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Ringed seal demography in a changing climate

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Abstract. Climate change is affecting species' distributions and abundances worldwide. Baseline population estimates, against which future observations may be compared, are necessary if we are to detect ecological change. Arctic sea ice ecosystems are changing rapidly and we lack baseline population estimates for many ice-associated species. Provided we can detect them, changes in Arctic marine ecosystems may be signaled by changes in indicator species such as ringed seals (*Pusa hispida*). Ringed seal monitoring has provided estimates of survival and fertility rates, but these have not been used for population-level inference. Using matrix population models, we synthesized existing demographic parameters to obtain estimates of historical ringed seal population growth and structure in Amundsen Gulf and Prince Albert Sound, Canada. We then formalized existing hypotheses about the effects of emerging environmental stressors (i.e., earlier spring ice breakup and reduced snow depth) on ringed seal pup survival. Coupling the demographic model to ice and snow forecasts available from the Coupled Model Intercomparison Project resulted in projections of ringed seal population size and structure up to the year 2100. These projections showed median declines in population size ranging from 50% to 99%. Corresponding to these projected declines were substantial changes in population structure, with increasing proportions of ringed seal pups and adults and declining proportions of juveniles. We explored if currently collected, harvest-based data could be used to detect the projected changes in population stage structure. Our model suggests that at a present sample size of 100 seals per year, the projected changes in stage structure would only be reliably detected by mid-century, even for the most extreme climate models. This modeling process revealed inconsistencies in existing estimates of ringed seal demographic rates. Mathematical population models such as these can contribute both to understanding past population trends as well as predicting future ones, both of which are necessary if we are to detect and interpret future observations.

Key words: climate change; general circulation models; matrix population model; monitoring; power analysis; Pusa hispida; *sea ice; snow depth.*

INTRODUCTION

With substantial climatic change predicted for the coming decades (IPCC, 2014), scientists and managers have been tasked with anticipating and detecting resulting changes in species' distributions and abundances. Imperative for the detection of these changes are baseline measurements of historical populations, against which we may compare new observations.

Mathematical models can be used both to understand historical patterns and to predict future trends. Further, models may be helpful for ensuring consistency between past studies and highlighting knowledge gaps. Looking ahead, as ecologists work to predict population trends in novel environmental conditions, a range of modeling approaches may be helpful (Sutherland 2006). Approaches for assessing species' vulnerability include standard forecasting (phenomenological) models, expert opinion, trait-based approaches, and systems biology models (Sutherland 2006, Evans 2012, Pacifici et al. 2015). Predictive (mechanistic) models are especially well suited for modeling populations in novel environmental conditions as they avoid the pitfalls of extrapolating patterns outside of the range of observed conditions (Berteaux et al. 2006, Pacifici et al. 2015). Regardless of model paradigm, models should provide predictions against which future measurements may be compared, with assumptions clearly stated and reevaluated as new information becomes available (Houlahan et al. 2017). Transparent, adaptable models with testable predictions of how a population may change under new environmental conditions are prerequisites for developing effective monitoring programs as well as evidence-based wildlife management (Sutherland 2006).

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The Arctic is warming much faster than the rest of the planet (Overland et al. 2016) and the life-history parameters of many Arctic species are correlated with changing environmental conditions (Mech 2000, Hunter et al. 2007, Chambellant et al. 2012, Nahrgang et al. 2014). Changes in the sea ice regime have already been linked to changes in sea ice ecosystems (Wassmann et al. 2011). Sea ice quality and phenology affect primary production, both within the sea ice as well as the timing and intensity of pelagic blooms during the summer ice free period (Arrigo 2014, Arrigo and van Dijken 2015). Changes in both the timing and abundance of primary production may affect the entire food web (Bluhm and Gradinger 2008). Furthermore, ice-associated marine mammals may depend on sea ice directly (e.g., as a substrate on which to give birth) or indirectly (e.g., protection from predators; Kovacs et al. 2011).

The responses of individuals, populations, and communities to these rapid environmental changes will likely include complex interactions between factors. There are many unknowns, including the speed and magnitude of environmental changes, the plasticity of species to these new conditions, the northward range expansion of more temperate species (Kovacs et al. 2011), and the introduction of new diseases (Burek et al. 2008). Detecting these changes in marine mammal populations requires estimates of abundance and key life-history parameters (e.g., survival and fertility). Unfortunately, even satisfactory baseline estimates are unknown for many ice-associated marine mammals (Laidre et al. 2015). In light of this uncertainty, mathematical models allow for exploration of those factors that are thought to be important but are not yet well understood.

Ringed seal populations, past and future

Due to their ecology, subnivean life stages, and remote habitat, ringed seals (*Pusa hispida*) are one such species for whom precise abundance estimates and life-history parameters remain elusive (Reeves 1998, Pilfold et al. 2014). Ringed seals are the most numerous Arctic pinniped and have a circumpolar distribution in ice-dominated marine ecosystems (McLaren 1958). They are the main prey of polar bears (*Ursus maritimus*; Stirling and Archibald 1977, Smith 1980), a significant food source for Arctic foxes (*Vulpes lagopus*), and an important species for northern communities (Smith 1987). They are a keystone species (Ferguson et al. 2005, Hamilton et al. 2015) and an indicator species for Arctic environmental monitoring (Laidre et al. 2008, Chambellant and Ferguson 2009).

Ringed seals are an ice-obligate species, dependent on the sea ice for pupping, nursing, and molting (McLaren 1958). They also depend on the presence of sufficiently deep snow drifts in spring to dig lairs for pupping and lactation (Smith and Stirling 1975). These life history events and the resultant survival and reproductive rates are thus sensitive to changes in ice phenology, ice quality, and snow depth, among multiple other factors (Smith 1987, Smith and Harwood 2001, Chambellant et al. 2012, Harwood et al. 2012*b*).

Episodic weather events throughout the Arctic have been linked to major atmospheric patterns operating on approximately decadal timescales (Vibe 1967, Tremblay and Mysak 1998, Proshutinsky et al. 2002). In the western Canadian Arctic, years of anomalously late ice breakup occurred approximately once a decade over the past half century (Mysak 1999, Harwood et al. 2012*b*). Decadal ice cycles affecting ringed seals have also been suggested for Hudson Bay, Canada (Ferguson et al. 2005, Chambellant et al. 2012). These events corresponded to fluctuations in ringed seal reproduction (Smith 1987, Stirling and Lunn 1997, Kingsley and Byers 1998, Harwood et al. 2012*b*), and body condition (Harwood et al. 2000, 2012*b*, Nguyen et al. 2017). Hypothesized mechanisms include the additional energy required to maintain breathing holes in heavier ice conditions (Harwood et al. 2012*b*) and a reduction in marine productivity resulting from reduced areas of open water (i.e., reduced leads and polynyas), and a shorter open water season (Harwood and Stirling 1992, Stirling and Lunn 1997). Furthermore, seals may experience increased predation pressure from polar bears, which use the ice as their hunting platform (Stirling et al. 1993, Stirling and Lunn 1997). Winters with heavy ice were arguably the most significant environmental stressors on ringed seals in the western Canadian Arctic from the 1960s through the early 2000s.

In contrast to past conditions, trends towards earlier ice breakup and a longer ice-free season have been observed in the western Canadian Arctic (Galley et al. 2008, Parkinson 2014, Stern and Laidre 2016) and these changes are anticipated to continue (Dumas et al. 2006, Notz and Stroeve 2016). As the effects of the changing climate have begun to be documented, hypotheses have been formed as to how environmental changes may affect ringed seal populations (Freitas et al. 2008, Chambellant 2010, Kelly et al. 2010). While it may intuitively seem that reduced ice concentrations may alleviate some of the stress experienced by ringed seals due to heavy ice in the past, benefits may be outweighed by new stresses caused by a warmer Arctic (Stirling and Smith 2004, Ferguson et al. 2005, Hezel et al. 2012).

Climate change is expected to affect ringed seals in myriad ways, including effects due to changing ecosystem productivity, food availability, and predation pressure from polar bears (Laidre et al. 2008, Kelly et al. 2010). In addition to these projected gradual changes, episodic events, including disease, can cause abrupt demographic changes on shorter timescales (Ferguson et al. 2017). We do not attempt to capture all of these factors here, but rather study the implications of two known mechanisms of demographic change (Kovacs et al. 2011).

First, a decrease in seal recruitment is expected to occur with earlier ice breakup but the mechanisms are poorly understood (Ferguson et al. 2005, Kelly et al. 2010). Ringed seals depend on stable sea ice until they have weaned and fully transitioned to pelagic feeding (Stirling 2005). Premature weaning caused by the separation of pups from their mothers is expected to negatively affect pup survival (Harwood et al. 2000, Laidre et al. 2008). Additionally, increased thermoregulation costs may affect seal pups forced into open water at an earlier age (Smith and Harwood 2001), and swimming is energetically costly for young pups (Smith et al. 1991, Lydersen and Hammill 1993). Following unusually early ice breakup, ringed seal pups have been documented as having significantly delayed moulting and poor body condition (Kingsley and Byers 1998, Smith and Harwood 2001).

Second, reduced ringed seal recruitment has also been linked to less spring snow accumulation on sea ice (Hammill and Smith 1991, Iacozza and Ferguson 2014). While annual precipitation in the Arctic is expected to increase in coming decades (Hassol 2004), the timing and type of precipitation are expected to result in a net decrease in the accumulation of snow on sea ice (Hezel et al. 2012). A shallower snow pack melts more quickly, and lairs may collapse before weaning (Ferguson et al. 2005, Kelly et al. 2010). In extreme cases, the formation of lairs may be precluded entirely (Kelly et al. 2010). Pups who do not have the protection of a stable birth lair are more susceptible to predation by polar bears, foxes, and avian predators (Lydersen and Smith 1989, Hammill and Smith 1991, Stirling and Smith 2004). In years of shallow snow accumulation, nearly total pup mortality has been observed (Lydersen and Smith 1989, Hammill and Smith 1991, Smith and Lydersen 1991, Ferguson et al. 2005).

Monitors in Amundsen Gulf and Prince Albert Sound, Canada, currently sample approximately 100 ringed seals from the annual subsistence harvest, with the main objectives of detecting both annual signals and longer term trends in body condition and reproduction (Smith 1987, Harwood et al. 2000, 2012*b*). The age or stage structure of harvest-based samples are also recorded (Chambellant 2010, Harwood et al. 2012*b*). Harvest samples collected in the autumn are thought to provide the best available estimate of the structure of the population, as all age classes are present and homogeneously distributed during the open water period (McLaren 1958, Smith 1987).

Geographic study area

This study focuses on the ringed seals of Amundsen Gulf and Prince Albert Sound (69°–71° N, 116°–124° W; Fig. 1). This region has historically been good ringed seal habitat, as it is protected from larger ocean storms and has extensive areas of stable fast ice during the winter (Smith 1987, Harwood et al. 2012*b*). Since the early 1970s, ringed seals in this region have been monitored through a partnership between scientists and Inuvialuit harvesters, providing an extensive body of literature on seals in this region (Smith 1987, Harwood et al. 2000, 2012*b*).

Modeling overview

Our goals were threefold: (1) to estimate a historical baseline population growth rate and population structure against which future population changes may be measured, (2) to project the population forward using existing environmental projections and formalizing hypotheses linking demographic rates to environmental states, and (3) to evaluate the ability of data already being collected through current monitoring practices to detect these projected changes.

We synthesized the available demographic information on ringed seals into a matrix population model (*Materials and methods: Structured population model*). Matrix population models provide a theory-rich modelling framework with which to explore population trends (see Caswell [2001] for a comprehensive overview). These models have been used to explore management options (Law 1979, Crouse et al. 1987, Rand et al. 2017) and to predict population trends under climate change (Jenouvrier et al. 2009, Hunter et al. 2010).

We first modeled a ringed seal population under the historically observed cycles of late ice breakup (*Materials and methods: Linking late production to historical late ice breakup*). We did this by working through environmental models of increasing complexity, from a constant environmental state, to a periodic environment with 10-yr cycles, to a stochastic Markovian environment (similar to the approach of Hunter et al. [2010]). This approach provided baseline estimates of population growth and structure. Sensitivity analyses described parameter importance, of relevance for future monitoring. Throughout this modeling process, we uncovered gaps and inconsistencies in our knowledge of ringed seal life-history parameters and thus suggest areas of future research.

Next, we linked demographic rates to predicted future environmental conditions by formalizing the hypothesized reduction in pup survival caused by earlier ice breakup and a shallower snowpack (*Materials and methods: Linking pup survival to projected early ice breakup and reduced spring snow depth*). We explored future population-level effects of reduced pup survival by coupling our matrix population model to ice and snow projections for years 2017 through 2100, available through the Coupled Model Intercomparison Project Phase 5 (CMIP5; Taylor et al. 2012).

Finally, we conducted power analyses to determine the ability of stage structured estimates obtained through current sampling procedures to detect these predicted changes in population structure from our estimated historical structure (*Materials and methods: Linking pup survival to projected early ice breakup and reduced spring snow depth: Power analyses for detection of population changes*).

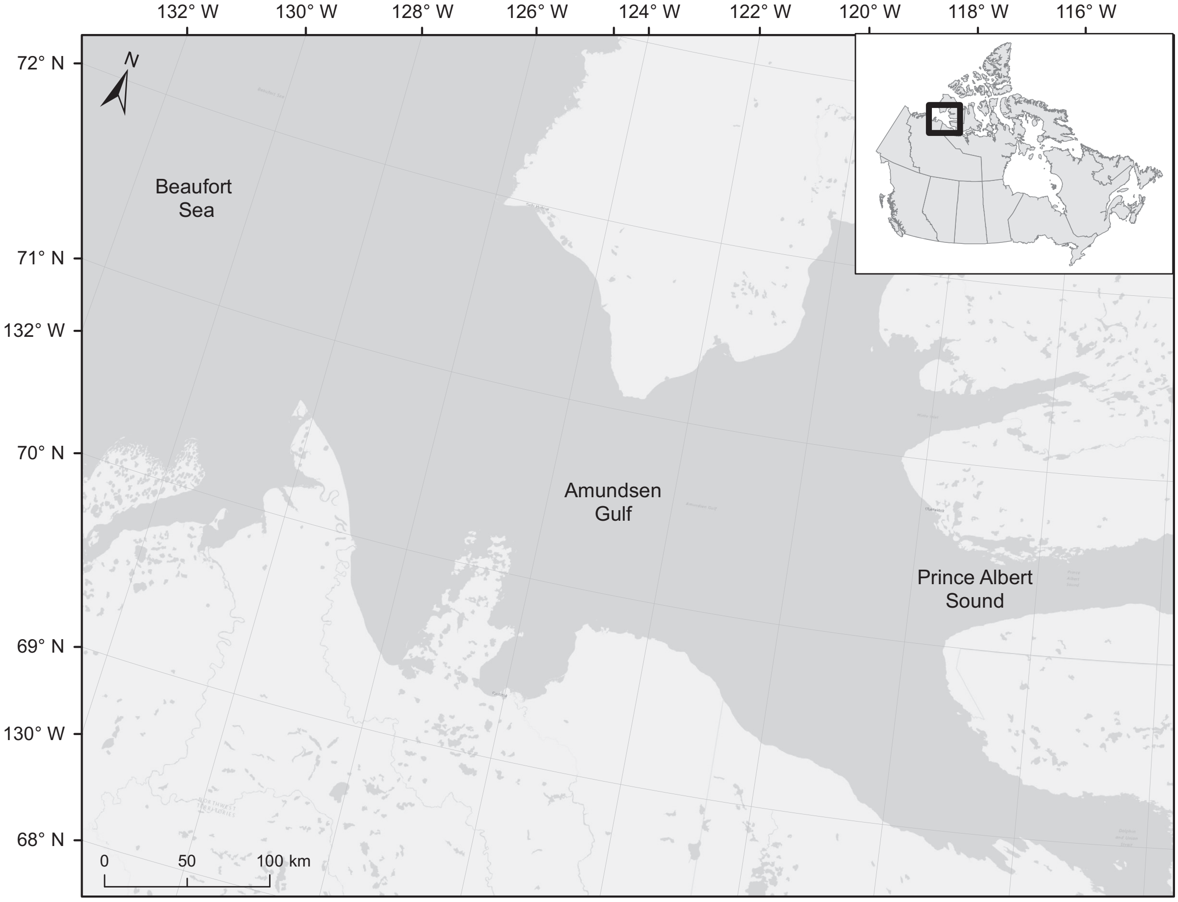

FIG. 1. Map showing location of Amundsen Gulf and Prince Albert Sound, Canada. Where possible, parameter estimates as well as snow and ice data and forecasts were taken from this area.

MATERIALS AND METHODS

Structured population model

We first created a general demographic model for ringed seals. We considered eight distinct stages corresponding to ages 0 (pups), 1 through 6 yr (juveniles), and 7+ yr (adults; Fig. 2). These three stages are commonly used throughout the ringed seal literature (Holst et al. 1999, Pilfold et al. 2012, Yurkowski et al. 2016). While the choice of age at which a seal becomes an adult differs between studies, age 7 has been used in this region (Pilfold et al. 2012) and corresponds to estimates of the age of first pregnancy (Harwood et al. 2012*b*).

Pups are <12 months old and experience high mortality due to predation (Stirling and Archibald 1977, Hammill and Smith 1991). Juveniles have not reached their maximum length, their survival rates are lower than those of adults, but they may be able to reproduce (age 1–6 yr). Seals may reproduce as young as 4 yr of age, but do not consistently do so (Harwood et al. 2012*b*). Adults have reached sexual maturity and have high annual survival rates (Smith 1973, 1987). We expect adult seals of all ages to respond similarly to environmental perturbations so we did not treat ages greater than 7 as distinct stages. We modeled only female seals, making the assumption that males are not limiting for reproduction (Smith and Hammill 1981). The date 15 April has been suggested as the nominal day of pupping in Amundsen Gulf (Smith 1987, Kingsley and Byers 1998), and we selected a model census time immediately following pupping.

We then linked the environmental state ξ to the demographic rates of individuals in each stage. For a seal in stage i, $P_i^{(\xi)}$ was the annual survival probability and $F_i^{(\xi)}$ denoted annual fertility in a year with environment ξ. Annual fertility was calculated as $F_i^{(\xi)} = m_i^{(\xi)} P_i^{(\xi)}$, where $m_i^{(\xi)}$ was the expected number of female offspring per female in one spring pupping season with environment ξ.

For each environmental state ξ, these rates were arranged as a Leslie matrix $\mathbf{A}^{(\xi)}$ (Caswell 2001). The population $\mathbf{x}(t+1) = [x_0(t), \ldots, x_7(t)]^\mathsf{T}$ at time $t+1$ was determined by

$$\mathbf{x}(t+1) = \mathbf{A}^{(\xi)}\mathbf{x}(t) \qquad (1)$$

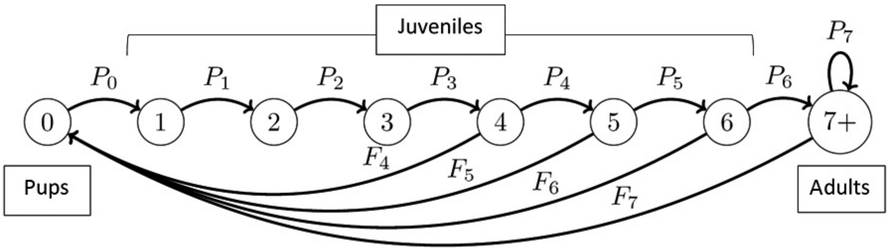

FIG. 2. Life history of female ringed seals. P_i and F_i are annual survival and fertility probabilities for a seal in state i, respectively.

with $\mathbf{x}(0) = \mathbf{x}_0$. Note that $\mathbf{A}^{(\xi)}$ depended on time (i.e., $\xi = \xi(t)$), but we simplified the notation. To project the population forward, we created models of the environment $\xi(t)$ from time t to $t+1$. This environmental variable could encompass a single environmental metric (e.g., sea ice breakup date), or could be a vector of environmental parameters. The environment could be constant or made to vary deterministically or stochastically.

Linking reproduction to historical late ice breakup

Data collected on ringed seal fertility from 1971 to 1981 found changes in fertility rates over three years associated with anomalously late ice breakup (1973–1975; Smith 1987). We designated 1973, 1974, and 1975 as late breakup years, denoted by $\xi = l_1, l_2$, and l_3, respectively. We used $\xi = n$ to denote the remaining years with normal breakup dates. The expected number of offspring in a given year depended on $\xi(t)$ (Table 1). As survival rates are not known to have varied over this period, we held survival rates constant for all four environments (Table 1). Note that fox predation on neonate pups has here implicitly been included in the fertility term.

We explored the demographic effects of these late breakup events through models with increasing environmental complexity (Hunter et al. 2010). Calculation of the population growth rate and stable structure for each environmental model followed standard matrix model methods (Caswell 2001).

We first considered a constant environment characterized by its ice breakup date. We calculated the population growth rate, $\log \lambda^{(\xi)}$, by calculating the dominant eigenvalue of $\mathbf{A}^{(\xi)}$ for each constant environment $\xi \in \{l_1, l_2, l_3, n\}$. We calculated the stable stage distribution predicted by each environmental state by calculating the right eigenvector corresponding to the dominant eigenvalue. We calculated the elasticity (proportional sensitivity) of the growth rate to each matrix entry.

Allowing for greater realism in the environmental model, we next considered a periodic model, allowing for environmental fluctuations roughly analogous to those observed in the western Canadian Arctic. We supposed that a series of years with late ice breakup, like 1973–1975, occurred once a cycle. Thus for each periodic cycle of h years, there were three consecutive years of late breakup, l_1, l_2, and l_3. The other $h-3$ years had normal ice breakup dates. The four environmental matrices $\left\{\mathbf{A}^{(n)}, \mathbf{A}^{(l_1)}, \mathbf{A}^{(l_2)}, \mathbf{A}^{(l_3)}\right\}$ constitute an ergodic set, so we were able to use established results on the behavior of populations subject to periodic environments. We let $\mathbf{A}^{(h)}$ denote the matrix describing the population over a period of h years,

$$\mathbf{A}^{(h)} = \left(\mathbf{A}^{(n)}\right)^{h-3} \mathbf{A}^{(l_3)} \mathbf{A}^{(l_2)} \mathbf{A}^{(l_1)}.$$

The annual growth rate $(1/h) \log \lambda^{(h)}$ was obtained by calculating the dominant eigenvalue of $\mathbf{A}^{(h)}$. We compared the population growth rates for cycles of different lengths h by changing the number of normal years. We

TABLE 1. Ringed seal annual demographic parameters and sources.

Demographic parameters	Stage i 0	1	2	3	4	5	6	7+	Source
Expected female offspring per seal									
$m_i^{(n)}$	0	0	0	0	0.098	0.144	0.195	0.406	1†
$m_i^{(l_1)}$	0	0	0	0	0.085	0.125	0.169	0.352	
$m_i^{(l_2)}$	0	0	0	0	0.046	0.067	0.091	0.188	
$m_i^{(l_3)}$	0	0	0	0	0.042	0.062	0.084	0.175	
Survival, P_i	0.65	0.80	0.82	0.84	0.86	0.88	0.90	0.92	2‡

Notes: Superscripts l_1 through l_3 denote rates for three years with anomalously late ice breakup, and n denotes assumed normal conditions.

Sources: 1, Smith (1987); 2, Kelly (1988) and Kelly et al. (2010).

†Fertility for stage 7+ was taken to be the mean of the reported fertilities for ages 7–20 yr, assuming the values for ages 12–20 yr were the same as that documented for age 11 yr.

‡See *Materials and methods: A note on parameter inconsistencies* for details.

calculated the elasticity of the growth rate to entries in each component matrix of one cycle.

Finally, we considered a stochastic environment, where $\xi(t) = \Xi(t)$ was a random variable. We allowed for autocorrelation between consecutive environments by using a discrete-state Markov chain to model a series of environmental states. The probability of transition between states was determined from observed transition frequencies. These transition frequencies were derived from the assumption that between 1971 and 2011, the years 1973–1975, 1984–1987, and 2004–2005 had reduced pup production linked to late ice breakup (Kingsley and Byers 1998, Harwood et al. 2000, 2012*b*).

To estimate transition rates between environmental states from year to year, we first considered two types of environmental states, with either late or normal breakup ($\xi = l$ or n). We let p be the probability of a late breakup year following a normal breakup year, and vice versa for q, so the Markov transition matrix between normal and late breakup years was

$$\mathbf{P} = \begin{pmatrix} 1-p & q \\ p & 1-q \end{pmatrix} \qquad 0<p,q<1.$$

For the years 1971–2011, p = 3/31, and q = 3/9, based on the studies noted above. The correlation between successive states was $\rho = 1 - p - q = 0.57$ (Tuljapurkar 1997, Caswell 2001), so we expected runs of the same environmental state. The dominant right eigenvector of **P** indicated that late breakup will occur with relative frequency 0.225.

Then, given a year with late breakup, we assumed conditions l_1, l_2, and l_3 occurred with equal probability. This resulted in the stochastic transition matrix

$$\mathbf{P} = \begin{pmatrix} 28/31 & 3/9 & 3/9 & 3/9 \\ 1/31 & 2/9 & 2/9 & 2/9 \\ 1/31 & 2/9 & 2/9 & 2/9 \\ 1/31 & 2/9 & 2/9 & 2/9 \end{pmatrix} \tag{2}$$

for states n, l_1, l_2, and l_3 respectively. For a realized sequence of environments $\Xi(0), \Xi(1), \ldots, \Xi(t)$, we modelled the population at time $t+1$ by projecting from an initial population vector $\mathbf{x}(0) = \mathbf{x}_0$ according to $\mathbf{x}(t+1) = \mathbf{A}^{\Xi(t)}\mathbf{A}^{\Xi(t-1)}\ldots\mathbf{A}^{\Xi(0)}\mathbf{x}_0$. We calculated the stochastic growth rate, $\log\lambda_s$, defined as the convergence of

$$\log\lambda_s = \lim_{t\to\infty}\frac{1}{t}\log\mathbf{x}(t).$$

We also simulated the population stage structure $\mathbf{w}(t)$ over 10,000 yr and recorded the ranges of observed stage proportions. We numerically calculated the elasticity of λ_s to each demographic rate in $\mathbf{A}^{\Xi(t)}$.

A note on parameter inconsistencies

For ringed seals in our study area, existing estimates of adult annual survival rates range from 0.85 to 0.9 (Smith 1987). When we initially set juvenile and adult survival rates to be 0.86 (Smith 1987) and had all remaining values the same as those we have used for normal, high fertility years ($m_i^{(n)}$ and P_0 in Table 1), we obtained a negative growth rate. Calculating the population growth rate in a constant environment following the same methods as in *Structured population model* yielded $\log\lambda^{(n)} = -0.018$. This implied rapid population decline inconsistent with the known persistence of populations of ringed seals. We suspect that these reported values are unreasonably low, given their implications for population persistence. These reported survival values were estimated from the age structure of harvested seals, which is a method known to often result in erroneous survival rates for long-lived animals (Polacheck 1985, Smith 1987). For this reason, we chose our estimate of annual adult survival to be $P_7 = 0.92$. This is similar to that of other phocids with similar life expectancies and life histories (Härkönen and Heide-Jørgensen 1990, Harding et al. 2007, Sundqvist et al. 2012). We assumed that the annual survival rate of juvenile seals is approximately 0.8 in their second year and then increases incrementally until they reach adulthood (Table 1; Kelly 1988, Kelly et al. 2010).

Linking pup survival to projected early ice breakup and reduced spring snow depth

To project the population in future conditions associated with climate change, we included spring snow depth as an additional environmental variable, so $\xi(t)$ was a vector of ice breakup date and spring snow depth in year t. We assumed both early ice breakup and insufficient snow depth contribute independently to pup survival. While predation pressure from polar bears will likely change in the coming decades, the strength and direction of this change are unknown, so we also assumed potential predation pressure to be constant. We represented stress from early ice breakup and from shallower snow as scaling factors P_{ice} and P_{snow}, placing additional stress on pups as compared to historical levels

$$P_0^{(\xi)} = P_{\text{ice}}^{(\xi)} \times P_{\text{snow}}^{(\xi)} \times P_0 \tag{3}$$

where $P_{\text{ice}}^{(\xi)}$ and $P_{\text{snow}}^{(\xi)} \in [0,1]$, and P_0 is as in Table 1.

Unlike in our treatment of the historical population, where we assumed the environment fell in one of four discrete states ($\xi = n, l_1, l_2, l_3$), here, we allowed ξ to take a continuous range of values representing ice breakup date and mean April snow depth.

We defined ice breakup as the first day that the mean sea ice concentration <50% (Etkin 1991, Stirling et al. 1999, Stirling 2005, Ferguson et al. 2017). A range of alternative definitions of breakup exist (Harwood et al. 2000, 2012*b*, Ferguson et al. 2005, 2017), but because we were using it as a proxy for the availability of a suitable pupping and nursing substrate, we used this definition and then studied sensitivity to it.

We assumed a positive linear relationship between ice breakup date and the pup survival factor P_{ice} from the nominal day of pupping (15 April) to weaning (Fig. 3). Weaning occurs approximately 39 d after birth (24 May; Hammill et al. 1991, Lydersen 1995), though up to two additional weeks of lactation have been suggested (Lydersen and Hammill 1993). Following weaning, we assumed no additional stress was placed on pups due to breakup date. We compared the implications of a functional breakup date 2 weeks on either side of the weaning date, which allowed us to explore different sensitivities of ringed seal pups to early breakup (Fig. 3).

Snow drifts sufficiently deep for the creation of pupping and nursing lairs require a minimum regional snowfall of 20–30 cm (Lydersen and Gjertz 1986, Smith et al. 1991, Kelly et al. 2010). We assumed a positive linear relationship between regional snow depth in April on the sea ice and the pup survival factor related to snow depth, P_{snow} (Fig. 3). For snow depths <20 cm, we assumed complete pup mortality. For snow depths >30 cm, we assumed no additional predation stress was placed on pups (Kelly et al. 2010, Iacozza and Ferguson 2014). We also considered the same linear relationship shifted both higher and lower by 5 cm to test sensitivity to the chosen values.

We used time series of the ice breakup date from nine climate models and time series of mean April snow depth from 10 models (*Ice and snow data*). From these environmental time series, we created time series of the corresponding pup survival rates according to Eq. 3. Combining these time series of pup survival rates and assuming fertility and the survival of all juvenile and adult stages to be constant at their typical historical values ($\xi = n$ in Table 1) resulted in a time series of demographic matrices $\mathbf{A}^{\xi(t)}$ for $t = 2017\ldots2100$. We let the initial population size be 25,000 (obtained by dividing the estimate of population size from Kingsley [1984] in half to roughly account for only females) and assumed the initial stage distribution $\mathbf{x}_0$ was the stable distribution predicted from $\mathbf{A}^{(n)}$, as calculated in *Structured population model*. We projected the population forward using Eq. 1 and recorded changes in population size and structure from 2017 to 2100.

Power analyses for detection of population changes.—We explored when existing monitoring practices might reliably detect the predicted population changes by conducting power analyses. Because ringed seal population size is not normally monitored, we considered the monitoring of population structure, as estimated from an autumn harvest structure. We assumed a monitoring program where managers compare the population structure in a given year with the historical population structure assumed from $\mathbf{A}^{(n)}$. We conducted power analyses for Pearson's chi-squared tests ($\alpha = 0.05$, df = 2), comparing the historical distribution and the projected distribution in a given year for a given sample size N (typically N = 100 in the study area), using package pwr (Champely 2015) in R (R Core Team, 2014). Power analyses were done for each combination of snow and ice model data, and for sample sizes ranging from N = 50 to 1,000 individuals. We use 0.8 as our acceptable power value (Cohen 1988).

Ice and snow data.—Atmosphere–ocean general circulation models are the foundation of climate projections. They inform global climate assessments such as those by the International Panel on Climate Change (IPCC, 2014). Coordinated climate model experiments from 20 international climate modelling groups from around the world have been archived as the latest phase of the

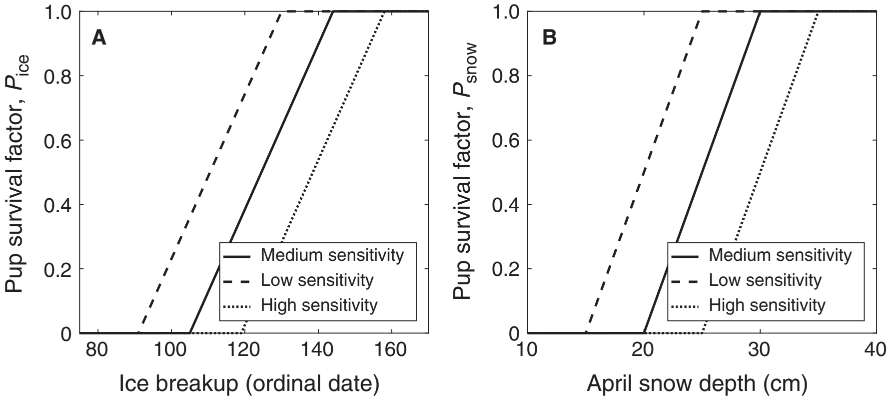

FIG. 3. (A) Assumed linear dependence of ringed seal pup survival on ice breakup date. The nominal day of pupping is 15 April (ordinal date 105), with weaning occurring approximately 39 d later. We shift the survival function 2 weeks in each direction to explore different levels of sensitivity to early breakup. Low and high sensitivities correspond to a functional breakup (i.e., the date at which breakup date affects pup survival) 2 weeks earlier and later than the projected breakup date, respectively. (B) Assumed linear dependence of pup survival on snow depth in April. Survival declines when snow depth is <30 cm, with complete cohort failure for snow depths <20 cm. We also consider lower and higher sensitivity to snow depth corresponding to declines in pup survival below 25 cm and 35 cm, respectively.

Coupled Model Intercomparison Project (CMIP5) at the Program for Climate Model Diagnosis and Intercomparison.

Consideration of future climate change scenarios required selection between four available greenhouse gas scenarios. We chose projections forced with the Representative Concentration Pathway (RCP) 8.5, colloquially known as the ``business as usual'' scenario. In this case, greenhouse gas emissions continue to increase until the end of the 21st century. While this scenario incorporates more extreme emissions than RCP 2.6, 4.5, or 6.0, we expected this to result in the most substantial projected changes in population size and structure. This was desirable, as we were interested in exploring our ability to detect changes, so large changes provided an optimistic detection baseline.

We downloaded model outputs of daily sea ice concentration and monthly snow depth on the sea ice in April from 1979 to 2100. Of the available models, 13 sea ice models and 14 monthly snow depth models met our baseline criteria of including a minimum of 10 grid cells in the study area. We considered only one model output from each modeling group. For years 1979–2005, we used outputs from historical experiments, and from 2006 to 2100, we used outputs from future projections forced by RCP8.5, as defined by CMIP5 (Taylor et al. 2012).

When possible, we retained only those models that best matched historical data. We obtained historical data on spring ice breakup from 1979 to 2016 from calibrated SSMI data from the National Snow and Ice Data Center (NSIDC), with 25-km resolution over the entire study area. NSIDC data were processed in Arc GIS ver.10.3.1 (ESRI, Redlands, California, USA). Ice concentrations were calculated from the mean of the pixel values within the defined study area. For comparison, we calculated both the Euclidean distance and the Dynamic Time Warping distance (a measure of distance between two numerical time series) between observed ice breakup dates and the historical model outputs from 1979 to 2016 using package TSdist (Mori et al. 2016) in R (R Core Team, 2014). The four models with the greatest distance from observed data were consistent for both distance metrics, thus we removed them and retained nine sea ice models, $\sim 70\%$ of available models (Appendix S2: Table S1), which we refer to as the ice model set.

Note that in the few instances where the mean ice concentration over the study area was not projected to fall below 50% in a given summer, we set the breakup date to be the latest recorded for that model. A list of these instances is included in Appendix S2.

We did not have sufficient historical records with which to compare snow depth model outputs. Instead, we took the mean values across models from 1979 to 2100. We then discarded the two models with the lowest means and the two with the highest means (i.e., we kept $\sim 70\%$ of models). We retained 10 models, which we refer to as the snow model set (Appendix S2: Table S1).

Unless stated otherwise, all simulations and analyses were conducted using MATLAB 2018a and all scripts are included as Supporting Information.

RESULTS

Historical population growth and structure

The population growth rate was greatest for the model with a constant environment with high reproductive success ($\xi = n$), more than double that of the periodic environment, and nearly double that of the stochastic environment (Table 2). Both the periodic and stochastic environmental models had growth rates indicative of a viable population.

The proportions of pups and juveniles in the population were lowest in constant environments with low reproductive rates ($\xi = l_2, l_3$; Table 2). The proportion of pups in the population ranged from <8% to nearly triple that in the stochastic environment (Table 2). Regardless of the environmental model, the growth rate was most sensitive to adult survival (Appendix S1: Fig. S2).

TABLE 2. Ringed seal population growth rate and stage structure for three environmental characterizations: a constant environment with either normal timing of ice breakup (n), or one of three documented years with anomalously late ice breakup (l_1, l_2, l_3); a periodic environment with 10 yr cycles (7 normal years, followed by the 3 yr of late breakup); or a stochastic (Markovian) environment with environmental probabilities estimated from historical ice records. Growth rates >0 suggest a long term increase in the population, while those <0 indicate a decline.

			Stage structure (%)		
Environmental model	Demographic matrix	Annual growth rate	Pups (age 0)	Juveniles (age 1–6)	Adults (age 7+)
Constant	$\mathbf{A}^{(n)}$	0.013	17.1	41.6	41.3
	$\mathbf{A}^{(l_1)}$	0.005	15.9	39.7	44.4
	$\mathbf{A}^{(l_2)}$	−0.026	11.1	30.4	58.5
	$\mathbf{A}^{(l_3)}$	−0.029	10.6	29.3	60.1
Periodic	$\mathbf{A}^{(10)}$	0.0054	8.7–19	33.8–45.8	39.6–49.3
Stochastic	$\mathbf{A}^{\Xi}$	0.0070	7.9–21.8	23.6–49.0	38.9–61.8

Notes: The stochastic growth rate and range of observed stage distributions are from a simulation over 10,000 yr. Time series of the population stage structure for the periodic and stochastic environments can be seen in Appendix S1: Fig. S1.

When we considered periodic cycles of varying lengths, the population growth rate increased with increasing cycle length h (Appendix S1: Fig. S3). The population growth rate fell below 0 for cycles ≤ 6 yr.

Projected population growth and structure

For conciseness, we here use the word "simulations" to mean the population simulations done for each combination of projections from the ice and snow model sets (90 combinations total, see Appendix S2: Table S1) and for each combination of the three sensitivities to ice and snow (Fig. 3).

In the case of low sensitivity to both decreased snow depth and earlier ice breakup, less than one-half of the simulated populations had declined below their original value by mid-century, and ~80% had declined by 2100 (Fig. 4, top left). In contrast, nearly all simulations assuming high sensitivity to snow and ice conditions had declined to less than half of their original value by mid-century, and by 2100, >90% of simulations were below 10% of their original size (Fig. 4, bottom right). For low sensitivity to snow depth, simulations tended to increase to mid-century before ultimately declining (Fig. 4, left column).

Assuming medium sensitivity to snow and ice conditions, the median modeled population declined to <10% of its original size by year 2100 (Fig. 5A). Across all ice and snow sensitivity combinations, median population declines ranged from ~50% to ~99% of the original population by 2100 (Appendix S1: Fig. S4). For medium sensitivity to snow and ice, corresponding changes in population structure displayed a trend towards an increase in the proportion of pups and adults and a decrease in juveniles (Fig. 5B, C). This was consistent regardless of snow and ice sensitivity levels (Appendix S1: Figs. S5–S7).

Detection of projected population changes.—The power to detect the predicted changes in population structure (Fig. 5) from the historical structure estimated from $\mathbf{A}^{(n)}$ (Table 2) reached 0.8 near the middle of the century, given the current sample size of 100 ringed seals per year (Fig. 6). Sample sizes of 300 obtained statistical power of 0.8 approximately 20 yr earlier (Fig. 6).

DISCUSSION

Historical population

Through the creation of an age-structured population model, we obtained estimates of historical ringed seal population growth and structure over the second half of the 20th century and the early 21st. The higher growth

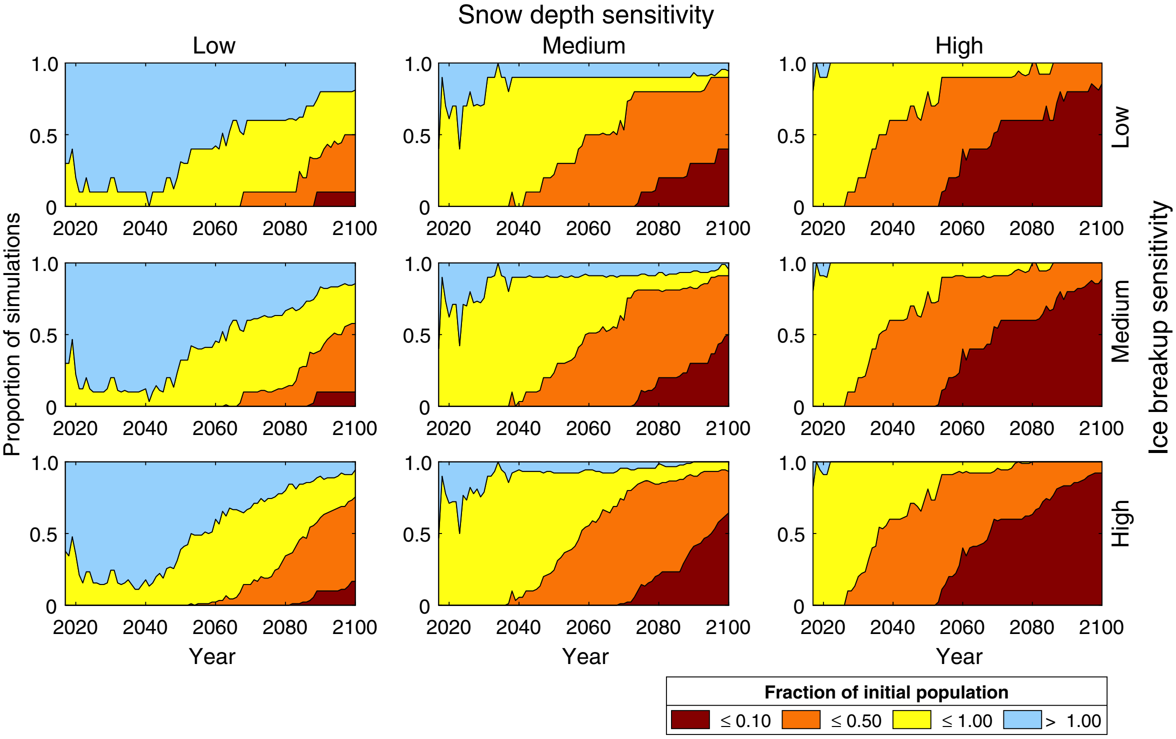

FIG. 4. Summary of changes in ringed seal population size (scaled) from 2017 to 2100 for populations with varying sensitivity to reduced snow depth and early ice breakup in Amundsen Gulf and Prince Albert Sound. For each sensitivity combination, the population was simulated 90 times (for each combination of ice and snow models; Appendix S2: Table S1). Blue represents simulations in which the population has increased from the initial population, while yellow, orange, and red represent population declines of increasing severity.

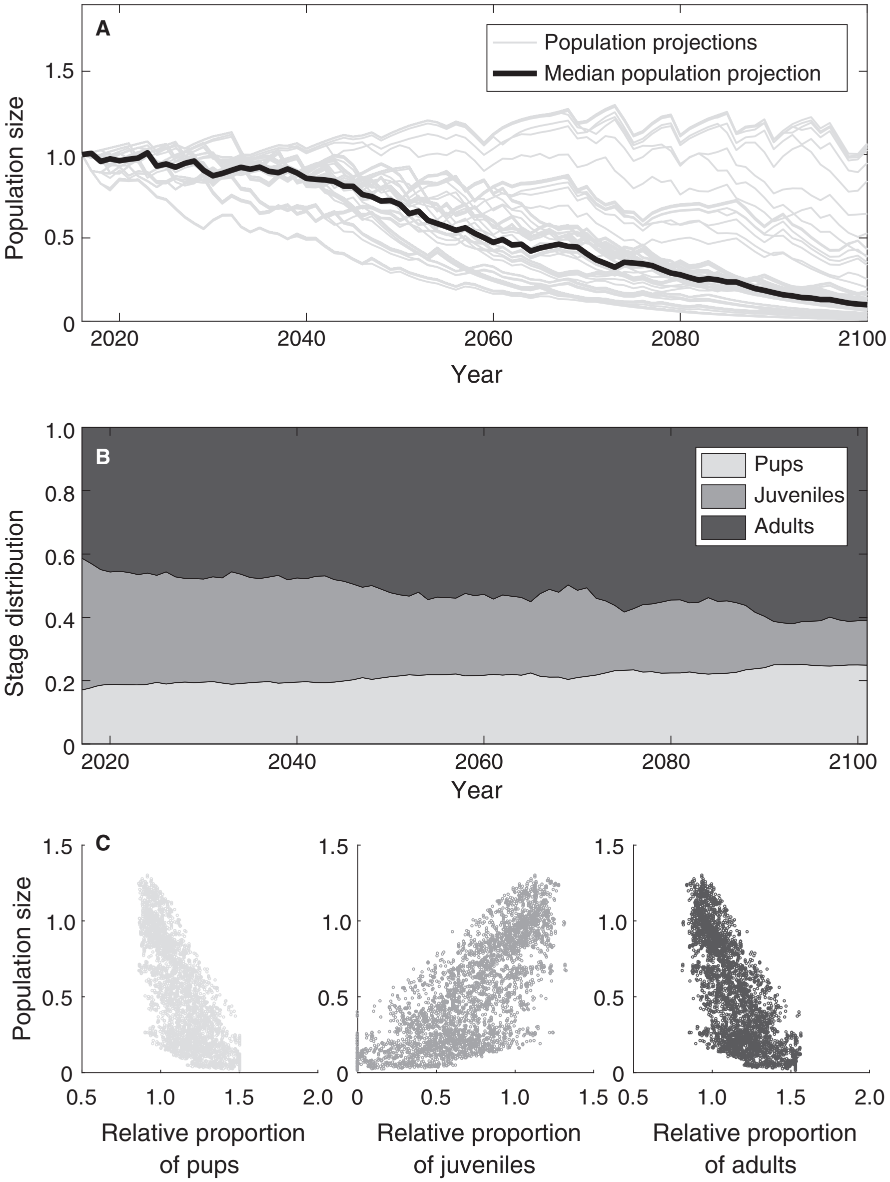

FIG. 5. (A) Projections of the ringed seal population size (scaled) from 2017 to 2100 for populations with medium sensitivity to both reduced snow depth and early ice breakup in Amundsen Gulf and Prince Albert Sound. Gray lines represent the population projection for each combination of ice and snow models. The black line is the median of all population projections. (B) The mean population stage structure corresponding to the population projections in the top figure. (C) Correlation between changes in population stage distribution and population size (scaled). Each point represents the population size and the relative proportion of stage *i* seals ([proportion stage *i* seals in the given year]/[historical proportion of stage *i* seals]) in a given year and for one snow and ice model combination, taken from the same simulations used in panels A and B. The point (1,1) in the graph describes a population that has not changed size and has not changed its proportion of stage *i* seals.

rate in the stochastic environment than in the periodic is unsurprising given that we created a periodic environment where late breakup years occurred more frequently than in the stochastic environmental model (30% as compared with 22.5% of years). Given the assumptions of our model, it appears that, for long-lived species with low annual reproductive rates, periodic occurrence of weak cohorts need not lead to population decline, as long as there is sufficient time for recovery (Appendix S1: Fig. S3).

In the process of compiling life-history parameter estimates from previous studies, preliminary results suggested that the historical population of ringed seals was in a rapid decline. We attributed this unrealistic result to the relatively low estimates of adult survival (*Materials and methods: A note on parameter inconsistencies*). We

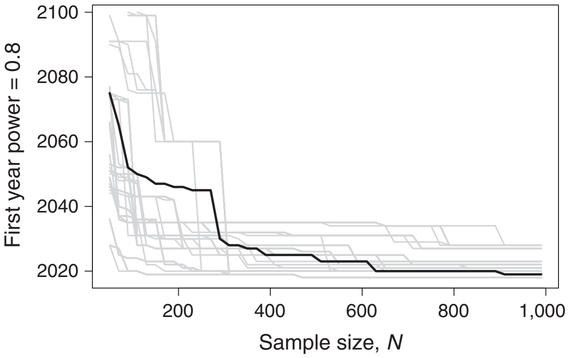

FIG. 6. The first year that the statistical power of a chi-squared test achieves 0.8 when attempting to detect differences in population stage structure between the estimated historical stage structure and that projected from each snow and ice model combination for 2017–2100, plotted against the sample size N (gray lines). The black line is the first year the power equals 0.8 when using the mean projected stage structure.

thus selected survival rates at the upper end of what was suggested in the literature. In spite of these optimistic parameter estimates, growth rates estimated for other ringed seal populations are higher than our values. Baltic ringed seal annual growth was estimated at $\log \lambda = 0.045$ from aerial surveys (Sundqvist et al. 2012). This higher growth rate may be because of the absence of predation on ringed seals from polar bears and Arctic fox in this region (Sundqvist et al. 2012). In the eastern Canadian Arctic, ringed seal growth was estimated at $\log \lambda = 0.0629$ (Law 1979) using values from a hypothetical, unharvested population (McLaren 1958). Adult survival rates were higher than those used in our study, hypothesized to be >0.95, contributing to the higher growth rate.

There are challenges with comparing our estimated population structures with historical harvest data from this region. During sampling in Amundsen Gulf and Prince Albert Sound, harvest proportions were 65.6% adults, 14% juveniles, and 20.5% pups (Harwood et al. 2012*b*), which most notably is a much higher percentage of adults and fewer juveniles than our estimates. It is important, however, to note that the majority of these samples were taken in June and July. This was before the optimal sampling period in August, when the area is largely ice free and seals of all stages are thought to be homogeneously distributed (Smith 1973, Holst et al. 1999). Our results support the hypothesis that sampling during early summer may under-represent juveniles, which is consistent with hypothesized spatial segregation of this stage in the spring (Crawford et al. 2012, Harwood et al. 2012*a*). However, our estimate of $\sim 17\%$ relative frequency of pups in the population immediately following pupping is consistent with other estimates (mean of 20.4% in [Miller et al. 1982], and 16–18% in [Frost 1985]).

Of the constant environments considered, higher growth rates were correlated with a higher proportion of juveniles. This is consistent with findings from Hudson Bay, Canada, where the population is believed to have been in decline in the 1990s and growing in the 2000s. Over these two decades, juveniles comprised ~27% and ~41% of the harvests in the 1990s and 2000s, respectively (Chambellant et al. 2012).

Elasticity of the population growth rate to demographic parameters indicated the importance of adult survival (Appendix S1: Fig. S2), which is consistent with other long-lived mammals (Heppell et al. 2000). Unfortunately, estimates of survival past the first year are scarce and imprecise (Smith 1987). Changes in the survival of mature seals brought about by changes in harvest pressure, disease, predation, or prey availability are not currently monitored through current harvest-based programs, but would have a profound effect on population viability.

Projected population

We projected the ringed seal population forward by linking ringed seal pup survival to ice and snow model forecasts. Given existing estimates for the minimal snow depth required for lair formation and our assumed dependence of pup survival on ice breakup, our model suggests that future reductions in mean April snow depth could be a more significant driver of reduced pup survival than early ice breakup. In the absence of better data on the response of pup survival to changes in snow and ice conditions, we chose the simplest justifiable demographic responses. As more years of early breakup or reduced spring snow depth occur, these response curves should be updated.

Changes in population structure were projected along with changes in abundance. There is, in general, no predictable relationship between a population's growth rate and a stable age distribution, let alone the age distribution in a time-varying environment such as we simulated here. However, for this life history, and with the assumed effects of the environment on the vital rates, our projections suggest a general trend in which ringed seal populations in decline have a reduced proportion of juveniles, and an increased proportion of pups and adults. These results were qualitatively consistent with the results from our historical population model; populations in decline had reduced proportions of juveniles. Since determining population size is difficult for ringed seals, population structure may conceivably be used to detect population changes. Managers and scientists should expect to see reduced juvenile frequency in the coming decades, and may use our model results to interpret this trend as being suggestive of population decline, especially if it is observed in conjunction with reports of reduced pup survival. While population decline cannot be concluded solely by observing changes in population structure, the consistency (or inconsistency) of new observations with the structure expected for a given trend may still be informative, especially if there is a greater known context of the demographic mechanisms involved.

For the same sample size as the current monitoring program (100 seals per year), our model predicts that the projected shift in age structure would not be reliably detected until mid-century. Larger annual sample sizes, practical implications aside, may shorten the time to detection. For example, increasing the sample size to 300 seals per year nearly halved the detection time (Fig. 6). Sampling more seals, less frequently (e.g., 300 seals every 3 yr, as compared with 100 seals every year) could also provide an alternative. However, if this ringed seal population declines, a smaller harvest in each community is likely, complicating any possible attempts to increase the sample size. Further, the current timing of harvest-based sampling overlaps both the spring ice-covered period and the late summer ice-free period. Only seals harvested in the late summer ice-free period, when seals of all ages are present, should be used to reliably assess the population age structure. Thus, the effective sample size for these purposes is currently smaller than 100. It is also important to note that we have used the most extreme emissions scenario, RCP 8.5, presumably resulting in the most dramatic shifts in ringed seal size and structure. Less extreme emissions scenarios may result in smaller population shifts that would be more difficult to detect. Note that the chi-squared test discussed here tests only for a difference between the historical and projected distributions, not for the specific trend of reduced juveniles and increased pups and adults. A more detailed statistical study treating sequential population distributions as a time series may be able to more effectively detect specific trends.

For all of these reasons, detecting changes in population structure using the current harvest-based monitoring program may not be feasible. Alternatively, periodic intensive birth lair surveys (Smith and Stirling 1975, Hammill and Smith 1989, Kelly and Quakenbush 1990) may be informative in the assessment of trends in pup production. Local measurements of spring snow depth on the ice may also help bridge our knowledge gap between regional snow accumulation estimates and the existing of localized drifts deep enough for subnivean lair formation. These methods, however, would not be sufficient to detect changes in pup recruitment due to early ice breakup.

Additional factors and limitations

A set of ideal conditions has been proposed for ringed seal recruitment, with ice breakup dates that are neither too early nor too late (Chambellant et al. 2012). Breakup dates near the middle of the historical range are thought to provide optimal recruitment. In light of trends toward earlier breakup, signs of population increase may be expected in coming decades, as late ice clearance becomes more rare, followed by a population decline as years of insufficient snow cover and early ice breakup occur with greater frequency. Nonlinear responses such as these to changes in sea ice complicate population projections (Grémillet et al. 2015). By splitting this study into historical and future models and allowing for no overlap between the two periods, we did not consider the historical implications of any years with early ice breakup or a shallow snowpack, nor the possibility that there may still be years with late ice breakup in the coming decades. Thus our results are, in this sense, optimistic, accounting for only select environmental stressors at a given time.

There are limitations in our understanding of ringed seal demography and the relationship to environmental variables. Our understanding of how demographic rates may change in response to environmental changes currently relies on few studies covering even fewer years. Juvenile ringed seals may emigrate to more favourable environments during years of adverse conditions, mitigating some of the effects (Smith and Stirling 1978, Kingsley and Byers 1998). The age at sexual maturity and first parturition may also change in response to the environment (Chambellant et al. 2012, Harwood et al. 2012*b*). Reduced body condition of several ringed seal populations, including the Beaufort Sea, has been observed in recent years for reasons that are poorly understood (Chambellant 2010, Harwood et al. 2012*b*). If these trends of reduced body condition continue, reduced pup production and, in extreme cases, reduced juvenile and adult survival may occur, which we have not accounted for here.

Other factors may also play a significant role in the viability of ringed seal populations in the coming decades. Plasticity in diet and behavior may ameliorate some effects of environmental change (Laidre et al. 2008, Yurkowski et al. 2016). Range expansion by both ringed seal predators and prey add further complexity (Laidre et al. 2008, Wassmann et al. 2011). Other physical variables, such as ocean acidity and temperature may also affect seals and their prey (Kelly et al. 2010). In years of early breakup, increases in primary productivity are expected, possibly leading to greater food abundance (Sallon et al. 2011).

Changes in community structure influence and are influenced by ringed seal abundance and distribution. In years of peak Arctic fox abundance, predation by foxes on ringed seal pups can significantly diminish seal pup recruitment (Lydersen and Gjertz 1986, Smith 1987). Ringed seals are the main prey of polar bears (Stirling and Øritsland 1995, Stirling 2002) and a decline in ringed seals has implications on the number of polar bears that may be sustained in an area. Changes in abundance and productivity of polar bear populations in the eastern Beaufort Sea were correlated with declines in ringed seal production both in the mid 1970s and 1980s (Stirling and Archibald 1977, Stirling and Øritsland 1995). A linear relationship has been suggested between the number of polar bears and ringed seals that an area can sustain (Stirling and Øritsland 1995). Thus a reduction in the number of ringed seals could cause a decrease in the polar bear population, or vice versa (Bromaghin et al. 2015), especially in areas like the western Canadian Arctic where there are few alternative prey species for polar bears (Thiemann et al. 2008, Cherry et al. 2011). While reductions in spring sea ice may cause pup survival to decline, it may also negatively affect polar bear hunting success, as polar bears rely on the sea ice to hunt in the spring. How this reduced spring predation pressure may change our projections remains to be studied.

Conclusion

We have established a baseline estimate of historical population structure and growth by synthesizing existing demographic rate estimates. This process has revealed inconsistencies in published rates, namely adult annual survival. Given the population's sensitivity to this parameter, a better understanding of factors affecting adult survival is important if we are to assess population viability as the Arctic climate changes. While we have focused our study on Amundsen Gulf and Prince Albert Sound, the large scale atmospheric forcing leading to past decadal cycles of ice conditions, and the general trend toward earlier ice breakup and a shallower snow pack are shared throughout ringed seals' range, making the results relevant for other Arctic ringed seal populations.

Across the range of snow and ice models, and for varying sensitivity to these changing snow and ice conditions, our projections indicate population declines in all but the most optimistic scenarios considered, with many of these declines projecting the population to less than one-half of its current size by the end of the century. This has implications for Arctic marine ecosystems, especially for polar bears whose diets rely heavily on ringed seals. While the current monitoring program includes other methods to assess demographic change, including assessing reproductive rates and body condition, it is important to consider that reduced pup survival may present a significant threat to ringed seal populations.

The chosen method of projecting a population forward and then evaluating our ability to detect future changes using existing monitoring techniques is applicable across taxa and environments. Even with only preliminary hypotheses of environmental effects, this exercise can illuminate possible future scenarios and help concentrate resources towards using the most informative monitoring methods to detect these changes. As an indicator species, ringed seals provide information on the health of Arctic marine ecosystems, but this information relies on our ability to detect the large scale changes resulting from climatic changes.

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