Trend- and population estimates of Gaviidae: Methodological overview

Moritz Mercker - BIONUM

January 12, 2019

Abstract

We present an integrative statistical approach to estimate trend- and population sizes of Gaviidae. The synergetic combination of different state of the art methods aims to obtain unbiased results as well as to maximise the statistical power. Especially, we combine distance-sampling methods with generalised additive [mixed] modelling (GA[M]M's), where variance-propagation between these two steps has been achieved using bootstrapping. The presented approach allows to integrate bird count data from different sources, namely observer-based aerial surveys, observer-based ship surveys, as well as digital-based aerial surveys. Here, qualitative and quantitative differences in distance-dependent and distance-independent detection (i.e., detection on the transect line) between the different methods have been considered.

The presented approach allows the estimation of log-linear as well as highly nonlinear trends while correcting for temporal autocorrelation on different time scales, namely on the scale of years as well as on the scale of subsequent sampling units. Population estimates are also model-based, providing population numbers (including confidence intervals) for arbitrary sub-areas. These population models can be used in future works for predictive modelling.

1. Introduction

Seabird population size estimates ("census") and those of population changes ("trends") are of great ecological concern. Amongst others, they are important indicators of large-scale and long-term changes in marine ecosystems [38]. Thus, statistical approaches estimating population sizes and trends are important e.g. in order to establish efficient warning systems for population declines.

The presented approach is based on offshore line transect data and aims at providing baseline information for assessing effects of anthropogenic impacts on Gaviidae in the German North Sea.

General challenges with bird count data

Reliable estimates of trends and population numbers are challenging; bird census and survey techniques [21, 12] as well as convenient statistical methods to extract the corresponding bird numbers and trends [16, 38, 47, 48] are thus versatile. Matters are complicated further since both – sampling and analytical techniques – depend on each other in a complex way. In the following, we summarise some of the most frequent challenges connected to the analysis of bird count data.

Data have been often collected in the context of different projects, each project using it's own preferred method/sampling strategy. If the aim is to use all available data, this heterogeneity has to be included appropriately into regression analyses.

A further challenge is given by the fact that bird detection is usually incomplete. Especially, there are several covariates (and their interactions) possibly affecting the visibility and thus the detection probability – such as the distance to the observer, the survey method, sea state, weather conditions, or bird flock size [46]. All these detection-related processes can be mainly separated into two categories:

1. processes/covariates influencing the "overall detectability" of birds (i.e., the distance-independent detectability respectively the detectability on the transect line); and

2. processes/covariates influencing the quantitative and qualitative decrease of detectability with the distance from the observer (i.e., the shape of the distance-dependent detection function).

Especially the latter has been extensively studied within the distance-sampling theory, and corresponding software and various modelling approaches are well established [11, 36, 12, 50]. In contrast, the correction for distance-independent detection of seabirds has been rarely considered so far.

A further challenge connected to bird count data is that such data can be rarely approximated by a Poisson distribution but rather show strong overdispersion, which poses the question of an appropriate probability distribution. Here – instead of log-transforming the count data in order to obtain normality – it is suggested to model count data explicitly within the framework of generalised linear or additive models, since this increases the power of the analysis and avoids several problems connected to a transformation of the outcome variable [19, 37, 15]. Various probability distributions for overdispersed count data have been proposed so far, including the quasi-Poisson-, negative binomial-, and the Tweedie-distribution, or more complex zero-inflated Poisson, zero-inflated negative binomial, and Hurdle models, or the introduction of an observation-level random intercept term [56, 30, 40, 62, 63].

Furthermore, biological data are frequently strongly temporally and/or spatially autocorrelated, aggravated by the fact that temporal correlation may appear on the scale of minutes (e.g., if a ship drives through a large flock of birds) as well as on the scale of years (e.g., if nonlinear trends are fitted via a (log-)linear regression model).

Finally, bird abundance may depend in highly nonlinear ways on several spatiotemporally varying covariates, making the use of additive models necessary [24, 59, 16, 22, 6].

Trend estimates

Previous approaches to estimate trends of waterbird populations have considered only partially the above mentioned aspects [38, 39, 45, 48, 41, 31]. However, a more comprehensive modelling framework aiming to integrate bird count data from different sources and assessing all above mentioned problems with appropriate statistical tools is still missing.

Census estimates

Traditionally, population size estimates are based on design-based estimates. I.e., total bird numbers are extrapolated from sampled plots to the entire study area [36, 50]. However, this approach has some strong drawbacks: e.g. counted plots have to be random throughout the survey region (in order to be representative); estimated confidence limits are unnecessarily wide since the amount of unexplained variance has not been decreased by the consideration of environmental covariates; and finally, neither temporal nor spatial autocorrelation is usually adequately taken into account [8, 4, 34].

Thus, as an alternative technique, model-based estimation methods are of increased interest and use [14, 36, 26, 3]. Here, bird distribution and density is explicitly modelled in time and space and as a function of additional (such as environmental) covariates [9, 10, 20, 26, 32]. Beside the fact that the model-based approach does not suffer from the above mentioned drawbacks of design-based methods, it can be additionally used to gain statistically grounded insight into relationships between bird distribution and (environmental) covariates, to plot continuous bird distribution maps, and also for predictive modelling.

Combined models and strategy

Both models - trend models as well as models for population estimates - are strongly related to each other, since the core of both approaches is an appropriate description of the spatio-temporal distribution patterns of Gaviidae. The key difference however lies only in the focus: in the trend model, the focus is on the temporal population development, and all other covariates (such as the spatially varying distribution or the dependency on environmental covariates) are only included in order to prevent for corresponding bias. In the census model in contrast, the main focus is on the spatially varying abundance and the dependency on additional covariates, eventually leading to realistic predictions. As we will see later, these different foci lead to slight differences in predictor-formulations, whereas most parts of both models are identical.

Overview

In this work we provide an integrative model-based approach to estimate both – population trends as well as population size of seabirds – based on different data sources. We therefore combine distance-sampling methods with generalised additive [mixed] modelling (GA[M]M's) within a two-step-procedure, where variance-propagation between these two steps has been achieved using bootstrapping. Additionally, the presented approach allows to integrate bird count data from different sources, namely observer-based aerial surveys, observer-based ship surveys, as well as digital-based aerial surveys. Here, qualitative and quantitative differences in distance-dependent and distance-independent detection (i.e., detection on the transect line) between the different methods have been estimated.

2. Material and Methods

In this section we present in detail the underlying data and applied methods. A sketch of the applied modeling scheme including all main steps is given in Fig. 1.

Instead of applying one self-contained statistical model to the data (such as a Bayesian hierarchical model [30, 27]), in this work, we rather combine ideas and specialised methods from different statistical fields and apply them in a multi-step procedure to the data. This approach appears to be favourable due to the heterogeneity and complexity of statistical problems which are connected to the data. That way, we can use state-of-the-art approaches for each of these sub-problems and profit from recent developments in corresponding specialised methods and software. Another reason why we decided against a Bayesian hierarchical model is the fact that final spatiotemporal GA[M]Ms are very complex and datasets are large, thus computation times for Markov chain Monte Carlo-based resampling would probably require too much computation time [30]. However, recent developments (making use of integrated nested laplacian approximation (INLA) [60]) are promising in order to solve the problem of tedious computation times in the context of Bayesian models in the nearest future.

Bird count raw data

Bird count data are given based on observer-based aerial or ship surveys as well as on digital-based aerial surveys from 2002-2017 and restricted to the spring (01.03.-15.05.).

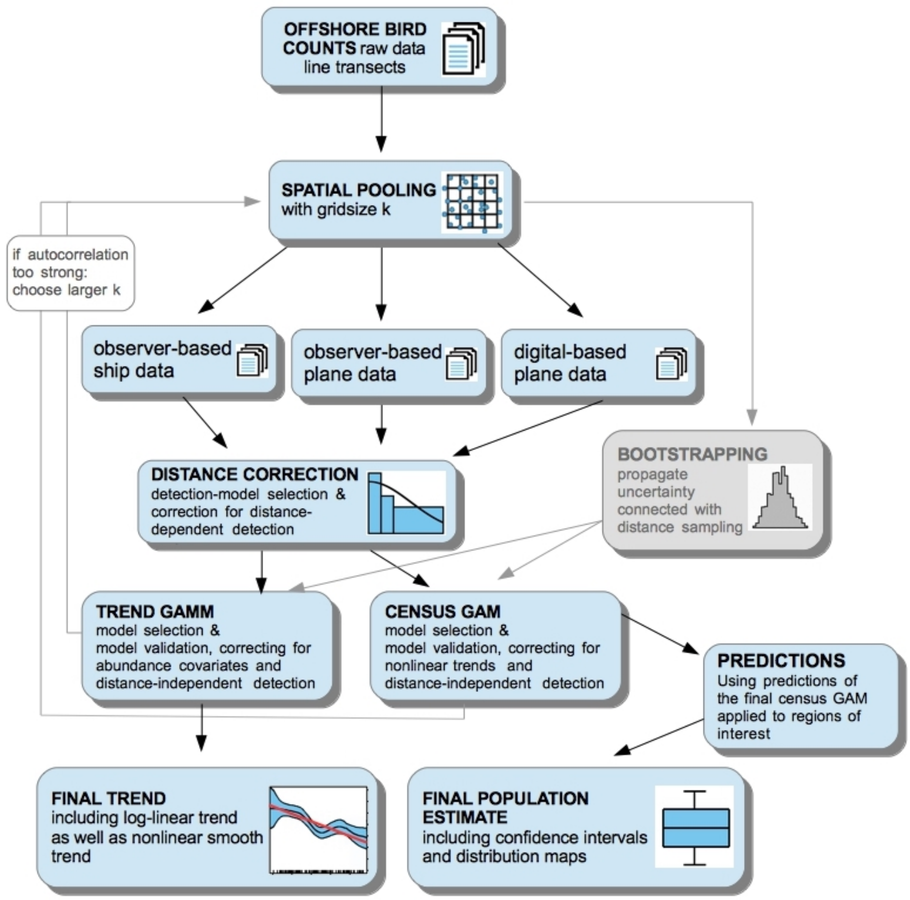

Figure 1: *Sketch of the applied modelling scheme leading from offshore line transect data to the final trend and population size estimates.*

Data pooling

Birds have been counted at minute intervals from the moving ship or airplane and for digital data up to eight picture per second. Using the raw-data without any pooling would result in an unmanageable amount of spatiotemporal auto-correlation. Furthermore, this would lead to mean-count values close to zero, which would make the use of Penalised Quasi Likelihood (PQL) techniques in mixed models inappropriate [7] and additionally the need of complex zero-inflated models more likely [35, 62, 30].

Previous studies thus pooled the data for each transect line to generate more appropriate sampling units. However, especially if transects are pretty large in one dimension (which is especially the case if aircrafts are used), such sampling units are spatially not very representative, since covariates will be averaged over long distances in only one direction, wich would result in a poor and anisotropic spatial resolution of these covariates. Other studies performed a segmentation of transect-lines into equidistant sub-parts [50]. However, this leads in principle to the same problem of anisotropy, even if moderated.

In this study, we use instead a pre-defined regular rectangular spatial grid of side length *k* as a basis [21] (c.f. Fig. 1). Based on this, each unique combination of survey-method, year, and time of year has been split into corresponding subunits defined by its intersections with these grid cells. This finally leads to spatially well separated and isotropic fragments (in the following termed as "sampling units"). For each of these sampling units, bird numbers have been summed up just as the monitored area within the grid cell, all other covariates (including the intra-annual decade as well as geographical coordinates) have been averaged instead. Thus, e.g. geographical coordinates usually do not represent the center of the pre-defined grid cell, but rather the center of the monitored area within the grid cell, which is more precise and eventually leads to a much higher effective spatial resolution.

The optimal grid cell side length k, however, is *a priori* not known. In contrast, it has to be evaluated during data analysis trying to find the optimal balance between a high local spatial resolution on the one hand (favouring small cells), and a manageable amount of autocorrelation and data-size on the other hand (favouring large cells).

Distance-dependent detection

Our recent works reveal for different seabird species that the detectability of bird flocks is the dominant distance-dependent detection process, whereas the detection of bird individuals within already detected flocks does not measurable depend on the distance (unpublished results). We thus concentrate in the following on a distance-correction considering the detection of bird flocks, and assume that birds within already detected flocks have been counted without errors.

For this purpose, we integrated the distance-correction step via a "two-stage-approach" [36] into our analysis (c.f., Fig. 1):

In the first step, we applied distance sampling methods (e.g., as presented in Ref. [11, 12]) to the observer-based raw data, where we tested different detection functions (half-normal vs. Hazart-rate) as well as various different predictor combinations (main-effects as well as interaction terms based on the predictors *sea state, bird flock size, log(bird flock size)*) via AIC-analysis [58, 17] separately for observer-based aerial and ship data. The best detection function has been subsequently used to correct the raw-data in a case sensitive manner (i.e. depending on the distance class, the method, and all other covariates appearing as predictors in the best detection model).

We want to point out that flying birds (if counted from ships) have not been corrected in this step, since they have been assumed as completely detected. Furthermore, correction of birds with no assigned distance has been based on the average detection probability, as predicted for the corresponding sampling unit. Importantly, raw data based on digital-based aerial surveys have not been distance-corrected, assuming that detection probability is distance-independent here.

In the second step, we pooled the corrected data and applied the final GA[M]Ms (which is explained more in detail within the following subsections) to these data.

Our approach slightly differs from recent works where detection probabilities estimated in the first step have been used as an offset in the final regression model [12, 36], which has the advantage that the probability distribution underlying the bird count data is not influenced by the correction step. However, we had to choose the "direct correction approach" as outlined above, since the detection probability has been determined on a finer scale (namely on the scale of the raw data) compared to the scale of sampling units as finally used for trend- and census analysis via GA[M]Ms.

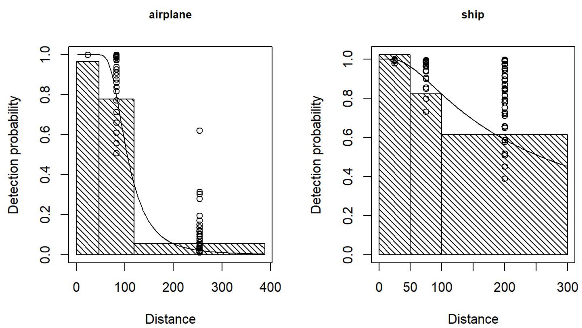

Figure 2: *Average detection functions in the context of distance sampling for observer-based counts from airplanes (left-hand side) as well as ships (right-hand side).*

Distance-independent detection

As outlined above, the detection on the transect line (hence the distance-independent detection) is also usually imperfect, and may depend on various covariates such as the survey method or the sea state. We incorporated these effects by testing the variables *method* and *sea_state* as additional predictors during AIC-based model selection [2] of the final population GA[M]M (applied to the already distance-corrected data). Thus, abundance-related and (distance-independent) detection-related covariates have been estimated simultaneously within the final GA[M]M.

Variance propagation

Both detection correction steps – the correction for distance-dependent detection and the correction for distance-independent detection – are connected to uncertainties, e.g. expressed via standard errors of corresponding regression coefficients. These uncertainties have to be propagated to final GA[M]M standard errors [36, 12]. E.g., should an uncertain determination of the detection model eventually result in an inflation of the final GA[M]M standard errors.

In the case of distance-independent detection, as described above, corresponding covariates (such as *method* and *sea_state*) are estimated simultaneously with all abundance-related covariates within final population GA[M]Ms. Thus, corresponding uncertainties directly/naturally influence all final standard errors in the desired manner.

Propagating the uncertainties from the decoupled distance-dependent step, however, is not straight forward. Different techniques have been proposed so far, including bootstrapping techniques, the Delta-method, or techniques based on GAM theory [12, 36, 31, 55, 54].

In this study, we used a bootstrapping-method in conjunction with standard GA[M]M-estimation techniques to estimate and propagate the above mentioned uncertainties. Especially, we used the following scheme:

1. We resample the observer-based raw data N times with replacement;
2. for each raw-data-resample, we fit the detection functions (separately for each method) and correct the raw data correspondingly;
3. for each corrected-data-resample, we fit the final GA[M]M's and produce again 100 resamples of (1) the regression coefficients of the trend-GAMM (using multivariate normal distribution based on the variance-covariance matrix and applied on the predictor scale), as well as (2) the population-estimates (based on the predict-function) of the census GAM.

Final standard errors and confidence intervals can than be calculated using quantiles based on the final N*100 regression coefficient respectively population estimate resamples [55].

In order to minimise the computation time required for bootstrapping, we (1) did not *a-priori* prescribe the number of bootstrap-resamples N but developed an algorithm stopping the resampling when sufficient convergence of the estimated variance has been achieved, and (2) we made use of parallel computing on a multi-core computer using the R-package *parallel*.

Covariates

Temporal covariates. Trend estimates can be deduced from appropriate formulated covariates in the context of regression analyses [47, 16, 47, 48]. Especially if relative short time frames are considered, population development can be often approximated by a simple (log-)linear trend. However, especially if population developments over longer periods are considered, their behavior can be highly nonlinear and pure (log-)linear regression models thus appear to be inappropriate or may show strong temporal autocorrelation. Possible alternatives are given by the use of generalised additive models (GAMs) [55, 16], or techniques based on Kalman-smoothing [23, 48].

In the present study, we are on the one hand interested in a statistical valid statement regarding the overall (log-linear) trend, but on the other hand also in a visualisation of the probably nonlinear population development. We thus fit always two different trend-GAMMs to each data frame, the first incorporating the variable *year* as a main effect (leading to the estimate of a log-linear trend), and secondly as a smooth, $s(year)$. Within the census GAM, we always only considered the smooth term $s(year)$.

Within trend-GAMM's, the variable *decade* (the intra-annual decade) has been introduced as a random factor (for that reason it is a GAMM instead of a GAM). Here, we choose a random factor over a fixed effect since (1) the relatively high total number of levels suggests to use it as a random factor [17, 62]; (2) introducing *decade* as a random factor leads to an increased power of the regression analysis since less parameter have to been estimated; and (3) an unbalanced design regarding the sample size per decade is automatically considered in the sense that low sample size cause a shrinkage towards the overall mean [30, 18]. The consideration of *decade* prevents for potential bias if the time points of bird surveys are not evenly distributed within a time of year. In census GAMs, however, this variable has been neglected, since otherwise bird numbers would have been calculated and averaged over all decades, leading together with the resampling (c.f., Section "Variance propagation") to extensive computing times.

Environmental/spatial covariates. As environmental covariates we considered smooth terms of the variables *dist_land* (= nearest distance to the mainland) and *depth* (=mean water depth). The aim was to further reduce the amount of unexplained variance and thus increase the power and quality of trend estimates and predictions in final regression models.

Furthermore, we introduced a 2D-spatial smooth predictor (especially a thin plate regression spline), depending on *Longitude* and *Latitude*. The aim was to account for additional spatial abundance heterogeneities not explained by the other used covariates. Since 2D thin plate splines are optimised for variables on the same scale [55], we rescaled geographical coordinates before analysis such that they are given in Kilometers.

Detection-related covariates. As introduced above, (distance-independent) detection-related covariates are given by the two variables *method* and *sea_state*. As we will see further down, population number estimates sensitively depend on these two variables and thus a correct and stable estimation of these two effects is of great importance. In order to facilitate a robust estimation, on the one hand, we renounced interaction terms between these variables for the sake of less but more stable estimated parameters. On the other hand, we merged the levels of the variable *sea_state* such that former level 0 and

1 has been fused to one level, and all levels ≥ 4 have also been fused to one level. Thus, the final variable *sea_state* is reduced to the levels 1-4, but not comprising any longer levels with sparse data.

Finally, for all smooth terms described above, the optimal amount of smoothing has been determined based on generalised cross-validation methods [55].

Dealing with autocorrelation

Count data are often spatially and/or temporally strongly autocorrelated [17, 58, 62, 30, 60]. Here, temporal autocorrelation may occur at two distinct different time scales:

On the one hand - especially in those trend-GAMM's where the nonlinear population development is not considered within the predictors – data are most probably autocorrelated between subsequent years. Here, time steps are equidistant, which means that autocorrelation can be implemented via a conventional autoregression (AR)-structure (nested within spatial grid cells used for the data pooling, c.f., Section "Data pooling").

On the other hand, subsequent sampling units may also be strongly spatio-temporally autocorrelated, especially if they consist of subsequents parts of the same transect, especially if birds have the tendency to spatially aggregate. Here, time step length is strongly heterogeneous, reaching from minutes up to several weeks. Due to limitations of the used regression software, this continuous small-scale autocorrelation had to be been included on the predictor scale rather than on the residual scale. Especially, we calculated bird numbers $n_{bird}(t)$ for each (chronological) time point $t = t_1, t_2, ...,$ and subsequently calculated for each time point t_j and each lag $L = 1, 2, 3$ the artificial predictors

$$lag_L = log\Big(n_{bird}(t_{j-L}) * exp\big(-(t_j - t_{j-L}) + 1\Big),$$

which have been used in subsequent regression analyses. It means that counted bird numbers may depend on the bird numbers counted at the 1-th, 2-th, or 3-th time point before, and that this dependency decays exponentially with increasing temporal distance (similar to the assumption in conventional AR-models [17]).

In order to validate this approach, we exemplarily fitted two models with equidistant time steps and strong temporal autocorrelation, where in one model the autocorrelation has been incorporated via an AR-3-structure, and in the second model with the above described approach. It appeared that estimated regression coefficients and standard errors differed by less than 1%, indicating that the inclusion of autocorrelation on the predictor scale (hence, as a Markov-process) differs only negligible from the AR-approach.

In order to choose the appropriate spatial grid size k for spatio-temporal data pooling (c.f., Section "Data pooling") we stepwise decreased the underlying spatial grid in $5\,km$ steps, starting with a grid size of $k = 30$ and performed for each k the distance-dependent correction, the model selection, and the final GA[M]M fits (including the newly calculated predictors $lag_1, ..., lag_4$; c.f., Fig. 1). The scheme stopped (and thus k has been fixed) as soon as lag_3 became a significant predictor – under the additional constraint that spatial autocorrelation (evaluated via semi-variogram- and bubble-plot-analyses of final regression model residuals [30, 58]) was not apparent. If the latter was violated, the size of the spatial grid was increased again until spatial autocorrelation has vanished.

Regression model structure

The "most complex" trend model GAMM (which has not yet been thinned regarding its predictors as described in the following subsection) is given by

$$\begin{aligned} log(y_{ji}) &= \beta_0 + u_i + method_j \qquad (1)\\ &+ sea\_state_j\\ &+ f(year) + s(depth_j)\\ &+ s(dist\_coast_j)\\ &+ s(latitude_j, longitude_j)\\ &+ lag_1 + lag_2 + lag_3\\ &+ \text{offset}(log(area_j)) + \epsilon_{ji}, \end{aligned}$$

with $\epsilon_j \sim N(0, \sigma^2)$ and $u_i \sim N(0, \sigma_u^2)$ i.i.d. Here, y_{ji} is the vector of bird numbers, where the index j refers to the observation number and i to the random intercept related to the (intra-annual) decade. Furthermore, β_0 is the fixed intercept, $s(.)$ depicts a cubic regression spline (where the optimal number on knots has been estimated via generalised cross-validation), and $f(year)$ depicts either the main effect *year* or the smooth term $s(year)$ (as outlined above, both variants have been fitted in order to evaluate the log-linear trend as well as to visualise the nonlinear population development). Additionally, since bird numbers have been counted related to a varying area per sampling unit, the logarithm of the area has been included as an offset [58, 30]. Furthermore, the terms lag_1, lag_2, lag_3 refer to the potential autocorrelation on the small temporal scale. Additionally, autocorrelation on the year-scale has been included as an appropriate AR-structure. Finally, an appropriate probability distribution as well as an appropriate subset of predictors has been selected based on AIC analysis [2] (c.f., following subsection).

As motivated above, for the estimation of population sizes, a slightly modified version of the model (a GAM instead of a GAMM) has been used, namely:

$$\begin{aligned} log(y_j) &= \beta_0 + method_j \qquad (2)\\ &+ sea\_state_j\\ &+ s(year) + s(depth_j)\\ &+ s(dist\_coast_j)\\ &+ s(latitude_j, longitude_j)\\ &+ lag_1 + lag_2 + lag_3\\ &+ \text{offset}(log(area_j)) + \epsilon_j. \end{aligned}$$

Model validation strategy

In order to obtain and validate the optimal GA[M]M-model, we modified the selection and validation strategies as described e.g. by Ref. [61, 62, 59, 63, 30, 17]. Especially – separately for the trend- and the census-model – we performed the following steps:

1. Based on the ”maximal complex model” (as given in the previous subsection) choosing an appropriate probability distribution / stochastic part of the model based on the Akaike Information Criterion (AIC) [2]. Namely we compared a Poisson-, negative binomial-, Tweedie- , and a zero-inflated Poisson-distribution among each other. All four probability distributions have been shown to describe the stochastic part in regression models of (p.r.n. overdispersed) count data reasonable well [13, 29, 28, 33, 52, 35, 63];

2. Using the favoured probability distribution, selecting an optimal subset of predictors (again based on the AIC). Especially, we permuted over all possible combinations and formulations of predictors leading in total to the comparison of > 100 different models;

3. based on the model with the favoured probability distribution and subset of predictors, performing model validation (mainly relied on graphical analysis via residual plots [61]) in order to test all required model assumptions.

Estimation of population sizes

Where trend estimates can be directly extracted from GAMM regression coefficients, the calculation of population sizes is not that straight forward. For this purpose we used the final fitted census-GAM to predict bird densities on a prediction map of the investigated area – the german north sea as well as sub-areas considered here. Prediction data had a resolution of 1 km^2 and included values for all required environmental covariates.

However, detection-related covariates (namely *method* and *sea_state*) are not naturally given but have to be chosen/set. Thus, we investigated which *method-sea_state*-combination leads to the highest predictions, and used corresponding factor levels subsequently within the predict-routine. This implies that at least for one *method-sea_state*-combination, detected bird numbers (after distance-correction) are close to the real bird numbers, i.e. detection on the transect line is in this case assumed to be close to 100 %.

Furthermore, the values for lag_1, lag_2 and lag_3 are not naturally given, and additionally may spatially vary. Hence, setting them in the predict data frame to their mean values (calculated based on the pooled bird count data frame) could cause spatial bias of the predictions, since spatial heterogeneity of the lag-values would not have been considered.

We thus performed the following approach: We fitted two different census regression models to the bird count data, the first including the lags and the second without the lags. For the first model, we set the lag-variables in the predict data frame to their mean values – as discussed above. Thus, the second model gives us an unbiased distribution/densities of birds whereas its confidence intervals (due to the lack of small-scale autocorrelation) are probably underestimated. In the second model, it is just the other way round.

Finally, we thus calculated the relative increase of the confidence bands (on the linear scale) of the first model vs. the second model, and extended the confidence limits of the second model correspondingly for final predictions. Hence, predictions are unbiased, and autocorrelation-driven inflation of the certainty (confidence interval length) has been adequately considered as well.

Software

All statistical analysis, validation procedures and visualisations have been performed using the statistical software R [44]. Especially, we used the following packages: *sp* [43] and *gstat* [42] for the analysis of spatial auto-correlation (e.g. via variograms and bubble-plots); *ggplot2* [53] for all other visualisations and plots; the *Rmisc* [25] and *matrixStats* [5] for different functions regarding data analysis and utility operations, *MASS* [51], *pscl* [1], and *mgcv* [55] for regression analyses, *Distance* [49, 50, 12, 36] for distance sampling-related procedures, and *parallel* [44] for the use of parallel computing.

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