Received: 6 June 2019 | Revised: 17 February 2020 | Accepted: 25 February 2020
DOI: 10.1111/gcb.15085

PRIMARY RESEARCH ARTICLE

Global Change Biology WILEY

Sea ice predicts long-term trends in Adélie penguin population growth, but not annual fluctuations: Results from a range-wide multiscale analysis

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Funding information
NSF, Grant/Award Number: 1341558; Institut Polaire Français Paul Emile Victor; BNP Paribas Foundation; CNRS

Abstract

Understanding the scales at which environmental variability affects populations is critical for projecting population dynamics and species distributions in rapidly changing environments. Here we used a multilevel Bayesian analysis of range-wide survey data for Adélie penguins to characterize multidecadal and annual effects of sea ice on population growth. We found that mean sea ice concentration at breeding colonies (i.e., "prevailing" environmental conditions) had robust nonlinear effects on multidecadal population trends and explained over 85% of the variance in mean population growth rates among sites. In contrast, despite considerable year-to-year fluctuations in abundance at most breeding colonies, annual sea ice fluctuations often explained less than 10% of the temporal variance in population growth rates. Our study provides an understanding of the spatially and temporally dynamic environmental factors that define the range limits of Adélie penguins, further establishing this iconic marine predator as a true sea ice obligate and providing a firm basis for projection under scenarios of future climate change. Yet, given the weak effects of annual sea ice relative to the large unexplained variance in year-to-year growth rates, the ability to generate useful short-term forecasts of Adélie penguin breeding abundance will be extremely limited. Our approach provides a powerful framework for linking short- and longer term population processes to environmental conditions that can be applied to any species, facilitating a richer understanding of ecological predictability and sensitivity to global change.

KEYWORDS
Antarctica, environmental variation, habitat suitability, niche, predictability, state-space, stochastic, uncertainty

1 | INTRODUCTION

The pace of global change has increased the urgency to understand how environmental conditions shape the dynamics of natural populations. Population growth rates are central to understanding contemporary ecological dynamics and evolutionary processes (Caswell, 2001; Sibly & Hone, 2002), and for forecasting species' viability under scenarios of future change (Ehrlén & Morris, 2015; Jenouvrier, 2013). Yet, identifying the spatial and temporal scales at which environmental processes affect population growth remains a considerable challenge. Short-term population fluctuations and longer term population trends jointly influence population viability (Che-Castaldo et al., 2017; Lande, 1993). Thus, approaches that can account for environmental effects operating at multiple temporal scales are needed to bridge the gap between short- and longer term forecasting needs (Dietze et al., 2018), and to provide a richer understanding of species sensitivity to global change (Jenouvrier, 2013).

The modern era is characterized by shifts in the biophysical environment that have generated long-term (i.e., multidecadal) trends in natural populations (e.g., Rosenberg et al., 2019). In cases where populations have not yet reached stable equilibria, studying the environmental correlates of population trends and associated annual fluctuations, provides a powerful opportunity to characterize the environmental niche of a species. Specifically, multiyear studies at sites across a species range can be used to identify the set of environmental conditions under which populations can maintain nonnegative mean growth rates (Ehrlén & Morris, 2015; Peterson, Doak, & Morris, 2018; Schurr et al., 2012). In general, the functional relationship between mean climate and mean population growth across the species range is likely to be a nonlinear function with some nonnegative intermediate optimum (Figure 1a). Simultaneously, at the short-term scale, interannual population growth rates may be affected by annual fluctuations in climate and weather (Figure 1b). If annual climate is a strong driver of annual growth rates, the sign of this relationship will depend on which "side" of the optimum a population sits, since short-term fluctuations essentially map out the local slope of this relationship (Figure 1c). For example, big sagebrush (*Artemesia tridentata*) populations respond positively to warmer temperatures in the colder part of their range and negatively in the warmer part of their range (Kleinhesselink & Adler, 2018). However, a variety of processes can decouple short- and longer-term population responses, such as transient dynamics (Iles, Salguero-Gómez, Adler, & Koons, 2016; Koons, Grand, Zinner, & Rockwell, 2005), dispersal (Tavecchia et al., 2016), density-dependence, and time-lagged carryover effects (Norris & Marra, 2007). Species interactions can also modify the effects of annual climate on populations, altering spatial patterns of climate sensitivity (Iles, Rockwell, & Koons, 2018). In these cases, the effect of short-term climate on particular populations may be inconsistent with the overall shape of the climatic niche, and thus fail to recapitulate the effects of long-term climate on longer term population trends. Thus, it is unclear if the shape of a species' climatic niche can be inferred from interannual responses at individual populations, or if long-term (i.e., multidecadal) studies from multiple populations are needed (Figure 1a).

Here we develop a unified multilevel analytical framework to simultaneously examine the effects of climate at multiple temporal scales on population growth (see related approaches in Amburgey et al., 2018; Kleinhesselink & Adler, 2018; Miller et al., 2018; Peterson et al., 2018). We apply this approach to understand the effects of sea ice on the population dynamics of Adélie penguins (*Pygoscelis adeliae*). Adélie penguins are strongly associated with Antarctic sea ice, and are considered indicators of climate change in the Southern Ocean because of their sensitivity to shifts in the availability of ice-dependent prey (Ainley, 2002; Ainley et al., 2010; Boersma, 2008). Sea ice is known to affect Adélie populations directly (i.e., as a physical feature of the environment that controls access to prey and nesting areas; Fraser & Trivelpiece, 1996; Le Guen et al., 2018; Trivelpiece & Fraser, 1996) and indirectly (i.e., by affecting the larger food web; Fraser & Hofmann, 2003; Massom & Stammerjohn, 2010). Through these pathways, sea ice can influence rates of survival, growth, reproduction, and dispersal (Ballerini, Tavecchia, Olmastroni, Pezzo, & Focardi, 2009; Dugger, Ainley, Lyver, Barton, & Ballard, 2010; Dugger, Ballard, Ainley, Lyver, & Schine, 2014; Emmerson & Southwell, 2008; Hinke, Trivelpiece, & Trivelpiece, 2014; e.g., Jenouvrier Barbraud, & Weimerskirch, 2006). Identifying the temporal scales at which overall effects on population growth are strongest, and how these effects differ across the

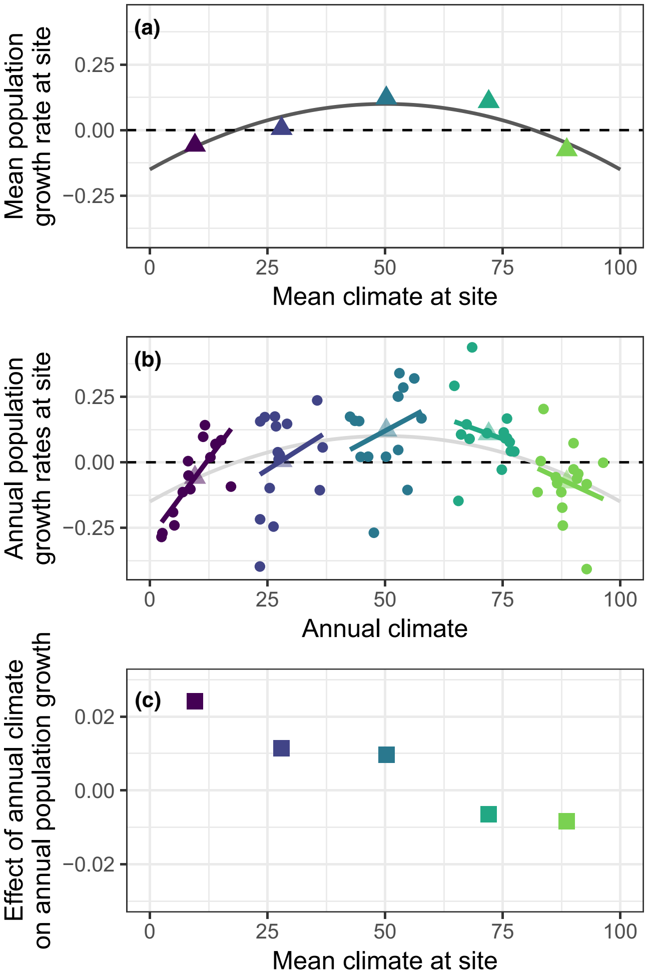

FIGURE 1 Conceptual model describing the short-term (i.e., annual) and longer term (i.e., multiyear mean) effects of a climate variable on population dynamics at multiple sites. In this example there are five sites that experience different prevailing climate conditions. (a) Mean population growth rate (e.g., over several decades) at a site is a nonlinear function (gray solid line) of mean climate at the site. (b) Annual population growth at each site is a function of annual climate. This functional relationship (shown by colored solid lines) differs at each site. Additional process variance (i.e., stochasticity) introduces scatter around these relationships. (c) If annual climate responses at individual sites (panel b) can be used to infer the climatic niche of a species (panel a), the effect of annual climate on annual population growth will be a negative function of mean climate (e.g., see Kleinhesselink & Adler, 2018)

species' range, is critical for understanding their sensitivity to ongoing climate change.

In the long-term, the effect of sea ice conditions on Adélie populations is thought to be reflected by their contemporary distribution; Adélie penguins are absent from areas that lack sea ice and from areas that are completely ice covered (e.g., by glaciers and ice shelves; Ainley, 2002; also see Figure S1). This pattern is also corroborated in the geologic record, such that ancient colonies of Adélie penguins are only present in the Ross Sea during periods of ice shelf retreat (Emslie, Berkman, Ainley, Coats, & Polito, 2003; Emslie, Coats, & Licht, 2007). Accordingly, Fraser and Trivelpiece (1996) proposed a conceptual "habitat-optimum" model (later expanded by Ainley, 2002; Smith et al., 1999; Trivelpiece et al., 2011) under which long-term Adélie penguin population growth rate is a hump-shaped function of average sea ice conditions and is maximized at locations with an intermediate frequency of heavy ice years. Empirical validation of this model is critically needed to provide explicit predictions for the range of conditions across which Adélie penguins can persist in a changing climate (Ainley et al., 2010). Within our framework, the effect of long-term climate on mean population growth rates (Figure 1a) provides a quantitative way to validate this "habitat-optimum" model.

In parallel, the influence of short-term sea ice variation on Adélie penguin population dynamics remains the subject of considerable debate (Ainley et al., 2003; Che-Castaldo et al., 2017; Croxall, Trathan, & Murphy, 2002; Forcada & Trathan, 2009; Jenouvrier et al., 2006; Lyver et al., 2014; Trivelpiece et al., 2011). This debate stems, in part, from apparent inconsistencies among the results of time series analyses from different regions of its Antarctic range. For example, Adélie breeding populations declined 5–6 years after heavy sea ice events in the Ross Sea (Wilson et al., 2001) and at Terre Adélie (Jenouvrier et al., 2006). These effects are consistent with an effect of sea ice on post-fledging survival of birds, which require 5 years to reach reproductive maturity. A similar effect was detected at the Ytre Hovdeholmen breeding colony in East Antarctica, but not at nine other nearby colonies (Kato, Ropert-Coudert, & Naito, 2002). In contrast, Forcada, Trathan, Reid, Murphy, and Croxall (2006) reported that Adélie breeding populations in the South Orkney Islands declined immediately following years of reduced sea ice, suggesting potential effects on adult survival or breeding effort. In some cases, the effects of short-term sea ice anomalies at individual colonies appear to be consistent with a habitat optimum model (reviewed in appendix A of Ainley et al., 2010). Nevertheless, an explicit test of this hypothesis is required to understand the degree to which short-term fluctuations in abundance are predicted by short-term environmental effects, and whether local-scale responses differ predictably across the species range. Our framework also allows us to test this hypothesis by examining whether the relationship between annual sea ice and annual population growth is predicted along a long-term sea ice gradient (e.g., Figure 1c).

Our approach relies on Bayesian analysis of multilevel population models, allowing us to integrate long-term count data from breeding colonies across the species' range. By examining the responses of Adélie penguin populations to sea ice dynamics at multiple scales, our study is designed to provide deeper insights into the factors that shape the climatic niche of this species and to simultaneously contextualize the utility of this species as an indicator of short-term environmental change. More generally, our approach can be applied to any species for which multiyear surveys exist at sites across its range, thereby providing a unified analytical framework for comparing species sensitivity to climate change at multiple scales.

2 | METHODS

2.1 | Penguin population data

We extracted available time series of Adélie penguin abundance from the Mapping Application for Penguin Populations and Projected Dynamics online database (MAPPPD; http://www.penguinmap.com); full details presented in (Humphries et al., 2017). Counts of nests, chicks, and/or adults are recorded during the breeding season, typically between December and February. An associated five-point precision score is also assigned to each observation to describe the potential for observed counts to differ from the true number of individuals present. We supplemented this dataset with additional counts (e.g., the Iles des Pétrels colony at Pointe Géologie) that were not in the public domain and are therefore not available in MAPPPD (available by request from C. Barbraud). We limited our investigation to time series consisting of counts in at least 10 years. In total, our analysis included time series from 38 colonies spanning the entire range of sea ice conditions experienced by Adélie penguins across their Antarctic range (Figure 2; Figure S1).

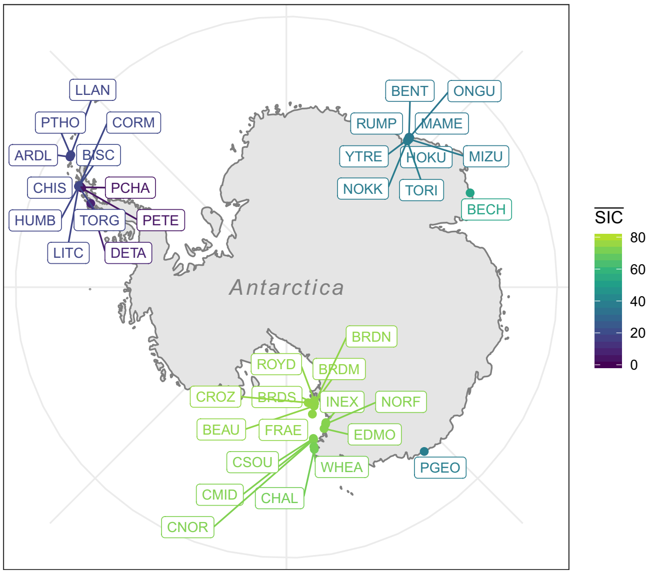

FIGURE 2 Map of breeding colonies included in analysis (i.e., sites with at least 10 years of count data from 1984 to 2017). Colonies are colored according to the long-term mean winter sea ice concentration during March–June across the duration of the study, denoted $\overline{SIC}$

2.2 | Sea ice covariates

To generate the sea ice covariates for each Adélie penguin colony, we extracted preprocessed monthly sea ice concentration data from the National Snow and Ice Data Center (Cavalieri, Parkinson, Gloersen, & Zwally, 2018) using methods outlined in Che-Castaldo et al. (2017). Sea ice concentration (SIC) is directly observed using passive microwave radiation and is provided at grid cells of 25 × 25 km. For each year, we calculated mean sea ice concentration from March to June within a 500 km radius of each colony. This temporal window corresponds to the period of the life cycle immediately following the breeding season during which Adélie penguins depart from breeding sites and make use of available pack ice to molt and feed (Ainley, 2002). Sea ice concentration during this period is highly correlated with conditions during the breeding season (i.e., median correlation with December SIC at breeding sites = 0.50, range = 0.18–0.69), and could additionally have strong effects on subsequent overwinter survival and annual energy budgets, with carryover effects to the following breeding season. A 500 km radius was used to capture large-scale regional effects that could plausibly influence conditions both at breeding sites and at sea (e.g., during migration, molt, and at overwintering sites), though preliminary results were qualitatively similar when generating covariates using a smaller (100 km) radius.

2.3 | State-space population model

We used a state-space framework to address our specific objectives (see Che-Castaldo et al., 2017). The model tracks the number of nests (i.e., population abundance) at each breeding colony and describes temporal dynamics using the time-varying exponential population model:

$$N_{s,t+1} = N_{s,t} e^{r_{s,t}}, \tag{1}$$

where *s* denotes site and *t* denotes year. We then adapted this model to decompose annual population growth rate at each colony, $r_{s,t}$, into two distinct components: the mean growth rate at the site (μ_s) and annual deviations from that mean ($\varepsilon_{s,t}$):

$$r_{s,t} = \mu_s + \varepsilon_{s,t}. \tag{2}$$

This allowed us to separately model the influence of (a) long-term sea ice averages on mean population growth rates, and (b) annual sea ice anomalies on fluctuations in annual population growth around the site-level mean.

First, to directly test the prediction that long-term sea ice conditions affect long-term population trends (sensu Smith et al., 1999), we modeled the effect of mean winter sea ice conditions at sites ($\overline{\text{SIC}}_s$) on mean population growth rates (i.e., population trends) using:

$$\mu_s \sim \text{Normal}\left(\beta_0 + \beta_1 \overline{\text{SIC}}_s + \beta_2 \overline{\text{SIC}}_s^2, \tau^2\right). \tag{3}$$

This equation describes the spatial variation in population trends driven by mean winter sea ice conditions and allows for a potential intermediate optimum effect. The parameter τ^2 measures the degree to which mean population growth rates deviate from this global response curve. Mean sea ice ($\overline{\text{SIC}}_s$) was calculated as the arithmetic average of $\text{SIC}_{s,t}$ across 34 years (1984–2017) at each site. We *z*-standardized these site-level covariates to facilitate model fitting but plot fitted results on unstandardized scale (see Figure 3 in Section 3).

Simultaneously, we modeled the influence of annual (i.e., short-term) sea ice anomalies on annual fluctuations in population growth around their site-level means. Previous work has shown that sea ice conditions in the winter leading up to the breeding season can influence breeding population size, possibly by affecting overwinter adult survival or breeding effort. For example, at Terre Adélie, adult survival is positively associated with warm temperatures (and less sea ice) in winter and spring. Additionally, several studies have reported effects of winter sea ice 5–6 years prior to the breeding season (Jenouvrier et al., 2006; Wilson et al., 2001), consistent with an effect of winter sea ice on survival of first year birds that require 5 years to reach reproductive maturity. We therefore estimated the effect of *z*-standardized sea ice anomalies (*z*SIC) during one, five, and six winters prior to the breeding season ($z\text{SIC}_{s,t-0}$, $z\text{SIC}_{s,t-4}$, and $z\text{SIC}_{s,t-5}$, respectively), using:

$$\varepsilon_{s,t} \sim \text{Normal}\left(\alpha_{1,s} z\text{SIC}_{s,t-0} + \alpha_{5,s} z\text{SIC}_{s,t-4} + \alpha_{6,s} z\text{SIC}_{s,t-5}, \sigma_s^2\right). \tag{4}$$

We note that the *z*SIC covariates are zero-centered and standardized such that their mean is 0 and *SD* is 1; they therefore represent annual deviations from the mean conditions at the site. As a result,

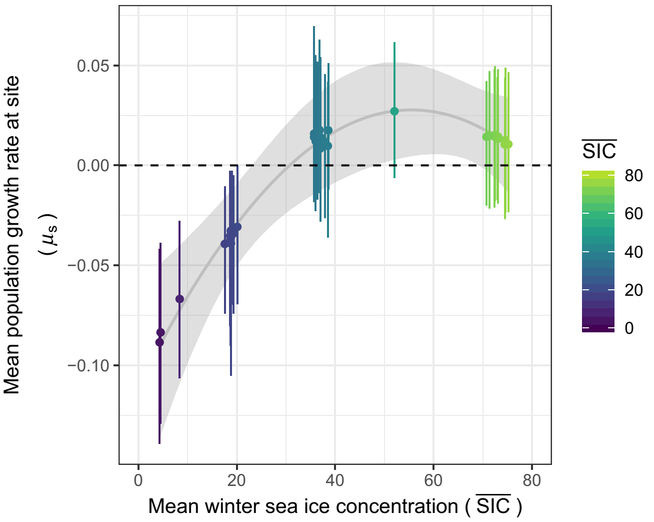

FIGURE 3 Relationship between mean winter sea ice concentration ($\overline{\text{SIC}}$) and mean population growth rate (i.e., long-term population trend) at sites. Colored points (and bars) correspond to median estimate (and 95% credible interval) for each site. Gray line (and ribbon) corresponds to predicted median population trend (and 95% credible interval) across the observed range of $\overline{\text{SIC}}$ based on fitted values from Equation (3) in our multilevel model

$\varepsilon_{s,t}$ also has an expectation of zero. The parameter σ_s^2 measures unexplained "process variance" in population growth. To improve model convergence and constrain estimates of process variance for sites with relatively few years of data, these terms were estimated as site-level random effects drawn from a shared lognormal distribution with mean and variance estimated from the data:

$$\sigma_s \sim \log\text{normal}\,(\gamma, \varphi). \tag{5}$$

We included a final level in our model that described the relationship between the site-level regression coefficients and mean winter sea ice conditions at sites ($\overline{\text{SIC}}_s$). This allowed us to examine how the effect of annual sea ice anomalies differed among breeding colonies, and to explicitly test if their effects depended on position within the species' range (i.e., stronger responses at the range edge vs. in the core). Thus, linear equations describing regression coefficients for each site were:

$$\alpha_{1,s} \sim \text{Normal}\left(A_{1,\text{intercept}} + A_{1,\text{slope}} \times \overline{\text{SIC}}_s, \epsilon_1^2\right), \tag{6}$$

$$\alpha_{5,s} \sim \text{Normal}\left(A_{5,\text{intercept}} + A_{5,\text{slope}} \times \overline{\text{SIC}}_s, \epsilon_5^2\right), \tag{7}$$

$$\alpha_{6,s} \sim \text{Normal}\left(A_{6,\text{intercept}} + A_{6,\text{slope}} \times \overline{\text{SIC}}_s, \epsilon_6^2\right). \tag{8}$$

We used the observation model outlined in Che-Castaldo et al. (2017) to relate observed counts to true population abundance. The model assumes observed population sizes are lognormally distributed with median equal to the true abundance. Thus, observed counts could be higher or lower than the true abundance of nests. This could occur due to genuine counting errors or biological processes that obscure the true nest abundance each year (e.g., undercounts caused by failure of nests prior to survey, or overcounts caused by presence of both members of a pair or nonbreeders in the colony). The magnitude of observation error variance was set according to predefined precision scores associated with each observation. The observation model assumes that counts of adults are less precise than counts of nests and that counts of chicks are potentially biased (see further details in Che-Castaldo et al., 2017).

2.4 | Parameter estimation and model diagnostics

We fit the population model in a Bayesian framework using JAGS version 4.3.0, interfaced with the R programming language using the *jagsUI* library. We specified diffuse priors on all model parameters (see Appendix A for full details of prior specification). After a burn-in of 250,000 iterations, we stored every 30th iteration until we accumulated 25,000 posterior samples from each of three Markov chain Monte Carlo chains. The model unambiguously converged; the Gelman–Rubin convergence statistic was less than 1.1 for all hyperparameters, site-level random effects, regression coefficients, and latent true abundances. We confirmed the ability of the model to generate data that are consistent with the observed data using posterior predictive checks (Appendix S1), which confirmed the model is well-calibrated.

To evaluate the ability of sea ice covariates to predict population growth rates, we quantified the proportion of variance in population growth rates explained by sea ice covariates (R^2) using the approach outlined in Gelman and Hill (2007; pp. 473–477). This approach entails calculating the total variance in the response explained by explicit covariates at each level of the multilevel model. First, we calculated the proportion of variance in population trends among sites that was explained by long-term mean sea ice conditions ($\overline{\text{SIC}}$). Second, for each breeding colony, we calculated the proportion of temporal variance in population growth rates that was explained by the linear combination of annual sea ice covariates (and associated regression coefficients) at that site. We note that R^2 can actually be negative in multilevel models, indicating that residual error variance is larger than the variance of the data at that level of the model.

3 | RESULTS

We found that breeding colonies in areas with relatively low mean winter sea ice concentration $\overline{\text{SIC}}$ (less than 25%) are declining ($\mu_s < 0$), while colonies in areas with intermediate were stable or increasing ($\mu_s \geq 0$; Figure 3). We found strong evidence for a nonlinear concave relationship between growth rate and sea ice concentration (see estimates of quadratic terms in Table 1), consistent with an optimum

TABLE 1 Median estimates and 95% credible intervals for hyperparameters in the multilevel Adélie penguin population model. Parameters correspond those used in Equations (3)–(8). Note that β_0, β_1, and β_2 were fit to *z*-standardized values of mean sea ice at sites and were back-transformed to produce fitted values in Figure 3

Parameter	2.5%	50%	97.5%
Effects of long-term sea ice conditions on long-term population growth rates:			
β_0	−0.003	0.023	0.048
β_1	0.010	0.024	0.038
β_2	−0.051	−0.029	−0.008
τ	0.000	0.010	0.034
Effects of annual sea ice anomalies on annual population growth rates:			
$A_{1,\text{intercept}}$	−0.015	0.011	0.034
$A_{1,\text{slope}}$	−0.001	0.023	0.047
ϵ_1	0.002	0.031	0.066
$A_{5,\text{intercept}}$	−0.029	−0.008	0.013
$A_{1,\text{slope}}$	−0.002	0.019	0.041
ϵ_5	0.000	0.008	0.030
$A_{6,\text{intercept}}$	−0.014	0.009	0.034
$A_{6,\text{slope}}$	−0.041	−0.017	0.007
ϵ_6	0.004	0.030	0.055
Hyperparameters describing site-level process variances:			
γ	0.176	0.207	0.241
φ	0.273	0.390	0.559

when $\overline{\text{SIC}}$ is approximately 50% (Figure 3; also see Figure S3 in Appendix). Furthermore, explained 83.1% of the variance in long-term population growth rates among the 38 breeding colonies in our study. This implies that the mean population growth rate at a site can be accurately predicted based solely on the knowledge of prevailing winter sea ice conditions at a site (i.e., $\overline{\text{SIC}}$).

In contrast, annual sea ice anomalies did not strongly predict fluctuations in annual population growth. Median effect sizes of annual SIC anomalies were less than 0.05 for most colonies and credible intervals generally broadly overlapped zero (Figure 4). Thus, a 1 *SD* change in local sea ice concentration resulted in less than 5% change in annual population growth rates (see Figure S4 in Appendix for presentation of unstandardized effects of annual sea ice). Parameters describing the effect of range position on population responses (i.e., $A_{1,\text{slope}}$, $A_{5,\text{slope}}$, $A_{6,\text{slope}}$) were also weak and credible intervals broadly overlapped zero (Table 1). Range position (i.e., mean winter sea ice concentration at the site, $\overline{\text{SIC}}$) was therefore not a strong predictor of population responses to sea ice anomalies; populations in ice-free and ice-heavy parts of the range responded similarly and weakly to sea ice fluctuations. Simultaneously, site-level

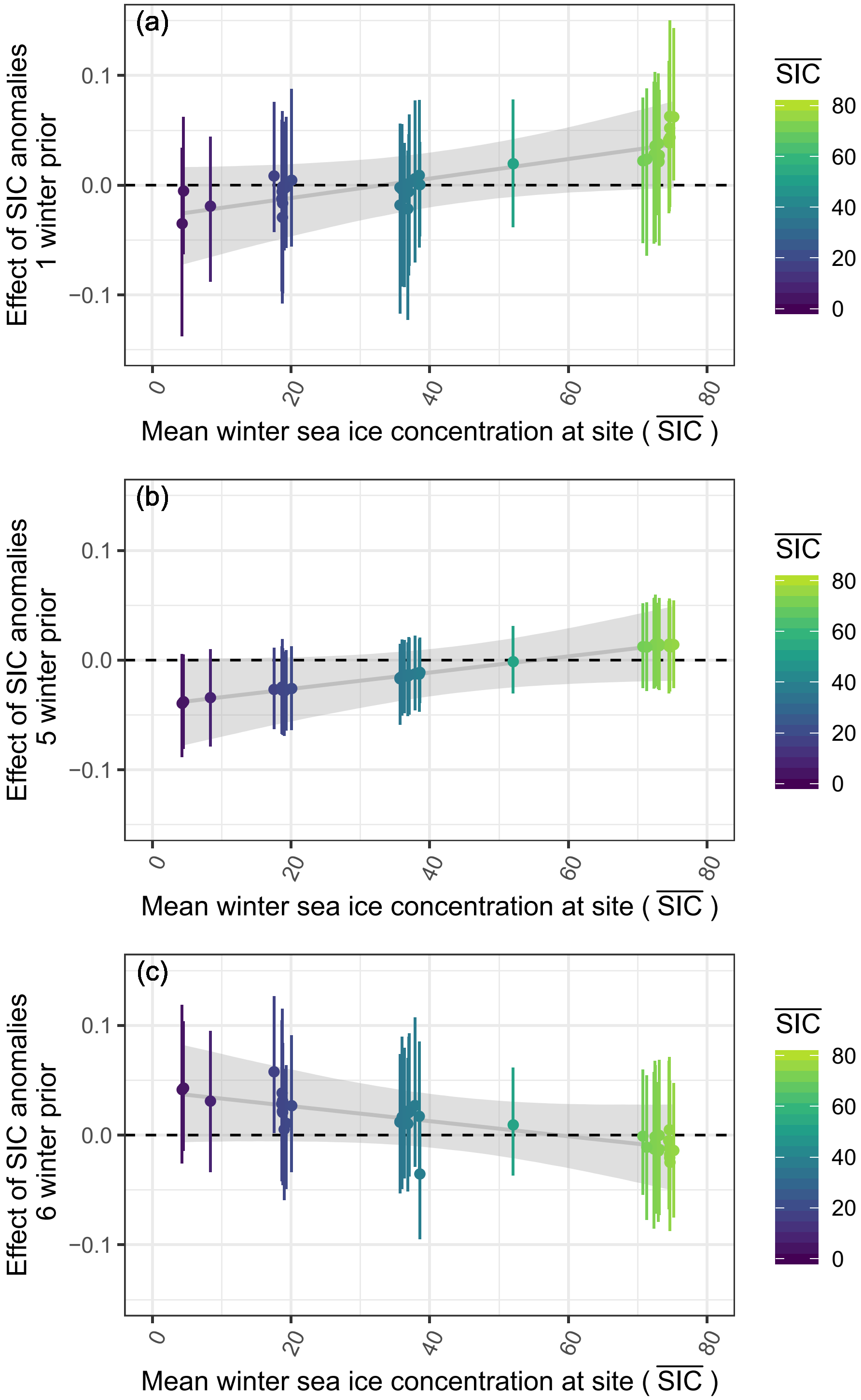

FIGURE 4 Effect of standardized annual sea ice concentration (SIC) anomalies on annual population growth rates. Effects at each site were estimated for three biologically relevant temporal windows: 1 (panel a), 5 (panel b), and 6 (panel c) winters prior to the breeding season. Gray lines and ribbons represent predicted mean effect (and 95% credible interval) across the range of sea ice conditions, based on Equations (6)–(8) in our multilevel model

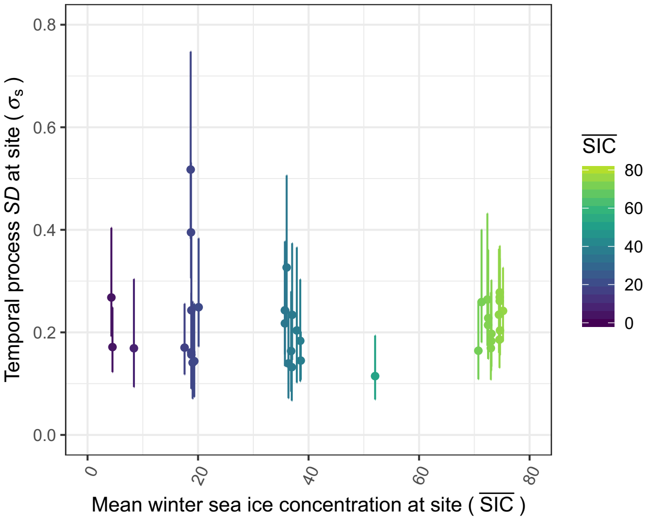

FIGURE 5 Unexplained temporal process variance in annual population growth rates at each of the 38 sites. Process variances (*y*-axis) are plotted against prevailing winter sea ice conditions at each site ($\overline{\text{SIC}}$; *x*-axis) to illustrate a lack of obvious pattern in process variance across the species range

process variances were generally large ($\sigma_s > 0.1$ for all colonies) and were themselves highly variable among colonies (Figure 5). The effects of explicit annual sea ice covariates were therefore relatively weak compared to large fluctuations in annual abundance caused by unexplained factors (i.e., process variance). As a consequence, sea ice anomalies generally explained an exceedingly small proportion of temporal variance in annual population growth rates (mean R^2 across all sites = .07; range = −.05 to .21 at individual sites). This implies that annual fluctuations in population growth at a site cannot be accurately predicted based on annual fluctuations in winter sea ice conditions.

4 | DISCUSSION

Our analysis confirms the hypothesis that Adélie penguin habitat suitability is strongly determined by prevailing sea ice conditions. Our results are also broadly consistent with a "habitat optimum" model (Ainley, 2002; Barbraud et al., 2012; Fraser & Trivelpiece, 1996; Smith et al., 1999) where mean population growth is a nonlinear function of long-term average winter sea ice concentration ($\overline{\text{SIC}}$; Figure 3). Our model predicts that population trends will be negative (and thus habitat is unsuitable for population persistence) at sites where mean winter SIC is below 31% (95% CRI: 23%–49%). While breeding colonies do currently exist below the lower threshold for population persistence, these colonies are in decline and some have already become extinct or abandoned (e.g., at Litchfield Island; Fraser, Patterson-Fraser, Ribic, Schofield, & Ducklow, 2013). Pre-satellite evidence suggests that warming has occurred extremely rapidly in this region of Antarctica in the second half of the 20th century (conditions are now the warmest in 500 years; Thompson et al., 1994), leading to large declines in sea ice (de la Mare, 1997; Smith et al., 1999). This explains the presence of Adélie penguin colonies at these currently unsuitable sites. On the other side of the habitat suitability curve, our model predicts negative population trends when mean winter SIC exceeds 80% (95% CRI: 74%–100%). We note that our empirical results could also be consistent with a model that predicts stable or positive growth rates for any SIC over 30%, given the lack of observations at extremely high values of (Figure 3). Nevertheless, an upper threshold on colony persistence when is greater than 80% is also surprisingly consistent with the current distribution of the species (Lynch & LaRue, 2014); no contemporary colonies are found in locations where long-term mean winter SIC is greater than 76% (Figure S1). These results are also consistent with geologic records that indicate that Adélie penguin colonies are absent during periods of extensive sea ice (Emslie et al., 2007). Our model therefore provides a dynamic understanding of the factors that determine Adélie penguin habitat suitability, which have led to their current and historical range limits, and further establishes Adélie penguins as true sea ice obligates.

While our results indicate sea ice is critical for Adélie population persistence, annual sea ice anomalies did not predict temporal fluctuation population growth at breeding colonies. Annual sea ice effects were weak (Figure 4) compared to the magnitude of annual fluctuations driven by unknown environmental or demographic factors (Figure 5). Thus, sea ice fluctuations explained a remarkably low proportion of temporal variation in population growth (often less than 6%). This finding is consistent with Che-Castaldo et al. (2017), who also reported that annual growth rates were highly stochastic and thus driven by largely unknown factors. There are several non-mutually exclusive explanations for this result. First, while multiple studies have detected effects of sea ice anomalies on rates of survival (e.g., Ballerini et al., 2009; Hinke et al., 2014) and reproduction (Dugger et al., 2014; e.g., Emmerson & Southwell, 2008), the overall effect on annual population growth is modulated by a variety of processes. In particular, life history tradeoffs (Stearns, 1992) and vital rate correlations (Iles, Rockwell, & Koons, 2019), fluctuating stage structure and associated transient dynamics (Koons, Iles, Schaub, & Caswell, 2016), and dispersal (Tavecchia et al., 2016) can obscure the effects of environmental drivers at the population level. Second, life history theory and empirical evidence suggests that long-lived species often evolve demographic mechanisms to dampen the effects of short-term environmental variation (Doak, Morris, Pfister, Kendall, & Bruna, 2005; Koons, Pavard, Baudisch, & Metcalf, 2009; Morris et al., 2008; Sæther et al., 2013). Adélie penguins are known to skip breeding (Massom et al., 2006), possibly as a bet-hedging strategy that maximizes long-term fitness at the expense of short-term reproductive output (Jenouvrier Barbraud, Cazelles, & Weimerskirch, 2005; Jenouvrier Barbraud, & Weimerskirch, 2005; Nevoux, Forcada, Barbraud, Croxall, & Weimerskirch, 2010). This behavior could strongly dominate short-term variation in breeding abundance, and simultaneously, be largely decoupled from long-term population trends. For Adélie penguins, it is unclear how breeding decisions are affected by environmental variation. For example, while breeding phenology is an important determinant of breeding successfully (Youngflesh, Jenouvrier, Li, et al., 2017), it may be largely determined by non-environmental stochastic processes (Youngflesh, Jenouvrier, Hinke, et al., 2017). If the decision to skip breeding is similarly dominated by true stochasticity, or an intractable combination of environmental and demographic factors, the ability to predict of short-term variation in population abundance may remain severely limited.

It remains an open question which aspects of the biophysical environment can be useful for short-term management feedback (also see Che-Castaldo et al., 2017). Year-to-year changes in Adélie penguin breeding abundance at individual colonies were often larger than ±40% (Figure 5) and appear to be driven by factors other than annual sea ice (Figure 4). Thus, short-term changes in breeding abundance are not reliable indicators of longer term population trends or habitat suitability. Short-term changes in population growth may be more strongly tied to other aspects of the marine environment, such as prey abundance (Trivelpiece et al., 2011), extreme weather events during particular parts of the life cycle (Barbraud, Delord, & Weimerskirch, 2015; Ropert-Coudert et al., 2015), or local-scale environmental conditions that are potentially uncoupled from large-scale sea ice conditions (Dugger et al., 2014). This raises the question as to whether lower level demographic processes such as reproductive performance may be more sensitive or more meaningful as an indicator of ecosystem conditions than abundance or annual population growth rate (Barbraud et al., 2015). Demographic theory predicts that reproductive success will often be the most responsive vital rate for long-lived species such as Adélie penguins, and will thus be more likely to track environmental conditions than more “buffered” vital rates such as adult survival (Koons et al., 2009; Lawson, Vindenes, Bailey, & Pol, 2015). Yet, empirical evidence suggests that the reproductive success of the Adélie penguin is also highly variable from year to year, largely decoupled from long-term trends, and idiosyncratic among species within the seabird community (Youngflesh, 2018). While regular population monitoring is clearly required to accurately estimate long-term trends, further work is needed to determine which aspects of the marine environment, if any, can be reliably inferred from short-term population processes. Caution is therefore warranted before ascribing environmental causation to year-to-year changes in abundance at local colonies, underscoring the need for examining responses across longer time horizons (this study) and across larger spatial scales (Che-Castaldo et al., 2017).

Our multilevel population modeling approach provides a potentially powerful framework for understanding species responses to climate change and forecasting long-term population viability under scenarios of climate change (also see Miller et al., 2018). Previous work has shown that many Adélie colonies will experience novel climate that falls outside the historical range of local conditions at those sites, casting doubt on the ability to extrapolate responses from individual colonies (Cimino, Lynch, Saba, & Oliver, 2016). However, our multilevel approach leverages information across sites and tests the degree to which a globally coherent response underlies spatial variation in population performance (also see similar approaches applied to other species; Amburgey et al., 2018; Kleinhesselink & Adler, 2018). For Adélie penguins, long-term count data are available from sites that span an extremely wide range of environmental conditions, ranging from mean winter SIC of 4%–75% (Figure 3). Furthermore, mean winter SIC explained over 80% of the variation in population trends across this range of conditions. Thus, efforts to fuse our population model with IPCC-class climate projections will avoid extrapolations into novel climate conditions and thereby provide robust insights into potential changes in Adélie distribution and abundance under scenarios of future change (Ballerini, Tavecchia, Pezzo, Jenouvrier, & Olmastroni, 2015; Iles & Jenouvrier, 2019; Jenouvrier, 2013; Jenouvrier et al., 2014).

Predictive modeling is an inherently iterative process (Dietze et al., 2018), and several aspects of our multilevel model are ripe for continued refinement. Our model assumes population growth is consistent with log-linear trends and first difference temporal random effects, but other models of temporal dynamics could be evaluated (e.g., using cross-validation; Link & Sauer, 2016), and could provide additional insights into penguin population viability (Holmes, Sabo, Viscido, & Fagan, 2007). Spatial and temporal autocorrelation terms could also be incorporated at multiple levels of our hierarchical model. These could facilitate improved predictions in years or sites with imprecise (or entirely missing) observations, and potentially help to identify additional environmental processes (e.g., Diniz-Filho, Bini, & Hawkins, 2003) or demographic structure (e.g., Hostetler & Chandler, 2015) that contribute to the substantial residual process variation we detected.

While our study relied on long-term range-wide survey data to provide insight into the niche-space of an iconic Antarctic predator, similar data are available for many other species. Improvements in remote sensing have the potential to provide updated population counts an unprecedented scale, especially for polar species experiencing rapid climate change (Fretwell et al., 2012; Fretwell, Scofield, & Phillips, 2017; LaRue et al., 2011; Lynch & LaRue, 2014). Comparative studies that extend our work to examine niche breadth and climate sensitivity (that together contribute to “population robustness”; Jenouvrier, 2013) for multiple species simultaneously is an important avenue of future research. Our framework links these concepts, while disentangling climate impacts on population dynamics at multiple temporal scales. Species responses to climate change will depend on the functional shape of the long-term response curve (e.g., Figures 1a and 3) and the effect of annual climate variation on annual population growth, potentially as a function of the range position (Figures 1c and 4). How the shapes of these responses differ across life histories (e.g., location of the climate optimum, width and curvature of response function, relationship between range position and annual climate effects, etc.) remains an open and important question. The multilevel approach we used provides a unified analytical framework to compare each of these facets of climate sensitivity among species, especially by examining responses of species to climate covariates that are projected to change dramatically in the coming century. Continued work that links short- and long-term population processes to climate will be necessary for estimating species viability, prioritizing conservation strategies, and guiding policy in a rapidly changing world.

ACKNOWLEDGEMENTS

This work was supported by NSF OPP award #1341558. The data at Pointe Géologie were collected by members of the scientific program 109 (resp. H. Weimerskirch) supported by the Institut Polaire Français Paul Emile Victor. C.B. acknowledges support from the BNP Paribas Foundation (program SENSEI – SENtinels of the Sea Ice), and the Zone Atelier Antarctique et Subantarctique – LTER France of the CNRS.

CONFLICT OF INTEREST

The authors declare they have no conflicts of interest.

AUTHOR CONTRIBUTIONS

D.I., H.L., R.J., and S.J. conceived of research ideas. D.I. and S.J. interpreted the data with additional input from H.L., R.J., C.B. and K.D. D.I. led statistical analysis with additional input from S.J. and H.L., C.B., and K.D. provided data that are not publicly available. S.J., R.J., and H.L. secured funding. D.I. led the writing of the manuscript. All authors edited and made critical contributions to drafts and gave final approval for publication.

COMPLIANCE WITH ETHICAL STANDARDS

The authors declare that they have complied with ethical standards.

DATA AVAILABILITY STATEMENT

Penguin population data are available on MAPPPD repository (http://www.penguinmap.com/mapppd) and are available upon request from C. Barbraud and K. Delord. Sea ice data are publicly available from the National Snow and Ice Data Center. R scripts to fully replicate analyses are available on GitHub at github.com/davidiles/Adelie-sea-ice-responses.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

How to cite this article: Iles DT, Lynch H, Ji R, Barbraud C, Delord K, Jenouvrier S. Sea ice predicts long-term trends in Adélie penguin population growth, but not annual fluctuations: Results from a range-wide multiscale analysis. *Glob Change Biol*. 2020;00:1–11. https://doi.org/10.1111/gcb.15085