

Multiple stressors: modeling the effect of pollution, climate, and predation on viability of a sub-arctic marine bird

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Abstract. Negative effects of long-transported pollutants, such as many persistent organic pollutants (POPs), on seabirds and other top predators have been documented for decades. Yet, the concentrations, and hence, the negative impacts of many POPs have recently declined in the Northern Hemisphere. However, organisms are exposed to multiple stressors and the impacts of pollution act in concert with both natural and other anthropogenic stressors. In theory, this means that even sub-lethal POP concentrations may cause adverse effects if they co-occur with increased levels of other stressors. We tested the multiple stress hypothesis on common eiders, a marine duck with a northern geographical distribution, by assessing the relative importance of pollution, climate (winter sea surface temperature; SSTw), and egg predation on population dynamics and viability (i.e., extinction risk) using Leslie-matrix population models. The model was parametrized by estimating reproduction and apparent adult survival using long-term data from a common eider population in sub-arctic Europe. Average annual adult survival was 0.80 (coefficient of variation [CV] = 22.00%) and showed a negative, both direct and delayed, relationship with SSTw. Average clutch size was 4.41 eggs (CV = 5.12%) and varied in time showing periods of both positive and negative trends, but showed no relationship with SSTw. We based immature survival on estimates from literature: 0.52 and 0.68 for juveniles and yearlings, respectively. Our model supported the multiple stress hypothesis as changes in a single stressor did not induce extinctions, unless the magnitude of our manipulations was extreme except for egg predation. The effect of pollution was, however, increasingly negative when it co-occurred with a warming climate and egg predation—and population viability was lowest when all the stressors occurred simultaneously.

Key words: Arctic; climatic vulnerability; computer experimentation; Cormack–Jolly–Seber models; fitness; Grindøya Nature Reserve, Tromsø, Norway; literature review; organochlorine contaminants (OCs); population viability analysis; *Somateria mollissima*; stress ecology.

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INTRODUCTION

A crucial task in ecotoxicology is to understand, and being able to predict the effect of pollutants on all aspects of biodiversity (varying from genes to communities and ecosystems). This is challenging as other stressors such as climate change act in concert with pollution (recently reviewed by Kimberly and Salice 2015, Mbaka et al. 2015). Yet, another challenge is that

such multiple stressors act on different spatiotemporal scales: Climate-induced stress generally acts on a large geographical scale in contrast to pollution, which is a local form of stress (Mbaka et al. 2015). Living organisms are thus exposed to multiple stressors that may either have additive or synergetic effects (Kimberly and Salice 2015) on life-history traits, such as reproduction and survival. Several authors advocate the need to use multiple stressor approaches in

ecotoxicology. Kimberly and Salice (2015:690), for instance, state that “the interaction with GCC (global climate change) and pollution may demand an increasing urgent understanding.” The concentrations of several persistent organic pollutants (POPs) have, however, recently declined in the Northern Hemisphere (Hung et al. 2016). Even though pollution levels in nature may be too low to be hazardous (as judged from laboratory studies), such low pollution levels may still have adverse effects when they co-occur with other stressors such as parasites (Bustnes et al. 2006) and food limitation (Bustnes et al. 2015). Ecological effects of pollution are thus likely to show spatiotemporal variation (Bustnes et al. 2006, 2015)—a variation that is, at least partly, explained by both natural and anthropogenic stressors. Multi-stress is, however, not only relevant in ecotoxicological studies. Numerous examples of this are found in ecology where food abundance is, for example, known to reduce negative density dependence (Ballesteros et al. 2013). Nonetheless, multi-stress is particularly relevant for ecotoxicology as many effect studies have been performed under controlled laboratory conditions where multiple stressors are not present.

Along these lines of reasoning, Van Straalen (2003) argues that ecotoxicology has come to a transition phase where it should take a new role in assimilating with the part of ecology commonly known as “stress ecology” where demographic modeling is highlighted as one area of research where ecotoxicology and ecology could meet. Demography, a central pillar of life-history theory, is a tool for studying the population dynamics as demography was developed to project population growth (Stearns 1992). Demographical science commonly involves the study of size, structure, and distribution of populations (demographics are any quantifiable characteristics of a pre-defined population). While human demography involves complex societal aspects such as education and ethnicity, demographical studies in ecology are more simplistic. Population ecology has largely been focused around population regulation and limitation (sensu, e.g., Sinclair and Pech 1996). In this context, population size one year ahead (N_{t+1}) may be viewed as a function of the so-called *BIDE* parameters (Puliam 1988): birth, immigration, death, and

emigration (often expressed as rates), along with current population size (N_t). Consequently, understanding how these *BIDE* parameters vary in space and time is thus the key to understanding population growth and thus population dynamics and viability. A potential large number of intrinsic and extrinsic factors affect the *BIDE* parameters (Forchhammer et al. 1998) and may consequently limit or regulate populations. A complicating issue is that interactions between intrinsic and extrinsic factors may occur; negative effects of climate become increasingly more negative as population density increases and vice versa (Bårdsen et al. 2010, 2014). Yet another complicating factor is that these intrinsic and extrinsic factors tend to be state dependent. Recruitment and mortality may, for instance, vary across individuals belonging to different age-, sex-, or size-classes (Bårdsen et al. 2011). Hence, mortality, or survival, reproduction, and other important demographic information are commonly expressed as rates (or vital rates, which is commonly referred to as average rates for individuals belonging to groups of similar states; Caswell 2001).

The common eider (*Somateria mollissima* L. 1758), the focal species of this study, is the largest duck in the Northern Hemisphere, where it is the only Anatidae that occupy marine environments throughout the whole year (Waltho and Coulson 2015). It is long-lived with a relatively high yearly reproductive potential (3–6 eggs) and has a European breeding distribution that extends from the Netherlands to as far north as Svalbard and Franz Josef Land in the high Arctic (Baillie and Milne 1982, Hanssen et al. 2016). Common eiders are benthic feeders relying on mussels and other invertebrates, typically at depths of 0–10 m (Guillemette et al. 1993, Bustnes and Lønne 1997), and usually wintering in coastal regions. Lagged effects of climate on the viability of eiders may thus reflect an indirect effect of climate on the eider food availability or food quality (Menge et al. 2008, Descamps et al. 2010, Guéry et al. 2017).

Life-history theory predicts that demographic traits with the lowest elasticity/sensitivity, that is, being of least importance for population growth, should be mostly affected by natural stressors such as environmental hazards (Gaillard et al. 1998, 2000). More recently, however, studies also

suggest that the same traits are the most sensitive to chemical toxicants. In general, this means that fecundity is more subject to stress than juvenile or adult survival (Forbes et al. 2010). This is further supported as many birds are long-lived organisms and as pollution has been shown to, for example, result in eggshell thinning, reduced embryonic development (that may also result in eggshell thinning), and impaired nest defense (occurring at levels 10–100 times lower than lethal concentrations; for recent reviews, see Hellou et al. 2013, Orłowski and Halupka 2015). For common eiders in Norway, negative effects of pollution on fecundity, but not survival, were documented as high levels of polycyclic aromatic hydrocarbons correlate negatively with breeding success (Bustnes 2013). Similarly, results from Canada suggest that sub-toxic levels of blood lead (Pb) concentrations had negative effects on reproductive success for North Atlantic eiders (*Somateria m. borealis* Brehm 1824) as later arriving birds and birds in poor condition had higher lead concentrations (Provencher et al. 2016). In the Wadden Sea, the eider population was reduced by 77% between 1960 and 1968 because of organochlorine pollutants (OCs; Swennen 1972). Female eiders were contaminated through their mussel prey during the non-breeding season, but died during incubation when they depleted their body lipids and OCs were released into their blood (Swennen 1972). After 1965, however, the concentration of toxic substances in the prey decreased, and after 1968, mortality due to OCs was no longer observed (Swennen 1972). For Pacific eiders (*S. m. v-nigrum* Bonaparte and Gray 1855), the probability of a nest containing ≥ 1 non-viable egg increased as a function of blood selenium concentrations in the females, whereas no other signs of compromised health in adults or ducklings were documented, nor were there any effect of lead (Wilson et al. 2007, see also Bustnes 2013 who showed an increased number of dead ducklings per female in a highly polluted area). Although few studies indicate that pollution limits the growth in eider populations, the same studies also indicate that (1) pollution mainly affect reproduction and not survival and (2) even low concentrations may, under certain circumstances, impose adverse effects.

Both avian and mammalian predators, such as polar bears (*Ursus maritimus* Phipps 1774) and

glaucous gulls (*Larus hyperboreus* Gunnerus 1767), may take a significant toll on eggs and chicks of seabirds (>90% of the nests and 90% of the eggs might be predated; see, e.g., Ahlén and Andersson 1970, Mehum 1991, Prop et al. 2015; Appendix S1). The eider is an open nesting species, and after egg-laying is completed, as much as 53% of the nests may lose all eggs because of egg predation by crows and gulls (Erikstad and Tveraa 1995). During egg-laying, daily nest predation rates may be up to 49%, although daily predation rates are reduced as female nest attendance increases toward the end of the egg-laying period (Hanssen et al. 2002). For common eiders, such losses may be reduced by human presence as trappers and down collectors may kill or chase away predators to protect the eiders (Hageland and Norderhaug 1975, Hanssen et al. 2013).

Both the 2001 IUCN Red List and the Norwegian Red List (IUCN Red List, www.iucnredlist.org; and Norw. Red List, www.artsdatabanken.no) consider the common eider near threatened (NT). Recent analyses of monitoring data found evidence of a dramatic decline of many seabird populations in the North Atlantic and in the Arctic Sea (Fauchald et al. 2015). According to Waltho and Coulson (2015:93), however, the global estimate of the number of common eiders has increased from 3,037,500 in 2002 to 3,643,500 in 2012 (i.e., a 20% increase). In spite of this, the population size in Norway and Russia was constant at 425,000 from 1997 to 2006, but then dropped to 410,000 in 2012 (Waltho and Coulson 2015:93). Even though this is not a dramatic decrease, it is important to keep in mind that according to Barrett et al. (2006), Norway contained 10–13% of the world population at the beginning of the third millennium (or 14% in 2002 according to Waltho and Coulson 2015:93). Fauchald et al. (2015:22) report that from 2003/2004 to present, the number of common eiders dropped from ~90,000 to 40,000 and ~75,000 to 40,000, that is, declines of 55% and 47%, in the North Sea/Skagerak and Norwegian Sea, respectively. The same study reports that the number of common eiders in the Barents Sea has been more stable during the same period.

The overall objective of the present study was to test the multiple stressor hypothesis on sub-arctic common eiders. We considered four different stressors: (1) the average and (2) variability of

winter climatic conditions, (3) egg predation, and (4) pollution. All these stressors are limiting factors commonly assumed relevant for Northern seabirds (Erikstad et al. 2013, Hanssen et al. 2013, Goutte et al. 2015, Prop et al. 2015). Specifically, we aim to (1) estimate long-term trends in adult apparent survival (Φ_a) and recruitment (using empirical data from our focal population), the two most important demographic processes affecting population dynamics, and (2) perform age-structured population viability analyses (PVA). Our PVA approach uses matrix modeling, which is a tool for assessing population growth, trajectories, and viability in structured populations (Caswell 2001, Morris and Doak 2002), and combines our own empirical estimates of Φ_a and recruitment with literature-based estimates of juvenile and yearling survival. Moreover, our model represents a computer experiment where we manipulate the level of each stressor separately and by manipulating several factors simultaneously to assess how multiple stressors interact in shaping population growth and viability.

METHODS

Study area

The study was conducted at Store Grindøya, which is a part of Grindøysundet Nature Reserve in Northern Norway (69°49' N, 18°15' E), an island of 0.65 km² that inhabits a population of 200–500 common eiders. Details about the study area and the focal population of interest are published elsewhere (Hanssen 2006, Hanssen and Erikstad 2013).

Study protocol

Our study was initiated in 1985 when 226 breeding adult female birds with unknown age were marked (i.e., ≥ 3 yr of age). Since then, fieldwork has been conducted annually with ringing and controls of already marked individuals. Based on this protocol, the raw data contained the following variables (following the same procedure as in Hanssen 2006):

1. ID—A tarsus ring, enabling unique recognition of individuals through a unique code, made it possible to recognize individuals (i.e., re-sighting) in order to estimate survival and recapture probabilities (Appendix S3).

2. Clutch size—The number of observed eggs laid per nest and the number of nests (N_{nests} ; data have only been collected from 1999 to present).

Empirical analyses

The effect of climate: winter sea surface temperature.—Our climate data consisted of winter sea surface temperatures (SSTw; downloaded from the International Council for the Exploration of the Sea [<http://ocean.ices.dk/data/surface/surface.htm>]), using annual March averages, from a pre-defined area of open-sea off the coast from our study area (Appendix S2). We conducted analyses of SSTw in several steps. First, we performed exploratory data analyses of temporal trends in SSTw using generalized additive models (GAMs: Wood 2006) in the mgcv library (Wood 2012). Second, we linked Φ_a and clutch size, *that is*, the averages for the Grindøya population, to winter SSTw. For clutch size, we used standard linear regression models (Appendix S3). For Φ_a , we added SSTw as a time-varying covariate in the survival analyses (Appendix S3). We expected winter climatic conditions to possess lagged effects as two previous studies on this population have shown a delayed effect of winter North Atlantic Oscillation, commonly referred to as NAO, on body mass (Descamps et al. 2010) and survival (Guéry et al. 2017). Such lagged effects might reflect indirect effects of climatic conditions on eider food availability or food quality (Menge et al. 2008, Descamps et al. 2010), so we created an a priori set of candidate models that consisted of SST with up to three years lag (Appendices S2, S3). All statistical tests were two-tailed, and statistical significance was evaluated at an α -level of 0.05.

Demographic data from Grindøya.—We fitted Cormack–Jolly–Seber models to estimate apparent survival (Φ) and recapture, or re-sighting probability (P) of the adults in the software MARK (details provided in Appendix S3). We were only capable of estimating adult apparent survival (Φ_a) as only breeding females were equipped with tags: Individuals were thus ≥ 3 yr of age when they were tagged. We extracted juvenile and yearling survival from the literature, as we were unable to tag the hatchlings as common eider chick leave their nest within 1–2 d (Appendix S1). We used clutch size (i.e., the

number of eggs laid) per nest as our empirical measure of reproduction (see below for how we re-defined this in the modeling exercise). In contrast to the estimation of Φ_a , clutch size does not take into account encounter probability—thus making this estimate negatively biased to an unknown extent. As a rough test for density-dependent regulation, we tested whether clutch size was related to N_{nests} (where this variable was used as a proxy for abundance as we lack data on this).

Estimates from the literature.—We performed a literature search in order to get information about juvenile and yearling survival, as well as egg predation levels in which we lack from Grindøya (details provided in Appendix S1).

Matrix population modeling

Overall model description.—Based on the estimated Φ_a and reproduction (clutch size) from Grindøya, as well as literature-based survival of juveniles and one immature age-class, we created a Leslie-matrix model (Caswell 2001). In our demographic model, different age-classes experience different survival and fecundity (reviewed by, e.g., Boyce et al. 2006), which we denoted as P and F . Our matrix model is based on four age-classes: a juvenile (0: <1 yr old), a pre-maturation class (1: 1 to <2 yr old), an adult but non-breeding class (2: 2 to <3 yr old), and a mature class (3+: ≥ 3 yr old) where the latter class is the only reproducing age-class (Appendix S4). Adult survival and reproduction estimated for the Grindøya population formed the basis for survival of the two oldest age-classes ($P_2 = P_{3+} = \Phi_a$) and fecundity (F_{3+}), whereas we based juvenile (P_0) and pre-maturation (P_1) survival on estimates from the literature (Appendix S1). Consequently, the transition matrix varied in time (A_t) through a random process (Appendix S4). F_{3+} , that is, fecundity in the 3+ age-class, was the only positive fecundity rate as all younger individuals were assumed immature (rationale provided in Appendix S4). Our model assumes a very simple form of regulation: We defined an upper ceiling, that is, an unrealistic form of density dependence, of 1000 individuals in the adult age-class (n_{3+}), whereas the number of chicks (n_0) and the two pre-maturation classes (n_1 and n_2) were unlimited (Appendix S4; Fig. S1). Moreover, we

assumed closed populations and hence no immigration or emigration.

Running the model.—Initial conditions were similar across all simulations as $n_0 = n_1 = n_2 = n_{3+} = 30$ so $n(t_0)$ was 120 (see also Appendix S2 for details). We also ran 100 different population trajectories, initialized similarly, in each run, in order to visually check whether the output was consistent across populations, but this seems not to be a problem. We ran these models and analyzed the output in R (R Core Team 2017) using the popbio package (Stubben and Milligan 2007). Terminal time was set to 500 yr, and the output, for example, population size (N) and population growth rates [$\lambda = \log_e(N_{t+1}) - \log_e(N_t)$], was presented as medians, including the 25th and 75th quantiles across the 100 population, from the last 26 yr of each simulation (Appendix S2).

Quasi-extinction.—We used a selection of matrices consisting of the last 26 yrs (for all the 100 populations; A_{sel}) to calculate stochastic populations growth rates using both a simulation (λ_s) approach and Tuljapurkar's (λ_T) approximation (Morris and Doak 2002:ch 7) using the stock.growth.rate (maxt = 10,000, $A = A_{\text{sel}}$) and the stock.quasi.ext ($A = A_{\text{sel}}$, nreps = 500, $N_x = n_0/2$, $n_0 = n_0$, tmax = 30, maxruns = 100) functions in the popbio package. The latter estimate the quasi-extinction probability, that is, the probability that the population is reduced by 50% during 30 yr provided that its initial population vector is similar to the initiation of the simulations above (n_0). This exercise was performed by simulation of a structured population in an independently and identically distributed stochastic environment (Stubben and Milligan 2007).

Computer experiments: manipulation of environmental conditions

Single stressors.—We manipulated multiple stressors for the common eiders in order to check the relative importance of these stressors in forming population growth and viability. The following stressors were added to the simulations (Table 1A):

1. Pollution—Pollution was a priori assumed to result in reductions in clutch size only, as chemical toxins have previously been associated with reduced reproductive success (details above). Hence, we included a potential

Table 1. Outline of the computer experiment where we manipulated (A) single stressors keeping the other stressors at their baseline values and (B) multiple stressors by manipulating more than one stress factor simultaneously.

Scenario	Pollution	Reduced effect of predation	Environmental conditions		Notes
			X	Y	
(A) Single stressors					
1. Pollution	min = 0, max = 2.5	1	$\bar{x} = 5.215$	$\hat{s} = 0.747$	†
2. Egg predation	0	min = 0, max = 1	\bar{x}	\hat{s}	‡
3. Environmental average	0	1	min = $\bar{x} \div 2.5 \hat{s}$, max = $\bar{x} + 2.5 \hat{s}$	\hat{s}	§
4. Environmental unpredictability	0	1	\bar{x}	min = $0.5 \hat{s}$, max = $2.5 \hat{s}$	
(B) Multiple stressors					
5. The good	min = 0, max = 2.5	0.750	\bar{x}	\hat{s}	†, ¶
6. The bad	0.444	0.250	min = $\bar{x} \div 2.5 \hat{s}$, max = $\bar{x} + 2.5 \hat{s}$	\hat{s}	†, ¶, #
7. The ugly	1.100	0.250	min = $\bar{x} \div 2.5 \hat{s}$, max = $\bar{x} + 2.5 \hat{s}$	\hat{s}	†, ¶, #

Note: The baseline for egg predation and pollution was that their effects were zero, whereas the baseline for environmental conditions was that its input for average (X) and SD (Y) was defined by the empirical estimates for SSTw (see main text for details).

† When reduced egg predation was set to 1, it means that human presence successfully prevented predation (100%).

‡ When reduced egg predation was set to 0, then actual predation equaled natural predation where the estimated mean (\bar{x}) and SD (\hat{s}) on logit-scale were $\bar{x} = -0.906$ and $\hat{s} = 1.239$; maximum value on natural scale = 0.779 (Appendix S1).

§ This manipulation of the average is extreme as 98.76% of the values for the initial distribution (assuming a normal distribution) are observed within ± 2.5 times the SD.

¶ When reduced egg predation was set to 0.5, it means that human presence reduced predation by 50% (i.e., half of the eggs normally lost to predation were saved).

Given the average clutch size on Grindøya means that a reduction in clutch size (induced by pollution) by 0.44 and 1.10 represented 10.08% and 24.97% reduction.

effect of pollution through reduction in clutch sizes (Appendix S4).

2. Reduced egg predation—Predation represents a proportion of eggs removed by predators, and it was normally distributed (using logit-transformation) where its average and standard deviation (SD) for 25 available estimates from the literature were used as input (Appendix S1). In the simulations, we manipulated various degrees of reduced egg predation assuming that the effect of natural predation could be proportionally reduced by human presence (see Appendix S4 for details on the implementation, see also Moe et al. 2012, Hanssen et al. 2013 for the rationale behind this). We thus separate between natural predation (using the average from the literature as a background mortality) and actual predation. The latter represents the number of eggs the predators actually remove from a population (and
3. Environmental average—Climate (i.e., SSTw) was generated from a normal distribution, that is, $N \sim (X, Y)$, where X and Y represent the distribution's average and SD, respectively. Consequently, we manipulated the input value for environmental average by changing the input value for X, while keeping the value for Y at its empirically estimated value.
4. Environmental unpredictability—We simulated increased values for Y when we generated climatic conditions keeping the value for X at the empirically estimated average for the distribution of our climatic variable.

Multiple stressors.—In the first four scenarios, we manipulated one stressor at a time while we kept the others constant either at zero (pollution

and egg predation) or using their empirical estimates (SSTw) as input (Table 1A). The remaining three multiple stressor scenarios consisted of the following manipulations (Table 1B):

1. The Good—The effect of pollution was manipulated creating a gradient from 0 to 2.5 while keeping egg predation at 7.5 (i.e., human presence saved 75% of the eggs usually taken by predators) and status quo for environmental conditions (i.e., the empirically estimate average and SD for SSTw as X and Y , respectively).
2. The Bad—Average environmental conditions were manipulated by creating a gradient in simulated average (X) ranging from ± 2.5 times the empirical estimated SD for SSTw. Pollution was kept constant at 0.44 eggs (i.e., a 10.08% reduction compared to the average clutch size from Grindøya), whereas human presence saved 25% of the eggs and the SD for environmental conditions was similar as in the good scenario.
3. The Ugly—Pollution reduced clutches additionally as a 1.10 egg reduction in clutch size occurred. Environmental conditions were the same as in the bad scenario. Consequently, the ugly scenario represented an additional $\sim 15\%$ reduction in clutch size relative to the empirical average from Grindøya compared to the bad.

Interpreting the computer experiments

In all scenarios, we kept all except one factor constant while for the variable factor we created a gradient of 80 equally spaced values between a minimum and maximum values (i.e., the varying stressor in each manipulation: Table 1). In each scenario, we fitted GAMs, using the *mgcv* library (Wood 2012), to each variable response variable (median across year and population values for the last 20 yr of each run) using the gradient as the predictor. We used GAMs as this method allows the degree of complexity, or smoothness, to be selected objectively (Wood 2006), which is an advantage in simulations assessing the effect of multiple stressors. We used cubic regression splines to model potential non-linear effects of the continuous manipulation, using the identity link and assuming a Gaussian family, applying

the following code: “`gam(response~s(continuous predictor, bs="cr", k=20))`.” Predictions, including their precision (standard errors), from these models were extracted using the `predict.gam` function in the *mgcv* package. Important output, such as the estimated degrees of freedom (edf), P -values, and the GAMs' adjusted R^2 , is provided on the figures (an approach similar to other modeling studies; see, e.g., Bårdsen et al. 2011, Bårdsen 2017).

RESULTS

Empirical analyses

Demographic data from Grindøya.—The annual average clutch size (average_{1986–2017} = 4.41 eggs; SD = 0.23; coefficient of variation [CV] = 5.12%) showed temporal variability, but no relationship with SSTw (Fig. 1). Clutch size varied from 3.98 ± 0.13 SD ($n = 56$) to 5.13 ± 0.35 ($n = 16$) eggs in 1986 and 2013, respectively. The annual sample size varied from 9 in 2014 to 146 in 1995 (with a total of 2057 clutches). Based on the GAM, four different periods of temporal dynamics were identified (Fig. 1A): (1) an initial increase period that ended around 1995; (2) a stable period lasting until to around 2005; (3) a second period of increase, which lasted until 2013; and (4) a final period of decrease. Finally, clutch size was subject to negative density dependence (Fig. 1C), using our rough proxy for density, and this simple model was selected over other candidate models where we added SSTw, using up to a three years lag, in addition to density (Appendix S2).

The annual average apparent adult survival (Φ_a), using the real parameters reported by MARK (Appendix S3), was 0.80 (on logit-scale: average = 1.38; SD = 0.30; CV = 22.00%), with a range of 0.69–0.92 (real parameters) and 0.60–0.95 (95% confidence intervals [CI]; Fig. 2A). The selected model contained a direct effect of SSTw and SSTw _{$t-3$} and was selected over a model including only time as a predictor of Φ_a (Appendix S3). Both SSTw and SSTw _{$t-3$} had negative effects on Φ_a , but the direct effect of SSTw was substantially more negative than the lagged one (Fig. 2C, D; see Appendix S3: Table S3 for effect sizes and their precisions). This indicates that SSTw was a potential driving factor affecting Φ_a even though survival showed temporal

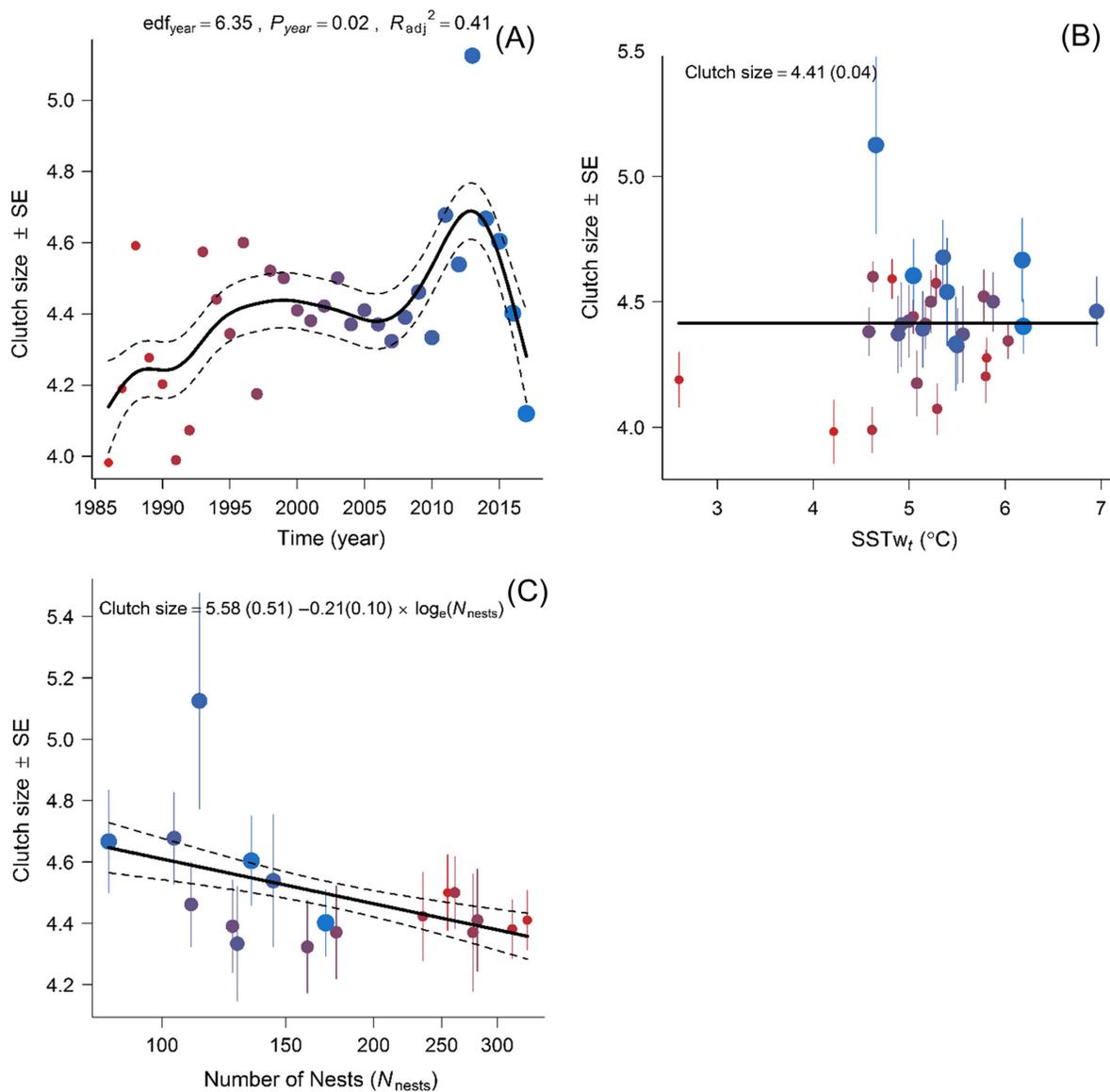


Fig. 1. Clutch size at Grindøya as a function of time (A), winter sea surface temperature (SSTw; B), and the number of clutches (N_{nests} ; data available since 1999; C; $R^2 = 0.23$). Temporal trends were analyzed applying generalized additive models similar to the temporal analyses of SSTw, whereas the analyses relating to SSTw and N_{nests} were performed using linear models (see Appendix S2 for details).

variability (Appendix S2: Fig. S2). The real parameters for recapture probability (P) varied between 0.03 (95% CI = 0.01, 0.10) and 0.56 (95% CI = 0.49, 0.62) and showed high variability (CV = 78.26%; Fig. 2D). In the selected model, P varied as a function of time and showed evidence of trap happiness (i.e., birds observed at

$t - 1$ showed an increased probability of being observed at t : Appendix S3).

The effect of climate: SSTw.—The initial GAM revealed a linear (edf = 1), but non-significant temporal trend in SSTw in our study area (adjusted $R^2 = 0.07$) even though analyses based on data from 1985 revealed a significant temporal

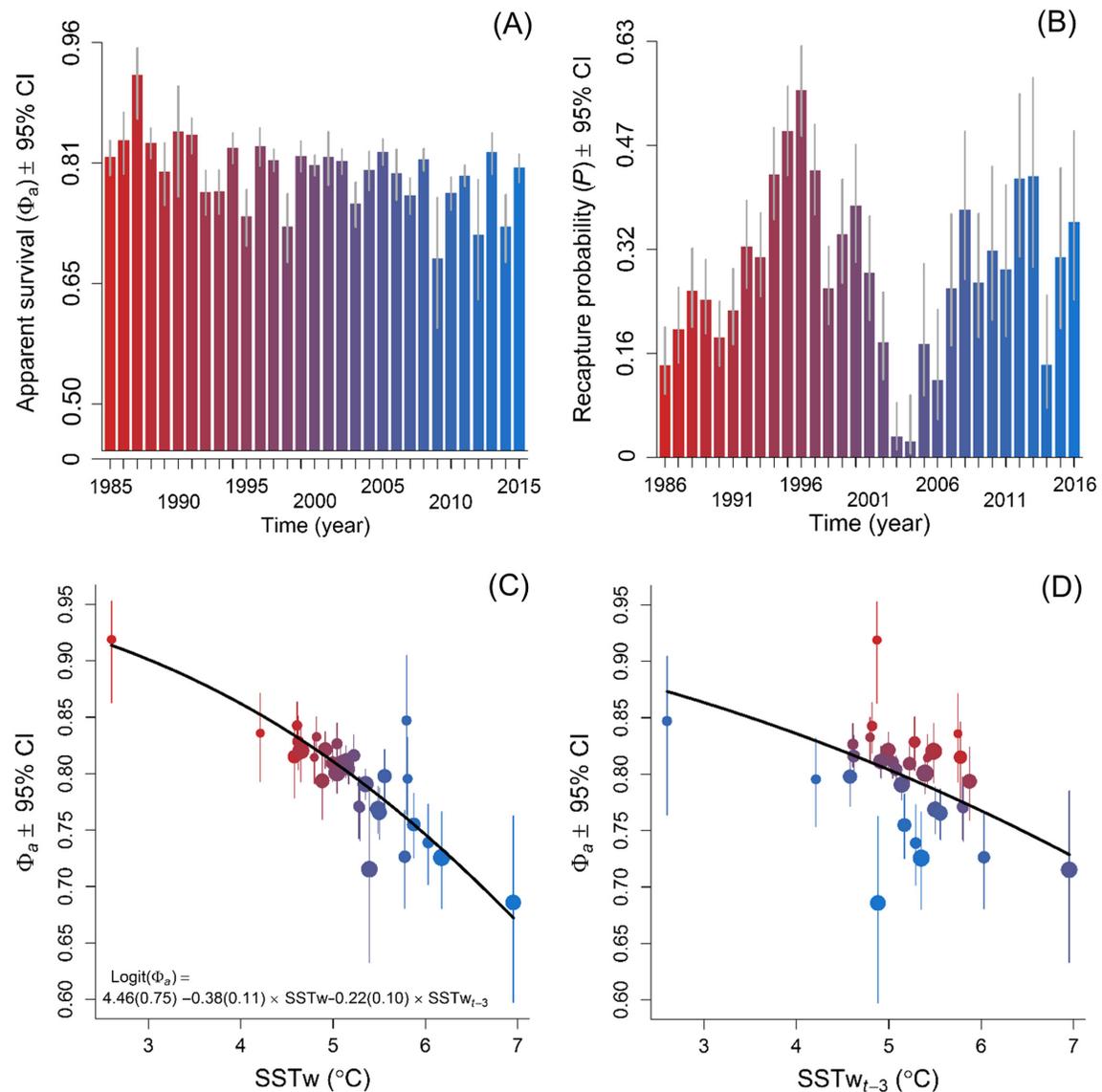


Fig. 2. Annual estimates of apparent adult survival (Φ_a ; A) and recapture, or re-sighting, probability (P ; B) for the Grindøya population (see also Appendix S3). Moreover, Φ_a was a function of winter sea surface temperature (SSTw) both directly (C) and with a temporal lag of three years (D; SSTw $_{t-3}$). Points and bars represent the real parameters reported in MARK, *that is*, predictions based on the annual averages for the covariates, and their associated 95% confidence intervals. Thick black lines show the effect of SSTw (C) and SSTw $_{t-3}$ (D), on Φ_a (transformed from logit- to probability-scale) keeping the other covariate at its empirical average. We also provide the estimated parameters on logit-scale, including their precision (standard error) in parentheses, for the survival component of the selected model (see also Appendix S3).

trend in SSTw (Appendix S2). From this analysis, it was also clear that annual average SSTw showed substantial temporal variation (average $_{1982-2016} = 5.23^{\circ}\text{C}$; CV = 14.38%; Appendix S2).

Estimates from the literature.—We found four estimates of apparent juvenile and yearling survival (Φ_j and Φ_y ; from one study in Canada and one in Europe: details provided in Appendix S1):

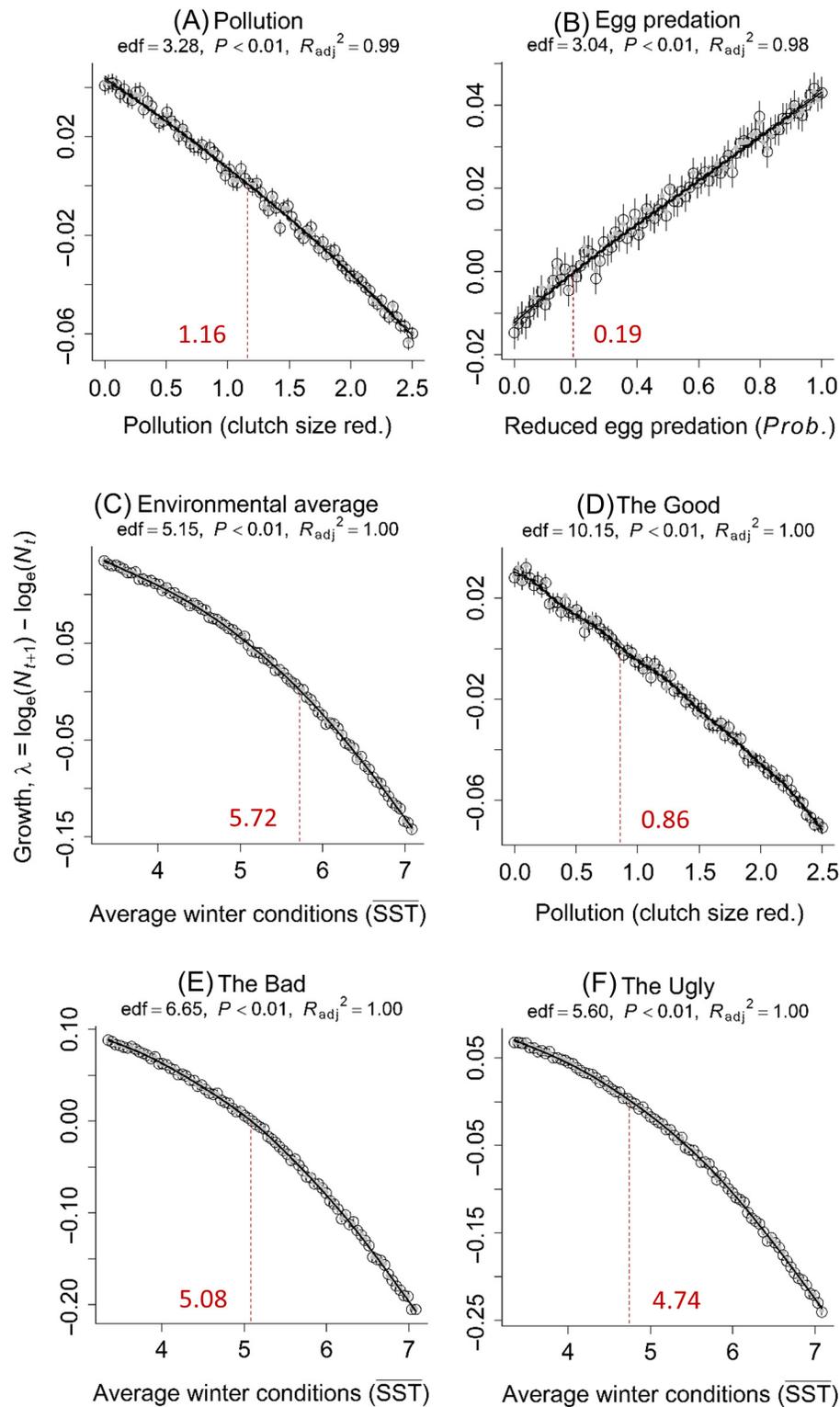


Fig. 3. Stochastic population growth rates using both a simulation (λ_s) approach, including 95% confidence intervals (vertical bars), and Tuljapurkar's (λ_T) approximation for the single and multiple stressor scenarios (see

(Fig. 3. *Continued*)

Table 1 for details). The single-stressor scenarios included (A) pollution, (B) egg predation, environmental average (C), and environmental unpredictable (Appendix S5) where we kept the other stressors at their baseline values. The multiple stressor scenarios included the good (D), the bad (E), and the ugly (F) in which more than one stress factor was manipulated simultaneously. Predictions including standard errors from a generalized additive model, fitted to each demographic manipulation separately, shown as thick solid and dotted lines, respectively. Please note the difference in the range of the y -axis.

$\Phi_j = 0.52$ (± 1 SD = 0.34, 0.70; CV = 867.42%) and $\Phi_y = 0.68$ (± 1 SD = 0.52, 0.80; CV = 84.86%); all estimates were back-transformed from logit- to probability-scale (i.e., based on logit-transformed probabilities). The large CV for Φ_j was partly related to the fact that the average for Φ_j was close to 0.5 (which has a logit = 0 and thus result in a large CV). The high CV for the juveniles was, at least partly, because these values were logit-transformed. A comparison of the SDs, based on logit values, for the juveniles and yearlings also supported this: 0.73 and 0.64. Similarly, we found 65 estimates of adult survival (Φ_a) from the literature (see Appendix S1 for a full reference list and data): average = 0.90 (± 1 SD = 0.82, 0.95; CV = 32.09%), which were significantly higher than the estimates from Grindøya (Appendix S1). Egg predation rates, which were treated similar as the survival estimates above, from the literature were on average 0.29 (± 1 SD = 0.11, 0.58), but highly variable (CV = 136.80%; Appendix S1).

Simulation results

Single stressors.—In the pollution scenario, a clutch size reduction of 1.16, or 27.20% reduction of the clutches compared to the empirical average from Grindøya, was necessary to induce extinctions (i.e., when $\lambda < 0$; Fig. 3A). In all manipulations, this effect was non-linear. In the pollution scenario, population abundance (N) was, for example, decreasing throughout the range in the simulated values for pollution, but the effect of pollution on N becomes increasingly more negative as pollution approximated the extinction threshold (Fig. 4A). Natural predation rates induced extinctions if $\geq 25.81\%$ of the eggs were lost to predation (i.e., when predation equals actual predation: Appendix S5). As average egg predation rate from the literature was slightly higher (see *Estimates from the literature*

section), egg predation as a single stressor induced extinctions assuming status quo (i.e., using the average from the literature). Remember that in the egg predation scenario, we did not manipulate egg predation directly. Instead, we manipulated the extent in which eggs normally lost to predation would be saved by human presence (e.g., by trappers actively protecting breeding eiders by shooting/chasing egg predators). In this scenario, a 0.19 reduction in egg predation rate was sufficient to prevent extinctions to occur (Figs. 3B, 4B). In the environmental average scenario, we show that increasing temperatures had a negative effect on population growth (due to the negative effect SSTw had on Φ_a ; Figs. 3C, 4C). Assuming status quo for SSTw, extinctions occurred when SSTw $\geq 5.72^\circ\text{C}$, which represents an increase in temperature of 0.51°C compared to the empirical average for SSTw. Environmental unpredictability had a negative effect on population growth and hence on population abundance, but within the range manipulated, this did not lead to extinction (Appendix S5). In sum, all single stressors affected common eiders population growth negatively. None of these stressors, except egg predation, were strong enough to be the sole cause of extinction within the range of the manipulations we applied.

Multiple stressors

In the good scenario, that is, when humans saved 75% of the eggs normally predated (Table 1), pollution-induced reduction of clutch size of ≥ 0.86 resulted in negative growth (Fig. 3D). Pollution thus had an increasingly negative impact on population size when it co-occurred with increased levels of egg predation (Fig. 4D) compared to when pollution was the only stressor being manipulated (Fig. 4A). In the bad scenario, humans saved 25% of the eggs usually predated and pollution reduced the clutches with 0.44 eggs (or 10.08% reduction compared to

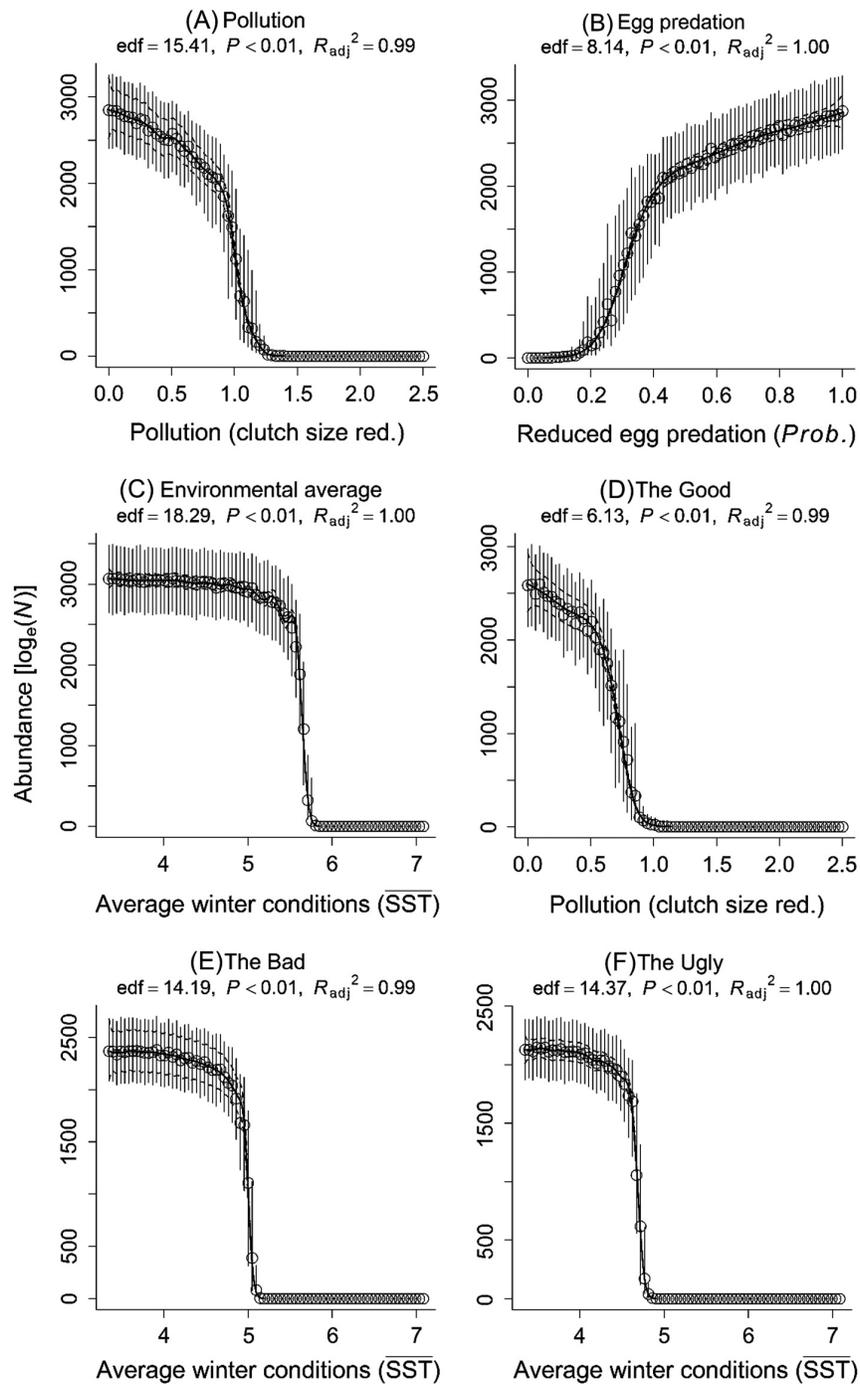


Fig. 4. Median population abundance (N), including the 25th and 75th quantiles for the 100 simulated trajectories and the last 25 yr of each run (vertical bars). The single-stressor scenarios included (A) pollution, (B) egg predation, (C) environmental average and environmental unpredictability (Appendix S5) where we kept the other stressors at their baseline values. The multiple stressor scenarios included the good (D), the bad (E), and the ugly (F) in which more than one stress factor was manipulated simultaneously (see legends for Fig. 3 for details). Please note the difference in the range of the y -axis.

the empirical average from Grindøya; Table 1). In this scenario, population growth became negative for $SSTw \geq 5.08^\circ\text{C}$ (a 0.64°C or an 11.20% reduction in temperature caused extinction compared to environmental average scenario), which is 0.13°C colder than the empirical average for SSTw or approx. the 40th percentile for its empirical distribution (Fig. 3E). In the ugly scenario, which was similar to the bad, except that pollution reduced clutch size with 1.10 eggs (or 24.97% compared to the empirical average; Table 1), population growth became negative when $SSTw \geq 4.74^\circ\text{C}$ (Fig. 3F). This means that a 0.98°C or a 17.13% reduction in temperature caused extinction in the ugly compared to the environmental average scenario. Increasing the effect of pollution thus caused extinctions in the ugly scenario to occur even for average temperatures being 0.34°C lower than the present-day average (representing roughly 0.5 SD or the 17th percentile for the empirical distribution of SSTw). In sum, the results support the multiple stressor hypothesis as extinctions occurred more easily when we manipulated more than one stressor at time. The threshold level for pollution to cause extinctions, for example, became lower when it co-occurred with increased predation pressure. Climatic warming, relative to present day, was needed for extinction to occur in the single-stressor manipulation of temperature, but in a multiple stress framework, extinction occurred even for temperatures lower than the present-day average (only six observed values for SSTw were lower than the extinction threshold from the ugly scenario).

The median probability (including the 2.5 and 97.5 percentiles) of quasi-extinction, that is, population reductions of $\geq 50\%$ over 30 yr, across our simulated population trajectories (see above for technical details), more than doubled if human presence saved 25% of the eggs instead of saving all the eggs (assuming status quo for SSTw). Specifically, the probability of quasi-extinction went from 0.20 (0.16, 0.23; Fig. 5A) to 0.52 (0.48, 0.56; Fig. 5B). Similarly, if no predation and pollution occur, the chance of quasi-extinction is practically zero assuming status quo for SSTw and assuming that 75% of the eggs were saved from predation (0.01 [0.00, 0.01] Fig. 6A). If, however, predation took a greater toll (only 25% of the eggs saved), but the effect of pollution was

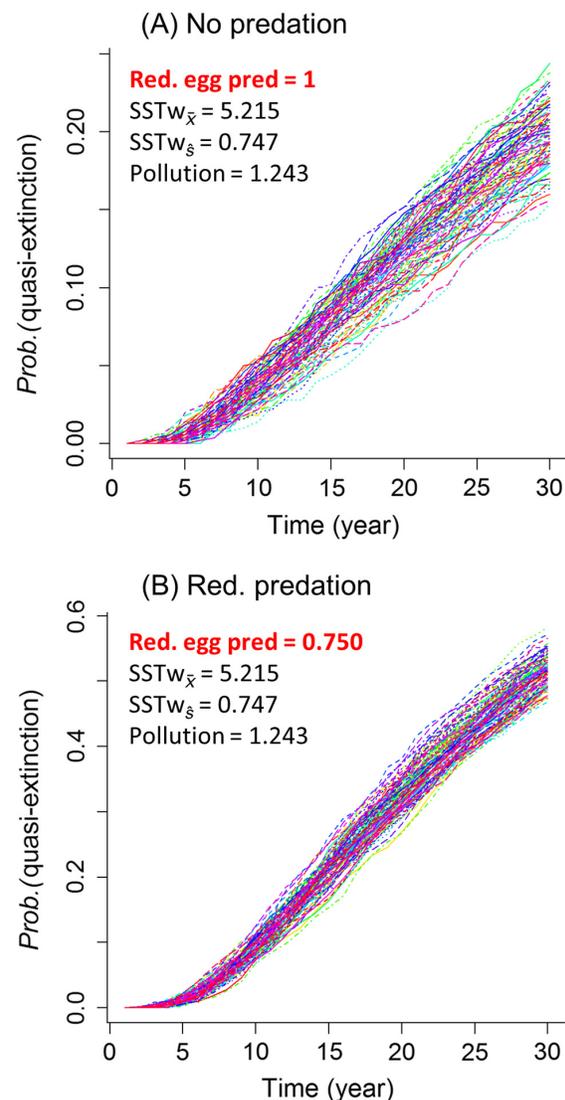


Fig. 5. Probability of quasi-extinction, that is, 50% reduction from an initial size of 120 individuals, over 30 yr based on matrices for the last 26 yr of 100 populations for the following scenarios (see main text for technical details): no predation (A) and reduced egg predation (B; 75% of the eggs were saved by humans). We assumed status quo for winter sea surface temperature (SSTw) and a pollution-induced reduction of clutched of 1.243 eggs. Note the difference in the range of the y-axis.

increased from 0.44 to 1.10, the probability of extinction increased dramatically going from 0.43 (0.39, 0.47; Fig. 6B) to 0.82 (0.78, 0.86; Fig. 6C). The latter show a dramatic effect of

increased pollution, assuming a pollution-induced reduction of the clutches representing 10% vs. 25% of the average clutch size from Grindøya, while the reduced egg predation increased. In sum, our assessment of quasi-extinction also supported the multiple stressor hypothesis.

DISCUSSION

We estimated reproduction (clutch size) and annual apparent adult survival (Φ_a) for common eiders, covering a period from 1985 to 2017, on Grindøya, a nature reserve in Northern Norway.

Average Φ_a showed a higher temporal variability ($CV = 22.00\%$) than the annual average clutch size ($CV = 5.12\%$). This was unexpected for a long-lived organism, such as common. Based on these findings, combined with information about juvenile and yearling apparent survival from the literature, we were able to apply a demographic population modeling approach. This enabled us to test the multiple stressor hypothesis: that is, the relative effect of pollution, SSTw (manipulating both average temperature and its variability), and egg predation on common eider population dynamics and viability (i.e., extinction risk).

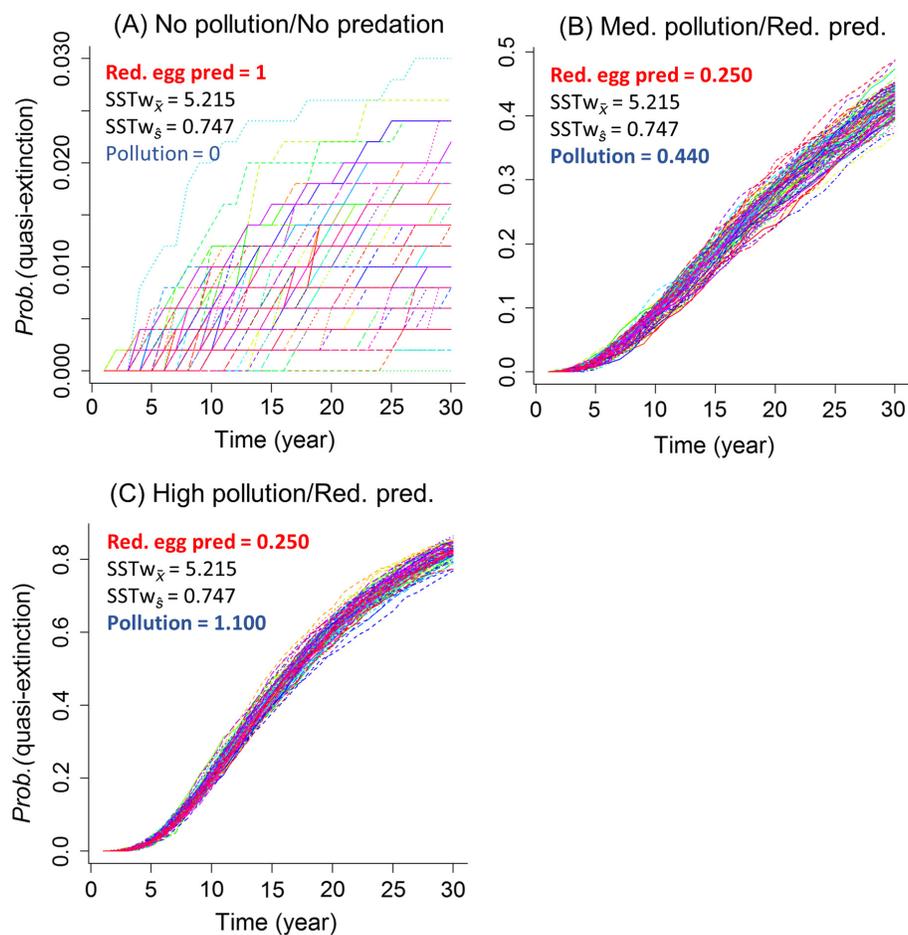


Fig. 6. Probability of quasi-extinction, that is, 50% reduction over 30 yr (see legends under Fig. 5 for technical details): no predation and no pollution (A; one simulation in the environmental average scenario); medium levels of pollution (B; from the bad scenario); and high pollution levels (C; the ugly scenario). In both (B) and (C), egg predation was reduced at a constant rate of 0.25, and we assumed status quo for winter sea surface temperature (SSTw) in all the plots. Note the difference in the range of the y-axis.

Empirical results

Reproduction.—The across-year average estimated clutch size on Grindøya was 4.41 clutch per nest, and the range for the annual averages was 3.98–5.13 eggs. We also found that the average clutch size varied significantly over time but no relationship between clutch size and SSTw. During the course of study, clutch size showed both evidence of increase (1985–1995 and 2005–2013) and decrease (2005–2013), as well as a period of no apparent trend (1995–2005). Mehlum (2012) reports positive temporal trends for Arctic common eiders, but a higher spatiotemporal variability compared to our study (CV = 37.17% across six colonies from 1981 to 2001: average = 3.39; SD = 1.26). Based on published annual clutch size averages from the United Kingdom (1958–1999: Coulson 1999:238), we calculated a temporal variability being more than twice as large as the one documented in our population (CV = 11.37%; average = 4.22; SD = 0.41). In another dataset from Scotland (Milne 1974:Table 4), a temporal CV of 28.95% was calculated (1961–1970; average = 4.11; SD = 1.19). Coulson (1999) was able to link clutch size to SSTw (January). Warm weather during winter and spring were in an Icelandic study positively related to nest numbers and clutch size (Jónsson et al. 2009), whereas time of ice break affected clutch sizes and fledging success negatively in Finland (Lehikoinen et al. 2006). The temporal trend for clutch size was in accordance with some of the previous findings from the literature even though the temporal variability for clutch size at Grindøya was small compared to other studies.

Nonetheless, while clutch size has varied over time, the size of the Grindøya population has decreased, and this together with the negative relationship between the number of nests and clutch size indicates that reproduction was subject to negative density dependence. This is in accordance with previous studies where negative density dependence has been documented (Hanssen et al. 2013). However, in the longer time series on eiders, periods of both increase and decrease have been found (Swennen 2002, Hario and Rintala 2009, Jónsson et al. 2009), along with both positive and negative effects of population size on reproduction such as nesting success and clutch size (Ahlén and Andersson

1970, Swennen 1983) as well as a lack of density dependence (Swennen 2002).

Survival.—The annual average adult survival (Φ_a) was 0.80, with a range of 0.69–0.92 (estimates), which is both lower and less variable than estimates from the literature. Our estimates of adult survival were related to SSTw, both directly and with a lag of three years. Surprisingly, adult survival varied more than reproduction for the Grindøya population, which is unexpected for long-lived animals such as common eiders (with an average life expectancy reported to be up to 26 yr: Baillie and Milne 1982), through a process called environmental canalization (Gaillard and Yoccoz 2003, see Pardo et al. 2013 for a seabird example). When examining the estimates from Grindøya, it might be questioned if we could classify individuals from this population as long-lived. Looking at the estimated Φ_a for Grindøya, the mean life span, calculated as $-1/\log_e(\Phi_a)$ in accordance with Seber (1982), was 4.67 yr with a range of 2.65–11.81 or 1.94–20.87 yr based on the range in the point estimates and the 95% CIs for survival (from our analyses of data from Grindøya).

In contrast, using the reported estimates for Φ_a from the literature yielded an average mean life span of 11.99 (± 1 SD = 6.63, 24.50) years. This seems to be within range of the estimated life expectancy reported by Waltho and Coulson (2015:236–237), although considerably lower estimates of average life expectancy and life span have also been reported (Baillie and Milne 1982, Coulson 1984). Our measure of life expectancy using the annual point estimates is simplistic as it assumes a time- and individual-constant adult survival. Nonetheless, it indicates that individuals in the Grindøya population have a life expectancy that is considerably lower (>50%) than for eiders in general (but see one population in Waltho and Coulson 2015:7 where life expectancy was 5.3 yr). This contrast fits well with the reported variability in fitness traits from the literature where the CV for juvenile survival was one order of magnitude larger than for yearlings, and the least variable estimate was adult survival, which had a CV that was <50% than the yearling estimate. Even though we only found four estimates of juvenile and yearling survival, this finding was as expected for long-lived organisms. In large herbivores, for

example, adult survival shows little variation, followed by the fecundity of prime-aged individuals and yearling survival, where juvenile survival and fecundity of young individuals vary the most (reviewed by, e.g., Gaillard et al. 2000). In sum, the apparent adult survival estimate and hence also the life expectancy, was lower at Grindøya compared to what is reported on common eiders in the literature. This could also explain why adult survival is more variable than what is expected from environmental canalization hypothesis.

Simulation results

Support for the multiple stressor hypothesis.—The key findings from the matrix population model, parametrized with data from Grindøya and the literature, were that no single stressor except egg predation was sufficient to induce extinctions unless the magnitude of the manipulations was quite excessive. Moreover, a rather small effect of human presence was needed, that is, humans saved <2 out of ten eggs subject to natural predation (assuming a natural average egg predation rate of 0.288), to prevent extinction. In the single-stressor scenario, the effect of pollution had to kill >27% of the eggs laid, that is, to reduce clutches with more than ca. 1.2 eggs on average, for extinctions to occur. Temperatures of 5.72°C, where the theoretic probability of reaching values above this is <0.25 assuming the empirical average and SD for SSTw [$N \sim (5.215, 0.747)$], were needed before extinction occurred in the single-stressor manipulation of average temperature.

Nonetheless, we found support for the multiple stressor hypothesis for sub-arctic common eiders. First, the good scenario showed that the effect of pollution was increasingly negative when it co-occurred with increased egg predation levels. Second, in the bad scenario the negative effect of climatic warming increased when it co-occurred with increased egg predation (25% of the eggs subject to predation were saved) and when pollution was assumed to reduce clutches with 0.44 eggs. This was sufficient to cause extinctions when our manipulation of warming reduced temperature by 0.13°C relative to empirical average for SSTw. Third, extinctions happened even more easily in the ugly scenario

where we manipulated an additional effect of pollution of 0.66 (representing a 25% change relative to the empirical average). In this manipulation, a reduction in average temperature of 0.5°C relative to empirical average, and ~1°C compared to the environmental average scenario, caused extinctions. We also observed similar patterns for the probability of quasi-extinction, which increased dramatically when comparing single- and multi-stressor scenarios.

Increasing the effect of pollution from 0.44 to 1.1 resulted in extinctions for far less extreme temperatures compared to the single-stressor simulation above. In the ugly scenario, extinctions occurred at 4.74°C, whereas extinctions happened at 5.08°C in the bad scenario. The difference between the two manipulations was 0.34°C, which might seem small in an absolute sense, but the corresponding increase in SSTw represent a 0.2 and 0.5 SDs when compared to the empirical temperature data. Based on the theoretical properties of a normal distribution, it is, however, clear that the probability of observing temperatures greater than or equal to 5.08°C is 57.17%, whereas the same for 4.74°C is 73.76% (compared to 24.95% for 5.72°C in the environmental average scenario). Consequently, the necessary temperatures to induce extinctions are far more likely for the ugly compared to the bad scenario, but the real contrast exists when we compare the multiple- and the single-stressor scenarios. An alarming finding in this respect is that both multi-stressor scenarios resulted in extinctions for temperatures being lower than the present-day average (0.1–0.3°C), whereas the single-stressor scenario predicted extinction if temperature increased by 0.5°C. We expect climate to become warmer at northern latitudes, and even though our SSTw time series showed no significant temporal trend, it seems to be increasing more than decreasing during the course of our study (Appendix S2). In sum, we found support for the multiple stressor hypothesis as neither pollution nor climate alone resulted in extinctions, whereas even small additional effects of pollution affected viability when it co-occurred with increased temperatures and predations (see also Dey et al. 2018 for a recent model where population sizes were predicted based on climate and nest predation).

Assumptions.—Our model is based on several important assumptions and simplifications that needs to be addressed. Similar to standard Leslie-matrix models, we assume that the vital rates represent the average across an homogenous group of similar-aged individuals (Caswell 2001). Even though we acknowledge that long-lived organisms have adopted complex life histories, for example, that they are capable of buffering environmental stochasticity (Erikstad et al. 1998, Bårdsen et al. 2008, 2014), our model assumes a more simplified response to changes in environmental conditions. For instance, we do not assume any evolutionary processes or take into account that real organisms have a wide behavioral repertoire, which might induce individual variability in how they respond to the increased stress levels. In this respect, we considered other modeling approaches that take this into account, such as agent-based models (Bårdsen et al. 2011, Bårdsen 2017, even though a recent model has been developed for *Somateria m. borealis*: Dey et al. 2018). Nonetheless, we ended up with the matrix models as we lack sufficient data on many of the proposed processes—and pollution in particular—to add such a degree of complicity into our model. We also follow only the female segment of the population and a 1:1 sex ratio, even though we suspect that the yearling and juvenile survival estimates from the literature do not discriminate between the sexes.

Pollution.—For common eiders, the levels of POPs in the blood may vary between populations (Bustnes et al. 2012, Fenstad et al. 2016). Nonetheless, as female eiders fast during the incubation, they may lose up to 40% of their body reserves (Swennen 1972, Korschgen 1977, Parker and Holm 1990), which again releases lipophilic contaminants into the blood and leads to dramatically increased blood levels of POPs (Bustnes et al. 2012). While birds in the Arctic are expected to be less exposed to pollution, they may have levels comparable to populations in more heavily polluted areas, a result that may be explained by the fact that Arctic birds need to metabolize more fat during incubation as they breed in a more temperature stressed habitats (Bustnes et al. 2010, 2012, Fenstad et al. 2016). In addition to the measured increased levels of POPs and other pollutants in the blood, the effect of pollution on common eiders in the literature is

mainly physiological (Wayland et al. 2003, Fenstad et al. 2016) even though DNA double-strand break frequency might be linked to POP levels (Fenstad et al. 2014). However, a few studies have suggested that eiders are vulnerable to ecological effects of pollutants (Swennen 1972, Wilson et al. 2007, Bustnes 2013). The abovementioned studies lack an explicit link to demographic responses (reproduction or survival in our case, even though Bustnes 2013 document a high number of dead ducklings in a highly polluted area). Our link to pollution was thus implemented as a hypothetical one, but from a theoretic perspective, we linked it to reproduction and not adult survival (Forbes et al. 2010). Nonetheless, our implementation of pollution is similar to a previous study where selenium had reproductive costs for Pacific eiders by increasing the chances of producing non-viable eggs (even though this study concludes that population-level effects were expected to be minor: Wilson et al. 2007).

Egg predation.—The estimates of predation used in our model are conservative for several reasons. First, we have not taken into account all reported estimates of complete losses of nests due to predation (i.e., when predators remove all eggs in the nest: see, e.g., Erikstad and Tveraa 1995 and Hanssen et al. 2003, for examples, from Grindøya). However, we base our model on 25 estimates from the literature reporting the proportion of eggs removed by predators (Appendix S1: Table S2). Even if we do not take into account that complete nest losses are a source for bias, many studies report high levels of partial egg predation, and it was difficult for us to separate these two sources of predation from each other. One study from Svalbard, for instance, reported that up to 90% the eggs ($n = 60$) was removed by predators (Ahlén and Andersson 1970:Table VI). The levels of egg predation rates from Grindøya seem to be lower: From 1986 to 1989, 30% ($n = 1987$) of the eggs were lost to predation (Erikstad et al. 1993:627). The estimate from Grindøya is thus close to the average across the studies from the literature. Second, we also assumed egg predation, in addition to pollution, to be the only source of mortality in the very beginning of life for the ducklings. This is an assumption, which we were unable to test using our empirical data. Nonetheless, several authors report that mortality in general seems to be low

as soon as the ducklings enter the water (Choate 1966:110, Milne 1974:144). This source of mortality was, however, taken into account in the juvenile survival rates that we used in our model. Hanssen et al. (2013) concluded that that human-induced limitation of predator activity had dramatic positive effects on population dynamics (λ and carrying capacity). The previous study utilized contrasting populations, but without any knowledge of neither the extent in which predation occurred nor how efficient humans controlled predators. In contrast, our study concludes that rather inefficient predation control, that is, humans needed to save <20% of the eggs subject to natural predation, was sufficient to induce population growth instead of decline. In sum, even though we acknowledge that predation is not the only source of mortality in eiders, especially in the early part of life in particular (Descamps et al. 2011, 2012), egg predation has had a special focus in the literature for decades (Appendix S1: Tables S1, S2).

CONCLUSIONS

When developing models, we wished to keep them as simple as possible without losing too much realism and precision. Levins (1966:422), for instance, prefers to “[s]acrifice precision to realism and generality. . . Since we are really concerned in the long run with qualitative rather than quantitative results.” We concur with this, as making overall predictions on how common eiders, and other long-lived seabirds, in general respond to future changes of multiple stressors is more important than making realistic and precise predictions about how local populations such as the Grindøya population may respond. This is further highlighted by the fact that quantitative research questions should be assessed by combining statistical analyses of observational data, experiments, and the development of models (review: Servedio et al. 2014), because these methods are associated with different strengths and weaknesses (Turchin 1995). In contrast to empirical analyses, models such as the ones we use are useful for assessing mechanisms that might occur in the real world—they may be thought of as thinking aids used to investigate the logic and assumption behind arguments (Kokko 2007, Servedio et al. 2014). The point is that this study

combines several methods as we link more pattern-oriented empirical studies (statistical analyses of empirical data) with more process-oriented population modeling tools. The latter requires implementation of mechanisms while the output of these models may be highly sensitive to a single or a few parameters. In fact, our assessment of the different scenarios represents an attempt to predict how common eiders’ population growth and abundance may be sensitive to future environmental changes. This also means that our modeling approach identifies knowledge gaps, which represent mechanisms, or patterns, where we currently have insufficient information (i.e., lacking or unprecise empirical estimates). The extent and strength of egg predation represent such a gap as we are uncertain of whether these estimates are unbiased or not. Consequently, once more, we concur with Levins (1966:430) that “The validation of a model is not that it is ‘true’ but that it generates good testable hypotheses relevant to important problems” (see also Servedio et al. 2014 for a recent review about the utilization of models in addition to other scientific approaches). Based on our model, further studies should address juvenile and yearling survival in more detail, and how they relate to environmental conditions, pollution, and other stressors such as diseases.

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