

An evaluation of density-dependent and density-independent influences on population growth rates in Weddell seals

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Abstract. Much of the existing literature that evaluates the roles of density-dependent and density-independent factors on population dynamics has been called into question in recent years because measurement errors were not properly dealt with in analyses. Using state–space models to account for measurement errors, we evaluated a set of competing models for a 22-year time series of mark–resight estimates of abundance for a breeding population of female Weddell seals (*Leptonychotes weddellii*) studied in Erebus Bay, Antarctica. We tested for evidence of direct density dependence in growth rates and evaluated whether equilibrium population size was related to seasonal sea-ice extent and the Southern Oscillation Index (SOI). We found strong evidence of negative density dependence in annual growth rates for a population whose estimated size ranged from 438 to 623 females during the study. Based on Bayes factors, a density-dependence-only model was favored over models that also included environmental covariates. According to the favored model, the population had a stationary distribution with a mean of 497 females (SD = 60.5), an expected growth rate of 1.10 (95% credible interval = 1.08–1.15) when population size was 441 females, and a rate of 0.90 (95% credible interval = 0.87–0.93) for a population of 553 females. A model including effects of SOI did receive some support and indicated a positive relationship between SOI and population size. However, effects of SOI were not large, and including the effect did not greatly reduce our estimate of process variation. We speculate that direct density dependence occurred because rates of adult survival, breeding, and temporary emigration were affected by limitations on per capita food resources and space for parturition and pup-rearing. To improve understanding of the relative roles of various demographic components and their associated vital rates to population growth rate, mark–recapture methods can be applied that incorporate both environmental covariates and the seal abundance estimates that were developed here. An improved understanding of why vital rates change with changing population abundance will only come as we develop a better understanding of the processes affecting marine food resources in the Southern Ocean.

Key words: Antarctica; climate; density dependence; *Leptonychotes weddellii*; population dynamics; population growth rate; Weddell seal.

INTRODUCTION

Understanding the relative roles of density and extrinsic factors such as climatic variation on population dynamics remains an important challenge in basic and applied ecology (Lande et al. 2005). To improve our understanding, long-term studies are needed that relate changes in demographics to population density, other biotic variables, and abiotic factors. Beyond providing basic information about the features governing dynamics, information on long-term dynamics is also of great interest in applied ecology. For example, knowledge of long-term population sizes and sources of variation in sizes provides a useful baseline when evaluating possible future changes that may occur and for predicting

population responses to changes in climate or other forcing factors (e.g., Barbraud and Weimerskirch 2001, Stenseth et al. 2002, Jacobson et al. 2004).

Until recently, the difficulties of analyzing time series of population abundance estimates that are affected by measurement error and process variation prevented proper analyses of many data sets (Freckleton et al. 2006). Accordingly, knowledge of the relative roles of stochastic and density-dependent factors is poor. Fortunately, recently developed Bayesian and frequentist methods for analyzing time series of abundance estimates using state-space models surmount previous difficulties and provide adequate flexibility for modeling the complex processes that generate population data (De Valpine and Hastings 2002, Buckland et al. 2004, Clark and Bjørnstad 2004, Dennis et al. 2006). Also, Bayesian methods of evaluating competing models and making multi-model inferences now exist that can be applied to

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state-space models (Link and Barker 2006). Thus, much useful progress can now be made as shown in several recent studies (Stenseth et al. 2003, Jamieson and Brooks 2004, Viljugrein et al. 2005).

Now that improved methods are available for modeling population time series, analyses of time series for Antarctic populations would be especially valuable as they would provide information from one of the more pristine environments on earth and because such high-latitude systems are thought to be particularly sensitive to possible climate change (Croxall et al. 2002). Within the Southern Ocean, the Ross Sea is of special interest due to its unique combination of attributes (Smith et al. 2007). The Ross Sea is one of the most productive areas of the Southern Ocean (Arrigo et al. 1998), has a relatively simple trophic web (La Mesa et al. 2004), and has been studied less extensively than have other sectors of the Southern Ocean (Trathan et al. 2007). Also, in striking contrast to trends in the Antarctic Peninsula (Vaughan et al. 2001) and Arctic regions (Walsh 2008), the Ross Sea is experiencing a general cooling of air temperatures and a lengthening of the sea-ice season (Doran et al. 2002).

Here, we use long-term data that are available from a mark-resight study of Weddell seals in Erebus Bay of the Ross Sea (e.g., Siniff et al. 1977, Cameron and Siniff 2004) to (1) evaluate the influence of density-dependent and density-independent factors on population dynamics and (2) characterize the population's dynamics for 1982–2003, a period with a wide range of environmental conditions (Hadley et al. 2006, Proffitt et al. 2007). Specifically, we use Bayesian methods and a set of competing state-space models to relate changes in abundance to previous population size, seasonal sea-ice extent, and the Southern Oscillation Index (SOI). Sea-ice extent, which varies widely across seasons and years, has been shown to play a major role in marine productivity (Constable et al. 2007) and to be related to the population dynamics of diverse predator species (e.g., Barbraud and Weimerskirch 2001, Croxall et al. 2002). SOI and other related broad-scale measures of atmospheric-oceanic conditions have been shown to be involved in environmental forcing of ice extent and concentration, sea surface temperatures, marine productivity, and the dynamics of several apex predators in the Southern Ocean (e.g., Testa et al. 1991, Kwok and Comiso 2002, Yuan 2004, Trathan et al. 2007).

METHODS

Study area and population

The Erebus Bay study area is located in southeastern McMurdo Sound, Antarctica (77°37'12" to 77°52'12" S, 166°18' to 167° E; see Cameron and Siniff [2004] for description and map of study area). Eight to 14 Weddell seal breeding colonies are located within this study area (Stirling 1969a). Colonies are associated with tidal cracks that form in the sea ice each austral spring, creating areas where adult female seals haul out to have

pups (see Plate 1 and Appendix A). Marking and resighting of this population have occurred each year since 1969. Over this period, both the proportion of the population that is marked, and the proportion of marked animals that are of known age have gradually increased (Cameron and Siniff 2004). As of 2003, which is the most recent year used in analyses presented here, approximately 80% of the female seals in this population were marked, and over 80% of these marked individuals were of known age.

Typically, 300–600 pups are born per year at colonies in Erebus Bay, and females surviving to reproductive age are strongly philopatric, returning to breed in Erebus Bay (Cameron and Siniff 2004). Age at first reproduction for females is variable and averages 7.6 ± 1.7 years (mean \pm SD; Hadley et al. 2006). Upon recruiting to the breeding population, females typically produce a pup every 1.5–2.2 years depending on previous breeding experience and environmental conditions (Hadley et al. 2007a). Mothers and pups are highly visible on the ice, typically in close proximity to one another, and spend much of their time hauled out on the sea ice, especially in the few weeks immediately following birth. Females who have not yet had a pup (pre-breeders) or those who are skipping pupping also haul out in the study area each year.

Data collection

Each year from 1969 until the present, Weddell seal pups born within the Erebus Bay study area have been individually marked (usually within about five days of birth) with plastic livestock tags attached to the interdigital webbing of each rear flipper. From 1969 to 1981, the proportion of pups that were tagged varied, and since 1982, which is the first year used in the analyses presented here, all pups in the study area have been tagged. In addition, any seal with a broken or missing tag was retagged, and untagged adults were tagged opportunistically upon sighting and capture. The majority of the tagging effort occurred from approximately 15 October to 15 November each year, during the peak of parturition when colonies were visited every two to three days to tag newborn pups. Beginning in early November of each year, six to eight resighting surveys were carried out throughout the study area with surveys typically separated by three to five days. Seals in this population could be readily approached within 0.5 m, and thus, observers were able to read tags on all marked animals that were observed.

Data analysis

Data analysis consisted of two key components: (1) estimating the number of females in the breeding population each year and (2) evaluating competing models for changes in the size of the annual population of breeding females. To estimate the size of the breeding population that used the study area in each year, we used Schwarz and Arnason's (1996) superpopulation

approach on the data collected from multiple within-year surveys. To evaluate competing models of changes in population size where annual population sizes were estimates affected by measurement error, we used Bayesian methods to obtain estimates of posterior model probabilities and to make multimodel inference (Link and Barker 2006).

Estimating population sizes.—The female breeding population consists of females with pups (active breeders in the current year) and females who have had pups in previous years but are skipping breeding in the current year (skip breeders). Data for estimating the number of females present in the study area comes from known-age females (tagged as pups) and females of unknown-age (tagged as adults). Because all mother–pup pairs are detected in the study area each year (Hadley et al. 2006), we know the number of active breeders in the female population each year. This information also allows us to know the breeding history for each known-age female and to assign each to the pre-breeder (P), active breeder (A), or skip breeder (S) state in each year of the study. Therefore, analysis of data from known-age females was straightforward: for each year, we estimated the number of known-age females in states P, A, and S based on data collected during multiple within-year surveys using Schwarz and Arnason's (1996) superpopulation approach and results from a set of competing models. The estimated numbers of known-age females in states A and S were subsequently combined with results from analyses of females of unknown age to yield annual estimates of the size of the female breeding population each year. The estimates of numbers in states P and S were used to help inform the analysis of data from females of unknown age.

Analysis of data for females of unknown age was complicated by the fact that we did not have complete breeding histories for such females. Thus, we could not distinguish whether an unknown-age female without a pup in a given year was in state P or S unless she had been observed in state A in a previous year. Also, some unmarked adult females that were encountered were released unmarked back into the population. Accordingly, estimation of population size for females of unknown age was done in three phases. First, working only with data from tagged females in each year, we assigned each female to one of three breeding states: A, S, or Q (questionable state, which was used for non-breeding females tagged as adults and who had not yet been known to be a mother) and used Schwarz and Arnason's (1996) superpopulation approach and a set of competing models to estimate the number of females of unknown age in each of those states in each year.

Second, we estimated how many unknown-age females in state Q were skip breeders based on the estimated proportion of known-age females (≥ 2 yr old) that were in state S each year (π^S). We estimated π^S and its variance using the binomial distribution and data from 1992–2003. We started with 1992 to allow $\hat{\pi}^S$ (the

estimate of π^S) for known-age females to stabilize, which was necessary because all known-age females were originally tagged as pups meaning that the known-age population consisted entirely of pre-breeders early in the study. From 1992 forward, the estimate was quite stable ($\hat{\pi}^S = 0.38$, $SD = 0.03$ as years were added from 1992 to 2003). Each year's estimate of the number of animals in state S was then adjusted upward as follows:

$$\hat{N}_t^S(\text{adjusted, unknown}) = \hat{N}_t^S(\text{original, unknown}) + \hat{N}_t^Q(\text{unknown}) \times \hat{\pi}^S.$$

In the third phase of the analysis of unknown-age females, we accounted for females that were encountered and released unmarked and completed the estimation of the number of females of unknown age that were in states A and S for each year. We first determined how many unmarked females were in state A based on field records for the tagged status of each mother in the population each year. We then created a pseudo-encounter history for each untagged mother based on the relevant model-averaged parameter values for known- and unknown-age mothers in that year. The remaining encounters of unmarked animals were added to the input file for marked females of unknown age. Each of these was assigned to state Q and treated as a loss on capture; estimation was then done using methods detailed in Siniff et al. (1977) and Hadley et al. (2006) to properly adjust the estimated numbers for the unmarked animals. With the encounters for unmarked animals included, we re-ran the set of competing models of the superpopulation size (Schwarz and Arnason 1996) to estimate the number of females in each state in each year. The number of females in state S was again adjusted upward using the estimated number of females in state Q as described above but using the new results. The estimates from analysis of data from unknown-age females were then combined with those from the known-age females to obtain the overall estimates of the number of females in states A and S for each year.

At each of the multiple steps involved in these analyses, we took care to carry variances and model-selection uncertainty forward when developing estimates and when transforming estimates. When transformations were done, the delta method was used for estimating variances on the new quantities (Seber 1982). Despite the multiple steps involved, we were able to obtain precise estimates for the parameters of interest because a large proportion of the population was marked, the detection rates for animals present in the study area were high, and females were highly philopatric to the site.

For data from known-age females, we evaluated a set of 45 competing models and based our estimates on annual model-averaged estimates of the number of females in states A and S. For data from females of unknown age, 12 models were considered, and annual estimates of the number of females in the breeding

population were based on model-averaged estimates of the number of females in states Q, A, and S, as well as our estimate of π^S . All modeling was conducted in Program MARK (White and Burnham 1999) to implement the Schwarz and Arnason (1996) model. The fundamental parameters estimated for each year were (1) ϕ_i , the probability of a female surviving and remaining in the population between sampling occasions i and $i + 1$ given that she was alive and present on occasion i ; (2) p_i , the probability of capture at occasion i when present; (3) β_i , the probability that a female entered the population between sampling occasions i and $i + 1$ given that she was alive and present during that year; and (4) N , the superpopulation size consisting of all females that were available for capture on at least one sampling occasion. Every model estimated N separately for females in states A, S, and Q and for age-specific classes of state P (1-, 2-, 3-, and ≥ 4 -yr-old). The competing models consisted of all possible combinations of five (known-age data) or three (unknown-age data) different parameterizations of $\hat{\phi}_i^{\text{state}}$, and three (known-age data) or two (unknown-age data) parameterizations each for \hat{p}_i^{state} and $\hat{\beta}_i^{\text{state}}$. All parameters were allowed to vary with occasion in all models, and the competing parameterizations varied in terms of whether $\hat{\phi}_i^{\text{state}}$, \hat{p}_i^{state} , and/or $\hat{\beta}_i^{\text{state}}$ for different states and age classes were constrained to follow the same temporal pattern or not. Goodness of fit was evaluated for each data set with Program RELEASE (Burnham et al. 1987) as implemented in Program MARK.

Evaluating competing models of annual change in population size.—We evaluated eight competing models of changes in population size. Each model was a discrete-time, state-space model with a Gompertz form of density dependence (Reddingius 1971, Dennis and Taper 1994, Dennis et al. 2006). The set of eight models included all-possible additive combinations of three large-scale atmospheric-oceanographic metrics. We kept our a priori model list simple and considered only additive combinations of covariates because scientific literature regarding features that might affect Weddell seal population dynamics provides indications of several factors but has not yet developed to the point that we were comfortable developing interaction models, especially given the length of our time series. The state-space approach for analyzing our time series of population estimates allowed us to incorporate our estimates of measurement error for annual population size while evaluating competing models that included process noise and various combinations of environmental covariates (De Valpine and Hastings 2002).

The two components of the state-space approach were (1) an observation model that related population estimates (\hat{N}_t , observed variable) to true underlying abundance (N_t , unobserved latent variable) and (2) a process model for changes in true population abundance. The observation model linked estimated abundance to true abundance as $\hat{N}_t \sim N(N_t, \text{SE}_t^2)$, where SE_t

was our estimate of measurement error for each year's population estimate. Our process model was built upon the Gompertz model, wherein the population's growth rate depends on the logarithm of abundance (Dennis et al. 2006 give an overview of the properties of the model and its history). In the process model used here, μ was the equilibrium value for the logarithm of population size, $\log(N_t) = \mu + y_t$, and $y_t \sim N(\alpha_t, \sigma_{\text{pr}}^2)$, where σ_{pr}^2 was process variation. The process model was $\alpha_t = \beta^{\text{Ab}}(y_{t-1}) + \beta^{\text{Env1}}(\text{env1}_t) + \beta^{\text{Env2}}(\text{env2}_t) + \beta^{\text{Env3}}(\text{env3}_t)$, where the abundance coefficient β^{Ab} was $1 + \beta^{\text{DD}}$, β^{DD} represented the coefficient for density dependence, and β^{EnvX} represented the coefficient relating environmental covariate X to α_t . We assumed that process variation and measurement errors were independent. Negative values of the estimate $\hat{\beta}^{\text{DD}}$ are evidence of negative density dependence, $\hat{\beta}^{\text{DD}} = 0$ would indicate no density dependence, whereas positive values provide evidence of positive density dependence (Dennis and Taper 1994). Based on previous reports that concluded the population to be at equilibrium in earlier decades (Stirling 1969a, Testa and Siniff 1987), we predicted that we would find evidence of negative density dependence. Our focus was on testing for direct density dependence but given the possibility of time delays in the process (Berryman and Turchin 2001), we also did exploratory analyses that evaluated the need to include abundance estimates from years $t - x$ ($x > 1$).

The environmental covariates considered were (1) summer sea-ice extent (Sum) measured in February of year t soon after pupping and mating occurs in year $t - 1$; (2) winter sea-ice extent (Win) just prior to the pupping season in September of year t ; and (3) the Southern Oscillation Index (SOI) just prior to and during the pupping season (September–November) in year t . Extensive sea ice during summer reduces the amount of open water available for phytoplankton blooms and thus, may reduce available food resources and reduce foraging success of Weddell seals during summer as evidenced by annual changes in female body mass (Proffitt et al. 2007). Accordingly, we predicted that Sum would be negatively related to equilibrium population size. In contrast, we predicted that Win would be positively related to equilibrium population size. Extensive winter sea ice may protect fish from open-water predators (Olivier et al. 2005), increase abundance of krill (*Euphausia crystalloporphias*) through positive effects on ice algae during winter (Loeb et al. 1997), and thereby benefit fish species such as *Pleuragramma antarcticum*, a primary food item for Weddell seals (Dearborn 1965). Although winter sea ice has been shown to have profound effects, it is only one of several factors that likely affect the abundance and spatial distribution of marine prey species and their predators (Croxall et al. 2002). In the Ross Sea, SOI is a more integrative metric of environmental conditions that has been shown to be positively associated with the extent and concentration of sea ice and also to be negatively

associated with atmospheric pressure and sea-surface temperatures (Kwok and Comiso 2002, Yuan 2004). Testa et al. (1991) found pupping rates in the study population to generally be in phase with SOI. Thus, we predicted that SOI would be positively related to equilibrium population size.

Sea-ice extent was measured over the Ross Sea sector of Antarctica from passive microwave satellite images (Comiso 1999). The strength of the El Niño-Southern Oscillation (ENSO) was measured by SOI whereby negative values are associated with El Niño episodes (Kwok and Comiso 2002) and calculated as a three-month running average (data *available online*).⁴ Before being used in modeling, values of environmental covariates were standardized to have a mean = 0 and SD = 1.

We evaluated the set of candidate models and made multi-model inferences using the Bayesian paradigm and Bayes factors as described by Link and Barker (2006). One of the challenges to implementing Bayesian multi-model inference was the selection of prior distributions for the parameters of the model (μ , $1/\sigma_{pr}^2$ [or τ_{pr}], and β^j for $j = DD, SOI, Sum, Win$). We used the approach provided by Link and Barker (2006) to attempt to maintain a constant total variance in the linear predictor across models. To do so, we used a flat normal prior on μ , which was present in all models, set an overall precision parameter τ for the linear predictor, and set the prior variance for τ_{pr} and each of the β^j in the model to $(1/\tau)/n$, where n is 1 plus the number of β^j in the model. For identifiability, we fixed $y_1 = 0$. We used a gamma prior distribution for τ with both hyperparameters set to 0.001.

We began the analysis by using equal prior probabilities for all models to obtain Markov chain output to compute initial approximations of posterior model probabilities and Bayes factors. Next, in the interest of having all models and the Markov chain adequately sampled, we used the approximate Bayes factors to choose non-equal priors that would yield nearly equal posterior model probabilities and reran the analysis. We generated chains of length 6.375 million, recording every 25th observation, thus producing chains of length 255 000 (computation took ~ 8 h on a 3.2-GHz processor). We discarded the first 5000 values as a burn in, and used the remaining 250 000 observations for posterior inference. The results of the second analysis were then used to recalculate the Bayes factors, obtain estimates of parameters for each model, and calculate posterior model weights. To ensure that good mixing was achieved and that simulations were long enough, we examined within-chain autocorrelation and compared results from five additional chains. All calculations were conducted in GAUSS (Aptech Systems, Black Dia-

mond, Washington, USA) and WinBUGS (Lunn et al. 2000).

When evaluating the modeling results, we were interested in whether there was evidence (1) for density dependence in population changes and (2) relationships between population size and any of the environmental covariates considered. We began by examining Bayes factors (BF) that compared the support for our simplest model to the support for each of the other models. We did so using the categorization provided by Kass and Raftery (1995) for weights of evidence in favor of one model over another: “not worth more than a bare mention” ($1 < BF \leq 3$), positive ($3 < BF \leq 20$), strong ($20 < BF \leq 150$), and very strong ($BF > 150$). We also considered posterior model weights (w_j), which sum to one and can be interpreted as the relative degree of support for model j within the model set (Link and Barker 2006). The w_j were calculated as $(1/BF_{1,j})/(1/\Sigma BF_{1,j})$. Finally, we evaluated the relevant coefficients and associated measures of precision from the competing models.

RESULTS

The estimated number of female seals in the breeding population ranged from 438.3 to 622.7 and averaged 526.9 during 1982–2003 (Appendix B: Fig. B1). Estimates were precise ($SE = 4.3$ seals, range = 2.0–9.5; average CV = 0.01). Such precision was possible because five to eight surveys were done each year, per-survey detection probability was typically quite high (0.6–0.9), and individuals tended to be present for most if not all surveys. Accordingly, in each year all models produced similar estimates of population size, and estimated population size was the number of unique seals observed plus one to eight additional seals. Evaluation of the results of goodness-of-fit tests indicated that the models fit the data adequately. For the 22 years of data, P values for χ^2 statistics averaged 0.57 for analyses of data for known-age and 0.54 for data from unknown-age females. In four of the 44 analyses, there was an indication of possible fit problems: in each case the problem was with data for active breeders late in the season, and close inspection indicated that some active breeders became difficult to sight late in the season (we suspect that these were females who had lost their pup earlier in the season). We note that the four fit issues that occurred did not affect our estimates of the number of active breeders in those years because all pups were born and counted with their mothers on numerous occasions before the time that some mothers became difficult to detect in those years.

When competing models of change in population size were evaluated, a model containing a density-dependent parameter but no environmental covariates received the greatest support and was favored over all models except one containing a density-dependent parameter and SOI (Appendix C). The Bayes factor comparing the density-dependence-only model with the second-best model

⁴ <http://www.bom.gov.au/climate/>

TABLE 1. Characteristics of estimated coefficients from competing models of changes in the size of the breeding population of female Weddell seals in Erebus Bay, Antarctica, 1982–2003.

Model	$\Delta\hat{\beta}^{DD}$	β^{SOI}		β^{Sum}		β^{Win}	
		$\Pr(\beta^{SOI} > 0)$	Median	$\Pr(\beta^{Sum} > 0)$	Median	$\Pr(\beta^{Win} > 0)$	Median
β^{DD}	0.015						
$\beta^{DD} + \beta^{SOI}$	−0.003	0.859	0.028				
$\beta^{DD} + \beta^{Win}$	−0.002					0.777	0.020
$\beta^{DD} + \beta^{Sum}$	0.016			0.454	−0.003		
$\beta^{DD} + \beta^{SOI} + \beta^{Sum}$	−0.007	0.902	0.038	0.236	−0.021		
$\beta^{DD} + \beta^{SOI} + \beta^{Win}$	−0.008	0.798	0.024	0.498	−0.001	0.613	0.005
$\beta^{DD} + \beta^{Sum} + \beta^{Win}$	−0.001			0.461	−0.003	0.778	0.020
$\beta^{DD} + \beta^{SOI} + \beta^{Sum} + \beta^{Win}$	−0.007	0.855	0.036	0.250	−0.020	0.529	0.002

Notes: Variables are β^{DD} , the coefficient for density dependence; β^{SOI} , the coefficient for Southern Oscillation Index; β^{Win} , the coefficient for winter sea-ice extent; and β^{Sum} , the coefficient for summer sea-ice extent. The values for $\Delta\hat{\beta}^{DD}$ are the difference between the posterior mean for $\hat{\beta}^{DD}$ from a specific model and the overall mean $\hat{\beta}^{DD}$ (−0.947, SD = 0.112) and were obtained from all models using the prior model probabilities in Appendix C. “Median” is median values of the estimated coefficient.

($\beta^{DD} + \beta^{SOI}$) was only 2.3, and thus, the latter model received some support from the data. The weight of evidence favoring the density-dependence-only model over other models was positive ($3 < BF \leq 20$) for most comparisons and strong ($20 < BF \leq 150$) when the most complex model was considered.

In the density-dependence-only model, $\hat{\beta}^{DD} = -0.93$ (SD = 0.11, 95% credible interval of −1.15 to −0.71), which provided strong evidence of negative density dependence in the rate of annual population change. This model estimated μ as 6.20 (SD = 0.01, 95% credible interval of 6.18 to 6.22) and σ_{pr}^2 as 0.12, which when converted to the original scale of measurement using equations provided by Dennis et al. (2006) yield a stationary distribution for the population with a mean of 496.9 females (SD = 60.5). Estimates of β^{DD} were stable across all models (Table 1) and regardless of whether prior probabilities for models were equal ($\hat{\beta}^{DD} = -0.94$, SD = 0.11) or not ($\hat{\beta}^{DD} = -0.95$, SD = 0.11). Results of exploratory analyses did not support models that included abundance estimates from years prior to year $t - 1$ ($\hat{\beta}_{t-x}^{DD}$ ranged from −0.03 to 0.01 for $x = 2$ to 5; SD = 0.10 to 0.11; J. Rotella, unpublished data).

Evidence for environmental effects was weaker, but the data did provide some support for the prediction that positive values of SOI in the months leading into the breeding season of year $t + 1$ would be associated with increased population size between years t and $t + 1$. The estimate of β^{SOI} was positive in all models that included the effect, and the probability of $\hat{\beta}^{SOI} > 0$ ranged from 0.80 to 0.90 (Table 1). In the most supported model that included SOI, $\hat{\beta}^{SOI} = 0.028$ with an 86% chance of being > 0 and a 95% credible interval of −0.025 to 0.085.

In keeping with our predictions, all of our estimates of β^{Sum} were negative, and all estimates of β^{Win} were positive. However, the weight of evidence provided by the data favored models without these effects, and the probability that β^{Sum} (β^{Win}) was less (greater) than 0 never exceeded 0.76 (0.78) in any model (Table 1). Further, our estimates of process variation decreased little as environmental covariates were added to the

Gompertz model: in our most complex model, $\hat{\sigma}_{pr}$ was 0.117 (SD = 0.020) compared with estimates of 0.122 and 0.118 for the two best-supported models.

DISCUSSION

Using a 22-year time series and analysis methods that accounted for measurement error associated with population estimates, we found clear evidence of direct, negative density dependence in annual population growth rates for a population of Weddell seals. The results indicate only moderate variation in population size for this apex predator of the Ross Sea during the period 1982–2002 (equilibrium population size = 497 females, CV = 11%, Appendix B). The expected population growth rate declined from an estimate of 1.10 (95% credible interval = 1.08 to 1.15) for a population of 441 females to an estimate of 0.90 (95% credible interval = 0.87 to 0.93) for a population of 553 females. Such information adds to a growing literature on population regulation that relies on rigorous analyses of population growth rates (e.g., Nichols et al. 2000, Freckleton et al. 2006) and can serve as a useful baseline for future studies of population responses to environmental change in the Southern Ocean (e.g., Barbraud and Weimerskirch 2001). The results do not, however, provide definitive information about the shape of density-dependence, a topic of interest in population dynamics (e.g., Fowler 1981, Sibly et al. 2005), because, as is common in such analyses (Brook and Bradshaw 2006, de Little et al. 2007), the range of abundances was not wide enough to allow us to discern among competing models such as the Ricker and Gompertz (Dennis and Taper 1994).

Underlying causes of negative density dependence in Weddell seal populations are not known because food resources are not monitored, overt competition for resources has not been reported among the animals, and predation rates on the seals are unknown. Based on characteristics of pinnipeds, Bowen et al. (2003) argued that food and space may become limiting as abundance increases. As reviewed by Trites and Donnelly (2003), reductions in per capita food supply have been shown to



PLATE 1. A mother and pup Weddell seal exiting a tide crack using an access hole that has been enlarged by the mother, Erebus Bay, Antarctica. Photo credit: J. J. Rotella.

lower rates of survival, body growth, metabolism, and late-gestation pregnancy in marine mammals. However, the role of food in regulating Weddell seal numbers cannot currently be resolved: data on fish abundance do not exist for the area and will be difficult to obtain for this often-ice-covered marine environment. Space for parturition and pup-rearing may also be limiting for Weddell seals (Stirling 1969a). During the breeding season, Weddell seals generally occupy shore-fast ice close to land, remain within several meters of a crack, and maintain access holes in cracks by abrading the ice with their teeth (Stirling 1969b). There may be limits to how many females can use a given access hole, and the number of suitable holes may limit population size (Siniff et al. 1977, Siniff 1981). Although we do not see overt competition above the ice, competition might occur below the ice and underwater cameras might be used to evaluate how behaviors change with seal abundance. Density-dependent changes in predation rate may also contribute to regulation of the population. Leopard seals (*Hydrurga leptonyx*) and killer whales (*Orcinus orca*) are both potential predators of Weddell seals (Testa and Siniff 1987) and known to occur within a few kilometers of our study site during the breeding season (Ainley et al. 2005). Although Weddell seals are afforded protection from predation by shore-fast ice when it is present, ice is sometimes absent, and seals may use pack ice areas during the non-breeding season (Testa

1994). Leopard seals have been reported to limit populations of Antarctic fur seals (*Arctocephalus gazella*; Boveng et al. 1998), but it will be difficult to evaluate if this is also true in Weddell seals due to the logistic challenges for estimating predation rates on Weddell seals using open water or pack ice.

Given the results of direct density dependence reported here and recent assessment of annual variation in vital rates for the study population (Cameron and Siniff 2004, Hadley et al. 2006, 2007a), we can speculate about which demographic rates may covary with density. Although a number of studies of pinnipeds have reported that body condition and survival rates for pups are negatively affected by density (e.g., Bradshaw et al. 2000, de Little et al. 2007), such changes would not account for the direct density dependence that we observed because effects of changes in pup survival would not be evident in the breeding population for ~5–10 years due to delayed maturity in this Weddell seal population (Hadley et al. 2006). Years of high population density may have been associated with low recruitment rates due to decreased breeding opportunities for young females or decreased prey availability as shown in other pinnipeds (Reiter and Le Boeuf 1991, Pistorius et al. 2001), but analyses conducted by Hadley et al. (2006) failed to detect such a relationship in our population. Given that, changes in adult survival rates, breeding probabilities, and/or rates of temporary

emigration for females in the breeding population were likely responsible for the direct density dependence detected in this study.

Adult survival rate is expected to be the last vital rate to change in response to increased density (Eberhardt 2002), but it may well have been negatively affected by density during the study as our population was quite close to its equilibrium size throughout the study period. During the study period, Hadley et al. (2007a) reported that annual survival rates for active and skip breeders ranged from 0.84 to 0.98 and 0.90 to 0.99, respectively, which would cause important changes in the size of the breeding female population. Pistorius et al. (2004) reported that variation in adult female survival was important to population regulation of southern elephant seals (*Mirounga leonina*), and evidence of density-dependent variation has been detected in adult survival rates of other Antarctic marine predators (Barbraud and Weimerskirch 2003). Given these results, we intend to conduct mark-recapture analyses that evaluate whether or not survival rates for breeding female Weddell seals are related to population density.

Intermittent breeding and abandonment of reproductive attempts are useful strategies in long-lived species (Goodman 1981) and are known to be employed by Weddell seals (Testa 1987). Successfully rearing a pup requires the transfer of a large proportion of body reserves in this capital breeder (Testa et al. 1989, Wheatley et al. 2006), which may induce costs of reproduction (Hadley et al. 2007a). We hypothesize that Weddell seals respond to high population density by lowering their breeding probabilities and by elevating the temporary emigration rate for skip breeders. Such a flexible strategy would help them to minimize reproductive costs to their own survival and future reproduction when population conditions are such that pups produced have impaired chances of survival. Hadley et al. (2007a) reported that breeding probabilities for experienced breeders ranged from 0.48 to 0.78, but it is not yet known if annual variation is related to population size. Rates of temporary emigration have not been estimated for our study population, but we suspect that there may be substantial annual variation in the rate of temporary emigration for females that are skipping breeding. Hadley et al. (2006) reported the average annual detection probability for skip breeders in our population as 0.78 (range 0.60 to 0.89), and those rates can reasonably be considered as approximations of the probability that a female did not temporarily emigrate in a given breeding season ($1 - [\text{rate of temporary emigration}]$). In the population estimation work reported here, the estimated number of seals in the population closely matched the number detected in the field, which indicates that seals are detected if present and that failed detections are due to seals not being present, i.e., temporarily emigrating. If so, the temporary emigration rate might range from 0.11 to 0.40 for skip breeders and be worth investigating as a demographic response to

density and/or environmental variation using appropriate mark-recapture methods (Kendall et al. 1997). Such work would complement recent experiments on the influence of local density on dispersal (Hauzy et al. 2007) and provide much needed information for vertebrates (Matthysen 2005). Reverse-time (Nichols et al. 2000) and open robust design capture-recapture models (Kendall and Bjorkland 2001) now permit estimation of the relative contributions of adult survival rate, breeding probability, recruitment of new breeders (both local recruits and immigrants), and temporary emigration of skip breeders to population growth while accounting for effects of population size and environmental variation.

By working at the level of the individual vital rates, which may respond differently to changes in various environmental factors (Hadley et al. 2007a, b), we may further our knowledge of which vital rates contribute to annual changes in population size and gain a better understanding of connections between the population's dynamics and environmental variation. In the work presented here, we were not able to find strong connections between environmental variation and population changes. We did find evidence that the population's equilibrium size was positively related to SOI as measured in late winter-early spring, but the strength of inference for the relationship was modest, process variation was only slightly reduced when SOI was incorporated, and the biological effect was not large: the point estimate of equilibrium population size increased by ~ 14 breeding females for every 1 SD increase in SOI. Although our hypothesis for the relationship depends on SOI-mediated changes in per capita food resources, the actual underlying reasons for the positive relationship between SOI and seal numbers will remain elusive until data on actual foods that are eaten by seals are collected at a variety of spatial scales. As data accumulate for key production zones such as the Ross Sea polynya and our understanding of the teleconnections between SOI, climate, and marine productivity improves (e.g., Yuan 2004), we will be able to better understand how changes in the physical environment affect populations of marine predators and make better sense of conflicting results from different species (Barbraud and Weimerskirch 2001, Croxall et al. 2002, McMahon and Burton 2005).

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APPENDIX A

A picture of a Weddell seal colony in Erebus Bay, Antarctica, during late October, 2006 (*Ecological Archives* E090-063-A1).

APPENDIX B

Estimated number of females in the breeding population of Weddell seals at Erebus Bay, Antarctica during 1982–2003 (*Ecological Archives* E090-063-A2).

APPENDIX C

Model-selection results for competing models of changes in the size of the breeding population of female Weddell seals in Erebus Bay, Antarctica, 1982–2003 (*Ecological Archives* E090-063-A3).