

The consequences of seabird habitat loss from offshore wind turbines, version 2

Displacement and population level effects in 5 selected species

Author(s): Tobias van Kooten, Floor Soudijn, Ingrid Tulp, Chun Chen, Daniel Benden and Mardik Leopold Wageningen University & Research report C063/19



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Summary

Introduction

The planned large-scale development of offshore wind farms (OWFs) in the North Sea has potential consequences for many marine organisms, including seabirds. The response of seabirds to wind farms varies depending on species: some may be attracted to the wind farms leading to risk of collisions, some will avoid them and some do not respond. Those birds that avoid wind farms do not suffer from collisions but may suffer from habitat loss if OWFs are built in areas they use, which may in turn negatively affect the populations of seabirds using the Dutch continental shelf. Adverse effects of offshore wind farms on seabirds potentially lead to a trade-off between societal demands for marine nature conservation and clean energy. Seabirds are important target species in European conservation frameworks. In this report, we develop and apply a method for assessing the effect of habitat loss on five seabird species: red-throated divers (*Gavia stellata*), northern gannets (*Morus bassanus*), sandwich terns (*Thalasseus sandvicensis*), razorbills (*Alca torda*) and common guillemots (*Uria aalge*). To our knowledge, this is the first study that calculates effects on the full life cycle and the larger North Sea population.

Assessment method

To assess the effect of OWF related habitat loss on the larger North Sea population of the seabirds listed above, we aim to answer the following research questions:

- 1. What is the importance of the areas to be occupied by OWFs, and what fraction of the populations is confronted with OWFs?
- 2. What is the degree of displacement by OWFs of each of the species?
- 3. What is the cost of habitat loss (in terms of the survival probability) as a result of the placement of OWFs?
- 4. What are the population consequences of these changes in vital rates?

Key aspects of the assessment method are:

- It translates effects that are measurable in the field to population level indicators that are relevant for policy
- It takes a precautionary approach in dealing with uncertainty, and is able to quantify the uncertainty in the predictions
- It can differentiate spatial configurations/locations of OWFs, and can be used for future scenario studies
- It takes the OWF plans of other North Sea countries into account
- It is reproducible and built on the basis of good scientific practice

To answer our research questions we use a research method with three steps. First, we describe the population distribution based on habitat maps that are constructed based on seabird distribution data and abiotic explanatory variables. Second, we determine the cost of habitat loss using an individual based energy-budget model, the habitat model predictions and the degree of displacement. We calculate the 'cost' of habitat loss in terms of reduced survival rates of bird redistribution due to a change in the availability and configuration of the foraging area for several OWF scenarios. Finally, we use population models to project the effect of the reduction in survival rates on the population level.

We used all available information from scientific literature and expert judgement. Nonetheless, many steps in the calculations are characterised by uncertainties. For the habitat models we have quantified this uncertainty in uncertainty maps. For the individual based model and the population model we translated this uncertainty into two scenarios: a realistic and a precautionary scenario. For the realistic approach, we use the best available estimate for the degree of displacement, whereas in the precautionary case we use complete displacement. In addition to the reduced survival rates estimated with the IBM, we use a scenario where 90% of all displaced individuals survive (based on the previously

proposed 10% mortality method). We ran each scenario for situations without wind farms, for Dutch wind farms only, for foreign wind farms only and for all wind farms combined.

Results

For three species (northern gannet, razorbill and common guillemot), habitat suitability maps covered the entire North Sea. Due to data limitations, the habitat suitability maps for red-throated diver and sandwich tern were limited to the Dutch continental shelf area. It is technically possible to calculate tern and diver abundance outside the input data locations, but doing so implies that the relationships determining bird abundance in Dutch areas translate 1:1 to the rest of the North Sea. We have no data to study whether or not this is the case and have therefore chosen not to extrapolate for these two species.

The habitat model contains different significant explanatory variables depending on the species. All habitat models include a random spatial field. The overlap between bird populations and Dutch OWFs was generally found to be < 1.5% (0.4-1.3% overlap, depending on the species). For the species that were considered over the full North Sea area, international OWFs overlap more with the bird populations (2.4-6.1% overlap, depending on the species) than Dutch OWFs do.

In an un-impacted situation (without wind farms), the population models predict increasing populations for four out of five species. None of the OWF scenarios causes populations to become declining. Our results show, in thirty years' time, population sizes varying between 83% and 99% as compared to the situation without windfarms for precautionary IBM mortality scenarios, with all OWF (Dutch and Non-Dutch) in place. For all scenarios studied, the overlap between predictions for the un-impacted and impacted population is large. Given the variability in natural populations, we consider it unlikely that any of the OWF-related changes estimated in this assessment will be detectable in natural populations under realistic sampling effort.

The overall effect sizes of adding Dutch OWFs on the PGR and the chance of a >10% reduced population after 30 years are calculated as the percentage change in these criteria as Dutch OWFs are added. We do this compared to a situation without OWFs and compared to a situation where all non-Dutch OWFs are already in place. In all cases, effects of Dutch OWFs on population growth rate are well below 1%. The largest effect we find is a 0.7% decrease in population growth rate of northern gannets, which translates into a median population size of 83% after 30 years with all OWFs compared to a situation with no OWFs. The chance of a >10% smaller population after 30 years is below 5%, except for Northern Gannets where the effect of adding Dutch OWFs first is 12%. However, when the Dutch OWFs are added after all other OWFs, the effect is reduced to 2%.

The Wozep programme, of which this work is part, aims to reduce the need to rely on the precautionary approach in the assessment of ecological effects of OWFs. Our work has clearly contributed to this goal. The species we work on here have been selected based on their high sensitivity to OWF-related habitat loss in a previous study (van der Wal et al. 2018). We have constructed habitat models, individual based simulation models and population models, using all data and knowledge available to us. We have applied the resulting assessment framework using a consistent precautionary approach in every step.

Assumptions and uncertainties

To our knowledge, this is the first study that calculates OWF effects on seabirds based on the full life cycle and the larger population. OWFs are only one of the many sources of disturbance, next to e.g. shipping. The fact that we found only limited effects of OWFs does not preclude an effect in combination with other potential pressures. Furthermore, our results are specific to the particular spatial configuration of OWFs tested and effects may differ if planned OWFs would move to other locations. Finally, our results are specific for the species studied and different patterns may emerge for other bird species. The selection of bird species was not part of this study.

We used existing information to the best of our knowledge. Yet, there are still large sources of uncertainty that may influence the outcome. While our current analysis has taken into account

uncertainty in the population-level parameter values, we based our analysis on the average predicted values from the habitat models. As the habitat model is the first step in the analysis that we used in our approach, there are two sources of uncertainty that are not incorporated. Firstly, the uncertainties derived from the habitat maps are not propagated into the individual based simulation models. This means that a large contribution to the overall uncertainty is not visible in the population model outcomes. More fundamental however is the unbalanced nature of the available bird distribution data, on which we based the habitat models, which is an important source of the uncertainty in the habitat maps. If OWF areas would have higher (lower) habitat quality, this may lead to larger (smaller) population effects of those OWFs. The actual effect of OWFs on seabirds ultimately depends on how OWFs influence the vital rates of seabirds. We have assumed, in our individual-based model, a mechanism based on general ecological principles, but the specific mechanisms driving the survival of seabirds at sea are largely unknown.

Potential improvements

habitat modelling

For sandwich terns, the MWTL sampling programme is sufficient in space because they are strongly coastal. However, an extension in time to better cover the breeding- and postbreeding seasons would strengthen the knowledge base for assessment of OWF (and other anthropogenic) effects.

Red-throated divers are difficult to count because they are easily disturbed. One potential improvement to data collection for this species would be systematic monitoring using high definition cameras from planes flying at high altitude.

We are confident that data coverage for the Dutch part of the North Sea is sufficient and that all existing data for that area, as brought together in the MWTL and ESAS databases, were used in this study. Unfortunately, data coverage of other parts of the North Sea is not well balanced and the habitat model quality for gannets, razorbills and guillemots has suffered as a result. Maintaining the ESAS database has proven difficult in the last ten years or so, and not all survey data collected in these years have been forwarded to ESAS to be incorporated into the database. That survey data are missing from the ESAS database is evident based on habitat model analysis from different countries (see e.g. Evans et al. 2018; Mendel et al. 2019). Moreover, much of the national survey effort, including in The Netherlands, has been directed towards national waters. Wide ranging, international surveys have become increasingly rare. Within ESAS, suggestions have been made to let ICES host the (new) ESAS database and work towards international coordination of seabird surveys in corporation with fisheries institutes around the North Sea (potentially coupling fisheries surveys and seabird surveys). Support from governments of the North Sea countries, e.g., via the ICES delegates could be a great help here.

Individual based model

The IBM uses general principles from behavioural ecology and physiology: individuals move towards higher quality habitat, and if and individual does not feed enough it eventually dies. While these principles hold for the birds we study, they are most likely not enough to predict future behaviour of individual birds. Seabirds possess advanced navigation skills and learned behaviour, which are not incorporated in our individual based model. For seabirds feeding on cryptic prey species it can be challenging to instantaneously asses habitat quality. Instead foraging decisions are likely based on a individual specific cognitive spatial maps of foraging habitats, which are build-up and updated throughout their life. For example, tracking studies have shown that seabirds have individual strategies and can show strong fidelity to specific foraging areas (e.g. for Gannets, Wakefield et al. 2015). Ongoing advances in animal telemetry may lead to more insight into these aspects of seabird ecology also for other poorly studied species. While we cannot speculate how this would change our results, a better mechanistic treatment of behaviour could increase the credibility of our IBM.

For certain species it is worth exploring the potential to expand our model to the breeding season. This is particularly interesting for species which are highly mobile even within the breeding season, with a relatively small number of breeding locations which are well-studied. Northern gannets and sandwich terns would be the most likely candidate among the species studied here. This would allow for a better

estimate of the OWF effects on productivity (reproductive rate), which we currently have not incorporated. In addition, density dependence seems most important during the breeding season. Since the planned OWFs are placed inside the breeding habitat of northern gannets and sandwich terns (and to a lesser degree also of guillemots and razorbills), the OWFs could potentially impact the "breeding carrying capacity". An extension of our IBM modelling approach with crowding or local food depletion may yield better insights into these potential effects.

Population modelling

Generally, the quality of the life history parameters of the birds is good, except for the red-throated diver, for which little information is available. In addition, for razorbills some of the parameter estimates are fairly uncertain. This translates into large uncertainties in the results for these two birds. Better knowledge of life-history parameters would improve the predictive power for these species.

An important source of uncertainty in the population modelling is the entanglement of mortality estimates with migration. A better understanding of meta-population dynamics across colonies (the degree of exchange of older birds and new breeders between colonies, and the mechanisms behind the exchange) would greatly help. This would allow for better estimates of the mortality parameters and better understanding the importance of immigration and emigration for the population dynamics. Such an analysis is particularly relevant for sandwich terns breeding in the Netherlands and the UK, which are known to switch between colonies easily.

Density dependent population regulation has a strong effect on population dynamics. Unfortunately, there is not enough information available regarding density dependent mechanisms to include them in the population models for the birds under study here. Especially the importance of density dependent mechanisms in regulating meta-populations on the level of the whole North Sea unknown. Thorough, international studies of the bird populations during winter as well as the breeding season on the level of the entire North Sea or the European level are essential to better understand the population dynamics.

1 Introduction

1.1 Background

The work in this report is part of the Rijkswaterstaat Wozep programme, financed by the ministry of Economic Affairs and Climate. Wozep is directed towards obtaining a better understanding of the potential (cumulative) impact of multiple offshore windfarms on relevant and potentially vulnerable nature conservation values. It aims to enable a more science-based policy to achieve an ecologically sound approach on the offshore energy transition.

The planned large-scale development of offshore wind farms (OWFs) in the North Sea has potential consequences for many marine organisms, including seabirds. Some seabird species avoid wind farm areas (Dierschke et al. 2016). Such species may suffer from habitat loss if OWFs are built in areas they use, which may in turn negatively affect the populations of such species using the Dutch continental shelf or the larger North Sea area. Adverse effects of offshore wind farms on seabirds potentially lead to a trade-off between societal demands for marine nature conservation and clean energy. Seabirds are also important target species in European conservation frameworks such as the Marine Strategy Framework Directive and the Bird- and Habitat Directives.

Large-scale development of offshore wind farms is considered an essential part of a transition to carbonneutral energy production in The Netherlands and other North Sea countries. In order to develop the Dutch offshore wind agenda in an ecologically sound way, as outlined in the policy document 'Energieakkoord voor duurzame groei' (2013, English: Agreement on Energy for Sustainable Growth), the KEC ('Kader Ecologie en Cumulatie' English: Framework for Ecology and Cumulation of impacts) was compiled (RWS 2016). This document gives an overview of species and populations that may suffer from the planned OWF development, and highlights potential mitigating measures to prevent these problems. The work presented in this report follows directly from the KEC, in which a ranking is developed of seabird species deemed most at risk from the Dutch offshore wind farms through displacement and concurring habitat loss. In this work, we develop and apply a framework for assessing these effects on the 5 species indicated as the most sensitive in the KEC. The work in the KEC applies an identical method to a large number of species. This means that it applies strong generalizations and relies heavily on precautionary approach assumptions. By conducting a more detailed and species-specific assessment for the species indicated as most sensitive in the KEC, this study aims to reduce uncertainty in the assessment for the given species. Hence, this study quantifies in more detail the sensitivity of those species indicated most at risk in the KEC.

The aim of the work reported here is to develop and apply an assessment method to estimate population effects from OWF plans in Dutch waters, caused by OWF-induced habitat loss. Key aspects of the assessment method are:

- It translates effects that are measurable in the field to population level indicators that are relevant for policy
- It takes a precautionary approach in dealing with uncertainty, and is able to quantify the uncertainty in the predictions
- It can differentiate spatial configurations/locations of OWFs, and can be used for future scenario studies.
- It takes the OWF plans of other North Sea countries into account
- It is reproducible and built on the basis of good scientific practice

1.2 Research questions

The aim of this analysis is to quantify the effects, as a result of habitat loss, of OWF development in Dutch waters on the population development of five seabird species: red-throated diver (*Gavia stellata*), northern gannet (*Morus bassanus*), sandwich tern (*Thalasseus sandvicensis*), razorbill (*Alca torda*) and common guillemot (*Uria aalge*). This analysis consists of a number of elements of OWF-induced habitat loss which together allow us to assess the (potential) influence of habitat loss for individual birds on the population of these birds. Three sub-questions can be formulated that are the focus of different parts of the analysis and which together address the overall goal. The sub-questions are:

- 1. What is the importance of the areas to be occupied by OWFs, and what fraction of the population is displaced?
- 2. What is the (direct) cost of this habitat loss (in terms of time and/or energy)? And, how do the results of the above questions combined change the population vital rates (e.g. reproduction, survival) as a result of the placement of Dutch OWFs?
- 3. What are the population consequences of these changes in vital rates?

The approach to each of the elements of this analysis is based on a common framework for the five species studied here. It is adapted to reflect species-specific knowledge regarding the ecology, life history and the data availability for each of the species.

Question 1 will be answered using state-of-the-art habitat models, which couple bird survey data to biotic and abiotic independent variables.

Question 2 will be answered using individual based energy-budget models. The habitat model will be used, together with the OWF scenarios to be developed and the degree of displacement, to calculate the energetic costs of bird redistribution due to a change in the availability and configuration of the foraging area. Finally, we determine the 'cost' of the scenarios in terms of reduced survival rates. This requires a translation of energetic costs into changes in survival and will be done using a behavioural simulation model.

Question 3 will be answered using population models. These models will also be used to conduct estimates of sensitivity of the results to parameter uncertainty.

1.3 Scope of this study

1.3.1 Spatial

For northern gannets, razorbills and guillemots, we restrict our analysis to the area between -4° and 10° longitude and between 50° and 62° latitude. This covers the greater North Sea area (Figure 1.1). Within this area we ignore waters that are not part of the 'Greater North Sea' (e.g. the Wadden Sea, Bristol Channel and Irish Sea). For red-throated divers and sandwich terns, we have used a smaller spatial extent (2.5-7.5° longitude and 51-56° latitude), because we have little observational data for the remaining area. For all prediction maps (result of the habitat modelling) and effect calculations (individual-based simulation models) we use a spatial resolution of 0.01° in each direction, corresponding to pixel sizes of approximately 1.1 km (north-south) by 0.6 km (east-west). This resolution ensures that even the smallest OWFs will encompass several map pixels.



Figure 1.1: Spatial domain of the study. The black rectangle indicates the reduced spatial extent used for red-throated divers and sandwich terns

1.3.2 Temporal

The seabird survey data includes annual sightings in the period between 1991 and 2017. These data are a collation of many incidental and more systematic surveys, and are collected throughout the year. The habitat models do not use any time-dependent explanatory variables, like temperature or salinity. While this may limit their fit to the data, such models would be unusable for our purpose, as they require our scenario studies (individual-based simulation models) to include future predictions for those time-dependent variables. This is beyond the scope of this work, as we are interested in quantifying general effects of OWFs on populations. The parameters in the habitat models we use explain less variation than would be the case if time-dependent explanatory variables would be used. However we overcome this partly by the use of spatial statistics (R-INLA). Much of the unexplained variation caused by such variables is now covered by the spatial field that is part of the habitat model.

1.3.3 Populations

The research questions for this study pertain to population-level effects of OWFs on the Dutch Continental Shelf (DCS). Hence, we are primarily interested in the subset of birds which can be expected to frequently visit the DCS. For colony breeders, this implies that we include all breeding colonies of which the members are expected to use the DCS (this means, for example, that we exclude colonies on the British west coast, although they may interbreed with individuals from east coast colonies). There are three important issues associated with this approach:

- 1. It is impossible to assign birds sighted at sea to a breeding colony
- 2. There is always exchange of birds between colonies that do and those that do not use the DCS, and the magnitude of this exchange is largely unquantified
- Population models are generally based on 'closed' populations, where birth, growth and death, rather than emigration and immigration, are the dominant processes affecting population dynamics

The first issue implies that we cannot infer the relevant colonies from observations. The second issue implies that even if we do choose the relevant colonies, we cannot be sure that they are a population in

the sense of the 3rd issue. For the colony breeders (all except red-throated diver) we deal with these issues by considering the breeding colonies in a wide range around our focus area as part of the relevant population (Table 2.3).

For the birds that are mainly confronted with OWFs on the DCS during the winter season, we consider the birds that use the North Sea during the winter season as 'the population'. This implies that we consider the North Sea as a 'closed' area, in which the population resides during the whole winter season. We consider this a precautionary approach assumption, because mixing with other populations would effectively increase the population size, thereby decreasing the per capita effect and hence the effect of OWF on the population level.

1.3.4 Effect scenarios

OWF placement scenarios

The OWF scenarios we study are focused on establishing the effects of the Dutch OWF development. However, the Dutch OWFs cannot be studied in isolation, but must be viewed in the context of international OWF developments. Therefore, we study 3 OWF placement scenarios:

- 1. The addition of only the Dutch OWFs
- 2. The addition of only the non-Dutch OWFs
- 3. The addition of all OWFs (1. and 2. above) simultaneously

With these 3 scenarios we cover the effects of the Dutch plans in isolation as well as the Dutch plans within the context of the wider development of OWFs in the North Sea. We use the OWF data as presented in van der Wal et al. (2018), which document the areas of all existing and planned North Sea OWFs.

Displacement and mortality scenarios

We study the effects of these OWF placement scenarios using a 'realistic' and a 'precautionary' approach. These names reflect the philosophy underlying each: the realistic scenario consistently uses best estimates based on current knowledge, whereas the precautionary approach uses the lower bound of the estimated uncertainty. For the realistic approach, we use the best available estimate for the degree of displacement (Dierschke et al. 2016), whereas for the precautionary approach we use complete displacement: all birds inside planned wind farms will move elsewhere. For each scenario, we use two mortality options. The first assumes 90% survival of displaced birds, based on the 10% mortality assumption previously proposed for the effect of habitat loss (Leopold et al. 2014). The second is based on the IBM, which produces a frequency distribution of survival probabilities from a large number of stochastic simulations. The realistic approach uses the survival probability at the median of this frequency distribution, while the precautionary approach uses the 5th percentile of the survival frequency distribution. For the 5th percentile, survival will be equal to or smaller than the value used in only 5 out of 100 estimations, whereas in 95 of 100 estimates it will be higher (where the actual effect is 95% certain to be smaller; Table 1.1).

The 10% mortality is assumed to occur over a full year of presence in an area with OWFs. The additional mortality is corrected for the length of the period that each of the birds spends in the area with the wind farms (Table 2.1). For red-throated diver, razorbill and common guillemot, OWFs are assumed to affect survival only in the non-breeding season (Table 2.1). The distribution of those species during the breeding season is strongly constrained by the locations of breeding colonies. Though some OWFs are planned close to specific colonies, we have assumed here that plasticity in the breeding locations prevents OWF-induced mortality during the breeding season. The rationale for this assumption is that colonies near OWFs will become less attractive breeding sites so that newly breeding individuals are more likely to settle in other locations. Gannets are affected both in the summer and winter period, while sandwich terns are affected only in the breeding season (Table 2.1).

Table 1.1 Mortality and displacement scenarios

population model scenario

degree of displacement survival of displaced individuals

precautionary	100%	1.	90%
		2.	5 th percentile of simulation
			model estimate
realistic	best available estimate for	1.	90%
	each species	2.	Median (50 th percentile) of
			simulation model estimate

2 Materials and Methods

2.1 Outline of the analysis

The analysis framework applied here consists of 3 steps.

The first step is a habitat model, which couples bird observations to abiotic variables at the place of the sighting. This model can be used to generate a habitat map, which predicts abundance at each location on the map based on the relevant abiotic variables at that location. Because we are interested in estimating the effects of planned OWFs, rather than in explaining spatiotemporal patterns in the past, we are limited to using abiotic variables that are constant in time (over the years), such as depth. For example, if we would use temperature data, we would need spatially resolved temperature predictions for the next 30 years. While this means our model may be crude compared to some published seabird distribution models, those models are not suitable for our purpose.

The values on the prediction map from step 1 are used as a measurement of habitat quality. Using the map, an individual-based simulation model is used to assess the effect of OWF on seabird survival. This model simulates a large number of individual birds, moving around on the prediction map. Each individual in the simulated population has an energy budget, which can increase in good locations (with high bird densities as a proxy for food) and decreases in bad locations (low bird densities). Once energy runs out, an individual is assumed to die. This model does not include reproduction. We calibrate the model so that at the end of the season (Table 2.1), without OWFs, the survival corresponds to a known value for each specific bird and life stage. We then add the OWFs and displacement to the model and run it again. This yields the new survival value in the presence of OWFs. This method assesses only the direct effect of the inaccessibility of the areas where OWFs are located. It does not take the potential effect of reduced carrying capacity into account, because there is not sufficient information available regarding the importance of density-dependent in regulating seabird populations (see section 4.4).

The final step in our analysis is an estimate of the population level effects of changes in survival due to OWFs, as derived above, using a matrix population model. This allows us to study the OWF effects on population growth rate, population development over 30 years, and a number of other relevant criteria. We assess changes in survival rates for several different scenarios (realistic and precautionary).

2.2 Habitat suitability models

2.2.1 Data sources

Habitat suitability modelling requires data on the spatial distribution of birds and on the other (biotic and abiotic) conditions. We have used the following data sources for the habitat models:

Bird observation data

For modelling at-sea seabird distribution, data are needed on seabird counts at sea (density estimates) that are geo-referenced. We used two sources of data:

- 1. the ESAS (European Seabirds At Sea) database (mostly ship-based counts of seabirds), kept at JNCC, Aberdeen, covering the entire North Sea.
- the MWTL database (Monitoring Waterstaatkundige Toestand des Lands, plane-based counts, available via Noordzeeloket, Rijkswaterstaat), for the Dutch section of the North Sea only, also including the ship-based Shortlist Masterplan Wind data collected in 2010-2011 (Van Bemmelen et al. 2011).

ESAS contains both ship-based (ESAS-ship) and aerial surveys (ESAS-fly), which were treated separately. From each database, only observations were used from 1991 to the most recent data available (2017). For an overview of the locations of observations in these two data sets, see Figure 2.1.

Handling bird data

Distance sampling is a widely used methodology for estimating animal density or abundance (Buckland and Turnock 1992; Buckland et al. 1993). A key underlying concept is that the probability of detecting an animal decreases as its distance from the observer increases. The distance sampling methodology is based on detection functions, which model the probability of detecting an animal as a function of distance from the observer trajectory in transects. Distance sampling was applied to arrive from the observed sightings to densities.

ESAS ship

ESAS sampling effort is strongly directed by specific projects often connected to wind farm locations or special protection zones. The ship-based observations in ESAS are made using a strip-count with series of strips on one or both sides of the ship. Based on density sampling theory and on the assumption that the birds were evenly distributed before the observing ship entered the area, and that equal densities should be present at all distances from the ship's track line, species-specific correction factors were derived to compensate for birds missed at greater perpendicular distances (Table 4.2 in Leopold et al. 2014, for details see Fijn et al. 2015).

MWTL

The survey design of this programme has been restructured both temporally and spatially in 2014 and was shifted from a strip-transect analysis to line-transect (Distance) analysis. In the analysis we did not correct for this transition in methods. Sampling surface was calculated as effective-strip-width × speed × time. For methods used to arrive at densities see Van der Wal et al. (2018).

From an airplane with a survey altitude of 500 ft. as conducted in the MWTL monitoring programme a number of sea bird species is indistinguishable from each other, e.g. 'razormots', i.e., razorbills/common guillemots. For these, the ship-based observations from the same season and area have been used to split these 'combi-species' into the respective single species, using the method previously described by Leopold et al. (2014). The small divers, red-throated diver and black-throated diver are difficult to distinguish in the field, but we also know that red-throated divers greatly outnumber black-throated divers in the North Sea. Therefore, we refer to red-throated divers throughout the text.

For every bird species, first the species-specific appropriate seasons were determined for which habitat models should be formulated. This was based on the spatial and temporal coverage of different surveys (by mapping monthly distribution for each species). For razorbill, common guillemot and red-throated diver winter (non-breeding period) numbers were used. For sandwich tern the breeding season and for northern gannet both the non-breeding season and the breeding season were selected, but gannets visiting Dutch waters during the breeding season were assumed to be non-breeding individuals (juveniles, immatures and/or 'floaters').

Table 2.1. The selected months for every species used in the habitat and IBM models.

species	selected months	period for which a habitat model was constructed	data source used
red-throated diver	Oct-March	non-breeding season	MWTL
northern gannet	Sept-March	non-breeding season	ESAS + MWTL
northern gannet	April-Aug	breeding season	ESAS + MWTL
sandwich tern	April-August	breeding season	MWTL
razorbill	Oct-March	non-breeding season	ESAS + MWTL
common guillemot	July-April	non-breeding season	ESAS + MWTL

2.2.2 Abiotic data

The explanatory variables are the abiotic factors prevailing at the location of each observation. For all species the same set of abiotic variables was considered in the habitat models:

- depth (smoother)
- day of season (smoother)
- distance to the nearest colony (common guillemot, razorbill, northern gannet. For sandwich tern distance to coast was highly correlated to distance to colony, so only distance to coast was used)
- distance to the nearest coast
- sediment type
- slope of the sea floor
- aspect of the sea floor
- survey (sampling) type
- surface area surveyed

An overview of several of the above variables is given in Figure 2.2. The distribution of the different species is likely to be affected by the combination of all these (abiotic) parameters. However, in the final selection of the relevant parameters, the ultimate goal of the habitat models was leading: to arrive at a time-invariant predicted density map. Because of this we could not include explanatory variables which change in time and for which future predictions are not readily available (temperature and salinity). For the same reason, a year effect was not included. Given that all species considered are long-lived, we also do not expect a strong year effect. Aspect of the seafloor (the direction of the slope) was considered as an explanatory variable since it was mentioned in some publications, but an exploratory analysis (GAM) indicates no relationship with density, therefore, it was excluded from the final model. Due to computational limits no interactions between explanatory variables were considered.

An important variable which is missing in the above list is the (fish) food for the seabirds. While we have some knowledge of the long-term average distribution of the various species in the diet of the birds, its spatiotemporal distribution is highly variable and not well studied. The explanatory relationship found with some of the above variables may hence describe a relationship with prey fish, which in turn are related to seabird abundance. For example, sandeel are important prey fish, which have a strong association with particular sediment types. A relationship between seabird abundance and sediment could thus be a proxy for a relationship between sandeel and seabirds. Because adequate data on sandeel distribution is unavailable, our analysis does not deal with such causal nuances.

Distance to coast

Coastline data were obtained from OpenStreetMap at http://openstreetmapdata.com/data/coastlines. Zoom level 5 was used in all calculations.

Day of season

For each observation, day of season was calculated as the number of days between the start of the current season (Table 2.1) and the observation date. This captures seasonal variation but not variation between years.

Water depth

Bathymetry data were obtained at a 30 arc-second resolution from the GEBCO Digital Atlas published by the British Oceanographic Data Centre on behalf of the Intergovernmental Oceanographic Commission and the International Hydrographic Organization, 2014.

Sediment

Seafloor habitat data were obtained from Emodnet. We used the dataset 'EUSeaMap 2016: Marine Strategy Framework Directive MSFD Benthic Broad Habitat Types'. The classifications used include aspects other than sediment type. We used a simplification of the habitat classification in the data (Table 2), because the full classification includes depth information, which we included separately.

Slope and aspect of the sea floor

The slope of the seafloor (in degrees) was calculated from the depth map, based on the depth difference with adjacent grid cells, using the function 'terrain' in the R package 'raster'. The aspect is the direction of the slope (0 to 360 degrees, where 0 and 360 indicate a northerly slope).

type	description sediment	grouped category
A5.13	infralittoral coarse sediment	coarse sediment
A5.14	circalittoral coarse sediment	coarse sediment
A5.15	deep circalittoral coarse sediment	coarse sediment
A5.23	infralittoral fine sand	fine sand/muddy sand
A5.24	infralittoral muddy sand	fine sand/muddy sand
A5.25	circalittoral fine sand	fine sand/muddy sand
A5.26	circalittoral fine sand	fine sand/muddy sand
A5.27	deep circalittoral sand	sand
A5.33	infralittoral sandy mud	sandy mud
A5.35	circalittoral sandy mud	sandy mud
A5.37	deep circalittoral fine mud	fine mud
A5.44	circalittoral mixed sediments	mixed

Table 2.2. Eunis classification level 5 and simplified groups.

Distance to colony

For common guillemots, razorbills and northern gannets, information on breeding colony locations was obtained from 'Seabird populations of Britain and Ireland' (Mitchell et al. 2004). For guillemots the Helgoland colony was excluded because it is small in comparison to other colonies, and its inclusion would lead to an inflated assignment of observed birds to that colony. In other words, many more bird observations would have these small colonies as 'nearest colony' than actually breed there. The colony locations were simplified to combine clusters of adjacent colonies (Table 2.3). For sandwich tern, colony data were examined but since distance to colony was highly correlated with distance to coast, only the latter was used.

Table 2.3: Locations of breeding colonies of gannets	s, common guillemots a	nd razorbills (WGS84
coordinates).		

species	colony	longitude	latitude
northern gannet	Shetland Islands	-1.194546	60.406036
	Bass Rock	-2.640667	56.077719
	Bempton Cliffs	-0.126189	54.132481
	Troup Head	-2.297285	57.700378
	Guernsey	-2.239297	49.704769
	Helgoland	7.897865	54.18325
	Scottish mainland south	-1.994228	55.780047
	Norway	5.635605	59.108856
razorbill	Bempton Cliffs	-0.126189	54.132481
	Shetland Islands	-1.194546	60.406036
	Orkney Islands	-2.805229	59.031799
	Scottish mainland north	-1.998647	57.314904
	Scottish mainland south	-1.994228	55.780047
common guillemot	Bempton Cliffs	-0.126189	54.132481
	Shetland Islands	-1.194546	60.406036
	Orkney Islands	-2.805229	59.031799
	Scottish mainland north	-1.998647	57.314904

2.2.3 Statistical analysis

R-INLA

The bird data we are dealing with are complex. The reason for this is that birds tend to occur in clusters, resulting in spatially and temporally correlated data: An observation at one point in space is more similar to a point close by than to a point further away. The same holds for points in time: the number in year 1 is more similar to the number in year 2 than to the number in year 5. Data are correlated in both space and time and we need to account for this in the analysis. Furthermore, we are dealing with data that come from different sources, collected from planes and ships, by different observers, and these sources of variation also need to be taken into account. That can be done by using hierarchical models: models that take into account variation on different levels that we know affect the observations, but that we are not necessarily interested in. Hierarchical models are widely used in ecology to represent complex dependency structures in data. The most advanced way to incorporate all these requirements to the data analysis is using R-INLA and Gaussian Markov random field, under the Bayesian statistics framework (Rue et al. 2009; Lindgren et al. 2011).

Hurdle model with spatial random field

In the analysis we applied a two-step hurdle model. In a hurdle model we focus on two questions, namely (i) what is driving absence and presence of birds? And (ii) once birds are present, what is driving their abundance? The first question requires a Bernoulli GLM (or GAM) and the second part a log-normal GLM (or GAM). For the positive density model we tried different distributions: truncated Poisson (for count), gamma (for square root transformed density). A log-normal distribution was chosen because it provided the best model diagnostics and is relatively simple.

A so-called mesh is defined for the study area. This means that a large number of connecting triangles are created; see Annex 1. The mesh consists of a large number of nodes (i.e. the vertices of the triangles). The mesh we used for northern gannet, common guillemot and razorbill has 820 nodes (within the entire area), the mesh used for the sandwich tern and red-throated diver has 4604 nodes (within the Dutch continental shelf only), which means that the software will estimate values for each node. In the

mesh with 820 nodes the mean distances between the nodes are 50 km, in the mesh with 4606 nodes this distance is ca 5-10 km. The choice for a specific mesh is a compromise between a biologically sound spatial distance and reasonable computation complexity. Computation time directly relates to mesh size (finer meshes take more time). For sandwich tern and red-throated diver we were able to use a finer mesh, because the area was limited to the MWTL data, which provided a better sample quality, allowing to investigate the spatial resolutions better and obtain a more precise and biologically sound spatial component of the distribution map (see Annex 1). For simplicity the same mesh is applied to both the first (presence-absence) and second model (positive density).

Using the mesh, the model estimates a spatially correlated random effect. Instead of estimating the spatial random effects directly, we will estimate one value at each node. To estimate this term, a mathematical model is imposed on the covariance matrix of the spatial random effects, namely the so-called Matérn correlation function. This function dictates that sites close to each other have similar spatial random effects, and the further sites are away from each other, the less similar are the spatial random effects. Based on the values in each of the mesh nodes, the spatially correlated random value is calculated as a weighted average of the surrounding values. The mesh is also used to calculate the parameters of the Matérn correlation. Note that any estimation outside the sampled area is extrapolated and thus should be interpreted with care.

An important aspect of our type of data is that they suffer from an observer effect: different observers have differing detection probabilities. This is a well-known problem of bird count data (van der Meer and Camphuysen 1996), which can be corrected for. However, our long-term data set contains too many observers (>100) and this factor contains too many missing values to carry out a meaningful correction. Therefore, we have not taken this into account.

Most ESAS samples were collected in very few years, and the data in terms of year, survey type and spatial distribution are therefore very unbalanced (cf. Fig. 2.1). However, we assume that there is no change in the relationship between seabirds and explanatory variables over the years and thus ignore the year effect and serial correlated spatial random field. As a result, we are able to obtain a time-invariant density map.

It is known that water depth exhibits a non-linear relationship with density. Therefore, in all models, it was modelled as a smoother using cubic regression spline (knots=4). Similarly, the density might peak during the middle of the season. Thus, a smoother (or polynomial) is also preferred for day of the season covariate. However, from the exploratory analysis (GAM) on our bird data, we either did not observe a peak-at-middle-season effect, or observed no effect (e.g. sandwich terns). Therefore, to compromise with the computation limits, we only applied day as a cubic regression spline (knots=4) for red-throated diver, while for other species we kept a linear relationship.

In the end, the following Bernoulli GAM with time-invariant spatial random field was fitted for presenceabsence of bird:

$$bird_i^{01} \sim \text{Bernoulli}(\pi_i)$$
$$E(bird_i^{01}) = \pi_i, \quad \text{var}(bird_i^{01}) = \pi_i \times (1 - \pi_i)$$

 $logit(bird_i^{01}) = intercept + f(depth) + slope_i + dis_coast_i + dis_colony_i + days_season_i + data_source_i + sediment_i + u_i$

The response variable $bird_i^{01}$ refers to the absence and presence of the bird at location *i*, which follows a Bernoulli distribution with a probability π_i of presence. Model covariates are described in Section 2.2.4: water depth, slope, distance to coast, distance to colony, days after the beginning of breeding (or non-breeding) season, data sources, sediment type. Water depth effect was modelled as a smoother using cubic regression spline (knots=4). Additionally, a spatial random effect u_i was included to estimate the spatial correlated effect.

The following log-normal GAM with time-invariant spatial random field was fitted for the positive density:

$$\log(bird_i^+) \sim N(\mu_i, \sigma^2)$$

$$E(\log(bird_i^+)) = \mu_i$$
, $var(\log(bird_i^+)) = \sigma^2$

 $log(bird_i^+) = intercept + f(depth) + slope_i + dis_coast_i + dis_colony_i + days_season_i + data_source_i + sediment_i + u_i$

The response variable $bird_i^+$ refers to the positive density of the bird at location *i*. The log transformed density follows a Normal distribution with mean μ_i and variance σ^2 . To be consistent with the presence-absence model, the same covariates were kept in the log-normal GAM model.

The main purpose of this study is to use environmental covariates to interpret and extrapolate density (i.e. provide a best fitted distribution map), rather than understanding the causal relationships. Therefore, we did not apply strict rules to prevent correlated covariates, such as depth, distance to coast, and distance to colony, or survey type vs. area. It is not useful to conduct a model selection procedure if the covariates are correlated and the main goal of the model is to offer predictions rather than finding causal relationships. Therefore, we did not apply a model selection procedure. Instead, for every species we applied a model with and without the spatial random field to investigate whether applying a spatial random field improves the model. These models are compared using the Watanabe-Akaike information (WAIC). Models with lower WAIC value indicate a better fitting.

The statistical analysis was conducted using R Core Team (2014) and R-INLA package at www.r-inla.org (Rue et al. 2009; Lindgren et al. 2011; Zuur et al. 2017).



Figure 2.1. Overview of observer effort per year for the two data sources. Dots indicate locations of observations. Colours correspond to MWTL (blue) and ESAS (red) data sources.

Prediction maps

To obtain the distribution of the mean density map, we conducted a simulation-based approach. First, we simulated a set of regression parameters and spatial random effects from their joint posterior distribution, for the presence-absence (model 1) and positive density models (model 2), respectively. From the parameters we calculated the estimated presence probability as well as positive density at each location of the map. In model 2, since the response is based on log-transformed data, we applied the exponential function to back-transform the model 2 response to the original scale. The estimated mean density given this set of parameters, is then the multiplication of the model 1 and model 2 response at each location on the map. We then repeat this process for 1000 times. As a result, a marginal posterior distribution for the mean density was obtained from the 1000 simulations at each location of the map. At each location, the median of this distribution was used as the value for the mean map, and the 2.5% and 97.5% percentiles were used as the 95% credible intervals (the Bayesian analogue to confidence intervals). We computed the difference between the 97.5% and 2.5% percentile maps as a straightforward and rough way to illustrate the precision/uncertainty of the estimated mean map. Thus, a higher value on the precision map indicates a higher uncertainty in the mean density estimation.



northern gannet: distance to colony



common guillemot: distance to colony



Figure 2.2. Covariates used in the habitat models (distance to coast is used for sandwich terns but not shown here). The grey areas (Norwegian coast and far north) are very deep, and there were very few bird observations for this area. Any prediction for this area would be very speculative and hence we exclude it from the prediction.

2.3 Individual based model

For each species we used an individual based simulation model to assess the effect of OWF-related habitat loss on survival rate. This model uses an energy budget approach to quantify this effect. In a first step, the model was calibrated in absence of planned OWFs to yield the value for survival that has been observed for the birds in the field (Table 2.4). The calibrated model was then used to calculate the change in survival as a result of adding the planned OWFs.

2.3.1 Behavioural simulation

The model simulates a large number of birds (100,000) each occupying a location on a map, which is the output from the habitat model for that species, normalized by the maximum abundance on the map. Individual birds move to adjacent map cells each 4 hours. OWFs are implemented as cells on the map which are (partially) inaccessible, with the accessibility set to zero in the precautionary scenario and to a species-specific estimated value in the realistic scenario (Table 1.1). Survival is calculated as the number of individuals at the end of the simulation relative to the number at the start of the simulation. Simulations are run for the relevant species-specific season length (Table 2.1).

As an illustration of this process, Figure 2.3 shows the spatial distribution of simulated razorbills at the end of a simulation. The OWFs are visible as (black) shadows between the birds (shown in white). We can see that the distribution closely follows the habitat quality and that the birds clearly avoid the windmill areas but not completely.



Figure 2.3 Spatial razorbill distribution at the end of a realistic displacement simulation.

2.3.2 Individual model

Energetics

The model assumes individual birds have an amount of energy E(t) available at time t. As units of this energy, we choose 'normalized habitat quality'. This is convenient because it prevents the necessity to scale from habitat quality to actual food availability and energy content, and it allows us to use the

values in the habitat map directly as energetic gain. We assume that individuals have an intake of energy I(t) at time t, which equals the normalized habitat quality of their location at time t. Finally, energetic costs T per time step are assumed constant. We can now calculate the dynamics of the energy budget of an individual bird over time as

$$E(t) = E(t-1) + I(t) - T.$$

Which relates the available energy at time t, to the energy in the previous time step, E(t - 1), plus the energy acquired at the current time step, minus the energetic cost per time step.

Behaviour

We assume that individuals either stay where they are or move to adjacent cells (8 nearest neighbour cells) on the map. The probability of moving to any potential location is proportional to the relative habitat quality of the 9 cells (8 nearest neighbour cells plus the current location). If one or more adjacent cells are on land, outside the map or inside OWF areas, there is a reduced chance to move to those locations (either zero or a reduced chance in case of partial displacement). This is included in the relative habitat quality, which hence can be zero. The individual then moves randomly following the derived probability distribution. For OWF locations the relative habitat qualities of the OWF cells are downscaled, so that individuals are less likely to move into and more likely to leave OWFs (Table 2.5). The chance to move to an OWF cell c_i is downscaled with 1 - displacement, while the remainder $c_i \cdot displacement$ is distributed over the neighbouring non OWF cells proportionally to the habitat quality of each non-OWF cell, such that the chance to move there becomes higher. The displacement values are given in Table 2.5.

2.3.3 Calibration

The goal of the calibration is to tune *T* in such a way that the survival (the number of birds at the end of the simulation divided by the numbers at the start) equals the correct value, which we take from the literature. We find the value T^* corresponding to the desired survival probability by solving S - S(T) = 0. We solve the equation using the bisection method. For each value of *T* we run the model 10 times, and T^* is reached when the desired value for survival equals the mean of the simulations for a given *T*. The number of runs is low due to computational time constraints. For calibration we use a scaled habitat map without the projected Dutch OWFs. The calibration procedure is carried out separately for each stage or age class in each population model which has its own survival parameter value.

2.3.4 OWF effects on survival

In order to estimate the effects of OWFs, we use the T^* derived in the calibration step, incorporate the OWF scenario in the habitat map, then re-run the simulation to obtain the survival probability corresponding to the OWF scenario. We do this last step a large (1000) number of times so that we can estimate the effect of the stochasticity inherent in the movement process. Going forward to the population models, we use the survival value at the 5th percentile of the distribution for the precautionary scenario, and for the realistic scenario we use the median survival.

2.3.5 Initial conditions

For both calibration and simulation the model needs an initial energy and an initial position on the habitat map for each bird. For the initial energy we arbitrarily use the mean value of the habitat map multiplied by 2. Testing showed that the actual initial value is irrelevant as long as it is sufficiently high to prevent immediate starvation, and this choice guaranteed that a sufficiently high value was chosen. A weighted discrete random distribution is used to determine the initial position of each bird. For each cell on the map the chance for a bird to start in this cell is weighted with the value of that cell in the habitat map.

2.3.6 Parameterization

Table 2.4 describes the general parameters used for calibration and simulations. The survival probabilities were only used during calibration. The season length is equal to the number of months a bird population uses the study area (Table 2.1). Although razorbills and guillemots are present all year, their dispersal in the breeding season follows other rules due to the central-place foraging associated with breeding. Gannets appear all over the area throughout the breeding season (but with a different distribution), and therefore we have conducted separate simulations for the breeding and non-breeding season. To calculate the number of time steps, we use the season length and the assumptions that birds move to another cell every 4 hours and that each month has 30 days.

For each species we defined a survival scenario (see Table 2.4). The annual survival S_y is scaled to seasonal survival S_m where m is the length of the season in months. The scaling follows:

$$S_m = e^{\frac{m\ln(S_y)}{12}}.$$

The best estimates for the displacement rates (Table 2.5) are based on the review by Dierschke et al. (2016) of bird displacement by wind farms in European waters. In the review, (red-throated) diver and northern gannet are categorized as 'strong avoiders' of wind farms, while razorbill, guillemot and sandwich tern are qualified as 'weak avoiders' of wind farms. In addition, a mean displacement score is calculated. The review does not explicitly define a best estimate of displacement. To estimate this value we used the information of areas for which displacement was quantified. This resulted in the following values per species:

- For the (red-throated) diver, displacement >80% was found in one study area (Dierschke et al. 2016). This was however non-significant, most likely due to limited sample size. We chose a value of 0.8 as a best estimate of the displacement rate for the diver, as we are not aware of other studies.
- Observations of gannets show a significant displacement >50% in two areas and a nonsignificant effect >80% in another area (Dierschke et al. 2016). We chose a value of 0.8 as a best estimate of the displacement rate for the gannet.
- For the sandwich tern, observations show a significant displacement >50% in one area, while multiple studies report indifference (Dierschke et al. 2016). We chose a value of 0.5 as a best estimate of the displacement rate for the sandwich tern.
- Razorbill observations show significant displacement <50% in 2 areas and non-significant displacement >50% in 3 areas (Dierschke et al. 2016). We chose a value of 0.5 as a best estimate of the displacement rate for the razorbill.
- Guillemot observations show significant displacement >50% in two areas, non-significant displacement >80% in one area, significant displacement < 50% in one area and no signs of displacement were found in three areas (Dierschke et al. 2016). We chose a value of 0.5 as a best estimate of the displacement rate for the guillemot.

Table 2.4 General parameters for calibration and simulations

survival	species	season length (m)	time steps	annual
				survival

red-throated diver	7 months	1260	0.84
northern gannet (breeding)	5 months	900	0.9
northern gannet(non-breeding)	7 months	1260	0.9
sandwich tern	5 months	900	0.95
Razorbill	7 months	1260	0.9
common guillemot	10 months	1800	0.94

Table 2.5 Windfarm displacement parameters

species	realistic	precautionary
red-throated diver	0.8	1
northern gannet (breeding)	0.8	1
northern gannet (non-breeding)	0.8	1
sandwich tern	0.5	1
razorbill	0.5	1
common guillemot	0.5	1

2.3.7 Stability, accuracy and precision

We tested the model for stability, accuracy and precision of the obtained solution. The model is invariant to the initial conditions, so the simulated survival is equally independent of the initial conditions. The model also has high accuracy: the simulation returns a survival very close to the survival used during the training if we run it without any OWFs. The precision is defined as the difference between the 95% percentile and the 5% percentile of the survival distribution. The precision of the model is ± 0.001 . A more detailed description of the results and methods can be found in Annex 4.

2.4 Population models

2.4.1 Matrix model structure

We use stage-structured matrix population models for all five bird species. Depending on the species, we choose a different number of life stages. A higher number of stages can be used when the resolution of the knowledge of life-history parameters is higher. Below we describe the setup and analysis of the matrix models in general terms. Per species we discuss the stage structure of the model, the setup of the projection matrices, the parameter values and sources of population data.

For stages that comprise multiple year classes, transition rates are estimated based on the assumption of a stable age distribution. Following Crouse et al. (1987):

$$P_{i} = \left(\frac{1 - p_{i}^{d_{i}-1}}{1 - p_{i}^{d_{i}}}\right) p_{i},$$
(1)

the probability of surviving and remaining in the same stage P_i , is calculated based on p_i , the annual survival probability, and d_i , the number of years individuals remaining in the stage. The probability that an individual survives and passes to the next stage G_i is given by:

$$G_i = \frac{p_i^{d_i}(1-p_i)}{1-p_i^{d_i}}.$$
(2)

Survival and ageing from one breeding season to the next is described by the matrix M_w . This is an example based on a model with four stages (sandwich tern):

$$M_{w} = \begin{pmatrix} P_{1} & 0 & 0 & 0\\ G_{1} & P_{2} & 0 & 0\\ 0 & G_{2} & P_{3} & 0\\ 0 & 0 & G_{3} & P_{4} \end{pmatrix}.$$
 (3)

In the breeding season, reproduction occurs following matrix M_s . Each reproducing adult produces F_i offspring in the breeding season. Part B_A of the adults skips reproduction (so-called 'floaters'). This results in the following matrix based on a model with a total of four life stages, two of which are reproducing stages:

$$M_{S} = \begin{pmatrix} 1 & 0 & (1 - B_{A})F_{3} & (1 - B_{A})F_{4} \\ 0 & 1 & 0 & 0 \\ 0 & 0 & 1 & 0 \\ 0 & 0 & 0 & 1 \end{pmatrix}.$$
 (4)

The annual projection matrix is calculated as $A = M_w * M_s$. The order of the seasonal matrices in the matrix multiplication implies that the annual projection matrix calculates the number of birds after the winter, just before the breeding season begins. At this point, newborns from the previous year have (in model terms) already become 1 year old. Turning the multiplication of the seasonal matrices around would result in a different annual projection matrix. However, analysis of this matrix would result in an identical population analysis. It would just be looking at the population at a different moment in the year.

2.4.2 Model analysis

To analyse the models, we calculate the population growth rate and do a perturbation analysis of the population growth rate to changes in the values of the parameters. The population growth rate is equal to λ , the real part of the dominant eigenvalue of the annual projection matrix (Caswell 2001). To test the effect of small changes in the parameter values on the population growth rate, we do a sensitivity and elasticity analysis of the population growth rate. Sensitivities of λ to lower-level parameters are given by Caswell (2001). For any parameter x, it holds that:

$$\frac{\partial \lambda}{\partial x} = \sum_{i,i} \frac{\partial \lambda}{\partial a_{ij}} \frac{\partial a_{ij}}{\partial x}.$$
(5)

The sensitivity of λ to changes in parameter x depends on partial derivatives of all matrix elements a_{ij} to parameter x and the partial derivative of λ to matrix element a_{ij} .

Elasticities of λ to lower-level parameters (x) are given by:

$$\frac{x}{\lambda}\frac{\partial\lambda}{\partial x} = \frac{x}{\lambda}\sum_{i,j}\frac{\partial\lambda}{\partial a_{ij}}\frac{\partial a_{ij}}{\partial x}.$$
(6)

This is equal to the sensitivity of λ to changes in parameter x, multiplied by x divided by the population growth rate. This means that elasticities are sensitivities, corrected so that they are comparable across parameters.

We use the software package R for all model analyses (R Core Team 2014). Population projections are done using the R-package 'popbio'.

2.4.3 Parameter uncertainty

We determine uncertainty in the model output due to uncertainty in the model parameters using a Monte Carlo (MC) method. In short, we calculate a large number (50,000) of projection matrices, each based on a set of parameter values drawn randomly from the probability distributions of the parameter estimates. This method assumes that the different parameters vary independently (they are uncorrelated to each other) and are constant through time. This method thus results in fully deterministic matrix models. A comparison of the MC method with stochastic matrix models shows that the MC method gives the most cautionary results for uncertainty in the model outcomes (for a detailed discussion of the methods for uncertainty calculations see annex 2).

In most cases, the data underlying the parameter values are binomially distributed. The survival probability, breeding success and skipped breeding probability either take the value '0' or '1' on the individual level. As a consequence, the variability around the mean parameter values $\bar{\mu}$ and variance σ follows a beta distribution, with parameters $\alpha = \bar{\mu}^2 (\frac{1-\bar{\mu}}{\sigma^2} - \frac{1}{\bar{\mu}})$ and $\beta = (\alpha - \bar{\mu} \alpha)/\bar{\mu}$. A beta distribution is appropriate to describe the uncertainty around the mean chance of a 'failure/success' type of process,

such as survival and producing a single offspring. Sandwich terns and red-throated divers produce either 0, 1 or 2 fledglings and fecundity data thus follow a multinomial distribution. For these species we assume a sex ratio of 50% and use female offspring for the fecundity parameter so that the variability in the value can be described using a beta distribution.

Since we generally do not have access to the original datasets used to estimate the life history parameters and do not know the original sample sizes, we do Monte Carlo simulations of the distributions around the mean parameter values. We use reported mean values and standard deviations to calculate the distribution parameters α and β . In case there are no standard deviations available, we use the range rule to estimate the standard deviation. This rule defines the standard deviation as $(\mu_{max} - \mu_{min})/4$.

2.4.4 Scenarios

The effect of OWF-related habitat loss is modelled as a 'press disturbance'. In other words, the bird populations suffer from the same additional mortality due to the windfarms throughout the 30-year period that we consider. We subtract the estimated mortality probability due to windfarms from the estimated survival probabilities for the season spent in our study area for all stages in the model. We assume that the effect of the wind farms affects individuals in all bird life stages except for the sandwich tern, which spends its immature years in the overwintering area. In case the IBM predicts a positive effect of OWFs on the survival¹, we assume there is no effect of OWFs on the survival of the birds. Using the estimates for average survival probabilities for the scenarios, we repeat the model analysis described above, except for the elasticity and sensitivity analyses. For the model uncertainty analysis, we assume that the mean of the parameter values is affected by the presence of OWFs, but that the variance is not.

The population level effect of offshore wind farm deployment is calculated for six different scenarios, consisting of two displacement and mortality scenarios, for each of three OWF placement scenarios (see 1.3.4 for details). From this, we calculate the proportion of the population that will die as a result of OWF-induced habitat loss (see Table 3.17 in the results section).

2.4.5 Metrics of population-level OWF effects

We use four metrics to quantify the population-level effect of OWF:

- Population growth rate (PGR), with its 5th and 95th percentile
- Percentage of the outcomes that show a population decline of 10% or more after 30 years (P10%30Y)
- Ratio of impacted to unimpacted (No OWFs) median population size after 30 years
- Percentage of unimpacted (No OWFs) PGRs that lie beneath the median impacted PGR, and thus also have a smaller population size.

Note that our metrics relate to the 'percentage of x...' rather than to the 'chance that x...' or 'probability that x...'. While equivalent in practice, it would be technically incorrect if we used the latter formulation, because of the Monte Carlo approach we use. In this method, the parameter values for each of a large number of model simulations are sampled from representative distributions, but are constant within each simulation. Strictly speaking, our method hence calculates the frequency (expressed as a percentage of the total) with which 'x' occurs. The 'chance that x' formulation would be correct if the outcome of our model simulation itself would vary.

¹ Positive effects could theoretically arise when OWFs are located in an unfavorable area, so that birds are concentrated in more suitable habitat with OWFs. Alternatively, very small positive effects (within the range of the precision of the model) could be the result of a negligible negative effect combined with stochasticity.

Population growth rate (PGR)

The population growth rate is an accepted metric to indicate the health of a population and to measure population-level effects of disturbance (Caswell 2001; Cook and Robinson 2016). A value >1 indicates an exponentially growing population, while a smaller value indicates a declining population. We present the 5th and 95th percentile, based on the Monte Carlo analysis described above. Given the uncertainty in the parameter values, 90% of our outcomes predict a PGR above (5th) or below (95th) these values.

Population decrease of 10% over 30 years

A population decrease of 10% or more occurs when the annual population growth rate is equal to or smaller than $\sqrt[30]{0.9} = 0.996$. By keeping track of this statistic for all simulations in the Monte Carlo analysis, we obtain the P10%30Y metric. We have chosen 10% because it is reasonable to assume that such a change can be detected in a well-studied population, and 30 years because it is the period of validity of recent Dutch OWF permits as well as the current life expectancy of an OWF. Hence, this metric indicates the likelihood of a measurable reduction in the abundance of the population after the planned lifetime of an OWF. It is strongly related to the PGR, but integrates the effect of parameter uncertainty into a single metric.

Relative population size

The relative median population size after 30 years is equal to the ratio between the median population size in the Monte Carlo simulations with OWFs divided by that without OWFs. Since the population size at the start of the time period is the same for all scenarios, we calculate this metric based on the PGR. The ratio between the population growth rates over a 30-year period (PGR^{30}) is equal to the ratio between the population sizes after 30 years. A value <1 indicates a smaller population size as a result of OWFs. This metric is related to the OWF-induced relative change in PGR, but is more intuitive and relates to the planned lifetime of OWFs.

Overlap of unimpacted and impacted

The percentage of unimpacted PGRs that lie beneath the median impacted PGR (Figure 2.4) is the most complex but also the most informative metric. Essentially, this metric indicates the overlap between the outcomes of the unimpacted and impacted scenarios. It indicates the chance that a population develops similarly to an unaffected population, given the magnitude of the OWF effect and the parameter uncertainty. If it is far below 50%, it is highly unlikely that a population will develop 'as if it were unaffected'. It is the chance (expressed as a percentage) that an unaffected population has a smaller PGR than the median (50th percentile) of the affected population and thus has a smaller population size. If an OWF has no effect at all, its value would be 50%, as the distributions (and medians) would be identical, so that half the Monte Carlo simulation outcomes would be below the median of the OWF-affected population. A value <50% indicates a negative effect of OWFs.



Population growth rate (PGR) \rightarrow

Figure 2.4: Diagram illustrating the 'percentage of un-impacted (No OWFs) PGRs that lie beneath the median impacted PGR' concept. The arrow indicates the effect of OWF on the median of the PGR distribution, shifting it from the un-impacted to the impacted distribution. The grey area under the un-impacted curve is the part that is at or below the median of the un-impacted distribution. An important aspect of this criterion is that it becomes smaller both with larger distance between the means (larger effect) and with narrower distributions (less uncertainty). An effect size of zero would imply the

distributions are perfectly overlaid, and exactly half (or 50%) of the un-impacted distribution would be below the median of the impacted distribution.

2.4.6 Red-throated diver model

The diver model contains a juvenile DJ (ages 0 and 1), immature DI (age 2) and adult DA (age 3+) life stage. We choose three stages based on the available mortality estimates (Table 2.4). Survival has been estimated for individuals at age 0, age 1 and age 3+. Since reproduction starts at age 3 (Horswill and Robinson 2015), we define an immature stage for individuals with age 2. Survival and ageing from one breeding season to the next are described by matrix M_{Dw} :

$$M_{DW} = \begin{pmatrix} \left(\frac{1-S_{DJ}}{1-S_{DJ}^{2}}\right)S_{DJ} & 0 & 0\\ \frac{S_{DJ}^{2}(1-S_{DJ})}{1-S_{DJ}^{2}} & 0 & 0\\ 0 & S_{DA} & S_{DA} \end{pmatrix}.$$
(7)

With survival of juveniles S_{DJ} , and immatures and adults S_{DA} . Part of the adults produces offspring in the breeding season. In the breeding season, reproduction occurs following matrix M_{Ds} :

$$M_{DS} = \begin{pmatrix} 1 & 0 & F_{DA}(1 - B_{DA}) \\ 0 & 1 & 0 \\ 0 & 0 & 1 \end{pmatrix}.$$
 (8)

Adults produce F_{DA} female offspring. The probability that individuals skip reproduction equals B_{DA} . The annual projection matrix is calculated as:

$$A_D = M_{Dw} * M_{Ds}$$

$$= \begin{pmatrix} \left(\frac{1-S_{DJ}^{1}}{1-S_{DJ}^{2}}\right)S_{DJ} & 0 & S_{DJ}\left(\frac{1-S_{DJ}^{1}}{1-S_{DJ}^{2}}\right)F_{DA}(1-B_{DA})\\ \frac{S_{DJ}^{2}(1-S_{DJ})}{1-S_{DJ}^{2}} & 0 & \frac{S_{DJ}^{2}(1-S_{DJ})}{1-S_{DJ}^{2}}F_{DA}(1-B_{DA})\\ 0 & S_{DA} & S_{DA} \end{pmatrix}.$$
(9)

Diver parameter values

Parameter values for the red-throated diver are taken from the review by Horswill and Robinson (2015). There are not many reports of life-history parameters for this species. A measure of the variance of the values is not available for the survival probabilities. The (relatively low) fecundity reported by Horswill and Robinson (2015) is based on studies at Shetland and Orkney, while Hemmingsson and Eriksson (2002) refer to studies in Sweden. Maximal clutch size is 2 eggs.

There is no information on the probability of skipping reproduction for the red-throated diver. Based on the range of estimates for other seabirds we choose a value of 0.05. The SD for this parameter is based on the range rule ((max-min)/4).

symbol	mean	unit	variance	description	remark	source
F _{DA}	0.348	Year ⁻¹	0.088 (SD)	fledged female offspring, age 5+	average across Sweden (0.41) and UK (0.2855)	1, 2, 3
B _{DA}	0.05		0.0-0.5 (min-max) 0.125 (SD range rule)	skipped breeding probability, all adult stages		-
S _{DJ}	0.61	-	0.014 (SD)	annual survival probability age 0-1	the SD value is quite low, but there are only	1, 2

Table 2.4 Default parameter values red-throated diver

					two estimates available	
					and they are very close	
S _{DA}	0.88	-	0.06 (SD)	annual survival probability immatures & adults, age 2+		2, 4
a_{Dm}	3	Years		age at recruitment		1
¹ Horswil	l & Robin	son (2015); ² Hemmings	son and Eriksson (2002); ³	³ Dierschke et al. (2017);	
⁴ Schmut	F7 (2014)					

2.4.7 Northern gannet model

The model contains the juvenile stages GJ_0 (age 0), immature stages GI_1 (age 1) and GI_2 (age 2), GI_3 (age 3) and GI_4 (age 4) and adult stage GA (age 5+).

Survival and ageing from one breeding season to the next is described by matrix M_{Gw} :

$$M_{GW} = \begin{pmatrix} 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ S_{G0} & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & S_{G1} & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & S_{G2} & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & S_{G3} & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & S_{GA} & S_{GA} \end{pmatrix}.$$
 (10)

With survival of juveniles S_{G0} , survival of immatures $S_{G1\cdots G3}$ and survival of adults S_{GA} . Adults produce offspring in the breeding season. Only part of the adults reproduces and we introduce a probability for reproduction. In the breeding season, reproduction occurs following matrix M_{GS} :

$$M_{GS} = \begin{pmatrix} 1 & 0 & 0 & 0 & 0 & \frac{F_{GA}}{2}(1 - B_{GA}) \\ 0 & 1 & 0 & 0 & 0 & 0 \\ 0 & 0 & 1 & 0 & 0 & 0 \\ 0 & 0 & 0 & 1 & 0 & 0 \\ 0 & 0 & 0 & 0 & 1 & 0 \\ 0 & 0 & 0 & 0 & 0 & 1 \end{pmatrix}.$$
 (11)

Adults produce $\frac{F_{GA}}{2}$ female offspring. The probability that individuals skip reproduction equals B_{GA} for young and old adults.

The annual projection matrix is calculated as:

$$= \begin{pmatrix} 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ S_{G0} & 0 & 0 & 0 & 0 & S_{G0} \frac{F_{GA}}{2} (1 - B_{GA}) \\ 0 & S_{G1} & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & S_{G2} & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & S_{G3} & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & S_{GA} & S_{GA} \end{pmatrix}.$$
 (12)

Northern gannet parameter values

Parameter values for the gannet are taken from the review by Horswill and Robinson (2015). There are a number of reports of life-history parameters for this species. The values in the review are based on studies of gannet colonies in the UK. Maximal clutch size is a single egg (Wanless et al. 2006). No estimate is available of the incidence of missed breeding for the northern gannet. Based on the range of estimates for other seabirds we choose a value of 0.05. The SD for this parameter is based on the range rule ((max-min)/4).

 $A_G = M_{GW} * M_{GS}$

Table 2.5 Northern gannet life-history parameters

symbol	mean value	variance	unit	description	remark	source	
F _{GA}	0.7	0.082 (SD) 0 - 1 (min- max)	year-1	fledged offspring, national average UK	area specific estimates (UK), available	1	
B _{GA}	0.05	0.125 (SD range rule) 0.0-0.5 (min- max)	-	skipped breeding probability, all adult stages		-	
S_{G0}	0.424	0.007 (SE)	-	annual survival probability age 0		1	
S_{G1}	0.829	0.004 (SE)	-	annual survival probability age 1		1	
S_{G2}	0.891	0.003 (SE)	-	annual survival probability age 2		1	
S_{G3}	0.895	0.003 (SE)	-	annual survival probability age 3		1	
S _{Ga}	0.919	0.042 (SD)	-	annual survival probability immatures & adults, age 4+		1	
a_{Gm}	5		years	age at recruitment		1	
¹ Horswill & Robinson (2015)							

Northern gannet windfarm scenarios

The gannet population distribution overlaps with the OWFs both in the breeding and the non-breeding season. The effect of the windfarms is therefore calculated in two steps. We assume that in the summer, the whole population is present and deduct the mortality probability for the breeding season from the summer survival (normally 1 on the diagonal of matrix M_{Gs}). In winter, only part of the population stays at the North Sea. Therefore, we apply mortality in winter due to the windfarms only to the proportion of the population that is present compared to the summer population. We estimate this proportion based on the mean density estimate of gannets in the breeding and non-breeding season from the habitat suitability models (Table 3.1).

2.4.8 Sandwich tern model

We use a juvenile *TJ* (age 0), immature *TI* (age 1 and 2), young adult *TM* (age 3 and 4) and old adult *TA* (age 5+) stage. The immature and young adult stage each last two years. We group immatures of one and two years old together because estimated mortality rates are identical. Maturation in the sandwich tern occurs at age 3 (van der Jeugd et al. 2014). Adults of age 3 and 4 have a significantly lower breeding success than adults of 5 years and older (Veen 1977). Therefore, we define an adult class for inexperienced (young) and an adult class for experienced (old) adults separately.

Survival and ageing from one breeding season to the next is described by matrix M_{Tw} :

$$M_{Tw} = \begin{pmatrix} 0 & 0 & 0 & 0 & 0 \\ S_{TJ} & \left(\frac{1-S_{TI}}{1-S_{TI}^2}\right) S_{TI} & 0 & 0 \\ 0 & \frac{S_{TI}^2(1-S_{TI})}{1-S_{TI}^2} & \left(\frac{1-S_{TA}}{1-S_{TA}^2}\right) S_{TA} & 0 \\ 0 & 0 & \frac{S_{TA}^2(1-S_{TA})}{1-S_{TA}^2} & S_{TA} \end{pmatrix}.$$
 (13)

With survival of juveniles S_{TJ} , survival of immatures S_{TI} and survival of adults S_{TA} . Part of the adults produce offspring in the breeding season. In the breeding season, reproduction occurs following matrix M_{Ts} :

$$M_{TS} = \begin{pmatrix} 1 & 0 & F_{TM}(1 - B_{TA}) & F_{TA}(1 - B_{TA}) \\ 0 & 1 & 0 & 0 \\ 0 & 0 & 1 & 0 \\ 0 & 0 & 0 & 1 \end{pmatrix}.$$
 (14)

Young and old adults produce respectively F_{TM} and F_{TA} female offspring. The probability that individuals skip reproduction equals B_{TA} for young and old adults.

The annual projection matrix is calculated as:

$$A_{T} = M_{Tw} * M_{Ts},$$

$$= \begin{pmatrix} 0 & 0 & 0 & 0 \\ S_{TJ} & \left(\frac{1 - S_{TI}}{1 - S_{TI}^{2}}\right) S_{TI} & S_{TJ} \frac{F_{TM}}{2} (1 - B_{TA}) & S_{TJ} \frac{F_{TA}}{2} (1 - B_{TA}) \\ 0 & \frac{S_{TI}^{2} (1 - S_{TI})}{1 - S_{TI}^{2}} & \left(\frac{1 - S_{TA}}{1 - S_{TA}^{2}}\right) S_{TA} & 0 \\ 0 & 0 & \frac{S_{TA}^{2} (1 - S_{TA})}{1 - S_{TA}^{2}} & S_{TA} \end{pmatrix}.$$
(15)

Sandwich tern parameter values

The parameter values (Table 2.6) are based on studies of the Wadden Sea sandwich tern colonies. Survival probabilities and breeding success are based on a recent study (van der Jeugd et al. 2014), which uses 40 years of ringing data from Griend to estimate survival. Breeding success measurements of the same colony from 1990 to 2010 are included in the study. Sandwich terns clutch size varies between 1-2 eggs.

Breeding success is reported to be much lower in 3- and 4-year-old adults than in adults of age 5 and older (Veen 1977, page 54). Veen (1977) reports that the breeding success for 3- and 4-year-old individuals is about 30% of that of older adults. For individuals with age 5+, we have used a weighted average based on colony size (unpublished data Hans Schekkerman, SOVON). For the younger adults we use a value of 30% of the older adult fecundity number.

There is no information on the probability of skipping reproduction for the sandwich tern. Based on the range of estimates for other seabirds we choose a value of 0.05. The SD for this parameter is based on the range rule ((max-min)/4).

symbol	mean value	variance	unit	description	remark	source
F _{TM}	0.3 <i>F_{TA}</i>	depends on values for F_{TA}	year-1	fledged female offspring, adults age 3 and 4		1
F _{TA}	0.275	0.095 (SD)	year-1	fledged female offspring, adults age 5+	weighed reproduction (based on colony size)	2
B_{TA}	0.05	0.125 (SD range rule) 0.0-0.5 (min-max)	-	skipped breeding probability, all adult stages		
S _{TJ}	0.302	0.125 (SD)	-	annual survival probability juveniles, age 0		3
S _{TI}	0.956	0.028 (SD)	-	annual survival probability immatures, age 1 and 2		3
S _{TA}	0.945	0.099 (SD)	-	annual survival probability adults, age 3+		3

Table 2.6	Default	narameter	values	sandwich	tern		
10010 2.0	DClaute	parameter	values	Sanawich	luin		
a_{TM}	3	-	years	age at		3	
--	---	---	-------	------------	--	---	--
				maturation			
¹ Veen (1977); ² Data Sovon; ³ Van der Jeugd et al. (2014).							

Sandwich tern windfarm scenarios

The sandwich tern population distribution overlaps with the OWFs in the breeding season only. After their first migration to the overwintering area (at age 0), the terns do not return to the breeding area until they are reading to start breeding (at age 3-4). We therefore incorporate an effect of OWF for individuals in the stages *TJ*, *TM* and *TA*, but not for stage *T*.

2.4.9 Razorbill model

The model contains the juveniles RJ (ages 0 and 1), immatures RI (ages 2-4) and adults RA (age 5+). Survival and aging from one breeding season to the next is described by matrix M_{Rw} :

$$M_{Rw} = \begin{pmatrix} \left(\frac{1-S_{RJ}}{1-S_{RJ}^{2}}\right) S_{RJ} & 0 & 0\\ \frac{S_{RJ}^{2} (1-S_{RJ})}{1-S_{RJ}^{2}} & \left(\frac{1-S_{RA}^{2}}{1-S_{RA}^{3}}\right) S_{RA} & 0\\ 0 & \frac{S_{RA}^{3} (1-S_{RA})}{1-S_{RA}^{3}} & S_{RA} \end{pmatrix}.$$
 (16)

With survival of juveniles S_{RJ} and survival of immatures and of adults S_{RA} .

Part of the adults produce offspring in the breeding season. Reproduction occurs following matrix M_{Rs} :

$$M_{Rs} = \begin{pmatrix} 1 & 0 & \frac{F_{RA}}{2}(1 - B_{RA}) \\ 0 & 1 & 0 \\ 0 & 0 & 1 \end{pmatrix}.$$
 (17)

Adults produce $\frac{F_{RA}}{2}$ female offspring. The probability that individuals skip reproduction equals B_{RA} .

The annual projection matrix is calculated as: $A_R = M_{Rw} * M_{Rs}$

$$= \begin{pmatrix} \left(\frac{1-S_{RJ}^{2}}{1-S_{RJ}^{3}}\right)S_{RJ} & 0 & \left(\frac{1-S_{RJ}^{2}}{1-S_{RJ}^{3}}\right)S_{RJ}\frac{F_{RA}}{2}(1-B_{RA})\\ \frac{S_{RJ}^{3}(1-S_{RJ})}{1-S_{RJ}^{3}} & \left(\frac{1-S_{RA}^{1}}{1-S_{RA}^{2}}\right)S_{RA} & \frac{S_{RJ}^{3}(1-S_{RJ})}{1-S_{RJ}^{3}}\frac{F_{RA}}{2}(1-B_{RA})\\ 0 & \frac{S_{RA}^{2}(1-S_{RA})}{1-S_{RA}^{2}} & S_{RA} \end{pmatrix}.$$
(18)

Razorbill parameter values

Parameter values for the razorbill (Table 2.7) are taken from the review by Horswill and Robinson (2015). There are a number of reports of life-history parameters for this species. The values in the review are based on studies of razorbill colonies in the UK. Yet, the juvenile survival estimate is based on a ringing programme in Canadian razorbill colonies (Horswill and Robinson 2015, Lavers et al. 2008). Maximum clutch size is one egg.

Horswill and Robinson (2015) give an estimate of 3% for the incidence of missed breeding. No standard deviation was available for the incidence of skipped breeding. Therefore, we calculated the SD for this parameter based on the range rule ((max-min)/4).

Table 2.7 Default parameter values Razorbill

symbol	mean value	variance	unit	description	remark	source		
F_{RA}	0.57	0.247 (SD)	year⁻ ¹	fledged offspring, age 5+		1		
B _{RA}	0.03	0.125 (SD range rule) 0.0-0.5 (min-max)	-	skipped breeding probability, all adult stages		1		
S _{RJ}	0.788	0.133 (SD)	-	annual survival probability age 0 and 1	based on Canadian colonies, derived annual value from original study	1, 2		
S _{RA}	0.895	0.067 (SD)	-	annual survival probability immatures & adults, age 2+		1		
a_{Rm}	5	-	years	age at recruitment		1		
¹ Horswill	¹ Horswill and Robinson (2015); ² Lavers et al. (2008);							

2.4.10 Common guillemot model

The guillemot matrix model contains the juvenile stages UJ_0 (age 0), UJ_1 (age 1) and UJ_2 (age 2), immatures UI (age 3-5) and adults UA (age 6+). Survival and ageing from one breeding season to the next is described by matrix M_{Uw} :

$$M_{UW} = \begin{pmatrix} 0 & 0 & 0 & 0 & 0 & 0 \\ S_{U0} & 0 & 0 & 0 & 0 \\ 0 & S_{U1} & 0 & 0 & 0 \\ 0 & 0 & S_{U2} & \left(\frac{1 - S_{UA}^2}{1 - S_{UA}^3}\right) S_{UA} & 0 \\ 0 & 0 & 0 & \frac{S_{UA}^3(1 - S_{UA})}{1 - S_{UA}^3} & S_{UA} \end{pmatrix}.$$
 (19)

With survival of juveniles S_{U0} , S_{U1} and S_{U2} , and survival of immatures and adults S_{UA} . Adults produce offspring in the breeding season. Only part of the adults reproduces and we introduce a probability for reproduction. In the breeding season, reproduction occurs following matrix M_{US} :

$$M_{US} = \begin{pmatrix} 1 & 0 & 0 & 0 & \frac{IUA}{2}(1 - B_{UA}) \\ 0 & 1 & 0 & 0 & 0 \\ 0 & 0 & 1 & 0 & 0 \\ 0 & 0 & 0 & 1 & 0 \\ 0 & 0 & 0 & 0 & 1 \end{pmatrix}.$$
 (20)

Adults produce $\frac{F_{UA}}{2}$ female offspring. The probability that individuals skip reproduction equals B_{UA} for young and old adults.

The annual projection matrix is calculated as:

$$A_{U} = M_{UW} * M_{US}$$

$$= \begin{pmatrix} 0 & 0 & 0 & 0 & 0 & 0 \\ S_{U0} & 0 & 0 & 0 & S_{U0} \frac{F_{UA}}{2} (1 - B_{UA}) \\ 0 & S_{U1} & 0 & 0 & 0 & 0 \\ 0 & 0 & S_{U2} & \left(\frac{1 - S_{UA}^{2}}{1 - S_{UA}^{3}}\right) S_{UA} & 0 & 0 \\ 0 & 0 & 0 & \frac{S_{UA}^{3} (1 - S_{UA})}{1 - S_{UA}^{3}} & S_{UA} \end{pmatrix}.$$
(21)

Common guillemot parameter values

Parameter values for the guillemot (Table 2.8) are taken from the review by Horswill and Robinson (2015). There are a number of reports of life-history parameters for this species. The values in the

review are based on studies of common guillemot colonies in the UK. The incidence of skipped breeding is estimated to be between 5-10% (Harris and Wanless 1995). No standard deviation was available for the incidence of skipped breeding. Therefore, we calculated the SD for this parameter based on the range rule ((max-min)/4). Maximum clutch size is one egg.

symbol	mean value	variance	unit	description	remark	source
F _{UA}	0.627	0.147 (SD)	Year ⁻¹	fledged offspring, age 5+	area specific estimates (UK), available	1
B _{UA}	0.08	0.0125 (SD) 5-10% (min- max)	-	skipped breeding probability, all adult stages	SD based on range rule	1,2
S _{U0}	0.56	0.013 (SD)	-	annual survival probability age 0		1
S_{U1}	0.792	0.034 (SD)	-	annual survival probability age 1		1
S _{U2}	0.917	0.022 (SD)	-	annual survival probability age 2		
S _{UA}	0.939	0.067 (SD)	-	annual survival probability immatures & adults, age 3+		1
a_{UM}	6	-	Years	age at recruitment		1
¹ Horswill	& Robinson	(2015): ² Harris	and Wan	less (1995)		

Table 2.8 Default parameter values common guillemot

orswill & Robinson (2015); ²Harris and Wanless (1995)

3 Results

In this chapter the results per species are presented. For every species we present:

- 1. The resulting habitat suitability map (the predicted distribution based on the habitat models), that provides input to the next step.
- The habitat suitability map is then used in the individual based models, to calculate the proportion of birds that will be affected through reduced survival because of habitat loss under different OWF- scenarios.
- 3. The resulting changes in survival rates are incorporated in population models to arrive at population projections under the different OWF-scenarios.

3.1 Population density estimates

Table 3.1 gives a summary of the density predictions for all bird species based on the habitat suitability maps. These are obtained by multiplying the predicted bird density at each map grid cell by the size of each cell, and summing all cells on the map. Also the number of birds in Dutch and foreign windfarms are estimated.

Based on the percentage of the bird populations found in Dutch and international wind farms, we estimate additional OWF mortality using the 10% rule (see section 2.3.4). This is simply a multiplication of mortality (depending on the length of the period spent near the OWFs) with the percentage overlap with the precautionary and realistic displacement estimate. We use these mortality estimates, in addition to the IBM results, to calculate population level effects of OWF deployment in the North Sea in section 3.2-3.6.

Table 3.1 Mean, high and low population estimates (based on habitat suitability models: estimates of number of birds in whole study area, in Dutch and foreign wind farms). In sandwich tern and redthroated diver, the estimated number based on the habitat map cannot be compared to previous estimates, as the latter include a larger area than we have used here.

species		total estimated number	previous estimates	n birds in Dutch OWFs	%	n birds in foreign OWFs	%
red-throated diver	mean	11,637	490,001 ¹	92	0.8%	275	2.4%
	high	27,507		231	0.8%	795	2.9%
	low	4,642		27	0.6%	70	1.5%
northern gannet non-breeding	mean	644,698		3,388	0.5%	21,224	3.3%
	high	2,404,808		9,669	0.4%	74,231	3.1%
	low	0		0		0	
northern gannet breeding	mean	712,937	1,300,000 ²	3,027	0.4%	25,438	3.6%
	high	2,349,559		8,338	0.4%	76,295	3.2%
	low	0		0		0	
sandwich tern	mean	16,800	36,000 ³	217	1.3%	474	2.8%
	high	32,551		435	1.3%	1,213	3.7%
	low	8,238		93	1.1%	146	1.8%
razorbill	mean	85,159	324,000 ¹	820	1.0%	5,236	6.1%
	high	179,620		958	0.5%	10,063	5.6%
	low	42,863		699	1.6%	2,517	5.9%

common guillemot	mean	842,469	1,562,000 ¹	3,296	0.4%	54,059	6.4%
_	high	1,546,662		3,695	0.2%	72,752	4.7%
	low	491,334		2,931	0.6%	39,288	8.0%
¹ Skov et al. (2007); ² Birdlife Red list 2015; ³ Sovon: https://www.sovon.nl/nl/soort/6110							

3.2 Red throated diver

3.2.1 Density predictions

For red-throated diver the model fit was conducted using only the MWTL data. These data are of a much smaller spatial area than the ESAS data. Consequently, to avoid over-extrapolating the model results, the area for which we do habitat quality predictions is reduced to a smaller portion of the North Sea, for which the input data are representative. It is technically possible to calculate diver abundance outside the input data locations, but doing so implies that the relationships determining bird abundance in Dutch areas translate 1:1 to the rest of the North Sea. We have no data to study whether or not this is the case and have therefore chosen not to extrapolate to other areas.

Statistically significant predictors for the presence-absence (model 1) are depth, distance to coast, day of season, and sediment. Numbers increased with increasing slope and decreased with distance to coast. The sediment category fine sediment showed lower densities than the coarse sediment (which is the reference category in the table). For areas where divers are present (model 2), densities were higher in areas with mixed sediment as compared to coarse sediment. Water depth and day of the season were included as a smoother and showed clearly that red-throated divers occur mainly up to a depth of 25 m, with the highest densities in the shallowest part. The day of the season smoother shows that the occurrence of diver increases until the peak around mid-March, which is likely to be in accordance with their migration season. On the other hand, in the positive density model, the density reaches maximum around late November and remains at a constant level afterwards (Annex 1).

The WAIC shows that for both models the model including the covariates and the spatial random field fits better than the models without the spatial random field (Table 3.3).

Species		model 1 (presence-absence)	model 2 (density)
red-throated diver	covariate	coefficient	coefficient
	Intercept	-4.97	1.67
	slope	0.01	-0.01
	distance to coast	-1.28	0.05
	sediment_deep_sand	0.17	0.25
	sediment_fine	-0.30	-0.16
	sediment_fine_mud	0.08	0.37
	sediment_mixed	0.19	0.70
	sediment_sandy_mud	-0.33	-0.15
	log surface area	0.30	

Table 3.2: Coefficients and significance of covariates in the habitat model for red-throated diver. Significant covariates are printed bold. The reference category of sediment covariate is coarse sediment.

Table 3.3. WAIC values of the two models with and without a spatial random field. The best models are indicated by the lowest WAIC value.

Model	covariates only	covariates + SRF
model presence/absence	16860	16313
model positive density	5990	5852



Figure 3.1. Habitat suitability map (left) and precision map (right) for red-throated diver. White hatched areas are the internationally planned OWFs, blue hatched areas are Dutch planned and constructed OWFS. Grey areas are areas of missing data or too far outside the parameter range of the data.

3.2.2 OWF effects on mortality

Table 3.4 shows the simulated change in mortality rate of the red-throated diver, with only the Dutch, only the international and all OWFs. The additional mortality is the difference between the median or the 5th percentile and the mortality rate without OWFs. Generally, there is very little variation in outcomes, which means that the differences between the 5th and the 50th percentile (the median) are minimal, indicating that all simulations give a highly similar outcome.

Table 3.4 Effects of OWF (realistic and precautionary scenario) on red-throated diver monthly mortality rate during the period of OWF exposure: 5th percentile and median additional mortality from OWFs.

	used for stage	5th percentile	Median additional monthly
		additional	mortality from OWF
		from OWF	
Precautionary			
Dutch OWF			
	DJ	2.8E-04	0.0E+00
	DI, DA	9.9E-05	0.0E+00
International OWF			
	DJ	2.8E-04	0.0E+00
	DI, DA	9.9E-05	0.0E+00
All OWF			
	DJ	2.8E-04	0.0E+00
	DI, DA	9.9E-05	0.0E+00
Realistic			
Dutch OWF			
	DJ	2.8E-04	0.0E+00
	DI, DA	2.0E-04	0.0E+00
International OWF			
	DJ	1.4E-04	0.0E+00
	DI, DA	9.9E-05	0.0E+00
All OWF			
	DJ	2.8E-04	0.0E+00
	DI, DA	9.9E-05	0.0E+00

3.2.3 Population level effect

Since the habitat model is limited to the North Sea around the Netherlands, the red-throated diver population we modelled only overlaps partly with international wind farms (Table 3.1). A higher percentage of the population in the study area occurs in international than Dutch OWFs (2.4 vs. 0.8%). The red-throated diver population model predicts a slow decline of the population without wind farms. The median diver population growth rate is 0.996 (Table 3.5). While an increase of the population is included in the 90% range of possible outcomes of the model, the majority of the outcomes predict a decrease of the population (Figure 3.2). Without wind farms, a population decline of 10% or more over a 30-year period is shown by 50.2% of the outcomes. With windfarms, this is maximally 52%.

The population growth rate decreases only slightly with additional OWF mortality (Figure 3.2). Both the precautionary and realistic scenarios show a small effect of OWF mortality on all population metrics. For all scenarios, the median population size for the 'OWF impacted' scenario is at least 0.926 of the median population size without wind farms. In addition, at least 48% of the outcomes without OWFs predict

population sizes lower than the median with all OWFs. All realistic scenarios show a negligible effect of OWF mortality on all population metrics. In summary, we do not find a strong effect of OWF related habitat loss on the population level for red-throated divers.

The perturbation analysis for divers (Annex 3) shows that population growth rate is most strongly affected by changes in adult survival, which result in an order of magnitude larger effect per unit change (elasticity) than any other parameter.

Table 3.5 Red-throated diver population growth rate for all model scenarios. The median annual population growth rate (PGR), the 5% and 95% percentile, the proportion of the calculations (out of 50,000) that predict a 10% decline (or greater) of the population over a period of 30 years, the median population size after 30 years relative to the scenario without OWFs for all model scenarios and the percentage of the results without OWFs that predict a population size lower than the median of the results for each of the OWF scenarios

	PGR	PGR 5% percentile	PGR 95% percentile	P10%30yr (%)	relative population size after 30 years	results unaffected lower than median affected (%)
without OWFs	0.996	0.875	1.081	50.2%		
precautionary s	cenario IBM					
Dutch OWFs	0.994	0.873	1.079	52.0%	0.929	48.5%
foreign OWFs	0.994	0.873	1.079	52.0%	0.930	48.0%
all OWFs	0.994	0.873	1.079	51.0%	0.945	49.0%
realistic scenari	o IBM					
Dutch OWFs	0.996	0.875	1.081	50.0%	0.998	50.0%
foreign OWFs	0.996	0.874	1.080	51.0%	0.980	50.0%
all OWFs	0.996	0.874	1.080	50.0%	0.990	50.0%
precautionary s	cenario 10%)				
Dutch OWFs	0.995	0.875	1.080	51.0%	0.975	49.0%
foreign OWFs	0.994	0.875	1.079	51.0%	0.946	49.0%
all OWFs	0.994	0.872	1.078	52.0%	0.926	48.0%
realistic scenari	o 10%					
Dutch OWFs	0.996	0.875	1.080	51.0%	0.978	50.0%
foreign OWFs	0.995	0.874	1.079	51.0%	0.958	49.0%
all OWFs	0.995	0.872	1.080	51.0%	0.956	49.0%



Figure 3.2 Red-throated diver median population growth rate, with 5 and 95% percentile, relative median population size after 30 years and percentage of outcomes of the scenario without OWFs that lies lower than the median of the results for each of the scenarios with Dutch OWFs.

3.3 Northern gannet

3.3.1 Density predictions

Non-breeding gannets:

Significant predictors for presence-absence (model 1) were: day of season and data source. Presence decreased with distance to colony, decreased with day of season and was lower in MWTL data. Densities (model 2) decreased with distance to colony, increased with day of the season, were higher in the MWTL set and in fine mud. In the non-breeding season gannets occur mainly deeper than 25 m (Annex 1). The WAIC shows that for both models the model including the covariates and the spatial random field fits better than the models without the spatial random field (Table 3.6).

Breeding gannets:

Significant predictors for presence-absence (model 1) were: distance to colony, day of season and data source. Presence decreased with day of season and was lower in the MWTL data. Densities (model 2) increased with slope, decreased with distance to colony and day of the season and were higher in MWTL. Similar to non-breeding birds, the depth distribution of breeding gannets is mainly limited to areas of 25 m or deeper (Annex 1).

The WAIC shows that for both models the model including the covariates and the spatial random field fits better than the models without the spatial random field (Table 3.7).

The estimated mean density map and its precision are illustrated in Figure 3.3 and Figure 3.4. Results indicate that northern gannets are mostly distributed along the UK coast, UK north island and North Sea between Netherlands and UK. In the non-breeding season, they are spread over a larger area between the Netherlands and UK. However, the estimates were everywhere highly uncertain. This is partially due to low sampling coverage and sample size over the entire North Sea area as well as the ESAS survey area (Annex 1). Additionally, the high density and high uncertainty along the north edge in the non-

breeding map was caused by the high depth (artefacts from smoother) and low sample size at these high depths.

Table 3.6. Coefficients and significance of covariates in the model for northern gannet in the nonbreeding period and for non-breeding gannets in the breeding period. Significant covariates are printed bold.

species		model 1 (presence-absence)	model 2 (density)
northern gannet breeding	covariate	coefficient	coefficient
	Intercept	211.46	0.61
	slope	-0.01	0.04
	distance to coast	-0.02	-0.02
	distance to colony	-0.44	-0.10
	day of season	0.06	-0.06
	data source_MWTL	-0.61	0.10
	sediment_deep_sand	-0.02	0.05
	sediment_fine	0.08	-0.04
	sediment_fine_mud	0.08	0.18
	sediment_mixed	0.53	0.12
	sediment_sandy_mud	-0.13	0.09
	log surface area	0.25	
northern gannet non- breeding			
	Intercept	265.96	0.60
	slope	-0.01	-0.003
	distance to coast	-0.06	-0.002
	distance to colony	-0.36	0.04
	day of season	-0.62	0.03
	data source_MWTL	-0.48	0.21
	sediment_deep_sand	-0.01	0.03
	sediment_fine	0.10	-0.04
	sediment_fine_mud	-0.06	0.10
	sediment_mixed	-0.90	0.18
	sediment_sandy_mud	0.16	0.06
	log surface area	0.20	

Table 3.7. WAIC values of the two models with and without a spatial random field. The best models are indicated by the lowest WAIC value.

	model	covariates only	covariates + SRF
northern gannet breeding	model presence/absence	43986	42390
	model positive density	22201	16605
northern gannet non-breeding	model presence/absence	52041	49929
	model positive density	23255	18014



Figure 3.3. Habitat suitability map (left) and precision map (right) for northern gannets in the **breeding season**. White hatched areas are the internationally planned OWFs, black areas are Dutch planned and constructed OWFS. Grey areas are areas of missing data or too far outside the parameter range of the data.

Figure 3.4. Habitat suitability map (left) and precision map (right) for northern gannets in the **nonbreeding season**. White hatched areas are the internationally planned OWFs, black areas are Dutch planned and constructed OWFS. Grey areas are areas of missing data or too far outside the parameter range of the data.

3.3.2 OWF effects on mortality

Table 3.8 shows the simulated change in mortality rate of northern gannets using realistic and precautionary displacement, with only the Dutch, only the international and all OWFs. The additional mortality is the difference between the median or the 5th percentile and the mortality rate without OWFs. Generally, there is very little variation in outcomes, which means that the differences between the 5th and the 50th percentile (the median) are minimal, indicating that all simulations give a highly similar outcome.

Table 3.8 Effects of OWF (realistic and precautionary scenario) on northern gannet monthly mortality rate during the period of OWF exposure: 5th percentile, median and median additional mortality from OWFs.

	used for stage	5th percentile additional monthly mortality	Median additional monthly mortality from OWF	<i>5th percentile additional monthly mortality from OWF</i>	Median additional monthly mortality from OWF
Non		from OWF Realistic		Precautionary	
breeding					
Dutch OWF					
	GJ ₀	2.09E-04	0.00E+00	4.18E-04	0.00E+00
	GI_1	2.09E-04	0.00E+00	2.09E-04	0.00E+00
	GI2, GI3, GI4, GIA	9.26E-05	0.00E+00	9.26E-05	0.00E+00
International OWF					
	GJ₀	8.38E-04	6.27E-04	1.05E-03	6.27E-04
	GI_1	4.18E-04	2.09E-04	4.18E-04	2.09E-04
	GI ₂ , GI ₃ , GI ₄ , GI _A	1.85E-04	9.26E-05	1.85E-04	9.26E-05
All OWF					
	GJ₀	8.38E-04	6.27E-04	8.38E-04	6.27E-04
	GI_1	4.18E-04	2.09E-04	4.18E-04	2.09E-04
	GI ₂ , GI ₃ , GI ₄ , GI _A	1.85E-04	9.26E-05	1.85E-04	9.26E-05
Breeding					
Dutch OWF					
	GJ_0	4.18E-04	0.00E+00	4.18E-04	0.00E+00
	GI_1	2.09E-04	0.00E+00	2.09E-04	0.00E+00
	GI2, GI3, GI4, GIA	9.26E-05	0.00E+00	9.26E-05	0.00E+00
International OWF					
	GJ₀	4.18E-04	0.00E+00	4.18E-04	0.00E+00
	GI_1	4.18E-04	2.09E-04	4.18E-04	2.09E-04
	GI2, GI3, GI4, GIA	3.71E-04	1.85E-04	3.71E-04	1.85E-04
All OWF					
	GJ ₀	4.18E-04	0.00E+00	4.18E-04	0.00E+00
	GI1	4.18E-04	2.09E-04	4.18E-04	2.09E-04
	GI2, GI3, GI4, GIA	2.78E-04	1.85E-04	2.78E-04	1.85E-04

3.3.3 Population level effect

The northern gannet population overlaps most strongly with the international (foreign) wind farms (3.3-3.6%, Table 3.1). Only 0.4-0.5% of the population overlaps with Dutch wind farms. Without wind farms, the gannet population model predicts a slow increase of the population. The median of the population growth rates is 1.008 (Table 3.9). The possibility of a population growth rate smaller than one is included in the 90% of possible outcomes of the model (Figure 3.5). Without wind farms, 36.9% of the outcomes predict a population decline of 10% or larger over a period of 30 years. For the precautionary scenario the number is higher: ~44%.

The population growth rate decreases due to the additional OWF mortality (Table 3.9). For all scenarios, the median population size is at least 0.8 of the median population size without wind farms. In addition, at least a substantial 41.2% of the outcomes without OWFs predict population sizes lower than the median with all OWFs. In summary, we find an effect of OWF related habitat loss on the population level for the gannet for the IBM scenarios, for the 10% mortality scenarios the effect is small.

When the Dutch OWFs are considered alone, the effect on all the metrics that we consider is negligible. The additional effect of the Dutch OWFs when the international OWFs are already present (the difference between 'foreign OWFs' and 'all OWFs' in Table 3.9) causes a very small change to the outcome of the assessment for gannets.

The perturbation analysis for gannets (Annex 3) shows that population growth rate is most strongly affected by changes in adult survival, which have over an order of magnitude larger effect per unit change (elasticity) than any other parameter.

Table 3.9: Northern gannet population growth rate for all model scenarios. The median annual population growth rate (PGR) with 5% and 95% percentile, the proportion of the calculations (out of 50,000) that predict a 10% decline (or greater) of the population over a period of 30 years, the median population size after 30 years relative to the scenario without OWFs for all model scenarios and the percentage of the results without OWFs that predict a smaller population size than the median of the OWF scenarios.

	PGR	5% percentile	95% percentile	P10%30yr	relative populatio n size after 30 years	percentage results unaffected lower than median affected
without OWFs	1.008	0.941	1.049	36.9%		
precautionary sce	nario IBM					
Dutch OWFs	1.004	0.938	1.045	41.3%	0.891	45.1%
foreign OWFs	1.000	0.936	1.042	45.2%	0.805	41.2%
all OWFs	1.001	0.936	1.043	44.3%	0.829	42.4%
realistic scenario I	BM					
Dutch OWFs	1.008	0.942	1.049	36.6%	1.009	50.3%
foreign OWFs	1.004	0.939	1.046	40.8%	0.899	45.5%
all OWFs	1.004	0.938	1.046	40.6%	0.905	45.7%
precautionary sce	nario 10%					
Dutch OWFs	1.008	0.942	1.048	37.2%	1.002	50.1%
foreign OWFs	1.005	0.940	1.046	40.1%	0.920	46.4%
all OWFs	1.004	0.939	1.046	40.5%	0.906	45.8%
realistic scenario 1	L 0 %					

Dutch OWFs	1.008	0.941	1.048	36.7%	1.012	50.5%
foreign OWFs	1.006	0.939	1.047	39.2%	0.943	47.5%
all OWFs	1.005	0.939	1.047	39.4%	0.932	47.0%



Figure 3.5 Northern gannet median PGR, with 5 and 95% percentile, relative population size after 30 years and the percentage of outcomes without OWFs that predicts a population size smaller than the median for each of the scenarios.

3.4 Sandwich tern

3.4.1 Density predictions

For sandwich terns the model fit was conducted using only the MWTL data. These data are of much smaller spatial area than the ESAS data. Consequently, to avoid over-extrapolating the model results, the area for which we do habitat quality predictions is reduced to a smaller portion of the North Sea, for which the input data are representative. It is technically possible to calculate sandwich tern abundance outside the input data locations, but doing so implies that the relationships determining abundance in Dutch areas translate 1:1 to the rest of the North Sea. We have no data to study whether or not this is the case and have therefore chosen not to extrapolate to other areas.

Since the exploratory analysis showed no day effect on density of sandwich terns, it was excluded from both models. The significant predictors for presence-absence (model 1) were depth and distance to coast

(Table 3.10). Presence decreased with distance to coast. For positive densities (model 2) only depth was significant. The depth smoother showed that sandwich terns occur mainly in the zone up to 25 m depth and within that zone densities tend to be highest in the shallowest part (Annex 1). The WAIC shows that for both models the model including the covariates and the spatial random field fits better than the models without the spatial random field (Table 3.11).

The estimated mean density map and its precision are illustrated in Figure 3.6. Consistent to our observation, sandwich terns adhere to the coast. The "high" density area has around 1-2 birds per km². The two high density clusters are associated to their colonies along the Dutch coast. The precision alongside the Dutch coast is high. The two high uncertain spots in the precision map are caused by zero sample coverage in these area, thus causing the estimated spatial random fields to be highly uncertain in these areas (Annex 1).

Table 3.10: Coefficients and significance of covariates in the model for sandwich tern. Significant covariates are printed bold.

	model 1 (presence-absence)	model 2 (density)
covariate	coefficient	coefficient
Intercept	-3.61	1.40
Slope	0.08	0.01
distance to coast	-1.83	-0.20
sediment_deep_sand	0.16	0.09
sediment_fine	0.02	0.001
sediment_fine_mud	0.08	0.28
sediment_mixed	-0.40	0.40
sediment_sandy_mud	-0.22	0.12
log surface area	0.27	
	covariate Intercept Slope distance to coast sediment_deep_sand sediment_fine sediment_fine_mud sediment_mixed sediment_sandy_mud log surface area	covariatecoefficientIntercept-3.61Slope0.08distance to coast-1.83sediment_deep_sand0.16sediment_fine0.02sediment_fine_mud0.08sediment_mixed-0.40sediment_sandy_mud-0.22log surface area0.27

Table 3.11: WAIC values of the two models with and without a spatial random field. The best models are indicated by the lowest WAIC value.

model	covariates only	covariates +	SRF
model presence/absence	26960		26038
model positive density	10928		11809

sandwich tern mean



sandwich tern mean

Figure 3.6. Habitat suitability map (left) and precision map (right) for the sandwich tern in the breeding season. White hatched areas are the internationally planned OWFs, blue hatched areas are Dutch planned and constructed OWFS. Grey areas are areas of missing data or too far outside the parameter range of the data.

3.4.2 OWF effects on mortality

Table 3.12 shows the simulated survival probability of the sandwich tern, with only the Dutch, only the international and all OWFs. The additional mortality is the difference between the median or the 5th percentile and the mortality rate without OWFs. Generally, there is very little variation in outcomes, which means that the differences between the 5th and the 50th percentile (the median) are minimal, indicating that all simulations give a highly similar outcome.

	used for stage	5th percentile monthly additional mortality from OWF	Median additional monthly mortality from OWF
Precautionary			
Dutch OWF			
	TJ	5.6E-04	0.0E+00
	ΤΜ, ΤΑ	8.8E-05	0.0E+00
International OWF			
	TJ	5.6E-04	0.0E+00
	ΤΜ, ΤΑ	8.8E-05	0.0E+00
All OWF			
	TJ	5.6E-04	0.0E+00
	ТМ, ТА	8.8E-05	0.0E+00
Realistic			
Dutch OWF			
	TJ	5.6E-04	0.0E+00
	ΤΜ, ΤΑ	8.8E-05	0.0E+00
International OWF			
	ΤJ	5.6E-04	0.0E+00
	ΤΜ, ΤΑ	8.8E-05	0.0E+00
All OWF			
	TJ	5.6E-04	0.0E+00
	TM, TA	8.8E-05	0.0E+00

Table 3.12 Effects of OWF (realistic and precautionary scenario) on sandwich tern monthly mortality rate during the period of OWF exposure: 5th percentile and median percentage additional mortality from OWFs.

3.4.3 Population level effect

Since the habitat model is limited to a smaller area, the sandwich tern population we modelled only overlaps partly with international wind farms (Table 3.1). A higher percentage of the population in the study area occurs in international than in Dutch OWFs (2.8 vs. 1.3%).

Without wind farms, the sandwich tern population model predicts an increase of the population. The median of the population growth rates is 1.033 (Table 3.13). While a decrease of the population is included in the inner 90% of model outcomes, the minority of the outcomes predicts a decrease of the population (Figure 3.7). Without wind farms, 25.6% of the outcomes predicts a population decline of 10% or more over a period of 30 years. For the precautionary scenario, this is ~25.7%; a negligible difference with the value without wind farms.

The population growth rate decreases most with OWFs for the 10% mortality scenarios (Table 3.13). For all IBM mortality scenarios the effect of the OWFs on all population level metrics is negligible. For all

scenarios, the median population size is at least 0.952 of the median population size without wind farms. In addition, at least a substantial 48.4% of the outcomes without OWFs predict population sizes lower than the median with all OWFs. All realistic scenarios show a negligible effect of OWF mortality on all population metrics. In summary, we do not find a strong effect of OWF related habitat loss on the population level for the sandwich tern.

When the Dutch OWFs are considered alone, the effect on all the metrics that we consider is negligible for all scenarios. The additional effect of the Dutch OWFs when the international OWFs are already present (the difference between 'foreign OWFs' and 'all OWFs' in Table 3.13) causes a very small change to the outcome of the assessment for terns.

The perturbation analysis for sandwich terns (Annex 3) shows that population growth rate is most strongly affected by changes in adult survival, which has almost an order of magnitude larger effect per unit change (elasticity) than any other parameter. The population growth rate is particularly insensitive to changes in the breeding success of young adults and the breeding probability.

Table 3.13 Sandwich tern population growth rate for Dutch OWF scenarios. The median annual population growth rate (PGR) with 5% and 95% percentile, the proportion of the calculations (out of 50,000) that predict a 10% decline (or greater) of the population over a period of 30 years, the median population size after 30 years relative to the scenario without OWFs for all model scenarios and the percentage of the results without OWFs that show a population size smaller than the median of the results for each of the OWF scenarios.

	PGR	PGR 5% percentile	PGR 95% percentile	P10%30yr (%)	relative population size after 30 years	results unaffected lower than median affected (%)
without OWFs	1.033	0.816	1.098	25.6%		
precautionary scen	nario IBM					
Dutch OWFs	1.033	0.814	1.098	25.7%	0.993	49.8%
foreign OWFs	1.033	0.815	1.097	25.6%	0.983	49.5%
all OWFs	1.033	0.816	1.097	25.7%	0.993	49.8%
realistic scenario I	BM					
Dutch OWFs	1.033	0.815	1.098	25.8%	0.993	49.8%
foreign OWFs	1.033	0.813	1.098	25.8%	1.002	50.1%
all OWFs	1.033	0.814	1.098	25.8%	1.003	50.1%
precautionary scen	nario 10%					
Dutch OWFs	1.033	0.816	1.097	25.7%	0.987	49.6%
foreign OWFs	1.032	0.811	1.097	26.0%	0.974	49.2%
all OWFs	1.032	0.817	1.096	25.7%	0.952	48.4%
realistic scenario 1	.0%					
Dutch OWFs	1.033	0.816	1.097	25.5%	0.986	49.6%
foreign OWFs	1.033	0.813	1.096	26.0%	0.977	49.3%
all OWFs	1.033	0.820	1.096	25.5%	0.981	49.4%



Figure 3.7 Sandwich tern median PGR with 5 and 95% percentile, relative population size and percentage of results without OWFs that shows a population size smaller than the median of the results for each of the scenarios.

3.5 Razorbill

3.5.1 Density predictions

Significant predictors for presence-absence (model 1) were: slope, day of season, data source, sediment (mixed, sandy mud, Table 3.14). Presence decreased with slope and increased with day of the season, was lower in the MWTL database and was higher over mixed and sandy-mud sediment than over coarse sediment. Densities (model 2) only showed significantly lower values in the MWTL data. The depth smoother shows an optimum at depths of 25-50 m. Occurrence shallower and deeper is lower compared to this zone. Densities decrease with depth (Annex 1).

The WAIC shows that for both models the model including the covariates and the spatial random field fits better than the models without the spatial random field (Table 3.15).

The estimated mean density map and its precision are illustrated in Figure 3.8. Results show that razorbills are mainly active between the Netherlands and UK. In this area, razorbills have a relatively low density compared to the other species in the study, around 0.6-0.8 birds per km², and the precision is relatively high. Note that the area outside the DCS contains considerably fewer samples and the estimates are based on the same covariate effect as inside the intensively sampled area and the extrapolation of the spatial random field (Annex 1). Therefore, these estimates should be interpreted with caution.

Table 3.14. Coefficients and significance of covariates in the model for razorbill. Significant covariates are printed bold.

species	model 1	model 2
	(presence-absence)	(density)

razorbill	covariate	coefficient	coefficient	
	Intercept		-2.67	1.42
	slope		-0.04	-0.002
	distance to coast		0.002	0.15
	distance to colony		-0.29	0.02
	day of season		0.14	0.01
	data source_MWTL		-0.71	-1.04
	sediment_deep_sand		-0.13	0.04
	sediment_fine		0.08	-0.03
	sediment_fine_mud		-0.10	0.11
	sediment_mixed		0.60	-0.11
	sediment_sandy_mud		0.23	0.13
	log surface area		-0.41	

Table 3.15. WAIC values of the two models with and without a spatial random field. The best models are indicated by the lowest WAIC value.

Model	covariates only	covariates + SRF
model presence/absence	70440	69561
model positive density	31969	30972



Figure 3.8: Habitat suitability map (left) and precision map (right) for the razorbill in the non-breeding season. White hatched areas are the internationally planned OWFs, black areas are Dutch planned and

constructed OWFS. Grey areas are areas of missing data or too far outside the parameter range of the data.

3.5.2 OWF effects on mortality

Table 3.16 shows the simulated change in mortality rate of razorbills using realistic and precautionary displacement, with only the Dutch, only the international and all OWFs. The additional mortality is the difference between the median or the 5th percentile and the mortality rate without OWFs. Generally, there is very little variation in outcomes, which means that the differences between the 5th and the 50th percentile (the median) are minimal, indicating that all simulations give a highly similar outcome.

Table 3.16 Effects of OWF (realistic and precautionary scenario) on razorbill monthly mortality rate during the period of OWF exposure: 5th percentile, median and median additional mortality from OWFs.

	used for stage	5th percentile additional monthly mortality rate from OWF	Median additionalmonthly mortality rate from OWF
Precautionary			
Dutch OWF			
	RJ	1.0E-04	0.0E+00
	RI, RA	9.3E-05	0.0E+00
International OWF			
	RJ	1.0E-04	0.0E+00
	RI, RA	1.9E-04	9.3E-05
All OWF			
	RJ	1.0E-04	0.0E+00
	RI, RA	1.9E-04	9.3E-05
Realistic			
Dutch OWF			
	RJ	1.0E-04	0.0E+00
	RI, RA	9.3E-05	0.0E+00
International OWF			
	RJ	1.0E-04	0.0E+00
	RI, RA	9.3E-05	0.0E+00
All OWF			
	RJ	1.0E-04	0.0E+00
	RI, RA	9.3E-05	0.0E+00

3.5.3 Population level effect

The razorbill population overlaps more with the international wind farms than with the Dutch ones (6.1 vs 1%, Table 3.1). Without wind farms, the razorbill population model predicts an increase of the population. The median of the population growth rates is 1.015 (Table 3.17). While the possibility of a

population growth rate smaller than one is included in the inner 90% of model outcomes, most outcomes predict an increase of the population (Figure 3.9). Without wind farms, 41% of the outcomes show a population decline of 10% or more over a period of 30 years. For the precautionary scenarios, this is maximum 43.3%.

The population growth rate decreases most with OWFs for the 10% mortality scenarios (Figure 3.9). For all IBM mortality scenarios the effect of the OWFs on all population level metrics is negligible. For all scenarios, the median population size after 30 years is at least 0.871 of the median population size without wind farms. In addition, at least 47.7% of the outcomes without OWFs predict population sizes lower than the median with all OWFs. In summary, we find a small effect of OWF related habitat loss on the population level for the razorbill for the 10% mortality scenarios.

The perturbation analysis for razorbills (Annex 3) shows that the population growth rate is most strongly affected by changes in adult survival, which has a more than 3-fold larger effect per unit change (elasticity) than any other parameter.

When the Dutch OWFs are considered alone, the effect on all the metrics that we consider is negligible in all scenarios. The additional effect of the Dutch OWFs when the international OWFs are already present (the difference between 'foreign OWFs' and 'all OWFs' in Table 3.17) causes a very small change to the outcome of the assessment for razorbills.

Table 3.17 Razorbill population growth rate for all model scenarios. The median annual population growth rate (PGR), the 5% and 95% percentile, the proportion of the calculations (out of 50,000) that predict a 10% decline (or greater) of the population over a period of 30 years (P10%30yr), the median population size after 30 years relative to the scenario without OWFs for all model scenarios and the percentage of the results without OWFs that show a population size smaller than the median of each of the OWF scenarios

	PGR	PGR 5% percentile	PGR 95% percentile	P10%30yr (%)	relative population size after 30 years	results unaffected lower than median affected (%)
without OWFs	1.015	0.860	1.133	41.0%		
precautionary scen	nario IBM					
Dutch OWFs	1.015	0.861	1.133	41.1%	0.996	49.9%
foreign OWFs	1.015	0.859	1.133	41.2%	0.987	49.8%
all OWFs	1.014	0.858	1.132	41.4%	0.980	49.7%
realistic scenario I	ВМ					
Dutch OWFs	1.016	0.861	1.133	40.8%	1.020	50.3%
foreign OWFs	1.016	0.860	1.133	40.7%	1.023	50.4%
all OWFs	1.015	0.859	1.132	41.0%	1.003	50.1%
precautionary scen	nario 10%					
Dutch OWFs	1.015	0.861	1.133	41.1%	1.003	50.1%
foreign OWFs	1.012	0.857	1.129	42.5%	0.910	48.4%
all OWFs	1.011	0.855	1.130	43.3%	0.871	47.7%
realistic scenario 1	L 0 %					
Dutch OWFs	1.015	0.860	1.133	41.4%	0.993	49.9%
foreign OWFs	1.013	0.858	1.131	41.9%	0.941	48.9%
all OWFs	1.013	0.858	1.131	41.9%	0.944	49.0%



Figure 3.9 Razorbill median PGR, with 5 and 95% percentile, relative population size and percentage of results without OWFs that shows a population size lower than the median of each of the scenarios.

3.6 Common guillemot

3.6.1 Density predictions

Significant predictors for presence-absence (model 1) were: slope, distance to coast, distance to colony, day of season, data source, sediment (fine, sandy mud, Table 3.18). Presence showed decrease with slope and distance to colony, increase with distance to coast, increase with day of the season, was lower for the MWTL set and was higher in fine sediment and sandy mud. Densities (model 2) were lower further from the coast, further from the colonies, at a later day in the season and were lower in the MWTL set and differed depending on sediment. Occurrence of common guillemot increases with depth but densities decrease in the range between 0 towards 50 m depth (Annex 1).

The WAIC shows that for both models the model including the covariates and the spatial random field fits better than the models without the spatial random field (Table 3.19).

The estimated mean density map and its precision are illustrated in Figure 3.10. Results show that common guillemots are mainly active along the north UK coast. However, the estimates were highly uncertain everywhere. This is partially due to low sampling coverage and sample size over the entire North Sea area as well as in the ESAS survey area (Annex 1).

Table 3.18: Coefficients and significance of covariates in the model for common guillemot. Significant covariates are printed bold.

species		model 1 (presence-absence)	model 2 (density)
common guillemot	covariate	coefficient	coefficient
	Intercept	-1.46	1.43
	slope	-0.04	0.003
	distance to coast	0.32	-0.18
	distance to colony	-0.59	-0.10
	day of season	0.06	-0.20
	data source_MWTL	-1.69	-0.27
	sediment_deep_sand	-0.04	0.11
	sediment_fine	0.09	0.05
	sediment_fine_mud	-0.03	0.19
	sediment_mixed	-0.36	-0.47
	sediment_sandy_mud	0.20	0.18
	log surface area	-0.21	

Table 3.19: WAIC values of the two models with and without a spatial random field. The best models are indicated by the lowest WAIC value.

model	covariates only	covariates + SRF
model presence/absence	175732	172343
model positive density	31969	30972



Figure 3.10. Habitat suitability map (left) and precision map (right) for the common guillemot in the nonbreeding season. White areas are the internationally planned OWFs, black areas are Dutch planned and constructed OWFS. Grey areas are areas of missing data or too far outside the parameter range of the data.

3.6.2 OWF effects on mortality

Table 3.20 shows the simulated change in mortality rate of common guillemots using realistic and precautionary displacement, with only the Dutch, only the international and all OWFs. The additional mortality is the difference between the median or the 5th percentile and the mortality rate without OWFs. Generally, there is very little variation in outcomes, which means that the differences between the 5th and the 50th percentile (the median) are minimal, indicating that all simulations give a highly similar outcome.

	used for	5th percentile additional	Median additional
	stage	monthly mortality from OWF	monthly mortality from OWF
Precautionary			
Dutch OWF			
	UJ ₀	3.34E-04	1.67E-04
	UJ ₁	2.09E-04	1.04E-04
	$U_{A,}$ $U_{I,}$ UJ_{2}	8.87E-05	0.00E+00
International OWF			
	UJ ₀	6.69E-04	3.34E-04
	UJ ₁	2.09E-04	1.04E-04
	U _A , U _I , UJ ₂	8.87E-05	0.00E+00
All OWF			
	UJ ₀	6.69E-04	5.02E-04
	UJ ₁	3.13E-04	2.09E-04
	U _A , U _I , UJ ₂	8.87E-05	0.00E+00
Realistic			
Dutch OWF			
	UJ ₀	3.34E-04	1.67E-04
	UJ ₁	2.09E-04	0.00E+00
	U _A , U _I , UJ ₂	8.87E-05	0.00E+00
International OWF			
	UJ ₀	5.02E-04	1.67E-04
	UJ ₁	2.09E-04	1.04E-04
	$U_{A,}$ $U_{I,}$ UJ_2	8.87E-05	0.00E+00
All OWF			
	UJ ₀	5.02E-04	3.34E-04
	UJ ₁	2.09E-04	1.04E-04
	<i>U</i> _A , <i>U</i> _I , <i>U</i> J ₂	8.87E-05	0.00E+00

Table 3.20: Effects of OWF (realistic scenario) on guillemot monthly mortality rate during the period of OWF exposure: 5th percentile, median and median percentage additional mortality from OWF.

3.6.3 Population level effect

The guillemot population overlaps more with the international than with the Dutch wind farms (6.4 vs 0.4%, Table 3.1). Without wind farms, the guillemot population model predicts an increasing population. The median population growth rate is 1.043 (Table 3.21). While the possibility of a population growth rate smaller than one is included in the inner 90% of model outcomes, the majority of the outcomes predicts an increase of the population (Figure 3.11). Without wind farms, 23.7% of the outcomes shows a population decline of 10% or greater over a period of 30 years. For the precautionary scenario, this is maximum 27.1%. In case only the Dutch OWFs are considered, this is a maximum of \sim 24.7%.

The population growth rate decreases most with OWFs for the 10% mortality scenarios (Figure 3.11). For all IBM mortality scenarios the effect of the OWFs on all population level metrics is negligible. For all scenarios, the median population size is at least 0.82 of the median population size without wind farms. In addition, at least 44.6% of population sizes without OWFs are smaller than the median with all OWFs. In summary, we find a small effect of OWF related habitat loss on the population level for the guillemot for the 10% mortality scenarios.

When the Dutch OWFs are considered alone, the effect on all metrics is negligible. The additional effect of the Dutch OWFs when the international OWFs are already present (the difference between 'foreign OWFs' and 'all OWFs' in Table 3.21) causes a very small change to the outcome of the assessment for guillemots.

The perturbation analysis for guillemots (Annex 3) shows that population growth rate is most strongly affected by changes in adult survival, which has over an order of magnitude larger effect per unit change (elasticity) than any other parameter.

Table 3.21 Common guillemot population growth rate for all model scenarios. The median annual population growth rate (PGR), the 5% and 95% percentile, the proportion of the calculations (out of 50,000) that predict a 10% decline (or greater) of the population over a period of 30 years (P10%30yr), the median population size after 30 years relative to the scenario without OWFs and the percentage of the results without OWFs that show a population size smaller than the median of each of the OWF scenarios.

	PGR	PGR 5% percentile	PGR 95% percentile	P10%30yr (%)	relative population size after 30 years	results unaffected lower than median affected (%)
without OWFs	1.043	0.897	1.089	23.7%		
precautionary scenario IBM						
Dutch OWFs	1.042	0.896	1.089	24.7%	0.954	48.7%
foreign OWFs	1.042	0.895	1.088	24.7%	0.954	48.7%
all OWFs	1.042	0.897	1.088	24.6%	0.953	48.6%
realistic scenari	o IBM					
Dutch OWFs	1.043	0.897	1.089	23.9%	0.994	49.8%
foreign OWFs	1.042	0.895	1.089	24.2%	0.979	49.4%
all OWFs	1.043	0.897	1.089	24.0%	0.992	49.8%
precautionary scenario 10%						
Dutch OWFs	1.043	0.896	1.089	24.3%	0.988	49.7%



Figure 3.11 Common guillemot annual population growth rate with 5% and 95% percentile, relative median population size after 30 years and percentage of predictions without OWFs that show a population size smaller than the median of each of the scenarios.

3.7 Effect sizes

Using the effect criteria from the previous paragraphs, we now calculate, using the IBM under the precautionary scenario, the effect sizes of the addition of the Dutch OWFs in addition to the international OWFs, the Dutch OWFs in isolation, the foreign OWFs, or all (Dutch and foreign) OWFs at once, for each species (Tables 3.22-26). We calculate the percentage change in the population growth rate and the P10%30yr (risk of a population decrease of 10% or more after 30 years). We choose these criteria because they are the best estimators of the expected effect (PGR) and of the risk including uncertainty (P10%30yr). These results are the answers to the objective of this work: quantify the effects of the Dutch OWF plans on the populations of five seabird species deemed at risk from OWF-related habitat loss. The results presented here show that the effects of OWFs on the capacity for population growth (PGR) are less than 1% in all cases. The risk of a measurably smaller population size after 30 years generally increases <5%, except for northern gannets, where it runs up to 23% when the effects of foreign OWFs are considered. However, the results also show that for this species, the effect of the Dutch OWF plans are negligible when considered in addition to the OWF plans of the other North Sea countries. In fact, the addition of only the Dutch OWFs shows a slight positive effect. This increase is most likely an aftefact of our computational methods, but it is negligibly small.

Table 3.22: Effect sizes of adding OWF on PGR and P10%30yr for red-throated divers.

	percentage change in:		
effect of:	PGR	P10%30yr	
Dutch OWF in addition to INT	0.00%	0.00%	
Dutch OWF in isolation	-0.20%	3.59%	
Foreign OWF only	-0.20%	3.59%	
All OWF	-0.20%	1.59%	

Table 3.23: Effect sizes of adding OWF on PGR and P10%30yr for northern gannets.

	percentage change in:		
effect of:	PGR	P10%30yr	
Dutch OWF in addition to INT	0.10%	0.00%	
Dutch OWF in isolation	-0.38%	11.96%	
Foreign OWF only	-0.72%	22.59%	
All OWF	-0.62%	20.30%	

Table 3.24: Effect sizes of adding OWF on PGR and P10%30yr for sandwich terns.

	percentage change in:		
effect of:	PGR	P10%30yr	
Dutch OWF in addition to INT	0.00%	0.39%	
Dutch OWF in isolation	0.00%	0.39%	
foreign OWF only	0.00%	0.00%	
all OWF	0.00%	0.39%	

Table 3.25: Effect sizes of adding OWF on PGR and P10%30yr for razorbills.

	percentage change in:		
effect of:	PGR	P10%30yr	
Dutch OWF in addition to INT	-0.10%	0.49%	
Dutch OWF in isolation	0.00%	0.24%	
foreign OWF only	0.00%	0.49%	
all OWF	-0.10%	0.98%	

Table 3.26: Effect sizes of adding OWF on PGR and P10%30yr for guillemots.

	percentage change in:		
effect of:	PGR	P10%30yr	
Dutch OWF in addition to INT	0.00%	0.00%	
Dutch OWF in isolation	-0.16%	4.19%	
foreign OWF only	-0.16%	4.14%	
all OWF	-0.16%	3.90%	

4 Discussion

4.1 Habitat models

The habitat maps show distributions for five species during the period they are present. For red-throated diver, razorbill and common guillemot the analysis was limited to the non-breeding season, for sandwich tern to the breeding season and for northern gannet the analysis was carried out both for the breeding and non-breeding season. Seasonal variation in bird numbers is accounted for by incorporating day of the season in the models (and making the predictions for the situation at the median date). Sandwich tern and red-throated diver are confined to the coastal area, whereas northern gannet, razorbill and common guillemot have a much wider distribution. In the habitat models we did not use any time-dependent explanatory variables, like temperature, salinity or food (other than within-season). This was a deliberate choice as such models would be unusable for our purpose, since they would require our scenario studies to include future predictions for those time-dependent variables. However, this greatly reduces the explanatory power (and therefore also predictive power) of the simplified habitat models we used. Part of this unexplained variation will be covered by the spatial random field that we apply. This is illustrated by the fact that in all cases models with a spatial random field performed better.

The habitat models describe the general distribution of the five species in the seasons in which they use the North Sea. This is based on the information of the period since 1991. Most ESAS samples were collected in very few years (Figure 2.1). Therefore, the data in terms of year, survey and spatial distribution are highly unbalanced. We assumed that there is not much change of the bird density distribution over the years and thus ignore the year effect and serial correlated spatial random field. Major changes in both seabird and sea mammal redistribution took place in the period just before 1990, possibly related to shifting food distributions (Camphuysen 2004; Frederiksen et al. 2007; Anderson et al. 2014). Our predicted distributions are based on the more recent situation. Future shifts in abiotic conditions or the food distribution may alter the habitat maps.

In the habitat mapping we present the distributions resulting from two models: presence-absence and positive densities. The quality of the habitat maps greatly depends on the quantity and quality of the bird data they are based on. The area covered by the MWTL data has a higher resolution than the remaining areas. E.g. the German Bight and the area off the UK coast are only covered in four years in the whole period. This pattern is visible in several habitat maps where the MWTL area stands out, despite the fact that it was incorporated in the model as a covariate. For the coastal species, red-throated diver and sandwich tern this is not a problem. However, for razorbill, common guillemot and northern gannet, the suggestion that the DCS is the preferred habitat over other areas is unrealistic. The uncertainty maps indicate areas of high uncertainty, which are generally the areas that are poorly covered by the surveys. For red-throated divers they include coastal areas off the Belgian and German coasts. For northern gannets during the breeding season, the areas close to the UK breeding colonies and the Gemini windfarm stand out. For sandwich terns, all un-surveyed areas have high uncertainty. For razorbills this applies to areas close to the UK coast and outside the DCS, and for guillemots to areas around the Shetlands and Orkneys.

As the habitat model is the first step in the analysis that we used in our approach, there are two sources of uncertainty that are hitherto not incorporated. Firstly, the uncertainties derived from the habitat maps are not propagated onto the individual models. This means that a large contribution to the overall uncertainty is not visible in the population model outcomes. More fundamental is the fact that the habitat models are based on an unbalanced dataset (as explained above), in which large areas are poorly covered, which is an important source of the uncertainty of the habitat maps. This could mean that uncertainties are in fact much larger than the ranges given in Table 3.1. Compared to the uncertainties

and assumptions related to the individual based models and habitat models, the uncertainties related to the data availability are likely much higher.

4.2 Individual-based simulation model

The individual based simulation model (IBM) which we have developed here is based on simple assumptions about individual behaviour: individuals move around in response to local gradients in habitat quality, do not move long distances at once and do not have a memory. However, as long as we simulate a large enough number of birds and enough opportunities for the birds to relocate over small distances, adding more complexity to the behaviour of the simulated birds does not necessarily change the patterns we obtain from the simulation. Just as it is now, it will be driven by the underlying habitat quality. This would only change if bird distributions are very strongly driven by fixed behavioural patterns, and would ignore information they get from the environment. However, if that were the case, there most likely would not be any habitat loss from offshore wind farms, as the birds would simply enter them, following their pre-programmed patterns. Of course, a change in the habitat quality would affect the predicted distribution.

The energy budget we use is also highly simplified: there is a cost to being alive, and energy is gained from feeding. In reality, the cost depends on behaviour. Flying in particular is an energy-expensive behaviour, and birds that frequently relocate most likely have a higher energetic cost than those that move around less. High mobility could hence be seen as a high-risk high-gain strategy, contrary to a more defensive sedentary behaviour. It is unclear if and how the presence of such different strategies would affect our results but it is difficult to hypothesize how it could increase OWF effects.

We have shown that the IBM model results are stable and precise: the distribution of results from a large number of runs with identical settings is similar to a normal distribution. We have also verified that our results are insensitive to the computational settings (e.g. the number of iterations) we use. Therefore, we are confident that the results are meaningful estimates of the effects of OWFs on seabird survival.

The OWF effects we observe using the IBM simulation are sometimes much weaker than those obtained from the earlier used `10% rule'. This is the case for example for the effect of international OWFs on razorbills and guillemots. On the other hand, the IBM results lead to stronger effects of OWFs on northern gannets in all scenarios as compared to the `10% rule' results, indicating that the 10% assumption is not precautionary for all species.

4.3 Population models

4.3.1 Red-throated diver

Red-throated divers are very sensitive to disturbance. Birds have been reported to take flight in response to approaching vessels several kilometres away (Schwemmer et al. 2011). One of the consequences of this behaviour is that the birds are hard to count at sea. There is little information available about the diver population (trends) in Europe. It is therefore not possible to compare the negative population trend that our population model predicts with population data. While the divers return to the same lake each year to breed, the breeding sites are widely spread out and the sizes of breeding populations are not well known either. As a result, population trends are generally uncertain (BirdLife International 2015). The divers undertake long distance migrations and the origin of individuals that overwinter on the North Sea is unknown.

The quality of the parameter estimates is low for this species. There is no measure of the variance in survival probabilities of juvenile red-throated divers (Horswill and Robinson 2015). The measures of breeding success are more reliable since individuals return to the same lake to breed each year. An

estimate of the breeding probability is lacking, we currently use a value of 0.05 which seems reasonable for seabirds in general (Horswill and Robinson 2015).

4.3.2 Northern gannet

The population model predicts a slowly increasing population. Gannet breeding colonies have been observed to increase everywhere in Europe (BirdLife International 2015). This is particularly true for Scottish colonies, of which some display exponential growth (Murray et al. 2015). The parameter estimates that we use are based on colonies in the UK. This area contains most of the breeding individuals that are relevant for the North Sea area. The population growth rate is relatively close to 1. A good estimate of the breeding probability is lacking, we currently use a value of 0.05 which seems reasonable for seabirds in general (Horswill and Robinson 2015).

4.3.3 Sandwich tern

The population model predicts an increasing sandwich tern population. Both fluctuations and positive trends are common in sandwich tern populations across Europe (BirdLife International 2015). In the months prior to and after breeding (and even within the breeding period itself), the sandwich tern is known to forage outside the coastal zone on the Dutch Continental Shelf (Fijn et al. 2017). This is the area in which the OWFs have been and are being planned. In addition to a suboptimal documentation of the distribution of the birds in this period (see section 4.1.1), there is no information available on the origin of these birds.

The sandwich tern is studied a lot in the Netherlands and the parameter estimates are quite reliable. An estimate of the breeding probability is lacking. We currently use a value of 0.05 which seems reasonable for seabirds in general (Horswill and Robinson 2015). The sensitivity analysis of the population model in our study shows that the population growth rate is highly sensitive to the adult survival probability. Currently, for the Netherlands only for the Wadden Sea population survival estimates are available. Outside the Netherlands, there is not much information available to estimate sandwich tern survival (Horswill and Robinson 2015). Estimates of survival probabilities are sensitive to exchange rates between colonies. Exchange between nearby colonies is known to occur frequently in the sandwich tern. It is unclear how often birds change colonies over larger distances, better information regarding migration rates would improve the reliability of the survival estimates. In addition, emigration and immigration to and from colonies outside the Dutch/Belgian area could affect the population dynamics. If many adult birds would leave or arrive, this would have a similar impact on the population growth rate as a change in the adult survival probability.

4.3.4 Razorbill

The median population growth rate shows an increase of the razorbill population. The razorbill abundance increases in some areas of Europe and decreases in others (BirdLife International 2015). The source colonies of overwintering birds have not been resolved, and it is therefore not possible to link birds on the North Sea to specific colonies.

The range of uncertainty in the outcomes of the population model is rather large. This stems from the large parameter uncertainty reported by Horswill and Robinson (2015). Especially the breeding success seems variable. In addition, for juvenile survival only few data are available, which were collected in Canada (Horswill and Robinson 2015). However, the outcomes of the razorbill population model are most sensitive to changes in adult survival. Razorbills generally display high colony-fidelity, which reduces the risk of underestimation of the adult survival rates.

4.3.5 Common guillemot

The median population growth rate shows an increase of the guillemot population. The abundance of the guillemot increases in some areas of Europe and decreases in others (BirdLife International 2015). The source colonies of overwintering birds have not been resolved, and it is thus not possible to link to specific colonies.

The guillemot is quite common in the North Sea area and the parameter estimates of this species are generally good. Adults tend to return to the same colonies to breed, reducing the risk of underestimation of the adult survival rates. Juveniles however, may switch between colonies, affecting the measurability of juvenile survival.

4.4 Density dependence

Density dependence is thought to be one of the most important structuring and regulating factors at the population level. Yet, density dependence is hard to detect in the field and it is often even harder to determine the exact mechanism through which density dependence acts. Moreover, many seabirds display a complex life cycle, in which their habitat is split over multiple locations. This makes it yet harder to determine where and when regulation of the population occurs. In addition, density dependent processes in population models can mask the effect of disturbances through compensation in the form of reduced density-dependent mortality or increased density-dependent productivity. A population model without density dependence is thus under most circumstances the correct implementation of the precautionary approach. We have therefore decided not to include any density dependent effects in our analysis. In the individual based model as well as the population model we assume that process rates (mortality, productivity) are independent of bird density. Below we give an overview, based on the review by Horswill & Robinson (2015), of documented effects of density for the five species of seabirds in our study. In addition, we explain under which circumstances density-dependence could affect the predictions of our model framework. And, hoe a rough proxy of effects of OWFs for situations where the population is close to the carrying capacity can be calculated.

4.4.1 Observed effects of density

Below we summarize published evidence for density dependence in various life history processes for the bird species under study here. In summary, there is clear evidence for density-dependence in the breeding season, when individuals commute between the colony and feeding grounds. We have not found documentation of density dependence during the non-breeding season. In addition, the importance of density dependence on the meta-population level is unclear, most evidence is based on studies of specific colonies.

Red-throated diver

There is no documented evidence of density-dependent processes for the red throated diver (Horswill & Robinson 2015).

Northern gannet

For the northern gannet, there is evidence for density dependence in migration between breeding colonies (Moss et al. 2002), in colony growth (Lewis et al. 2001), of foraging range around colonies (Lewis et al. 2001; Wakefield et al. 2013) and in the number of foraging trips (Wakefield et al. 2013). The population trends for certain Scottish northern gannet colonies also show indications of density-dependent effects, as their growth appears to level off (Murray et al. 2015).

Sandwich tern

There is no documented evidence of density dependent processes for the sandwich tern (Horswill & Robinson 2015). Numbers in Dutch sandwich tern colonies fluctuate strongly (Stienen 2006, Thesis). The slower growth of the total number of individuals in the Netherlands observed over the last decade (Chen

et al. 2018) could indicate that the Dutch sandwich tern population approaches the carrying capacity, or could be due to fluctuations in external conditions.

Razorbill

The Isle of May colony count shows a levelling off (Harris et al. 2015b), which could be an indication of density-dependence in colony growth. The Barents Sea colonies show a different trend (Fauchauld et al. 2015). Birds from Scandinavian colonies also use the North Sea as overwintering area. Both the age of recruitment (Horswill & Robinson 2015) and the foraging range around colonies (Wakefield et al. 2013) are reported to be density dependent. However, the relationship between age of recruitment and colony size could also arise because new colonies are generally formed by young adults.

Common guillemot

Colony size has been reported to affect age at recruitment (Votier et al. 2008), migration (Crespin et al. 2006) and egg production (Harris et al. 2015a). There is also evidence that the distribution at sea around colonies is density-dependent (colony size, Wakefield et al. 2017). The Isle of May colony count shows levelling off (Harris et al. 2015a), which may be a sign that the colony is approaching its carrying capacity. Guillemot colonies in Norway (Fauchald et al. 2015) do not show any sign of slow growth. Birds from Scandinavian colonies also use the North Sea as overwintering area (SEAPOP, 2018).

4.4.2 Potential density dependent effects of OWF displacement

The individual based model used in this study investigates the effect of differences in the food quality that birds encounter due to displacement from OWF-areas. The model is based on the assumption that the food quality of the habitats will not change due to the displacements of the birds. In other words, there is no local food depletion as a result of feeding. Theoretically it is possible that displacement due to OWFs leads to higher densities of birds around the OWF areas, and that this negatively affects the local food density. While there is evidence that food intake is affected by bird density for colony-breeding seabirds during the breeding (Wakefield et al. 2013; Bolton et al. 2018), there is no documented evidence of resource-competition outside the breeding season. Outside the breeding season birds have more space available (no nest to return to) and have more time to feed (no time lost flying back and forth; though the advantage is offset by shorter day length in winter). It seems intuitively unlikely that space or food are limiting on the population level during the non-breeding season, and we have not found any evidence in the literature that this may occur. However, the lack of evidence should not be interpreted as evidence for its absence, as such studies would be difficult to carry out.

For the current assessment only small parts of the North Sea are occupied by wind farms. It is important to note, that when larger parts of the North Sea are to be covered with wind farms, density dependence will eventually become more important. In its current form, our framework is not suitable to study density-dependent effects. However, under the assumption that the populations are currently already at carrying capacity we can make a rough estimate of the effect for a situation with strong density dependence. If the carrying capacity is impacted by windfarm deployment, the *absolute* population size will decrease by the number of displaced birds. The predicted decrease in population size under these assumptions equals the percentage of the population displaced by OWFs (Table 3.1). For a displacement of 100%, this decrease would range from 3-7%. These effects are stronger than currently predicted by our model framework in absence of density dependence (Tables 3.22-3.26).

Based on the evidence that is available, potential density dependent effects are most relevant for razorbills and guillemots as they seem the most likely candidates for being close to their carrying capacity, with, for example, the Isle of May colony count levelling off. Again, however, there is no evidence available for density-dependent effects on the "winter season population" (consisting of individuals from multiple colonies). In addition to the UK, guillemots and razorbills use the Scandinavian coastline for breeding. A study of the meta-populations of the birds on the European/North Sea level has not yet been undertaken.

The growth in sandwich tern numbers in the Netherlands has seemed to slow down over the last decade. However, it is unclear how numbers in other countries, which are also part of the North Sea metapopulation, are developing, and no effects of high density have been documented. No relevant knowledge is available for red-throated divers.

Many gannet colonies are still increasing rapidly, indicating that density-dependent effects are unlikely. In summary, meta-population studies of the North Sea populations are necessary for all the bird species treated here, before it is possible to assess whether OWFs could affect the carrying capacity.

4.5 OWF scenarios

4.5.1 OWF effects

In all realistic and precautionary scenarios, the effect of wind farms on the population size and indicators of the five bird species is small. For the effect of the Dutch wind farms alone, either in isolation (contrasting no OWF and Dutch OWF scenarios) or in addition to the international wind farms (contrasting the all OWF and international OWF scenarios), the effects are even smaller. The northern gannet, razorbill and common guillemot population show a negligible effect of Dutch windfarms. Amongst all species, the gannet population is affected most strongly, probably because the effect of OWFs adds mortality both in the breeding and the non-breeding season, while for all other species their presence on the North Sea is seasonal. However the OWFs are only one of the many sources of disturbance, next to e.g. shipping. The fact that we find only small effects of OWFs does not preclude an effect in combination with other potential pressures.

Since the habitat model is limited to the area around the Netherlands for the sandwich tern and redthroated diver populations, we considered only the effect of wind farms in this area for these species. Some of the international wind farms are located within this area. It is known that the winter distribution of divers includes areas outside that included in our habitat model, but we have no data to extrapolate to these areas. Also, there is exchange between Dutch and foreign sandwich tern colonies. However, we are currently unable to quantify this exchange and hence are limited to calculating the effects of OWF-related habitat loss in near-Dutch waters only.

4.5.2 Uncertainty of population estimates

The population numbers that are estimated by the habitat models are a rough estimate of the actual population size at the median date during the period in which they are in the area. Both parts of the habitat model (presence/absence and densities) had large uncertainties (not shown), which means that also the resulting population size is very imprecise. Moreover, in reality the population may be larger than estimated, because birds could continuously enter and leave the area that we consider. However, the approach that we have chosen allows for the calculation of the maximum effect on the population level, by assuming that all birds are present throughout the season, so that the population experiences the maximum exposure level.

The population level indicators that we have chosen are independent of population size. The population indicators are all calculated based on the population growth rates, which are determined based on the life history parameters only.

4.5.3 Displacement behaviour

The estimates of displacement are mostly based on comparisons of counts of birds inside and outside windfarms (Dierschke et al. 2016). These observations do not take factors such as feeding behaviour into account. Therefore, the precautionary scenario assumes 100% avoidance for the mortality calculations. On the other hand, many of the observations on avoidance of OWFs are done during or shortly after the construction phase. It is likely that habituation to the OWFs may occur for all species studied here, except perhaps for the red-throated diver. The red-throated diver is very sensitive to disturbance (Schwemmer et al. 2011) and the regular presence of a maintenance boat such as is common in wind farms may be enough to keep these birds away from OWF areas. On the other hand, the sandwich tern, northern gannet, razorbill and common guillemot may not lose foraging habitat in the long run. This implies that our scenarios assume more impact than will occur in reality. For the gannet, however, not avoiding OWFs may result in an increase of the risk of collision mortality. The first studies of habituation
of seabirds to OWFs have only recently been done. So far, there is no clear picture of habituation behaviour of the birds that we studied here.

4.5.4 Timing of OWF effects and OWFs already present

In addition to a number of choices in developing our assessment framework, also our implementation of the OWF scenario is precautionary. We implement all planned OWFs up to 2030 simultaneously from the start of the simulations. We allow no habituation and no transition period with fewer OWFs. In our 'no OWF' calculations, we have assumed that all OWFs that are already present in the North Sea are not there. While this is potentially problematic because in some of the distributional data and some of the data underlying parameter estimates of the population models, these OWFs were already present, this means that in the distributions and parameter estimates their effects are already included. However, these OWFs are few and small compared to the planned OWFs for the next decade, so we expect this effect to be small. In any case, it conforms to the precautionary approach because if anything, our approach results in an overestimation of the OWF effects.

4.5.5 Effects on fecundity

Our analysis has focused on OWF effects on survival, rather than effects on fecundity. This has several reasons. Our elasticity analysis shows that for all species, adult survival is the most important determinant of population growth rate – and hence all other population metrics. This is not surprising, because all species are long-lived and have low annual fecundity. It does imply that OWF effects on fecundity, although they may be present and even may be substantial, will have relatively little effect on the population metrics. A further reason that the effect on fecundity is likely to be smaller, is plasticity in nesting location. If a nesting location becomes severely affected by nearby OWFs, birds are likely to relocate to other areas, either because individual birds move or because offspring do not return to their parental breeding location. Including this dynamic would not only necessitate the inclusion of explicit colony dynamics but also an assessment of the availability of unused breeding locations, both of which are beyond the scope of this study.

4.5.6 Effects of habitat change

The large scale at which windfarms are currently planned may involve considerable changes in the underwater habitat. The predominant habitat currently consisting of sandy bottom will partly be replaced by hard structures. In addition, the placement of the piles may affect mixing of water layers and both effects may change fish communities and can have both positive and negative effects on predators. Finally, harvesting wind energy can alter the transfer of energy from air to sea, affecting waves and currents. Such system-level changes are not part of the current study, but would affect the results in this study, since they would affect both wind patterns and the distribution of prey fish, i.e. the food availability/distribution of the birds.

4.6 Conclusions and recommendations

We have estimated population effects of OWF avoidance for five seabird species in the North Sea. To our knowledge, this is the first study to consider effects for the full life cycle and the larger population. Most studies of this effect focus on the reproductive success of a single breeding colony. The framework we use for these calculations relies on established methodological components, but the combination of components to scale up from local OWF-related habitat loss to effects on populations is novel.

The Wozep programme, of which this work is part, aims to reduce the need to rely on the precautionary approach in the assessment of ecological effects of OWFs. Our work has clearly contributed to this goal. The species we work on here were selected based on their high sensitivity to OWF-related habitat loss in a previous study (van der Wal et al. 2018). We have constructed habitat models, individual based simulation models and population models, using all data and knowledge available to us. We have applied

the resulting assessment framework using a consistent precautionary approach in every step. Our results show that for none of the species, any of the OWF scenarios lead to negative population growth rate (indicative of a declining population). The largest effect we see, using our IBM approach to estimate OWF mortality, is a 0.7% decrease in population growth rate of northern gannets when all internationally planned OWFs are considered. The contribution of the Dutch OWFs is negligible. For guillemots and razorbills, the effects are considerably smaller. For red-throated divers and sandwich terns, the relative effects of the Dutch OWF (as part of the total, international OWF plans) are larger, but the overall effects are small.

For all scenarios studied, the overlap between outcomes for unimpacted and impacted populations is large. Given the variability in natural populations we consider it unlikely that any of the OWF-related changes calculated in this assessment will be detectable in natural populations under realistic sampling effort. Even if detectable, it is unlikely that these effects can be attributed to OWFs.

We expect that our results for red-throated divers and sandwich terns are applicable to other strongly coastal species: the Dutch OWFs have little effect because they are too far offshore. We also expect our results for northern gannets, common guillemots and razorbills to hold for similar colony-breeding birds which have their breeding grounds well outside the Netherlands. Except for birds that show a different pattern in habitat use of the North Sea. If additional locations for OWFs elsewhere on the Dutch Continental Shelf would be appointed, novel calculations of the Dutch contribution to population effects would have to be conducted. The assessment framework developed in this study is readily available to conduct such further analyses.

4.6.1 Recommendations for improved future assessment quality

Improving habitat modelling

The quality of habitat models depends on the quality of the data used to construct them. That accounts both for the bird counts as well as for the explanatory variables.

For sandwich terns, because they are strongly coastal, the MWTL sampling programme is sufficient in space. However, an extension in time to better cover the breeding and post breeding seasons would strengthen the knowledge base for assessment of OWF (and other anthropogenic) effects.

Red-throated divers are difficult to count because they are easily disturbed. One potential improvement to data collection for this species may be systematic monitoring using high definition cameras from planes flying at high altitude.

We are confident that the data coverage of the Dutch part of the North Sea is sufficient and that all existing data for that area, as brought together in the MWTL and ESAS databases, were used in this study. Unfortunately, data coverage for other parts of the North Sea is not well balanced and the habitat model quality for gannets, razorbills and guillemots has suffered as a result. Maintaining the ESAS database has proven difficult in the last ten years or so, and not all survey data collected in these years have been forwarded to ESAS to be incorporated into the database. In addition, new parties have emerged that have been collecting seabirds at sea data and these have not all become ESAS partners. That survey data are missing from the ESAS database is evident based on habitat model analysis from different countries (see e.g. Evans et al. 2018; Mendel et al. 2019). Moreover, much of the national survey effort, including in The Netherlands, has been directed towards national waters. Wide ranging, international surveys have become increasingly rare. For future, international studies of seabird distribution patterns in the North Sea, a revitalization of ESAS is thus urgently needed as is new, international survey effort that covers the entire North Sea, rather than just national waters. These two might go hand in hand, and new, jointly undertaken survey work may entice parties to update ESAS. Within ESAS, suggestions have been made to let ICES host the (new) ESAS database and work towards international cooperation with the fisheries institutes around the North Sea. This would perhaps allow a

coupling between fisheries surveys and seabird surveys. Support from the governments of the North Sea countries, e.g., via the ICES delegates could be a great help here.

Finally, many of the abiotic variables explaining the abundance of seabirds may actually be abiotic factors contributing to the likely abundance of food for seabirds. Better understanding of the distribution, dynamics and behaviour of these fish species (e.g. sandeel) would greatly help in constructing better habitat suitability maps for fish-eating seabirds. While there are regular scientific surveys for fish, these are generally designed to inform fisheries management and are therefore annual surveys at a fixed moment during the year, which is of very limited use for our purposes.

Improving the IBM

The IBM uses general principles from behavioural ecology and physiology: individuals move towards higher quality habitat, and if and individual does not feed enough it eventually dies. While these principles hold for the birds we study, they are most likely not enough to predict the behaviour of individual birds. We know that there is also a tendency of many species to move closer to the breeding locations as the breeding season draws closer, and that many birds stay near the breeding sites after breeding.

Furthermore, seabirds possess advanced navigation skills and complex learned behaviour, which would enable them to more easily cross areas of low quality to reach better, sites. Such directional longerdistance movement would enable birds to move against gradients of deteriorating habitat quality, which they are currently unlikely to do. This could lead to higher concentration of seabirds in areas of high quality. The behaviour of seabirds, far out at sea, is difficult to study. Hence it is unsurprising that little published information exists. Ongoing advances in animal telemetry may lead to more insights into these aspects of seabird ecology in the near future.

For northern gannets and sandwich terns it is worth exploring the potential to expand our model to the breeding season. This is interesting since these species are highly mobile even within the breeding season, with a relatively small number of breeding locations, which are well-studied. Such studies would allow for a better estimate of the OWF effects on productivity (reproductive rate), which are not incorporated currently. In addition, the literature overview presented in the discussion indicates that density dependence is most important during the breeding season. Since the planned OWFs are placed within the breeding habitat of northern gannets and sandwich terns (and to a lesser degree also that of guillemots and razorbills) these could potentially impact the "breeding carrying capacity". An extension of our IBM modelling approach, which includes the potential for crowding or local food depletion, may yield better insights into this important life history period.

Improving population modelling

Generally, the quality of the life history parameters of the birds is good, except for the red-throated diver, for which little information is available. For razorbills some of the parameter estimates are fairly uncertain. This translates into large uncertainties in the results for these two birds. Better knowledge of life-history parameters would improve the predictive power for these species.

An important source of uncertainty in the population modelling is that it is hard to disentangle mortality and migration. A good understanding of the meta-population dynamics between colonies (the degree of exchange of older birds and new breeders between colonies, and the mechanisms behind the exchange) would greatly help. This would allow for better estimates of the mortality parameters. In addition, better understanding the importance of immigration and emigration for the population dynamics. Such an analysis is particularly relevant for sandwich terns breeding in the Netherlands and the UK, which are known to switch between colonies easily.

Density dependent population regulation has a strong effect on population dynamics. The literature overview presented in the discussion shows that there is not enough information available regarding

density dependent mechanisms to include them in the population models for the birds under study here. Especially the importance of density dependent mechanisms in regulating meta-populations on the level of the whole North Sea is not known. Thorough, international studies of the bird populations during winter as well as the breeding season on the level of the whole North Sea or the European level are essential for understanding the population dynamics.

Quality Assurance

Wageningen Marine Research utilises an ISO 9001:2015 certified quality management system. This certificate is valid until 15 December 2021. The organisation has been certified since 27 February 2001. The certification was issued by DNV GL.

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Justification

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

Approved:

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Date:

5th of July 2019

1 Annex: Details on habitat modelling

red-throated diver



Presence (red) and absence (black)



Relationship between presence of red-throated diver and depth (left, model 1) and between density and depth (right, model 2).



Relationship between presence of red-throated diver and day of the season (left, model 1, right, model 2). Day 0=1st1 October.

Mesh and sampling points for model 1 (left) and model 2 (right, only non-zero observations)



Constrained refined Delaunay triangulation



Constrained refined Delaunay triangulation

northern gannet non-breeding



Presence (red) and absence (black)



Relationship between presence of northern gannet in the non-breeding period and depth (left, model 1) and between density and depth (right, model 2)

Constrained refined Delaunay triangulation



Mesh and sampling points for model 1 (left) and model 2 (right, only non-zero observations)

northern gannet breeding



Presence (red) and absence (black)



Relationship between presence of northern gannet in the breeding period and depth (left, model 1) and between density and depth (right, model 2)

Constrained refined Delaunay triangulation



Mesh and sampling points for model 1 (left) and model 2 (right, only non-zero observations))

sandwich tern



Presence (red) and absence (black)



Relationship between presence of sandwich tern and depth (left, model 1) and between density and depth (right, model 2).

Constrained refined Delaunay triangulation

Constrained refined Delaunay triangulation



Mesh and sampling points for model 1 (left) and model 2 (right, only non-zero observations)

Razorbill



Presence (red) and absence (black)



Relationship between presence of razorbill and depth (left, model 1) and between density and depth (right, model 2).



Mesh and sampling points for model 1 (left) and model 2 (right, only non-zero observations)

common guillemot



Presence (red) and absence (black)



Relationship between presence of common guillemot and depth (left, model 1) and between density and depth (right, model 2)



Mesh and sampling points for model 1 (left) and model 2(right, only non-zero observations)

2 Annex: Implementation methods for analysis parameter uncertainty

A. Potiek, F.H. Soudijn & T. van Kooten

2.1 Introduction

Parameter estimates are usually reported with a measure of variance, often in the form of a standard deviation. Variability in parameter values may stem from measurement error and/or natural variability in parameter values. Measurement error is an inherent part of any measurement and the measurement process. For example, if the measured adult survival rate is 90%, it is possible that the 'true' survival is actually 91%. A large measurement error indicates that the estimate is relatively uncertain. Natural variability in parameter values is caused by fluctuations in environmental conditions such as food availability and the weather. In a year with favourable environmental conditions, survival and fecundity are likely to be higher than in other years. It is often not possible to separate the causes for variability in the parameter values. However, the impact of the two on the outcome of a population model may strongly differ.

Here, we study to what extent the source of parameter uncertainty (measurement error or natural variability) matters for the outcome of our main study, the effect of OWF-related displacement on the population dynamics of seabirds.

In theory, if all variance is explained by measurement error, the demographic rate is (slightly) under- or overestimated every single year in the population model. Hence, the effect adds up over time. In contrast, variation between years results in some years with above-average parameter values, and some years with below-average parameter values. Over time, the average will move towards the estimated value. Several demographic rates vary between years. In our population models, input parameters are juvenile survival, immature survival, adult survival, fecundity and probability of non-breeding. These demographic rates may vary independently, or the variation may be correlated. Such correlations would occur if natural variability was caused by 'good' and 'bad' years, in which all parameters would be positively or negatively affected. In addition to the source of the variation, we study the effect of correlated variability in parameter values.

This is essentially an analysis of model assumptions. The effect of the various assumptions will be qualitatively similar for any of our studied species. Therefore, we do the analysis only for the common guillemot, for which we have the best data on variance of parameter values. The results can, in a qualitative sense, be extrapolated to the other species.

These results will allow us to choose the most appropriate way to incorporate parameter value uncertainty in our main analysis. An important guiding principle in this choice will be the precautionary principle. If one assumption will lead to larger effects of OWFs and we have no data to choose between the different possibilities, the precautionary principle requires us to choose the most conservative method.

2.2 Aim

This Appendix covers four different subprojects:

Measurement error

- 1. Test the impact of measurement error on the uncertainty of the outcomes of the population model.
- <u>Natural variability</u>
- Test the effect of stochastic fluctuations in the parameter values through time on the uncertainty of the outcomes of the population model. In contrast to the analysis on the impact of measurement error (1), the parameter values are here (2) assumed to vary between years.
- 3. Test the effect of within-year correlations between values of the parameters (survival and fecundity) on the uncertainty of the outcomes of the population model. In subproject 2, we assumed that demographic rates varied independently, whereas in subproject 3 we run the model for different strengths of correlations.
- Empirical natural variability: evidence for correlated demographic rates
- 4. Analyse multi-annual parameter datasets of some of our model species (Wozep habitat loss and collision victims) to determine how parameter values naturally vary through time and to what extent demographic rates are correlated.

2.3 Methods

We study the effect of the source of measurement error (subprojects 1-3) using the population model of the common guillemot. The model details are described in the main section of this report.

2.3.1 Measurement error

2.3.1.1 Subproject 1

The uncertainty in the model output due to measurement error can be estimated using Monte Carlo methods. This method implies random sampling from the probability distributions of all parameter estimates. For subproject 1, we follow the assumption that the deviation from the mean in parameter values is independent for each parameter. In addition, this method assumes that the uncertainty stems from inaccurate measurements of parameter values rather than from temporal changes. Hence, parameter values do not vary in time. The choice for the probability distributions of the parameter estimates depends on the availability of the data for the species that is under study. If very little data are available for a certain species, the range from which a parameter value is drawn will be wider than when good data are available.

We calculate all model output (e.g. population growth rates, sensitivity analysis and population sizes) for a large number of random draws from the parameter probability distributions. Based on the results of these simulations we determine confidence intervals around the model output.

2.3.2 Natural variability

2.3.2.1 Subproject 2

A stochastic matrix model allows for variability of the parameter values through time. At each time step, parameter values are drawn randomly from a probability distribution of the parameter values. The shape of the probability distributions is based on the information that is available for the species under study. Using this method, we run 10,000 simulations, in which demographic rates are independently, randomly drawn from the probability distribution. Based on the results of the simulations we determine confidence intervals around the model output.

2.3.2.2 Subproject 3

We also investigate the effect of covariance between the parameter values on the model outcome. If the correlation between survival and reproduction is strong, this means that a good year for survival is also a good year for reproduction. In contrast, if they are uncorrelated, survival and fecundity vary

independently. To analyse the impact of such a correlation, we use a similar approach as described for subproject 2. However, we define an additional parameter C, which is the degree of correlation between demographic rates. This parameter C varies between 0 and 1, corresponding to uncorrelated to completely correlated demographic rates.

2.3.3 Empirical natural variability: correlation in measured parameters

2.3.3.1 Subproject 4

Using datasets of life history parameters that consist of multiple years of data from the same colony, we analyse the effect of "natural" environmental stochasticity on the model output. The previous step in the analysis will help us understand how correlated parameter values may affect the model outcomes. A dataset with "natural" environmental stochasticity shows us how strong the correlation between *Table 3.1 Overview of data used for testing correlations*

parameter values and also the frequency of "good" and "bad" years is in reality. The previous step in the analysis is needed because there is not a lot of multi-year data of life history parameters available. As the level of correlation between parameter values varies between species, we perform this analysis for several species. However, this analysis requires high-quality and long-term data, the availability of which will be limited.

We searched the literature for papers reporting survival rates as well as fecundity. An overview of the available data is shown in Table 3.1. Correlations between demographic rates in the same year were tested on significance, as well as delayed effects of survival in the previous year on breeding success in

Source	Species	Parameters	Area	Time period
Meade <i>et al.</i> (2013)	Guillemot	immature survival, adult survival, breeding success	Skomer (UK)	1992-2004
Crespin <i>et al.</i> (2006a, b)	Guillemot	immature survival, adult survival, breeding success	Isle of May (UK)	1983-1994
Ebbinge <i>et al.</i> (2002)	Brent goose	adult survival, breeding success (% juveniles in winter)	Western Europe (wintering area)	1956-1998
CEH (Center for Ecology and Hydrology, UK) monitoring programme	Guillemot, kittiwake, razorbill, puffin	return rate, breeding success	Isle of May (UK)	2007-2018

the present year.

In addition to the data found in published literature, more recent data from Isle of May was collated based on annual newsletters from the CEH long-term monitoring programme, in which among others guillemot, kittiwake, puffin and razorbill are monitored (https://www.ceh.ac.uk/our-science/projects/isle-may-long-term-study). These newsletters report breeding success (fledglings per breeding pair) and return rates for adults. Return rates can be used as a proximate for annual survival. Although return rates underestimate annual survival, it can be assumed that this is the case for all years within the monitoring program (2007-2018).

2.3.4 Input data population models, basis for subproject 1-3

2.3.5 Species: common guillemot

We assume that the data underlying all parameter values follow a binomial distribution. Therefore, uncertainty around a mean parameter value \overline{Sa} with variance σ_{Sa}^2 can be described by a beta distribution with $\alpha = \overline{Sa}^2(\frac{1-\overline{Sa}}{\sigma_{Sa}^2} - \frac{1}{\overline{Sa}})$, $\beta = (\alpha - \overline{Sa} \alpha)/\overline{Sa}$.

As we do not have the data and we do not know n_i , we simulate data based on the beta distributions as described above. We repeat this for all parameter values. The variance is taken as the standard deviation

cubed. Note that although the used parameter distribution is the same for subprojects 1-3, the assumed source of variation differs. In the first subproject, we assume that the variation is due to measurement error. The parameter values are drawn at the start of a simulation, and used for each year within that simulation. For a new simulation, new parameter values are drawn. Hence, each simulation uses different demographic rates, which are constant over time. In the second subproject, demographic rates vary over time. Within each simulation, new values for each demographic rate are drawn every year. For the third subproject, the simulation starts with the definition of the degree of correlation. Subsequently, a parameter defining year quality is drawn. Depending on the degree of correlation, the effect of year quality on demographic rates can be strong (high degree of correlation) or weak (low degree of correlation).

Symbol	Mean value	Variance	unit	Description	Remark	Source
F _a	0.627	0.147 (sd)	Year ⁻¹	Fledged offspring		1
D	0.08	0.03 (sd)	-	Skipped breeding probability, all adult stages	No source for SD, the value is arbitrary	1
S ₀	0.56	0.013	-	Annual Survival probability age 0		1
<i>S</i> ₁	0.792	0.034	-	Annual Survival probability age 1		1
<i>S</i> ₂	0.917	0.022	-	Annual Survival probability age 2		
S _a	0.939	0.067 (sd)	-	Annual Survival probability immatures & adults, age 3+		1
a _m	6		Years	Age at recruitment		1
1 Horewill	9 Dobincon (7	015)				

Table 3.2: Parameter values and sources used in the population model

Horswill & Robinson (2015)

2.4 Results

For each of the scenarios, we show a frequency distribution of the population growth rates, calculated over 10,000 runs.

2.4.1 All variation due to measurement error



Figure 3.1 Population growth rates (with mean, red solid line and 5% and 95% edge of results, red dashed lines) and inner 90% of population projections (with mean of all projections, red solid line) for Monte Carlo simulations. Parameter values are as given in Table 2.

2.4.2 All variation due to natural variability



Figure 3.2 Frequency distribution of population growth rates assuming all variation is due to natural variability. Demographic rates within years are assumed to be independent (not correlated, C=0). Continuous line represents median population growth rate, and dashed lines the 90% confidence interval.



Figure 3.3 Frequency distribution of population growth rates with varying degree of correlation between parameters (Low C: weak correlation, C=1: fully correlated values). Continuous line represents median population growth rate, and dashed lines the 90% confidence interval.

2.4.4 Empirical natural variability: correlation in measured parameters

Demographic rates for guillemots reported by Meade et al. (2013) and Crespin et al. (2006a, b) were not significantly correlated.

For brent goose, we analysed data from Ebbinge et al. (2002) to test for correlations between demographic rates. In this study, breeding success in year i is defined as the percentage of first-winter birds in the following winter. We tested for correlations between breeding success and adult survival in the year prior to the breeding season, as well as to the year following the breeding season. We found no correlation between the breeding success and the adult survival in the following year. However, we found a significant negative correlation between adult survival prior to the breeding season and breeding success (Figure 3.4). This significant negative correlation suggests that a year with low adult survival is likely followed by high breeding success. This was contrasting with our expectation that individuals are in poorer body condition after a strong winter with high mortality, and therefore have lower breeding success. This has been interpreted as density-dependence in reproductive output (Ebbinge et al 2002), but might also be an artefact of the type of data collection. With both measures depending on the number of adults, a relatively low number of adults in a certain year suggests low adult survival

compared to other years. In the calculation of breeding success, the number of first-year individuals is divided by a relatively low number of adults. In case the number of first-years is comparable between years, this gives a relatively high proportion of first-years.





Data on the breeding success and return rates of guillemot, kittiwake, razorbill and puffin from the CEH long-term monitoring programme did not show significant correlations for kittiwake and razorbill. For both guillemot and puffin, there seems to be a significant positive relationship between breeding success and return rate in the year before as well as after the breeding season (Figure 3.5). However, the cause of these correlations is a single data point of extremely low breeding success. In all cases, the exclusion of this data point results in a non-significant correlation.



Figure 3.5 Correlations between breeding success and the return rate of the year prior to the breeding season (left panel), and between breeding success and the return rate of the year following the breeding season (right panel).

2.5 Conclusions

- Stochastic simulations with complete correlation give the widest variance in population growth rate distribution, but we see no support for such strong correlations in any of the data examined.
- Uncorrelated and weakly correlated temporal variation of parameter values leads to the narrowest population growth rate distributions
- Time-invariant measurement error (Monte Carlo approach) leads to higher variation in population growth rate distribution.
- There is no empirical basis to distinguish between temporal variations in parameter values and measurement error.
- Applying the precautionary approach leads us to choose the Monte Carlo approach, because it results in the highest uncertainty among assumptions with equal plausibility.
- Long-term studies and repeated measures of parameters are needed to empirically distinguish between the assumptions tested here.

3 Annex: sensitivity analysis population models





Figure 3.1 Red-throated diver perturbation analysis of (annual) population growth rate (without OWFs). Elasticities and sensitivities of population growth rate to individual parameters, error bars represent 5% and 95% percentile of the outcomes. Population growth rate as a function of the diver adult survival probability S_{DA} , the breeding probability B_{DA} and the breeding success F_{DA} , the red solid line indicates the boundary where a population increase switches to a decrease. Note the log axis for sensitivities and elasticities.

3.2 Northern gannet





Figure 3.2 Northern gannet perturbation analysis of (annual) population growth rate (without OWFs). Elasticities and sensitivities of population growth rate to individual parameters, error bars represent 5% and 95% percentile of the outcomes. Population growth rate as a function of the gannet adult survival probability S_{GA} , the breeding probability B_{GA} and the breeding success F_{GA} , the red solid line indicates the boundary where a population increase switches to a decrease. Note the log axis for sensitivities and elasticities.



Figure 3.3 Sandwich tern perturbation analysis of (annual) population growth rate (without OWFs). Elasticities and sensitivities of the population growth rate to individual parameters, error bars represent 5% and 95% percentile of the outcomes. Population growth rate as a function of the tern adult survival probability S_{TA} , the breeding probability B_{TA} and the breeding success F_{TA} , the red solid line indicates the boundary where a population increase switches to a decrease. Note the log axis for sensitivities and elasticities.



Figure 3.4 Razorbill perturbation analysis of (annual) population growth rate (without OWFs). Elasticities and sensitivities of the population growth rate to individual parameters, error bars represent 5% and 95% percentile of the outcomes. Population growth rate as a function of the razorbill adult survival probability S_{RA} , the breeding probability B_{RA} and the breeding success F_{RA} , the red solid line indicates the boundary where a population increase switches to a decrease. Note the log axis for sensitivities and elasticities.

3.5 Common guillemot



Figure 3.5 Common guillemot perturbation analysis of (annual) population growth rate (PGR, without OWFs)._Elasticities and sensitivities of the population growth rate to individual parameters, error bars represent 5% and 95% percentile of the outcomes. Population growth rate as a function of the guillemot adult survival probability S_{UA} , the breeding probability B_{UA} and the breeding success F_{UA} , the red solid line indicates the boundary where a population increase switches to a decrease (PGR = 1.0). Note the log axis for sensitivities and elasticities.

4

Annex: Stability, Accuracy and Precision of the individual-based simulation model

For the individual based model, we did a stability analysis for the initial energy and the number of time steps. We used the razorbill parametrisation with an annual survival of 0.9. For the simulation we ran the model 200 times without any OWF locations. We expected that the survival probability calculated by the simulation would be equal to the true survival rate, that is the survival rate used during the calibration and thus independent of the initial energy and of the number of time steps.

Also we say something about the accuracy and precision of the model. The accuracy of the model is defined as the absolute difference between the 50th percentile of the estimated distribution and the true (input) survival probability. The precision is defined as the difference between the 95% percentile and the 5% percentile of the estimated distribution.

For the different initial energies we used a multiple of the mean of the habitat quality values, as multiplication factors we used: 0.001, 0.01, 0.1, 0.25, 0.5, 1, 2.5, 5, 10.

The result is shown in Figure A, where we see that the simulated survival probability is as expected to be very close to the true survival probability. Figure B shows how precise and accurate the model is. We see that the simulated survivability is fairly close to the true survival probability and that the precision is a bit under 0.002. This means that the results of the model can be interpreted as having a precision of ± 0.001 .



Figure A Results of the stability analysis for the indiviual based model varying the initial energy



Figure B Accuracy and Precision of Individual based model

For the number of time steps, we varied the time interval between moving events. Again we used the razorbill parametrisation with an annual survival of 0.9.


Figure C Results of the stability analysis for the individual based model while varying the number of time steps.

We used 3040, 1520 760 for the number of time steps, with a season length of 7 months these corresponding with moving to another cell every 2 hours, every 4 hours and every 8 hours. Also in this case we see as expected that the simulated survival probability matches the true survival probability very close. If we look at the accuracy and precision in Figure D we see again that the accuracy is very high and the precision around 0.002. Again indicating that the simulation outcome can be interpreted as having a precision of ± 0.001

Figure D Accuracy and precision of the individual based model while varying the number of time steps.







Figure D Accuracy and precision of the individual based model while varying the number of time steps.

4.1 Red-throated diver uncertainty

Figure 4.1 and Figure 4.2 show the distribution of the calculated survival values for the different scenarios for the red-throated diver. The distributions are approximated well by a normal distribution, the mean value is a good choice as an approximation of the survival change. However we see also a lot of overlap between the distributions of the estimated survival therefor we use as precaution the 5th percentile.

Table 4.1 Survival values used	l for the individual based model
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Survival	used for stage
0.60	DJ
0.84	DI, DA

Diver precautionary



Figure 4.1 Uncertainty of the red throated diver breeding precautionary scenarios

Diver realistic



Figure 4.2 Uncertainty of the red throated diver breeding realistic scenarios

4.2 Northern gannet uncertainty

Table 4.2 Survival values used for the individual based model

Survival	used for stage
0.4	GJ0
0.8	GI1
0.9	GI2, GI3, GI4, GIA

4.2.1 Northern gannet breeding

Figure 4.3 and Figure 4.4 show the distribution of the calculated survival values for the different scenarios for the northern gannet (breeding). The distributions are approximated well by a normal distribution, the mean value is good choice as an approximation of the survival change. However, we see also a lot of overlap between the distributions of the estimated survival and therefore we use as precaution the 5th percentile.



Figure 4.3 Uncertainty of the northern gannet breeding precautionary scenarios



Northern gannet breeding realistic

Figure 1.4 Uncertainty of the gannet breeding realistic scenarios

4.2.2 Northern gannet non-breeding

Figure 4.5 and Figure 4.6 show the distribution of the calculated survival values for the different scenarios for the northern gannet (non-breeding). The distributions are approximated well by a normal distribution, the mean value is good choice as an approximation of the survival change.

However we see also a lot of overlap between the distributions of the estimated survival therefor we use as precaution the 5^{th} percentile.

Northern gannet non breeding precautionary



Figure 4.5 Uncertainty of the gannet non-breeding precautionary scenarios

Northern gannet non breeding realistic



Figure 4.6 Uncertainty of the gannet non-breeding realistic scenarios

4.3 Sandwich tern uncertainty

Figure 4.7 and Figure 4.8 show the distribution of the calculated survival values for the different scenarios for the sandwich tern. The distributions are approximated well by a normal distribution, the mean value is good choice as an approximation of the survival change.

However we see also a lot of overlap between the distributions of the estimated survival and therefore we use as precaution the 5^{th} percentile.



Table 4.3 Survival values used for the individual based model



Figure 4.8 Uncertainty of the sandwich tern realistic scenarios

4.4 Razorbill uncertainty

Figure 4.9 and Figure 4.10 show the distribution of the calculated survival values for the different scenarios for the sandwich tern. The distributions are approximated well by a normal distribution, the mean value is good choice as an approximation of the survival change.

However we see also a lot of overlap between the distributions of the estimated survival and therefore we use as precaution the 5^{th} percentile.



Table 4.4 Survival values used for the individual based model

used for stage

Survival

Figure 4.9 Uncertainty of the razorbill precautionary scenarios



Guillemot realistic

Figure 4.10 Uncertainty of the razorbill realistic scenarios

4.5 Common guillemot uncertainty

Figure 4.11 and Figure 4.12 show the distribution of the calculated survival values for the different scenarios for the sandwich tern. The distributions are approximated well by a normal distribution, the mean value is good choice as an approximation of the survival change.

However we see also a lot of overlap between the distributions of the estimated survival and therefore we use as precaution the 5^{th} percentile.

Survival	used for stage
0.5	UJo
0.8	UJ ₁
0.94	U_{A}, U_{I}, UJ_{2}

Table 4.5 Survival values used for the individual based model

Guillemot	precautionary
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Figure 4.11 Uncertainty of the guillemot precautionary scenarios

Guillemot realistic

Without OWF 400 All OWF S=0.5 d=0.5 Dutch OWF S=0.5 d=0.5 300 International OWF S=0.5 d=0.5 200 200 100 0 0.498 0.500 0.502 0.496 600 Without OWF All OWF S=0.8 d=0.5 Dutch OWF S=0.8 d=0.5 400 International OWF S=0.8 d=0.5 count 200 0 0.796 0.797 0.798 0.799 0.800 0.801 0.802 0.803 Without OWF 800 All OWF S=0.94 d=0.5 Dutch OWF S=0.94 d=0.5 600 International OWF S=0.94 d=0.5 count 400 200 0 0.9380 0.9385 0.9390 0.9395 0.9400 0.9405 0.9410 0.9415 0.9420 Survival

Figure 4.12 Uncertainty of the guillemot realistic scenarios

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