Model-based assessment of marine bird population status using monitoring of breeding productivity and abundance

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Vertebrate populations are often monitored as part of broader assessments of ecosystem status, where they are expected to provide information on the ability of the ecosystem to support higher-level predators. However, because many vertebrates are long-lived and often only subsets of their populations can be monitored, abundance may not be sufficiently responsive to ecosystem status to provide early warnings of impending changes. Marine birds are often used as indicators of ecosystem status, but due to their long lifespan and delayed recruitment to the breeding population, changes in abundance are generally slow and often difficult to interpret. Their breeding productivity is however also widely monitored and much more responsive to ecosystem status, but the relevance of variation in productivity may be difficult to assess. We propose a model-based indicator, which integrates monitoring of abundance and breeding productivity through demographic matrix models. The metric of the proposed indicator is the expected population growth rate, given the observed level of breeding productivity. This expected growth rate is then compared to a threshold derived from the criteria employed for red-listing of threatened species by the International Union for the Conservation of Nature. We demonstrate the suggested approach using data from Black-legged Kittiwakes *Rissa tridactyla* in the Greater North Sea region, Northwest Europe. The proposed indicator shows that the current level of breeding productivity is expected to lead to a population decline of 3-4% per year, which is equivalent to a red-list status as Endangered for the species in this region. Our indicator approach is used in OSPAR's Quality Status Report 2023 and is expected to be used by European Union member states for reporting under the Marine Strategy Framework Directive in 2024. While our approach represents a major step forward in assessing the status of marine bird populations, the ideal next step would be to develop a coherent Integrated Population Modelling (IPM) framework that would allow inclusion of all data on population abundance and demography collected across the large and diverse marine ecosystems involved.

Keywords: Breeding success; indicator; Marine Strategy Framework Directive; seabirds

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One of the common uses of biodiversity monitoring is to allow management agencies to assess the status of ecosystems, as well as the success of policies and management initiatives to improve their status. Population abundance is often monitored as part of such broader monitoring programmes, rather than because the species monitored serve as specific ecological indicators directly linked to e.g. pollutant levels, or require specific management. Such monitoring programmes can be taxonomically based (Brlík *et al.* 2021) or involve true ecosystem-based monitoring with regular assessments of the status of various ecosystem components, which can be both abiotic and biotic (Christensen *et al.* 2020). In either case, the aim is typically to provide a broad assessment of the ecological status of an area or an ecosystem and to provide early warning signals of ecological change. For long-lived organisms with delayed maturity, assessment of abundance alone is often not regarded as sufficient to reflect current ecosystem status, mainly because abundance typically changes slowly in response to environmental impacts on reproduction (Parsons *et al.* 2008). This is further exacerbated for species such as colonially breeding birds, where often only the adult segment of the population can be monitored, and where impacts of e.g. reproductive failures on abundance can take several years to manifest. Therefore, demographic parameters such as age structure or reproductive output are sometimes monitored to provide a more immediate reflection of status. However, the interpretation of variation in such demographic parameters is less obvious than for abundance. For instance, would the observed variation in reproductive output have a measurable impact on the future state of the population? Population models have the capacity to answer such questions, but are rarely integrated into broader monitoring programmes (but see Robinson *et al.* 2014).

Marine birds (or seabirds) are long-lived organisms, with low annual fecundity and delayed recruitment to the breeding population, often at ages 3-10 years (Schreiber & Burger 2002, Horswill & Robinson 2015). Standard monitoring of abundance usually only covers the breeding segment of the population, because they are much easier to count when aggregated at breeding colonies than at other times of the year when they are dispersed over large areas of ocean. Therefore, changes in reproduction are only reflected in the recorded counts with several years' delay. Monitoring of breeding productivity may provide an 'early warning' of impending changes in population abundance, if population growth is sensitive to variation in this demographic rate. Compared to abundance, breeding productivity is likely more sensitive to short-term changes in environmental status, and thus more informative of current conditions. In long-lived organisms, adult survival is typically less variable between years than breeding productivity (Sæther & Bakke 2000), and also less sensitive to variation in environmental status (Gaillard & Yoccoz 2003). However, temporal variation in adult survival has a strong impact on population growth rate (Lebreton & Clobert 1991), and observed variation in survival can therefore be very informative of drivers of population change. Monitoring of demographic parameters (or vital rates) can have at least three functions in an ecosystem-based monitoring programme: 1) track variation in environmental status, 2) inform on potential drivers of population change, and 3) enable projections of future population change.

The European Union (EU) Marine Strategy Framework Directive (MSFD) requires the regular assessment of Good Environmental Status (GES) of regional seas by member states. GES includes several aspects covered by a set of descriptors. Descriptor 1 addresses biodiversity and includes several criteria for each ecosystem component, including marine birds. Whereas abundance is a primary criterion and therefore required, demographic characteristics (e.g. breeding productivity) is a secondary criterion that member countries are not obliged to monitor. These criteria should be assessed at the species level, and for each regional sea or sub-region thereof as appropriate (European Commission 2017). In practice, monitoring is conducted nationally, while indicators corresponding to the MSFD descriptors are defined and calculated by the commissions responsible for the relevant Regional Sea Conventions, including the OSPAR Commission (www.ospar.org) for the Northeast Atlantic and the Baltic Marine Environment Protection Commission (HELCOM) (www.helcom.fi) for the Baltic Sea, and used in their regular status assessments as well as for national MSFD reporting.

In the OSPAR area, an indicator of marine bird breeding success/failure was used in the 2017 Intermediate Assessment (OSPAR 2017). The indicator collated data on breeding failure (i.e. virtually no chicks being produced at a colony) across breeding sites and years, and produced an index of the frequency of breeding failure in a specific area. This indicator was shown to be more responsive to e.g. fisheries impacts than abundance-based indicators (Cook *et al.*, 2014). However, a challenge with this approach is interpretation: is the observed frequency of breeding failure actually a problem for the population? Also, the binary nature of the success/failure indicator (at the site level) may hide impacts of less than catastrophic declines in breeding productivity. We therefore developed an alternative approach, which uses monitoring data on breeding productivity in conjunction with the established indicator of breeding abundance to assess the impact of variation in breeding productivity on population growth potential. Development of this new approach was initiated during annual meetings of the OSPAR/HELCOM/ICES Joint Working Group on Marine Birds (JWGBIRD) (ICES 2018, ICES 2020) and was adopted by OSPAR Contracting Parties. An assessment of the indicator was completed in preparation for OSPAR's Quality Status Report (QSR) 2023 (https://oap.ospar.org/en/ospar-assessments/quality-status-reports/qsr-2023/), where it has replaced the success/failure indicator. The aim of this study is to demonstrate the value of an integrated demographic indicator that uses information on both abundance and breeding productivity to improve assessments of current environmental status. An indicator that incorporates observations of both abundance and productivity can lead to a more meaningful assessment of population status than one that relies on abundance alone.

METHODS

General approach

We reasoned that breeding productivity in recent years would, all else being equal, provide an indication of the near-future growth potential of the population. However, observed values of breeding productivity would need to be interpreted in the context of the species' life history and recent changes in population size. This requires a demographic modelling approach. Given that breeding abundance and productivity are monitored much more widely than other demographic parameters, particularly survival, we used a reverse modelling approach to identify mean values of survival that, in combination with observed values of breeding productivity, could have produced the observed changes in abundance. This approach assumes that monitoring of breeding abundance and productivity is sufficiently representative to provide realistic time series of both parameters. We then used our models to calculate the expected annual population growth rate, given recent observed values of breeding productivity.

To provide threshold values to which we could compare the expected population growth of our model populations, we reformulated the thresholds of population change used for red-listing by the International Union for the Conservation of Nature (IUCN) as annual growth rates, adapted to the life history of each species.

Data

Monitoring data on breeding abundance and productivity of marine birds were collected as part of national monitoring programmes (e.g. Walsh *et al.* 1995, Koffijberg *et al.* 2011, Anker-Nilssen *et al.* 2022). OSPAR Contracting Parties reported these data to a joint database held at the International Council for the Exploration of the Seas (ICES, https://www.ices.dk/data/data-portals/Pages/Biodiversity.aspx).

Data on both abundance and productivity were provided from four of the five OSPAR Regions: Arctic Waters, Greater North Sea, Celtic Seas, Bay of Biscay and Iberian Coast (see https://www.ospar.org/convention/the-north-east-atlantic). No data were available from the Azores – the only land mass in the 'Wider Atlantic' Region. For the abundance indicator, the Greater North Sea Region and the Norwegian part of the Arctic Region were divided into smaller 'sub-divisions' (https://odims.ospar.org/en/submissions/ospar_marine_birds_au_2022_06/).

Subsequently, data up to 2020 were extracted from these four OSPAR Regions, although in many cases the last year with available data was 2019. Breeding abundance data contained counts of all birds in a colony ('total colony count') and counts of birds within one or more smaller sample plots within a colony ('plot counts'), and in some cases both approaches were used in the same colony. All counts were done following the species-specific methods and recommendations described in detail in the Seabird monitoring handbook for Britain and Ireland (Walsh *et al.* 1995), which serves as the international standard for such work in the OSPAR area. Briefly, these data were processed as follows (for details, see Dierschke *et al.* 2023): First, missing data points in each time series of annual counts for each colony with at least three years of data were imputed using generalised additive models, using year as the explanatory variable. At some colonies, observed and imputed plot counts were scaled up to estimate change in numbers of birds across the entire colony, using the most recent total colony count for the colony. Next, the completed time series from each colony in an OSPAR Region or sub-division were combined and weighted according to the size of the total regional or sub-divisional population. The weightings are required because the proportion of a population that is monitored and contained in the dataset varies between species and between the different countries in each Region and sub-division. To apply a regional or sub-division weighting, each annual estimate of abundance in each assessment unit was divided by a proportion p, which is the proportion of the total population that is present within the sites or colonies included in the data provided (Dierschke *et al.* 2023).

Finally, each time series was converted to an index of relative abundance by dividing by a baseline set at the start of the time series, following the methodology used in the OSPAR marine bird abundance indicator (Dierschke *et al.* 2023). This was done to allow easy comparison among species and to be able to apply a common threshold value for the GES indicator.

Walsh *et al.* (1995) also describe the methods used for monitoring breeding productivity. The reported monitoring data for this parameter consisted of numbers of breeding pairs within designated monitoring plots, and the total number of chicks fledged by these pairs. Breeding productivity was then estimated for each plot as the average number of chicks fledged per pair (i.e. the ratio between the number of chicks fledged and the number of breeding pairs monitored). The minimum data requirement for each species in each OSPAR Region was set to ten years and two sites (typically breeding colonies, where each colony may include several study plots).

Sufficient data on both abundance and productivity were available for 25 species in one or more OSPAR Regions. To illustrate our approach, we present results from the Greater North Sea OSPAR Region for a well-monitored marine bird species, the Black-legged Kittiwake *Rissa tridactyla*, which is regarded as globally threated by IUCN (red-listed as Vulnerable, https://www.iucnredlist.org/species/22694497/155617539). Indicator output for the remaining Regions and species are reported as part of OSPAR QSR in 2023 (Frederiksen *et al.* 2023), while parameter values of the pertaining matrix models will be reported separately.

Constructing time series of breeding productivity

For breeding productivity, not all sites were monitored annually. Therefore, we calculated estimated marginal means (across colonies in each OSPAR Region) and their standard errors for each year using the R package emmeans (Lenth 2021), based on a linear model with a main effect of year (as a factor) and weighted by sample size. To obtain a time series with less year-to-year variation, we next calculated a 6-year retrospective running mean (i.e., the value for 2019 was calculated as the arithmetic mean of the estimated marginal means for 2014-2019; Fig. 1). In rare cases when marginal means and their standard errors could not be estimated for individual years due to missing data, we used instead the arithmetic means of the mean and standard error for all years with available data. Overall mean breeding productivity and between-year standard deviation were calculated based on the annual estimated marginal means.

Baseline demographic model

We constructed baseline demographic matrix models with a pre-breeding census (Caswell 2001) for each marine bird species, with the number of age classes as well as parameter values informed by expert knowledge and available literature. In practice, we mainly used parameter values based on Horswill and Robinson (2015), with the additional assumption that 90% of all breeding-age individuals bred each year (Acker *et al.* 2022) (Table 1).

Tuning the model to observed population growth

In the next step, we substituted annual values of breeding productivity, drawn from normal distributions with the estimated marginal means and standard errors, into the baseline model. Using 10,000 random draws and a starting age distribution based on the baseline model, we simulated population growth over the period with available data. We calculated the annual stochastic growth rate λ_s of the breeding population for each simulation as

$$\sqrt[t_{end}-t_{start}]{N_{end}/N_{start}},$$

where t_{start} and t_{end} indicate the first and last year of the available time series, and N_{start} and N_{end} indicate the breeding population size (oldest age class, in arbitrary units) in the first and last year (i.e., the geometric mean of the annual growth rates). We then took the arithmetic mean across simulations of the stochastic growth rates. For comparison, we estimated the observed annual population growth rate λ_o by fitting a linear regression to the log-transformed abundance time series, and back-transforming the estimated slope.

We then adjusted survival of one or (in most cases) several age classes so that the mean λ_s was identical (with a tolerance of 0.001) to λ_o. There is no unique way to make this adjustment, and the choices made reflect our general knowledge of marine bird life histories. For example, we have generally assumed that survival increases with age over the pre-breeding period, with the largest difference between the first and second years of life (e.g. Wanless *et al.* 2006, Frederiksen *et al.* 2008). We refer to the results of this step as the tuned model.

Next, we adjusted breeding productivity so that the expected annual asymptotic growth rate λ was 1; the adjusted value was denoted BP_{stable}. This stable version of the tuned model was then used to estimate generation time using the R package popbio (Stubben & Milligan 2007).

Thresholds for demographic indicators

IUCN assigns species to different categories of conservation concern on its Red List, using thresholds for observed population decline over 10 years or three generations, whichever is the longer. The following thresholds apply, unless the decline has ceased, the reasons are understood, and the decline is reversible (exceptions that rarely occur) (IUCN 2012):

- CR (critically endangered): ≥ 80 % decline
- EN (endangered): ≥ 50 % decline
- VU (vulnerable): ≥ 30 % decline

For the marine bird species considered in our analyses, three generations is always more than 10 years. To derive threshold values of λ (the annual asymptotic growth rate) for a specific species or population, we used estimates of generation time from the stable version of the tuned model. We then calculated λ^T as

$$\sqrt[3*GT]{(1 - T^{IUCN})},$$

where GT = generation time and T^{IUCN} = IUCN threshold value (0.8, 0.5 or 0.3, as appropriate). To illustrate the potential impact of uncertainty in the values of survival used, we repeated this step using stochastic versions of the same model, with 10,000 simulations including random draws of survival parameters from beta distributions with the tuned value as mean and a standard deviation of 0.05 for adult survival and 0.1 for survival of all other age classes, values similar to those often found for long-lived species (Horswill & Robinson 2015) (Fig. 2).

Potential impacts of observed demographic variation

We substituted the estimated retrospective running means of breeding productivity into the tuned model and calculated the expected asymptotic growth rate for each year. These growth rates illustrate the expected impact on long-term population growth, given that the observed level of breeding productivity (in the most recent six years) is maintained, and that other demographic parameters remain constant. The expected growth rates were then graphically compared to the thresholds derived from IUCN red-list criteria (λ^T).

All demographic models were created in R 4.2.0 (R Core Team 2019). Script and data for black-legged kittiwake are available on Dryad (Frederiksen *et al.* 2023).

RESULTS

The breeding productivity of Black-legged Kittiwake was monitored in 70 colonies in the Greater North Sea OSPAR Region in at least one year in the period 1986-2019, with data available for 20-121 study plots per year. The emmeans model with year as a factor was highly significant ($P < 2*10^{-16}$, $r^2 = 0.20$), indicating some among-colony synchrony in breeding productivity over time. Breeding productivity was highly variable between years (overall mean 0.716 chicks fledged/pair, SD = 0.187), with the six poorest seasons spread from 1997 to 2013 (Fig. 1).

The baseline demographic model

$$\begin{bmatrix} 0 & 0 & 0 & 0.9 * 0.69 * 0.5 * 0.79 \\ 0.854 & 0 & 0 & 0 \\ 0 & 0.854 & 0 & 0 \\ 0 & 0 & 0.854 & 0.854 \end{bmatrix}$$

(see also Table 1) gave an asymptotic growth rate of 1.005, while the observed mean population growth rate λ_o was 0.961. Using the annual estimates of breeding productivity (p_t), the mean simulated growth rate λ_s was 1.008. We tuned the model to obtain a λ_s of 0.961 by reducing the parameter values of first-year survival from 0.79 (which seemed biologically unrealistic) to 0.49, and second-year survival from 0.845 to 0.79.

$$\begin{bmatrix} 0 & 0 & 0 & 0.9 * p_t * 0.5 * 0.49 \\ 0.79 & 0 & 0 & 0 \\ 0 & 0.854 & 0 & 0 \\ 0 & 0 & 0.854 & 0.854 \end{bmatrix}$$

For the tuned model, a mean breeding productivity of 1.15 fledged chicks/pair was required to stabilise the population, and the generation time was 9.8 years. Threshold values of population growth rates λ^T and their approximate uncertainties were calculated (Table 1).

The expected population growth rate was consistently below λ^T (EN), throughout the study period (Fig. 3), corresponding to an expected decline over three generations of 50-80% and thus warranting red-listing as Endangered. For the years 2005-2009 (corresponding to mean breeding productivity in 2000-2009), the expected population growth rate was below λ^T (CR), which in isolation would warrant red-listing as Critically Endangered. Results appear to be in accordance with the marine bird abundance indicator of the OSPAR QSR 2023 (Dierschke *et al.* 2023). For comparison, the abundance indicator for Black-legged Kittiwake in the Greater North Sea OSPAR Region showed a decline of 64% over the period 1991-2019, which is almost exactly equal to three Kittiwake generations (i.e. 29.4 years).

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DISCUSSION

Our approach produces an easily interpretable answer to the question: for a given species in a given region, is the current level of breeding productivity sufficient to avoid future population declines (assuming that survival remains at recent levels)? Furthermore, the approach quantifies the expected population growth rate and allows a tiered assessment of the severity of an observed (low) level of breeding productivity, consistent with the widely used IUCN criteria for red-listing of threatened and vulnerable species and populations. By collating results across species and regions, higher-level assessments of GES for e.g. regions or functional species groups (feeding guilds) are possible, as required under the MSFD. Results of such assessments are presented as part of the OSPAR QSR 2023. More detailed comparative analyses of time series of expected growth rates across species and regions could be highly informative, e.g. for identifying drivers of population change. Overall, we believe this approach provides a powerful tool that is likely to lead to major improvements in understanding and communicating the status and trends of European marine bird populations, and that could also easily be adapted to other areas and taxa, where suitable data are available.

Nevertheless, there are several important limitations of our approach, and of the data it is based on.

1. Our approach is fairly data-hungry, as it requires sufficient data for annual estimates of breeding productivity as well as population abundance. Colonially nesting birds are therefore obvious candidates for applying the approach, as collection of large amounts of data is relatively easy. In principle, dispersed nesters could be assessed using the same approach, and this is likely to be practically possible for some well-monitored species (e.g. some passerines, raptors). However, our approach is likely to be less useful for species occurring at low density, or those where one or the other type of data is difficult to collect.
2. Ideally, the assessment should take place for areas that are ecologically well defined and reasonably homogeneous, as marine bird breeding productivity can vary over relatively small spatial scales (Frederiksen *et al.* 2005b, Olin *et al.* 2020). However, limits to data availability will in general lead to assessments taking place on a spatial scale that is larger than optimal.
3. Linked to this, monitoring data should be representative of temporal patterns in abundance and breeding productivity within each region. However, such data are uncommon. For example, our study area includes some long-term monitoring programmes, but even here, data coverage is generally highly heterogeneous in space. In the North Sea, many more sites are monitored for marine bird breeding productivity in the UK and the Netherlands than in other countries. The weighting of the abundance indicator by national population total should ideally to some extent compensate for the uneven coverage. In general, breeding productivity is monitored at much fewer sites than abundance, and some countries monitor only abundance and thus do not contribute to the indicator of breeding productivity. The breeding productivity indicator is likely to be less representative than the corresponding abundance indicator, which should be kept in mind when interpreting the results. Coverage also differs among species, with monitoring of some species restricted to a few sites. However, the Black-legged Kittiwake, the focus of our case study, is among the most widely monitored seabird species.
4. The tuning of survival parameters to fit the observed abundance trend is somewhat subjective. Because several age classes are involved, there are several age-specific parameter values that can be adjusted with no unique solution. The choice of values to

adjust was based on expert opinion (general understanding of marine bird life histories), as well as the weight of evidence behind the starting values. In the case of the Black-legged Kittiwake, our assessment was that the value for particularly first-year survival (0.79) given in Horswill and Robinson (2015) was unrealistically high and based on one very old reference (Coulson & White 1959). On the other hand, the value for adult survival (> 2 years old: 0.845) was based on two more recent published studies and a report (Oro & Furness 2002, Frederiksen *et al.* 2004, Taylor *et al.* 2010). We therefore adjusted first-year survival to 0.49, close to the value of 0.50 which was found to be useful for reconstructing the population trajectory in one study colony by Frederiksen *et al.* (2004). A small further adjustment was necessary, and we therefore reduced the value of second-year survival (for which no value was given by Horswill and Robinson (2015)) from 0.845 to 0.79. For some other species, tuning survival to reflect population trend was more complex.

5. The assumption that age-specific survival and breeding propensity have remained constant over the 35-year study period is unrealistic. All demographic parameters will show some variation in response to the environment, although adult survival is generally expected to show less year-to-year variation than breeding productivity (Sæther & Bakke 2000). Long-term trends in mean survival are also possible. At the same time, for long-lived species such as marine birds, annual population growth rate is much more sensitive to variation in adult survival than in breeding productivity (Lebreton & Clobert 1991). The expected growth rates should therefore be interpreted with caution, with the caveat that they are valid if mean survival and breeding propensity (including age of first breeding) have remained fairly constant over the study period. Systematic trends in survival will lead to bias in the expected growth population growth rates, and potentially to incorrect assignment to IUCN threat categories (see Supporting Information).
6. The models used here ignore dispersal between OSPAR Regions, or to and from regions outside the OSPAR Maritime Area. For most species this omission is probably of small importance, but for species which are rapidly spreading northwards, population trends can only be realistically reproduced if dispersal is included.

In addition to time series of expected growth rates, our approach produces additional output which could be useful for research and management of European marine birds. The tuned values of age-specific survival represent our best informed ‘guesstimates’ of mean survival over a 30-year period, consistent with observed breeding productivity and trends in abundance. These values should be useful as starting points for future demographic modelling work, e.g. as part of environmental impact assessments of infrastructure developments, incidental mortality (fisheries bycatch) or other anthropogenic impacts. The tuned values can also be compared to available empirical estimates of survival, as noted above for Black-legged Kittiwake. The mean breeding productivity required for a stable population is another useful quantity, e.g. for assessing the status of individual colonies. For the Black-legged Kittiwake, the value of 1.15 fledged chicks/pair is high, and while similar values are regularly observed in individual years and colonies, the mean in the Greater North Sea OSPAR Region has been below this level in every year 1986-2019 (Fig. 1). This may suggest that survival of one or more age classes has been so low that even near-optimal values of breeding productivity are insufficient to maintain a stable population (Frederiksen *et al.* 2004). In the North Pacific, Black-legged Kittiwakes generally show much higher adult survival, and much lower breeding productivity, than in European waters (Frederiksen *et al.* 2005a, Suryan *et al.* 2009). Finally, our approach produces an estimate of generation time that reflects local conditions, which may also be useful for e.g. status assessments. Tuned values of age-specific survival, breeding productivity required to sustain a population, as well as generation time, will be reported separately for all species and regions included in OSPAR QSR 2023 (https://oap.ospar.org/en/ospar-assessments/quality-status-reports/qsr-2023/indicator-assessments/).

Our approach does not fully exploit the information in the existing demographic data. The ad hoc modelling approach does not allow full error propagation from raw data to model predictions, and existing data on e.g. survival are not incorporated directly. As the next step, therefore, a set of Integrated Population Models (IPMs) should be developed, based on the data we have used here as well as any other empirical data on demography for the same species in the same regions. This would require a systematic collation of demographic data (other than breeding productivity), which are currently not necessarily included in national monitoring programmes, and not reported to OSPAR. IPMs allow the full integration of all data on population abundance and demography into a single, mathematically coherent framework (Schaub & Abadi 2011, Robinson *et al.* 2014), and can be used for population projections. Species- and region-specific IPMs would thus allow explicit projections of expected population development, incorporating uncertainty and environmental stochasticity, and could also integrate available data on the magnitude of human-induced mortality from e.g. fisheries bycatch or collisions with wind turbines. While applying an IPM to a single population is fairly straightforward, this is not the case for the complex multi-population (or metapopulation) setup that would be needed for regional demographic indicators. New model frameworks would thus need to be developed.

Conclusion

We propose a model-based approach to assessment of population status of birds, which integrates monitoring data on abundance and breeding productivity and allows comparison with established thresholds for population threat level. Our approach allows agencies responsible for biodiversity monitoring to assess whether populations are likely to be self-sustainable in the medium term, and should be easily generalizable from marine birds in the Northeast Atlantic to other cases where abundance and breeding productivity are monitored.

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Tables

Table 1. Model structure and values of demographic parameters in the baseline and tuned models for Black-legged Kittiwake. In the models used here, the number of age classes is determined by the mean age of first breeding *m*. Individuals younger than *m* are assumed not to breed, and all individuals aged *m* or older are assumed to have the same values for survival, breeding propensity and breeding productivity. The table also shows the observed population growth rate λ_o, as well as the breeding productivity required for stability BP_{stable}, the estimated generation time, and the threshold levels of population growth corresponding to IUCN red-listing as Vulnerable (VU), Endangered (EN) and Critically Endangered (CR) (with 2.5th and 97.5th percentiles). Values for age-specific survival in the baseline model are taken from Horswill & Robinson (2015).

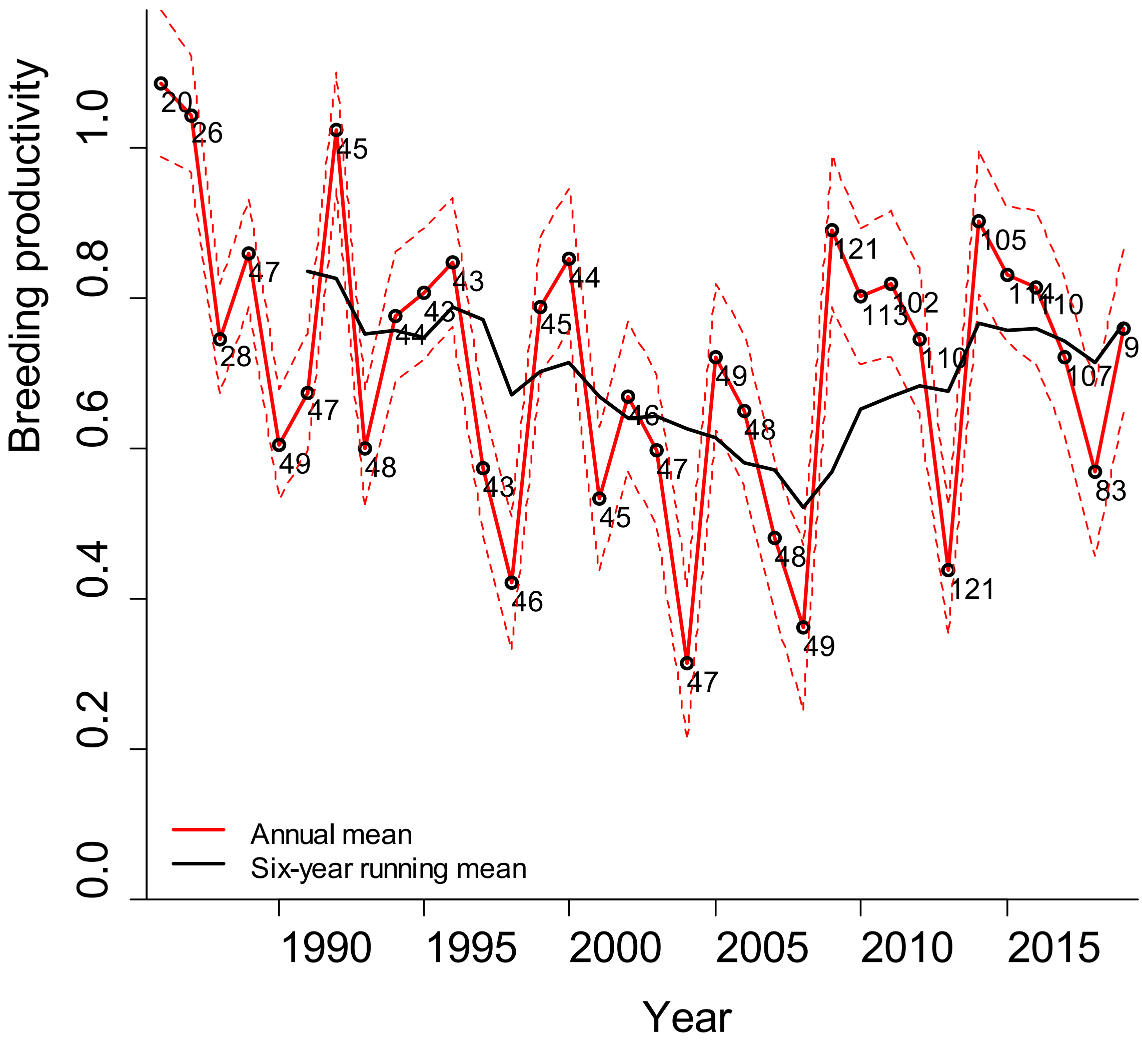
	Black-legged Kittiwake	
λ_o	0.962	
	Baseline model	Tuned model
Age of first breeding (years)	4	4
Breeding productivity (fledged chicks/pair)	0.69	Time series
Sex ratio	0.5	0.5
Breeding propensity	0.9	0.9
First-year survival	0.79	0.49
Second-year survival	0.854	0.79
Third-year survival	0.854	0.854
Fourth-year survival	0.854	0.854
Adult survival	0.854	0.854
BP_{stable}	-	1.15
Generation time (years)	-	9.8
λ^T (VU)	-	0.988 (0.984-0.992)
λ^T (EN)	-	0.977 (0.969-0.985)
λ^T (CR)	-	0.947 (0.930-0.966)

Figures

Fig. 1. Time series of mean breeding productivity (fledged chicks/pair) of Black-legged Kittiwake in the Greater North Sea OSPAR Region during 1986-2019. The solid red line shows the estimated marginal means for each year, with dashed lines indicating 95% confidence limits. Labels below the data points show the number of survey plots with available data for each year. The solid black line shows the retrospective six-year running mean.

Fig. 2. Illustrative examples of the beta distributions used to draw random values of survival. Here shown for mean = 0.9 and SD = 0.05 (solid line), and for mean = 0.5 and SD = 0.1 (dashed line). These combinations are roughly illustrative of survival values commonly found in long-lived marine bird species, in adult and first-year birds respectively (Horswill and Robinson 2015).

Fig. 3. Time series of expected population growth rate of Black-legged Kittiwake in the Greater North Sea OSPAR Region during 1991-2019 (black line). Each point on the line represents the expected population growth rate based on the six-year retrospective running mean breeding productivity (Fig. 2). The background colours illustrate the species-specific thresholds derived from IUCN red-listing criteria for the categories Vulnerable (VU, yellow), Endangered (EN, orange) and Critically Endangered (CR, red).



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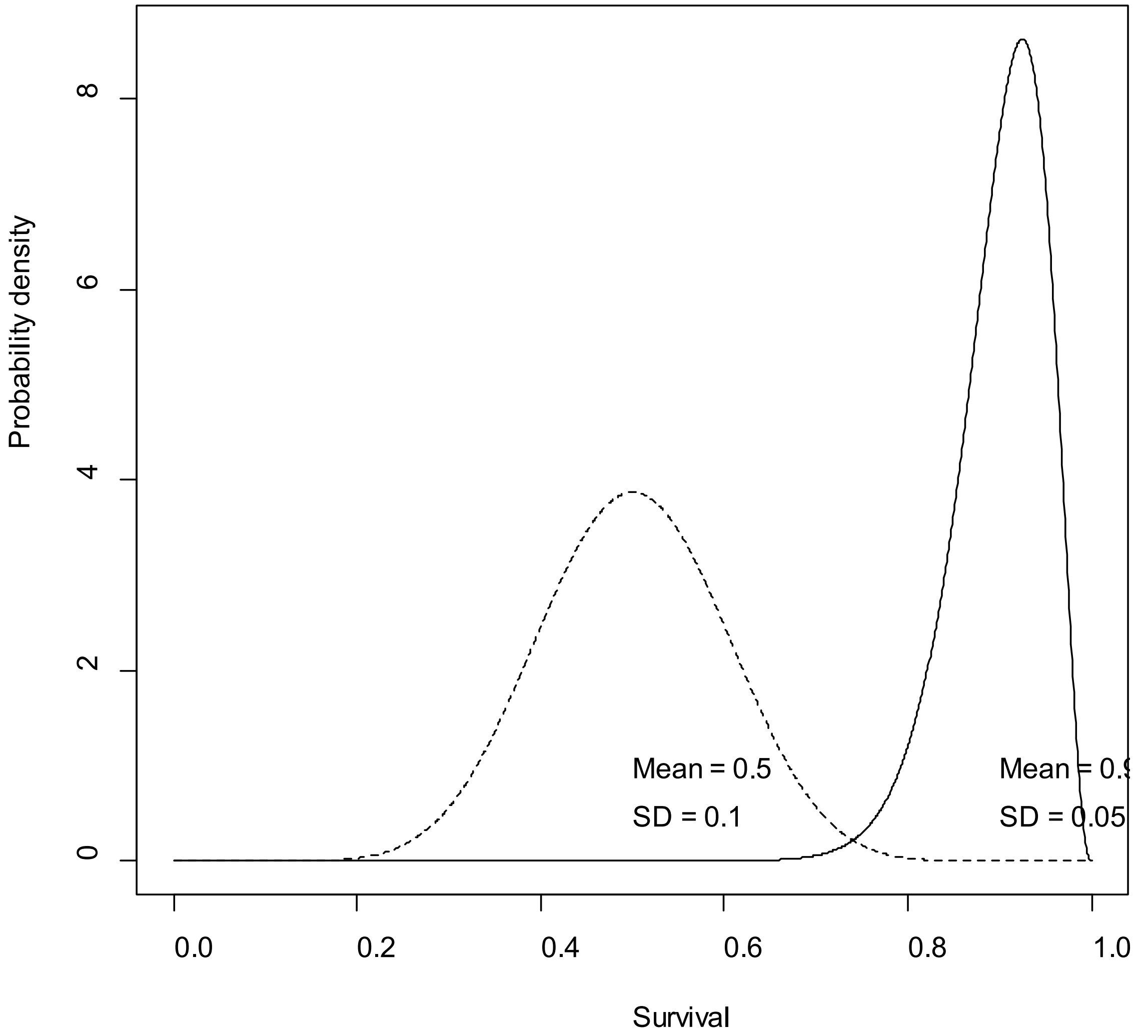

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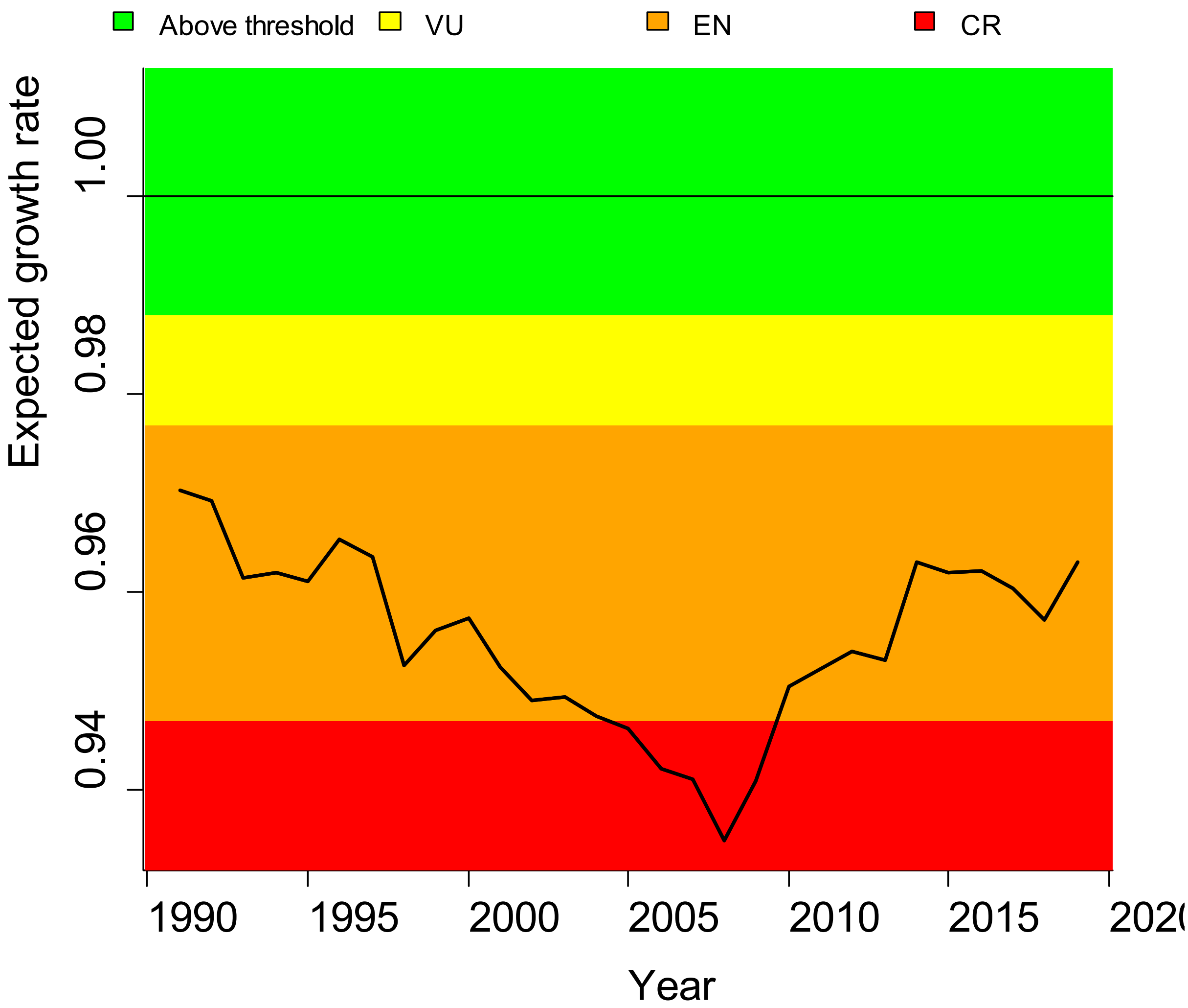

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