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RESEARCH ARTICLE

Path analysis reveals combined winter climate and pollution effects on the survival of a marine top predator

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Abstract

1. Marine ecosystems are experiencing growing pressure from multiple threats caused by human activities, with far-reaching consequences for marine food webs. Determining the effects of multiple stressors is complex, in part, as they can affect different aspects of biological organisation (behaviour, individual traits and demographic rates). Determining the combined effects of stressors, through different biological pathways, is key to predict the consequences for the viability of populations threatened by global change.
2. Due to their position in the food chain, top predators such as seabirds are considered more sensitive to environmental changes. Climate change is affecting the prey resources available for seabirds, through bottom-up effects, while organic pollutants can bioaccumulate in food chains with the greatest impacts on top predators. However, knowledge of their combined effects on population dynamics is scarce.
3. Using a path analysis, we quantify the effects of climate change and pollution on the survival of adult great black-backed gulls, both directly and through effects of individuals' body mass.
4. Warmer ocean temperatures in gulls' winter foraging areas in the North Sea were correlated with higher survival, potentially explained by shifts in prey availability associated with global climate change. We also found support for indirect negative effects of organochlorines, highly toxic pollutants to seabirds, on survival, which acted, in part, through a negative effect on body mass.
5. The results from this path analysis highlight how, even for such long-lived species where variance in survival tends to be limited, two stressors still have had a marked influence on adult survival and illustrate the potential of path models to improve predictions of population variability under multiple stressors.

KEYWORDS
adult survival, Bayesian inference, capture-mark-recapture, climate change, great black-backed gull, *Larus marinus*, path analysis, persistent organic pollutants

1 | INTRODUCTION

Natural populations are facing increasing pressure from anthropogenic stressors (Jackson et al., 2021; Simmons et al., 2021). A key challenge in ecology is measuring the effect of multiple stressors, which can act through alternative pathways (e.g. via various life-history traits). Multiple stressors can interact in complex ways, combining to have a negative total impact that is greater (or less) than the sum of their independent effects (Darling & Côté, 2008). Understanding their combined effects and the mechanisms behind them is crucial to assess the overall consequences of global change and accurately predict populations' viability. Our knowledge of the mechanisms behind multiple stressor effects is limited because analyses and experiments often only consider effects of a single stressor, which can lead to underestimation or overestimation of the risk to biodiversity (Simmons et al., 2021).

Assessing causal pathways between variables, for example between environmental stressors and a population's demographic rates, requires experimental manipulations, which are often not feasible in natural populations and so we tend to rely on observational data. Path analysis is a multivariate regression technique to formalise and confront hypothesised scenarios using observational data (Shipley, 1997). Path models are traditionally used to test causal relationships, which can be direct or indirect, between multiple variables, and such models have been widely employed in ecological studies (Pugesek et al., 2003; Shipley, 2016). The model reflects a hypothesised causal structure for which we can estimate the effects of variables, through direct and indirect paths, given this structure. Capture-mark-recapture or resighting (CMR) models provide a general and flexible framework for survival estimation (among other parameters) in the face of imperfect detection. For long-lived species, the survival of mature adults is the most influential demographic rate driving population growth (Gaillard et al., 1998). While CMR models are widely used to estimate the effects of time- and individual-varying factors on demographic parameters (Pollock, 2002), they generally do not consider multiple effect pathways. Recently, path analyses have been implemented in CMR models (Cubaynes et al., 2012; Gibson et al., 2023; Gimenez et al., 2012), with great—but still largely unharnessed—potential in studies of multiple stressor effects on population dynamics. Furthermore, Bayesian approaches to path models allow for the propagation of the uncertainty among the estimated relationships between variables in the proposed causal structure and allow for missing data (Fan et al., 2016).

Marine ecosystems are experiencing intense and growing pressure from human activities (OSPAR, 2009). Overfishing, climate change and the presence of organic pollutants have irreversibly altered the structure and stability of marine food webs (Halpern et al., 2008; Maxwell et al., 2013). Top predators are particularly sensitive to such anthropogenic impacts as a result of trophic accumulation of pollutants as well as their life history characteristics such as long lifespans and delayed maturation (Heithaus et al., 2008). The population dynamics of marine predators are largely driven by changes lower in the food chain, making them more vulnerable to shifts in food resources (Frederiksen et al., 2006). In long-lived species, the survival of mature adults is expected to be canalised against temporal variation, compared to recruitment, because a populations' growth rate is highly sensitive to changes in adult survival (Gaillard et al., 1998). Seabirds are top marine predators. They are also considered the world's most threatened bird group and many populations are undergoing strong declines (Croxall et al., 2012). There are numerous well-documented threats to seabirds including pollution, climate change, bycatch and overfishing (Cury et al., 2011; Dias et al., 2019).

Climate change is having widespread, detrimental consequences for seabirds (Grémillet & Boulinier, 2009; Sydeman et al., 2012) largely through changes in the availability of prey resources (Frederiksen et al., 2006; Reiertsen et al., 2014). However, phenomena such as increased extreme weather events also directly affect survival rates (Guéry et al., 2019). Changes in the abundance and distribution of prey resources are caused by warming ocean temperatures and associated changes in oceanographic conditions (Perry et al., 2005). Seabirds are considered especially at risk from the effects of climate change as most are migratory. Migratory species experience different environmental conditions at discrete sites, making them less able to predict changes in conditions. This applies to species spending at least part of the year in the Arctic, where ocean warming is occurring at a faster rate than the global average (Rantanen et al., 2022).

While pollution is considered an important threat to seabirds, our understanding of its impact on population dynamics is limited, particularly in the context of multiple stressors (but see e.g. Bårdsen & Bustnes, 2022; Bustnes et al., 2015). The most damaging pollutants to wildlife, and top predators in particular, are those that persist and bioaccumulate. For instance, methylmercury, a potent neurotoxin which bioaccumulates in marine food chains, has been found at extremely high concentrations in predatory fish (Schartup et al., 2019). Persistent organic pollutants (POPs) can negatively affect seabirds, where individuals with higher levels of POPs can have increased parasite loads (Sagerup et al., 2000) and reduced individual condition (Bustnes et al., 2002). This, in turn, has negative implications for their reproduction (Bustnes et al., 2003), survival (Erikstad et al., 2013; Goutte et al., 2015) and population viability (Bustnes et al., 2003). Subarctic and arctic marine ecosystems currently have relatively high levels of several long transported persistent POPs (Burkow & Kallenborn, 2000), and even low levels of POPs can have ecological consequences, especially under poor environmental conditions (Bustnes et al., 2015; Goutte et al., 2015). Organochlorines (OCs) are chemical pesticides and are distributed globally with toxic, biomagnifying effects on wildlife (Jones & De Voogt, 1999). OCs are considered to have the most detrimental effects on marine top predators of all POPs (Bustnes, Erikstad, et al., 2008; Bustnes, Fauchald, et al., 2008, Murphy et al., 2018). Although they are no longer in use, these compounds are still contaminating terrestrial and aquatic environments worldwide (Buccini, 2003). Some pollutants, such as OCs, are released into the blood when fats are metabolised and redistributed into vital organs (Bustnes et al., 2012), meaning an individuals' physiological state can affect circulating levels of pollutants and thereby mediate effects on survival or reproduction (Bustnes et al., 2015; Henriksen et al., 1998). Consequently, other stressors, for example climate change, may exacerbate the negative impacts of pollution by affecting individuals' condition. Conversely, contaminant exposure can also alter individual responses to environmental conditions, via the regulation of stress hormones (e.g. Nordstad et al., 2012). Such mechanisms may be particularly relevant for Arctic breeding seabird species that store large fat reserves prior to the breeding season (Henriksen et al., 1998).

There is a need to study the combined effects of multiple stressors on populations' demographic rates to predict the consequences for their viability. Studies applying path models (e.g. confirmatory path analysis or structural equation models) in a multiple stressor context illustrate their promise, across taxa and environmental pressures (e.g. Layton-Matthews et al., 2020; Selonen et al., 2021; Texeira et al., 2012), although examples of their application to survival responses to multiple stressors remain limited (but see Gibson et al., 2023; Gimenez et al., 2012). Despite the requirement for individual-based, longitudinal data to fit such models, CMR-path models present a holistic approach to study multiple stressors effects on survival, which is of particular importance for the population dynamics of long-lived species. They also account for imperfect detection, a recognised issue in many studies (Gimenez et al., 2008). Here, we used a path model to integrate CMR data from a long-lived marine top predator (great black-backed [GBB] gulls, *Larus marinus*), with known individual contaminant (OC) levels and climate data from their non-breeding areas, to disentangle their effects on survival. We tested for direct effects of ocean warming and both direct and indirect (via individual condition) effects of OC contamination on adult survival rates.

2 | MATERIALS AND METHODS

2.1 | Study system and species

Great black-backed (henceforth 'GBB') gulls are coastal species with a recorded lifespan of 10–23 years and typically become breeding adults at 4–5 years old. GBB gulls are top predators and their diet consists mainly of marine invertebrates and fish, as well as other seabirds' eggs and chicks during the breeding season (Furness & Barrett, 1985). Seabirds deposit a portion of contaminants in their eggs (Verboven et al., 2009). Therefore, gulls feeding on eggs are at even greater risk of accumulating heavy pollutant loads (Bustnes et al., 2000). The study was carried out at an Arctic seabird breeding colony, Hornøya (70°23′ N, 31°09′ E), in the southern Barents Sea.

2.2 | Population size

To estimate the change in the numbers of breeding pairs, we used annual counts of monitored plots. Three plots were counted each year from 2008 to 2017, except for 2009 when no data were collected. We fitted a state-space model to these data (Besbeas et al., 2002; De Valpine & Hastings, 2002), which is defined by a state process (true population sizes) and an observation process (observation of the true population sizes). Counts, y_t, were assumed to have a Poisson distribution conditional upon the true abundance N_t, so that $y_t \sim \text{Pois}(N_t)$. We modelled the latent variable N, at year $t+1$ as $N_{t+1} \sim N_t \lambda_t$, where λ_t is the population growth rate from year t to $t+1$. The state-space model was fitted to counts and implemented in a Bayesian framework using Markov chain Monte Carlo (MCMC) simulations to estimate posterior distributions of model parameters. Three chains of length 200,000 were run, where the first 50,000 was discarded as burn-in.

2.3 | Biometric and pollutant data

Breeding adults were caught using nest traps during the incubation period (May–June) in 2001 and 2002. Once caught, birds were weighed, and the head and bill length were measured. GBB gulls were sexed using measurements of head and bill length as they are size dimorphic (see Bustnes, Fauchald, et al., 2008 for details). Individuals' body mass (weight) was used as a measure of individual quality. The activities of capturing, handling and tagging the birds were performed through SEAPOP (Norwegian Research Council Grant #192.141, https://seapop.no/en/) and SEATRACK (https://seapop.no/en/seatrack/) programmes and all applicable and/or institutional guidelines and necessary approvals for the sampling of birds were followed and obtained. The County governor of Finnmark approved and provided a special permit to conduct fieldwork in Hornøya and Reinøya Nature Reserve (ref 2020/3215).

Blood concentrations of several OCs were measured in 158 individuals during field campaigns in 2001 and 2002. Approximately 10 mL of blood was drawn from the brachial vein. Levels of OCs were analysed at the Environmental Toxicology Laboratory at the Norwegian School of Veterinary Science (see Bustnes, Fauchald, et al., 2008). Samples were analysed for hexachlorobenzene (HCB), *p,p′*-dichlorodiphenyldichloroethylene (DEE), oxychlordane and the total polychlorinated biphenyl (PCB) congeners. Blood concentration (ng/g wet weight) was used as a measure of an individual's relative OC level. Other studies suggest a relatively high stability of OC blood concentrations in incubating gulls under stable conditions, indicating that blood concentration is a reliable measurement of an individual's relative OC burden (Bustnes et al., 2001, 2005). For analysis, data of OC concentrations had a left-skewed distribution and so were log transformed to approximate a normal distribution (Supporting Information S1, Figure S1). Each OC variable was then normalised (mean equal to 0 and standard deviation [SD] equal to 1) within year (separately for values from 2001 and 2002) to account for differences in the timing of capture and background levels of contaminants between years. The first principal component (PC1) from a principal component analysis (PCA) was used to represent individuals' overall contamination level (Supporting Information S1, Figure S2). The PCA was applied to the log-transformed and scaled values of the measured compounds (HCB, DDE, summed PCBs and oxychlordane). The first axis of the PCA (PC1) explained 88% of the total variance in OC concentrations (see Supporting Information S1, Figure S2). No additional permits were required for sampling of blood for contaminants in 2001 and 2002.

2.4 | Non-breeding season distribution

We estimated gulls' core foraging areas during the non-breeding season using geolocation data from 2012–2015 (Figure 1). Ten adult birds were equipped with miniature year-round, light-based tracking devices (geolocators) attached to a plastic leg ring. Light data from the geolocators were processed using the BASTrak software package (British Antarctic Survey, Fox, 2010) and positions were calculated using a threshold method (Lisovski et al., 2020). Raw positions were filtered with distance, speed, loess filters and unreliable positions around the equinoxes, between 7 September–19 October and 24 February–5 April, were excluded. Utilisation distributions (10%, 30%, 50% and 70%) were estimated as kernel density distributions using the "kernelUD" function in the "adehabitatHR" package (Calenge, 2006). Based on the geolocation data, individuals also forage close to the breeding colony at Hornøya during spring prior to breeding (Figure 1). After breeding, they travel to the North Sea around the east coast of the UK and most remain there during the winter. During late winter, individuals migrate back to the southern Barents Sea area (Figure 1). Permits to handle and tag seabirds with geolocators were given by the Norwegian Food Safety Authority (FOTS ID 23259) and licences and permits to capture and ring birds were given by the Norwegian Environment Agency (ref 2018/607).

2.5 | Climate data

We selected climate variables reflecting non-breeding season conditions that may affect survival rates, which were available at different

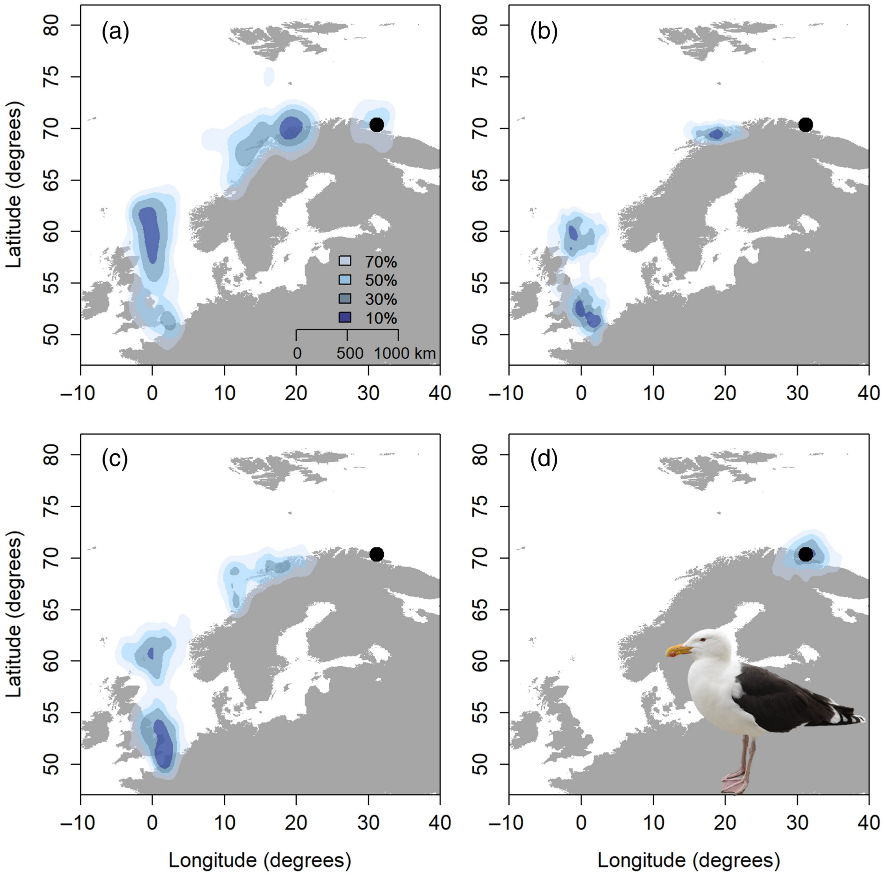

FIGURE 1 Year-round non-breeding areas of adult great black-backed gulls from Hornøya based on positions from individuals with geolocators (GLS) during the years 2012–2015 for autumn [September–October (a)], early winter [November–December (b)], late winter [January–February (c)] and spring [April (d)] seasons.

spatial scales; North Atlantic Oscillation (NAO), Atlantic Water (AW) inflow, land temperature, sea surface temperature (SST) and mean sea level pressure (MSLP).

North Atlantic Oscillation and AW inflow were available as monthly values. The NAO index reflects large-scale weather patterns and specifically cyclone activity in the North Atlantic and is widely used as a proxy for indirect effects of climate conditions on seabirds via changes in prey distributions and abundances (Stenseth et al., 2003). Annual, monthly values of NAO index are openly available from www.cpc.ncep.noaa.gov. In the Barents Sea, ocean conditions are largely determined by fluctuations in the inflow of warm and saline AW (Ingvaldsen et al., 2004; Loeng, 1991), again affecting seabirds through changes in prey availability (Barrett et al., 2017). Cyclones, in part, modulate the influx of AW, and so this can be related to NAO (Heukamp et al., 2023). Data of AW inflow were available at a monthly scale from the Norwegian Meteorological Institute (https://api.met.no/product/THREDDS). NAO and AW inflow were aggregated for two periods: winter (November–February) and spring (March–April).

Land temperature (airT), SST and MSLP were available as gridded data and were extracted from within seabirds' seasonal foraging ranges (Supporting Information S2, Figure S3) and were available from the European Centre for Medium-Range Weather Forecasts (ECMWF) Re-Analysis Interim Project (‘ERA-Interim’). ERA-Interim is a gridded model dataset at a resolution of 0.70° or approximately 79 km based on data assimilation of meteorological station data and satellite data, among others (Dee et al., 2011; Mesquita et al., 2015). Values of MSLP, SST and airT were extracted from areas reflecting the utilisation distributions, for the relevant seasonal periods (Supporting Information S2, Figure S3). Annual covariates were aggregated to four periods: Autumn (September–October, Aut), early Winter (November–December, Ewin), late Winter (January–February, Lwin) and Spring (March–April, Spr), for the years 2001–2017. Values were extracted from the North Sea region for Autumn, early Winter and late Winter (NNS/SNS, Figure S3). For spring, values were extracted from around the breeding colony at Hornøya (HRN, Figure S3). See Supporting Information S2, Figure S4 for plots of the annual time series.

2.6 | Model selection

We used individual-level capture-mark-resight (CMR) data collected between 2001 and 2017. Only mark-recapture data from individuals with known levels of OCs ($N=158$) that were caught and sampled in either 2001 or 2002 were included in the analysis. During first capture, birds were marked with a unique numbered metal ring and individually coded colour ring for future resighting, which is possible with a telescope or binoculars. Each year, visual searches were made for marked birds, predominantly at the same colony where initial capture and ring-marking took place.

All CMR analysis were based on a Cormack–Jolly–Seber (CJS) model framework (Lebreton et al., 1992). For model selection, apparent survival and re-sighting rates were estimated using MARK via the program RMark (Laake, 2013) run in R (version 4.2.2, R Core Team, 2023). The goodness of fit (GOF) of this model to the data was assessed using UCARE (Choquet et al., 2009). One of the GOF test components indicated a significant deviation from the model assumptions: Test 2.CT showed trap-dependence (dependence of resighting rates across years, $\chi^2=40.86$, df = 10, $p<0.001$). We corrected for this by including a trap-dependence effect in the resighting model, where resighting rates of individuals the year after first capture are estimated separately from those that were not resighted the previous year. Correcting for this effect sufficiently improved the model fit ($\chi^2=12.30$, df = 10, $p=0.27$).

We first obtained the best structure for a model without covariates (Supporting Information S3, Table S1). Given the large number of climate variables, candidate models of survival were then fitted including climate variables. Model selection was based on Akaike's information criterion corrected for small sample size ($\mathrm{AIC_c}$; Anderson & Burnham, 2002). A maximum of two covariates per model was set and variables with a correlation of 0.4 or higher were not included in the same model, which is a relatively restrictive threshold to avoid potentially incorrect model selection (Dormann et al., 2013). Models with lower $\mathrm{AIC_c}$ are preferred; if models differed by <2 $\mathrm{AIC_c}$ units, they were regarded as equally well supported (unless they differ in the number or parameters, in which case the most parsimonious model within this set was favoured). We report the difference ($\Delta\mathrm{AIC_c}$) between the $\mathrm{AIC_c}$ of each covariate model and the null model and also the proportion of variance explained (R^2) by that covariate model, which was calculated as

$$\frac{\text{Deviance(covariate model)} - \text{Deviance(null model)}}{\text{Deviance(time} - \text{dependent model)} - \text{Deviance(null model)}}.$$

Since some of the climate covariates displayed temporal trends, models that had a lower $\mathrm{AIC_c}$ than the intercept model were tested in a de-trended version as well, to ensure effects were not spurious (see Supporting Information S3, Table S2). In this case, covariates were linearly detrended using the ‘detrend’ function in the R package ‘*pracma*’ (Borchers, 2019).

To determine the best model of body mass, we fitted the individual-level body mass data using a linear model, assuming body masses were normally distributed. We formulated candidate models with terms including only an intercept, OC level, sex (female/male) and a model with an interaction between OC level and sex. As oxychlordane is considered an especially toxic OC compound (Bustnes, 2006), we tested for both effects of oxychlordane levels alone and PC1 of all measured compounds. Model fits were also compared using the $\mathrm{AIC_c}$ described above.

2.7 | Path model

The path model was fitted to individual capture histories and implemented in a Bayesian framework using MCMC simulations to estimate posterior distributions of model parameters, following the methodology outlined in Gimenez et al. (2012). The path model estimates survival ($\Phi_{i,t}$) and resighting probabilities ($p_{i,t}$), which included a year and a trap dependence (TD) effect. The probability of resighting on the logit scale for individual *i* in year *t*, can be expressed as:

$$\text{logit}(p_{i,t}) \sim \alpha_p \times \text{TD}_{i,t} + \varepsilon_{p,t}.$$

The temporal residual term, $\varepsilon_{p,t}$, was assumed to be normally distributed with a zero mean and variance equal to σ_p^2. We developed a CMR model for GBB gulls, with a direct effect of climate conditions (time varying) and both a direct and indirect effect of OC contaminant levels (individually varying) on adult survival, with body mass (individually varying) as a mediating variable. Body mass was normalised so that the overall mean was zero and the SD of the data was one. Total contaminant level (PC1) was fitted as an individual-level covariate (OC_i). The probability of survival on the logit scale for individual *i* and year *t* was modelled as a function of body mass (BM_i), climate variable(s) from the best fitting model (clim_t) and OC levels (i.e. a direct effect of individual contaminant level):

$$\text{logit}(\Phi_{i,t}) \sim \alpha_1 + \beta_1 \times \text{BM}_i + \beta_2 \times \text{clim}_t + \beta_3 \times \text{OC}_i.$$

βs refer to the regression coefficients. Body mass (BM_i) was included as both a predictor variable (of adult survival) and a response variable. When fitted as a response, BM was assumed to be normally distributed with a variance equal to σ_{BM}^2 with weakly uninformative priors. The linear model for body mass (BM_i) against contaminant level and sex (sex_i) can be written as:

$$\text{BM}_i \sim \alpha_2 + \beta_4 \times \text{OC}_i + \beta_5 \times \text{sex}_i.$$

The product of β_1 and β_4 captures the indirect effect of individual level contamination on survival rates, accounting for annual variation in climate conditions and sex differences in body mass. An interaction effect between OC and sex was not included given the results from the model selection, which are shown in Table 2.

Following Gelman et al. (2008), we used weakly informative default priors for parameters to aid convergence (Supporting Information S4, Table S3). Normal distributions were specified for the intercepts and Cauchy priors for the regression coefficients (β), as recommended for standardised data (Gelman et al., 2008). Normal distributions were specified with variance terms with uniform priors. Three chains were run of length 200,000, where the first 50,000 was discarded as burn-in. Both the state-space model of counts and the path model were implemented in JAGS (Plummer, 2003), via the program JAGSUI, version 1.5.2 (Kellner, 2015) and implemented in R version 4.2.2 (R Core Team, 2023). Convergence was assessed by ensuring $\hat{R}$ values for each parameter were less than 1.1 (Brooks & Gelman, 1998). Parameter estimates are reported as means with 95% credible intervals and probabilities of posterior distributions being greater or less than zero (note posterior probabilities are rounded to two decimal places).

3 | RESULTS

3.1 | Population size trend

Mean numbers of breeding pairs from monitored plots of GBB gulls on Hornøya were estimated to be 26 pairs [2.5% CRI: 18, 97.5% CRI: 36] in 2008 to 10 pairs [6, 17] in 2017 and showed a decline over this period (Figure 2a), where the mean population growth rate was 0.94 [0.73, 1.30].

3.2 | Adult survival model selection

The best fitting model of adult survival without climate covariates, included a negative linear trend over time (Supporting Information S3, Table S1). Annual estimates of survival (fixed year effect) are shown in Figure 2b. Based on this model, mean survival was 0.81 [0.78, 0.84] and the temporal trend was −0.09 [−0.15, −0.03] on the logit scale (see Supporting Information S3, Figure S5 for predicted survival probabilities for the trend model and recapture probabilities). The next best model of survival, which was within 2 AIC_c units, also included an effect of sex, where females had higher survival than males (Table S1) however, the first model was the most parsimonious. The best fitting model of resighting probability included a year-specific and trap-dependence effect. The mean recapture probability was 0.45 [0.23, 0.68] and the TD effect was 2.03 [1.37,

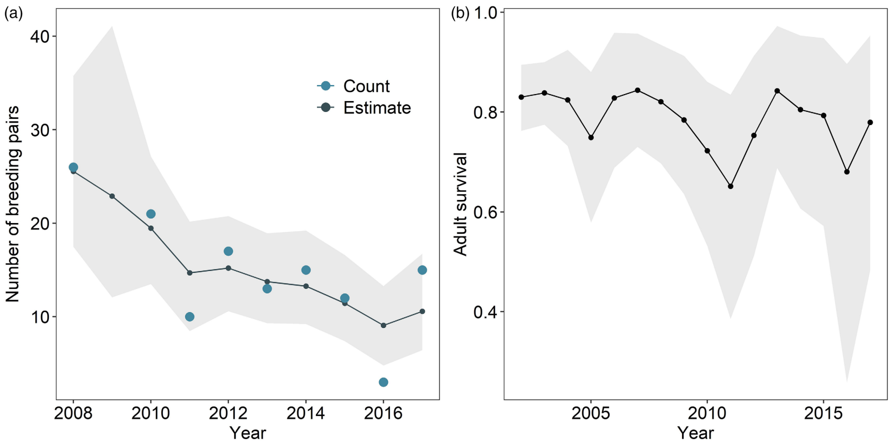

FIGURE 2 (a) Estimated numbers of breeding pairs from monitored plots from 2008 to 2017, estimated using a state-space model (see Section 2). Black points are mean estimates with 95% credible intervals shown as grey shading and blue points are observed counts. (b) Estimate annual mean survival for the years 2002–2017 (year reflects $t+1$) using the survival model fitted with an intercept and random year effect.

2.69] on the logit scale, indicating that birds caught the previous year were more likely to be caught the following year, that is 'trap happiness'.

The best fitting model of survival with climate covariates included positive effects of SST in late winter in the North Sea (SST_{Lwin}, 0.29 [0.00, 0.59]) and mean sea-level pressure in spring around Hornøya ($MSLP_{spr}$, 0.33 [−0.03, 0.69]), where these covariates together explained 48% of the variance in survival. However, a model with only SST_{Lwin} (slope = 0.45 [0.14, 0.76]) was within 2 AIC_c units and explained 35% of the annual variation in survival rates alone. This model was therefore considered the most parsimonious as it had one fewer parameter. All of the described covariate models were a better fit than the baseline model of survival with a temporal trend and the intercept model (Table 1).

3.3 | Body mass model selection

The best-fitting model of body mass included additive effects of PC1 and sex but not an interaction effect between them (Table 2). Mean levels of OCs in breeding individuals were 3.611 ng/g wet weight (SD = 3.06) for HCBs, 14.03 ng/g (13.28) for DDEs, 76.95 ng/g (88.09) for summed PCBs and 2.18 ng/g (3.13) for oxychlordane. A higher PC1 value (the first axis of the PCA where OC variables were log-transformed and scaled) was correlated with a lower body mass (−0.13 [95% confidence intervals: −0.17, −0.08]). Body mass was also higher for males than females on average (male–female contrast = 1.80 [1.64, 1.97]).

3.4 | Path model

Based on the model selection results, a path analysis CMR model was fitted where adult survival was regressed against SST_{Lwin}, body mass and individual OC level (PC1) (Figure 3a). Posterior distributions are shown in Figure 3b. Based on the path model, estimated mean adult survival was 0.80 [95% credible intervals: 0.77, 0.83]. Adult survival was positively correlated with body mass (Figure 3a) although 95% credible intervals overlapped zero and the posterior probability, $Pr(\beta_1 > 0)$, was 0.78. Survival also increased with late winter SST ($Pr(\beta_2 > 0) = 0.99$) (Figure 3b). The direct effect of OC levels on survival was negative ($Pr(\beta_3 < 0) = 0.94$). In the same model, body mass was also fitted as response variable with OC level and sex as predictor variables. Individual body mass was lower at higher levels of OCs, where $Pr(\beta_4 < 0)$ was 1.00 (Figures 3c and 4c). Body mass was also higher overall for males than females ($Pr(\beta_5 > 0)$ was 1.00, Figures 3c and 4c).

While the direct effect of OC levels on survival (β_3) was −0.08 [−0.18, 0.02], the product of the regression coefficients β_1 and β_4, reflecting the indirect effect via body mass, was −0.01 [−0.04, 0.01].

TABLE 1 Candidate models of climate effects on adult survival.

Survival model	df	AIC_c	ΔAIC_c	Weight	R^2
$0.29SST_{Lwin} + 0.33MSLP_{spr}$	18	1150.62	0.00	0.43	0.48
$0.45SST_{Lwin}$	17	1151.75	1.13	0.25	0.35
$0.44MSLP_{spr}$	17	1152.95	2.34	0.14	0.30
−0.09trend	18	1154.33	3.72	0.07	0.33
$airT_{Ewin}$	17	1156.83	6.21	0.02	–
NAO_{win}	18	1157.11	6.49	0.02	–
year	27	1157.20	6.59	0.02	–
$MSLP_{Ewin}$	18	1157.88	7.26	0.01	–
SST_{aut}	18	1158.60	7.99	0.01	–
SST_{spr}	18	1159.79	9.17	0.00	–
$airT_{Lwin}$	19	1160.97	10.36	0.00	–
SST_{Ewin}	18	1161.58	10.97	0.00	–
$airT_{spr}$	18	1161.85	11.23	0.00	–
AW_{spr}	19	1161.92	11.31	0.00	–
–	18	1162.64	12.03	0.00	–
AW_{win}	19	1162.90	12.28	0.00	–
$MSLP_{aut}$	19	1164.05	13.44	0.00	–
$airT_{aut}$	19	1164.39	13.77	0.00	–
NAO_{spr}	19	1164.43	13.82	0.00	–
$MSLP_{Lwin}$	19	1164.62	14.00	0.00	–

Note: For all models, the recapture model included year and trap dependence effects. Slope estimates are included for the "c" the top models.

Abbreviations: AIC_c, Akaike's information criterion corrected; AW, Atlantic Water; MSLP, mean sea level pressure; NAO, North Atlantic Oscillation; SST, sea surface temperature.

TABLE 2 Candidate models of covariate effects on body mass.

OC[PC1]	Sex	OC[PC1]:sex	Oxychlordane	Oxychlordane:sex	df	AIC$_c$	ΔAIC$_c$	Weight	R^2
−0.13	1.81				4	236.63	0.00	0.74	0.75
−0.13	1.81	−0.0006			5	238.76	2.13	0.26	0.75
	1.78		−0.23		4	248.66	12.03	0.00	0.73
	1.74		−0.26	0.08	5	250.27	13.65	0.00	0.73
	1.67				3	264.18	27.55	0.00	0.70
					2	451.46	214.83	0.00	–
			0.08		3	452.85	216.22	0.00	0.01
0.01					2	453.50	216.87	0.00	0.01

Notes: Candidate models included sex (female/male, where the slope effect is for females), OC level and an interaction between the two terms. OC levels were represented in two ways; either as oxychlordane alone (the most toxic compound) or as the first principal component (OC[PC1]) of all compounds after log transformation.

Abbreviations: AIC$_c$, Akaike's information criterion corrected; OC, organochlorine.

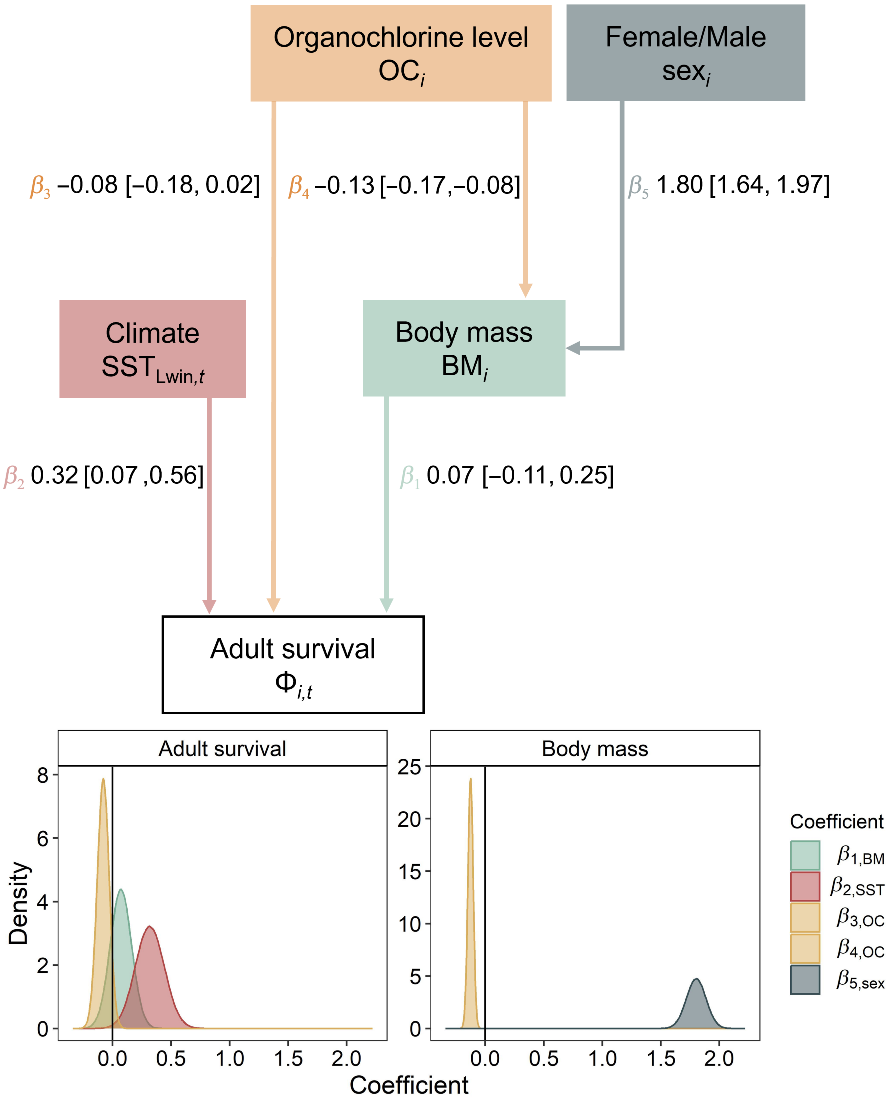

FIGURE 3 (a) Effects [credible intervals] of organochlorine levels (OC) and sex on body mass and of OC levels, winter sea surface temperature (SST_{Lwin}) and body mass on adult survival. Posterior distributions of estimated regression parameters from the path model representing the effect of (b) body mass (β_1, green), SST (β_2, red) and OC levels (β_3, yellow) on survival rates and (c) OC levels (β_4, yellow) and sex (slope for males $=\beta_5$, grey) on body mass.

An increase of 1 SD in PC1 (1 SD = 1.87), which reflects variation in OC levels, would increase blood concentrations of contaminants (averaged across measure components HCBs, DDEs, PCBs and oxychlordane) from the overall mean 24.19 ng/g wet weight to 78.31 ng/g. Given the effect size of β_1 and β_4, this would reduce survival by 0.003, that is a 0.37% decline in survival through reduced body condition. While a 1 SD increase in PC1 would reduce survival by 2.48% through the direct pathway (β_3). Overall, this indicates a negative effect of pollution, in part, through a reduction in body mass and that survival was higher under favourable conditions (high SST), acknowledging parameter uncertainties (Figure 4d).

4 | DISCUSSION

Anthropogenic pressure on oceans is increasing. Despite this, quantifying and predicting effects of isolated stressors on marine populations remains the norm. However, recent studies using path models to determine multiple stressor effects have illustrated their potential in disentangling multiple effect pathways (e.g. Selonen et al., 2021). Path models quantify the relative impact of stressors, through different biological pathways, and to what extent they explain declines in populations' demographic rates and abundances. For long-lived species, survival of mature adults is a key demographic rate in driving population growth. In ecology, the use of path models to study effects of multiple stressors on survival remains limited (but see Cubaynes et al., 2012; Gimenez et al., 2012; and more recently Gibson et al., 2023). By combining classical CMR modelling with path analysis in a Bayesian framework, we estimated the relative effects of two key widespread threats, climate change and pollution, on the survival of a long-lived marine top predator, through different biological pathways, while accounting for imperfect detection. Although such models can be fitted as separate, single regressions in more classical frequentist frameworks, Bayesian hierarchical models present a holistic approach, allowing for more complete error propagation (Maunder & Punt, 2013). Quantifying the relative importance of stressors, in the presence of uncertainty, is particularly relevant for threatened populations such as this gull population, where both adult survival rates and numbers of breeding pairs have declined over the study period. While warmer ocean temperatures in the North Sea appeared to increase gull survival rates, pollution reduced survival rates via direct and indirect pathways (i.e. individual condition).

Identifying the seasonal environmental drivers of population dynamics is imperative and especially for declining populations such

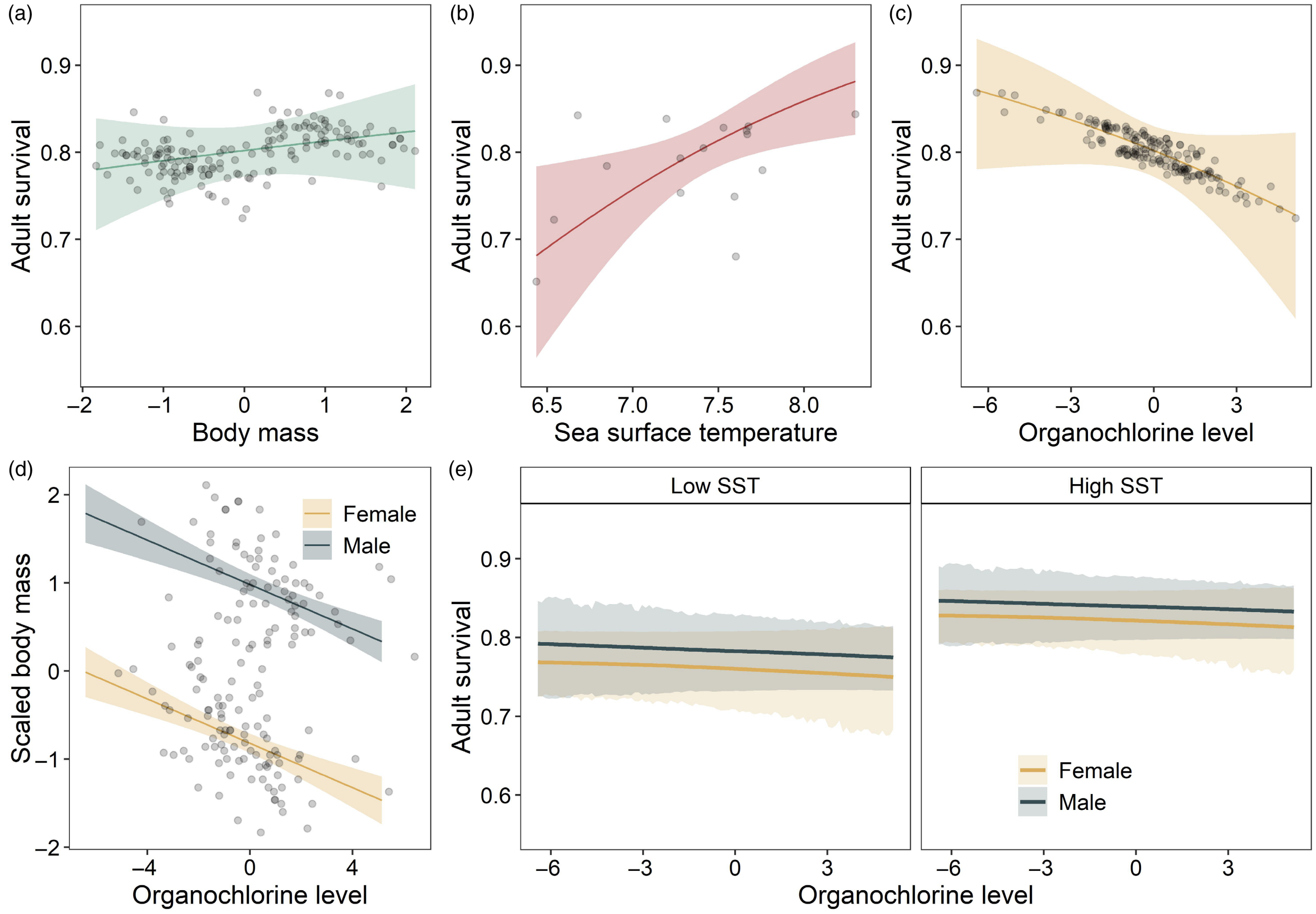

FIGURE 4 Model predictions (mean and 95% confidence intervals) for adult survival as a function of (a) body mass and (b) late winter sea surface temperature (SST) in the North Sea ($\mathrm{SST}_{\mathrm{Lwin}}$) and (c) organochlorine (OC) level and for (d) body mass as a function of OC level for females (yellow) and males (grey). (e) The indirect effect of organochlorine levels on adult survival, via a negative effect of OC on mass ($\beta_1 \times \beta_4$), where survival was predicted at the 25th and 75th quantile of observed SSTs. Scaled values are shown for all variables except $\mathrm{SST}_{\mathrm{Lwin}}$ (b).

as this population of Arctic-breeding gulls. Similarly, adult survival, a key process driving population trends in long-lived species (Sæther & Bakke, 2000), has also declined over the study period. However, given that we modelled apparent survival rates, we cannot confirm whether declines are due to mortality or permanent emigration.

Demographic consequences of anthropogenic stressors can be direct (e.g. mortality caused by extreme weather or bycatch by fishing vessels) or indirect, reducing an individual's condition and thereby their future survival or reproductive potential. In Cassin's auklets (*Ptychoramphus aleuticus*), the availability and quality of food resources affected breeding adults' body mass in spring and thereby their subsequent fledging success (Johns et al., 2018). POPs can directly cause mortality in seabirds (e.g. Bustnes et al., 2003; Erikstad et al., 2013; Goutte et al., 2015). Alternatively, POPs can reduce individuals' condition (Bustnes et al., 2002, 2003, 2015; Bustnes, Erikstad, et al., 2008; Nordstad et al., 2012) by increasing levels of stress hormones (Nordstad et al., 2012) and disease (Sagerup et al., 2000; Sonne et al., 2020), which in turn can reduce survival and reproductive rates (Bustnes et al., 2002, 2003, 2015; Bustnes, Fauchald, et al., 2008; Nordstad et al., 2012). Here, higher OC levels were negatively correlated both directly with survival rates and indirectly via individuals' body mass. This is supported by studies from other gull populations, where OCs have been shown to reduce individual condition (Bustnes et al., 2003; Helberg et al., 2005), as well as delay laying dates and reduce clutch sizes (Helberg et al., 2005). In other colonies, especially in the high Arctic, far higher levels of OCs have been recorded (Steffen et al., 2006). Despite relatively low levels of pollutants at our study site in the low Arctic, there was a strong negative association between levels of OCs and body mass (proxy for individual condition) and a direct, negative correlation with survival rates. It is important to note that our study was an observational analysis and so we cannot infer causal links between variables. Although we modelled body mass as a function of blood levels of contaminants, the causal link may be the reverse: individuals experiencing mass loss due to high stress from poor environmental conditions are known to release contaminants into the bloodstream as they burn fat reserves (discussed above). However, we do not have annual measurements of body mass, rather one measurement per individual meaning that, in this case, body mass may reflect individual quality rather than within- or between-season variation in condition. Either way, it is plausible that individuals of low quality or condition—caused by, or else evidenced by, high contamination—are more susceptible to adverse climatic conditions than individuals of higher quality or condition, leading to a cumulative effect of different pressures on survival.

Body mass measured during the breeding season was positively correlated with survival. Despite having only one mass measure per individual, this path analysis provides quantitative evidence of an indirect pathway from individual OC levels to survival. In long-lived species, fluctuations in reproductive rates and survival of younger age classes in response to environmental conditions are often greater than in adult survival (Gaillard & Yoccoz, 2003; McKnight et al., 2018). In line with this, several studies have found evidence of negative effects on OC levels on seabird breeding success, even at relatively low contamination levels (Bustnes et al., 2015; Bustnes, Erikstad, et al., 2008; Bustnes, Fauchald, et al., 2008; Helberg et al., 2005), while evidence of pollutant effects on survival is more limited. At high Arctic Bjørnøya, OC compounds in glaucous gulls have been recorded at far higher levels than those measured at Hornøya (concentrations measure at Bjørnøya in ng/g HCB = 11.3, oxychlordane = 16.7, DDE = 61.2 and PCBs = 288.9, Bustnes et al., 2003) and OC contamination had a stronger negative effect on survival rates than in our study (Bustnes et al., 2003; Erikstad et al., 2013). Thus, the small indirect effect of OC levels on survival through body mass points to additional pathways for example effects on fecundity that may explain the stronger direct effect, alternatively, this may be related to having only one sampling occasion per individual. Nevertheless, even a small change in survival has the potential to affect population viability given its importance in driving population trends, particularly when considered in the context of other stressors associated with human activities.

A large proportion of this gull population migrates to the North Sea during the autumn and remains there until spring. The North Sea represents an important area for many seabirds and other migratory birds (Dunnet et al., 1990). Adult gulls' survival was improved under warmer ocean temperatures during late winter in the North Sea. The Northeastern Atlantic has been strongly affected by climate change in recent decades, with associated shifts in the abundance and distribution of many species across the marine food web (Barton et al., 2016; Lenoir et al., 2011). Distributional shifts associated with climate change have been recorded at lower trophic levels, which have, in turn, affected the abundance of prey for seabirds (Frederiksen et al., 2013). The consequences appear greatest for more specialised, piscivorous species (Sydeman et al., 2021). In contrast, larger gull species are generalists in their prey selection (Harris, 1965; Kubetzki & Garthe, 2003) and can feed on terrestrial food sources (Gyimesi et al., 2016) as well as the eggs and young of other seabirds (Harris, 1965). Studies of GBB gulls indicate that their diet predominantly consists of fish and marine invertebrates, crabs in particular (Rome & Ellis, 2004; Steenweg et al., 2011). Swimming crabs (such as *Liocarcinus* spp.) were also shown to be a major dietary component for lesser black-backed gulls in the southeast North Sea (Schwemmer & Garthe, 2005). Warming ocean temperatures in the North Sea have been associated with increased abundances of swimming crabs and subsequent increases in the breeding success of lesser black-backed gulls (Luczak et al., 2012; Schwemmer et al., 2013). Although anecdotal, such changes in the coastal feeding ecology provide a feasible mechanism for the positive relationship between annual fluctuations in GBB gull survival and winter ocean temperatures in the North Sea.

The best-fitting—albeit not most parsimonious—model of apparent survival also included a positive effect of MSLP in spring, around the breeding colony in the southern Barents Sea, higher MSLP reflects a greater frequency of high-pressure systems in the area. High sea level pressure creates clear skies and blocks the passage of storms, while low pressure systems reflect stormier weather. Stormy conditions may increase energetic costs associated with foraging behaviours and can even prevent feeding for extend periods, potentially resulting in starvation (Guéry et al., 2019).

The North Sea is projected to warm by 2.4°C (range 1.2–4.6°C under IPCC AR6 SSP1-2.6 and SSP5-8.5 scenarios) by 2100 (Good et al., 2019; Kennedy et al., 2019), compared to the average SST for 1991–2020. Given that there was no significant temporal trend in late winter SST over our study period, the positive relationship between survival and SST may only hold true under observed conditions. Additionally, extreme events such as winter storms (Acker et al., 2021; Frederiksen et al., 2008) and marine heatwaves (Semmouri et al., 2023), which may increase in frequency with climate change (Cornes et al., 2023), could play an increasingly important role in driving gull population dynamics. Thus, changes in SST from 2002 to 2017 may have represented a temporary increase in prey resources (e.g. swimming crabs) for gulls but we cannot know the consequences of future increases in ocean temperatures. Thanks to international legislation, background levels of organic pollutants such as OCs are predicted to decline, hopefully limiting their negative impacts on top predators like seabirds.

As we found positive effects of ocean temperatures over the study period and as data of pollution and individuals' body masses were only available from a single year (per individual spanning 2 years), we cannot confirm the cause of the negative trends in survival rates and breeding numbers observed in this population, although the combined negative effect of OC levels via direct and indirect pathways was considerable. Nevertheless, this gull population and others along the coast of Norway are undergoing rapid declines and should be of extreme concern in terms of the long-term viability and risk of extinction. The North Sea is also under pressure from other human activities (e.g. commercial fishing, offshore wind farms, oil and gas production and shipping), all known to be important threats to seabirds, particularly during the non-breeding season. Furthermore, here, we focused on core non-breeding areas however, individuals from this population also utilise other areas that are affected by for example climate change, fishing competition to differing degrees, which can also impact their survival and population trend. While ocean warming is one potential threat, there are several others which may explain the observed declines in adult survival and breeding population sizes. This emphasises the need for monitoring data that captures changes in anthropogenic pressures and wildlife populations, at a sufficient temporal and spatial resolution and the wider adoption of path models to provide predictions of future population viability under ecosystem change.

AUTHOR CONTRIBUTIONS

Kjell Einar Erikstad, Hanno Sandvik, Jan Ove Bustnes conceived the ideas, and Kate Layton-Matthews designed the methodology with input from Hanno Sandvik, Michael D. S. Mesquita and Nigel G. Yoccoz. Kjell Einar Erikstad, Jan Ove Bustnes and Tone K. Reiertsen collected the data. Kate Layton-Matthews analysed the data with advice from Hanno Sandvik, Kjell Einar Erikstad, Tone K. Reiertsen and Kevin Hodges and maps were produced by Manuel Ballesteros. Kate Layton-Matthews led the writing of the manuscript. All authors contributed to discussions of the results and critically to the drafts and gave final approval for publication.

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CONFLICT OF INTEREST STATEMENT

The authors have no conflicts of interest to declare.

DATA AVAILABILITY STATEMENT

Data are available from the Dryad Digital Repository https://doi.org/10.5061/dryad.t4b8gtj9k (Layton-Matthews et al., 2024).

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REFERENCES

Acker, P., Daunt, F., Wanless, S., Burthe, S. J., Newell, M. A., Harris, M. P., Grist, H., Sturgeon, J., Swann, R. L., & Gunn, C. (2021). Strong survival selection on seasonal migration versus residence induced by extreme climatic events. *Journal of Animal Ecology*, *90*, 796–808.

Anderson, D. R., & Burnham, K. P. (2002). Avoiding pitfalls when using information-theoretic methods. *The Journal of Wildlife Management*, 912–918.

Bårdsen, B. J., & Bustnes, J. O. (2022). Multiple stressors: Negative effects of nest predation on the viability of a threatened gull in different environmental conditions. *Journal of Avian Biology*, *2022*, e02953.

Barrett, R. T., Erikstad, K. E., & Reiertsen, T. (2017). Ocean climate and egg investment in the black-legged kittiwake *Rissa tridactyla*. *Marine Ecology Progress Series*, *579*, 129–137.

Barton, A. D., Irwin, A. J., Finkel, Z. V., & Stock, C. A. (2016). Anthropogenic climate change drives shift and shuffle in North Atlantic phytoplankton communities. *Proceedings of the National Academy of Sciences of the United States of America*, *113*, 2964–2969.

Besbeas, P., Freeman, S. N., Morgan, B. J., & Catchpole, E. (2002). Integrating mark–recapture–recovery and census data to estimate animal abundance and demographic parameters. *Biometrics*, *58*, 540–547.

Borchers, H. W. (2019). *pracma: Practical numerical math functions*. R package version, 2, 519.

Brooks, S. P., & Gelman, A. (1998). General methods for monitoring convergence of iterative simulations. *Journal of Computational and Graphical Statistics*, *7*, 434–455.

Buccini, J. (2003). The development of a global treaty on persistent organic pollutants (POPs). *Persistent Organic Pollutants*, 13–30.

Burkow, I. C., & Kallenborn, R. (2000). Sources and transport of persistent pollutants to the Arctic. *Toxicology Letters*, *112*, 87–92.

Bustnes, J., Erikstad, K., Bakken, V., Mehlum, F., & Skaare, J. (2000). Feeding ecology and the concentration of organochlorines in glaucous gulls. *Ecotoxicology*, *9*, 179–186.

Bustnes, J., Fauchald, P., Tveraa, T., Helberg, M., & Skaare, J. (2008). The potential impact of environmental variation on the concentrations and ecological effects of pollutants in a marine avian top predator. *Environment International*, *34*, 193–201.

Bustnes, J., Folstad, I., Erikstad, K., Fjeld, M., Miland, Ø., & Skaare, J. (2002). Blood concentration of organochlorine pollutants and wing feather asymmetry in glaucous gulls. *Functional Ecology*, *16*, 617–622.

Bustnes, J. O. (2006). Pinpointing potential causative agents in mixtures of persistent organic pollutants in observational field studies: A review of glaucous gull studies. *Journal of Toxicology and Environmental Health, Part A*, *69*, 97–108.

Bustnes, J. O., Bourgeon, S., Leat, E. H., Magnusdóttir, E., Strøm, H., Hanssen, S. A., Petersen, A., Olafsdóttir, K., Borgå, K., & Gabrielsen, G. W. (2015). Multiple stressors in a top predator seabird: Potential ecological consequences of environmental contaminants, population health and breeding conditions. *PLoS One*, *10*, e0131769.

Bustnes, J. O., Erikstad, K. E., Lorentsen, S.-H., & Herzke, D. (2008). Perfluorinated and chlorinated pollutants as predictors of demographic parameters in an endangered seabird. *Environmental Pollution*, *156*, 417–424.

Bustnes, J. O., Erikstad, K. E., Skaare, J. U., Bakken, V., & Mehlum, F. (2003). Ecological effects of organochlorine pollutants in the Arctic: A study of the glaucous gull. *Ecological Applications*, *13*, 504–515.

Bustnes, J. O., Moe, B., Hanssen, S. A., Herzke, D., Fenstad, A. A., Nordstad, T., Borgå, K., & Gabrielsen, G. W. (2012). Temporal dynamics of circulating persistent organic pollutants in a fasting seabird under different environmental conditions. *Environmental Science & Technology*, *46*, 10287–10294.

Bustnes, J. O., Skaare, J. U., Berg, V., & Tveraa, T. (2005). Interseasonal variation in blood concentrations of organochlorines in great black-backed gulls (*Larus marinus*). *Environmental Toxicology and Chemistry: An International Journal*, *24*, 1801–1806.

Bustnes, J. O., Skaare, J. U., Erikstad, K. E., Bakken, V., & Mehlum, F. (2001). Whole blood concentrations of organochlorines as a dose metric for studies of the glaucous gull (*Larus hyperboreus*). *Environmental Toxicology and Chemistry: An International Journal*, *20*, 1046–1052.

Calenge, C. (2006). The package "adehabitat" for the R software: a tool for the analysis of space and habitat use by animals. *Ecological Modelling*, *197*(3–4), 516–519.

Choquet, R., Lebreton, J. D., Gimenez, O., Reboulet, A. M., & Pradel, R. (2009). U-CARE: Utilities for performing goodness of fit tests and manipulating CApture–REcapture data. *Ecography*, *32*, 1071–1074.

Cornes, R., Tinker, J., Hermanson, L., Oltmanns, M., Hunter, W., Lloyd-Hartley, H., Kent, E., Rabe, B., & Renshaw, R. (2023). Climate change impacts on temperature around the UK and Ireland. *MCCIP Science Review*, *2023*, 18.

Croxall, J. P., Butchart, S. H., Lascelles, B., Stattersfield, A. J., Sullivan, B., Symes, A., & Taylor, P. (2012). Seabird conservation status, threats and priority actions: A global assessment. *Bird Conservation International*, *22*, 1–34.

Cubaynes, S., Doutrelant, C., Grégoire, A., Perret, P., Faivre, B., & Gimenez, O. (2012). Testing hypotheses in evolutionary ecology with imperfect detection: Capture–recapture structural equation modeling. *Ecology*, *93*, 248–255.

Cury, P. M., Boyd, I. L., Bonhommeau, S., Anker-Nilssen, T., Crawford, R. J., Furness, R. W., Mills, J. A., Murphy, E. J., Österblom, H., & Paleczny, M. (2011). Global seabird response to forage fish depletion—One-third for the birds. *Science*, *334*, 1703–1706.

Darling, E. S., & Côté, I. M. (2008). Quantifying the evidence for ecological synergies. *Ecology Letters*, *11*, 1278–1286.

De Valpine, P., & Hastings, A. (2002). Fitting population models incorporating process noise and observation error. *Ecological Monographs*, *72*, 57–76.

Dee, D. P., Uppala, S. M., Simmons, A. J., Berrisford, P., Poli, P., Kobayashi, S., Andrae, U., Balmaseda, M. A., Balsamo, G., Bauer, P., Bechtold, P., Beljaars, A. C. M., van de Berg, L., Bidlot, J., Bormann, N., Delsol, C., Dragani, R., Fuentes, M., Geer, A. J., … Vitart, F. (2011). The ERA-Interim reanalysis: Configuration and performance of the data assimilation system. *Quarterly Journal of the Royal Meteorological Society*, *137*(656), 553–597.

Dias, M. P., Martin, R., Pearmain, E. J., Burfield, I. J., Small, C., Phillips, R. A., Yates, O., Lascelles, B., Borboroglu, P. G., & Croxall, J. P. (2019). Threats to seabirds: A global assessment. *Biological Conservation*, *237*, 525–537.

Dormann, C. F., Elith, J., Bacher, S., Buchmann, C., Carl, G., Carré, G., Marquéz, J. R. G., Gruber, B., Lafourcade, B., & Leitão, P. J. (2013). Collinearity: A review of methods to deal with it and a simulation study evaluating their performance. *Ecography*, *36*, 27–46.

Dunnet, G., Furness, R., Tasker, M., & Becker, P. (1990). Seabird ecology in the North Sea. *Netherlands Journal of Sea Research*, *26*, 387–425.

Erikstad, K. E., Sandvik, H., Reiertsen, T. K., Bustnes, J. O., & Strøm, H. (2013). Persistent organic pollution in a high-Arctic top predator: Sex-dependent thresholds in adult survival. *Proceedings of the Royal Society B: Biological Sciences*, *280*, 20131483.

Fan, Y., Chen, J., Shirkey, G., John, R., Wu, S. R., Park, H., & Shao, C. (2016). Applications of structural equation modeling (SEM) in ecological studies: An updated review. *Ecological Processes*, *5*, 1–12.

Fox, J. W. (2010). *Geolocator manual v8* (March 2010). British Antarctic Survey.

Frederiksen, M., Anker-Nilssen, T., Beaugrand, G., & Wanless, S. (2013). Climate, copepods and seabirds in the boreal Northeast Atlantic–current state and future outlook. *Global Change Biology*, *19*, 364–372.

Frederiksen, M., Daunt, F., Harris, M., & Wanless, S. (2008). The demographic impact of extreme events: Stochastic weather drives survival and population dynamics in a long-lived seabird. *Journal of Animal Ecology*, *77*, 1020–1029.

Frederiksen, M., Edwards, M., Richardson, A. J., Halliday, N. C., & Wanless, S. (2006). From plankton to top predators: Bottom-up control of a marine food web across four trophic levels. *Journal of Animal Ecology*, *75*, 1259–1268.

Furness, R. W., & Barrett, R. T. (1985). The food requirements and ecological relationships of a seabird community in North Norway. *Ornis Scandinavica*, *16*, 305–313.

Gaillard, J.-M., Festa-Bianchet, M., & Yoccoz, N. G. (1998). Population dynamics of large herbivores: Variable recruitment with constant adult survival. *Trends in Ecology & Evolution*, *13*, 58–63.

Gaillard, J.-M., & Yoccoz, N. G. (2003). Temporal variation in survival of mammals: A case of environmental canalization? *Ecology*, *84*, 3294–3306.

Gelman, A., Jakulin, A., Pittau, M. G., & Su, Y.-S. (2008). A weakly informative default prior distribution for logistic and other regression models. *The Annals of Applied Statistics*, *2*(4), 1360–1383.

Gibson, D., Riecke, T. V., Catlin, D. H., Hunt, K. L., Weithman, C. E., Koons, D. N., Karpanty, S. M., & Fraser, J. D. (2023). Climate change and commercial fishing practices codetermine survival of a long-lived seabird. *Global Change Biology*, *29*, 324–340.

Gimenez, O., Anker-Nilssen, T., & Grosbois, V. (2012). Exploring causal pathways in demographic parameter variation: Path analysis of mark–recapture data. *Methods in Ecology and Evolution*, *3*, 427–432.

Gimenez, O., Viallefont, A., Charmantier, A., Pradel, R., Cam, E., Brown, C. R., Anderson, M. D., Brown, M. B., Covas, R., & Gaillard, J.-M. (2008). The risk of flawed inference in evolutionary studies when detectability is less than one. *The American Naturalist*, *172*, 441–448.

Good, S., Embury, O., Bulgin, C., & Mittaz, J. (2019). *Level 4 analysis climate data record*, *version 2.1*. Centre for Environmental Data Analysis.

Goutte, A., Barbraud, C., Herzke, D., Bustamante, P., Angelier, F., Tartu, S., Clément-Chastel, C., Moe, B., Bech, C., & Gabrielsen, G. W. (2015). Survival rate and breeding outputs in a high Arctic seabird exposed to legacy persistent organic pollutants and mercury. *Environmental Pollution*, *200*, 1–9.

Grémillet, D., & Boulinier, T. (2009). Spatial ecology and conservation of seabirds facing global climate change: A review. *Marine Ecology Progress Series*, *391*, 121–137.

Guéry, L., Descamps, S., Hodges, K. I., Pradel, R., Moe, B., Hanssen, S. A., Erikstad, K. E., Gabrielsen, G. W., Gilchrist, H., & Jenouvrier, S. (2019). Winter extratropical cyclone influence on seabird survival: Variation between and within common eider *Somateria mollissima* populations. *Marine Ecology Progress Series*, *627*, 155–170.

Gyimesi, A., Boudewijn, T. J., Buijs, R.-J., Shamoun-Baranes, J. Z., de Jong, J. W., Fijn, R. C., van Horssen, P. W., & Poot, M. J. (2016). Lesser black-backed gulls *Larus fuscus* thriving on a non-marine diet. *Bird Study*, *63*, 241–249.

Halpern, B. S., Walbridge, S., Selkoe, K. A., Kappel, C. V., Micheli, F., d'Agrosa, C., Bruno, J. F., Casey, K. S., Ebert, C., & Fox, H. E. (2008). A global map of human impact on marine ecosystems. *Science*, *319*, 948–952.

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

Heithaus, M. R., Frid, A., Wirsing, A. J., & Worm, B. (2008). Predicting ecological consequences of marine top predator declines. *Trends in Ecology & Evolution*, *23*, 202–210.

Helberg, M., Bustnes, J. O., Erikstad, K. E., Kristiansen, K. O., & Skaare, J. U. (2005). Relationships between reproductive performance and organochlorine contaminants in great black-backed gulls (*Larus marinus*). *Environmental Pollution*, *134*, 475–483.

Henriksen, E. O., Gabrielsen, G. W., & Skaare, J. U. (1998). Validation of the use of blood samples to assess tissue concentrations of organochlorines in glaucous gulls, *Larus hyperboreus*. *Chemosphere*, *37*, 2627–2643.

Heukamp, F. O., Aue, L., Wang, Q., Ionita, M., Kanzow, T., Wekerle, C., & Rinke, A. (2023). Cyclones modulate the control of the North Atlantic Oscillation on transports into the Barents Sea. *Communications Earth & Environment*, *4*, 324.

Ingvaldsen, R. B., Asplin, L., & Loeng, H. (2004). The seasonal cycle in the Atlantic transport to the Barents Sea during the years 1997–2001. *Continental Shelf Research*, *24*, 1015–1032.

Jackson, M. C., Pawar, S., & Woodward, G. (2021). The temporal dynamics of multiple stressor effects: From individuals to ecosystems. *Trends in Ecology & Evolution*, *36*, 402–410.

Johns, M. E., Warzybok, P., Bradley, R. W., Jahncke, J., Lindberg, M., & Breed, G. A. (2018). Increased reproductive investment associated with greater survival and longevity in Cassin's auklets. *Proceedings of the Royal Society B*, *285*, 20181464.

Jones, K. C., & De Voogt, P. (1999). Persistent organic pollutants (POPs): State of the science. *Environmental Pollution*, *100*, 209–221.

Kellner, K. (2015). *jagsUI: A wrapper around rjags to streamline JAGS analyses*. R package version, 1.

Kennedy, J. J., Rayner, N., Atkinson, C., & Killick, R. (2019). An ensemble data set of sea surface temperature change from 1850: The Met Office Hadley Centre HadSST. 4.0. 0.0 data set. *Journal of Geophysical Research: Atmospheres*, *124*, 7719–7763.

Kubetzki, U., & Garthe, S. (2003). Distribution, diet and habitat selection by four sympatrically breeding gull species in the south-eastern North Sea. *Marine Biology*, *143*, 199–207.

Laake, J. L. (2013). *RMark: An R interface for analysis of capture-recapture data with MARK*. AFSC Processed Rep. 2013-01.

Layton-Matthews, K., Erikstad, K. E., Sandvik, H., Ballesteros, M., Hodges, K., Mesquita, M. D. S., Reiertsen, T. K., Yoccoz, N. G., & Bustnes, J. O. (2024). Data from: Path analysis reveals combined winter climate and pollution effects on the survival of a marine top predator. *Digital Dryad Repository*. https://doi.org/10.5061/dryad.t4b8gtj9k

Layton-Matthews, K., Hansen, B. B., Grøtan, V., Fuglei, E., & Loonen, M. J. J. E. (2020). Contrasting consequences of climate change for migratory geese: Predation, density dependence and carryover effects offset benefits of high-arctic warming. *Global Change Biology*, *26*, 642–657.

Lebreton, J.-D., Burnham, K. P., Clobert, J., & Anderson, D. R. (1992). Modeling survival and testing biological hypotheses using marked animals: A unified approach with case studies. *Ecological Monographs*, *62*, 67–118.

Lenoir, S., Beaugrand, G., & Lecuyer, E. (2011). Modelled spatial distribution of marine fish and projected modifications in the North Atlantic Ocean. *Global Change Biology*, *17*, 115–129.

Lisovski, S., Bauer, S., Briedis, M., Davidson, S. C., Dhanjal-Adams, K. L., Hallworth, M. T., Karagicheva, J., Meier, C. M., Merkel, B., & Ouwehand, J. (2020). Light-level geolocator analyses: A user's guide. *Journal of Animal Ecology*, *89*, 221–236.

Loeng, H. (1991). Features of the physical oceanographic conditions of the Barents Sea. *Polar Research*, *10*, 5–18.

Luczak, C., Beaugrand, G., Lindley, J., Dewarumez, J.-M., Dubois, P., & Kirby, R. (2012). North Sea ecosystem change from swimming crabs to seagulls. *Biology Letters*, *8*, 821–824.

Maunder, M. N., & Punt, A. E. (2013). A review of integrated analysis in fisheries stock assessment. *Fisheries Research*, *142*, 61–74.

Maxwell, S. M., Hazen, E. L., Bograd, S. J., Halpern, B. S., Breed, G. A., Nickel, B., Teutschel, N. M., Crowder, L. B., Benson, S., & Dutton, P. H. (2013). Cumulative human impacts on marine predators. *Nature Communications*, *4*, 2688.

McKnight, A., Blomberg, E. J., Golet, G. H., Irons, D. B., Loftin, C. S., & McKinney, S. T. (2018). Experimental evidence of long-term reproductive costs in a colonial nesting seabird. *Journal of Avian Biology*, *49*, e01779.

Mesquita, M. D. S., Erikstad, K. E., Sandvik, H., Barrett, R. T., Reiertsen, T. K., Anker-Nilssen, T., Hodges, K. I., & Bader, J. (2015). There is more to climate than the North Atlantic Oscillation: a new perspective from climate dynamics to explain the variability in population growth rates of a long-lived seabird. *Frontiers in Ecology and Evolution*, *3*, 43.

Murphy, S., Law, R. J., Deaville, R., Barnett, J., Perkins, M. W., Brownlow, A., Penrose, R., Davison, N. J., Barber, J. L., & Jepson, P. D. (2018). Organochlorine contaminants and reproductive implication in cetaceans: a case study of the common dolphin. *Marine Mammal Ecotoxicology*, 3–38.

Nordstad, T., Moe, B., Bustnes, J. O., Bech, C., Chastel, O., Goutte, A., Sagerup, K., Trouvé, C., Herzke, D., & Gabrielsen, G. W. (2012). Relationships between POPs and baseline corticosterone levels in black-legged kittiwakes (*Rissa tridactyla*) across their breeding cycle. *Environmental Pollution*, *164*, 219–226.

OSPAR. (2009). *Trend analysis of maritime human activities and their collective impact on the OSPAR maritime area*. OSPAR Commission.

Perry, A. L., Low, P. J., Ellis, J. R., & Reynolds, J. D. (2005). Climate change and distribution shifts in marine fishes. *Science*, *308*, 1912–1915.

Plummer, M. (2003). JAGS: A program for analysis of Bayesian graphical models using Gibbs sampling. *Proceedings of the 3rd international workshop on distributed statistical computing* (pp. 1–10). Vienna, Austria.

Pollock, K. H. (2002). The use of auxiliary variables in capture-recapture modelling: An overview. *Journal of Applied Statistics*, *29*, 85–102.

Pugesek, B. H., Tomer, A., & Von Eye, A. (2003). *Structural equation modeling: Applications in ecological and evolutionary biology*. Cambridge University Press.

R Core Team. (2023). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing.

Rantanen, M., Karpechko, A. Y., Lipponen, A., Nordling, K., Hyvärinen, O., Ruosteenoja, K., Vihma, T., & Laaksonen, A. (2022). The Arctic has warmed nearly four times faster than the globe since 1979. *Communications Earth & Environment*, *3*, 168.

Reiertsen, T. K., Erikstad, K. E., Anker-Nilssen, T., Barrett, R. T., Boulinier, T., Frederiksen, M., González-Solís, J., Gremillet, D., Johns, D., & Moe, B. (2014). Prey density in non-breeding areas affects adult survival of black-legged kittiwakes *Rissa tridactyla*. *Marine Ecology Progress Series*, *509*, 289–302.

Rome, M. S., & Ellis, J. C. (2004). Foraging ecology and interactions between herring gulls and great black-backed gulls in New England. *Waterbirds*, *27*, 200–210.

Sæther, B.-E., & Bakke, Ø. (2000). Avian life history variation and contribution of demographic traits to the population growth rate. *Ecology*, *81*, 642–653.

Sagerup, K., Henriksen, E. O., Skorping, A., Skaare, J. U., & Gabrielsen, G. W. (2000). Intensity of parasitic nematodes increases with organochlorine levels in the glaucous gull. *Journal of Applied Ecology*, *37*, 532–539.

Schartup, A. T., Thackray, C. P., Qureshi, A., Dassuncao, C., Gillespie, K., Hanke, A., & Sunderland, E. M. (2019). Climate change and overfishing increase neurotoxicant in marine predators. *Nature*, *572*, 648–650.

Schwemmer, H., Schwemmer, P., Ehrich, S., & Garthe, S. (2013). Lesser black-backed gulls (*Larus fuscus*) consuming swimming crabs: An important link in the food web of the southern North Sea. *Estuarine, Coastal and Shelf Science*, *119*, 71–78.

Schwemmer, P., & Garthe, S. (2005). At-sea distribution and behaviour of a surface-feeding seabird, the lesser black-backed gull *Larus fuscus*, and its association with different prey. *Marine Ecology Progress Series*, *285*, 245–258.

Selonen, V., Helle, S., Laaksonen, T., Ahola, M. P., Lehikoinen, E., & Eeva, T. (2021). Identifying the paths of climate effects on population dynamics: Dynamic and multilevel structural equation model around the annual cycle. *Oecologia*, *195*, 525–538.

Semmouri, I., De Schamphelaere, K. A., Mortelmans, J., Mees, J., Asselman, J., & Janssen, C. R. (2023). Decadal decline of dominant copepod species in the North Sea is associated with ocean warming: Importance of marine heatwaves. *Marine Pollution Bulletin*, *193*, 115159.

Shipley, B. (1997). Exploratory path analysis with applications in ecology and evolution. *The American Naturalist*, *149*, 1113–1138.

Shipley, B. (2016). *Cause and correlation in biology: A user's guide to path analysis, structural equations and causal inference with R*. Cambridge University Press.

Simmons, B. I., Blyth, P. S., Blanchard, J. L., Clegg, T., Delmas, E., Garnier, A., Griffiths, C. A., Jacob, U., Pennekamp, F., & Petchey, O. L. (2021). Refocusing multiple stressor research around the targets and scales of ecological impacts. *Nature Ecology & Evolution*, *5*, 1478–1489.

Sonne, C., Siebert, U., Gonnsen, K., Desforges, J.-P., Eulaers, I., Persson, S., Roos, A., Bäcklin, B.-M., Kauhala, K., & Olsen, M. T. (2020). Health effects from contaminant exposure in Baltic Sea birds and marine mammals: A review. *Environment International*, *139*, 105725.

Steenweg, R. J., Ronconi, R. A., & Leonard, M. L. (2011). Seasonal and age-dependent dietary partitioning between the great black-backed and herring gulls. *The Condor*, *113*, 795–805.

Steffen, C., Borgå, K., Skaare, J. U., & Bustnes, J. O. (2006). The occurrence of organochlorines in marine avian top predators along a latitudinal gradient. *Environmental Science & Technology*, *40*, 5139–5146.

Stenseth, N. C., Ottersen, G., Hurrell, J. W., Mysterud, A., Lima, M., Chan, K. S., Yoccoz, N. G., & Ådlandsvik, B. (2003). Studying climate effects on ecology through the use of climate indices: The North Atlantic Oscillation, El Nino Southern Oscillation and beyond. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, *270*, 2087–2096.

Sydeman, W. J., Schoeman, D. S., Thompson, S. A., Hoover, B. A., García-Reyes, M., Daunt, F., Agnew, P., Anker-Nilssen, T., Barbraud, C., & Barrett, R. (2021). Hemispheric asymmetry in ocean change and the productivity of ecosystem sentinels. *Science*, *372*, 980–983.

Sydeman, W. J., Thompson, S. A., & Kitaysky, A. (2012). Seabirds and climate change: Roadmap for the future. *Marine Ecology Progress Series*, *454*, 107–117.

Texeira, M., Baldi, G., & Paruelo, J. (2012). An exploration of direct and indirect drivers of herbivore reproductive performance in arid and semi arid rangelands by means of structural equation models. *Journal of Arid Environments*, *81*, 26–34.

Verboven, N., Verreault, J., Letcher, R. J., Gabrielsen, G. W., & Evans, N. P. (2009). Nest temperature and parental behaviour of Arctic-breeding glaucous gulls exposed to persistent organic pollutants. *Animal Behaviour*, *77*, 411–418.

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Supporting Information S1. Organochlorine (OC) variables and results from principal component analysis.

Supporting Information S2. Extraction of climate covariates from core foraging areas.

Supporting Information S3. Baseline survival model selection.

Supporting Information S4. Priors for parameters modelled in the path model.

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