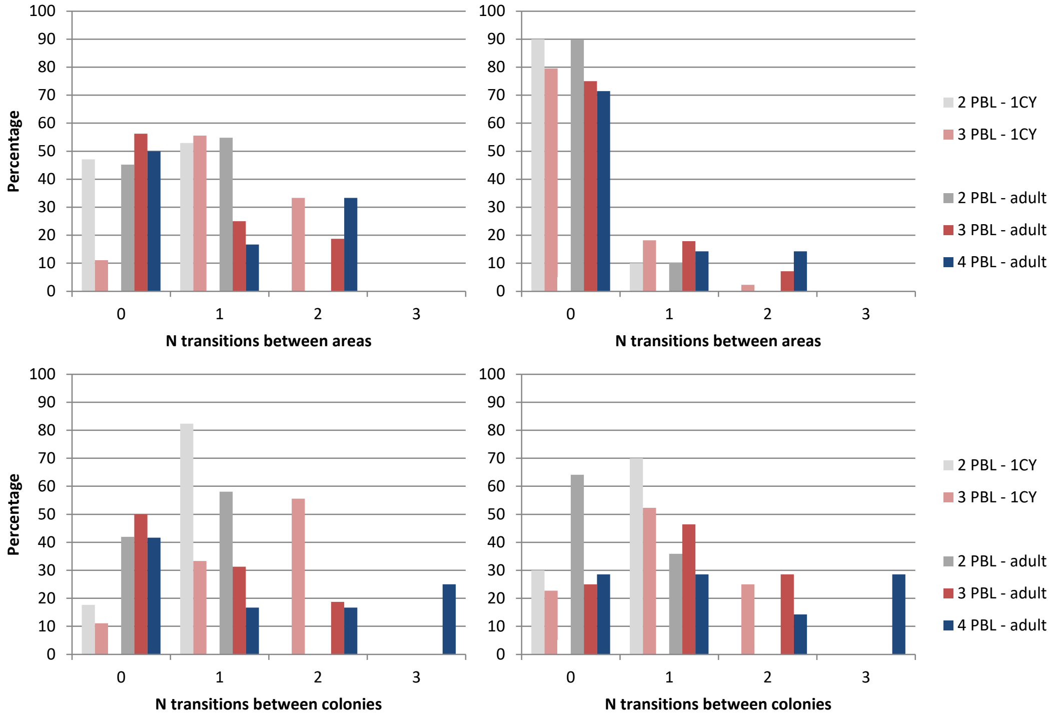

Figure 8.14 *Number of transitions between the S and N Netherlands and outside of the study area (upper panels) and between colonies (lower panels) for birds ringed as 1CY and as adult in the S (left panels) and N Netherlands (right panels).*

Patterns of colonization

Since the start of the colour-ring project, large new colonies formed in De Putten and more recently in Waterdunen. This presents us with an opportunity to analyze the origin of the Sandwich Terns colonizing these new breeding locations.

Sandwich Terns first bred in De Putten in 2016. In 2017, 119 young adults out of a total of 132 Sandwich Terns of known origin were born in Delta N. Weighted for the number of birds still alive from the different ringing locations, Sandwich Terns from Delta N accounted for 38% of the birds of known origin in the Putten (Figure 8.15). An equal proportion originated in Texel and 24% came from Ameland where the colony was flooded and predated by gulls and rats in that year. In the following years, the relative proportion of birds from the Delta N and Texel remained comparable while the proportion of birds from Ameland and Griend increased slowly. In 2021, a significant number of young adults from Griend (58% of the total of birds of known origin) had their PBL in De Putten. Unfortunately, older adult Sandwich Terns were colour-ringed a bit too late to calculate their importance in the colonization of De Putten. In 2020 and 2021, older adults from other colonies made up respectively 16 and 32% of the total of birds with known origin. Caution is advised though, as the number of older adults ringed and resighted is much smaller than the number of birds ringed as 1CY. Also, birds from other colonies where no colour-rings were applied were obviously not taken into account in the colony composition.

Even more recently, a large colony of Sandwich Terns settled in newly created breeding habitat in Waterdunen (Zeeland) in 2021. Most of these birds probably originated from the nearby colony at the Hooge Platen which was deserted in 2021, but the total number at Waterdunen was much higher than the original number at Hooge Platen. With a camera placed in the colony, 67 colour-rings of birds probably breeding (52 ringed as 1CY and 12 as adult) were read in this colony. This allowed to estimate the proportional abundance of birds of different age-classes and colonies. While the number of young adults was larger than that of birds previously caught as breeder, older adults were relatively more abundant than younger birds (58 vs 42%). Most older adults came from De Putten (where the colony was flooded in 2021) and the Delta N area, while younger birds came from Delta N (19%), the lost colony of Ameland (14%) and Texel (10%).

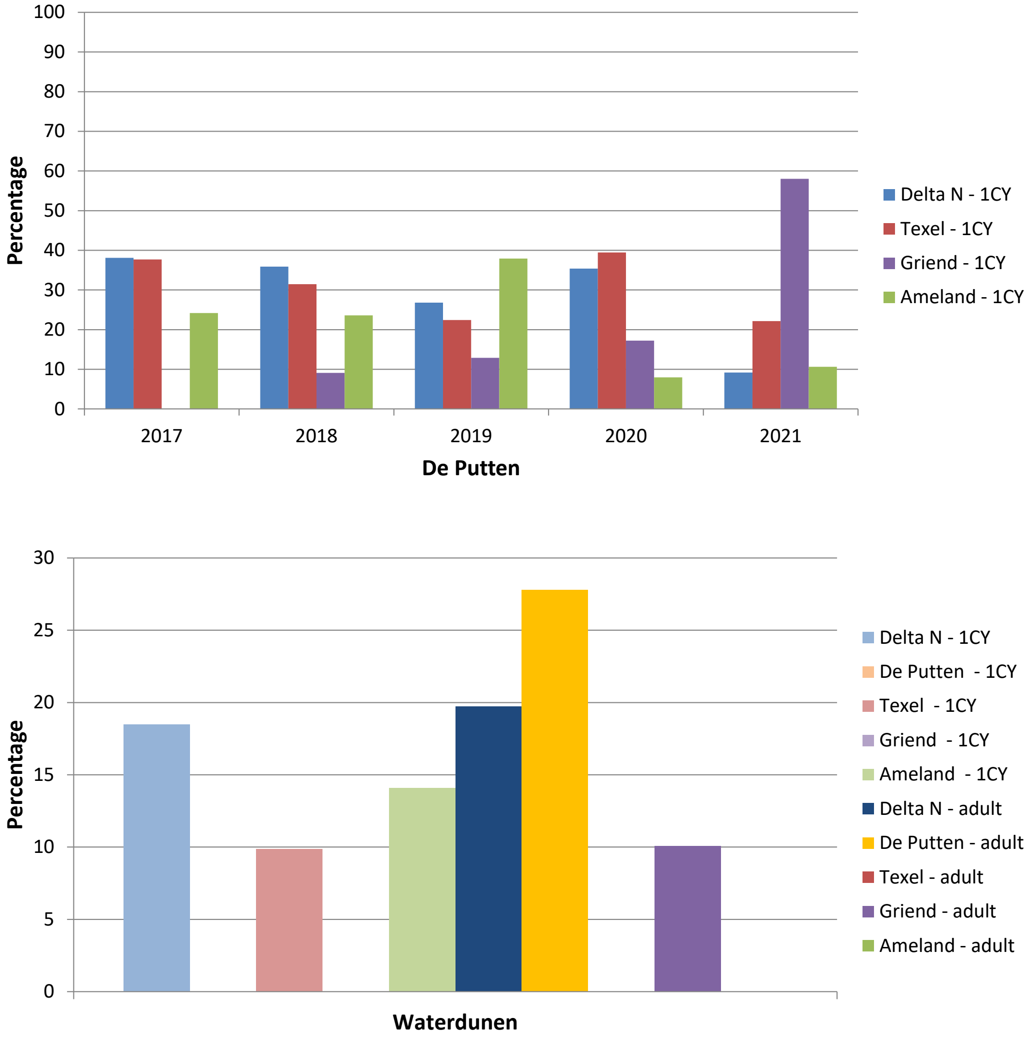

Figure 8.15 *Origin of birds breeding in De Putten in 2017-2021 (upper panel) and of the Sandwich Terns colonizing Waterdunen in 2021 (lower panel).*

8.5 Discussion

8.5.1 Survival

Previously published survival estimates for Sandwich Terns show a lot of variation (Table 10). Pre-breeding survival estimates range from 0.2 (Robinson 2010) to 0.55 (Jiménez-Muñoz *et al.* 2019). Adult survival rates were found to be less variable but still range between 0.76-0.83 (Brenninkmeijer & Stienen 1992) and 0.95 (van der Jeugd *et al.* 2014), both for a part of the Dutch Sandwich Tern population. In a later report, Brenninkmeijer & Stienen (1997) used an alternative methodology and increased sample size, leading to estimated adult survival rates of 0.90. Our estimates by the Burnham model for the whole period for the S and N Netherlands are comparable to these studies, both for pre-breeding survival (respectively 0.27 ± 0.01 (or 0.65*0.65*0.65, cf Figure 8.7) and 0.34 ± 0.01) and for adult survival (respectively 0.92 ± 0.02 and 0.91 ± 0.01). Adult survival for 5-year periods ranged between 0.85 and 0.94 for both parts of the study area.

Table 8.10 Survival estimates of immature (pre-breeding, 1-3Y) and adult Sandwich Terns. Only estimates assuming first breeding after their 3Y are reproduced or calculated.

Pre-breeding survival	Annual adult survival	Reference
0.46	0.82	Green *et al.* (1990)
0.34	0.76-0.83	Brenninkmeijer & Stienen (1992)
-	0.9	Brenninkmeijer & Stienen (1997)
0.2	0.9	Robinson (2010)
0.28	0.95	Van der Jeugd *et al.* (2014)
0.55	0.87	Jiménez-Muñoz *et al.* (2019)
0.27-0.34	0.92-0.91	**this study (Burnham model, S & N Netherlands)**
0.40 - 0.43	4-7Y: 0.94 Adult: 0.91-0.92	**this study (CR-analysis, S & N Netherlands)**

Applying a Burnham model, survival estimates could be calculated for only two age classes (1-3Y or immatures and 3Y+ or adults). Further separation of age lead to erroneous results, mainly because most of the immature birds stay in the winter areas and consequently generate almost no resightings in the breeding areas during the breeding season. Also the very low number of dead recoveries caused problems running the model. The survival rates for immatures and adults are thus not age-dependent but are given as an annual mean for all ages at a given time. Although the colour-ring dataset of Sandwich Terns is still rather limited in time, analysis of the data (without using a modeling approach) lead to valuable and somewhat different insights in the survival of the different age-classes. The most notable is the very high survival of especially 3Y (0.98-0.99) but also 4Y old birds (0.96-0.98). This leads to a pre-breeding survival estimate very different from the Burnham estimates. In the latter case, pre-breeding survival is to be calculated by multiplying the survival estimate by the number of years (here 3). For the S Netherlands between 2011 and 2020 this means 0.67*0.67*0.67 = 0.30 and for the N Netherlands 0.70*0.70*0.70 = 0.34. Based on the colour-ring analysis this is respectively 0.40 (0.41*0.98) and 0.43 (0.43*0.99). The analysis of the colour-ring data further suggests that survival in the first years of adult life (young adults) is higher (a mean of 0.94 ± 0.04 for 4-7Y old birds) than that of older adults (0.91 ± 0.06 for the S Netherlands and 0.92 ± 0.10 for the N Netherlands).

Several studies on long-lived seabirds revealed age-specific patterns in survival. Bradley *et al.* (1989) found an increase in survival of Short-tailed Shearwaters *Ardenna tenuirostris* in the first 10 years, while California Gulls *Larus californicus* studied by Pugesek *et al.* (1995) showed a slow decline in survival between 4 and 12Y (from 0.92 to 0.90). The pattern in age-related survival emerging from the analysis of the colour-ring data does not fit either of these, due to the very high survival of 3 and 4Y birds and a slow decrease afterwards, but this has been described in other taxa nonetheless (e.g. Loison *et al.* 1999). Other studies found a decrease in survival in older individuals due to senescence (Bradley *et al.* 1989, Pugesek *et al.* 1995). In this study, the difference in survival between young and older adults as derived from the colour-ring data might hint towards a decreasing survival with age in Sandwich Terns as well. Nisbet & Cam (2002) found a similar difference in survival between known-aged Common Terns *Sterna hirundo* (0.91) and birds of unknown age (0.88) and attributed this to heterogeneity in this group. While the monitoring programme might at this moment be too short to truly distinguish between age-related patterns in survival and short-term environmental variation and certainly for studying senescence patterns (Aubry *et al.* 2011), these results underline the high potential of thorough and long-lasting colour-ringing programmes to unravel such patterns in long-lived seabirds.

The importance of correctly assessing both pre-breeding and adult survival is illustrated by Figure 8.16. The difference between the estimates by the Burnham model and the analysis of the colour-ring database (annual estimates for the first 7Y as derived from birds ringed as 1CY and constant survival for older adults) leads to a difference in demographic composition. When applying the Burnham estimates, about 25% less birds recruit as breeders than expected based on the colour-ring data. This difference gradually decreases as the birds grow older due to the higher adult survival estimate from the modeling approach. Compared with other estimates from literature, especially the curve by van der Jeugd *et al.* (2014) compares well with the Burnham curve.

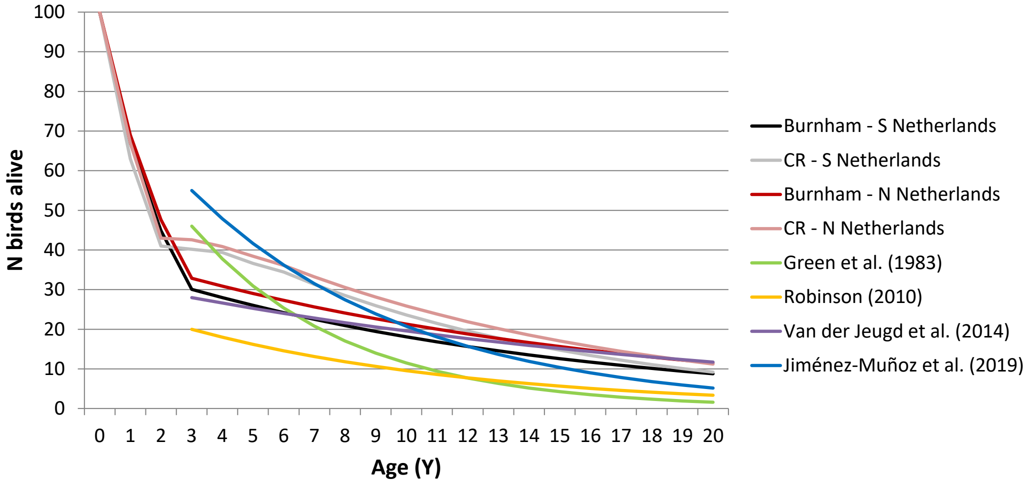

Figure 8.16 Number of Sandwich Terns alive (out of 100) per year of age according to the estimates from the Burnham model and the analysis of the colour-ring dataset. For comparison, also the numbers resulting from the estimates of Green et al. (1983), Robinson (2010), Van der Jeugd et al. (2014) and Jiménez-Muñoz et al. (2019) are given.

Some caution has to be taken though, as especially for the N Netherlands the time series for older and to a lesser extent also young adults is still short and the number of colour-ringed adults in some cohorts is rather low. Also, despite applying a correction factor for the lower chance to be coded alive by backfilling in the last years, survival in the later years is probably still an underestimation. On the other hand, the tendencies in both areas are very similar and even the patterns for the different colonies show a comparable trend. Another aspect that has to be taken into account is loss of colour-rings. While this is very hard to note (only when a bird is found dead or caught alive or if the metal ring is read in the field, this can be determined), a total of eight colour-rings have been recorded as 'lost' over the past years based on recaptures or resightings. As a consequence, the estimates should probably be regarded as minimum survival estimates as lost rings augment mortality. Using minimum survival estimates in population modeling on which impact assessments are based, is in line with the 'precautionary principle' that is one of the foundations of European nature legislation.

8.5.2 Between-colony migration

As already suggested in earlier studies, this study confirms that Sandwich Terns belong to a select group of colonial breeding (sea)birds that show rather low site fidelity and high dispersion rates. In a West-European context, Mediteranean Gull *Ichthyaetus melanocephalus* and Slender-billed Gull *Chroicocephalus genei* also show this behaviour (Zielińska *et al.* 2007, Francesiaz *et al.* 2017, Acker *et al.* 2018). This group received not much attention in survival studies, but it has become clear that for species that show low philopatry, it is particularly difficult to obtain reliable estimates of survival. While site fidelity is incorporated in the Burnham model by means of the *F*-parameter, multi-state models are the best option to quantify emi- and immigration. Most studies using multi-state modeling have one or more of the following characteristics in common: they are conducted in relatively small colonies (often with few birds emigrating), have a high detection probability, a very high percentage of birds marked and continued for a (very) long time period (e.g. Cam & Monnat 2000, Ratcliffe *et al.* 2008, Gaulthier *et al.* 2009, Szostek & Becker 2012, Acker *et al.* 2018). Except for the high detection probability of colour-rings, Sandwich Terns show none of these characteristics. This makes maintaining the ringing and resighting effort in the coming years all the more important. With the current ring-reading effort continued, we expect that within about 5 years we could run a multi-state model with success. More so, it would be wise to perform especially colour-ringing at a larger geographical scale (including Germany and France) so that an overview of the entire meta-population can be obtained.

Using resightings of colour-ringed individuals we found remarkable differences in the probability of exchange between northern and southern colonies, which strongly determines the current composition of these colonies. Colonies in the Dutch Delta (Delta N) are mainly composed of ‘own’ birds, either ringed as a 1CY or as an adult. On the other hand, in the N Netherlands – especially the newer colonies at Texel and de Putten – hold much higher proportions of non-local birds. They clearly attract birds from the Dutch Delta. Here it must be mentioned that there are no data available from the Hooge Platen, a large colony in the Delta area that was occupied until 2020 and where unfortunately no birds were ringed or read. This is an import lack in our knowledge because ring-readings by camera in the newly established colony of Waterdunen (whereto the colony of the Hooge Platen relocated) in 2021, indicated the attraction of a higher percentage of northern birds than found in the Delta N colonies. It is not clear if this was an effect of the sudden availability of a huge, highly suitable breeding site or that the northern birds had first established at Hooge Platen and then moved to Waterdunen in 2021. The latter would mean that the net flux from S to N might in reality be less pronounced than calculated based on the available data.

One note of caution here is that we used a standardized method to assign probable breeding locations. In colonies with a very high ring-reading intensity, the number of birds to which a PBL is assigned could be an overestimation. Visiting birds (non-breeders) that only spend a short time in or near a colony on Texel or De Putten have a higher chance of being detected than in the colonies in the S Delta so it is possible that relatively more birds are assigned as a breeder to the most-watched colonies. As a consequence, the amount of exchange between colonies or areas should be treated as an order of magnitude rather than a ‘hard number’. In a later stage, a database of all certain breeders in all colonies and years could be compiled and even more precise calculations could be made.

In other terns, young birds often show a greater tendency to move to another colony than 'established' adults (e.g. 2-6 times higher in Dougall's Terns *Sterna dougallii*; Lebreton *et al.* 2003). In Sandwich Terns, the precise magnitude of between-colony migration for young and older adults is not easy to estimate due to for example the large and sometimes difficult access to the colonies and the unevenly distributed ringing effort. Nevertheless, the probability of birds relocating to another colony seems to be age-related as well. Brenninkmeijer & Stienen (1997) calculated that 29 % of all alive Sandwich Terns previously born on Griend were found breeding there in 1995. The percentage of alive adults previously ringed there as a breeding bird and to be found there again in 1995, was much higher with 93 %. In this study, we found this to be respectively 38 and 74 % on the Scheelhoek in 2019. The probability of moving to another area or colony also differs between the S and N. While northern birds are much more faithful to their part of the study area than southern birds, they are more prone to moving to another colony within that area. This may be a result of the active management of landowners such as Natuurmonumenten and Staatsbosbeheer that has created a network of potential breeding sites for Sandwich Terns, especially in the N along the entire coastline. This may have led to an increase in movements, especially of adult birds. Fijn *et al.* (2014) have shown that adults actively 'taste the atmosphere' in other colonies before, during and after the breeding season, possibly to test the local breeding conditions. Apparently, the Sandwich Tern meta-population is characterized by a high degree of exchange between colonies and relatively low site fidelity.

One question remaining is why the Delta N population is still present although it obviously loses high proportions of birds to the newly established colonies at Texel and De Putten. This might be due to the difference in population size between the S and N Netherlands. In most years the number of breeding pairs in the north was 1.5-2.5 times that of the southern colonies. While the chance of migration from N to S is smaller than vice versa, the number of birds involved is relatively larger due to the larger population size. Also a difference in breeding success could play a role with the Delta N population functioning as a ‘source population’. Schekkerman *et al.* (2021) indicates this is not the case with at least the mean breeding success in the N (2005-2016) and S (2010-2019) Netherlands being comparable. An unknown factor is the degree of ‘import’ of foreign birds to the different regions.

A red line through this work is that one has to keep in mind that only Dutch birds from colonies where colour-rings were applied are taken into account. This means that although they are certainly ‘in the mix’, birds from for example Hooge Platen, the old Zeebrugge colony, 1CY birds from De Putten and birds from outside the Netherlands, are not detected. Resightings of both metal and colour-rings certainly indicate that the Sandwich Tern meta-population extends beyond the borders of the study area (Fijn *et al.* 2014; Courtens *et al.* 2020). Exchange with colonies in France, the UK, Germany and Denmark occurs but the order of magnitude is unknown. This could potentially lead to a masking of the effects of OWFs. In case of a structural emigration surplus (more individuals leaving Dutch colonies than joining), the growth rate of the Dutch population is probably lower than estimated based on the current population model structure and would be less resilient to changes (e.g. potential negative impacts due to the increasing presence of OWFs). On the other hand, an immigration surplus (more individuals join Dutch colonies than leave) would mean that the population growth rate could be higher than estimated and the population would be more resilient to changes than expected. This would also mean that OWF deployment in the Dutch waters could negatively affect birds from other countries. The same holds for the intra-country movements.

We provide reliable data on age-specific survival rates as well as on colony site fidelity which is essential knowledge to develop a reliable population model for this species. Other valuable model input is, however, still missing. In the first place there is not much known about the variation in age of first breeding. Recoveries used in this study predominantly relate to birds seen in the colony (often multiple times) but of which it is not certain whether or not they did breed. Especially young birds may hang around in the colony without breeding. These individuals are probably less restricted to the colony and may thus undertake longer foraging trips and may be more at risk of colliding with wind turbines. Furthermore, the nomadic behaviour of this species in general, as described in this report, complicates population modelling a lot and asks for further, more specific knowledge of colony attendance. Given that a large percentage of all Sandwich Terns breeds in another colony every year, potential negative effects of OWFs on a particular colony extend beyond that colony itself, probably to a large part of the Sandwich Tern entire meta-population.

Furthermore, even within a breeding season, Sandwich Terns often visit multiple colonies, thereby potentially passing multiple OWFs which heightens collision hazards. Also post-breeding visits of various colonies by adults and juveniles seems a common behaviour in this species. This nomadic behaviour (within-years, between-years and post-breeding) makes it very difficult to model collision mortality based on colony-specific features. We expect that such will result in an underestimate of true collision rates. Individual based models using multiple transition probabilities may solve this problem and figures on migration probabilities as provided in this report are certainly needed in these models. Beside these figures more insight is needed in the 'colony-hopping' behaviour of this species before individuals decide to join a certain colony as well as movements of failed breeders and post-breeding movements.

This leads to some final recommendations:

1. While this report presents reliable estimates for age-related survival and between-area migration, the timespan of the colour-ring dataset is still short, especially in the N Netherlands. In order to refine the numbers presented in this work, the **continuation of colour-ringing in the largest colonies** is crucial. Around 200-300 1CY birds per colony should suffice. Catching adults on the nest is not self-evident in many locations. Given the added value of resightings of established adults for both the survival and migration estimates, it is advised to colour-ring yearly at least 40 adults in the colonies where this is possible. Especially the **inclusion of the Western Scheldt colonies** would yield important insights that are lacking at this moment.
2. Together with the deployment of colour-rings, a **sustained reading effort** in the most important colonies is mandatory. Ring-readers should be made aware of the importance of ticking the boxes 'Behaviour' and/or 'BreedingCode' when a bird is noticed breeding in a colony.
3. Intensive ring-reading sessions in all colonies in the same year with the aim of detecting as much breeding birds as possible would greatly help to **clarify colony composition** further.
4. The compilation of a database with all probable or certain breeders for all Dutch colonies in all years would improve the calculations of migration numbers. This would entail 'manually' checking all sightings of all birds during the breedings eason instead of automatically assigning PBL based on the number of sightings.

5. In several countries (such as the UK, Denmark and Ireland, and from a different geographical region Bulgaria and Italy) colour-ring projects comparable to the Dutch programme have been deployed in recent years. Despite the rather short time-period of these projects, an analysis of these data would lead to a more complete **picture of inter-country migration** and ultimately of the impact of OWFs on the entire Sandwich Tern meta-population.
6. Difficult to tackle is the issue of **adults skipping breeding seasons**. While a number of studies have managed to calculate the chance of birds not breeding in a particular year, this was mainly done in colonies without much emi- or immigration and a large part of the birds identifiable. As Sandwich Tern often migrate between colonies, the establishment of a bird as a certain breeder in a certain year is complicated. In order to calculate this for Sandwich Terns, a huge effort should be done to read colour-rings in as many colonies as possible (both in and outside the Netherlands).

Acknowledgements

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9 Colony size and breeding success of Sandwich terns in De Putten and the Delta region between 2019 and 2021.

R.C. Fijn, S. Lilipaly, R.S.A. van Bemmelen, J.W. de Jong

Abstract

Data on colony size and breeding success of Sandwich Terns in the Netherlands as well as colonies around the North Sea were collected in high resolution between 2010 and 2021. These data are collected by direct observation and using Unmanned Aerial Vehicle (UAV or ‘drone’) surveys.

9.1 Introduction

Sandwich Terns *Thalasseus sandvicensis* breed in the Dutch coastal areas with about 15.000 – 20.000 pairs per year (Sovon 2021). These are spread over a limited number of large colonies (with usually a few hundred to thousands of pairs) in the Delta area, North Holland and the Wadden Sea area (Figure 9.1). In this study, breeding numbers of Sandwich Terns in the Netherlands and along the North Sea coasts of surrounding countries were collated as reference material for other parts of this research (e.g. Chapter 6 and 8) and for future research. Specific reference is made to the colonies in De Putten and the Delta, as these were part of the two Wozep studies ‘GPS tagging coastal birds project’ and ‘Onderzoek Grote Stern 2019-2021 project 31147211’.

9.2 Methods

Annual counts of the number of breeding pairs per colony were collected for colonies around the southern North Sea in between the Strait of Dover in the south, the Scottish border in the northwest and the Kattegatt in the northeast. In some colonies, counts were only done once during the egg phase, in other colonies, more specifically in the colonies in the Dutch delta and in De Putten, multiple visits were made to get a more precise estimate of breeding numbers and breeding success.

The colony size and breeding success of Sandwich Terns breeding in the Netherlands were determined by human visits to the colonies and/or by using Unmanned Aerial Vehicles (UAVs) in some colonies. In a few Delta colonies, vegetation made it difficult to conduct complete counts as the season progressed. Estimates of breeding success were therefore made, based on sample counts of ringed and unringed birds following visits by Deltamilieu Projecten in late June / early July, during which several hundred young were ringed as part of ongoing (voluntary) research of the Bird Ringing Group Delta.

Figure 9.1 *Photograph of De Putten on the 4 June with the southern island in the foreground and the eastern and northern islands in the distance (picture Bureau Waardenburg).*

9.3 Results and Discussion

9.3.1 Delta

Colony counts

In 2020, a total of 6,463 breeding pairs of Sandwich Tern were counted in the Delta area (RWS data). This represents an increase compared to the previous five-year mean of 5,387 breeding pairs. Numbers in 2020 were notably high, having only been higher in four years since 1979, the maximum being 7,733 pairs in 2013 (Lilipaly *et al.* 2020). In 2021, even higher numbers of breeding Sandwich Terns were found in the Delta area with a total of 6,998 breeding pairs. The main part of this increase was formed by the significantly larger number of breeding pairs at Waterdunen than the numbers that bred at Hooge Platen in previous years (where most of the birds breeding at Waterdunen are thought to originate from). Numbers of pairs and the number of juveniles per pair per colony in 2020 are presented in Table 9.1.

Table 9.1 Estimated number of breeding pairs and young per colony in 2020 and 2021 in the Delta area.

2020	**Breeding pairs**	**Number of young**	**Young per pair**
Hooge Platen	3,450	3,220	0.93
Scheelhoekeilanden	995	-*	0.50**
Slijkplaat	1,925	1,300	0.67**
Kaarspolder	96	103	1.07
Waterdunen	15	0	0
Totaal	6,481		
2021	**Breeding pairs**	**Number of young**	**Young per pair**
Hooge Platen	50	50	1
Scheelhoekeilanden	137	0	0
Slijkplaat	1,875	1,770	0.94**
Kaarspolder	83	93	1.12
Waterdunen	4,850	4,550	0.94
Neeltje Jans	1	2	2
Totaal	6,998		

* no final estimate due to high vegetation, ** based on fraction of colourringed and unringed juveniles at that location

Distribution after the breeding season

Juvenile Sandwich Terns are fed by their parents for some time after fledging. In the first month after fledging, the young are left in a so-called crèche where they are fed occasionally or from where they make short food flights with a parent. Such crèches can consist of groups of up to many hundreds of birds.

In July, large groups were only noticed in a few places: Zeebrugge (max. 2,000), Waterdunen (max. 3,280), Neeltje Jans Plaat (max. 1,145), the Verklikkerstrand (max. 1,630) and the Maasvlakte II (max. 3,300). Smaller numbers were present in the Flaauwers and Weversinlagen (200) and Het Zwin (300). It is likely that at least 6,000 to 7,000 Sandwich Terns were present simultaneously in the Delta area between 15 July and early August. Ring readings showed that the majority of the birds during this period came from colonies in the Delta.

From the second week of August, the numbers in the Voordelta and Oosterschelde declined rapidly. During this period the young birds are large enough to forage for food themselves. A substantial part of the population migrates northwards and stays in the northern part of the North Sea (mainly Denmark and Scotland) for a few weeks before moving towards the wintering areas in Africa. This is also the time when the proportion of ringed birds from the Wadden Sea, Germany and Denmark increased.

In the beginning of September a few thousand of Sandwich Terns were still present in the Voordelta. In October only a few hundred were left.

9.3.2 De Putten

Colony counts

Unlike other colonies of Sandwich Terns, the settlement phase of the colony in De Putten is widespread. Up until mid-June, large numbers of breeding pairs settle. These settlers may be failed breeders from elsewhere but also included new recruits. This spread settlement is one of the reasons that it is very difficult to determine breeding success in this colony. Another reason is that De Putten attracts a lot of parents and juveniles from elsewhere shortly after fledging. Since the colony at De Putten starts slightly later than other colonies it is impossible to distinguish the origin of juveniles if they are not colour-ringed just before the chicks from De Putten fledge (as they have mixed with other chicks).

In 2019, the largest number of breeding pairs was found in De Putten with about 3,500 pairs (Table 9.2). In this year, the terns mainly bred on the northern and eastern island. No breeding occurred on the southern island. In 2019, the breeding season seemed normal with birds starting breeding in the first week of May. In 2020, the breeding season developed very differently. In late April, a Red Fox *Vulpes vulpes* managed to circumnavigate the fence and predated on at least 16 adult Sandwich Terns. This caused the departure of all prospecting breeders for some time, until from 19 May onwards a stable colony formed. In 2020, about 2,500 breeding pairs were present on the northern and southern island. In 2021, settlement of the colony was again delayed relative to other colonies and spread out in time. Although breeding commenced in the second week of May, numbers stayed low for a long time. It was only by the end of May that larger numbers of breeding birds were found in De Putten. A complete count was carried out by unmanned aerial vehicle (UAV) on 4 June. The total number of breeding Sandwich Terns on that day was 2,086 breeding pairs. On 15 June however, the Sandwich Tern clusters had grown substantially, with 2,800 birds present, but many of these were not yet breeding. After heavy rainfall around 19 June, counts on 22 June indicated a substantial loss of nests and chicks. Unfortunately, we cannot estimate the total percentage lost, as we do not have precise counts of the birds just before the rainfall. Based on counts later that season, a total of at least 2,659 pairs must have bred in 2021 in De Putten, but due to the delay in settlement and the flooding this figure needs to be treated with caution.

Table 9.2 Estimated number of breeding pairs and young in the Putten in 2019 - 2021.

Jaar	Breeding pairs	Number of young	Young per pair
2019	3,500	no estimate	no estimate
2020	2,500	no estimate	no estimate
2021	min. 2,659	no estimate	no estimate

9.3.3 Netherlands and the rest of the southern North Sea

No major changes in breeding numbers in North Sea colonies have been registered over the last ten years. The average breeding population size is about 33,000 breeding pairs (Figure 9.2). The year 2020 had the highest number of breeders, totalling to 39,229 pairs. Note that colony counts for Denmark, Germany and the UK are incomplete for 2021.

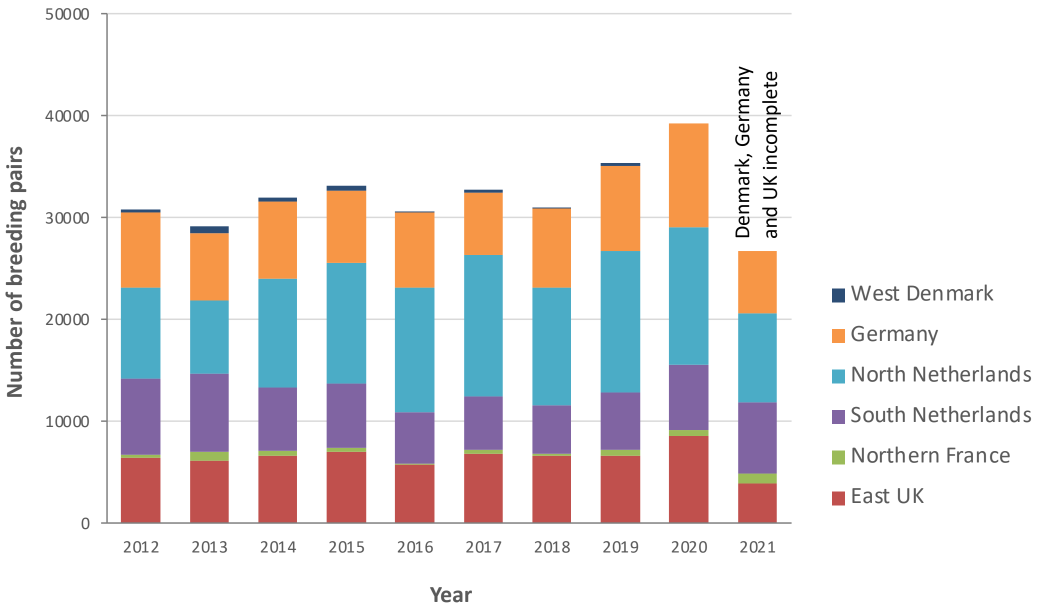

Figure 9.2 *Population estimates (in breeding pairs) of Sandwich terns in North Sea colonies for the last ten years.*

Acknowledgements

Thanks to all who provided colony counts; C. Redfern (Newcastle University), P. Morrison (RSPB) and A. Wilson (Natural History Society of Northumbria) for the colonies of the National Trust (Farne Islands) and Royal Society for the Protection of Birds (Coquet Island), N. Lawton (NE) for the Norfolk colonies, Pierre Thellier for the Platier d'Oye (FR) colony, W. Courtens (INBO) for the Zeebrugge colony (BEL), Deltamilieu Projecten for the colonies in the Dutch Delta, E. Menkveld (NM) for the colony in De Putten, and him together with B. Spaans (Vogelwerkgroep Texel) and M. Plomp (Vogelinformatiecentrum Texel) for the Texel colonies (NL), Date Lutterop (NM) for the colony on Griend, A. Brenninkmeijer for the Ameland colony, B. Hälterlein (Landesbetrieb für Küstenschutz, Nationalpark und Meeresschutz) for the Schleswig-Holstein colonies (GER), Kees Koffijberg (SOVON, Nationalpark Niedersächsisches Wattenmeer and TMAP database) for the Niedersachsen colonies (GER), and T. Bregnballe & J. Gregersen (Aarhus University) for all of the Danish colonies.

10 Adult and chick diet of Sandwich Terns *Thalasseus sandvicensis* in the Dutch Delta area in 2013-2021

W. Courtens, C. Mouton, R.C. Fijn & E.W.M. Stienen

Abstract

The Borssele offshore wind farm (OWF) is located in the foraging range of the Sandwich Terns breeding in the Western Scheldt colony (Waterdunen/Hooge Platen). The presence of an OWF could have fitness consequences for these birds since they may lose part of their foraging area and may have to shift to less profitable foraging areas. Because GPS-tagging of breeding birds was not allowed in these colonies, we had to fall back to the use of the birds' diet as a possible indicator of foraging behaviour. Diet data of adult Sandwich Terns and their chicks were collected in the Western Scheldt colony and compared with reference material from other locations in the Dutch Delta area (Grevelingen and Haringvliet basins) between 2013 and 2021. Prey brought to the Western Scheldt colony during the first three weeks of chick-rearing in 2021 consisted mainly of (very) small clupeids and differed markedly from the prey brought to the reference colonies. Also, the sandeels brought to the Western Scheldt colonies were very small compared to those delivered to the chicks in the other Delta colonies. As we made no observations of chick diet in the reference colonies in 2021, no direct comparison of chick diet is possible and these small prey fish might either point towards a typical feature of Sandwich Terns breeding in Western Scheldt or reflect a highly atypical year in the wider Delta Area. As small prey fish are often caught in the immediate vicinity of the colony, we would expect little interaction with the Borsele OWF in the first 2 weeks of age. As foraging duration (distance to colony) increases with prey size, especially in the weeks before fledging, possible effects of the Borsele OWF could be expected. Extensive sampling of the diet of incubating adult Sandwich Terns indicates the presence of between-year variation in diet composition rather than between colonies in the same year and this method could potentially be used as a proxy for prey availability in a larger spatial context such as the Delta Area as a whole. Intensive, repeated faeces sampling further shows strong intra-seasonal variation in the presence of different age classes of clupeids and sandeels in the diet. Future studies should take the between-year and intra-seasonal variation in both adult and chick diet of Sandwich Terns into account when comparing the post-construction phase of the Borssele OWF with the T0 situation.

10.1 Introduction

Along the Dutch coast, several offshore wind farms (OWFs) will be constructed within the foraging range of a number of large Sandwich Tern *Thalasseus sandvicensis* colonies. Besides increasing collision risks, OWFs might displace birds from their (favoured) foraging habitat (Drewitt & Langston 2006, Masden *et al.* 2010). Sandwich Terns avoid OWFs during both the construction phase (Harwood *et al.* 2017) and the operational phase (Dierschke *et al.* 2016 – updated by Vanermen & Stienen 2019, and Chapter 4). This might force the birds to shift to less profitable foraging areas (with different species or length classes available) which in turn could have fitness consequences such as lower chick condition and/or breeding success.

The Borssele OWF will be constructed in the foraging habitat of Sandwich Terns breeding in the important Western Scheldt colonies (Hooge Platen and Waterdunen). Ideally, adult breeding birds should be equipped with GPS-loggers to delineate their foraging range and to allow before/after construction comparison. As this is not possible in the Western Scheldt colonies due to accessibility issues, knowledge of the diet of the Sandwich Terns in these colonies in the T0-period is especially important as it is the only way to check for potential changes in the foraging habitat caused by the Borssele windfarm.

During the breeding season, when terns become central place foragers, they have to balance the demands of self- and offspring-provisioning within the constraints imposed by foraging from a fixed colony site (Orians & Pearson 1979). Birds attempt to maximize the rate of energy provisioning to offspring. Seabirds do so by selecting more proficient prey (larger size or more energy rich species, e.g. Dänhardt *et al.* 2011) for their chicks than when self-feeding, resulting in a different diet composition (Wilson *et al.* 2004, Ito *et al.* 2009). This ‘optimal sharing theory’ also predicts that adults will select different prey sizes at different distances from the colony (Burke & Montevecchi 2009). Moreover, small chicks are often not yet able to eat large prey which means selection for a certain prey size might also depend on the chick age (e.g. Shealer 1998). Prey availability also shows spatial variation ánd within-season and between-season variability (e.g. Ito *et al.* 2009). Consequently, a diet study should ideally encompass the degree of variation of both chick and adult diet in space and time and present an estimation of the foraging duration for different prey types.

In the framework of this Wozep project, we collected new data on both adult and chick diet in the Delta colonies and supplemented these with data from multiple colonies in previous years acquired in other projects (notably the PMR-NCV project and studies on own initiative). The aim of this work is to present the Sandwich Tern diet data of multiple years and colonies in the Dutch Delta area and to illustrate the degree of variability herein. Additionally, advice for good practice in setting up future diet studies (should this be deemed appropriate) is given to link offshore habitat use and breeding success to dietary research.

10.2 Study sites

In the framework of this Wozep project, data on the diet of incubating adult Sandwich Terns were collected in the colonies of Hooge Platen (2020) and Waterdunen (2021) in the Western Scheldt, and Scheelhoek (2020) and Slijkplaat (2021) in the Haringvliet (Figure 8.1).

For comparison, these were supplemented with data collected as part of earlier projects (PMR-NCV project and own study INBO) in several colonies in the Dutch Delta area:

- Scheelhoek and Slijkplaat in the Haringvliet in 2013-2019
- Markenje in Grevelingen in 2013-2016
- Hooge Platen in 2014-2019

Although sampled in earlier years, most of these additional samples from Hooge Platen were processed during this Wozep project.

Chick diet data (species composition and length) was collected at the Western Scheldt colony (Waterdunen) in 2021. While a Sandwich Tern colony was present on the Hooge Platen in 2020, it proved to be impossible to make trustworthy observations of birds flying with prey to the colony due to the very large distance. The Western Scheldt data are supplemented with chick diet data of the Haringvliet (2009-2018) and Grevelingen (2011-2016) colonies collected during the PMR-NCV project.

10.3 Methods - Adult diet

10.3.1 Collection of samples

Incubating Sandwich Terns defecate next to the nest. This results in a layer of faeces at the end of the incubation period (which lasts for about 24 days). We applied two sampling methods to obtain information about the adults' diet composition: extensive and intensive sampling.

The extensive method consisted of gathering one single sample just before the hatching of the first chicks (mostly in the last 10 days of May). Each extensive sample consists of the faeces collected around 15 to 20 nests in the study colony. These samples thus give an overview of the adult diet during the entire incubation period and allow comparison with similar samples collected in other colonies or years. Only faeces samples collected in the 4th and 5th week after May 1st were retained for analysis. The samples collected in the Western Scheldt in 2017 and 2018 were omitted because they were retrieved respectively very late and very early which might lead to a bias in composition and size of prey.

Also, the results of the 2021 sample collected at Waterdunen were omitted as this sample was collected during the only (very early) visit at the colony on May 7th.

Intensive sampling consisted of collection of consecutive faeces samples with a known time-interval. This method gives insight into the temporal variation in the adult diet but is labour intensive and requires frequent visits to the colony. The first diet sample was collected on the first visit to the colony (a few days after the first eggs were laid) by scraping the layer of faeces from around about 20 nests. To be able to collect a successive series of samples of adult faeces after this first sample, 10 plates were put between the nests of incubating birds. Each plate collected faeces of incubating adults of 1 to maximum 4 surrounding nests. At each consecutive visit the plates were collected and replaced by new ones. In this project the plates were replaced every 7 to 10 days. The plates were put out as long as there were birds incubating eggs. New birds often join already settled birds throughout the breeding season. As they frequently do so in sub-colonies at the border of the existing colony, we were able to collect adult diet samples even after the chicks had hatched in other parts of the colony. By putting the plates only between nests being incubated, contamination with faeces of chicks was avoided and only adults without chicks were sampled. After gathering the plates they were taken to the lab. Here, the faeces was scraped off with a soft scraper (in order not to break the diet remains) and put in a plastic container. The plates were rinsed and cleaned twice with water that was poured in the container as well. The recipients were labelled and stored in a freezer at -18°. The recipients were analysed later, following the protocol described in Courtens *et al.* (2017).

10.3.2 Species composition

The diet of adult Sandwich Terns in several colonies in the southern Delta area was described for the period 2007-2015 based on faeces samples (Courtens *et al.* 2017). This study showed that adults are extreme food specialists with only three prey types found in large numbers in their diet: clupeids *Clupeidae* sp., sandeels *Ammodytidae* sp. and ragworms *Nereididae* sp. All sagittal otoliths and teeth of ragworms *Nereididae* sp. were collected and stored in Eppendorf tubes. Vertebrae of pipefish *Syngnathidae* sp. were counted as the otoliths of these species are so small they are very easily overlooked. Sagittal otoliths were photographed with a Leica camera attached to a Leica stereo microscope. They were identified to the lowest possible taxonomic level using identification guides (Härkönen 1986. Leopold *et al.* 2001, Camphuysen & Henderson 2017, Tuset *et al.* 2008) and a reference collection of otoliths cut from fish of known species and length.

All otoliths of juvenile and adult clupeids were identified to species level. Otoliths of (post)larval specimens of clupeids were impossible to identify to the species level. But while Twaite Shad *Alosa fallax* and Sardine *Sardina pilchardus* have been found in small numbers in adult Sandwich Tern diet (Courtens *et al.* 2017), Herring *Clupea harengus* and Sprat *Sprattus sprattus* are the only clupeids occurring in large numbers in the southern North Sea. Larval and postlarval clupeids should be considered as Herring, Sprat or a mixture of both.

Three species of sandeel are known to occur in the Dutch Delta area: Lesser Sandeel *Ammodytes tobianus*, Raitt's Sandeel *Ammodytes marinus* and Greater Sandeel *Hyperoplus lanceolatus* (Tien *et al.* 2017). Based on current knowledge, it is not possible to identify the otoliths of sandeel to species level with certainty. Specimens found dead in the colony and catches of sandeel below foraging Sandwich Terns indicate that the majority of sandeel consumed by Sandwich Terns in the Dutch Delta area are Lesser Sandeel, with a small percentage of Raitt's and some Greater Sandeel.

10.3.3 Prey size

The width (OW) of sagittal otoliths of clupeids and sandeels was measured (to 0,1 µm) with ImageJ©. Several reference works and otolith identification books (e.g. Härkönen 1986, Leopold *et al.* 2001, Camphuysen & Henderson 2017) provide linear regression equations for the conversion of otolith length (OL) or width (OW) to total fish length (TL). While these are adequate for larger specimens (larger juveniles and adults), they frequently give an under- or overestimation of TL for small otoliths. As these small otoliths make up a substantial proportion of the total number found in adult Sandwich Tern faeces (Courtens *et al.* 2017), we used regression formulas based on our own reference collection (Table 10.1).

Table 10.1 Regression equations (with R²) used to calculate Total Fish length (TL in cm) from OW (in µm) for clupeids and sandeels. N gives the number of individuals used to build the equations. These equations are slightly different to the ones used in Courtens et al. (2017) as more specimens were added to the analysis.

Species	Equation	R^2	n
Herring	TL (cm) = (0.000006501*OW^2) - (0.0007996*OW) + 3.072	0.94	339
Sprat	TL (cm) = (0.000004093*OW^2) + (0.003965*OW) + 1.367	0.94	209
Clupeid sp.	TL (cm) = (0.000005315*OW^2) + (0.001355*OW) + 2.353	0.93	548
Sandeel sp.	TL (cm) = (-0.000000007322*OW^3) + (0.00002385*OW^2) - (0.01208*OW) + 6.205	0.92	206

10.3.4 Age classes of prey fish

Sagittal otoliths of sandeels and clupeids retrieved from previously processed faeces samples could be subdivided in age classes based on macrostructure characteristics (presence and size of the rostrum and sulcus, shape of dorsal, ventral and caudal sides and presence of annuli; Courtens *et al. in prep.*). These age classes corresponded well with the multiple modi seen in the OW frequency distribution diagrams. This way, four age classes for both clupeids and sandeels could be distinguished and cut-off values of OW between the classes were delineated (Table 10.2). Clupeids were separated in larval, 'postlarval', juvenile (with two types in Herring) and adult. While larval and postlarval clupeids were left unidentified, all juvenile and adult clupeids were identified to species level. Sandeels were divided in larval, juvenile (with two types) and adult (Age 1 and older). The cut-off values in Table 10.2 were used to attribute the age classes to the otoliths retrieved from the samples in this study.

Table 10.2 Age classes of clupeids and sandeels with cut-off values for OW and ranges of total fish length (TL in cm) per age class for adult and chick diet.

Ageclass preyfish	OW (µm)	Adult (cm TL)	Chick (cm TL)
Larval clupeid	< 477	< 4,2	< 4,2
Postlarval clupeid	477 - 693	4, 2 - 5,8	4, 2 - 5,8
Juvenile Sprat	693 - 977	5,8 - 9,1	5,8 - 9,1
Juvenile Herring Type 1	693 - 1000	5,6 - 8,8	
Adult Sprat	> 977	> 9,1	9,1 - 13,5
Juvenile Herring Type 2	> 1000	> 8,8	> 13,5
Larval sandeel	< 475	< 5,0	< 5,0
Juvenile Type 1 sandeel	475 - 726	5,0 - 7,2	5,0 - 7,2
Juvenile Type 2	726 - 986	7,2 - 10,5	7,2 - 10,5
Adult sandeel	> 986	> 10,5	> 10,5

10.4 Methods - Chick diet

10.4.1 Collection of chick diet data

At Waterdunen, half-hour observational bouts of adult Sandwich Terns carrying prey to the colony were made once or twice per week between 26/5/21 and 28/6/21 (Table 10.3). Sometimes these were shortened due to e.g. bad weather. We aimed to spread the observations over the same part of the day (between 10:30 and 16:30 h). Most returning adults followed the same route towards the colony and passed the observer at a distance of 10-50 m. This allowed for reliable identification of prey family and size. Prey brought to the colony was categorised as ‘clupeid’, ‘sandeel’ or ‘other fish’. Prey size was estimated in quarter bill lengths (BL = 5.43 ± 0.25 cm, *see* Stienen *et al.* 2000).

We aimed to identify all prey seen. When this was not possible because too many birds passed at the same moment, we randomly picked a bird, recorded the prey and moved to the next individual while looking through the binoculars. In doing so we avoided a bias towards a certain prey type or size. All observations were made by the same experienced observer (WCO) to exclude observer bias and recorded with a voice recorder.

The results are plotted against the data of chick diet of Sandwich Terns breeding in Grevelingen (Markenje) in 2011-2016 (no observations in 2014) and Haringvliet (Scheelhoek and Slijkplaat) in 2009-2018 (no observations in 2011) collected during the PMR-NCV project. The observations in Grevelingen were comparable to those in the Western Scheldt. They were made from two vantage points along the dike of the Grevelingen. All prey items seen during observation bouts of 30 minutes were identified and the size estimated. The protocols in the Haringvliet colonies were made from a blind next to an enclosure. In most cases these lasted for at least several hours during which all prey items brought to a selection of chicks or to all chicks in the enclosure were identified and measured.

The results are expressed per week of age of the chicks. The mean day of birth of the chicks in the enclosures in the Grevelingen and Haringvliet colonies was taken as the start of the first week of age. On Waterdunen, the first chicks hatched on May 19th (camera-observations). We used May 21st as the mean date of first hatching and the start of the first week of life.

10.4.2 Prey size

In order to be able to compare adult and chick prey size, TL in cm was calculated by assigning a randomly generated dummy length of (BL ± 0.125 BL) * 5.43 cm to all fish lengths in BL. For example, prey of 1.25 BL was assigned a random length between 6,1 and 7,5 cm, prey of 2.75 BL a random length between 14,3 and 15,6 cm.

10.5 Results - Adult diet: Extensive samples

A total of 20 extensive diet samples of the Western Scheldt, Haringvliet and Grevelingen colonies are included in this work (Table 10.3). From these, 15.856 prey remains were extracted of which 5.413 during this study.

Over all years and colonies, clupeids and sandeels were by far the main ingredient of the diet (90 ± 8 %, Table 10.3). Other fish species (mostly *Gobiidae* sp., *Gadidae* sp. and *Cyprinidae* sp.) were present in very limited numbers (2 ± 1 %). Ragworms were somewhat more important in numbers, making up 9 ± 8 % of the total diet composition of all investigated colonies. In what follows we will focus on the clupeids and sandeels as these are both the most abundant and energetically most important component of the diet of both incubating adults and chicks.

The ratio of clupeids and sandeels differed significantly between years for all basins (X^2-test, $p < 0.001$). Remarkably, in the four years a colony was present in both Haringvliet and Grevelingen, there were no significant inter-colony differences in the clupeid to sandeel ratio. On the other hand, whenever comparison between Haringvliet and Western Scheldt was possible, a significant difference was found between these locations. When looking at the age class composition of both families for all years and locations, the variation in age class composition was significantly greater between years than between colonies in the same year (ANOSIM, $R = 0.72$, $p < 0.001$). Differences between colonies in the same year were not significant.

Obvious differences in age class composition of both clupeids and sandeels between years are notable in Figure 10.1. In 2013, larval clupeids made up 47 and 57 % of the adult diet in Grevelingen and Haringvliet, respectively. Postlarval clupeids were almost absent before at least the end of May in that year. In 2014, a relatively large number of juvenile Herring was found in the diet of incubating Sandwich Terns, in most years these only show up later in the season. 2015 was a year with a lot of Sprat in the adult Sandwich Tern diet in all three basins. In 2016, sandeels < 1 year old were almost absent from the samples of Grevelingen and Haringvliet, respectively 90 and 87 % of the sandeels were adult (1 year or older). The ratio clupeids to sandeels in Grevelingen/Haringvliet and the Western Scheldt respectively, was almost the same in 2014 (46/44 % clupeids vs. 42 % clupeids) while in 2015 a much larger proportion of the adult diet consisted of clupeids (61/60 vs. 80 %). In 2019 and 2020, the inverse was observed, a much larger proportion of clupeids was found in Haringvliet than in the Western Scheldt (68 vs. 29 % in 2019 and 45 vs. 9 % in 2020).

Table 10.3 *Diet composition of adult Sandwich Terns in the Western Scheldt, Grevelingen and Haringvliet in 2013-2021 based on extensive faeces samples. The X²-column presents the results of X² tests for the ratio of clupeids to sandeels between respectively the Haringvliet colonies (reference) and the Grevelingen and Western Scheldt colonies (n.s.= not significant, * = $p < 0.05$, **= $p < 0.01$, *** = $p < 0.001$). Samples indicated in grey were omitted from the analyses.*

Year	Colony	Date	Clupeid	Sandeel	Other fish	Ragworm	Total	% Clupeid	% Sandeel	% Other fish	% Ragworm	X²
2013	Grevelingen	27/05/2013	2670	1086	44	62	3742	71	29	1	2	n.s.
2013	Haringvliet	3/06/2013	360	230	22	110	722	50	32	3	15	
2014	Westerscheldt	29/05/2014	116	163	10	5	294	39	55	3	2	*
2014	Grevelingen	22/05/2014	260	308	22	28	618	42	50	4	5	n.s.
2014	Haringvliet	21/05/2014	241	303	15	59	618	39	49	2	10	
2015	Westerscheldt	26/05/2015	332	85	4	5	426	78	20	1	1	***
2015	Grevelingen	26/05/2015	284	183	3	14	484	59	38	1	3	n.s.
2015	Haringvliet	26/05/2015	159	104	6	34	303	52	34	2	11	
2016	Grevelingen	26/05/2016	178	206	6	1	391	46	53	2	0	n.s.
2016	Haringvliet	26/05/2016	210	251	8	22	491	43	51	2	4	
2017	Westerscheldt	23/06/2016	19	74	5	13	111	17	67	5	12	
2017	Haringvliet	26/05/2017	331	485	9	150	975	34	50	1	15	
2018	Westerscheldt	16/05/2018	26	175	5	49	255	10	69	2	19	
2018	Haringvliet	25/05/2017	522	408	8	441	1379	38	30	1	32	
2019	Westerscheldt	28/05/2019	72	193	2	30	297	24	65	1	10	***
2019	Haringvliet	29/05/2019	1435	704	14	142	2295	63	31	1	6	
2020	Westerscheldt	27/05/2020	63	661	6	30	760	8	87	1	4	***
2020	Haringvliet	27/05/2020	186	228	5	87	506	37	45	1	17	
2021	Haringvliet	28/05/2021	195	452	3	10	660	30	68	0	2	
2021	Westerscheldt	7/05/2021	285	213		31	529	54	40	0	6	
Mean	Westerscheldt							**37 ± 26**	**57 ± 24**	**1 ± 1**	**4 ± 4**	
Mean	Grevelingen							**54 ± 11**	**42 ± 10**	**2 ± 1**	**2 ± 2**	
Mean	Haringvliet							**43 ± 10**	**43 ± 12**	**1 ± 1**	**13 ± 9**	

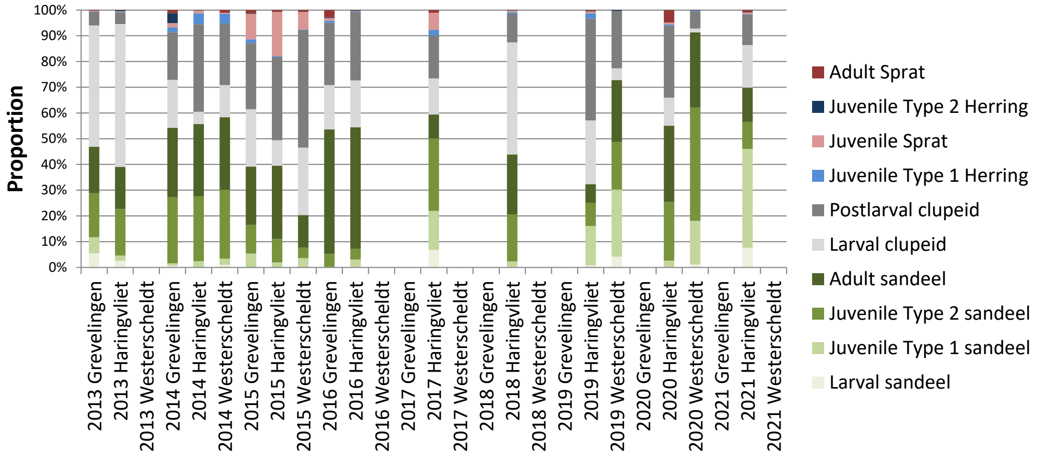

Figure 10.1 *Age class composition of the clupeids and sandeels in the diet of adult Sandwich Terns in the Western Scheldt, Grevelingen and Haringvliet in 2013-2021 based on extensive faeces sampling.*

Figure 10.2 shows the mean length ± SD of the different age classes of sandeels. While there is no obvious trend in the length of the 3 different classes of non-adult sandeels, simple linear regression indicated a significant decrease in length of adult sandeels with 2.5 ± 0.1 mm per year ($p < 0.001$, $R^2 = 0.1$) over the study period.

The mean length of the different age classes of the clupeids is presented in Figure 10.2. The majority of clupeids in the diet of incubating Sandwich Terns are smaller than 5 cm. Clupeids of 6 cm and more (juvenile Herring and juvenile and adult Sprat are present in numbers only in some years (e.g. in 2015).

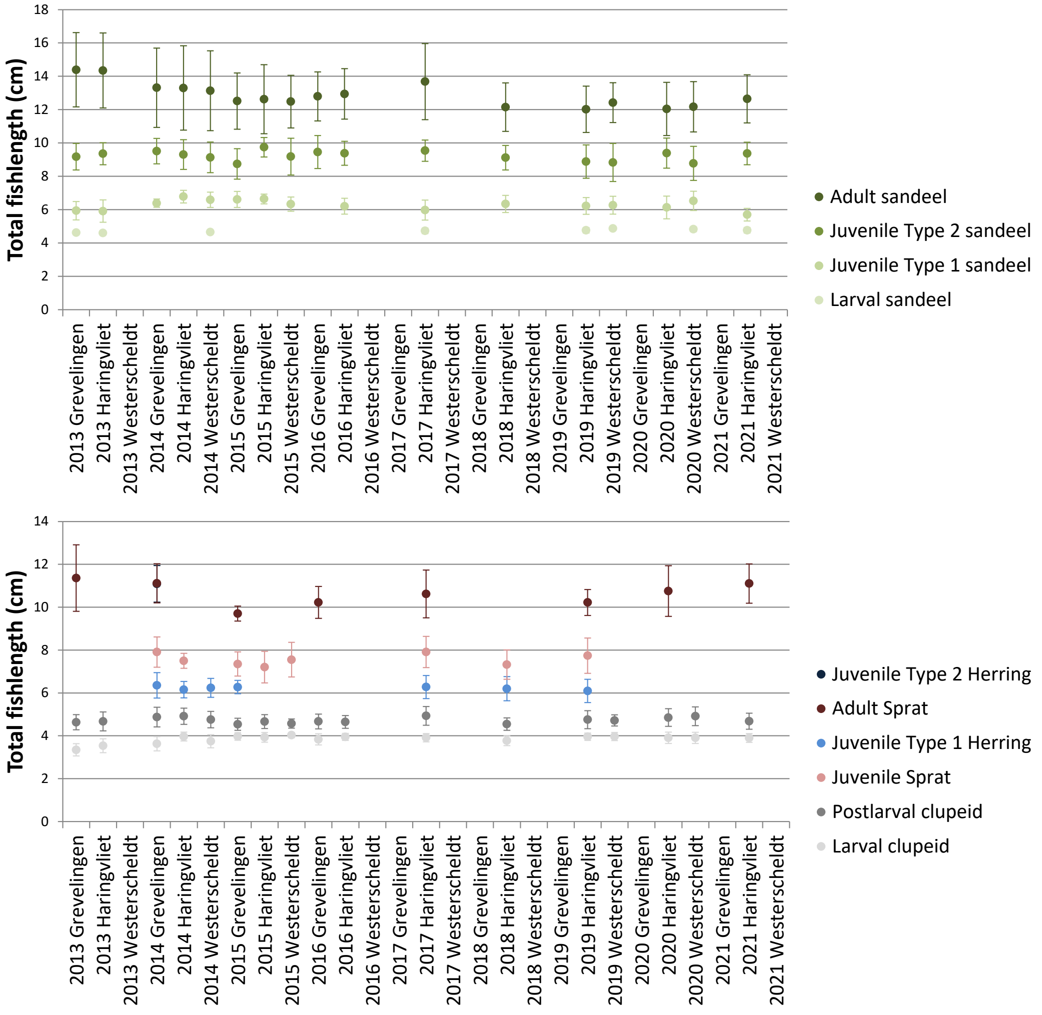

Figure 10.2 Mean length in cm (± SD) of the sandeels (upper panel) and clupeids (lower panel) per age class in the diet of adult Sandwich Terns in the Western Scheldt, Grevelingen and Haringvliet in 2013-2021 based on extensive faeces sampling.

10.6 Results - Adult diet: temporal variation

The consecutive faeces samples collected in 2015 in the Sandwich Tern colony of the Western Scheldt (Hooge Platen) and in 2020-2021 in the Haringvliet colonies (Scheelhoek and Slijkplaat respectively) were processed during this Wozep project. A total of 11.004

prey items were sorted, identified, and measured. An additional 4.506 prey items of the 2015 sampling campaign in the Haringvliet that were processed during the PMR-NCV project were included for comparison with the Western Scheldt data of 2015 (Table 10.4).

Table 10.4 Number of prey items and proportions of the different categories based on intensive sampling of adult Sandwich Tern diet in the Western Scheldt in 2015 and Haringvliet in 2015, 2020 and 2021.

Year	Location	Date	Clupeid	Sandeel	Other fish	Ragworm	Total	% Clupeid	% Sandeel	% Other fish	% Ragworm
2015	Westerscheldt	12/05/2015	40	149	9	33	231	17	65	4	14
2015	Westerscheldt	26/05/2015	2516	518	19	10	3063	82	17	1	0
2015	Westerscheldt	12/06/2015	920	318	14	6	1258	73	25	1	0
2015	Westerscheldt	24/06/2015	431	74	2	6	513	84	14	0	1
2015	Haringvliet	8/05/2015	63	123	12	38	236	27	52	5	16
2015	Haringvliet	12/05/2015	4	194	7	33	238	2	82	3	14
2015	Haringvliet	15/05/2015	42	123	7	13	185	23	66	4	7
2015	Haringvliet	20/05/2015	137	198	6	54	395	35	50	2	14
2015	Haringvliet	22/05/2015	120	86	5	6	217	55	40	2	3
2015	Haringvliet	25/05/2015	224	141	4	11	380	59	37	1	3
2015	Haringvliet	27/05/2015	189	62	11	11	273	69	23	4	4
2015	Haringvliet	29/05/2015	380	61	9	10	460	83	13	2	2
2015	Haringvliet	1/06/2015	505	230	9	6	750	67	31	1	1
2015	Haringvliet	3/06/2015	342	43	8	4	397	86	11	2	1
2015	Haringvliet	5/06/2015	97	35	3	1	136	71	26	2	1
2015	Haringvliet	8/06/2015	301	65	5	10	381	79	17	1	3
2015	Haringvliet	10/06/2015	156	21	7	2	186	84	11	4	1
2015	Haringvliet	12/06/2015	95	19	2	11	127	75	15	2	9
2015	Haringvliet	15/06/2015	102	24	6	13	145	70	17	4	9
2020	Haringvliet	8/05/2020	154	101	9	78	342	45	30	3	23
2020	Haringvliet	15/05/2020	272	418		166	856	32	49	0	19
2020	Haringvliet	22/05/2020	177	503	6	117	803	22	63	1	15
2020	Haringvliet	28/05/2020	149	252		50	451	33	56	0	11
2020	Haringvliet	3/06/2020	247	85	1	68	401	62	21	0	17
2020	Haringvliet	10/06/2020	550	144	8	144	846	65	17	1	17
2020	Haringvliet	16/06/2020	109	24	10	79	222	49	11	5	36
2020	Haringvliet	19/06/2020	94	8		10	112	84	7	0	9
2021	Haringvliet	28/05/2021	195	452	3	10	660	30	68	0	2
2021	Haringvliet	11/06/2021	323	177	9	10	519	62	34	2	2
2021	Haringvliet	16/06/2021	240	59	12	1	312	77	19	4	0
2021	Haringvliet	25/06/2021	326	70	9	10	415	79	17	2	2

Figure 10.3 and Figure 10.4 respectively show the temporal variation in the age class composition of clupeids and sandeels in the consecutive samples collected in 2015 at Scheelhoek (Haringvliet) and Hooge Platen (Western Scheldt) and in 2020-2021 in Haringvliet (respectively at Scheelhoek and Slijkplaat). All graphs show a strong temporal pattern in diet composition. In the beginning of 2015, sandeels made up the bulk of the adult diet in Haringvliet. As the breeding season progressed, clupeids became more important. Although much less samples were collected, a similar pattern is visible at the Western Scheldt colony in that year. In 2020 a similar pattern is visible at the Haringvliet colony, although the peak in sandeel abundance in the diet is reached later in the season. The first sample in 2021 was collected too late to get an impression of the temporal variation during incubation, but the trend towards more clupeids and less sandeels remains clear.

While the age class composition of the sandeel fraction in the 2020 and 2021 samples in Haringvliet do not show a trend (Figure 10.3, Figure 10.4, and Figure 10.9 in Appendix), in

2015 less adult sandeels are found towards the end of the breeding period in both the Western Scheldt and Haringvliet. The age class composition itself differs between years with for example a large fraction of the samples taken in 2021 consisting of Type 1 juveniles, an age class largely absent from the 2020 samples.

In contrast to the sandeel fraction, the age class composition of the clupeids shows a strong temporal pattern recurring in the different years and locations (Figure 10.3, Figure 10.4 and Figure 10.10 in Appendix). At the start of the incubation period, mostly larval and to a lesser extent postlarval clupeids are preyed upon. Towards the end of May, an increasing amount of postlarval clupeids are found in the diet. As June progresses, juvenile Herring and Sprat become increasingly abundant. The clupeid composition at Haringvliet in 2015 shows a somewhat aberrant pattern as already by mid-May, a large fraction consisted of juvenile Sprat.

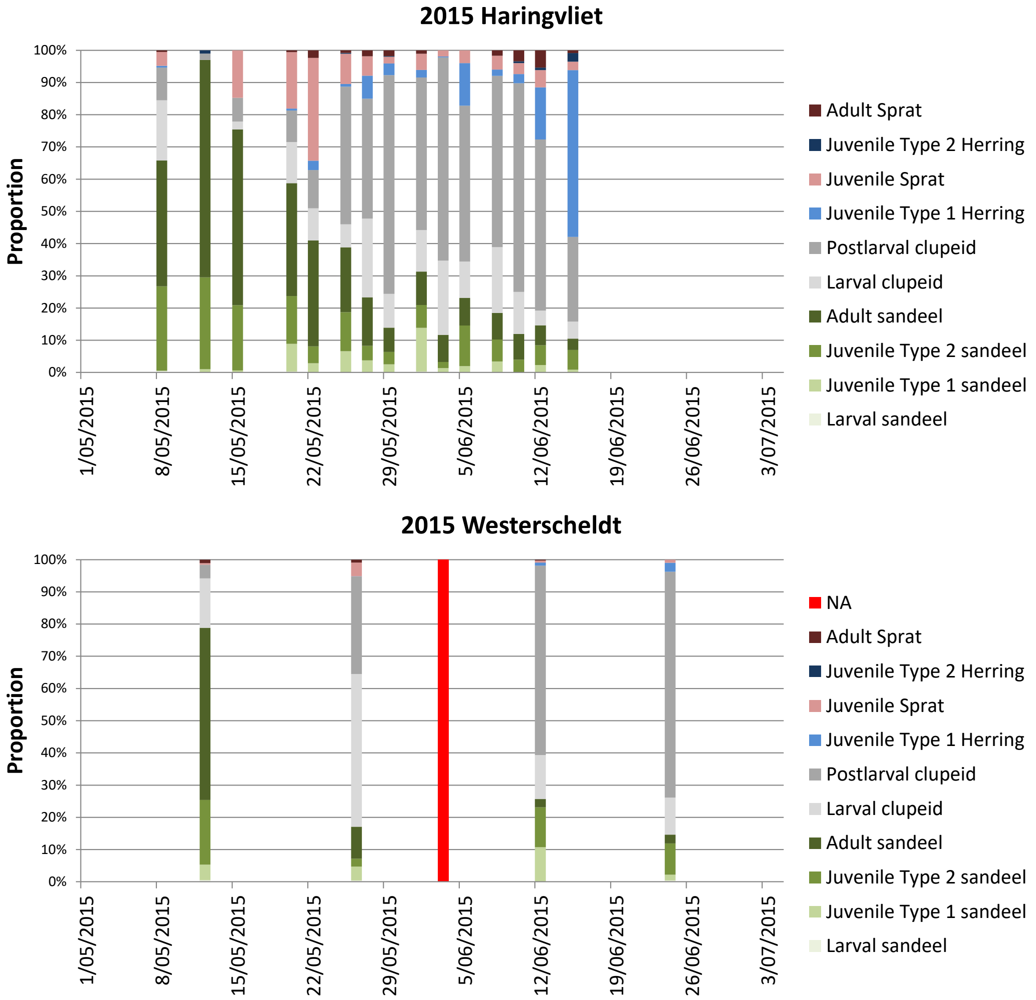

Figure 10.3 *Temporal variability in the age class composition of clupeids and sandeels in the diet of adult Sandwich Terns in the Haringvliet (upper panel) and Western Scheldt (lower panel) in 2015 based on intensive faeces sampling. The red bar in the lower graph represents a missing sample, as a consequence the 12/06/2015 sample represents the adult diet between 5/6/2015 and 12/6/2015.*

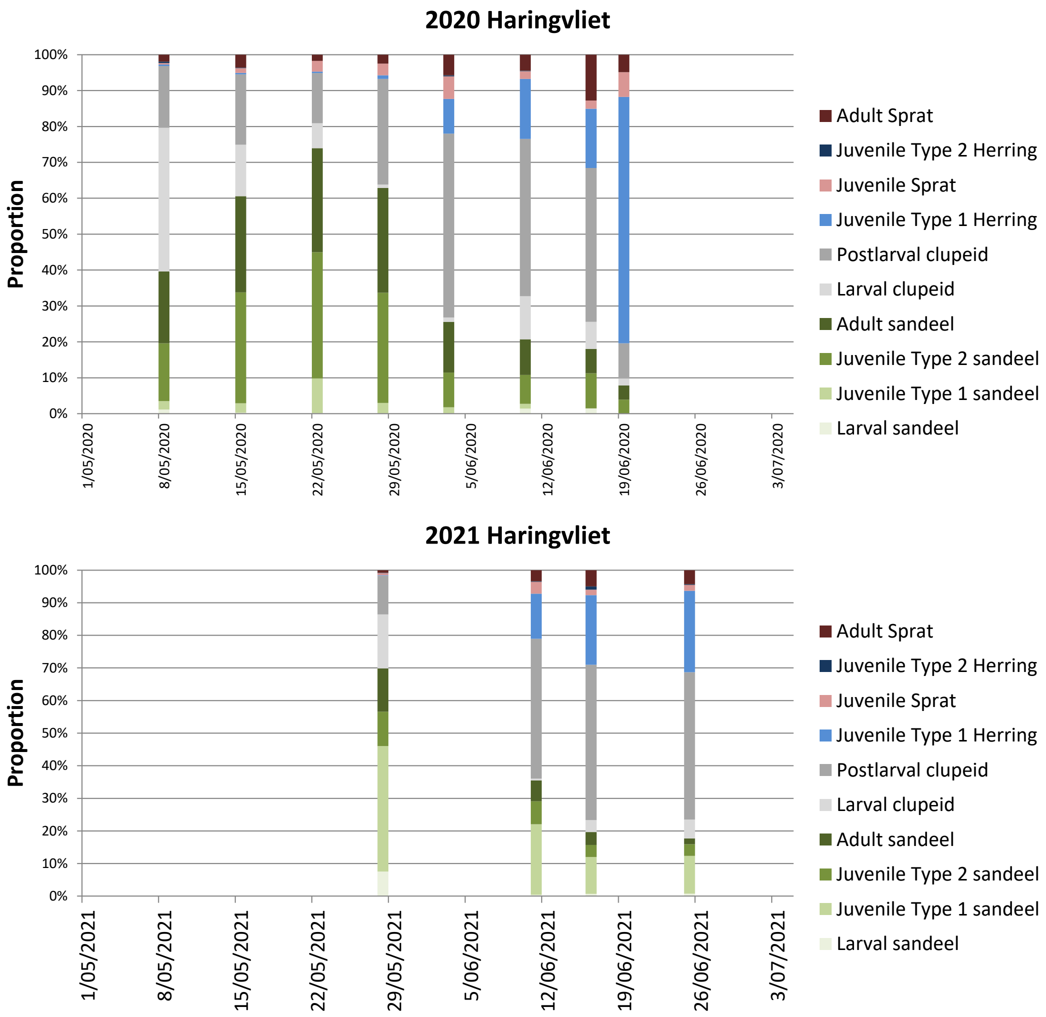

Figure 10.4 *Temporal variability in the age class composition of clupeids and sandeels in the diet of adult Sandwich Terns in the Haringvliet in 2020 and 2021 based on intensive faeces sampling.*

10.7 Results - Chick diet

At the Waterdunen colony, a total of 25 observational bouts good for 704 minutes of observation were made on 8 days between 26/5/21 and 28/6/21 (Table 10.5). 3.275 prey items were identified of which 2.386 clupeids (72.9 %), 818 sandeels (25.0 %) and 71 other fish sp. (2.2 %). These data are compared with the data of the Grevelingen (9.637 prey items) and Haringvliet reference colonies (10.144 prey items).

Table 10.5 Characteristics of observation bouts (n minutes, n bouts) and composition of prey items brought to chicks in the Sandwich Tern colony on Waterdunen per date in 2021. Means are given ± SD.

Colony	Date	N minutes	N bouts	N clupeid	N sandeel	N other fish	N total	% clupeid	% sandeel	% other fish
Waterdunen	26/05/2021	54	2	84	9	3	96	88	9	3
Waterdunen	31/05/2021	60	2	232	38	2	272	85	14	1
Waterdunen	4/06/2021	45	2	89	49	1	139	64	35	1
Waterdunen	7/06/2021	60	2	164	77	1	242	68	32	0
Waterdunen	14/06/2021	120	4	258	120	6	384	67	31	2
Waterdunen	17/06/2021	136	5	440	341	14	795	55	43	2
Waterdunen	21/06/2021	109	4	449	38	13	500	90	8	3
Waterdunen	28/06/2021	120	4	670	146	31	847	79	17	4
Total		704	25	2386	818	71	3275			

The majority (75 ± 12 %) of prey brought to the colony were clupeids on all observation dates (Figure 10.5). Sandeels made up 24 ± 12 % of the chick diet and 2 ± 1 % were other fish species. Compared to the reference colonies in Grevelingen and Haringvliet, especially in the beginning of the chick-rearing period, the composition of the chick diet at Waterdunen in 2021 was markedly different. In the 1st and 2nd week of chick life (comparable with the 4th and 5th week after May 1st) respectively 90 and 86 % of the diet were clupeids. This is significantly higher (X^2-test, $p < 0.01$) than the mean of 65 and 56 % in the 1st and 65 and 48 % in the 2nd week in respectively the Grevelingen and Haringvliet. During the 3rd and 4th week of age, prey composition in the three basins was comparable with between 60 and 70 % clupeids (X^2-test, $p > 0.05$). In the week of fledging (5th week of life), the proportion clupeids was again very high with 92 % of the diet consisting of this prey type and significantly different from Haringvliet (X^2-test, $p < 0.001$) but not from Grevelingen (X^2-test, $p > 0.05$).

In all colonies, the mean length of both the clupeids and sandeels brought to the colony increased with chick age (Figure 10.6). In the first chick week (4th week of May), the clupeids and sandeels were respectively 4.9 ± 1.4 cm and 9.2 ± 1.4 cm long. By the time the chicks fledged, this was respectively 12.4 ± 1.9 cm and 13.9 ± 3.5 cm. Except in the 4th week of chick age, the clupeids brought to the chicks at Waterdunen were significantly smaller than those at the Haringvliet colonies (t-tests, $p < 0.05$). Sandeels brought to chicks of up to three weeks old were also significantly smaller than those in the Haringvliet colonies (t-tests, $p < 0.01$). In the 4th and 5th week of chick age there was no significant difference between the sandeel-prey at Waterdunen and the Haringvliet (t-tests, $p > 0.05$).

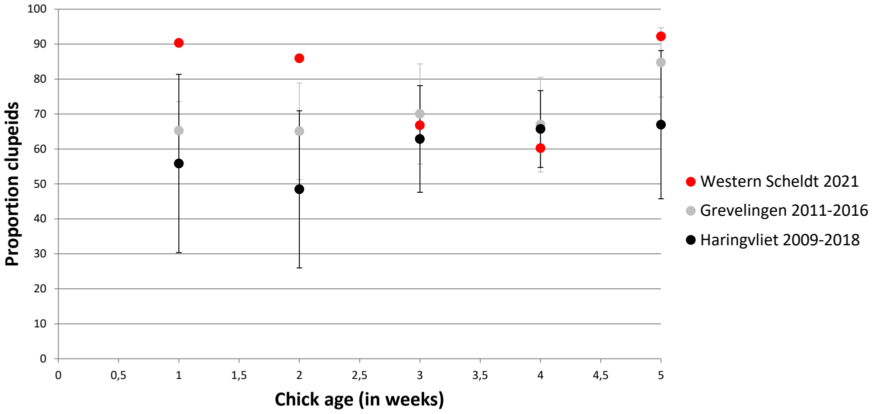

Figure 10.5 *Proportion of clupeids in the prey brought to Sandwich Tern chicks in the Western Scheldt Sandwich Tern colony (Waterdunen) in 2021. Proportions are expressed per week of age of the chicks. The mean proportion (± SD) of clupeids for the Grevelingen colony (Markenje) averaged over the period 2011-2016 and the Haringvliet colonies (Scheelhoek and Slijkplaat) over the period 2009-2018 are presented for comparison.*

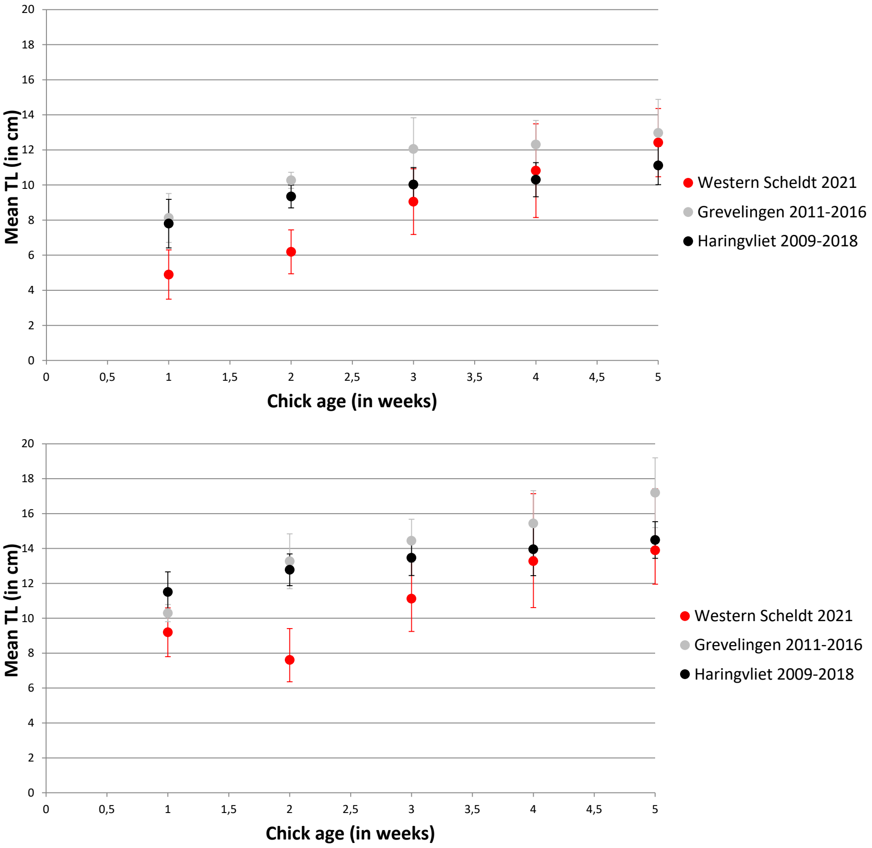

Figure 10.6 *Mean total length of clupeids (upper panel) and sandeels (lower panel) in cm ± s.d. brought to Sandwich Tern chicks in the Western Scheldt Sandwich Tern colony (Waterdunen) in 2021. Lengths are expressed per week of age of the chicks. The mean lengths ± SD for the Grevelingen colony (Markenje) in 2011-2016 and the Haringvliet colonies (Scheelhoek and Slijkplaat) in 2009-2018 are presented for comparison.*

10.8 Adult vs chick diet: 2021

While the mean percentage of clupeids in the diet of incubating adult (75 ± 8 %) and chicks (74 ± 12 %) of Sandwich Terns over the whole chick rearing period is comparable, Figure 10.7 indicates that parents select older and larger age classes of both clupeids and sandeels while chick feeding (see also Figure 10.11 in Appendix). Between 31/5/21 and 28/6/21, 60 ± 28 % of the sandeels in the chick diet were adult specimens compared to 16 ± 4 % in that of incubating adult Sandwich Terns. Moreover, where the proportion of adult sandeels in the adult Sandwich Tern diet remained fairly constant (10 to 20 %), in the chick diet a strong increase of this age class is notable towards the end of the chick rearing period (from 13 % at the end of May to 97 % at the end of June). Another obvious difference is the proportion of small juvenile sandeels (Juvenile Type 1) that made up a fairly constant 61 ± 3 % of the adult diet compared to 16 ± 22 % of the chick diet. This age class was especially abundant in the diet of young chicks (observations of 31/5/21) and almost disappeared when the chicks grew older. Not only is there a strong selection toward adult sandeels to feed to the chicks, the average length of the adult sandeels that were brought to the colony gradually increased during chick rearing (Figure 10.8). Whereas the mean length of adult sandeels in the adult diet remains at 12.5-13.0 cm, the mean length in the chick diet was 15.5-17.5 cm in the week of fledging.

The age class composition of the clupeids in the diet of incubating adults shows a fairly constant pattern during the whole chick rearing period (Figure 10.7). Postlarval clupeids made up the largest part of the adult diet (63 ± 3 %) and 31 ± 3 % were juvenile Sprat or small juvenile Herring (Juvenile Type 1 Herring). Larger clupeids were almost absent in the adult diet. Chick-feeding Sandwich Terns show an even more pronounced selection for the larger age classes of clupeids than in the sandeels. Postlarval clupeids were almost exclusively brought to small chicks and disappeared from the chick diet after the end of May. The bulk of the chick diet was made up of juvenile Sprat/small juvenile Herring (30 ± 20 %) and especially consisted of adult Sprat/larger juvenile Herring (50 ± 22 %). Adult Herring, an age class absent from the adult diet, was an important part of the diet of Sandwich Tern chicks, especially in the week before fledging (12 ± 13 %). Over the whole chick rearing period, small age classes show a decreasing trend in favour of the larger age classes. Total fish length of the different age classes is comparable between the chick and adult diet (Figure 10.8), except for the juvenile Sprat/Juvenile Herring Type 1 group. Whereas adults mainly took small juvenile Herring (Figure 10.7) with a length of about 6.5 cm, the mean length of this class in the chick diet (7.5-8.0 cm) indicates that mainly juvenile Sprat were brought to the colony.

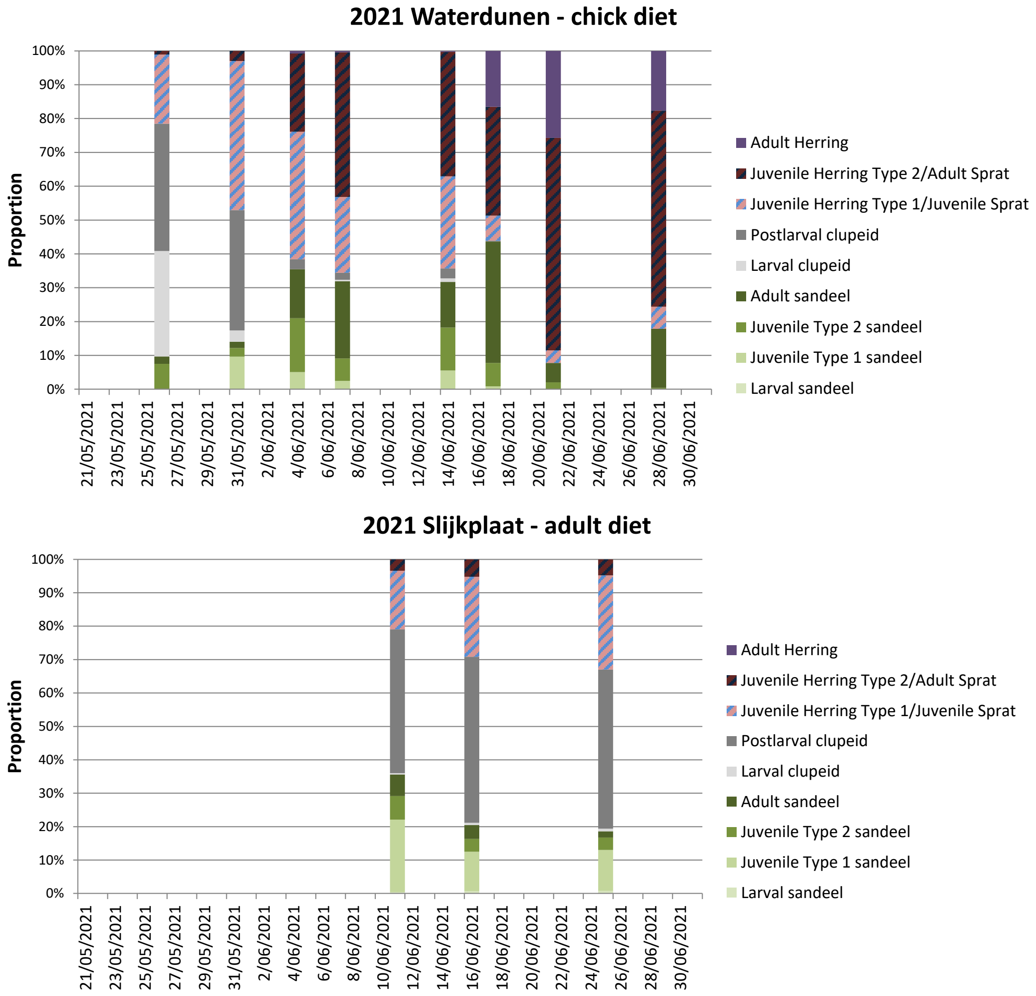

Figure 10.7 *Temporal variability in the age class composition of clupeids and sandeels in the diet of chick (upper panel) and incubating adult (lower panel) Sandwich Terns in respectively the Waterdunen and Slijkplaat colonies in 2021.*

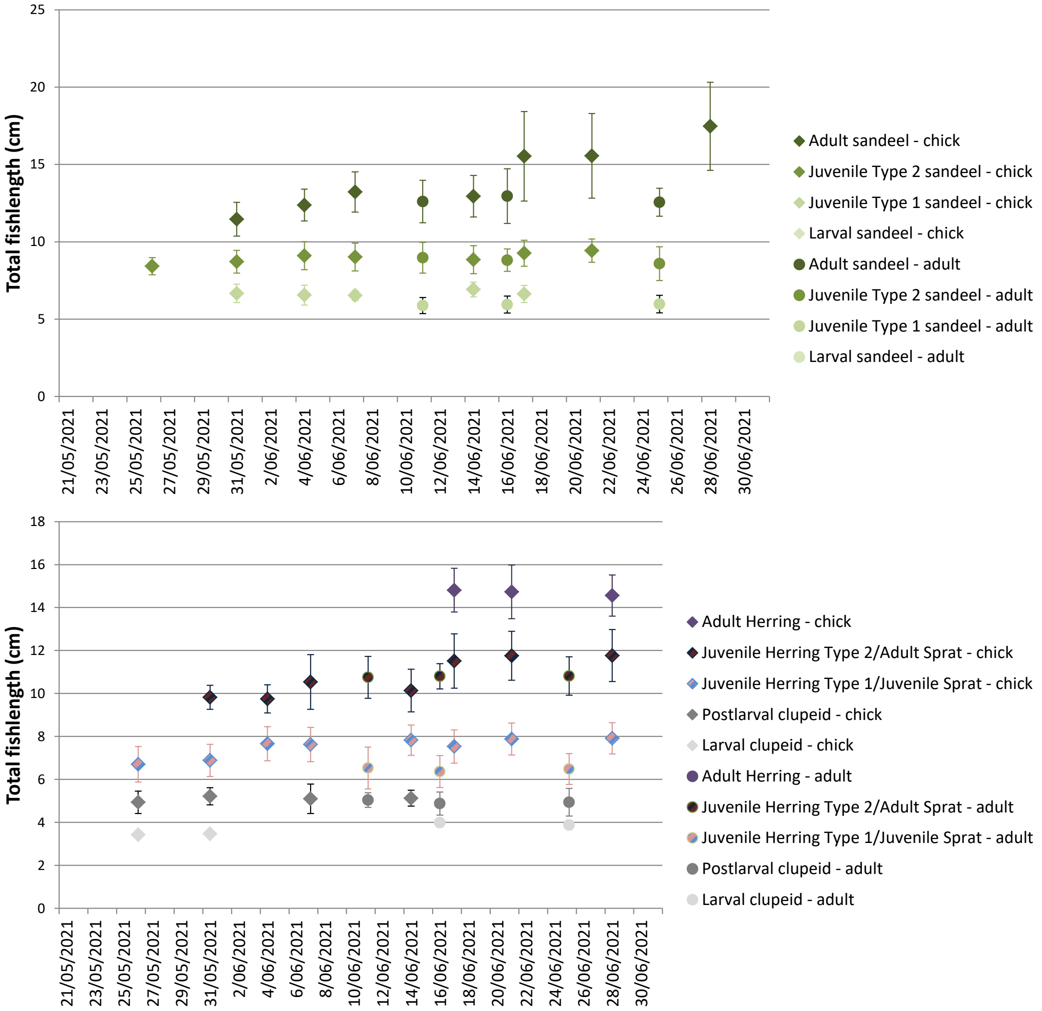

Figure 10.8 *Temporal variability in the total fish length (in cm ± s.d.) of the different age classes of sandeels (upper panel) and clupeids (lower panel) in the diet of chick and adult Sandwich Terns in respectively the Waterdunen and Slijkplaat colonies in 2021.*

10.9 Discussion

During this Wozep project, new data on Sandwich Tern chick diet were collected at the Western Scheldt colony of Waterdunen in 2021. Compared to reference data collected in earlier years during the Project Mainportontwikkeling Rotterdam and Natuur Compensatie Voordelta (PMR-NCV) project at colonies located in Grevelingen and Haringvliet, adult birds brought proportionally more and smaller clupeids to the colony in the first weeks of chick life. The clupeids transported to the Waterdunen colony during the first two weeks of chick rearing were the smallest thus far recorded. The same was true for the sandeels in the first three weeks. Despite this, breeding success in the colony was very good. This probably indicates high prey availability in the vicinity of the colony, as a high prey delivery rate could compensate for the low energy content of these small fish. Observations of individually marked adult birds and the construction of an enclosure were not possible, so data on foraging duration and prey delivery rates to the chicks that might support this theory are unfortunately not available. Furthermore, GPS-tracking combined with prey observations was not possible in the colony closest to OWF Borssele, so we cannot be sure where these prey items come from, but all signs point to a small foraging distance and thus no major interaction with OWF Borssele.

Because only one year of chick diet data is available for the Western Scheldt colony and no reference material could be collected in other colonies in 2021, care has to be taken with conclusions. While especially the size of clupeids and sandeels in the first two weeks of chick life was exceptionally small, this might as well have been the case in the other basins in 2021. On the other hand, a high transport rate of particularly small fishes was also noted in the nearby colony of Zeebrugge the early 2000s (Vanaverbeke *et al.* 2007), which could point towards a general pattern in these colonies. Adult diet data could have provided an indication to support this but as only in the reference colony samples could be collected, comparison was not possible. If these small clupeids would indeed have been caught in the immediate vicinity of the colony, we would expect little interaction with the Borssele OWF in the first 2 weeks of age. As foraging duration (distance to colony) increases with prey size (Fijn *et al.* 2017 & 2019), potential effects of the Borssele OWF can be expected especially in the weeks immediately before fledging.

Chick diet data gathered during the PMR-NCV project show a strong temporal pattern, especially in prey length. Both clupeids and sandeels brought to the study colonies increased in length as the chicks grew. Whenever comparison with the adult diet could be made, the data show a strong selection for the larger age classes and individuals by chick-feeding parents. The temporal pattern in the diet of the chicks is probably a function of chick age rather than of prey availability. Should particular prey lengths of fish species occur within OWF Borssele, this could have an attractive effect to the area, however, spatial data on length distributions of forage fish are not available.

Extensive sampling of faeces proves to be very useful to distinguish between year and between colony patterns in the adult diet in a non-time consuming way. It also permits to discern general trends as a decreasing length of adult sandeels in the adult diet over the last 9 years. Extensive diet sampling indicates that patterns of availability of age classes of prey may strongly differ between years, but less so between nearby colonies in the same year. It does, however, not allow to estimate the short-term variation in prey availability, while these are expected to be very important given the highly variable patterns in larval transport and temperature induced changes in the distribution of prey fish (e.g. Ito *et al.* 2009). The results from the intensive sampling indeed show a high degree of temporal variation in the adult diet composition on a short-term scale (i.e. within a breeding season). The fact that clear, yearly recurring patterns of prey composition are visible indicates that this could reflect (variation in) prey availability. For chick growth and survival, it might be very important that the timing of such patterns matches the onset of the chick-rearing period (which is rather static in Sandwich Terns). If certain prey fish or crucial prey lengths do arrive too late in the coastal waters of the Delta area, there might be a mismatch that can have strong repercussions. Here we show that intensive sampling of adult diet could serve as a sensitive proxy for such shifts in prey abundance.

10.10 Guidelines for future diet studies

Given the occurrence of strong within-seasonal patterns in both chick and adult diet ánd the fact that both are very different in age class composition of prey, care should be taken when comparing diet data of different locations and years when these are not collected in a standardised way. The next paragraphs delineate some guidelines of good practices for (Sandwich Tern) diet studies to allow proper comparison.

10.10.1 Chick diet

1) Diet sampling should take place with regular intervals over the entire chick rearing season to avoid an effect of chick age on diet composition and prey length. Preferably observations should be made during good conditions as strong wind or heavy rain have an impact on prey brought to the colony.
2) Diet sampling should take place with regular intervals over a sampling day to avoid effects of time of the day and potential tidal effects.
3) Diet protocols from a hide near an enclosure are preferred over observations of flyby adults with prey. Protocols are much more precise, as the observer is very close to the action. Protocols near an enclosure also allow the gathering of important additional information such as exact age of the chicks, fate of the prey (kleptoparasitism by e.g. Black-headed Gulls *Larus ridibundus* can cause a lot of prey loss) and foraging duration (see 4). Disadvantages are additional disturbance to the colony, the visibility of the hide in the colony and the fact that it is time-consuming.
4) When diet protocols are not an option, observations of flyby adults can be made. These should be conducted along the main flight path(s) towards the colony. Maximal observation distance should be around 100 m when using binoculars. When a telescope can be used, 300 m can be considered as a maximum.
5) To avoid bias towards a certain prey type, all prey should be identified and measured. When that is not possible (when too many birds pass at once), one could limit oneself to the prey carried by all of the birds effectively seen by binoculars. Prey length should be estimated in 0.25 bill lengths.
6) All observers should be experienced with the identification of the potential prey species and estimation of length. Length estimation should be calibrated between observers at the beginning of the season and multiple times afterwards. This can be done by independently estimating the same prey and comparing the estimates.

10.10.2 Adult diet

1) Preferably both extensive and intensive sampling should be done. Extensive sampling allows easy comparison between years and colonies and intensive sampling allows the recognition of temporal patterns in prey availability.
2) Most extensive samples in the Delta area have been collected between May 25th and May 29th, just before hatching of the eggs produced during the peak of laying (Sandwich Terns are highly synchronised and timing of laying is rather constant between years, except for incidental events caused by predation events for example)

Future samples should preferably be collected in the same time-frame to allow reliable trustworthy comparison.

3) Intensive sampling should be initiated at the latest one week after the first eggs in the colony are laid. The samples should be collected at regular intervals and at least every week until egg-laying ceases.

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Appendix

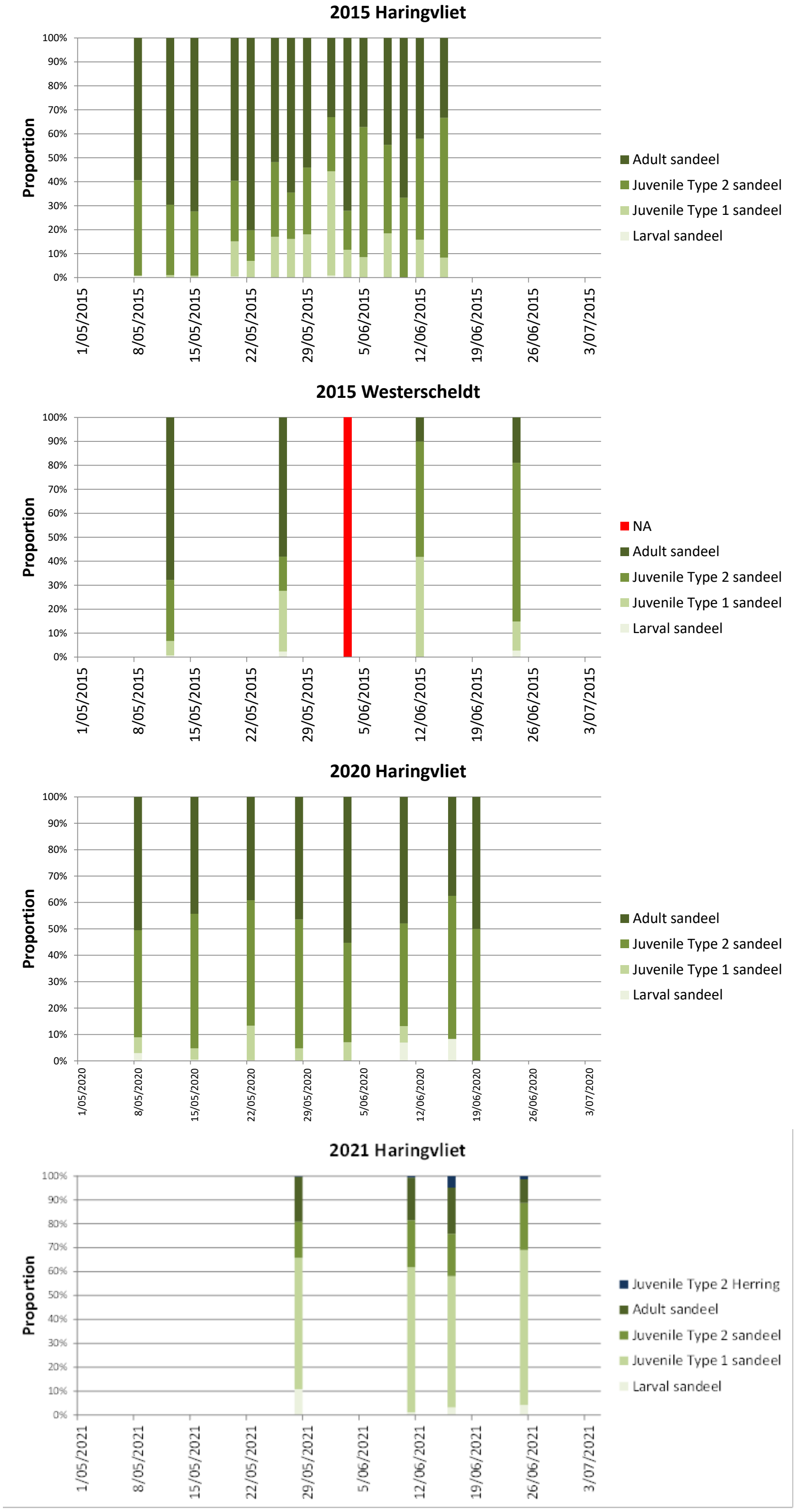

Figure 10.9 *Temporal variability in the age class composition of sandeels in the adult diet of Sandwich Terns in the Western Scheldt in 2015 and the Heringvliet colonies in 2015, 2020 and 2021.*

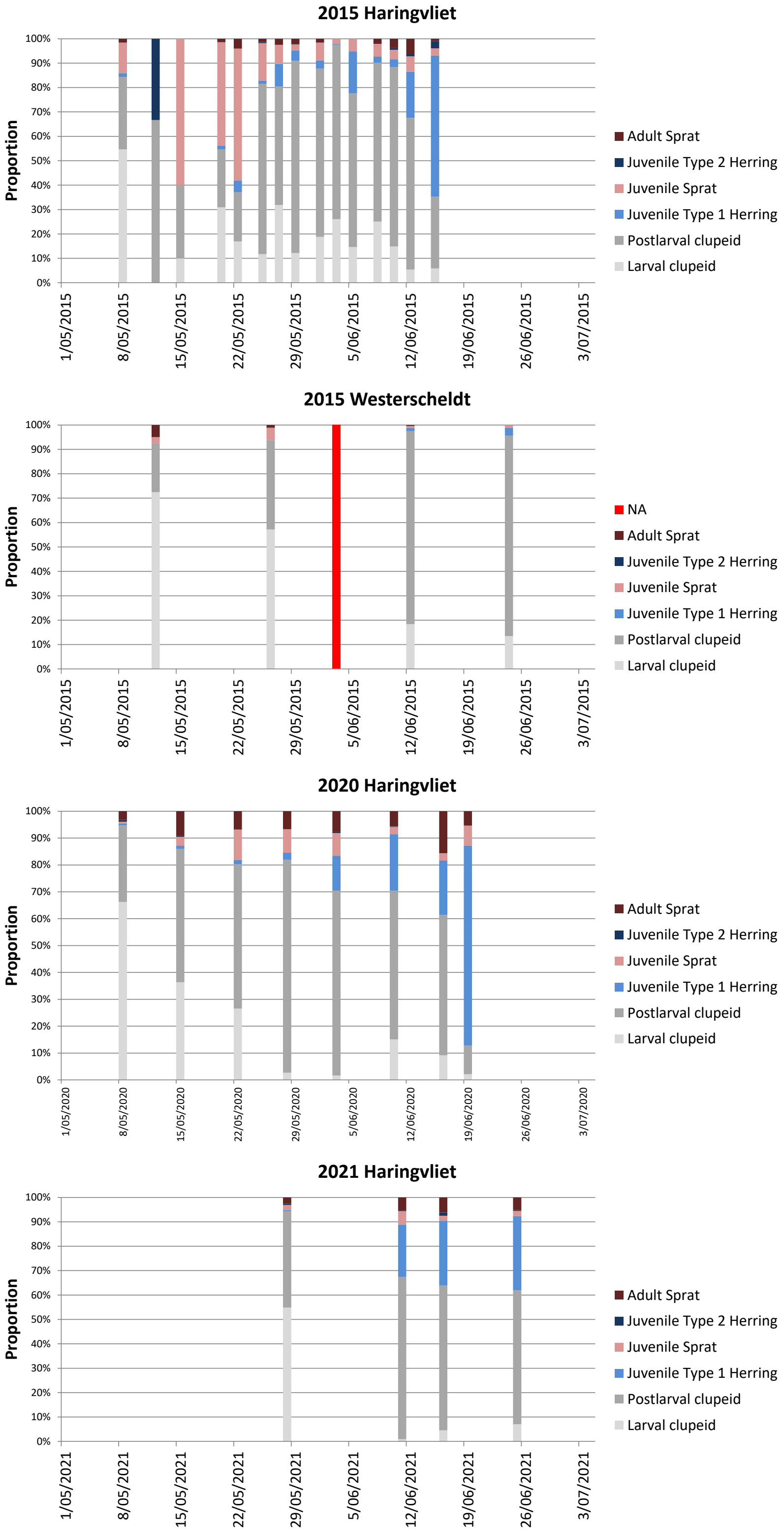

Figure 10.10 *Temporal variability in the age class composition of clupeids in the adult diet of Sandwich Terns in the Western Scheldt in 2015 and the Haringvliet colonies in 2015, 2020 and 2021.*

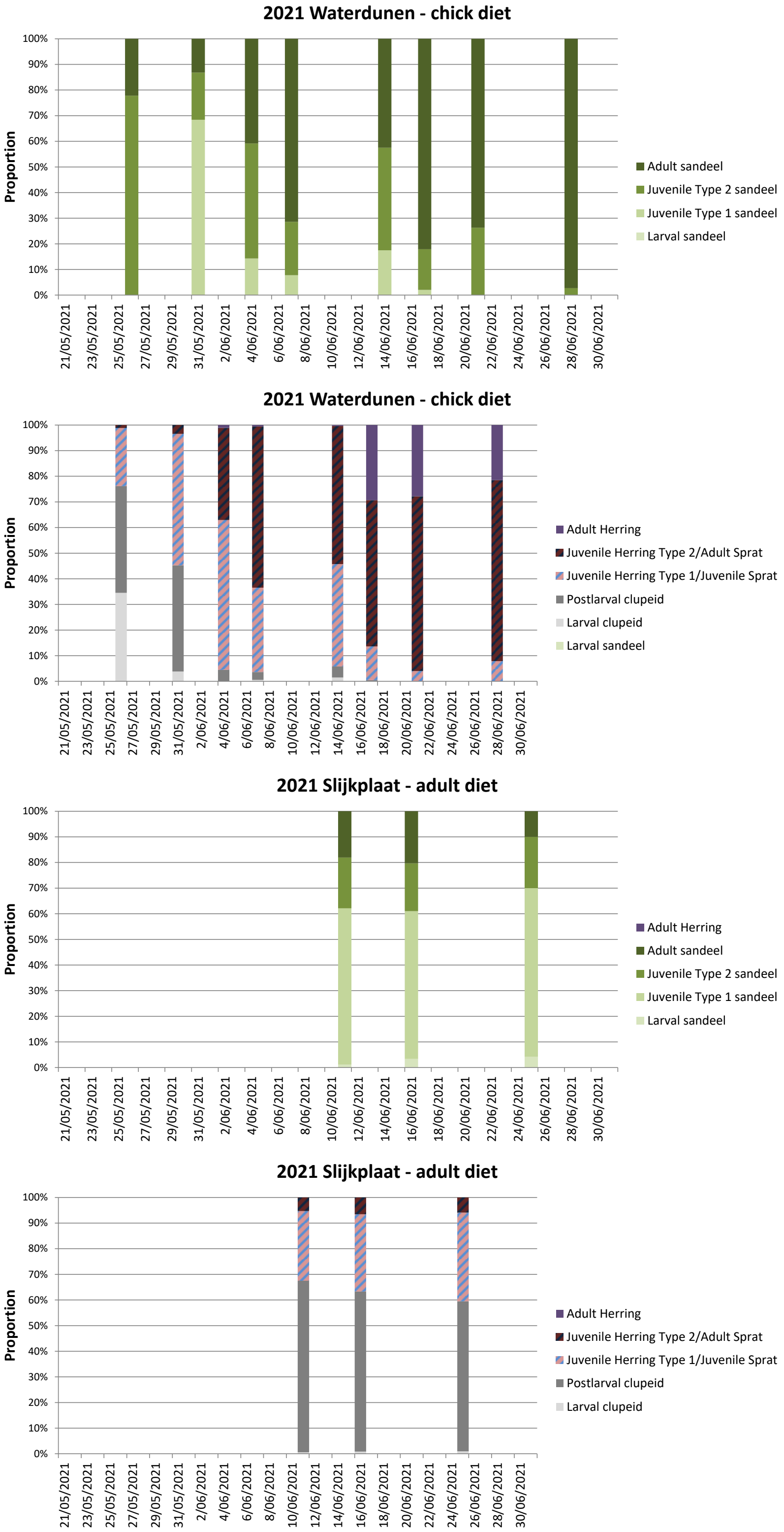

Figure 10.11 *Temporal variability in the age class composition of sandeels and clupeids in the diet of chick (upper panel) and adult (lower panel) Sandwich Terns in respectively the Waterdunen and Slijkplaat colonies in 2021.*

11 Conclusions and recommendations

R.S.A. van Bemmelen, R.C. Fijn

11.1 Which knowledge gaps have been filled?

This report combines data and results from several projects to fill important knowledge gaps concerning Sandwich terns and the potential impact of OWFs on this species. These knowledge gaps, identified by van Kooten *et al.* (2019), focus on 1) the distribution of Sandwich Terns, especially during the breeding period, 2) avoidance of OWFs and 3) demography, including age-dependent survival and emi- and immigration between colonies.

11.1.1 At-sea distribution of Sandwich Terns

Previous models to estimate population-level effects of OWFs on Sandwich Terns relied for distribution data on the ESAS and MWTL datasets. However, these datasets poorly covered Dutch Continental Shelf (1991-2014) and the breeding season (2014-2018). Since 2018, the MWTL monitoring now includes surveys in April and June providing better coverage of coastal waters during the breeding season. In addition, the ESAS database has been updated to include more (recent) ship-based surveys. Thus, both datasets should now provide improved general distribution data of Sandwich Terns to cover this knowledge gap.

At the same time, GPS-tracking of Sandwich Terns has produced a wealth of new knowledge on the at-sea distribution and behaviour of individual birds. In **Chapter 3**, we show to what degree the home ranges of birds from Scheelhoek/Slijkplaat and De Putten colonies overlapped with OWFs during 2019-2021. These tracking datasets, together with tracking data obtained at Scolt Head (United Kingdom) and Texel (data collected by WRM) and in combination with annual colony counts across the southern North Sea, were used to model the annual at-sea distribution of Sandwich Terns (**Chapter 6**). These modeled distributions show how overlap with OWFs changes as a function of the size and location of colonies.

11.1.2 Avoidance of offshore wind farms by Sandwich Terns

An important parameter required to model the potential population effects of OWFs on birds, is the amount of macro-avoidance of OWFs. Using tracking data from De Putten and Scolt Head, we were able to show a 5% macro-avoidance of OWFs by birds from Scolt Head, and 22% macro-avoidance by birds from De Putten (**Chapter 4**).

Another important parameter is the overlap between the rotor zone of wind turbines and the distribution of flight heights, as only birds that are within the rotor zone can potentially collide. We show that the majority of Sandwich Terns fly below rotor heights of the Borssele

OWF (**Chapter 7**). However, 4.1% of the birds fly at rotor height during foraging trips, which is much higher than the previous estimate of 1.8% generally used in Collision Rate Models.

11.1.3 Demography and diet

Colour-ring resightings indicate a high annual survival rate of adults, confirming the species is a long-lived bird (**Chapter 8**). Sandwich Terns were already long known for the large annual variations in colony size and locations but were also thought to be largely faithful to colonies if these were occupied. We now have quantified the degree to which individual Sandwich Terns switch between colonies from year to year.

Chapter 9 and 10 provide background information on the breeding numbers, breeding success and diets of Sandwich Terns on the Dutch coast. The research program at hand does not provide data on the direct link between habitat use and diet, neither does it provide data on the link between habitat use and breeding success (potentially via diet). However, the data collected do present a high-quality measure of various aspects of the breeding and feeding ecology of these birds that can be compared with the data collected before OWF developments (data collected within PMR-NCV) and future data collection to investigate whether changes have occurred over time. For example, in the past years more and smaller clupeidsa and sandeels were brought to the Waterdunen colony compared to previous years in colonies in the Northern Delta region. Despite this, breeding success in the colony was very good. This probably indicates high prey availability in the vicinity of the colony, as a high prey delivery rate could compensate for the low energy content of these small fish. This points to a small foraging distance and thus no major interaction with OWF Borssele. However, foraging duration (and distance to colony) increases with prey size (Fijn *et al.* 2017 & 2019), interaction of foraging Sandwich terns with Borsele OWF can be expected especially in the weeks before fledging. Furthermore, if OWF Borssele proves to be an area with high abundance of the right size of prey items, it might even lead to attraction of foraging Sandwich terns. This mechanism is however not studied yet.

11.1.4 Summary: how vulnerable are Sandwich Terns to OWF developments?

In summary, Sandwich Terns 1) avoid entering OWFs for 5-22%, 2) show distributional overlap of up to 0.6% during breeding with OWFs that are nearshore and close to colonies, 3) generally fly at low altitudes although 4.1% of the flux flies at rotor heigt, 4) are long-lived (annual survival rate of 0.92 for adults) and show 5) low year-to-year fidelity to breeding colonies.

This indicates that OWFs that are nearshore and close to colonies pose a potential threat to Sandwich Terns in a given year: they regularly encounter OWFs and avoid entering OWFs only in a minority of instances. Furthermore, because Sandwich Terns are long-lived and regularly switch between breeding colonies between years, the number of individual birds breeding in a colony is much greater across years than in any given year. Hence, also the number of individual terns that will interact with any given OWF will be very large over the life span of an OWF. On the other hand, Sandwich Terns' collision rates with offshore wind turbines may be relatively low considering some macro-avoidance takes place, and they normally stay below rotor heights. On the other hand, in previous CRMs a smaller proportion of birds flying at rotor height has been used, so mortality rates may have been underestimated.

Finally, if future OWFs are built outside the foraging ranges of breeding Sandwich Terns, the exposure of them to OWFs during the breeding season will be much reduced and potentially negligible in that period. That said, aerial surveys show that outside the breeding season Sandwich Terns do spend time far offshore, so in another part of the season interaction between OWFs and these birds might still occur.

11.2 Future studies

Despite the many knowledge gaps that have been filled in this report, some important issues remain.

11.2.1 Distribution

The amount of collected tracking data is substantial but does not cover the entire annual cycle or at least the period that Sandwich Terns are in the North Sea. These periods include the periods between spring arrival in the North Sea and settlement in a colony, the early incubation period, the post-fledging period, and the autumn migration period. The pre-breeding period is characterized by prospecting flights to many colonies and may include flights across the North Sea when visiting colonies on both sides. Colour-ring data show that such movements are performed. During the early incubation stage, birds are probably moving in similar ways as during late incubation and again prospecting to other colonies has been regularly recorded. However, movements will be more restricted to the vicinity of the colony than during pre-breeding. After fledging of the chicks, adults and their accompanying offspring have been recorded foraging far offshore. Finally, the migration period will include birds from elsewhere in Europe. Even (colour-ringed) birds from the colonies on the Atlantic coasts of France have been recorded traveling north towards the Netherlands post-breeding. It is not clear how long individual birds stage in the Netherlands before commencing migration to African wintering quarters, but foreign colour-ring data from e.g. Denmark and France could shed light on this. We also lack tracking data of immatures in the period between fledging and first breeding. We know that during their first and second summer (second and third calendar year), immatures usually remain in the wintering quarters, but their whereabouts in later years until first breeding are unknown. Hence, whether birds of these age-classes differ from adults in their spatial behaviour and the degree to which they avoid OWFs is unknown.

The tracking data are also unevenly spread in terms of sampled colonies. The largest colonies that have not been sampled are the colonies at the Hooge Platen/Waterdunen and colonies in the Dutch Wadden Sea. Griend has been very poorly sampled in one year only and the multiple colonies at Texel have been sampled in two years, but concern relatively small numbers of loggers. Missing GPS-tracking data from Hooge Platen/Waterdunen is especially problematic as these colonies are close to the Borssele OWFs and foraging Sandwich Terns were recorded in the vicinity of the OWF during ship-based (**Chapter 7**) and aerial surveys. We aimed to solve this gap by modeling of the distribution based on other colonies (**Chapter 6**). Still, tracking data from these colonies would be more than welcome and would also increase the predictive power of the distribution model from Chapter 6. The same applies to the Wadden Sea colonies. The few data that we have now indicate that the movements of birds from these colonies may differ substantially from colonies along the coast, given the differences in bathymetry and water currents, which may lead to different spatio-temporal dynamics of potential foraging opportunities.

11.2.2 Avoidance behaviour and flight altitudes

Although a better estimate for macro-avoidance is now available, estimates of meso- and micro-avoidance are still lacking. Meso-avoidance could potentially be estimated from digital aerial surveys - which are currently carried out in the Borssele OWFs. Preliminary results from these surveys will be included in the final version of this report. Meso-avoidance could also be estimated based on tracking data, in a similar fashion as for our macro-avoidance estimate in Chapter 3. The robustness of such an estimate depends of course on the number of GPS-positions within OWFs.

Flight altitudes have been measured outside the OWFs, but Sandwich Terns could show a behavioural response to turbines when within an OWF that may include adjustments in altitude. Therefore, measuring flight altitudes of Sandwich Terns within OWFs is advisable. In 2022, flight altitudes of Sandwich Terns will be monitored continuously using GPS-tagged breeding birds from Scolt Head. If these birds enter OWFs, flight altitudes can be compared between within and outside OWFs. Another option would be to do dedicated flight altitude measurements in and around turbines using a laser range finder.

11.2.3 Demography and diet

Using an extensive data set of colour-ring resightings, we were able to estimate age-dependent survival rates and emi- and immigration rates between colonies. Demographic parameters for which a robust estimate is still lacking, are the probability to skip a breeding season or to do a second breeding attempt within a single year, as well as age-dependent breeding success. We currently do not have the right data to estimate these parameters. This is because in capture-mark-recapture data, it is difficult to distinguish skipped breeding from a failure to detect breeding in a given year at a given colony. This is exacerbated by the fact that Sandwich Terns show low site fidelity. To assess age-dependent breeding success, success should be recorded for known-age birds, but these data have only scarcely been collected in the past within the PMR-NCV project, and we did not attempt to analyze these as this would have required a substantially higher time investment with rather uncertain perspectives.

Future efforts to study adult and chick-diets in colonies in the vicinity of OWF developments (Waterdunen, Hooge Platen, De Putten) will provide an insight in annual variation and trends over time of Sandwich tern diets and changes herein. Should there be effects of OWFs on the prey base of Sandwich terns these signals should be picked up from diet monitoring. This data combined with sampling efforts of pelagic forage fish in and around OWFs will shed even more light on the potential attractiveness and importance of OWFs for chick-feeding and self-provisioning Sandwich terns. If a positive or negative link would exist between OWFs and Sandwich terns, these data would be a prerequisite for a definite assessment of the relationship between the two.

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