Effects of climate change and variability on population dynamics in a long-lived shorebird

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Abstract. Climate change affects both the mean and variability of climatic variables, but their relative impact on the dynamics of populations is still largely unexplored. Based on a long-term study of the demography of a declining Eurasian Oystercatcher (*Haematopus ostralegus*) population, we quantify the effect of changes in mean and variance of winter temperature on different vital rates across the life cycle. Subsequently, we quantify, using stochastic stage-structured models, how changes in the mean and variance of this environmental variable affect important characteristics of the future population dynamics, such as the time to extinction. Local mean winter temperature is predicted to strongly increase, and we show that this is likely to increase the population's persistence time via its positive effects on adult survival that outweigh the negative effects that higher temperatures have on fecundity. Interannual variation in winter temperature is predicted to decrease, which is also likely to increase persistence time via its positive effects on adult survival that outweigh the negative effects that lower temperature variability has on fecundity. Overall, a 0.1°C change in mean temperature is predicted to alter median time to extinction by 1.5 times as many years as would a 0.1°C change in the standard deviation in temperature, suggesting that the dynamics of oystercatchers are more sensitive to changes in the mean than in the interannual variability of this climatic variable. Moreover, as climate models predict larger changes in the mean than in the standard deviation of local winter temperature, the effects of future climatic variability on this population's time to extinction are expected to be overwhelmed by the effects of changes in climatic means. We discuss the mechanisms by which climatic variability can either increase or decrease population viability and how this might depend both on species' life histories and on the vital rates affected. This study illustrates that, for making reliable inferences about population consequences in species in which life history changes with age or stage, it is crucial to investigate the impact of climate change on vital rates across the entire life cycle. Disturbingly, such data are unavailable for most species of conservation concern.

Key words: age structure; climatic variability; density dependence; environmental stochasticity; Eurasian Oystercatcher; Haematopus ostralegus; *nonlinearity; population viability analysis; Schiermonnikoog, The Netherlands; stochastic population dynamics; time to extinction; winter temperature.*

Introduction

Currently, the global climate changes at a rate much faster than experienced over most of earth's history, and this change is expected to continue in the future (IPCC 2007). Although it is well established that climate change can strongly affect population dynamics (e.g., Sæther et al. 2000, Coulson et al. 2001, McLaughlin et al. 2002), the general mechanisms causing climate-induced population change are still poorly understood.

Four major unresolved questions are: (1) Does climate change mainly affect population dynamics through its effects on survival or fecundity, and how does this vary between species and environments (Lack 1954, Sæther et al. 2004)? (2) How important is the contribution of climate change to population fluctuations in comparison to other stochastic and deterministic processes (Lande et al. 2003)? (3) What is the relative importance of changes in the mean and variability of climatic drivers (Boyce et al. 2006, Morris et al. 2008)? (4) Does increased interannual climatic variability typically reduce population viability as predicted by classical stochastic population theory (Lewontin and Cohen 1969, Lande and Orzack 1988), or can it also improve population viability as more recently put forward (Drake 2005,

Boyce et al. 2006, Morris et al. 2008)? Answering these questions and identifying the mechanisms involved are crucial for making general predictions about the population dynamical consequences of climate change and for identifying the species that are most at risk.

Most climate change studies either directly relate variation in climatic variables to changes in population size (e.g., McLaughlin et al. 2002, Drake 2005, Tyler et al. 2008) or examine how climate affects only one or a few vital rates (e.g., McMahon and Burton 2005, Nevoux et al. 2008, Votier et al. 2008). However, these approaches ignore the demographic mechanisms causing changes in population size. For example, does climate mainly act via an effect on fecundity or on survival? If we are to understand how climate change influences the population dynamics, we need to consider how different climatic variables affect the mean and variability of all major vital rates and then in turn how this will give rise to population changes (as advocated by Sillett et al. 2000, Ådahl et al. 2006, Morris et al. 2008, Visser 2008).

A demographic approach to the study of climate-induced changes of the population dynamics is a challenging task. First, it necessitates separation of deterministic from stochastic influences on population dynamics. This separation requires decomposition of how much of the temporal variation in, and covariation between, vital rates is explained by climatic variables, density dependence, demographic stochasticity, and (residual) environmental stochasticity (Lebreton 1990, Rotella et al. 1996, Dennis and Otten 2000). Furthermore, climatic responses of vital rates themselves may be density dependent (Turchin 1995, Coulson et al. 2001). Second, it requires identification of the major sources of age and stage structure in vital rates, as both age and stage structure can induce lagged responses to climatic variables (Lande et al. 2002). Third, climate change can manifest itself as changes in both the mean and variance of climatic variables (Easterling et al. 2001), which necessitates evaluation of their separate effects on each vital rate (Lande et al. 2003). Moreover, it requires examination of possible nonlinear dependencies between climatic variables and vital rates, as the shape of this relationship determines how increased environmental variability affects the means of vital rates (e.g., Ruel and Ayres 1999, Boyce et al. 2006). Fourth, quantifying all the abovementioned characteristics for vital rates over the entire life cycle requires detailed individual-based data. Additionally, such data must span long periods (typically decades for birds and mammals) in order to reliably decompose the temporal variance of the population process (Lande et al. 2003, Altwegg et al. 2006).

Recently, there is an increasing interest in the role of changes in climatic variability and the occurrence of catastrophic events (an extreme case of climatic variability; Boyce et al. 2006, Jentsch et al. 2007). Many studies have suggested that climatic variability can have important effects on population dynamics of a variety of animal and plant species (e.g., Sæther et al. 2000, Coulson et al. 2001, Green et al. 2003, Jenouvrier et al. 2003, Tews and Jeltsch 2007). However, to our knowledge no study has directly quantified the relative importance of changes in the mean versus changes in the interannual variability of climatic variables for population dynamics via their effect on each of the vital rates in the life cycle. Such a comparison is important, however, as it will help us to resolve the questions mentioned in the first paragraph.

Here we will investigate the impact of changes in the mean and variability of a major climatic variable (winter temperature) on the vital rates and population dynamics of Eurasian Oystercatchers (*Haematopus ostralegus*). This long-lived shorebird exhibits clear age, stage, and spatial structure, as well as density dependence in vital rates. Locally, mean winter temperatures are expected to increase, while interannual temperature variability is expected to decrease (van de Hurk et al. 2006). Interestingly, changes in winter temperature are expected not only to affect multiple vital rates in this species, but also to do so in opposing ways. Increasing winter temperature is predicted to enhance survival in all age and stage classes, because in warm winters oystercatchers have little problem meeting their daily energy requirements, while this is problematic in cold winters (Camphuysen et al. 1996, Atkinson et al. 2003). In contrast, warm winter temperatures are expected to adversely affect fecundity indirectly, because oystercatchers' main prey species during breeding are less abundant after warm winters (Beukema 1992, Philippart et al. 2003, Lawrence and Soame 2004). Furthermore, the effects of decreased interannual temperature variability on vital rates have not yet been investigated. Consequently, there is no a priori expectation for the direction and magnitude of the population dynamical consequences of climate change in this strongly declining species.

Using 24 years of data from the wild and a stage-structured stochastic population model, we will disentangle the relative importance of changes in climatic mean and variability for population dynamics. We will do this by quantifying whether a small change in mean winter temperature of $X°C$ results in larger or smaller changes in time to extinction than a $X°C$ change in the standard deviation of temperature. By further investigating the climatic effects on each vital rate we will investigate whether population consequences of climate change in oystercatchers are mainly caused by climate effects on survival or reproduction. More specifically, if an increase of $X°C$ increases persistence time with Y years, how much of this increase in Y is caused by temperature effects on survival and how much by effects on fecundity? Finally, we will discuss when climatic variability is expected to improve or reduce population viability and how this might depend on the life history of a species and on the vital rates affected. Our modeling framework is general and can be adapted to other
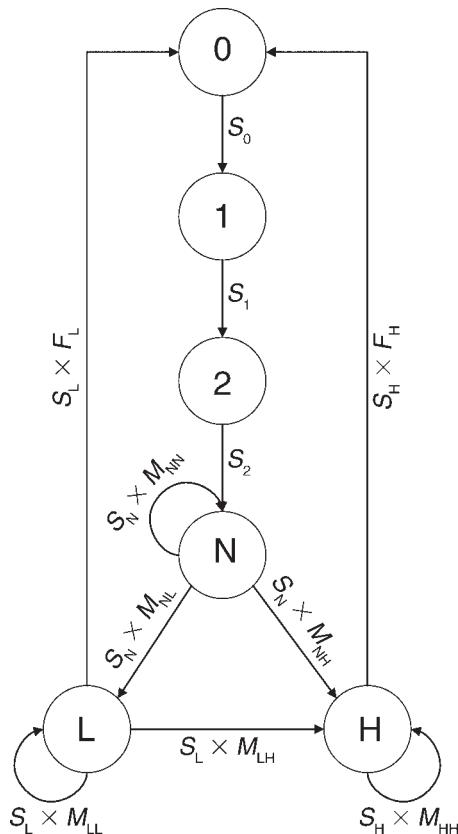
FIG. 1. Schematic view of the age-, stage- and spatially structured life cycle of the Eurasian Oystercatcher (*Haematopus ostralegus*) and the stage-dependent vital rates fecundity (*F*), survival (*S*), and movement probabilities between states (*M*). Six states are distinguished: 0, fledged offspring; 1, one-year-old juveniles; 2, two-year-old juveniles; N, adult nonbreeders; L, breeders in low-quality habitat; H, breeders in high-quality habitat. Note that $M_{NN} = 1 - M_{NL} - M_{NH}$, etc.

species with structured life cycles, provided that long-term individual-based data exist.

METHODS

Study species and population

Oystercatchers are long-lived monogamous shorebirds (>40 years), and their demography exhibits distinct age, stage, and spatial structure (e.g., van de Pol et al. 2007). Juveniles become sexually mature when they reach the age of three years; annual survival increases progressively from fledging to second year and remains approximately constant within adult stage classes. Due to the high site fidelity and despotic territorial system oystercatcher populations contain a surplus of adult nonbreeders that do not own a nesting territory; consequently delayed reproduction is common (age of first reproduction 3–12 years; Harris 1970, van de Pol et al. 2006). Oystercatcher populations typically exhibit a dichotomy in breeding habitat quality caused by permanent differences in the spatial organization of territories (Ens et al. 1992, Safriel et al. 1996). Some

pairs have adjacent nesting and feeding territories, allowing them to take their chicks to the food, whereas other pairs have spatially separated nesting and feeding territories and are forced to spend much energy to bring every food item to their chicks (see Ens et al. 1992: Fig. 1). Consequently, adjacent territories consistently produce two to three times more offspring annually than split territories. Henceforth, adjacent and split territories are denoted high- and low-quality habitat, respectively (cf. Ens et al. 1992, Bruinzeel and van de Pol 2004). The six life stages (0, fledged offspring; 1, one-year-old juveniles; 2, two-year-old juveniles; N, adult nonbreeders; L, breeders in low-quality habitat; H, breeders in high-quality habitat) and the age, stage, and spatial structure of oystercatcher's vital rates fecundity (*F*), survival probability (*S*), and movement probability between stages (*M*; conditional on survival) are depicted in Fig. 1. Fecundity was defined as the number of fledglings (day 30 of age) a breeding pair produced in a year multiplied by 0.5 (reflecting a fledgling sex ratio of 0.5; Heg et al. 2000a).

From 1983 to 2007 we studied a breeding population of oystercatchers on the Dutch island of Schiermonnikoog (53°29′ N, 6°14′ W). This area is considered core breeding habitat for this species and is part of the international Wadden Sea estuary consisting of many other nearby barrier islands. An intensive color-ringing program was initiated to mark all nonbreeders, breeders, and their offspring. The standard monitoring protocol is described in detail elsewhere (Ens et al. 1992, Heg et al. 2000b). In short, during each breeding season (May–August) population numbers were counted and we recorded which individuals were alive and what their stage class status and reproductive output was (~300 marked individuals and ~100 breeding territories annually). Mortality occurred mainly in winter, with subsequent stage changes finalizing before the start of the breeding season. The study population declined ~5% per year over the 24-year study period (van de Pol 2006), comparable to Dutch national trends (van Dijk et al. 2007).

Climatic, environmental, and density covariates

Winter temperature (*w*; mean of December–March) has been measured at the local weather station (2 km from the study site). However, as this weather station is relatively new, we instead used historical data since 1907 from the Eelde weather station located 35 km away (Royal Netherlands Meteorological Institute). Winter temperatures at both weather stations were strongly correlated (Pearson's $r = 0.98$; $n = 33$). By combining the historical data with four different climate models specifically developed for this region (van de Hurk et al. 2006), projections of winter temperature trends were generated for 1990–2100 (Fig. 2A). Mean winter temperature is projected to continue to increase, whereas the interannual variability of winter temperature is projected to decrease in the future (Fig. 2A, B). Based
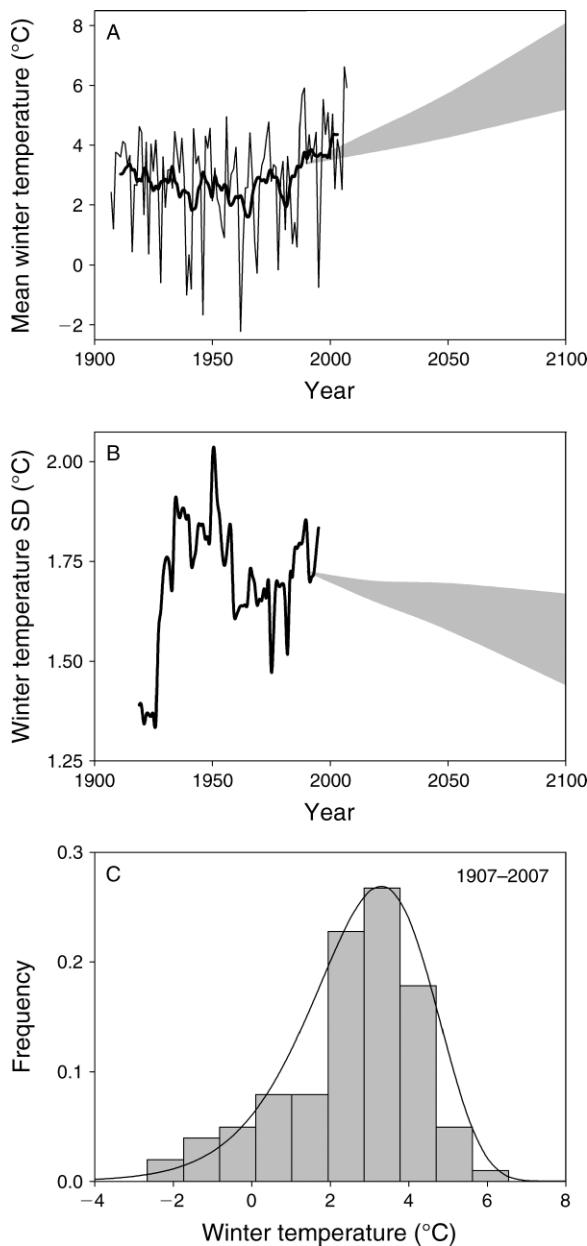
FIG. 2. Historical (1907–2007) and projected (1990–2100) changes in local winter temperature (data from the Royal Netherlands Meteorological Institute). (A) Mean winter temperature (thin line, annual fluctuations; thick line, 10-year running average; gray area, range of projections of mean temperature trends from four climate scenarios [van de Hurk et al. 2006]). (B) Standard deviation of winter temperature (thick line, 25-year running SD; gray area, range of projections of temperature standard deviance trends from four climate scenarios [van de Hurk et al. 2006]). (C) Distribution of historical mean winter temperature with a transformed lognormal distribution fitted to the data.

3.7°C and 1.7°C, respectively (similar to the study period 1983–2007). The standard deviation of w decreases as a function of the mean for this transformed lognormal distribution, as is also predicted by all four future climate scenarios (Fig. 2A, B).

We also considered whether vital rates were associated with various other large-scale and local climatic variables besides winter temperature (summer and winter Northern Atlantic Oscillation index and summer temperature, precipitation, and flooding events). In addition, we explored how vital rates depend on food availability, as the abundances of oystercatchers' main prey species (shellfish and worms) are known to depend on winter temperature (Beukema 1992, Philippart et al. 2003, Lawrence and Soame 2004). Food abundance was measured as the density of each main prey species (ragworm [*Nereis diversicolor*], lugworm [*Arenicola marina*], Baltic tellin [*Macoma balthica*], and cockle [*Cerastoderma edule*]) on the mudflats in the study area during the birds' peak of egg-hatching (van de Pol 2006). We included only prey items that are accessible to oystercatchers (i.e., in the top 15 cm of the mudflats) and selected by oystercatchers (i.e., bivalves <10 mm were excluded).

Density dependence of fecundity and survival probabilities was investigated by including competitor numbers as a covariate (total population size [N_{pop}] or size of a stage class [e.g., N_H]). In addition, we specifically investigated possible interactions between climatic and density variables. The density dependence of movement probabilities between stages was investigated differently, because the limited amount of high- and low-quality habitat is the main factor regulating this population. Many adult nonbreeders are despotically excluded from breeding, and removal experiments have shown that when given the opportunity they can reproduce (Bruinzeel and van de Pol 2004). Movement probabilities from the nonbreeder stage to the high- or low-quality breeding stages are thus expected to be a function of both the number of vacant territories (due to deaths of breeders; $(1 - S_H)N_H$ or $(1 - S_L)N_L$) and the number of surviving nonbreeders that compete for these vacancies ($S_N N_N$). In addition, vacancies in high-quality habitat are much more likely to be occupied by nearby breeders from low-quality habitat than by nonbreeders (Heg et al. 2000b). Therefore, we expected the number of vacancies for nonbreeders also to be a function of the number of breeders moving from the low- to high-quality habitat breeding stage ($S_L M_{LH} N_L$). More specifically, we expected

$$M_{NL} \approx \frac{(1 - S_L)N_L + S_L M_{LH} N_L}{S_N N_N}$$

$$M_{NH} \approx \frac{(1 - S_H)N_H - S_L M_{LH} N_L}{S_N N_N}$$

$$M_{LH} \approx \frac{(1 - S_H)N_H}{S_L N_L}.$$

on the historical data we approximated winter temperature by a transformed lognormal process ($w \sim 10 -$ lognormal($\mu - 10$, σ); Fig. 2C), with μ and σ chosen such that the mean and standard deviation of w are

Decomposition of variance in vital rates

We decomposed interannual variation in fecundity and survival rates over the 24-year study period into components due to demographic stochasticity, climatic and other environmental variables, density effects, and residual unexplained environmental stochasticity. The technical details of the estimation procedure will be described elsewhere; here we describe the major steps. As earlier studies showed no evidence for sex differences in vital rates (van de Pol et al. 2006, 2007), both sexes were pooled for parameter estimation. We decomposed temporal variation in each vital rate using generalized linear mixed models with year included as a random effect (intercept). We assumed that demographic heterogeneity in vital rates was sufficiently accounted for by the stage structure described in Fig. 1 and that the annual between-individual variation in fecundity and survival could be described by a Poisson and binomial probability distribution, respectively. Variation in fecundity was decomposed using a mixed model in program MLwiN 2.0 (Rasbash et al. 2004). Survival and movement probabilities were estimated simultaneously using a multistate mark–recapture–recovery model (model structure as in Fig. 1). Variance components were estimated in the global time-dependent model using the Bayesian Markov chain Monte Carlo random effects procedure implemented in program MARK (Burnham and White 2002). Selection between models with and without specific environmental and density covariates was based on the deviance information theoretic criterion (DIC, a hierarchical modeling generalization of the Akaike information criterion; Burnham and Anderson 2002).

Residual environmental covariation between fecundity and survival rates not caused by density, climatic, or other measured environmental variables was estimated using the shrinkage estimators of the annual residuals of each vital rate on either the log or logit scale (with base *e*). The 24 shrunken annual residuals of each vital rate were assumed to be normally distributed and residuals for each vital rate were used to calculate a variance–covariance matrix that describes the multivariate normally distributed residual environmental (co)variances among the vital rates (see Appendix).

Stochastic population model

Our stage-structured stochastic population model included demographic stochasticity, density dependence, the climatic effect of interest (i.e., winter temperature), other environmental effects, and residual environmental variance within and covariance between vital rates. The population model is asexual (i.e., tracks females only) with the following general form (Caswell 2001):

$$\mathbf{n}_{t+1} = \mathbf{A}_t \times \mathbf{n}_t \quad (1)$$

where $\mathbf{n}_t$ is the column vector of (female) stage sizes at time t and the elements of the projection matrix $\mathbf{A}_t$ are stochastic variables depending on the vital rates in the life cycle (cf. Fig. 1). We used a post-breeding census definition (each year birds first survive, then can move between stages, and finally reproduce) such that Eq. 1 becomes Eq. 2. The expressions determining the between-year expectation, variance, and covariances of the stochastic variables F, S, and M and their dependency on density, winter temperature, and other environmental variables are directly based on the statistical models, and parameter estimates are given in the Appendix. The observed sizes of stage classes in the last year of study were used as initial starting values in the simulations.

By assuming that individual fecundity and survival were generated by a Poisson and binomial process, respectively, the contribution of demographic stochasticity to temporal variation in each vital rate at a certain population size is given by the sampling variance of the specific distribution. Density regulation was modeled by including a ceiling for the number of high- and low-quality territories to account for the fact that breeding habitat is a limiting resource (cf. van de Pol et al. 2007; the ceiling was set to the maximum number of high- and low-quality territories from 1983 to 2007; $N_{H(max)} = 60$, $N_{L(max)} = 150$). A ceiling is based on the idea that at high density the breeding habitats become saturated and cannot be subdivided into smaller parts without their quality becoming below the territory acceptance threshold for nonbreeders (Kokko et al. 2001). Correspondingly, rates of recruitment to and breeding dispersal between high- and low-quality habitats (M_{NL}, M_{NH}, M_{LH}) were modeled as functions of the number of vacant breeding territories per competing nonbreeder. Moreover, breeders in low-quality habitat had priority over nonbreeders when competing for breeding vacancies in high-quality habitat (cf. Heg et al. 2000b). Although oystercatchers sometimes lose their territory ($[M_{HN}, M_{HL}, M_{LN}] > 0$), we did not model this explicitly, as these vacancies were typically reoccupied immediately and consequently this mainly concerns

$$
\begin{pmatrix} n_0 \\ n_1 \\ n_2 \\ n_N \\ n_L \\ n_H \end{pmatrix}_{t+1}
=
\begin{pmatrix}
0 & 0 & 0 & 0 & S_L F_L & S_H F_H \\
S_0 & 0 & 0 & 0 & 0 & 0 \\
0 & S_1 & 0 & 0 & 0 & 0 \\
0 & 0 & S_2 & S_N(1 - M_{NL} - M_{NH}) & 0 & 0 \\
0 & 0 & 0 & S_N M_{NL} & S_L(1 - M_{LH}) & 0 \\
0 & 0 & 0 & S_N M_{NH} & S_L M_{LH} & S_H
\end{pmatrix}_t
\begin{pmatrix} n_0 \\ n_1 \\ n_2 \\ n_N \\ n_L \\ n_H \end{pmatrix}_t
\quad (2)
$$

individuals swapping stages and thus does not affect the stage distribution of the model. Similarly, although some permanent emigration and immigration of non-breeders does occur (~4% annually; van de Pol 2006), we assumed immigration matched emigration and did not model migration explicitly (i.e., we focus on studying the local population dynamics).

Decomposing sensitivities

The sensitivity of population dynamics to climate change was assessed using computer simulations of the stochastic population model (Eqs. 1 and 2) in R (R Development Core Team 2007). We determined the sensitivity of the median time to extinction, because the stochastic population growth rate in a density-regulated population is density dependent itself and therefore less suitable for sensitivity analyses. Median time to extinction was defined as the number of "years" it took for 50% of 300 000 simulated populations to go extinct. As we are dealing with fecundity and survival rates that are approximately lognormally and logit-normally distributed, respectively, it is more convenient to study their effects on the log and logit scales, respectively (e.g., $x_i = \log[F_H]$ or $x_i = \text{logit}[S_1]$). We can decompose the effect of climate change in winter temperature (w) on the median time to extinction (T) into an effect due to changes in the expectation (E) of w and an effect due to the change in the standard deviation (σ) of w:

$$dT = \frac{\partial T}{\partial E(w)} dE(w) + \frac{\partial T}{\partial \sigma_w} d\sigma_w. \quad (3)$$

Eq. 3 allows a quantitative comparison of the impact of a $X°C$ change in $E(w)$ on T relative to the impact of a similar $X°C$ change in σ_w on T (is $|\partial T/\partial E(w)| >$ or $< |\partial T/\partial \sigma_w|$?). Eq. 3 can be further decomposed into how climate effects on each vital rate x_i contribute to the overall effect on dT:

$$dT = \left(\sum_{x_i} \frac{\partial T}{\partial E(x_i)} \frac{\partial E(x_i)}{\partial E(w)} \right) dE(w) + \left(\sum_{x_i} \frac{\partial T}{\partial \sigma_{x_i}} \frac{\partial \sigma_{x_i}}{\partial \sigma_w} \right) d\sigma_w. \quad (4)$$

Eq. 4 thereby permits a quantitative comparison of the relative contribution of climate-dependent fecundity and survival to extinction dynamics (e.g., by comparing the $|\partial T/\partial E(x_i) \times \partial E(x_i)/\partial E(w)|$ of fecundity vs. survival rates). Sensitivities were estimated numerically using small perturbations (<1%) of the variables of interest in the population model.

Results

Climatic and density effects on vital rates

All vital rates across the life cycle were directly or indirectly associated with winter temperature, with temperature explaining 32–46% of the total environmental variance in each vital rate (Fig. 3). Survival rates of all stage classes were strongly positively associated

with winter temperature (Fig. 3A–D; see the Appendix for parameter estimates). The effect of winter temperature on survival was strongest for juvenile age classes (see slopes in Fig. 3A, B vs. Fig. 3C, D). Winter temperature also explained 42–73% of the positive environmental covariances between stage-dependent survival rates (Appendix). Other environmental variables (e.g., food abundances, North Atlantic Oscillation index, summer temperature) did not explain any additional environmental variance in any of the stage-dependent survival rates, nor did we find any evidence for density-dependent survival (DIC increased >1 when including these covariates).

Movement probabilities between stages, specifically breeding dispersal from low- to high-quality breeding habitat (M_{LH}) and recruitment into the breeding population (M_{NL} and M_{NH}) were strongly dependent on the number of breeding vacancies per competitor. The number of vacancies in high-quality habitat per surviving competitor in low-quality habitat was a good predictor of M_{LH} (Fig. 3E). Similarly, the number of remaining vacancies in high-quality habitat per surviving nonbreeder was a good predictor of M_{NH} (Fig. 3F; similar results for M_{NL}). These results suggest that the climatic effects on recruitment and breeding dispersal are density dependent themselves, as these movement probabilities are determined by the product of the size of stage classes and climate-dependent survival rates (Fig. 3E, F).

Fecundity was indirectly dependent on winter temperature, by being positively correlated with ragworm abundance (Fig. 3G, H), oystercatchers' main food source during chick feeding (Bunskoeke et al. 1996). Cold winter temperatures promote egg production of ragworms (Lawrence and Soame 2004), and as expected the annual ragworm abundance was strongly negatively related to winter temperature in our study area (inset of Fig. 3I; $R^2 = 0.38$). Consequently, both F_H and F_L were indirectly negatively associated with winter temperature (Fig. 3I, J; see Appendix for parameter estimates). Fecundity was also negatively associated with flooding events during the breeding season (Fig. 3G, H), as these floods flushed away many nests. However, as there is currently no evidence that these flooding events will become systematically more or less frequent, we modeled flooding effects in the population model as a separate random (residual) environmental process that does not change systematically over time (see Appendix). Other environmental variables (e.g., summer temperature, precipitation, other food sources) did not explain any additional environmental variance in fecundity rates, nor did we find any evidence for density-dependent fecundity (DIC increased >1 when including these covariates). The fecundity of breeders in high- and low-quality habitat exhibit strong positive environmental covariance ($\sigma_{F_H, F_L} = 0.49 \pm 0.21$ [estimate $\pm$ SE]). However, this covariance disappeared after accounting for effects of food and floodings on
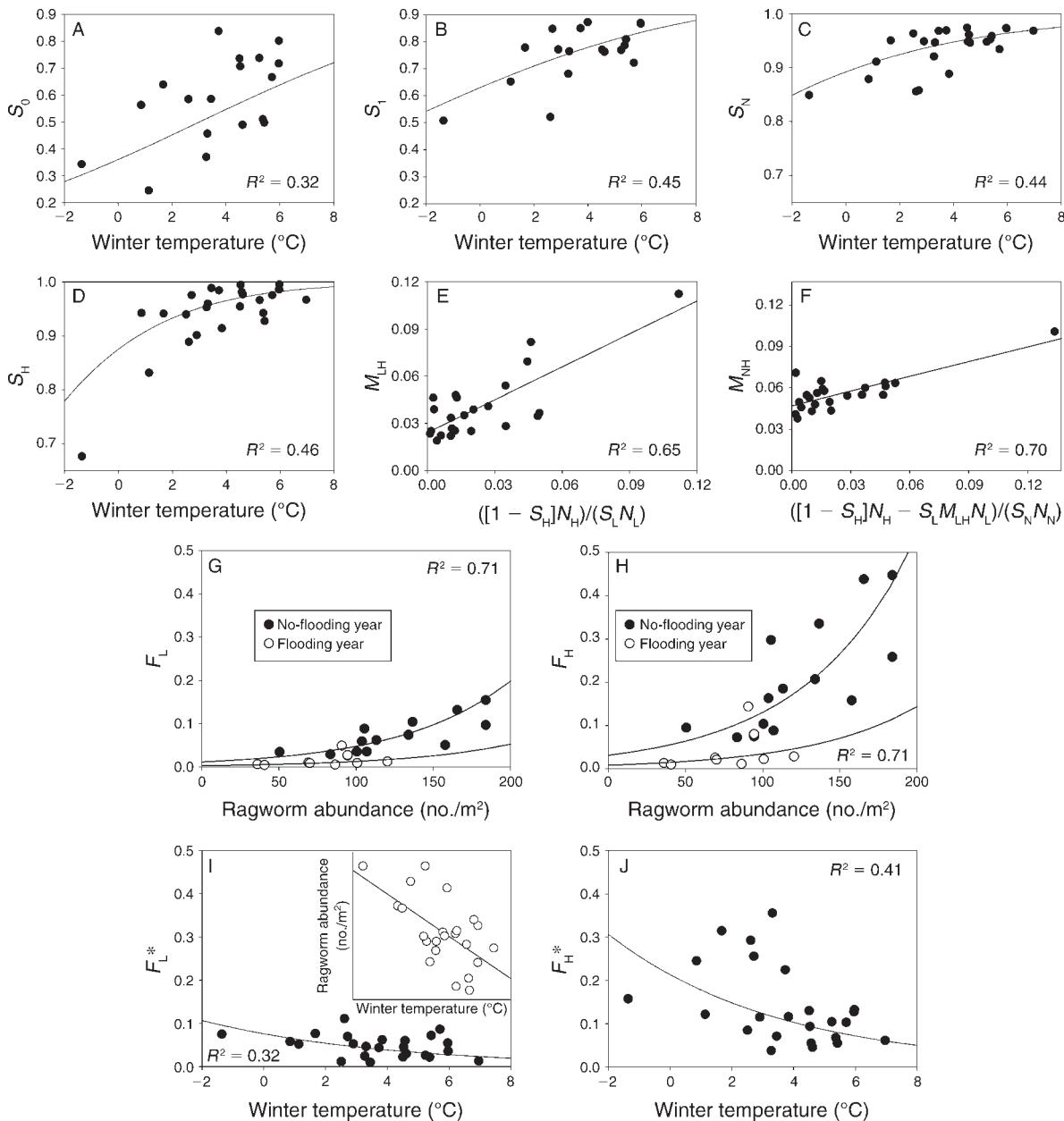
Fig. 3. Relationships of annual survival (S), movement (M), and fecundity (F) rates to winter temperature, competitor density, and other environmental variables (1983–2007). The competitor density term on the x-axis in panels (E) and (F) is explained in *Methods*. In panels (I) and (J), F_L^* and F_H^* are adjusted for flooding effects and for the dependency between ragworm abundance and winter temperature; see panels (G) and (H) and the subpanel within (I). All regression equations and parameter estimates with standard errors are given in the Appendix, including those not presented in this figure (S_2, S_L, and M_{NL}). Six states are distinguished: 0, fledged offspring; 1, one-year-old juveniles; 2, two-year-old juveniles; N, adult nonbreeders; L, breeders in low-quality habitat; H, breeders in high-quality habitat.

fecundity ($\sigma_{F_H, F_L} = 0.02 \pm 0.08$), which is consistent with the observation that breeders in high- and low-quality habitat are both affected by the same food stocks and flooding events.

Climate effects on population dynamics

Different realizations of the stochastic population model can give quite dissimilar trajectories (Fig. 4A),

and prediction intervals for time to extinction were wide (Fig. 4B). Under current environmental conditions this population is likely to go extinct, but the estimated median time to extinction for this strongly declining population (~5% annually from 1983 to 2007) was estimated to be still rather long at 413 years (Fig. 4B). The duration to extinction is typically long, because simulated populations can fluctuate for centuries at
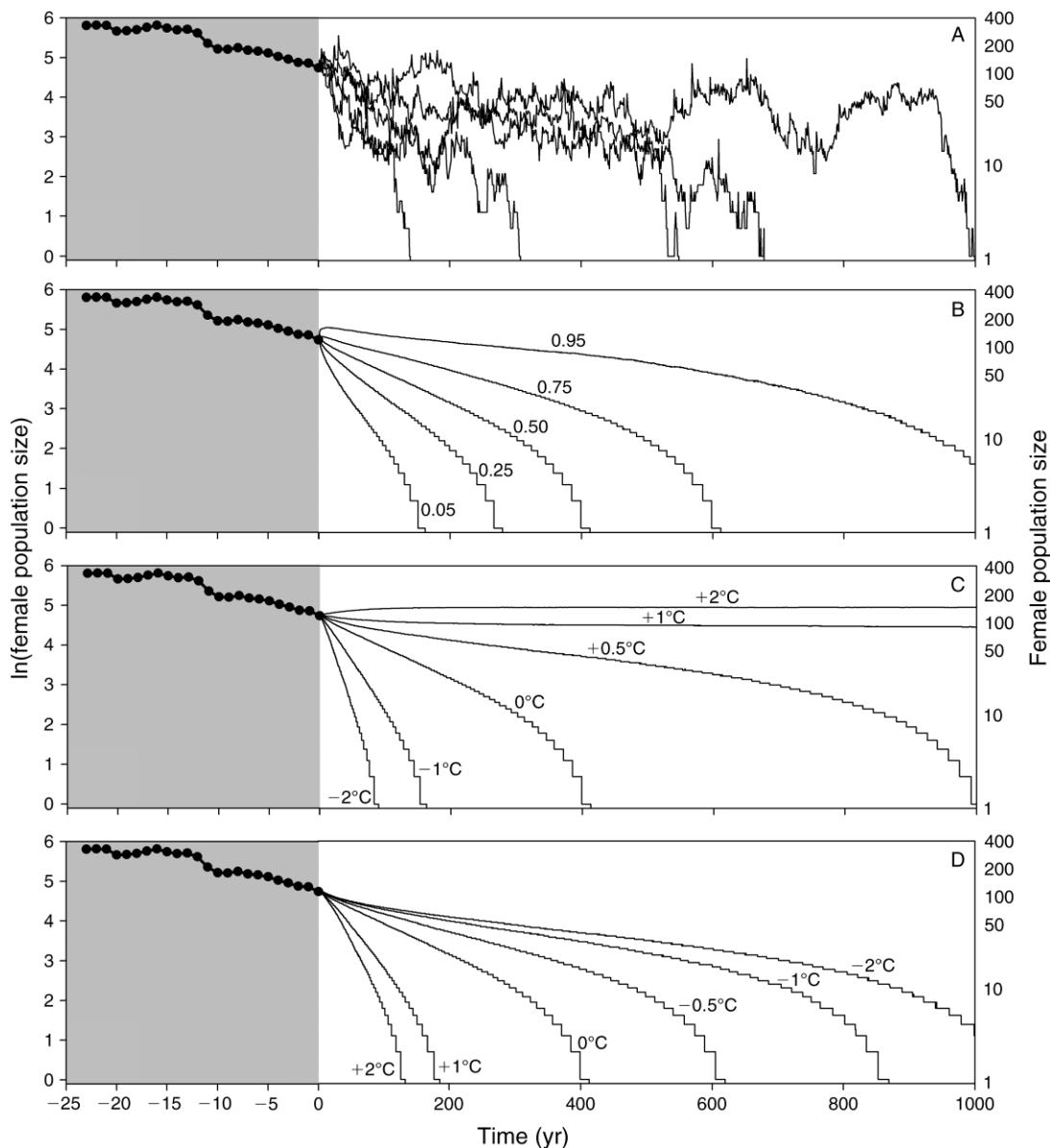
FIG. 4. Historical (gray panels) and projected (white panels) changes in population numbers for scenarios of changing winter temperature (w). (A) Time plots of five randomly selected realizations of a stochastic population model with no changes in the mean and SD of winter temperature. (B) Time plots of 5th, 25th, 50th, 75th, and 95th percentiles of the population size of 300 000 simulated populations of a stochastic population model with no changes in the mean and standard deviation of winter temperature. (C) The 50th percentile of population size for scenarios with changes in the expectation of winter temperature, $E(w)$, while keeping the standard deviation of winter temperature, σ_w, constant. (D) The 50th percentile of population size for scenarios with changes in σ_w, while keeping $E(w)$ constant. The point in time at which the 50th percentile reaches a population size of zero is defined as the median time to extinction, T. Note the logarithmic y-axes; the timescale on the x-axis differs between the gray and white panels (year 2007 set to time = 0).

intermediate population sizes (Fig. 4A). At intermediate population sizes all low-quality habitat is abandoned and only high-quality habitat is occupied ($N_{pop} < N_{H(max)}$), which increases the per capita productivity (as $F_H > F_L$) of this declining population to the point at which the population growth is close to zero. The final process of extinction can occur relatively abruptly (Fig. 4A), with growth rate becoming strongly negative again

($\sim$6% per year) at low population size ($N_{pop} < 20$) due to demographic stochasticity.

A rise in mean winter temperature, $E(w)$, increased median time to extinction, T, substantially; using small perturbations we estimated $\partial T/\partial E(w) = 543$, meaning that an increase in $E(w)$ of 0.1°C leads to an increase in T of $\sim$54 years. Increasing the standard deviation of winter temperature σ_w led to a decrease in T and we

estimated $\partial T/\partial \sigma_w = -364$, meaning that an increase in σ_w of 0.1 decreases T by roughly 36 years. Thus, a 0.1°C change in mean temperature is predicted to alter persistence time by 1.5 times (=54/36), as many years as would a 0.1°C change in the standard deviation in temperature, suggesting that the dynamics of oystercatchers are intrinsically more sensitive to changes in the mean than in the variability of this climatic variable ($|\partial T/\partial E(w)| > |\partial T/\partial \sigma_w|$). In addition, as climate models (van der Hurk et al. 2006) predict 10-fold larger changes in $E(w)$ than in σ_w until the year 2100 ($dE(w) = +1.5$°C to $+4.4$°C; $d\sigma_w = -0.1$°C to -0.3°C; Fig. 2A, B), the predicted effect of $|\partial T/\partial E(w) \times dE(w)|$ on T is expected to overwhelm the effect of $|\partial T/\partial \sigma_w \times d\sigma_w|$ on T even more strongly (see Eq. 3). Fortunately for oystercatchers, changes in the mean and variability of winter temperature both are expected to improve population viability, as future climate scenarios predict that $E(w)$ will increase but σ_w will decrease.

The sensitivities reported above deal only with small changes in $E(w)$; large changes in $E(w)$ are predicted to result in strongly nonlinear responses of T (Fig. 4C). If $E(w)$ increases by 1°C or more (as projected by all climate models; Fig. 2A) then $T \rightarrow \infty$, and populations typically fluctuate stochastically around a certain carrying capacity (Fig. 4C). Thus, an increase in $E(w)$ of ~1°C is expected to shift the population dynamics from almost certain extinction toward stationary fluctuations around a mean population size. Contrastingly, even a 1°C decrease in σ_w (which is much more than projected by all climate models; Fig. 2B), seems to have relatively little impact on T (Fig. 4D), again suggesting that oystercatcher population dynamics are more sensitive to changes in mean winter temperature than in variability of winter temperature.

Population impact of climate change decomposed per vital rate

In total the cumulative effect of changes in $E(w)$ through each vital rate was estimated to be positive, namely,

$$\sum_{x_i} \frac{\partial T}{\partial x_i} \frac{\partial x_i}{\partial E(w)} = 569$$

(see Table 1). Considering the finite number of simulations, this estimate is close to our earlier direct estimate of $\partial T/\partial E(w) = 543$, illustrating the consistency of our decomposition approach. Future climate change that increases $E(w)$ has a negative impact on T through its effects on stage-dependent fecundity rates, but has a positive impact on T through its effects on stage-dependent survival rates (Table 1). The cumulative sensitivity of T to effects of $E(w)$ on all survival rates was three times as large in magnitude, i.e.,

$$\sum_{x_i=\text{logit}(s_i)} \frac{\partial T}{\partial x_i} \frac{\partial x_i}{\partial E(w)} = 835$$

than the cumulative sensitivity of T to effects of $E(w)$ on all fecundity rates, i.e.,

$$\sum_{x_i=\log(f_i)} \frac{\partial T}{\partial x_i} \frac{\partial x_i}{\partial E(w)} = -276$$

showing that the effects on this population's time to extinction by the climate mean are largely mediated by mean temperature effects on survival. The stage-specific vital rates that had by far the largest positive and negative contributions to the overall effect of $E(w)$ on T were both vital rates of breeders in high-quality habitat (namely S_H and F_H; Table 1). The reason S_H and F_H contributed more strongly to the overall effect of $E(w)$ on T than other vital rates was because T is very sensitive to changes in S_H and F_H; S_H and F_H are not more sensitive to changes in $E(w)$ than other vital rates (Table 1).

The cumulative effect of changes in σ_w through all vital rates was estimated to be negative, namely,

$$\sum_{x_i} \frac{\partial T}{\partial \sigma_{x_i}} \frac{\partial \sigma_{x_i}}{\partial \sigma_w} = -316$$

(close to the direct estimate of $\partial T/\partial \sigma_w = -364$). Future climate change that increases σ_w positively impacts T through its effects on stage-specific fecundity rates, while it negatively impacts T through its effects on stage-specific survival rates (Table 1). The cumulative sensitivity of T to effects of σ_w on all survival rates was three times as large in magnitude, i.e.,

$$\sum_{x_i=\text{logit}(s_i)} \frac{\partial T}{\partial \sigma_{x_i}} \frac{\partial \sigma_{x_i}}{\partial \sigma_w} = -497$$

than the cumulative sensitivity of T to effects of σ_w on all fecundity rates, i.e.,

$$\sum_{x_i=\log(f_i)} \frac{\partial T}{\partial \sigma_{x_i}} \frac{\partial \sigma_{x_i}}{\partial \sigma_w} = 181$$

showing that climate variability effects on this population's time to extinction are largely mediated by temperature variability effects on survival. The vital rates that had the strongest positive and negative contributions to the overall effect of σ_w on T were the same vital rates that were the main contributors to the overall effect of $E(w)$ on T (namely S_H and F_H; Table 1).

DISCUSSION

We have quantified how climate affects the major vital rates over a structured life cycle of a long-lived species and determined the sensitivity of population dynamics to changes in the mean and variability of these vital rates. This demographic approach allowed us to investigate how climatic effects on each demographic rate give rise to changes in the population dynamics. We now discuss the implications of our results for some important unresolved questions in our field.

TABLE 1. Sensitivities of median time to extinction, T, to changes in expectation and standard deviation of winter temperature, $E(w)$ and σ_w, respectively, decomposed for each vital rate x_i (see Eq. 4) for a declining Eurasian Oystercatcher (*Haematopus ostralegus*) population on the Dutch island of Schiermonnikoog.

x_i	$\partial T/\partial E(x_i)$	$\partial E(x_i)/\partial E(w)$	$(\partial T/\partial E(x_i))(\partial E(x_i)/\partial E(w))$	$\partial T/\partial \sigma_{x_i}$	$\partial \sigma_{x_i}/\partial \sigma_w$	$(\partial T/\partial \sigma_{x_i})(\partial \sigma_{x_i}/\partial \sigma_w)$
log f_L	28	−0.182	−5	41	0.182	8
log f_H	1602	−0.169	−271	1024	0.169	173
Sum of fecundity			−276			181
logit s_0	559	0.190	106	−76	0.190	−14
logit s_1	380	0.182	69	−39	0.182	−7
logit s_2	60	0.200	12	−50	0.200	−10
logit s_N	4	0.195	1	−49	0.195	−10
logit s_L	79	0.235	18	−34	0.235	−8
logit s_H	1827	0.344	629	−1301	0.344	−448
Sum of survival			835			−497
Sum of all			559			−316

Notes: Sensitivities of stage-dependent fecundities, f_i, and survival, s_i, are on the log or logit scale, respectively (see *Methods*). Environmental conditions during the study period were $E(w) = 3.7°C$ and $\sigma_w = 1.7°C$, resulting in $T = 413$ years.

Impact of changes in climatic mean vs. variability

Global climate change not only results in changes in the mean of climatic variables, but also in their variance (Easterling et al. 2001), which has been shown to affect population dynamics (e.g., Drake 2005, Altwegg et al. 2006, Boyce et al. 2006). So far no study directly compared the relative importance of changes in mean and variance of climatic variables on population dynamics via their effect on each vital rate across the life cycle using empirical data. Eq. 4 shows there can be various mechanisms by which changes in the climatic mean or variability can affect time to extinction, i.e., multiple terms can cause

$$\sum_{x_i} \frac{\partial T}{\partial E(x_i)} \frac{\partial E(x_i)}{\partial E(w)} dE(w) \neq \sum_{x_i} \frac{\partial T}{\partial \sigma_{x_i}} \frac{\partial \sigma_{x_i}}{\partial \sigma_w} d\sigma_w.$$

In our study two mechanisms were important: (1) time to extinction was more sensitive to changes in the mean than in the standard deviation of most vital rates, i.e.,

$$\left| \frac{\partial T}{\partial E(x_i)} \right| > \left| \frac{\partial T}{\partial \sigma_{x_i}} \right|$$

(see Table 1) and (2) climate models predicted much larger changes in the mean than in the standard deviation of temperature ($|dE(w)| > |d\sigma_w|$; Fig. 2). Since in most animal and plant species the sensitivity of population dynamics to standard deviations of vital rates is much lower than the sensitivity to mean vital rates (Haridas and Tuljapurkar 2005, Morris et al. 2008), we would expect changes in climatic means to have often a stronger impact on population dynamics than changes in climatic variability (as long as climatic variability does not cause the catastrophic death of the entire population and projected changes in climatic variability are not much larger than those for climatic means). Potentially, our conclusion might thus hold for a wide variety of life histories.

The environmental canalization hypothesis suggests that the vital rates to which population growth is most sensitive in terms of changes in their mean values might also be the vital rates most resilient to environmental variation (Pfister 1998, Sæther and Bakke 2000, Gaillard and Yoccoz 2003). In long-lived species such as the oystercatcher, population growth is more sensitive to changes in the mean of adult than of juvenile survival (van de Pol et al. 2006). In line with the environmental canalization hypothesis we found that juvenile survival was more variable in time and more sensitive to winter temperature than adult survival (Fig. 3A, B vs. Fig. 3C, D). However, although juvenile survival was very sensitive to temperature variability, this variability barely affected the extinction dynamics (Table 1). In contrast, while adult survival of breeders in high-quality habitat was less sensitive to winter temperature variability, this low variability strongly affected the extinction dynamics (Table 1). Thus, although the vital rates to which population growth is most sensitive in terms of changes in their mean values might be more resilient to environmental variation, this does not mean that effects of climate change via such canalized vital rates are not important for population dynamics.

Does increased climatic variability reduce population viability?

Although classical stochastic population theory suggests that environmental variability reduces population viability (Lewontin and Cohen 1969, Lande and Orzack 1988), recent work suggests that increased climatic variability can sometimes also improve population viability, depending on the exact relationship between vital rates and climatic variables (Drake 2005, Boyce et al. 2006, Morris et al. 2008). In oystercatchers, fecundity rates have a decreasing convex relationship with winter temperature (Fig. 3I, J) and consequently increasing variance in winter temperature is expected to increase mean fecundity and, thereby, persistence time (due to Jensen's inequality; Caughley 1987, Ruel and Ayres 1999, Boyce et al. 2006). Conversely, due to the increasing concave relationship between survival and

winter temperature (Fig. 3B–D), increased variability in winter temperature is expected to decrease mean survival and thereby persistence time (Table 1). Thus, the key element in understanding the impact of climatic variability on vital rates is to be able to explain why some relationships between vital rates and climatic variables are convex and others concave.

It is possible that species' life histories can be used to make general predictions about the impact of climatic variability on vital rates. In species with low reproductive output most individuals typically do not produce any young at all in an average year. Thus, in such species fecundity cannot get much worse in bad years, whereas it can get much better in good years, resulting in a convex relationship between fecundity and climatic variables (Boyce et al. 2006). Similar arguments can be used to propose that the relationship between survival and climatic variables is typically concave for long-lived species, as survival is already so high that in good years it cannot get much better, while in bad years it can get much worse. Conversely, this hypothesis suggests that for short-lived species with low juvenile or adult survival (<50%) the relationship between survival and climatic variables might be convex and increasing climatic variability might actually increase these survival rates and thereby population viability. Our results on the Eurasian Oystercatcher, a species at the extreme of the low-productivity and longevity spectrum of life histories (Sæther and Bakke 2000), are well in line with these predictions on how life history might affect the impact of climatic variability on vital rates and population viability.

Decomposing climate effects per vital rate

Determining the critical periods affecting population dynamics is a first step in predicting the consequences of climate change on population fluctuations (Hallett et al. 2004, Sæther et al. 2004). Many studies have shown that climate affects the population dynamics through an effect on either fecundity during the breeding season or on the number of individuals that survive the nonbreeding season. In avian species, the dynamics of precocial birds seem to be especially strongly dependent upon climate during the breeding season, while the population fluctuations of altricial birds covary strongest with climatic variables during the nonbreeding season (Sæther et al. 2004). At first sight our results on semi-precocial oystercatchers seem to suggest both pathways are important, as climatic effects on both fecundity and survival affected population dynamics (Fig. 3, Table 1). However, the effect of climate on fecundity was not caused by (summer) climate during the breeding season, but was due to an indirect effect of winter temperature on the dynamics of oystercatchers' main prey species. Consequently, both fecundity and survival were affected by the same climatic variable during the nonbreeding winter season (albeit in opposing ways). Thus, when finding that population fluctuations are most strongly

associated with climatic variables during the nonbreeding season, this does not necessarily imply that this climatic variable only affects demography via survival during this season. In addition, it may be problematic to generalize across populations, as Sæther et al. (2007) and Grøtan et al. (2008) have shown that there is often large interpopulation variation in the critical season during which the strongest climate-induced influences on the population dynamics arise.

The spatial heterogeneity in habitat quality and the resulting stage structure and density dependence in vital rates strongly affect the extinction dynamics. As density decreases, first surplus nonbreeders will disappear and subsequently low-quality habitat will not be reoccupied, resulting in an increase of the per capita productivity with declining density (the "buffer effect"; Kluijver and Tinbergen 1953). Consequently, in our simulations the population typically fluctuated for long periods around an intermediate population size at which only high-quality territories are occupied ($N_{pop} < 60$ (=$N_{H(max)}$); Fig. 4A) with a realized growth rate close to zero. Only when by chance populations became small (<20 individuals) was the population growth further reduced due to demographic stochasticity, and typically extinction followed quickly (a stochastic Allee effect; Lande 1998; see Fig. 4A). An important consequence of this buffer effect is that the sensitivity of time to extinction was highest for vital rates associated with breeding in high-quality habitat (Table 1). Thus, although survival and fecundity in low-quality habitat were both affected by winter temperature (Fig. 3I, Appendix), this had little impact on population viability (Table 1). The huge variation in sensitivities among stage classes highlights the importance of investigating the impact of climate change on vital rates across the entire life cycle before making strong inferences about the population consequences. Furthermore, it underlines the critical role of density regulatory mechanisms in determining the population impacts of climate effects on vital rates.

Contribution of climate change to population change

Even small increases in mean winter temperature were expected to improve the population viability in our population model substantially. Due to nonlinearity in the dynamics we expect that somewhat larger increases of ~1°C will have a disproportional larger effect, and our results suggest that such warming could potentially save this population from extinction (Fig. 4C). However, predicting long-term consequences of climate change remains a problematic task, as climate models predict large changes in temperatures (+1.5 to +4.4°C). These large temperature rises mean that the domain of winter temperatures will shift to a range of which we still have little knowledge regarding the manner in which vital rates react to such temperatures. In addition, other aspects of the climate might also change in the future. It is still unclear how intra-annual climatic variability might change in the future (e.g., will cold spells become

more or less common?) and how this will affect vital rates (Hallet et al. 2004). Also, the predicted positive effect of rising winter temperatures might be counteracted by negative effects of flooding events (Fig. 3G, H), which seem to have become more frequent recently (van de Pol 2006). Finally, individuals might adapt to climate change (Visser 2008); for example, oystercatchers might shift to alternative food sources that are less sensitive to increased winter temperature. Although we are still a long way from accurately predicting long-term consequences of the large climatic changes many populations are facing nowadays, we hope this study illustrates that by decomposing the effects of small changes in climatic variables on vital rates and population dynamics we can gain important insight into the mechanisms determining how populations will respond to climate change. Disturbingly, the duration and level of detail of field data required to gain these insights is typically unavailable for the species for which these insights are actually most needed (i.e., those of conservation concern).

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APPENDIX

Estimates of model parameters used in the stochastic population model (*Ecological Archives* E091-085-A1).

Ecological Archives **E091-085-A1**

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Appendix A: Estimates of model parameters used in stochastic population model.

General modeling approach

By assuming that the fecundity in state k of individual i in year j is $F_{kij} \sim Poisson(f_{kij})$

and survival is $S_{kij} \sim Binomial(s_{kij})$, the temporal variation in fecundity and survival was

decomposed into components due to demographic variation, climatic and other

environmental variables, density effects and residual unexplained environmental

(co)variation using the following statistical model:

$$
\begin{bmatrix}
\log f_{Lij} \\
\log f_{Hij} \\
\text{logit } s_{oij} \\
\text{logit } s_{1ij} \\
\text{logit } s_{2ij} \\
\text{logit } s_{Nij} \\
\text{logit } s_{Lij} \\
\text{logit } s_{Hij}
\end{bmatrix}
=
\begin{bmatrix}
\beta_{f_L 0} \\
\beta_{f_H 0} \\
\beta_{s_0 0} \\
\beta_{s_1 0} \\
\beta_{s_2 0} \\
\beta_{s_N 0} \\
\beta_{s_L 0} \\
\beta_{s_H 0}
\end{bmatrix}
+
\begin{bmatrix}
\underline{\beta_{f_L Z}} \\
\underline{\beta_{f_H Z}} \\
\underline{\beta_{s_0 Z}} \\
\underline{\beta_{s_1 Z}} \\
\underline{\beta_{s_2 Z}} \\
\underline{\beta_{s_N Z}} \\
\underline{\beta_{s_L Z}} \\
\underline{\beta_{s_H Z}}
\end{bmatrix}
\underline{Z}_j
+
\begin{bmatrix}
\underline{\beta_{f_L N}} \\
\underline{\beta_{f_H N}} \\
\underline{\beta_{s_0 N}} \\
\underline{\beta_{s_1 N}} \\
\underline{\beta_{s_2 N}} \\
\underline{\beta_{s_N N}} \\
\underline{\beta_{s_L N}} \\
\underline{\beta_{s_H N}}
\end{bmatrix}
\underline{N}_j
+
\begin{bmatrix}
\underline{\beta_{f_L ZN}} \\
\underline{\beta_{f_H ZN}} \\
\underline{\beta_{s_0 ZN}} \\
\underline{\beta_{s_1 ZN}} \\
\underline{\beta_{s_2 ZN}} \\
\underline{\beta_{s_N ZN}} \\
\underline{\beta_{s_L ZN}} \\
\underline{\beta_{s_H ZN}}
\end{bmatrix}
\underline{Z_j N_j}
+
\begin{bmatrix}
u_{f_L 0 j} \\
u_{f_H 0 j} \\
u_{s_0 0 j} \\
u_{s_N 0 j} \\
u_{s_N 0 j} \\
u_{s_N 0 j} \\
u_{s_L 0 j} \\
u_{s_H 0 j}
\end{bmatrix},
$$

where $\underline{Z}_j$ is a column vector of climatic and other environmental variables (e.g., winter

temperature, food) and $\underline{N}_j$ is a column vector of conspecifics densities (e.g., N_{pop}, N_L)

observed during the study period. The beta's ($\beta_{f_k 0}$, $\beta_{s_k 0}$, and row vectors $\underline{\beta_{f_k Z}}$, $\underline{\beta_{s_k N}}$,

etc.) are constants estimated by the statistical model. We specifically considered

interactions between climate and density effects ($\underline{Z_j N_j}$). In addition, we estimated the

residual environmental process variance and covariance in demographic rates that was

not explained by Z_j or N_j, by including random intercepts (u_{0j}) that vary between

years.

Due to data limitations we were forced to constrain $u_{s_1 0j} = u_{s_2 0j} = u_{s_N 0j}$. Based on

preliminary data exploration it seemed reasonable to assume that $u_{f_k 0j}$ and $u_{s_k 0j}$ can be

approximated by a multivariate normal distribution (MVN) with mean zero and a

between-year variance-covariance matrix Ω_u:

$$\begin{bmatrix} u_{f_L 0j} \\ u_{f_H 0j} \\ u_{s_0 0j} \\ u_{s_N 0j} \\ u_{s_L 0j} \\ u_{s_H 0j} \end{bmatrix} \sim MVN(0, \Omega_u) : \Omega_u = \begin{bmatrix} \sigma^2_{u_{f_L 0}} & & & & & \\ \sigma_{u_{f_L 0 f_H 0}} & \sigma^2_{u_{f_H 0}} & & & & \\ \sigma_{u_{f_L 0 s_0 0}} & \sigma_{u_{f_H 0 s_0 0}} & \sigma^2_{u_{s_0 0}} & & & \\ \sigma_{u_{f_L 0 s_N 0}} & \sigma_{u_{f_H 0 s_N 0}} & \sigma_{u_{s_0 0 s_N 0}} & \sigma^2_{u_{s_N 0}} & & \\ \sigma_{u_{f_L 0 s_L 0}} & \sigma_{u_{f_H 0 s_L 0}} & \sigma_{u_{s_0 0 s_L 0}} & \sigma_{u_{s_N 0 s_L 0}} & \sigma^2_{u_{s_N 0}} & \\ \sigma_{u_{f_L 0 s_H 0}} & \sigma_{u_{f_H 0 s_H 0}} & \sigma_{u_{s_0 0 s_H 0}} & \sigma_{u_{s_N 0 s_H 0}} & \sigma_{u_{s_L 0 s_H 0}} & \sigma^2_{u_{s_H 0}} \end{bmatrix}$$

Note that we assume a multivariate normal distribution of (co)variances of vital rates on

the transformed log and logit scale (with base e). Between-year covariances between

fecundity and survival were based on fecundity in the breeding season and survival

during the preceding period (and not survival during the following period).

Model without climatic, density and other environmental covariates

We first fitted a multivariate model that only included an intercept and a separate year

random effect for each vital rate with a fully specified between-year variance covariance

matrix. All parameter estimates are given with standard errors between parentheses. The

model can be described by the following multivariate regression equation:

$$
\begin{bmatrix}
\log f_{L\,ij} \\
\log f_{H\,ij} \\
\text{logit } s_{o\,ij} \\
\text{logit } s_{1\,ij} \\
\text{logit } s_{2\,ij} \\
\text{logit } s_{N\,ij} \\
\text{logit } s_{L\,ij} \\
\text{logit } s_{H\,ij}
\end{bmatrix}
=
\begin{bmatrix}
-1.801(0.156) \\
-2.612(0.146) \\
0.126(0.153) \\
1.203(0.136) \\
3.358(0.165) \\
2.830(0.099) \\
3.057(0.116) \\
3.213(0.175)
\end{bmatrix}
+
\begin{bmatrix}
u_{f_L 0 j} \\
u_{f_H 0 j} \\
u_{s_0 0 j} \\
u_{s_N 0 j} \\
u_{s_N 0 j} \\
u_{s_N 0 j} \\
u_{s_L 0 j} \\
u_{s_H 0 j}
\end{bmatrix}
$$

with

$$
\begin{bmatrix}
u_{f_L 0 j} \\
u_{f_H 0 j} \\
u_{s_0 0 j} \\
u_{s_N 0 j} \\
u_{s_L 0 j} \\
u_{s_H 0 j}
\end{bmatrix}
\sim MVN(0, \Omega_u) : \Omega_u =
\begin{bmatrix}
1.210(0.349) \\
0.491(0.208) & 0.661(0.191) \\
0.117(0.183) & 0.064(0.133) & 0.641(0.185) \\
-0.215(0.140) & -0.120(0.101) & 0.275(0.112) & 0.351(0.101) \\
-0.167(0.161) & -0.179(0.122) & 0.379(0.138) & 0.310(0.106) & 0.491(0.142) \\
-0.095(0.236) & 0.038(0.174) & 0.471(0.196) & 0.363(0.147) & 0.395(0.170) & 1.094(0.316)
\end{bmatrix}
$$

Note that in this model Ω_u describes the variance within vital rates and covariances

between vital rates, which also includes (co)variation due to density dependence and

climatic or environmental variables.

Model with climatic, density and other environmental covariates

Below we give the final model that included three climatic/environmental variables

explaining a substantial amount of the temporal variation in vital rates (see Fig. 3 in the

main text). Models that included various density and other environmental variables were

not better supported by the data as determined by model selection procedures based on

information theoretic criteria (all ΔDIC>1). The model can be described by the following

multivariate regression equation:

$$
\begin{bmatrix}
\log f_{Lij} \\
\log f_{Hij} \\
\text{logit } s_{oij} \\
\text{logit } s_{1ij} \\
\text{logit } s_{2ij} \\
\text{logit } s_{Nij} \\
\text{logit } s_{Lij} \\
\text{logit } s_{Hij}
\end{bmatrix}
=
\begin{bmatrix}
-1.821(0.156) \\
-2.712(0.146) \\
0.126(0.153) \\
1.203(0.136) \\
3.358(0.165) \\
2.830(0.099) \\
3.057(0.116) \\
3.213(0.175)
\end{bmatrix}
+
\begin{bmatrix}
0 \\
0 \\
0.190(0.081) \\
0.182(0.067) \\
0.200(0.095) \\
0.195(0.053) \\
0.235(0.061) \\
0.344(0.093)
\end{bmatrix}(w-w^*)+
\begin{bmatrix}
0.0142(0.0044) \\
0.0132(0.0028) \\
0 \\
0 \\
0 \\
0 \\
0 \\
0
\end{bmatrix}(r-r^*)+
\begin{bmatrix}
-1.318(0.388) \\
-1.229(0.404) \\
0 \\
0 \\
0 \\
0 \\
0 \\
0
\end{bmatrix}(q-q^*)+
\begin{bmatrix}
u_{f_L 0j} \\
u_{f_H 0j} \\
u_{s_0 0j} \\
u_{s_N 0j} \\
u_{s_N 0j} \\
u_{s_N 0j} \\
u_{s_L 0j} \\
u_{s_H 0j}
\end{bmatrix}
$$

with three environmental variables winter temperature w (°C), ragworm abundance r

(individuals/m^2) and flooding event q (0 or 1) included. These variables were

standardized to mean 0 by subtracting the normalization constants $w^*=3.67$, $r^*=107.2$

and $q^*=0.375$ as determined over the study period 1983-2007. Ragworm abundance was

subsequently modeled as a function of the variable winter temperature (Fig. 3I):

$$r = 153.04(15.0) - 12.8(3.6)w + e_{r_j}.$$

Winter temperature was modeled as a random variable described by a transformed

lognormal process $w \sim 10 - LogNormal(\mu-10,\sigma)$, with μ and σ chosen such that

$E(w) = 3.67(0.44)$ and $\sigma_w = 1.71(0.49)$ as in the study period 1983-2007 (see Fig. 2C). In

this paper we focus on temperature effects (as this is the only variables for which we have

evidence that it will change systematically in the future) and therefore residual ragworm

process variance (e_{r_j}) and flooding events were modeled as random variables part of the

residual environmental stochasticity:

$$
\begin{bmatrix}
\log f_{Lij} \\
\log f_{Hij} \\
\text{logit } s_{oij} \\
\text{logit } s_{1ij} \\
\text{logit } s_{2ij} \\
\text{logit } s_{Nij} \\
\text{logit } s_{Lij} \\
\text{logit } s_{Hij}
\end{bmatrix}
=
\begin{bmatrix}
-1.821(0.156) \\
-2.712(0.146) \\
0.126(0.153) \\
1.203(0.136) \\
3.358(0.165) \\
2.830(0.099) \\
3.057(0.116) \\
3.213(0.175)
\end{bmatrix}
+
\begin{bmatrix}
-0.182(0.076) \\
-0.169(0.060) \\
0.190(0.081) \\
0.182(0.067) \\
0.200(0.095) \\
0.195(0.053) \\
0.235(0.061) \\
0.344(0.093)
\end{bmatrix}
+(w-w^*)+
\begin{bmatrix}
0.0142(0.0044) \\
0.0132(0.0028) \\
0 \\
0 \\
0 \\
0 \\
0 \\
0
\end{bmatrix}
+
\begin{bmatrix}
-1.318(0.388) \\
-1.229(0.404) \\
0 \\
0 \\
0 \\
0 \\
0 \\
0
\end{bmatrix}
e_{r_j}
+
\begin{bmatrix}
u_{f_L 0j} \\
u_{f_H 0j} \\
u_{s_0 0j} \\
u_{s_N 0j} \\
u_{s_N 0j} \\
u_{s_N 0j} \\
u_{s_L 0j} \\
u_{s_H 0j}
\end{bmatrix}
e_{q_j}
+
\begin{bmatrix}
u_{f_L 0j} \\
u_{f_H 0j} \\
u_{s_0 0j} \\
u_{s_N 0j} \\
u_{s_N 0j} \\
u_{s_N 0j} \\
u_{s_L 0j} \\
u_{s_H 0j}
\end{bmatrix}
$$

with ragworm process variance $e_{r_j} \sim N(0, \sigma_{e_r}) : \sigma_{e_r} = 31.5(9.1)$, flooding variance

$e_{q_j} \sim (Bin(\pi) - \pi): \pi = 0.375(0.049)$ and residual environmental (co)variances:

$$
\begin{bmatrix}
u_{f_L 0j} \\
u_{f_H 0j} \\
u_{s_0 0j} \\
u_{s_N 0j} \\
u_{s_L 0j} \\
u_{s_H 0j}
\end{bmatrix}
\sim MVN(0, \Omega_u) : \Omega_u =
\begin{bmatrix}
0.617(0.178) \\
0.021(0.088) & 0.300(0.087) \\
0.114(0.117) & -0.114(0.083) & 0.513(0.148) \\
-0.078(0.076) & -0.116(0.057) & 0.143(0.074) & 0.216(0.062) \\
0.010(0.0087) & -0.163(0.069) & 0.221(0.091) & 0.147(0.060) & 0.295(0.085) \\
-0.030(0.132) & -0.119(0.095) & 0.239(0.130) & 0.124(0.082) & 0.108(0.094) & 0.674(0.195)
\end{bmatrix}
$$

The contribution of variance component of environmental variable Z (or density variable

N) to total process variance in vital rate x_i was calculated using the formula:

$$
R^2_{Z, x_i} = \frac{\sigma^2_{u_{x_i 0} \text{ model without } Z} - \sigma^2_{u_{x_i 0} \text{ model with } Z}}{\sigma^2_{u_{x_i 0} \text{ model without } Z}}
$$