Environmental Variation and Cohort Effects in an Antarctic Predator

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ABSTRACT

Understanding the potential influence of environmental variation experienced by animals during early stages of development on their subsequent demographic performance can contribute to our understanding of population processes and aid in predicting impacts of global climate change on ecosystem functioning. Using data from 4,178 tagged female Weddell seal pups born into 20 different cohorts, and 30 years of observations of the tagged seals, we evaluated the hypothesis that environmental conditions experienced by young seals, either indirectly through maternal effects and/or directly during the initial period of juvenile nutritional independence, have long-term effects on individual demographic performance. We documented an approximately 3-fold difference in the proportion of each cohort that returned to the pupping colonies and produced a pup within the first 10 years after birth. We found only weak evidence for a correlation between annual environmental conditions during the juvenile-independence period and cohort recruitment probability. Instead, the data strongly supported an association between cohort recruitment probability and the regional extent of sea ice experienced by the mother during the winter the pup was in utero. We suggest that inter-annual variation in winter sea-ice extent influences the foraging success of pregnant seals by moderating the regional abundance of competing predators that cannot occupy areas of consolidated sea ice, and by directly influencing the abundance of mid-trophic prey species that are sea-ice obligates. We hypothesize that this environmentally-induced variation in maternal nutrition dictates the extent of maternal energetic investment in offspring, resulting in cohort variation in mean size of pups at weaning which, in turn, contributes to an individual’s phenotype and its ultimate fitness. These linkages between sea ice and trophic dynamics, combined with demonstrated and predicted changes in the duration and extent of sea ice associated with climate change, suggest significant alterations in Antarctic marine ecosystems in the future.
Introduction

In most ecological contexts the environments in which animal populations exist are inherently variable. Ecological studies of the impacts of environmental variation on animal population processes has a long and rich history and have demonstrated the direct and immediate influences of environmental variability on basic demographic processes (Turchin 2003). A more recent area of investigation is the influence of nutritional or developmental programming on the demographic performance of individuals subjected to differing environmental conditions during the early stages of life. Studies across a wide range of taxa are revealing that this phenomenon can result in cohorts produced during poor environmental conditions suffering reduced fitness, as indexed by survival, fecundity, or recruitment rates, compared to cohorts born under more favorable conditions (Lindström 1999). Such cohort effects have important consequences for understanding features of population dynamics such as variability, stability, and delayed density dependence (Beckerman et al. 2003, Lindström and Kokko 2002).

The study of cohort effects in long-lived, large-bodied mammals is particularly interesting because these animals have a prolonged developmental period that often extends for several years before adult body size and sexual maturity are attained. The developmental period for such animals can be partitioned into the maternal-dependency phase, which includes the intrauterine period from conception to birth and the subsequent period of maternal provisioning through lactation and nursing. The juvenile phase begins when an animal is weaned, thus becoming nutritionally independent, and continues until the animal attains maturity. Because development extends over multiple seasons and years, environmental conditions influencing an individual can vary considerably from one developmental period to the next, providing an
opportunity to evaluate the relative contribution of environmental conditions during various stages of development to any realized cohort effect.

Investigations of cohort effects in large mammals have been dominated by ungulate studies in temperate and high latitudes (e.g., Albon et al. 1987, Festa-Bianchet et al. 1998, Forchhammer et al. 2001). Ungulates generally accrue body reserves during the growing season of one year, breed in autumn at maximal body mass, and nourish the fetus through the winter period of energy restriction, primarily from body reserves. Birth occurs the following spring at the onset of the next growing season when mothers are at minimal body mass (Anderson et al. 1974, Parker et al. 1993). Mothers then feed on nutritious forages during the lactation period and gradually wean young near the end of the growing season. Using the capital-income typology for describing reproductive investment (Jönsson 1997) and standardizing its application to the entire reproductive cycle (Stephens et al. 2009), ungulate reproduction thus represents a blend of capital investment during the intrauterine period and income investment during the post-partum maternal provisioning period. A consequence of this capital-income sequence of energetic investment in ungulates is that the environmental conditions influencing the development of a cohort of young ungulates during the maternal dependency period span two growing seasons as well as a winter season, with the environmental conditions during the second growing season contributing to both the maternal dependency period and the initial period of juvenile independence.

Demographic studies of marine mammals, particularly of large phocids, provide opportunities to expand our understanding of cohort effects to a taxon that represent secondary consumers. These mammals have a considerably different pattern of energetic investment in reproduction from ungulates that enhances our ability to assess the relative contribution of
environmental variability experienced during the maternal-dependence and juvenile phase to any
realized cohort effect (Shultz and Bowen 2004). One of the largest phocids is the Weddell seal
(Leptonychotes weddellii), which is associated with the fast ice around the coast of Antarctica
and attains a body size of 500-580 kg (Wheatley et al. 2006, Proffitt et al. 2007a). Weddell seals
fast during lactation (mid-October through early December) and breed at the end of the period of
lactation, hence placing them at a seasonal low point in body reserves at the start of the
reproductive cycle. Implantation is delayed until mid-January to mid-February followed by a
prolonged gestation period with energetic intake supporting both fetal development and
replenishment of body reserves. Birth occurs from mid-October through November, when
female body mass is at its maxima at the end of the seasonal cycle, after which body reserves are
rapidly transferred to the developing young during the post-partum maternal provisioning period
(Stirling 1969). Thus, reproduction depends on income investment during the intrauterine period
and capital investment during the post-partum maternal dependency period. Recent energetic
studies in Weddell seals confirm that feeding during the nursing period contributes nominal
resources to support lactation (Wheatley et al. 2008). Thus the reliance on body reserves during
the maternal provisioning period provides an unambiguous demarcation between environmental
conditions that influence the maternal dependency period experienced during a single summer-
winter annual cycle and those experienced by newly independent juveniles during the subsequent
annual cycle.

Here, we use 30 years of data from a long-term demographic study of Weddell seals
occupying Erebus Bay in the southern Ross Sea to test the hypothesis that environmental
conditions experienced by young seals during early development, either indirectly through
maternal effects and/or directly during the initial period of juvenile nutritional independence,
have long-term effects on individual demographic performance. The objectives of this investigation included (1) characterizing variability in the probability of recruitment of cohorts of females born over periods with a wide range of environmental conditions, and (2) evaluating and contrasting the strength of correlations among indices of environmental conditions that were hypothesized to contribute to resources available during the maternal dependency and juvenile development periods. The Erebus Bay Weddell seals represent the world’s southernmost breeding mammal population, with life history traits likely linked to marine conditions that demonstrate substantial variability over multiple times scales (Cavalieri and Parkinson 2008, Massom and Stammerjohn 2010). These attributes, combined with the long-term study of highly detectable, known-age, individually marked seals (Hadley et al. 2007a, Rotella et al. 2009), enhance the ability to detect and understand the potential influence of environmental variation experienced during early stages of life on demographic performance.

High latitude systems are thought to be particularly sensitive to climate change (Croxall et al. 2002, Parkinson 2004), and thus studies of the linkages between environmental conditions and demographic processes in Antarctic populations contribute to understanding the ecological consequences of this global phenomenon. In this respect, the Ross Sea is of special interest, as it is one of the most productive areas of the Southern Ocean (Arrigo and van Dijken 2004), represents the most pristine marine environment remaining on the planet (Halpern et al. 2008), and, in striking contrast to trends in the Antarctic Peninsula (Vaughan et al. 2001, 2003) and Arctic regions (Parkinson and Cavalieri 2008, Walsh 2008), is experiencing an increase in sea ice coverage (Cavalieri and Parkinson 2008) and a gradual lengthening of the sea-ice season (Parkinson 2004).
Methods

Study area and population

The Erebus Bay study area is located in McMurdo Sound, the southernmost embayment of the Ross Sea, Antarctica (77°37'12" to 77°52'12" S, 166°18' to 167° E). Each austral spring, pupping colonies form along perennial cracks in the sea ice created by tidal movement of the fast ice against land or glacial ice. The fast ice associated with the pupping colonies is consistently present during the spring reproduction period with annual variation primarily limited to the thickness of the ice that, in turn, depends on annual variation in ice break out during the austral summer. Pupping occurs on the ice surface from mid October through November, and mothers remain in close association with their pups throughout the 30-45 day lactation period. Females who have not yet had a pup (pre-breeders) and parous females that are skipping pupping also haul out in the study area each year. Females come into estrous approximately 35 days after parturition, and breeding occurs within underwater territories centered on the ice cracks at each colony (Stirling 1969). Limited data from telemetry studies suggests that most seals move north into the Ross Sea after the breeding season and remain there until returning to traditional pupping colonies in spring. The estimated number of female seals in the breeding population ranged from 438 to 623 and averaged 527 during 1982–2003 (Rotella et al. 2009). Typically, 300–600 pups are born per year at colonies in Erebus Bay, and females surviving to reproductive age have strong natal philopatry (Cameron and Siniff 2004). Age at first reproduction for females is variable and averages 7.6 ± 1.7 years (mean ± 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). The oldest known animals in this population are 29 years old.
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 several 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, but since 1982 all pups in the study area have been tagged. In addition, most seals with a broken or missing tag were 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 and field work ending by mid-December. 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.

Response variable (the proportion of female pups recruited by 10 years of age)

The response variable of interest was the proportion of females from a given birth cohort that recruited to the breeding population by age 10. The choice of age 10 represents the best compromise that captures most recruitment while maximizing the number of cohorts that could be included in the analysis, as Hadley et al. (2006) found that 93% of breeding females produce their first offspring by age 10. Weddell seals have strong philopatry to their birth colony with little evidence of permanent dispersal (Cameron and Siniff 2004), and the vast majority of all young tagged in the Erebus Bay colonies are never detected after their birth year (Hadley et al. 2007b), thus it is likely that seals that have not recruited into the breeding population by age 10 died. The uninterrupted multi-decadal research effort using consistent tagging and resight
methodology, combined with strong philopatry of female seals to their natal area (Cameron and Siniff 2004) and nearly perfect detection probability of reproducing females (Hadley et al. 2006), provided high-quality encounter histories of females born in the Erebus Bay colonies for developing the response variable. Using these individual encounter histories we developed a dichotomous response variable by assigning a 0 or 1 to each tagged female pup in each cohort based on whether she recruited by age 10 or not. Based on those 0’s and 1’s we thus obtained an estimate of the proportion of females in each cohort that recruited. The numbers of pups annually tagged prior to 1980 were considered too low to provide a representative sample of the cohort, and 2009 was the most recent year for which resight data were available. Hence we included 20 cohorts from 1980 through 1999 in the analysis.

Environmental covariates

We evaluated seasonal covariates at three spatial scales that indexed environmental variation we suspected may influence primary production and other attributes of the marine system that result in variation in prey availability, and the distribution and abundance of other predators that compete for the same fish resources with Weddell seals. We considered these covariates for two time periods to evaluate the relative importance of environmental conditions during the maternal dependency period and the initial period of juvenile nutritional independence.

Southern Oscillation Index (SOI)

At the broadest scale there is strong evidence that the El Niño/Southern Oscillation (ENSO) phenomenon in the tropical Pacific linearly covaries with Antarctic sea ice fields and that this teleconnection is the most significant link with extra-polar climate variability (Yuan 2004; Yuan and Li 2008). We used the Southern Oscillation Index (SOI), which describes the ENSO atmosphere–ocean interactions in tropical and subtropical latitudes (Stenseth et al. 2003), and
calculated a three month running average of the monthly SOI for summer (Dec-Feb, SOIₜ) and winter (July-Sept, SOIₜₜ) periods (http://www.bom.gov.au/climate/current/soihtm1.shtml). SOI is negatively associated with atmospheric pressure and sea-surface temperatures and is positively associated with the extent and concentration of sea ice (Yuan 2004). SOI generally is in phase with pupping rates in the study population (Testa et al. 1991) and positively correlated with the size of the population (Rotella et al. 2009) and seal body mass (Proffitt et al. 2007a). Thus, we predicted that SOI would be positively related to measures of cohort demographic performance, such as the probability of recruitment.

**Antarctic Dipole (ADP)**

A second climate mode index, the Antarctic Dipole (ADP), was also considered as it represents the ENSO ‘footprint’ at the southern high latitudes, but has its own characteristics in space and time and persists after tropical forcing has diminished (Yuan and Li 2008). Similar to SOI, we calculated a three-month running average of the Antarctic Dipole for summer (Dec-Feb, ADPₜ) and winter (July-Sept, ADPₜₜ). ADP is a more recently developed climate mode and has not yet been employed much in biological studies, but we expected probability of recruitment to have the same relationship with ADP as with SOI.

**Sea ice extent (SIE)**

At the intermediate spatial scale of the Ross Sea sector, defined as that portion of the Southern Ocean between 160°E and 130°W, we considered measures of summer and winter sea-ice extent (SIE) as estimated from passive microwave satellite images (DMSP SSM/I, NASA team algorithm; ftp://sidads.colorado.edu/pub/DATASETS/seaice/polar-stereo/trends-climatologies/ice-extent/nasateam/) (Cavalieri et al. 1991). Winter sea-ice extent (SIEₜₜ) was defined as the September average and summer sea-ice extent (SIEₜ) was defined as the February
average; September and February are typically the months of maximum and minimum sea ice coverage, respectively, both in the Ross Sea and in the Southern Ocean as a whole (Cavalieri and Parkinson 2008). Extensive compacted sea ice during summer reduces the amount of open water available for phytoplankton blooms and atmospheric contributions of CO₂ to ocean waters (Arrigo and van Dijken 2007). Reduced primary production would likely cascade up the food chain, reducing the abundance of prey for apex predators like Weddell seals (Proffitt et al. 2007a,b) and resulting in a negative correlation between SIEs and probability of recruitment. Alternatively, increased sea-ice extent in summer may decrease the abundance of birds and whales in the ecosystem, competing predators that are not as well adapted to dense sea ice. This would suggest a positive rather than negative correlation between SIEs and probability of recruitment. Similarly, extensive sea ice during the winter would shift distributions of most predators further north, providing more extensive areas for Weddell seals to forage during the Antarctic winter with less competition, thus, we also predicted a positive correlation between SIEw and probability of recruitment.

**Open water index (OWI)**

At the most restricted spatial scale, we developed three seasonal covariates for the 804,000 km² ocean area of the Ross Sea that included the continental shelf and slope. Covariates describing summer (Oct to May) and winter (June-Sept) variation in open water within the Ross Sea were developed using the same passive microwave satellite data employed in constructing sea-ice extent covariates for the Ross Sea sector. Satellite data from alternate days for each seasonal period were processed with all pixels that were classified as open water (<15% sea-ice concentration) summed to obtain an estimate of total open water area within the Ross Sea for that day. The daily values were then summed to index the extent and duration of open water for the
summer (OWI_s) and winter (OWI_w) periods. No satellite data were available from 3 December 1987 thru 12 January 1988; therefore, we estimated 1987-88 OWI_s using the correlation between the OWI_s derived from complete data sets for the other 19 years in the time series and the OWI_s values obtained with the period of missing data in the 1987-88 data omitted. Similar to SIE_s, the influence of OWI_s on probability of recruitment could be positive due to influences on primary production or negative due to increased abundance of competing fish predators. The OWI_w covariate captures variation in the Ross Sea polynya as well as several smaller polynyas along the western Victoria Land coast that are maintained by strong katabatic winds originating on the Antarctic continent (Jacobs and Comiso 1989). While we suspect that the substantial annual variation in these polynyas influences the marine ecosystem and Weddell seals, the paucity of studies focused on the winter ecology of this food web makes it difficult to predict the direction of influence of OWI_w on measures of reproductive performance of females.

Prevalence of first-year ice (FYI)

Microbial communities that grow in close association with sea ice contribute substantially to annual primary production in the Ross Sea and account for up to 25% of total annual primary production in ice-covered waters (Arrigo and Thomas 2004). Most of this production occurs on the bottom of first-year sea ice that allows adequate sunlight penetration, with blooms of ice algae and bacteria occurring in spring prior to phytoplankton blooms (Garrison et al. 1986).

Hence, we developed a third covariate at the scale of the Ross Sea to index the prevalence of first-year sea ice in spring (FYI_s), when sea ice microbial communities would be most productive. We used the passive microwave satellite images processed to quantify open water, as previously described, and identified the date during the summer of year \( t-1 \) with the maximum open water, then took the amount of open water on that date and subtracted the minimum area of
open water quantified from daily images acquired the subsequent winter. We assumed this quantity indexed the maximum area that could potentially contain first-year ice in spring of year $t$. Because sea ice microbial communities contribute to annual primary production, and likely have a positive effect on crystal krill that are considered ice-obligate grazers, we predict that FYI$_t$ would be positively correlated with probability of recruitment.

Before employment in modeling, values for each of the environmental covariates were centered to have a mean of 0 and rescaled to have a standard deviation of 1.0. We assessed collinearity among environmental covariates by calculating pair-wise correlations and variance inflation factors. We also evaluated each time series of environmental covariates for temporal autocorrelation using a wide range of time lags.

**A priori and exploratory models**

In order to evaluate the relative contribution of environmental variation during summer and winter seasons and between the periods of maternal provisioning and the initial year of juvenile independence, we constructed four a priori model suites for confrontation with the data: summer-maternal (Mat$_s$), winter-maternal (Mat$_w$), summer-juvenile (Juv$_s$), and winter-juvenile (Juv$_w$). For the two seasonal model suites associated with the maternal provisioning period we developed a series of regression models that included combinations of the 5 summer environmental covariates (SOI$_s$, ADP$_s$, SIE$_s$, OWI$_s$, FYI$_s$) and another suite using combinations of the 4 winter environmental covariates (SOI$_w$, ADP$_w$, SIE$_w$, OWI$_w$) measured during year $t-1$ for the cohort born in year $t$. These models reflect the environmental conditions experienced by the mothers of pups born in that cohort when the mothers were accruing resources to nourish the pup while in utero and during the post-partum nursing period when mothers were fasting. Two additional model suites were similarly constructed for the juvenile-independence period using
the environmental covariates measured during year $t$ that reflected environmental conditions experienced by the pups during their first summer and winter seasons of nutritional independence.

To reduce the risk of over-fitting models (Knape and de Valpine 2010), we constrained all a priori models within each suite to include a maximum of only one environmental covariate from each of the 3 spatial scales (climate mode-SOI, ADP; Ross Sea sector-SIE; Ross Sea-OWI, FYI), as well as employing a null intercept-only model. This resulted in a total of 18 models in each of the summer-maternal and summer-juvenile suites and 12 total models in the winter-maternal and winter-juvenile suites. We kept our a priori model lists simple and considered only additive combinations of covariates because knowledge of environmental variation in the Ross Sea and its effects on the marine ecosystem is limited, providing little guidance for developing interaction models, especially given the number of cohorts available for this analysis.

Once we completed analysis of a priori models, we evaluated all possible combinations of those environmental covariates from each a priori model suite that were well-supported by the data in an exploratory analysis to further evaluate the relative contribution of environmental variability during the maternal-dependency and juvenile-independence periods. We also evaluated a duplicate set of these exploratory models that included a cohort size covariate as we speculated that cohort size might capture important annual environmental variation not described by our suite of environmental covariates. Not all reproductively mature females produce a pup every year and breeding probabilities (Hadley et al. 2006), as well as temporary emigration rates (Cameron and Siniff 2004), display considerable annual variation that might be associated with variability of food resources available to the females during the year prior to the pupping season,
when conception, implantation, and gestation would occur. Thus we expected a positive
correlation between cohort size and recruitment probability.

**Data analysis**

We modeled the number of female pups from each cohort that recruited into the breeding
population by age 10 using a logistic-binomial model (Gelman and Hill 2007), where the number
of females that recruited from a given cohort was the number of ‘successes’ and the size of the
cohort was the number of possible successes. We evaluated support for each model within a
suite and among suites using an information-theoretic approach and Akaike’s Information
Criteria (AIC) adjusted for possible overdispersion (QAIC) and sample size (QAICc). We
estimated overdispersion as the smallest dispersion value that was obtained when we evaluated
the most complex models in each of our 4 suites, using a logistic model of the counts and a
quasibinomial distribution of errors (Gelman and Hill 2007). The most complex models were
evaluated with and without cohort size as a covariate. We next evaluated each of the competing
models using the logistic-binomial model and adjusted the resulting AICc scores and standard
errors using our estimate of over-dispersion. We evaluated the strength of support for each of
the competing models both within and among suites. When calculating QAICc values, we added
1 to the number of parameters in the model being used, to account for the fact that we had to
estimate the amount of over-dispersion. Finally, to provide an approximate measure of the
proportion of deviance explained by covariates in the top model, we used analysis of deviance to
compute the ratio of differences in quasi-log-likelihood values and to provide a deviance-based
$r^2$ metric for covariates of interest (Skalski et al. 1993). The numerator contained the difference
in values for the top model and the intercept-only model. The denominator was the difference in
values for the global model and the intercept-only model.
Results

We obtained data from 4,178 female pups born into 20 different cohorts that were each monitored to determine how many of the females recruited to the pup-producing portion of the population within 10 years of birth. The cohorts under investigation here were born during the period 1980-1999 and, with the exception of 1981 when only about 50% of the pups were tagged due to early ice breakout, contained 165 to 275 female pups each year (mean = 209 females, SD = 22). The proportion of a cohort that recruited within 10 years averaged 0.20 (SD = 0.07) and ranged from 0.11 to 0.36 (Table 1). Data on environmental conditions during the maternal-provisioning and juvenile-dependency periods were available for all 20 cohorts, and conditions varied among years (Fig. 1). During the maternal-provisioning period, summer environmental covariate values had pair-wise-correlation values that averaged -0.06 (SD = 0.36; range from -0.55 to 0.45) and variance inflation factors that ranged from 1.33 to 1.82. During the juvenile-dependency period, summer environmental covariate values had pair-wise-correlation values that averaged 0.02 (SD = 0.33; range from -0.40 to 0.59) and variance inflation factors that ranged from 1.29 to 2.40. Correlations and variance-inflation factors for winter environmental conditions were similar to those for summer covariates. We did not find evidence of important levels of temporal autocorrelation among environmental covariates, as auto-correlation function values at lags of 1 to 13 years were modest: for lag 1 year, values averaged 0.04 (SD = 0.25, range = -0.40 to 0.35). We estimated over-dispersion in the counts of the number of recruits per cohort as 1.90. Accordingly, we used QAIC$_c$ based on an over-dispersion value of 1.90 in model-selection and to inflate variances and confidence intervals. In each suite, there was strong evidence that it was important to consider environmental covariates when modeling the
proportion of the cohort that went on to recruit to the breeding population within 10 years of
being born. Accordingly, the intercept-only model received little support within each suite
(ΔQAICc ≥ 14.8, Table 2).

**Summer-maternal covariate suite**

The top 2 models both included the Antarctic Dipole (ADPs) and open water index (OWIs), and
the 2nd best model also included sea ice extent (SIEs). The 3rd best model contained first year ice
(FYIs) and SIEs. Other models in this suite were not well supported by the data in within-suite
model comparisons (ΔQAICc ≥ 4.3, Table 2), and Southern Oscillation Index (SOIs) did not
appear in any well-supported models in the suite (ΔQAICc ≥ 4.64). In the top model, estimates
indicated that a female pup’s probability of recruiting was positively related to the ADPs
($\hat{\beta}_{\text{Mat-ADP}} = 0.16, \text{SE} = 0.06, \text{Fig. 2}$) and negatively related to OWIs ($\hat{\beta}_{\text{Mat-OWI}} = -0.21, \text{SE} = 0.06$)
during the maternal provisioning period, which was in accordance with our predictions regarding
these environmental covariates. Although SIEs was in the 2nd-ranked model the estimated
coefficient was small and may have been positive or negative ($\hat{\beta}_{\text{Mat-SIE}} = 0.025, \text{SE} = 0.070$).

**Summer-juvenile covariate suite**

As in the summer-maternal suite, the top model in the summer juvenile covariate suite included
the Antarctic Dipole (ADPs) and the open water index (OWIs). The top 6 models all included
ADPs and up to 1 or 2 other covariates; these were the only models receiving any weight in this
suite as all other models had ΔQAICc ≥ 11.9 (Table 2). The estimated coefficients for ADPs
were relatively stable among models and supported the prediction that a female pup’s probability
of recruiting was positively related to ADPs (top model: $\hat{\beta}_{\text{Juv-ADP}} = 0.25, \text{SE} = 0.06, \text{Fig. 2}$).
Estimated coefficients for all other environmental covariates were small and imprecisely
estimated.
Winter-maternal covariate suite

Sea ice extent (SIE$_w$) was in all models within 7.52 QAIC$_c$ units of the top model in the winter-maternal suite. The top model contained only SIE$_w$, whereas other well-supported models included 1 or 2 additional covariates (Table 2). The estimated coefficients for SIE$_w$ in this suite of models supported the prediction that a female pup’s probability of recruiting was positively related to SIE$_w$ (top model: $\hat{\beta}_{\text{Mat-SIE}} = 0.26$, SE = 0.05, Fig. 2). It appears that other top models in the suite gained support from the data because they included SIE$_w$: the estimated coefficient for SIE$_w$ remained stable and relatively large among well-supported models, while coefficients for other covariate effects were smaller in magnitude and imprecisely estimated. For example, in the 2nd-best model in the suite, $\hat{\beta}_{\text{Mat-ADP}} = 0.09$ (SE = 0.07) whereas $\hat{\beta}_{\text{Mat-SIE}} = 0.21$ (SE = 0.07).

Winter-juvenile covariate suite

As was found for the winter-maternal suite, sea ice extent (SIE$_w$) was in all models within 14.38 QAIC$_c$ units of the top model in the winter-juvenile suite (Table 2), and the estimated coefficient associated with SIE$_w$ was relatively stable and positive (top model: $\hat{\beta}_{\text{Juv-SIE}} = 0.34$, SE = 0.08, Fig. 2). SOI$_w$ was in the top two models ($\Delta$QAIC$_c < 0.52$), but, contrary to our prediction, had an estimated coefficient that provided evidence that recruitment probability was negatively related to SOI$_w$ ($\hat{\beta}_{\text{Juv-SOI}} = -0.15$, SE = 0.07). The coefficient for OWI$_w$ was estimated imprecisely enough that it could have been positive or negative.

Comparing across suites

When models from the four suites were compared against one another, the data provided the strongest support for models in the winter-maternal suite. The top six models (cumulative model weight = 0.77) were all from the maternal-winter suite and all were within 2.42 QAIC$_c$ units of the best model, which contained only sea ice extent (SIE$_w$) in the winter-maternal period (Table
The top model from the summer-maternal period was the 7th-best model ($\Delta QAIC_c = 3.41$), and the best model from the winter-juvenile period was the next best ($\Delta QAIC_c = 3.85$). Models from the summer maternal suite had a cumulative model weight of 0.09, with juvenile winter and summer model suites having cumulative model weights of 0.09 and 0.05, respectively. Thus, the evidence was strong that a female pup’s eventual recruitment probability was most strongly tied to environmental conditions that the mother experienced during the winter the pup was in utero. The cumulative weight for models containing the covariate for sea ice extent for the winter maternal period, Mat$_w$-SIE$_w$ covariate was 0.77 and was most strongly related to the probability of a female pup recruiting. In contrast, for other winter environmental covariates, cumulative model weights ranged from 0.20 to 0.26. In the top model, 61% of the deviance was explained by Mat$_w$-SIE$_w$, which represents an approximate $r^2$ value for this model. As recommended by one reviewer, we also evaluated additional models that considered the size of the recruited population of females in either year $t$ or year $t-1$ as possible covariates to explore potential density-dependent effects. We evaluated whether the data supported adding population size or the natural logarithm of population size in year $t$ or year $t-1$ to the top a priori model. None of the 4 models performed as well as the top model, and 95% CIs for estimated effects of abundance variables overlapped zero in all cases.

**Exploratory modeling**

We evaluated all possible combinations of 6 different environmental covariates that were supported by the data in our assessments of the a priori model suites (64 models). These covariates included Mat$_w$-SIE$_w$ (the only variable receiving support from the data in the top model); Mat$_w$-ADP$_w$ and Mat$_w$-OWI$_w$ (the two variables that were in the only summer-maternal model that was within 5 QAIC$_c$ units of the top model in among-suite comparisons); and Juv$_w$-
OWIw, Juvw-SIEw, and Juvw-SOIw (the three variables that were in the only winter-juvenile model that was within 5 QAICc units of the top model in among-suite comparisons). We also include a duplicate set of models that included cohort size, resulting in a total of 128 exploratory models. This analysis reinforced the results of the a priori analysis with respect to important environmental covariates, but also provided strong support for including cohort size (Fig. 3). The top-ranked exploratory model included cohort size and Matw-SIEw; the top-ranked a priori model that included only Matw-SIEw had a QAICc score that was 13.38 units worse. Thirty-eight different models were within 5 QAICc units of the top-ranked exploratory model. All of these models included cohort size, and 32 of the 38, including all models within 3 QAICc units of the top exploratory model, also contained Matw-SIEw. While other environmental covariates appeared in various combinations in these top-ranked models, cumulative model weights for models pertaining to each of the additional covariates were modest (weights ranged from 0.26 to 0.48) and lower than the cumulative weight of 0.90 for models containing Matw-SIEw. Model-specific coefficient estimates for cohort size and Matw-SIEw were positive in all cases, and model-averaged estimates had 95% confidence limits that only included positive values ($\hat{\beta}_{\text{cohort size}} = 0.004$, unconditional SE = 0.001, 95% confidence limits = 0.002 to 0.007; $\hat{\beta}_{\text{Matw-SIE}} = 0.165$, SE = 0.083, 95% confidence limits = 0.003 to 0.327). Model-averaging produced 95% confidence limits that overlapped zero for coefficients associated with all other covariates considered in exploratory modeling: ($\hat{\beta}_{\text{S,M-ADP}} = 0.01$, SE = 0.04, 95%CI = -0.06 to 0.08; $\hat{\beta}_{\text{S,M-OWI}} = -0.05$, SE = 0.07, 95%CI = -0.19 to 0.09; $\hat{\beta}_{\text{W,J-OWI}} = 0.09$, SE = 0.07, 95%CI = -0.04 to 0.23; $\hat{\beta}_{\text{W,J-SIE}} = 0.09$, SE = 0.09, 95%CI = -0.09 to 0.27; $\hat{\beta}_{\text{W,J-SOI}} = -0.08$, SE = 0.07, 95%CI = -0.22 to 0.06). When we used model averaging to evaluate the effects of changing cohort size and Matw-SIEw, we found that the proportion predicted to recruit for the smallest observed cohort size (n =
345 pups) ranged from 0.12 (SE = 0.02) to 0.21 (SE = 0.03), as conditions changed from the lowest to the highest levels of Mat\textsubscript{w}-SIE\textsubscript{w}. For the maximum cohort size observed (n = 546 pups), predicted proportions ranged from 0.21 (SE = 0.04) to 0.34 (SE = 0.04) (Fig. 3).

Discussion

Using data from 20 cohorts of tagged female Weddell seal pups and 30 years of observations of the tagged seals, we documented an approximately 3-fold difference in the proportion of each cohort that returned to the Erebus Bay pupping colonies and produced a pup within the first 10 years after birth. The strong support in the data for a priori models correlating this inter-annual variation in recruitment probability and environmental covariates we hypothesized could influence regional ecosystem trophic dynamics provides evidence of a substantial cohort effect and contributes to the growing body of literature demonstrating the effects of environmental conditions during the early stages of life on the subsequent demographic performance of individuals later in life (Forchhammer et al. 2001, Reid et al. 2003, Nevoux et al. 2010).

Proximate mechanism for cohort effect

Recruitment probability is a combination of prebreeding survival probability and age-specific breeding probability. Long-lived mammals tend to have low and variable juvenile survival with much less variable breeding probability (Gaillard et al. 2000). In contrast to many studies of long-lived mammals in both terrestrial and marine systems that have documented relatively low and variable juvenile survival during the maternal dependency period (Gaillard et al. 2000 Chambellant et al. 2003), Weddell seal pups have exceptionally high survival to weaning (Proffitt et al. 2010). Estimating annual post-weaning juvenile survival rates in Weddell seals, however, is challenging because, like many other marine birds and mammals, juvenile Weddell
seals temporarily emigrate from natal sites during the lengthy immature period resulting in low
detection probabilities (Testa and Siniff 1987). Despite this limitation, several analyses of the
mark-resight data from the Erebus Bay population have documented substantial annual variation
in juvenile survival estimates for the first several years of independence (Hastings et al. 1999,
Cameron and Siniff 2004, Hadley et al. 2006). All studies have consistently estimated mean
annual survival as approximately 0.50-0.60 for the first two years of life, despite difference in
analytical methodology and length of the time series used. Although substantial annual variation
in age-specific recruitment probability has also been documented in this population (Hadley et al.
2006), we suspect that variation in juvenile survival is the predominant contributor to variation in
the proportion of a cohort that recruits and plan to initiate an evaluation of cohort-based variation
in survival rates to assess this hypothesis.

Although we hypothesize that cohort-based variation in juvenile survival is the primary
demographic mechanism driving variation in the probability of recruitment by age 10 among
Weddell seal cohorts, we found only weak evidence for a correlation between annual
environmental conditions during the initial year of juvenile-independence and cohort recruitment
probability. Instead, the data strongly support an association between cohort recruitment
probability and environmental conditions that the mother experienced during the winter the pup
was in utero. These results, therefore, suggest that the primary driver of the observed cohort
effects were indirect maternal environmental effects rather than direct environmental effects
experienced by the juveniles during their first years of nutritional independence (Maestripieri and
Mateo 2009).

The most widely recognized maternal effect in mammals is the influence of maternal
nutrition on offspring size and growth (Maestripieri and Mateo 2009). This topic has been
investigated in a variety of pinnipeds where females invest a substantial proportion of their body mass in offspring through lactation (Bowen 2009). Weddell seal females invest approximately 40% of their post-parturition body mass in their pup during the 30-45 day nursing period, with pups typically tripling in mass from birth to weaning (Wheatley et al. 2006). Several investigations of Weddell seals have demonstrated a strong positive correlation between post-parturition maternal body mass and pup mass at weaning (Wheatley et al. 2006, Proffitt et al. 2007a), similar to studies of other phocid species (Arnbom et al. 1997, Mellish et al. 1999). In addition, Proffitt et al. (2007a,b) found correlations between annual variation in oceanographic and sea ice conditions and maternal post-parturition body mass, as well as annual mean pup weaning mass. Correlations between pup weaning mass and environmental variation experienced by female southern and northern elephant seals have also been reported (Vergani et al. 2001, LeBoeuf and Crocker 2005), with all these investigators concluding that pup weaning mass reflected foraging success of parturient females during the previous year. Given the evidence of a positive relationship between size of progeny and survival during the initial period of nutritional independence in pinnipeds (Hall et al. 2001, Beauplet et al. 2005, McMahon and Burton 2005), as well as ungulates (Albon et al. 1987, Clutton-Brock et al. 1992, Festa-Biachet et al. 1998), we conclude that annual variation in food resources available to pregnant females was likely the driver of variation in recruitment probability among cohorts.

Interpretation of environmental and cohort covariates

While we found consistent support from the evaluation of a priori model suites for a relationship between the probability of recruitment and the Antarctic Dipole in summer and sea-ice extent in winter for both the maternal provisioning and juvenile independence periods, the comparison of models across suites, as well as exploratory analyses, indicated overwhelming support in the data
for the importance of including the winter sea-ice-extent covariate. In addition, there was almost no support in the data for relationships between probability of recruitment and environmental covariates we hypothesized would be linked to primary production (summer indices of sea ice extent, open water, and first year ice). These results are consistent with Ainley et al.’s (2006) hypothesis that the Ross Sea marine ecosystem is strongly structured from the top down. During the open water season, the Ross Sea supports some of the highest densities of top trophic level species found in marine environments (Smith et al. 2007), including Adélie (Pygoscelis adeliae) and emperor (Aptenodytes forsteri) penguins, snow petrels (Pagadroma nivea), minke whales (Balaenoptera acutorostrata), killer whales (Orcinus orca), and Weddell seals. In addition, the large Antarctic toothfish (Dissostichus mawsoni) is a major component of the fish assemblage in the Ross Sea (Eastman 1993) and although population estimates are not available, limited scientific fishing and the recent development of a commercial fishery in the region indicates their numbers are substantial (Dunn and Hanchet 2006). Ainley et al. (2006) suggests that predation by this unusually abundant predator community depletes the mid-trophic level (silverfish and crystal krill), resulting in light grazing pressure on phytoplankton that is inferred from satellite-based assessments of chlorophyll concentrations (Arrigo and Thomas 2004).

Because all of these predators feed heavily on silverfish (Smith et al. 2007), strong exploitative, and potentially interference competition, between Weddell seals in the Ross Sea and other members of the apex predator community is likely during the brief summer open-water period. Most of these predators, however, cannot occupy areas of consolidated sea ice and hence move north out of the Ross Sea in the autumn, as sea ice begins to build and consolidate. Only emperor penguins, Antarctic toothfish, and Weddell seals remain in the Ross Sea during the annual periods of extensive sea ice (Smith et al. 2007). Competition between Weddell seals and
emperor penguins during the prolonged Antarctic winter is largely minimized by temporal and
geographic differences in habitat use (Burns and Kooyman 2001), and although Antarctic
toothfish may compete with Weddell seals for silverfish, Weddell seals also prey on Antarctic
toothfish (Ainley and Siniff 2009). Thus, we suggest that sea-ice extent indirectly influences
Weddell seals by moderating the abundance of competing predators in the Ross Sea, and
hypothesize that changes in abundance of predators underlie the strong correlation between
winter sea-ice extent and probability of recruitment of female pups observed in this study.
Because both of the two main mid-trophic species (crystal krill and Antarctic silverfish) that
either indirectly or directly influence prey availability for Weddell seals have important life
history stages linked to sea ice (Vacchi et al. 2004), it is also possible that variability in winter
sea-ice extent influences the abundances of these species, thus contributing to annual variability
of prey resources for Weddell seals. These linkages between sea ice and trophic dynamics,
combined with demonstrated and predicted changes in the duration and extent of sea ice due to
climate change (Cavalieri and Parkinson 2008, Massom and Stammerjohn 2010), suggest
significant changes in the Ross Sea ecosystem in the future.

While winter sea-ice extent was the dominant environmental covariate receiving support
from the data in our analyses, the data also provide modest evidence supporting our hypothesis
that the probability of recruitment is positively correlated with the summer Antarctic Dipole
covariate. This climate mode is specific to the high latitude southern oceans and has only
recently been developed; thus it has seen very limited use in biological studies compared to the
commonly used Southern Oscillation Index for the tropical Pacific (Stenseth et al. 2003). A
number of investigations of Antarctic and sub-Antarctic marine birds and mammals have
demonstrated correlations between SOI and various demographic measures and indices of body
condition (Wilson et al. 2001, McMahon and Burton 2005). Thus, the evidence is strong that
this global climate index influences biotic components of marine systems. Despite evidence
from previous studies of the influence of SOI on the biology of the Erebus Bay Weddell seals
(Testa et al. 1991, Proffitt et al. 2007a, Rotella et al. 2009), the lack of support for Southern
Oscillation Index in our analyses suggest that the more regionally-specific Antarctic Dipole may
better capture environmental variation in the region of interest in this study (Yuan and Li 2008).
Thus, we encourage other ecologists to incorporate the Antarctic Dipole in analyses to further
assess its utility as an index of environmental variation in the high southern latitudes.

Although our results clearly indicate that sea-ice extent and the Antarctic Dipole index
reflect aspects of environmental variation that are important to Weddell seals, such indices are
likely to be imperfect measures of the multitude of conditions experienced by organisms that
either directly or indirectly influence the seals’ complex life cycle and the adequacy of available
resources to meet physiological and life-history demands. We evaluated cohort size as a
potential covariate in exploratory analyses because we hypothesized that the number of seals that
produce pups in a given year may be a more integrative index of annual variation in
environmental conditions. The strong support in the data for this covariate affirms this
hypothesis. There is considerable evidence from studies of a variety of taxa that annual breeding
probability and fecundity are state-dependent, i.e., are influenced by an individual’s condition
(McNamara and Houston 1996). We interpret the existence of skip-breeders in the Erebus Bay
Weddell seal population as evidence of this phenotypic plasticity in breeding probability (Testa
and Siniff 1987). We hypothesize that the mechanism for this plasticity may involve the
approximately 6-8-week period from conception to implantation. If most of the accumulation of
body reserves necessary to support pregnancy and the subsequent lactation period are accrued
during the austral summer then the rate of mass gain, as dictated by prey availability, may
provide a signal that dictates whether the blastocyst implants or not. In years of lower prey
availability a larger proportion of the breeding females may fail to implant, hence prey
availability during the previous summer may dictate the size of the pup cohort born the following
spring. This interpretation is reinforced by an integrated mark-recapture analysis using 30 years
of data that found a positive correlation among survival and breeding probabilities across years,
and also provides further support for the influence of annual variation in environmental
conditions on numerous aspects of Weddell seal demographic performance (Rotella et al. In
review).

Cohort effects and individual phenotypic variation

In conclusion, we have demonstrated a cohort effect in our Weddell seal study population that
contributes to the growing body of studies in a variety of taxa, occupying diverse ecological
settings, and that have quantified the existence and magnitude of cohort effects in populations
(Lindström 1999). Similar to many other studies involving long-lived organisms, we argue that
the mechanism responsible for the measured cohort effect in this Weddell seal population is a
result of environmental variation influencing maternal investment in progeny, which in turn
contributes to an individual’s phenotype and ultimate fitness. Thus, cohort effects introduce
individual phenotypic variation into this, as well as other populations.

The consequences of cohort effects on the dynamics of a population, however, are not
easily understood, because there are a number of other processes that also contribute to
individual phenotypic variation. Clearly in all sexually reproducing organisms both maternal
and paternal genetic effects contribute to individual variation. In organisms with extended
parental care, there is also the potential for maternal (and in some species paternal) behavioral
effects (Maestripieri and Mateo 2009). In this respect, the Weddell seal is relatively unique among phocids, because of its long period of maternal care, which can last 30-45 days (Wheatley et al. 2006), with extensive mother-pup interactions both on the ice surface and in the water (Testa et al. 1989, Sato et al. 2003). All three types of maternal effects (genetic, environmental, and behavioral) represent latent or static traits that influence an individual’s phenotype and contribute to heterogeneity among individuals within a population. However, additional variability in an individual’s phenotype is introduced by dynamic traits that change over an individual’s life, such as age, reproductive experience, social status, and body mass (Bergeron et al. 2010). Some of these processes that contribute to individual phenotypic variation are aggregated across groups of individuals, such as the cohort effect demonstrated in this study, and others, such as genetic effects, introduce random phenotypic variation among individuals (Wilson and Nussey 2010).

The relative contribution of each of these sources of individual phenotypic variation, interacting with the life history characteristics of the organism, dictate the degree to which individual variation stabilizes or destabilizes the dynamics of a population (Lindström and Kokko 2002, Beckerman 2003). Advances in our understanding of these complex interactions in long-lived organisms will require long-term longitudinal studies of tractable species where individuals can be studied from birth to death and aspects of population dynamics, as well as individual demographic performance and attributes, can be carefully quantified (Clutton-Brock and Sheldon 2010). An ongoing challenge for these research programs will be quantifying individual phenotypic variation, identifying the relative contribution of the numerous underlying mechanisms leading to this variation, and evaluating the consequences of this variation on individual fitness and population dynamics.
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Proffitt, K. M. et al. 2010. Effects of pup age, maternal age, and birth date on pre-weaning survival rates of Weddell seals in Erebus Bay, Antarctica. – Oikos 119: 1255-1264.


Table 1. The number of Weddell seal pups born and tagged at traditional colony sites within Erebus Bay, Antarctica, over 20 consecutive years, and the proportion of the female pups in each cohort that returned to the colonies and recruited (produced a pup) within 10 years of birth. In all years except 1981, all pups in each cohort were tagged at birth. (Ignoring the anomalous year, 1981, the mean values for the remaining years are: 419 animals, 209 females, and 0.20 proportion of females recruited.)

<table>
<thead>
<tr>
<th>Cohort</th>
<th>No. animals</th>
<th>No. females</th>
<th>Propor. females recruited</th>
</tr>
</thead>
<tbody>
<tr>
<td>1980</td>
<td>422</td>
<td>207</td>
<td>0.106</td>
</tr>
<tr>
<td>1981</td>
<td>202*</td>
<td>108*</td>
<td>0.157</td>
</tr>
<tr>
<td>1982</td>
<td>385</td>
<td>201</td>
<td>0.134</td>
</tr>
<tr>
<td>1983</td>
<td>391</td>
<td>213</td>
<td>0.192</td>
</tr>
<tr>
<td>1984</td>
<td>390</td>
<td>203</td>
<td>0.128</td>
</tr>
<tr>
<td>1985</td>
<td>410</td>
<td>201</td>
<td>0.174</td>
</tr>
<tr>
<td>1986</td>
<td>413</td>
<td>196</td>
<td>0.214</td>
</tr>
<tr>
<td>1987</td>
<td>410</td>
<td>206</td>
<td>0.165</td>
</tr>
<tr>
<td>1988</td>
<td>423</td>
<td>201</td>
<td>0.149</td>
</tr>
<tr>
<td>1989</td>
<td>384</td>
<td>206</td>
<td>0.194</td>
</tr>
<tr>
<td>1990</td>
<td>440</td>
<td>208</td>
<td>0.216</td>
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<tr>
<td>1991</td>
<td>424</td>
<td>210</td>
<td>0.214</td>
</tr>
<tr>
<td>1992</td>
<td>345</td>
<td>165</td>
<td>0.182</td>
</tr>
<tr>
<td>1993</td>
<td>450</td>
<td>228</td>
<td>0.171</td>
</tr>
<tr>
<td>1994</td>
<td>378</td>
<td>182</td>
<td>0.165</td>
</tr>
<tr>
<td>1995</td>
<td>385</td>
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<td>1996</td>
<td>379</td>
<td>203</td>
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<td>1997</td>
<td>546</td>
<td>275</td>
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<tr>
<td>1998</td>
<td>490</td>
<td>237</td>
<td>0.333</td>
</tr>
<tr>
<td>1999</td>
<td>499</td>
<td>227</td>
<td>0.361</td>
</tr>
</tbody>
</table>

*Only ~50% pups tagged due to early ice breakout
Table 2. Model selection results comparing a priori models used to examine the effects of environmental covariates on variation in probability of recruitment within 10 years of birth for 20 cohorts of female Weddell seal pups born from 1980 through 1999 in Erebus Bay, Antarctica. A priori models were partitioned into four suites, representing summer and winter conditions experienced by the pups’ mothers prior to parturition (Maternal) and summer and winter conditions experienced by pups during their first year of nutritional independence following weaning (Juvenile). Environmental covariates are Southern Oscillation Index (SOI), Antarctic Dipole (ADP), Sea-Ice Extent (SIE), Open Water Index (OWI), and First-Year Ice Index (FYI), with subscripts deliniating summer (s) and winter seasons (w).

<table>
<thead>
<tr>
<th>Model structure</th>
<th>K</th>
<th>ΔQAIC&lt;sub&gt;c&lt;/sub&gt;</th>
<th>wi&lt;sub&gt;c&lt;/sub&gt;</th>
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</thead>
<tbody>
<tr>
<td><strong>Summer - Maternal</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>ADP&lt;sub&gt;s&lt;/sub&gt;+OWI&lt;sub&gt;s&lt;/sub&gt;</td>
<td>4</td>
<td>0.00</td>
<td>0.44</td>
<td>0.44</td>
</tr>
<tr>
<td>ADP&lt;sub&gt;s&lt;/sub&gt; + OWI&lt;sub&gt;s&lt;/sub&gt; + SIE&lt;sub&gt;s&lt;/sub&gt;</td>
<td>5</td>
<td>1.88</td>
<td>0.17</td>
<td>0.61</td>
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<tr>
<td>FYI&lt;sub&gt;s&lt;/sub&gt; + SIE&lt;sub&gt;s&lt;/sub&gt;</td>
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<td>2.89</td>
<td>0.10</td>
<td>0.71</td>
</tr>
<tr>
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<td>4.31</td>
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<td>0.76</td>
</tr>
<tr>
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<td>5</td>
<td>4.59</td>
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<td>0.81</td>
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<tr>
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<td>0.00</td>
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<tr>
<td><strong>Summer - Juvenile</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>ADP&lt;sub&gt;s&lt;/sub&gt; + OWI&lt;sub&gt;s&lt;/sub&gt;</td>
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<td>0.00</td>
<td>0.26</td>
<td>0.26</td>
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<td>1.82</td>
<td>0.11</td>
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<td>1.00</td>
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<tr>
<td><strong>Winter – Maternal</strong></td>
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</tr>
<tr>
<td>SIE&lt;sub&gt;w&lt;/sub&gt;</td>
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<td>0.27</td>
<td>0.27</td>
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<td>0.17</td>
<td>0.65</td>
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<tr>
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<td>0.98</td>
<td>0.17</td>
<td>0.82</td>
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<td>SIE&lt;sub&gt;w&lt;/sub&gt; + ADP&lt;sub&gt;w&lt;/sub&gt; + OWI&lt;sub&gt;w&lt;/sub&gt;</td>
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<td>2.27</td>
<td>0.09</td>
<td>0.91</td>
</tr>
<tr>
<td>SIE&lt;sub&gt;w&lt;/sub&gt; + SOI&lt;sub&gt;w&lt;/sub&gt; + OWI&lt;sub&gt;w&lt;/sub&gt;</td>
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<td>2.42</td>
<td>0.08</td>
<td>0.99</td>
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<tr>
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<td>20.42</td>
<td>0.00</td>
<td></td>
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<tr>
<td><strong>Winter - Juvenile</strong></td>
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<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Model</td>
<td>DF</td>
<td>AIC</td>
<td>BIC</td>
<td>Likelihood Ratio</td>
</tr>
<tr>
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<td>------------------</td>
</tr>
<tr>
<td>SIE&lt;sub&gt;w&lt;/sub&gt; + SOI&lt;sub&gt;w&lt;/sub&gt; + OWI&lt;sub&gt;w&lt;/sub&gt;</td>
<td>5</td>
<td>0.00</td>
<td>0.34</td>
<td>0.34</td>
</tr>
<tr>
<td>SIE&lt;sub&gt;w&lt;/sub&gt; + SOI&lt;sub&gt;w&lt;/sub&gt;</td>
<td>4</td>
<td>0.52</td>
<td>0.26</td>
<td>0.61</td>
</tr>
<tr>
<td>SIE&lt;sub&gt;w&lt;/sub&gt;</td>
<td>3</td>
<td>1.38</td>
<td>0.17</td>
<td>0.78</td>
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<tr>
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<td>0.10</td>
<td>0.88</td>
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<tr>
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<td>0.08</td>
<td>0.96</td>
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<tr>
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<td>0.04</td>
<td>1.00</td>
</tr>
<tr>
<td>Intercept-only</td>
<td>2</td>
<td>16.57</td>
<td>0.00</td>
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Table 3. Model selection results of among-suite comparisons that contrasted the most-supported models from each of four a priori model suites used to examine the effects of environmental covariates on variation in probability of recruitment within 10 years of birth of 20 cohorts of female Weddell seal pups born from 1980 through 1999 in Erebus Bay, Antarctica (see Table 2). A priori models were partitioned into four suites representing summer and winter conditions experienced by the pups’ mothers prior to parturition (Mat, and Mat, ) and summer and winter conditions experienced by pups during their first year of nutritional independence following weaning (Juv, and Juv, ). Environmental covariates are Southern Oscillation Index (SOI), Antarctic Dipole (ADP), Sea-Ice Extent (SIE), Open Water Index (OWI), and First-Year Ice Index (FYI), with subscripts deliniating summer (s) and winter seasons (w).

<table>
<thead>
<tr>
<th>Model structure</th>
<th>K</th>
<th>QAIC_c</th>
<th>ΔQAIC_c</th>
<th>w_ic</th>
<th>cum. w_ic</th>
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<td>Mat_w-SIE_w</td>
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<td>0.21</td>
<td>0.21</td>
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<td>Mat_w-SIE_w + ADP_w</td>
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<td>Mat_w-SIE_w + SOI_w</td>
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<td>0.90</td>
<td>0.14</td>
<td>0.50</td>
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<td>Mat_w-SIE_w + OWI_w</td>
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<td>0.13</td>
<td>0.64</td>
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<td>Mat_w-SIE_w + ADP_w + OWI_w</td>
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<td>97.88</td>
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<td>Mat_w-SIE_w + SOI_w + OWI_w</td>
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<td>2.42</td>
<td>0.06</td>
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<td>3.41</td>
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<td>Juv_w-SIE_w + SOI_w + OWI_w</td>
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<td>3.85</td>
<td>0.03</td>
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<tr>
<td>Juv_w-SIE_w + SOI_w</td>
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<td>99.98</td>
<td>4.37</td>
<td>0.02</td>
<td>0.86</td>
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</table>
Figure 1. The environmental covariate conditions in each year from 1979 through 1999 that were considered in a priori models of the probability of recruitment of female Weddell seals for 20 cohorts (1980-1999). Black lines depict winter conditions and gray lines depict summer conditions for each covariate. All covariate values are expressed as standardized values (mean = 0, sd = 1) with standardization performed separately for each covariate and season. Environmental covariates are Southern Oscillation Index (SOI), Antarctic Dipole (ADP), Sea-Ice Extent (SIE), Open Water Index (OWI), and First-Year Ice Index (FYI).
Figure 2. Correlations between the observed proportion of female Weddell seal pups (± 1 SE, with SE adjusted for overdispersion) from 20 cohorts (1980-1999) that recruited into the population within 10 years of birth versus the most important environmental covariate in each a priori model suite. Environmental covariates during the period of maternal pregnancy (Maternal) and the initial year of juvenile independence (Juvenile) were evaluated. Covariates were standardized, with the Antarctic Dipole climate mode during the summer (ADPs) and winter sea-ice extent in the Ross Sea sector (SIEw) most strongly correlated with recruitment probability (see Table 2).
Figure 2

- **Summer ADP (Maternal)**
  - Proportion Recruited vs. ADP
  - Data points with error bars

- **Summer ADP (Juvenile)**
  - Proportion Recruited vs. ADP
  - Data points with error bars

- **Winter SIE (Maternal)**
  - Proportion Recruited vs. SIE
  - Data points with error bars

- **Winter SIE (Juvenile)**
  - Proportion Recruited vs. SIE
  - Data points with error bars
Figure 3. Proportion of female pups recruiting within 10 years of being born presented as (a) model-averaged predictions across all a priori models as functions of cohort size and sea-ice extent during the winter (SIEw) before the pup was born (the upper solid line is for the largest cohort size observed [n = 546 pups], and the lower solid line is for the smallest cohort size observed [n = 345 pups]; dotted lines represent 95% confidence limits for predictions), and (b) annual proportions based on observed data (filled circles) and predictions from the best-supported a priori model (stars), best-supported exploratory model (open circles), and the null model (open squares).
Figure 3

(a) Probability of Recurrence within 10 years of Birth

(b) Probability of Recurrence within 10 years of Birth by Year

- observed
- best non model
- best exploratory model
- null model