



## Original Article

# Growth and condition in harp seals: evidence of density-dependent and density-independent influences

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Life history theory predicts that resource competition increases as a population increases, leading to changes in life history traits such as growth, survival, and reproduction. The Northwest Atlantic (NWA) harp seal population has increased from a low of 1.1 million animals in 1971 to over 7 million animals in 2014. Given this 7-fold increase in abundance, we hypothesized that density-dependent regulation might be reflected by changes in body growth. Gompertz curves fitted to size at age data for harp seals collected in the Gulf of St Lawrence over a 40 year period show a decline in female asymptotic length and mass. Body mass and condition were negatively related to reproductive rates the previous year, while a quadratic relationship ('inverse u') was observed between body measures and the ratio of the March:April first year ice cover, a measure of ice breakup. Condition was also negatively related to January ice cover. At high densities, reproduction is likely to be relatively more expensive for Northwest Atlantic harp seals, underlining the importance of females being able to access high energy food during the winter foraging period to build-up condition prior to pupping. A complex relationship between condition and the timing of ice-breakup likely reflects the influence of the timing of ice retreat on food resources and hence female ability to rebuild energy stores prior to moulting.

**Keywords:** density-dependence, ecology, Northwest Atlantic harp seal, *Pagophilus groenlandicus*, population regulation.

## Introduction

Understanding how density-independent and density-dependent processes affect the dynamics of populations is needed to understand how they might respond to environmental fluctuations and for developing effective conservation and management strategies (Bonenfant *et al.*, 2009; Troyer *et al.*, 2014; Bruggeman *et al.*, 2015). Density-independent factors act via external environmental stochasticity, which in turn can affect resource abundance such as food or habitat availability and quality. Density-dependent factors act via intraspecific competition for common resources, which leads to a negative feedback between population size and population growth, expressed through changes in reproduction, survival, and dispersal (Chamaillé-Jammes *et al.*, 2008). Early discussions emphasized the dichotomy between the two population regulation mechanisms, but by the 1990s mounting evidence suggested that the dynamics of populations resulted from interactions between

both processes (Bonenfant *et al.*, 2009). Thus, in addition to the underlying competition among individuals for available resources, temporal and spatial variation in environmental conditions can considerably modify resource abundance or availability to individuals, with the population response to these changes contingent upon its size relative to resource availability (Owen-Smith, 1990; de Little *et al.*, 2007; Bonenfant *et al.*, 2009; Hempson *et al.*, 2015).

Mammalian growth is a non-linear function of age that reflects the integration of food intake. Simplistically, individuals with access to high nutritional food resources often attain larger body sizes and better condition than individuals for which nutrition is inadequate, with subsequent influences on survival and reproduction (Parker *et al.*, 2009). Thus, body mass and length growth are key life history parameters that can influence survival, age of sexual maturity, and henceforth reproductive potential and success (Griffith and Brook, 2005).

Early indications of density-dependent regulation are expected to be reflected by changes in individual growth, followed by juvenile mortality, age at maturity, reproduction, and finally adult mortality (Scheffer, 1955; Eberhardt and Siniff, 1977; Kingsley, 1979; Innes *et al.*, 1981; Trites and Bigg, 1992). There is some evidence for density-dependence regulation among marine mammal populations (e.g. deLittle *et al.*, 2007; McMahon *et al.*, 2009), but overall, the number of studies is limited, probably because the necessary long-term datasets needed to detect density-dependence are few and far between and many populations were heavily overexploited and have not recovered sufficiently to exhibit density-dependence.

The harp seal is a medium-sized, migratory phocid distributed over continental shelf regions of the North Atlantic. Three populations are recognized (Sergeant, 1991); the White Sea/Barents Sea, the Greenland Sea, and the Northwest Atlantic (NWA). All three populations have a long history of commercial and subsistence exploitation throughout their range. There is some evidence for density-dependent changes in growth and reproduction in the White Sea/Barents Sea population between the 1960s and the 1990s, which has been linked to changes in resource abundance (Kjellqvist *et al.*, 1995; Frie *et al.*, 2003) and more recently, changes in the dynamics of the NWA harp seal population off the northeast coast of Newfoundland, Canada have been explained by density-dependent changes in reproduction and juvenile survival (Hammill *et al.*, 2015). However, marked inter-annual fluctuations in reproduction appear to be also driven by environmental factors such as the timing of ice breakup and capelin biomass (Stenson *et al.*, 2016).

Ice is very important in the life cycle of the harp seal and in all seasons they are often found close to pack-ice (Sergeant, 1991). Harp seals require pack ice as a platform for resting, to give birth and nurse their young. After weaning, the young of the year (YOY) remain with the ice, for several weeks, using it as a resting platform. A lack of suitable or insufficient ice appears to result in increased pup mortality (Sergeant, 1991; Stenson and Hammill, 2014). Based on stomach contents, harp seals off Newfoundland, Canada (Figure 1), generally consume a mixed diet of pelagic forage fish and invertebrates such as capelin (*Mallotus villosus*), Arctic cod (*Boreogadus saida*), sandlance (*Ammodytes* sp), euphausiids, and amphipods (Lawson *et al.*, 1995; Lawson and Stenson, 1997; Tucker *et al.*, 2009). In the Gulf of St Lawrence (Gulf), capelin, sandlance, euphausiids, amphipods, and mysids are important prey (Beck *et al.*, 1993a; Hammill *et al.*, 2005). The abundance of NWA harp seals declined considerably during the 1950s and 1960s, reaching a minimum of 1.1 million animals in 1971, but has increased to currently at around 7.4 million animals (Figure 2; Hammill *et al.*, 2015).

In this study, we examine age-specific growth in a sample of harp seals collected over a 40 year period from 1976 to 2015. If density-dependent factors are indeed affecting the dynamics of this population, we would expect to see changes in size at age, with animals declining in size (length and mass) as the population has increased. Similarly, if environmental variation drives the demographic and morphometric variation in this population, then we would also expect to see marked short-term fluctuations in body condition that can be linked to fluctuations in associated climatic/environmental variables and to recent demographic events.

## Material and methods

### Sampling and study area

NWA harp seals ( $N = 975$ ) were taken under licence by Fisheries and Oceans Canada (DFO) employees or contractors in February and March 1976 to 2015 from the St Lawrence Estuary (Godbout and Les Escoumins) and from the Gulf (Îles de la Madeleine; Figure 1). Growth and morphometric relationships using some of these data (1976–1992) have been described elsewhere (Innes *et al.*, 1981; Beck *et al.*, 1993b; Hammill *et al.*, 1995). Standard length (American Society of Mammalogists, 1967) was measured to the nearest centimetre, and body mass ( $\pm 0.5$  kg) was determined using a dial scale suspended from a tripod. A lower canine was extracted to age animals based on growth layers in the cementum of longitudinal sections from the tooth (Bowen *et al.*, 1983). The sampling protocol used in this study complies with the Fisheries and Oceans Canada standards on animal ethics and welfare (permit IML-2015-19).

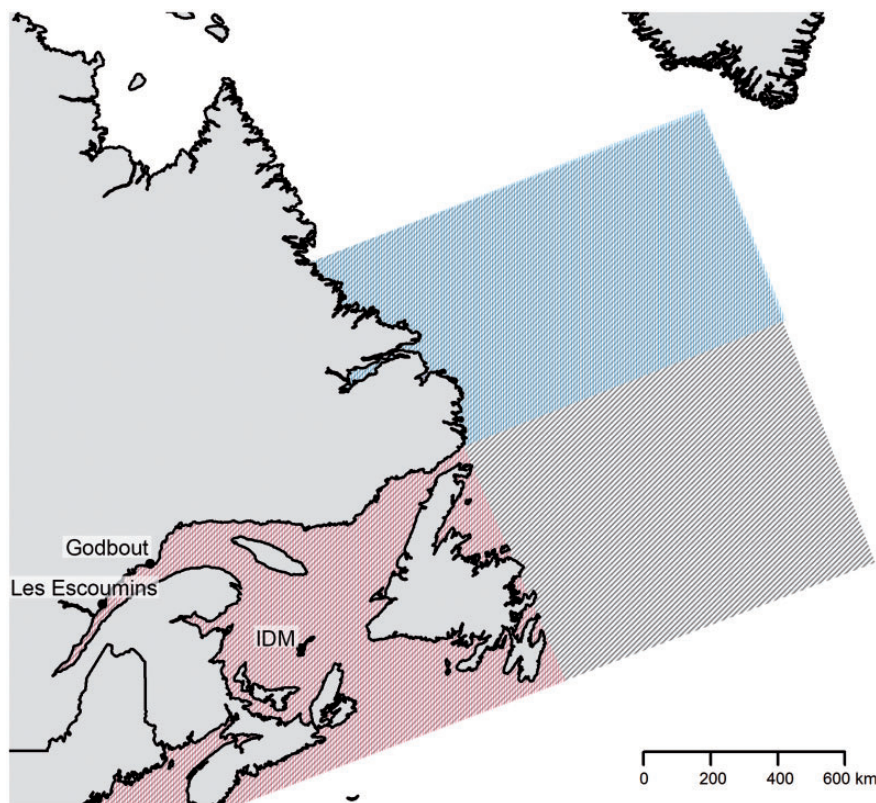
### Temporal changes in growth patterns

Since 1971, the population has increased. We divided the samples into three groups to represent different phases in the population trajectory: (1) Low population, near minimum, increasing slowly from 1976 to 1982, followed by (2) a rapid increase from 1983 to 2003, and (3) a relative stagnation from 2004 to 2015 (Figure 2; Hammill *et al.*, 2015).

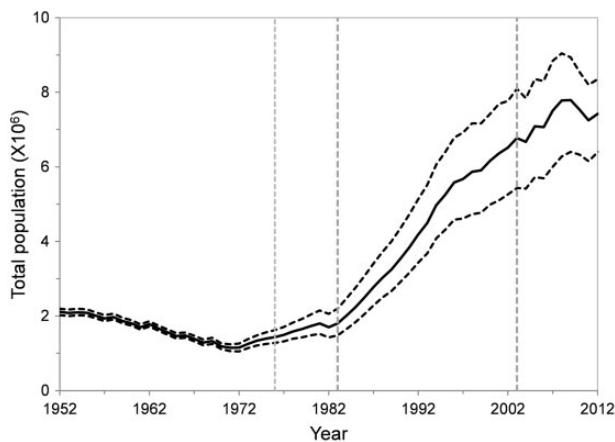
Size as a function of age was described using Gompertz growth curves:

$$S_t = S_\infty \times \left( \frac{S_0}{S_\infty} \right)^{\exp \left[ \frac{k_0 t}{S_0 \ln(S_0/S_\infty)} \right]}, \quad (1)$$

where  $S_t$  is the size at age  $t$ ,  $S_\infty$  is the asymptotic size,  $S_0$  is the size at birth, and  $k_0$  is the absolute growth rate at birth (Hammill *et al.*, 1995). Growth curves were fitted separately for each of the three time periods and for each sex for animals aged  $\geq 1$  year for both standard length and total body mass using the *nls* function in R (R Core Team, 2014). YOY were excluded from the models to avoid biases related to rapid postnatal growth and subsequent stagnation of growth until the second year (McLaren, 1993). Body mass and condition vary seasonally in harp seals, particularly during lactation, when most female samples were collected. For these animals, the effect of collection date on age-specific mass was assessed using a generalized linear model (GLM) using a  $\gamma$  distribution for error terms (link function: 'log'; *glm* function in R). Body mass was thus corrected to mass at parturition using age-specific generalized models predicting mass as a function of the number of days past 2 March for females aged 6–9 or  $\geq 10$  years, where 2 March was the mean date of pupping (Sergeant, 1991; Hammill *et al.*, 1995). Starting values for the models (Table 1) on standard length and total body mass were determined based on the results from earlier work (Hammill *et al.*, 1995; Chabot *et al.*, 1996). The asymptotic size is less sensitive to errors in age determination, to the age structure of the dataset and is independent of short-term fluctuations in size due to extraneous environmental effects of climate and food supply (Fitzhugh, 1975). As a result of its robustness, the asymptotic size ( $S_\infty$ ) was used for comparisons among periods based on overlap in confidence intervals (CIs) obtained by Jackknife resampling (*nls*tools packages;



**Figure 1.** Location of sampling areas in the St Lawrence Estuary (Les Escoumins and Godbout) and the Gulf of St Lawrence (Iles-de-la-Madeleine; IDM), Canada. Areas where ice coverage measurements were available are indicated by red, blue and grey patterns for the Gulf, southern Labrador and northeast Newfoundland (NF), respectively. The Atlantic region includes all three areas. Map generated using R (packages maps and mapdata; Becker *et al.*, 2013a, 2013b).



**Figure 2.** Trend in NWA harp seal population from 1952 to 2014 and the different phases of population growth used to compare changes in body size: (1) Low population, near minimum, increasing slowly from 1976 to 1982; (2) a rapid increase from 1983 to 2003 and (3) relative stagnation from 2004 to 2015. Figure reproduced from Hammill *et al.* (2015).

Baty *et al.*, 2015). Likewise, *t*-tests using the Tukey's honest significant difference method were performed on mean length and mass for animals aged  $\geq 10$  years (i.e. that reached their asymptotic size) to investigate for differences among periods.

The corrected body mass was related to length using:

Corrected body mass =  $10^x \times \text{standard length}^y$  (Innes *et al.*, 1981).

The estimation of the  $x$  and  $y$  coefficients describe the general relationship between mass at parturition (corrected body mass) and  $\text{length}^y$  for the entire sample. This relationship can be used to compute a condition index for individual  $i$  by comparing body mass of individual  $i$  to  $\text{length}^y_{\text{all}}$ , where:

(Hammill *et al.*, 1995). Animals with condition indices greater than 1 will be in better condition than animals with indices less than 1.

Condition Index  $\times_i = \text{corrected body mass}_i \times 10000 / \text{length}^y_{\text{all}}$

#### Harp seal demographic parameters

NWA harp seal population abundance and pup harvest data corrected for struck and loss from 1952 to 2014 are from Hammill *et al.* (2015). Annual late-term pregnancy rates for females aged  $\geq 8$  years are from Stenson *et al.* (2016). The reproductive samples are obtained from coastal regions around Newfoundland, including the west coast that borders the Gulf, but the majority of the samples is from the northeast Newfoundland coast (Stenson *et al.*, 2016).

Total abundance is estimated from a population model that includes information on reported harvests, animals that are killed but not recovered (struck and loss), unusual first year mortality because of poor ice conditions during the nursing period and age-specific reproductive rates. The model is then fitted to aerial

**Table 1.** Starting values used to fit Gompertz growth curves on harp seals.

Morphometric variable	$S_{\infty}$	$S_0$	$k_0$
Standard length (cm)	♀: 167.3	♀: 103.5	♀: 21.0
	♂: 169.5	♂: 104.0	♂: 20.5
Corrected total body mass (kg)	♀: 98.6	♀: 30.8	♀: 12.3
	♂: 102.6	♂: 34.2	♂: 11.3

survey estimates of pup production and the age specific reproductive rates data by adjusting three parameters, the initial population size, the adult mortality rate and environmental carrying capacity (Hammill *et al.*, 2015). As a result, the estimates of total abundance and the reproductive data are not independent, although as indicated above several other sources of information are included in the model in addition to the reproductive rate data. To examine the relationship between previous reproductive effort and population size on female body condition, annual reproductive rates were fitted to the population size estimates using a  $\beta$  regression. The residuals from this model were then used in the growth, mass, or condition model comparisons rather than the raw reproductive rates. These residuals represent an index of the density-independent variation in reproductive rates (hereafter referred to as *reprod* throughout this study).

#### Environmental variables

In addition to density-dependent factors, density-independent factors might also affect harp seal growth and condition in the Gulf. As outlined capelin, sandlance and Arctic cod are important prey for harp seals in the Gulf, but unfortunately there are no indices of abundance for these species in the Gulf and indices for the northeast coast of Newfoundland, an area connected to the Gulf via the Strait of Belle-Isle do not cover the entire temporal extent of this study. However, Buren *et al.* (2014) found that ice indices, particularly the timing of ice retreat in the spring, were good predictors of capelin biomass. Ice is also used by harp seals for breeding and resting; therefore, we examined how measures of ice cover and how an index of ice breakup might affect harp seal growth and condition, as well as the possible influence of two large scale climatic measures. The North Atlantic oscillation (NAO) is a large scale phenomenon exerting considerable influence on the North Atlantic climate. The winter (December through March) Hurrell NAO index used in this study is based on differences in normalized sea level pressures between Lisbon, Portugal and Stykkisholmur/Reykjavik, and Iceland (Hurrell, 2016). The Arctic Oscillation (AO) is a close relative to the NAO, but pressure anomalies are measured between the North Pole and 20°N. Monthly AO means are available from the US National weather service (<http://www.cpc.ncep.noaa.gov/>), from which a winter average was calculated using values from December through March. Weekly ice data were obtained for three regions: the Gulf of St Lawrence (Gulf), the southern Labrador Sea (referred to as the 'Front'), and the regional East Coast of Canada (referred to as 'Atlantic'; Figure 1) from the *Canadian Ice Service of Environment Canada* (<http://ice-glaces.ec.gc.ca>). Two ice measurements: percentage coverage of first year (FY) ice (ice > 30 cm thick) and percentage coverage of total ice were used as environmental variables to describe each region. These were converted to ice cover (kilometre square) by multiplying the cover of each ice

type (percentage) by the area of the region (kilometre square). Total ice cover was computed as the sum of FY ice, young ice (ice 10–30 cm thick), and new ice (recently formed ice: frazil ice, grease ice, slush, and shuga). Ice data were obtained for 29 January, 5 March, and 16 April, which represent conditions prior to pupping in January, ice available for pupping in March, and ice remaining post-pupping in April.). Ice breakup begins in late March and involves both spatial and temporal components, as the total amount of ice cover in each area declines over a short period of a few weeks. An index of breakup was developed by comparing the FY ice cover on 5 March, when animals are resting on the ice during the pupping period, with the amount of FY ice cover on the 16 April, which represents the post-pupping period. The index was calculated as:

$$\text{March: April FY ice ratio} = \frac{\text{FY ice coverage 5 March}}{\text{FY ice coverage 16 April}}.$$

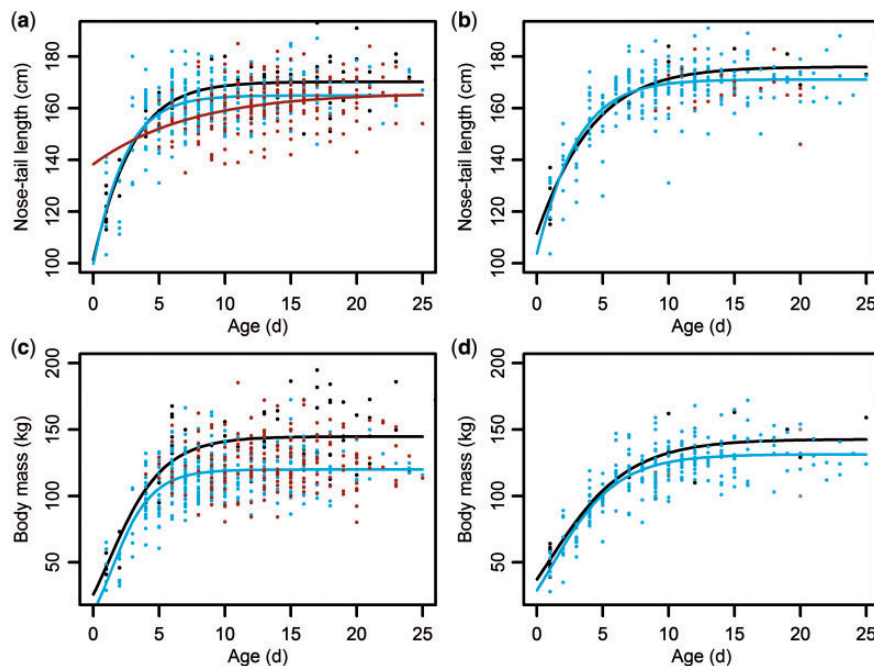
#### Analyses

Harp seal nose-tail length, body mass, and condition index were inserted as response variables in linear mixed models using demographic and climate parameters as fixed effects and year as a random effect to investigate the factors explaining the important inter-annual variability observed in morphometric data. These analyses included only females that had reached their asymptotic size (i.e. aged  $\geq 8$  years) when they were collected to eliminate the effect of age on morphometric variables. Pearson correlation coefficients between morphometric variables and age were computed for animals  $\geq 8$  years old to confirm that the effect of age was indeed eliminated.

Harp seal length is relatively constant during the first year of life, then increases rapidly until asymptotic size is reached (McLaren, 1993). Therefore, length in animals aged  $\geq 8$  years is likely determined by conditions that prevailed when they were aged 1–7 years. Nose-tail length was thus modelled as a function of mean population size calculated over the second to seventh year of life of the animal ( $mean_{2-7} \text{ abundance}$ ) and of YOY harvest the year the animal was born ( $harvest_{birth}$ ).

Body mass depends on growth during the first few years of life and also on current conditions favouring or limiting energy intake and storage. Explanatory variables considered for the body mass models thus included both  $mean_{2-7} \text{ abundance}$  and abundance when the animal was collected,  $abundance_{y_0}$ , the reported harvest of YOY when the animal was born ( $harvest_{birth}$ ), the reproductive rate in the previous year ( $reprod_{y-1}$ ), and the following climatic variables: current January FY ice and total ice concentrations, March and April FY ice and total ice concentrations lagged by one year, the March:April FY ice ratios lagged by one year, and current winter NAO and AO indices.

Body condition reflects an animal's energy reserves and muscle mass and depends mostly on recent environmental conditions. A condition index was thus modelled by variables describing the demographic and climatic conditions within the last 12 months. These include the current population size ( $abundance_{y_0}$ ), the reproductive rate in the previous year ( $reprod_{y-1}$ ), and the climatic variables described for the body mass models.



**Figure 3.** Harp seal nose-tail length (top panels) and total body mass (lower panels) fitted with Gompertz growth curves. Animals collected in 1976–1983, 1984–2003, and 2004–2015 are represented by black, blue and red circles and lines, respectively. Data from females are presented in left (a) and (c) panels, and right panels (b) and (d) present data from males.

### Model selection procedure

Assessing the relationship between environmental variables and biological traits requires considering numerous, often interdependent covariates. Model selection was based on the frameworks proposed by Grosbois *et al.* (2008) and van de Pol *et al.* (2016).

In a first step, baseline models including demographic parameters, but no climatic (i.e. ice, NAO, and AO) covariates were fitted to describe body length, mass, or condition. All possible subsets of the considered fixed effects included either as linear or as smooth terms in linear mixed models (LMM; function *lmer* from package *lme4*; Douglas *et al.*, 2015) or general additive mixed models (GAMMs; package *mgcv*; Wood, 2011) estimated by restricted maximum likelihood (REML), along with the model with an intercept only were tested. Every model included animal year of collection as a random factor. To be considered as significantly improving a model, a given variable had to induce a drop in the Akaike information criterion (AIC) of at least two points compared to the simpler model excluding the variable (Grosbois *et al.*, 2008). Although the use of the corrected AIC (AICc) is recommended for finite sample sizes (Sugiura, 1978), it is not implemented in R for GAMMs. The use of the AIC is considered appropriate for sample sizes considerably larger than the number of parameters estimated in the model, i.e. when  $n/k > 40$  (Burnham and Anderson, 2002), which is the case in the models considered in this study. AIC was thus used to compare models when the candidate models included GAMMs in a given selection procedure. The model with the lowest AIC in which all covariates significantly improved the fit was retained as the baseline model.

In a second step, climatic covariates were individually added to the body mass and condition index baseline models as either linear or quadratic terms. This resulted in a candidate model set in which each model contained a single climatic covariate. Since baseline models retained for body mass and condition index were

both LMMs, it was possible to compute their AICc (package *AICcmodavg*; Mazerolle, 2016). Candidate models were compared to the baseline model, on the base of their AICc. Those with  $\Delta\text{AICc} > 2$  (where  $\Delta\text{AICc} = \text{AICc}_{(\text{complex model})} - \text{AICc}_{(\text{baseline model})}$ ) were retained, and the climatic covariate was considered as a potential signal for body mass or condition index (Burnham and Anderson, 2002; Grosbois *et al.*, 2008). Quadratic effects were considered statistically supported when their inclusion in a model including the linear term for the same covariate induced a  $\Delta\text{AICc} > 2$  (Grosbois *et al.*, 2008).

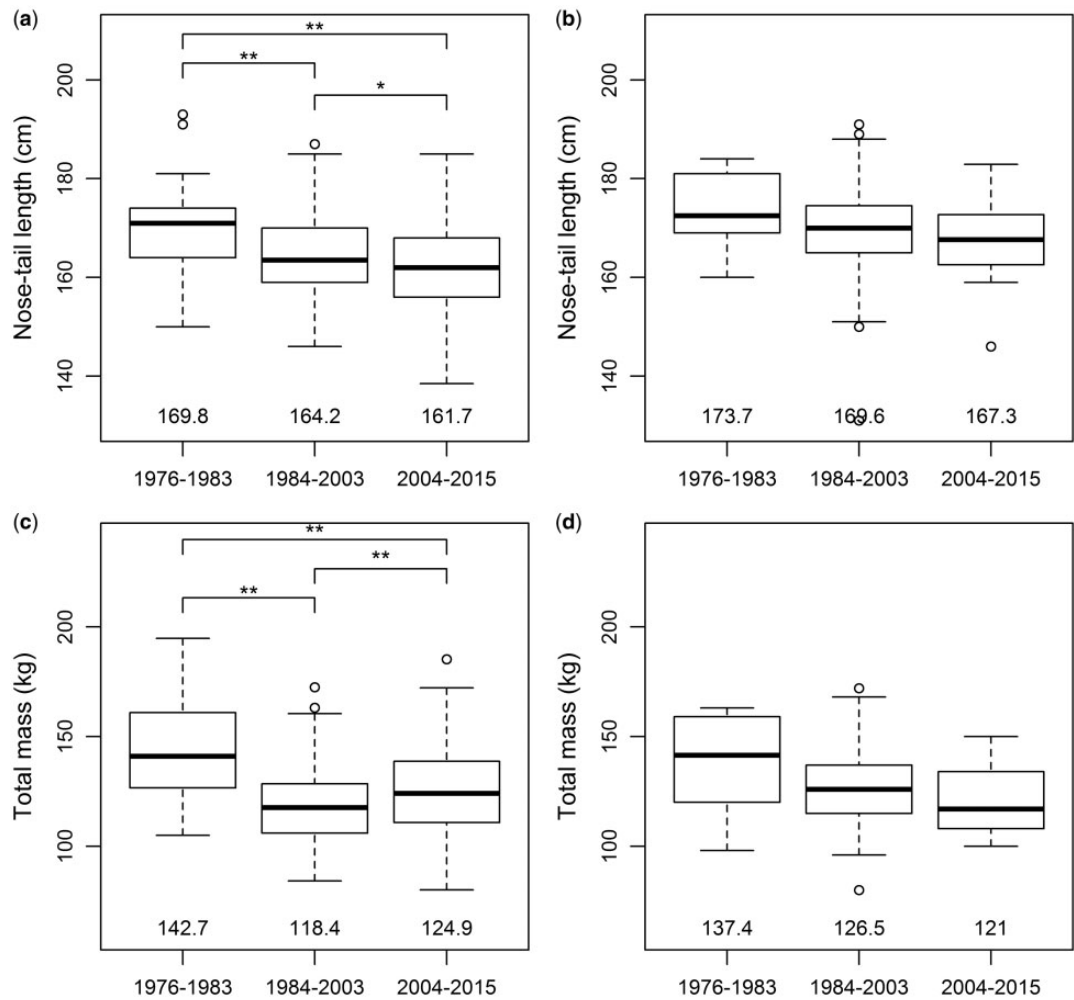
For each mixed effect model fitted in this study, parameter 95% CIs were calculated by bootstrap resampling (package *boot*; Canty and Ripley, 2016). In addition, the potential influence of a single year in the models was assessed using the *influence.ME* package (Nieuwenhuis *et al.*, 2012). A given fixed effect was not considered significant if removing a single year from the dataset resulted in a parameter estimation that was no longer different from zero. Normality of residuals and homogeneity of variance were visually checked by QQ plots and Pearson residuals (both including random effects) plotted against predicted values, respectively. For GAMMs, the *gam.check* function was used (*mgcv* package; Wood, 2011).

All statistical analyses were performed with R 3.1.0 (R Core Team, 2014). Results were considered significant at  $p < 0.05$  and are presented as means  $\pm$  standard errors (s.e.), unless stated otherwise. The entire set of models considered in the model selection procedures in this study is available online as [Supplementary Material 1](#).

## Results

### Temporal changes in growth patterns

Female asymptotic length and asymptotic body mass declined significantly from 1976–1983 to 1984–2003 ( $p < 0.05$ ), but the 2004–2015 length did not differ from the two previous periods ( $p$



**Figure 4.** Nose-tail length and total body mass from harp seal females (left panels (a) and (c)) and males (right panels (b) and (d)) that have reached asymptotic size (i.e. aged  $\geq 8$  years). Boxes extend from the first to the third quartiles, with a thin line indicating the median. \* $p < 0.05$ ; \*\* $p < 0.01$  for differences between the means using the Tukey's honest significant difference method.

**Table 2.** Asymptotic size estimated from Gompertz growth curves on harp seal morphometric data divided into three time periods.<sup>a</sup>

Sex	Period	Standard length (cm)			Total body mass (kg)		
		$L_{\infty}$ (95% CI)	$L_{\infty}$ s.e.	$n$	$W_{\infty}$ (95% CI)	$W_{\infty}$ s.e.	$n$
♀	1976–1983	<b>170.21 (167.77–172.57)</b>	1.08	88	<b>144.70 (137.65–151.31)</b>	3.13	88
	1984–2003	<b>164.91 (163.46–166.37)</b>	0.67	380	<b>119.87 (117.46–122.35)</b>	1.28	351
	2004–2015	165.95 (159.53–170.15)	3.32	187	NA	NA	188
♂	1976–1983	176.02 (169.76–181.34)	3.39	23	142.63 (119.33–161.22)	7.89	23
	1984–2003	171.09 (169.54–172.60)	0.84	249	131.31 (127.58–134.85)	1.82	230
	2004–2015	NA	NA	22	NA	NA	4

<sup>a</sup>Bold text indicates significant differences ( $P < 0.05$ ).

$> 0.05$ ; Table 2 and Figure 3). The 2004–2015 body mass model could not be estimated as there were no young ( $< 5$  years) animals in the sample. Comparisons of mean body length for animals aged  $\geq 10$  years decreased in female length from the earliest to the most recent periods (Figure 4). Female mean body mass decreased from  $142.7 \pm 3.0$  kg in 1976–1983 to  $118.4 \pm 1.1$  kg in 1984–2003 then increased slightly to  $124.9 \pm 1.5$  kg during the period 2004–2015.

No significant differences were observed for males, between periods in asymptotic nose-tail length and asymptotic body mass. Among males, the models for the period 2004–2015 did not converge because of the small sample sizes (Figure 3 and Table 2). There was no significant difference in mean male nose-tail length nor body mass among periods for animals aged  $\geq 8$  years, but sample sizes were small (Figure 4).

**Table 3.** Pearson correlation coefficients among climatic covariates considered in body mass and condition index models.

	Gulf						Front						Atlantic					
	January		March		April		January		March		April		January		March		April	
	FY ice	Total ice	FY ice	Total ice	FY ice	Total ice	FY ice	Total ice	FY ice	Total ice	FY ice	Total ice	FY ice	Total ice	FY ice	Total ice	FY ice	Total ice
NAO	1.00																	
AO	-0.13	0.35	0.31	0.05	0.16	0.032	0.02	0.33	0.25	0.09	-0.06	-0.07	-0.09	0.40	0.32	0.03	-0.07	-0.08
Gulf	1.00	0.22	0.53	0.33	0.38	0.38	0.41	0.53	0.40	0.06	0.27	0.83	0.79	0.53	0.55	0.21	0.48	0.69
		1.00	0.57	0.36	0.40	0.06	0.08	0.23	0.07	0.01	0.16	0.27	0.23	0.50	0.42	0.11	0.29	0.13
			1.00	0.42	0.48	0.30	0.31	0.70	0.55	0.42	0.39	0.48	0.41	0.79	0.90	0.37	0.52	0.38
Front				1.00	0.79	0.83	0.84	0.45	0.52	0.45	0.46	0.48	0.52	0.55	0.55	0.84	0.83	0.72
					1.00	0.68	0.72	0.36	0.57	0.12	0.30	0.50	0.54	0.44	0.59	0.50	0.86	0.64
						1.00	0.99	0.40	0.56	0.24	0.18	0.59	0.62	0.44	0.51	0.67	0.67	0.86
Atlantic							1.00	0.43	0.59	0.23	0.21	0.62	0.66	0.46	0.53	0.66	0.71	0.88
								1.00	0.77	0.63	0.69	0.46	0.45	0.95	0.82	0.57	0.63	0.49
									1.00	0.53	0.54	0.51	0.52	0.71	0.85	0.57	0.74	0.58
Atlantic										1.00	0.83	0.06	0.05	0.59	0.53	0.82	0.51	0.22
											1.00	0.19	0.20	0.65	0.51	0.72	0.71	0.30
												1.00	1.00	0.51	0.27	0.52	0.89	0.88
Atlantic														0.56	0.29	0.56	0.91	0.91
														1.00	0.87	0.58	0.65	0.53
															1.00	0.54	0.71	0.58
Atlantic																1.00	0.78	0.56
																	1.00	0.70
																		1.00
Atlantic																		1.00
																		1.00
																		1.00

### Climatic variables

The AO was not correlated ( $r < 0.6$ ) to any ice measure, while NAO was only correlated with Atlantic and Front ice measured in April (Table 3). Some FY and total ice measures were correlated for a given month and area, but this was not always the case. This is not surprising since ice in the Gulf is affected by upstream ice formation in the St Lawrence River Estuary, while ice at the Front will be affected by the southward drift of ice along the Labrador coast (Sergeant, 1991; Figure 1). The Atlantic ice for a given month was correlated with both the corresponding Gulf and Front ice measurements, as expected based on overlap in areas included in Atlantic and Gulf and Front ice measurements (Figure 1).

### Modelling factors affecting body length

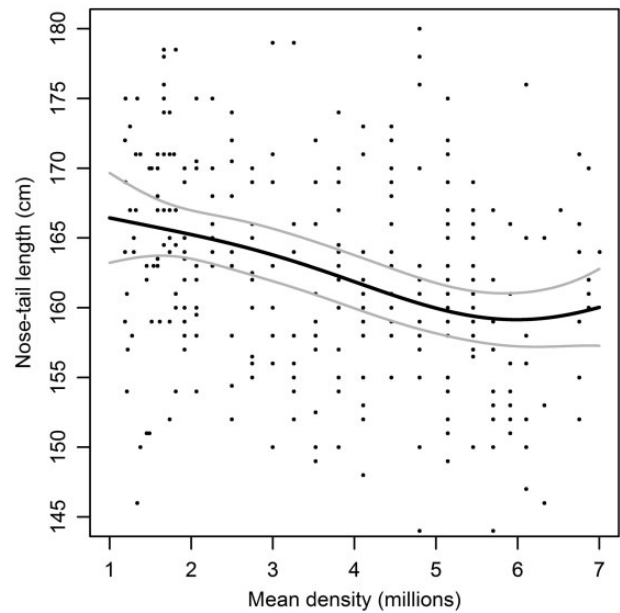
Age was not related to body length ( $R = 0.21$ ), body mass ( $R = 0.15$ ), nor condition index ( $R = 0.01$ ) for animals aged  $\geq 8$  years, confirming that these animals had reached asymptotic size and that morphometric data could be modelled without including age as a fixed effect.

Three LMM models fitted nose-tail length to abundance were more parsimonious than the model with an intercept only (AIC = 2235.0). The best of these models was a GAMM including mean population abundance during the maximal growth period (i.e. when animals were aged 1–7 years;  $mean_{2-7}abundance$ ) as a smooth term (AIC = 2224.8; Figure 5), while the second model was the equivalent LMM including  $mean_{2-7}abundance$  as a fixed term (AIC = 2225.0). The third model was a GAMM with both  $mean_{2-7}abundance$  and  $harvest_{birth}$  as smooth terms (AIC = 2225.6). All of these models indicated a significant ( $p < 0.05$ ) negative relationship between body length and population size. Models including the harvest in the year animals were born as sole covariate had higher AIC than the model with the intercept only, and in multiple covariate models including harvest, the coefficient for  $harvest_{birth}$  was never significantly different from zero, indicating no harvest effect on growth in length in a cohort.

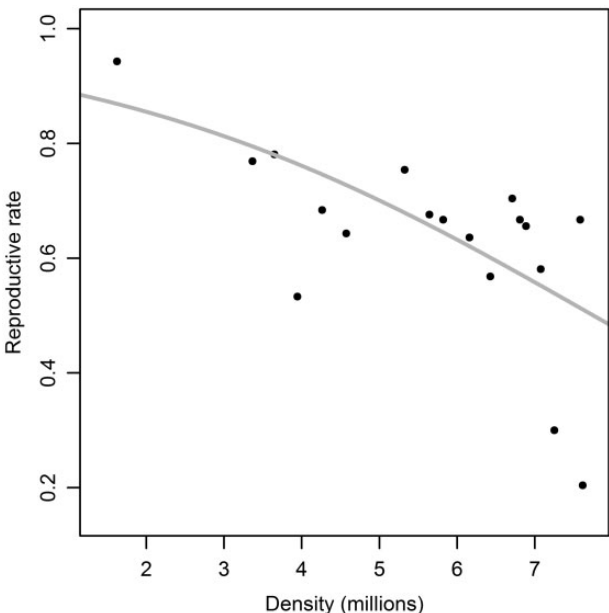
### Modelling factors affecting body mass

Reproductive rate as a function of population abundance was best described by a  $\beta$  regression including abundance as a linear term (Figure 6). The best model fitted to body mass included the reproductive rate from the previous year residuals ( $reprod_{y-1}$ ), and abundance as explanatory variables. However, the model including abundance did not have an AIC reduced by at least two points compared to the second best and simpler model containing  $reprod_{y-1}$  as sole covariate (Table 4). Moreover, the coefficient for abundance was not significantly different from zero (Table 4). Therefore, the  $mass \sim reprod_{y-1}$  model was retained as the baseline model. In this model, body mass was negatively correlated with the reproductive rate from the previous year (coefficient =  $-47.3 \pm 10.2$ ), suggesting that females tend to be heavier following years when reproductive rates were low.

When including climatic covariates in the baseline model LMM ( $Mass \sim reprod_{y-1}$ ) as either linear or quadratic terms, 22 variables improved the model by inducing an AICc drop of at least two points, as linear or quadratic terms, or both (see Supplementary material 1). However, only one climatic variable was associated with coefficients that significantly differed from zero based on their bootstrap CI: the March:April  $y-1$  FY ice ratio measured at the Front (Table 5, Figure 7).



**Figure 5.** Nose-tail length in harp seal females aged  $\geq 8$  years related to mean population abundance calculated over the maximal growth period (i.e. when animals were aged 1 to 7 years). Empty circles represent observations ( $n = 316$ ), while the black and grey lines illustrate predicted values and 95% CI from a GAMM with mean population abundance included as a smoothed term (estimated degrees of freedom = 2.512).



**Figure 6.** Relationship between annual reproductive rate and abundance ( $n = 16$ ). Black circles represent observations. The grey line illustrates the prediction curve from a Beta regression with abundance included as a linear term (coefficient =  $-0.31$ ,  $p < 0.01$ ).

**Table 4.** Best candidate baseline linear mixed models for body mass (*Mass*) from 316 harp seal females aged  $\geq 8$  years. Considered fixed effects were the annual reproductive rate residuals obtained from a Beta regression with abundance as sole covariate lagged by one year (*reprod y - 1*; see Figure 5), population abundance, and annual harvest on pups at birth (*harvest<sub>birth</sub>*). Year was included as a random effect in all models. Akaike weights ( $w_i$ ) were calculated considering all possible subsets ( $n = 16$ ) of the four considered fixed terms, including the model with the intercept only, and models with  $w_i > 0.01$  are presented.<sup>a</sup>

Model equation	AICc	Akaike weight ( $w_i$ )	Cumulative $w_i$	<i>reprod y-1</i> coefficient 95% IC	Abundance coefficient 95% IC
<i>Mass</i> ~ <i>reprod y-1</i> + <i>abundance y0</i> + (1  <i>year</i> )	1856.685	0.701	0.701	-75.0, -31.1	-3.1, 0.4
<b><i>Mass</i> ~ <i>reprod y-1</i> + (1 <i>year</i>)</b>	<b>1858.393</b>	<b>0.299</b>	<b>1.000</b>	<b>-67.7, -26.4</b>	-

<sup>a</sup>Model in bold type was retained as baseline model for further analyzes.

**Modelling factors affecting body condition**

Body mass was related to length by the relationship:  $Body\ mass = 10^{-2.54} \times standard\ length^{2.09}$ . The best model fitted to body condition index was a LMM including the reproductive rate from the previous year's residuals (*reprod y-1*) as the sole explanatory variable (Table 6). The second best model also included abundance, however the inclusion of this variable did not improve the simpler model by at least two AIC points. Moreover, the coefficient for abundance was not significantly different from zero based on the bootstrap CIs. The model with the lowest AIC was therefore retained as the baseline model for further analysis. In this model, condition index was negatively correlated with the reproductive rate from the previous year (coefficient =  $-16.18 \pm 4.79$ ). This indicates that in general, females tend to be in better condition following years with low reproductive rates.

When including climatic covariates in the baseline model LMM(*Condition* ~ *reprod y-1*) as either linear or quadratic terms, three variables improved the model by inducing an AICc drop of at least two points and were retained as potential climatic signals. These include the quadratic effects of the in March:April FY ice ratio  $y_{-1}$  in the Atlantic and at the Front, as well as the linear effect of total ice concentration at the Front in January (Table 7). Because Atlantic and Front ice ratios are closely related ( $r = 0.93$ ), the first and second models in Table 4 are conceptually equivalent. Results from Table 7 suggest that (1) there are optimal values for the March:April FY ice ratios (i.e., intensity of ice breakup in March and April) for which the harp seal condition index will be optimal the following year, and that (2) too much ice at the Front in January has a negative impact on harp seal condition (Figure 8). This model suggests that the effects of

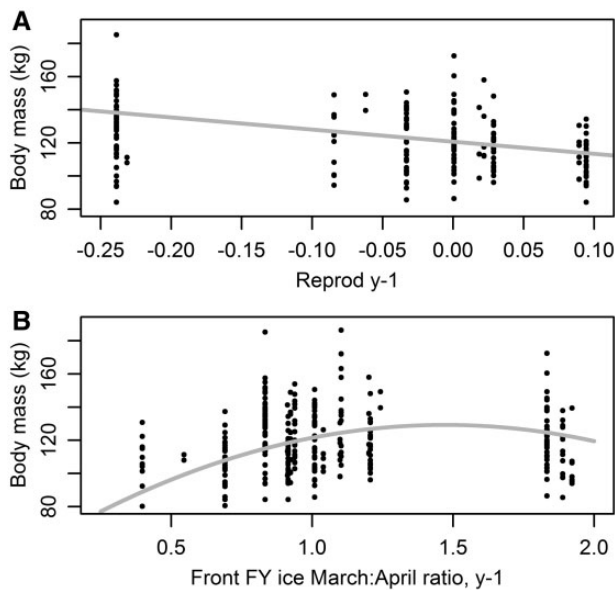
**Table 5.** Statistics from models fitted to harp seal body mass (*Mass*) by including climatic covariates one by one in the baseline model defined in Table 4. Models were fitted as linear mixed models using year as a random effect. The only significant climatic variable is the first year ice (*FYice*) ratio between 5 March and 16 April (*March:April*) measured in the Front (*Front*) lagged by 1 year (*y-1*).

Model equation	AICc	<i>reprod y-1</i> coefficient (95% IC)	Climatic variable linear coefficient (95% CI)	Climatic variable quadratic coefficient (95% CI)
$Mass \sim reprod\ y-1 + (Front\_FYice\_March:April\_y-1)^2 + (1 year)$	1846.9	-73.2 (-93.1, -46.0)	10.7 (3.62, 15.7)	-6.1 (-9.3, -1.0)

**Table 6.** Best candidate baseline linear mixed models for condition index (*Condition*) from 316 harp seal females aged  $\geq 8$  years. Considered fixed effects were the annual reproductive rate residuals obtained from a  $\beta$  regression with abundance as sole covariate lagged by one year (*reprod y-1*; see Figure 5), and population abundance. Year was included as a random effect in all models. Akaike weights ( $w_i$ ) were calculated considering all possible subsets ( $n = 8$ ) of the three considered fixed terms, including the model with the intercept only, and models with  $w_i > 0.01$  are presented.<sup>a</sup>

Model Equation	AICc	Akaike weight ( $w_i$ )	Cumulative $w_i$	<i>reprod y-1</i> coefficient 95% IC	Abundance coefficient 95% IC
<b><math>Condition \sim reprod\ y-1 + (1 year)</math></b>	<b>1203.773</b>	<b>0.561</b>	<b>0.561</b>	<b>-25.2; -7.6</b>	-
$Condition \sim reprod\ y-1 + Abundance + (1 year)$	1204.262	0.439	1.000	-24.3; -9.9	0.0; 1.0

<sup>a</sup>Model in bold type was retained as baseline model for further analyses.



**Figure 7.** Harp seal female body mass related to (a) the reproductive rate residuals from the previous year (*y-1*), obtained from a linear Beta regression with abundance, and (b) FY ice March:April ice ratio (*y-1*) at the Front, considered as an index of ice break-up between early March and mid-April. Grey lines illustrate prediction curves from models described in Table 4).

*Reprod y-1* and the March:April FY ice ratios on body mass and condition index are very similar (Figures 7 and 8).

Given the strong negative effect of reproductive rate on body mass and condition the following year, we tentatively tested the relationship between current reproductive rate residuals (*reprod\_y0*) and condition index. There was a positive linear relationship between these variables (coefficient =  $9.41 \pm 1.99$ ,  $p < 0.01$ ), suggesting that years when females are in good body condition are associated with high reproductive rates.

## Discussion

The discussion of density-dependence factors and their role in regulating populations are pervasive throughout the ecological literature, yet among marine mammals, examples of density-dependence and their mechanisms are limited. In this study, we showed that as the NWA harp seal population has increased from a low of 1.1 million in 1971 to 7.4 million in 2014, female body length and body mass have declined, which is consistent with a density-dependent response to a per capita decline in resources. The same general trend was also observed among males, but differences were not significant owing to small sample sizes. Since reproductive effectiveness depends on an individual's stage of physical development, then according to Eberhardt's paradigm for the regulation of populations, any force slowing juvenile growth is also likely to affect age of first reproduction and lead to a general decline in productivity (Eberhardt and Siniff, 1977). Such changes have been observed among NWA harp seals with mean age of maturity declining from 5.8 in 1954 to 4.1 years in 1979, which encompasses the period of population decline, remaining low ( $\sim 4.5$  years) for much of the 1980s, before increasing again to  $\sim 5.5$  years in the 1990s as the population increased (Sjare and Stenson, 2010; Hammill *et al.*, 2015). Since then as the growth of the population has slowed and possibly levelled off, the mean age of maturity has shown considerable inter-annual variability, fluctuating between 4.9 and 6.0 years (between 2000 and 2004), and variability in annual reproductive rates has also increased (Sjare and Stenson, 2010; Hammill *et al.*, 2015; Stenson *et al.*, 2016).

Body mass and condition are the integrators of location specific energy and protein demands and food intake, and the potential driver of demographic variation (Parker *et al.*, 2009). We observed that condition was affected by both a density-dependent related variable, population size, and density-independent variables representing environmental stochasticity, which we suggest likely affected local foraging conditions. Such changes in size at age and variability in condition provide a mechanism to account for observed changes in reproductive rates in this population (Hammill *et al.*, 2015; Stenson *et al.*, 2016).

**Table 7.** Statistics from models fitted to harp seal condition index (*Condition*) by including climatic covariates one by one in the baseline model defined in Table 3. All models were fitted as linear mixed models using year as a random effect. Climatic variables are the first year ice (FYice) ratios between March 5<sup>th</sup> and April 16<sup>th</sup> (March:April) measured either in the Atlantic (Atl) or in the Front (Front) lagged by one year (y-1), and current (y0) total ice concentration (Tot<sub>ice</sub>) measured in the Front on January 29<sup>th</sup> (Jan).

Model equation	AICc	reprod y-1 coefficient (95% IC)	Climatic variable linear coefficient (95% CI)	Climatic variable quadratic coefficient (95% CI)
<i>Condition</i> ~ <i>reprod</i> y-1 + (Atl_FYice_March:April_y-1) <sup>2</sup> + (1 year)	1198.816	−26.5 (−33.1, −21.1)	2.5 (1.1, 3.7)	−1.4 (−2.2, −0.5)
<i>Condition</i> ~ <i>reprod</i> y-1 + (Front_FYice_March:April_y-1) <sup>2</sup> + (1 year)	1199.559	−24.50 (−29.6, −19.8)	3.01 (1.2, 5.3)	−1.76 (−3.2, −0.6)
<i>Condition</i> ~ <i>reprod</i> y-1 + Front_Totice_Jan_y0 + (1 year)	1200.708	−17.78 (−26.6, −11.6)	−0.84 (−1.4, −0.4)	–

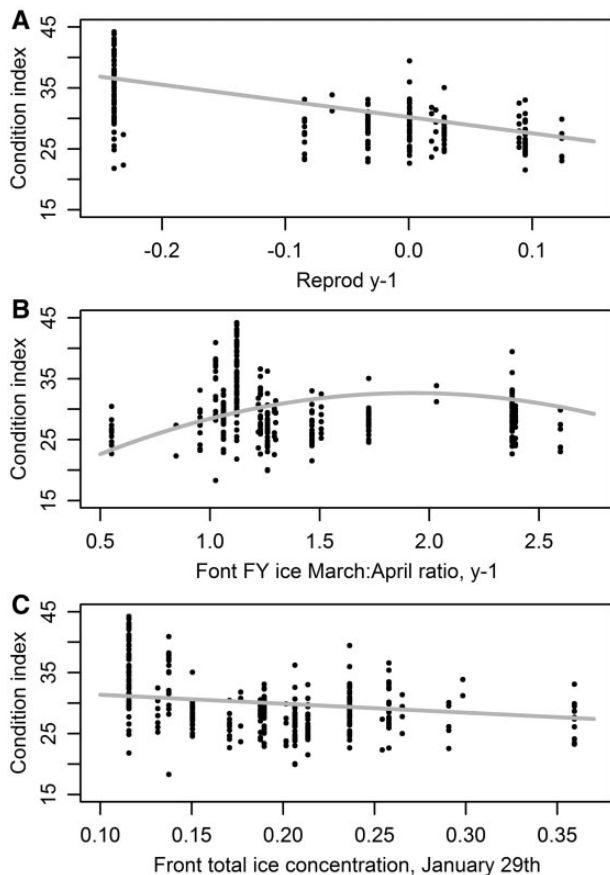
The greatest decline in length and mass occurred between the first and second periods of our analysis, between a period when the population was relatively small (1976–1983) and a period of rapid growth in the population (1984–2003). Beginning in 2004, the rate of growth in the harp seal population began to slow, possibly a result of a combination of factors that were initiated in the early to mid-1990s. At that time, in addition to an increasing harp seal population, there was a regime shift in the NWA: synergistic climatic and anthropogenic forcings contributed to declines in capelin biomass and changes in seabird biology and the collapse of stocks of top predators (deYoung *et al.*, 2004; Greene *et al.*, 2013; Buren *et al.*, 2014). Such ecosystem changes combined with a decade long resurgence in the harvesting of harp seals in Canada and Greenland, beginning in the mid-1990s, would have slowed the rate of increase in the NWA harp seal population (Hammill *et al.*, 2015) and may have dampened density-dependent effects, which could explain the slight increase in asymptotic length and mean body mass in females between the second (1984–2003) and third (2004–2015) periods observed in this study.

Harp seals from all three population undertake extensive seasonal movements, but those of the NWA population are the most extensive as harp seals migrate southwards from summering areas off the Baffin Island and Greenland coasts to arrive in the breeding areas off the southeast Labrador-northeast Newfoundland coasts and in the Gulf in the late fall (Sergeant, 1991). Animals returning from the Arctic show improved condition, but unlike Barents Sea harp seals, which build-up their energy supplies during summer, and appear to maintain energy levels until pupping (Nilssen *et al.*, 1995), NWA harp seals acquire a significant proportion of their energy during their last trimester of pregnancy (November–March) while on the southeast Labrador-northeast Newfoundland area feeding grounds and in the Gulf (Beck *et al.*, 1993b; Chabot and Stenson, 2002; Stenson *et al.*, 2016).

All animals examined in this study were sampled in the Gulf, which represents approximately 30% of the total NWA population, with the remaining animals breeding at the Front (Hammill *et al.*, 2015). NWA harp seals form a single stock for management purposes (Sergeant, 1991). Animals from both areas overlap in summer and during the spring, and fall migration (Sergeant 1991), and the Front area remains an important foraging area for Gulf harp seals, who do not begin moving into the Gulf until December via the Strait of Belle-Isle. Immature animals of Gulf origin remain at the Front throughout the winter and only move into the Gulf in later years during winter as they mature. In some years, entry into the Gulf may be delayed as a result of heavy ice in the Strait of Belle-Isle, while in others, the absence of ice in the Gulf probably results in animals overwintering at the Front and

pupping in that area as well (Sergeant, 1991; Stenson and Hammill, 2014). Due to the considerable overlap in distribution between the Gulf and Front herds, and the importance of ice conditions at the Front on our results, we believe that our findings are likely applicable to the entire population. However, a comparison between the two areas would confirm this.

Energy and time are limited, therefore individuals should allocate resources in an optimal way for maintenance, growth, and reproduction (Stearns, 1992). The decision to allocate resources to reproduction may incur costs which could affect future reproductive potential, such as reduced probability of reproduction the following year (Stearns, 1992; Hamel *et al.*, 2008), and this has been observed among several species including moose (*Alces alces*; Testa, 2004), red deer (*Cervus elaphus*; Clutton-Brock *et al.*, 1983), fur seals (*Arctocephalus gazelle*; Boyd *et al.*, 1995), and Weddell seals (*Leptonychotes weddelli*; Testa, 1987). To manage the fundamental trade-offs, different strategies have been developed to balance between female resource requirements and allocation of resources to their offspring. Capital and income breeding strategies represent extreme poles of a continuum of solutions to these trade-offs that are distinguished by the degree of using stored (vs. exogenous) energy to support reproductive costs (Stearns, 1992; Johnsson, 1997; Kerby and Post, 2013). Income breeders forage during the maternal care period to obtain energy supplies to support maintenance and lactation costs (Stearns, 1992; Johnsson, 1997). In contrast, capital breeders rely on these stored reserves to meet energy requirements for maintenance and lactation, and therefore their relative cost of reproduction depends on the ability to build-up stored energy reserves prior to reproduction, then to minimize expenditure during lactation. Among bighorn sheep (*Ovis canadensis*) and red deer, reproductive success was independent of female mass at low densities, but as density increased, the relative costs of reproduction increased for lighter females, who had greater difficulties in regaining sufficient mass after lactation and had reduced reproduction in the following year (Clutton-Brock *et al.*, 1983; Fiesta-Bianchet *et al.*, 1998), which contributes to an increase in inter-annual variability in reproductive success. Harp seals are generally considered to be capital breeders, but unusually high efficiencies of mass transfer, considerable time spent in the water by females and some evidence of feeding during lactation suggests that some females are adding some exogenous energy sources during lactation (Hammill *et al.*, 1995; Lydersen and Kovacs, 1996). Lighter females may attempt to offset the relatively higher costs of lactation by increasing foraging effort, particularly late in lactation as stored reserves are depleted, but the possibility of increased foraging in harp seals needs to be explored further.



**Figure 8.** Harp seal female condition index related to (a)  $y-1$  reproductive rate residuals obtained from a linear  $\beta$  regression with abundance, (b) FY ice March:April ice ratio at the Front, considered as an index of ice break-up between early March and mid-April, and (c)  $y0$  total ice concentration at the Front measured 29 January 29 (black circles). Grey lines illustrate prediction curves from models described in Table 4).

In this study, animals were collected during the breeding season, therefore, they had already exceeded some minimal threshold that enabled them to produce a viable pup. Nonetheless, we observed that in years when reproductive rates were high, females were in better condition, than in years when reproductive rates were low. We also observed a negative relationship between condition/mass and population size in the current year and reproductive rates the previous year. This suggests that at high densities, the decline in size has increased the relative cost of reproduction to breeding females, who now incur a significant cost that affects future fitness, which in turn could contribute to increased inter-annual variability in reproductive rates.

Female condition was affected by ice cover in January and the March:April FY ice ratio the previous year, the latter being a measure of the intensity of spring ice breakup. Early in this paper, we identified capelin as an important prey for harp seals and that foraging in southern waters is critical to building up energy reserves prior to pupping (Sergeant 1991; Stenson *et al.*, 2016). During winter, capelin are usually concentrated in large schools at a depth of 140–200 m (Winters, 1970). At this time, they also have high-fat content, representing an energy rich prey for harp seals, trying to stock up blubber reserves just prior to pupping

(Winters, 1970). Although ice during winter can be used as a platform to haul-out on, ice that is too heavy may reduce foraging opportunities because it limits seal movements and their ability to search and capture prey. This is because, unlike some other species, e.g. ringed seals (*Pusa hispida*), harp seals are unable to maintain breathing holes in the heavy winter ice, therefore they rely on ready access to cracks or open water between ice-pans to return to the surface and breathe. In this context, the negative relationship between January ice and harp seal condition index is likely due to a limiting effect of heavy ice concentrations on food accessibility for harp seal females prior to pupping.

After the pups are weaned, females undertake a short period of intensive foraging, to regain some of the mass lost during lactation prior to moult in April (Beck *et al.*, 1993b). Capelin and other small forage fish, as well as invertebrates continue to be important prey during this period (Beck *et al.*, 1993a; Lawson *et al.*, 1995; Lawson and Stenson, 1997). At this time, capelin are just beginning to forage, therefore lipid levels are still relatively high and relatively dense schools remain (Winters, 1970). Buren *et al.* (2014) proposed a mechanistic link between sea ice breakup and capelin availability, as a prey match/mismatch phenomenon, where the retreat of the sea ice in spring triggers the onset of the spring phytoplankton bloom, which in turn provides food for emerging *Calanus finmarchicus* (capelin's main prey) from diapause. If the spring bloom occurs too early, because of early ice breakup, then *Calanus* likely emerge too late to fully profit from the phytoplankton bloom, and *Calanus* biomass will remain low. In the absence of food, capelin will have difficulty foraging and may disperse earlier, to the detriment of harp seals. Conversely, a delayed breakup might limit seal access to capelin schools or may delay the phytoplankton bloom, with cascading effects on *Calanus* and capelin biomass. Thus changes in breakup would appear have food web consequences that might affect foraging opportunities for harp seals during this critical post-breeding feeding period. This is consistent with the convex relationship, suggesting the existence of optimal conditions, between the March:April ice ratio and seal condition and mass found in this study.

The overall decline in body length and mass of NWA harp seals as the population has increased shown in this study is consistent with a density-dependent response to reduced *per capita* resources. Such changes will impact vital rates and provide the mechanism to account for the general decline in productivity of this population reported by Stenson *et al.* (2016). In that study, increased variability in pregnancy rates was attributed to an increase in late-term abortions, which in turn was associated with increased variability in spring ice break-up (Buren *et al.*, 2014; Stenson *et al.*, 2016). Among pinnipeds, where ovulation and even early term reproductive rates appear to remain high, intrauterine mortality and late-term abortion appears to be an important mechanism to avoid the high costs of lactation when female stored energy reserves are low (Testa, 1987; Fay *et al.*, 1989; Stenson *et al.*, 2016). At high densities, reproduction is likely to be relatively more expensive for NWA harp seals, underlining the importance of females being able to access high energy capelin during the winter foraging period to build-up condition prior to pupping. A complex relationship between condition and the timing of ice-breakup likely also affects food resources and the female's ability to rebuild energy stores prior to moulting. Temporal variation that impacts the availability and duration of reliance on a key resource will increase the role of density in

regulating the population (Wang *et al.*, 2006, 2013) by increasing the frequency of large mismatches between population size and food resources (Chamaillé-Jammes *et al.*, 2008; Hempson *et al.*, 2015). Among ungulates, greater temporal variability of the key resource will also reduce mean population size, because populations decline more rapidly in poor years than they can recover in good years (Illius and O'Connor, 2000; Davis *et al.*, 2002). Currently, the NWA harp seal population is at the highest levels seen in over a century (Hammill *et al.*, 2011). An increase in environmental variability, which might be expected under climate change, will likely affect individual growth and condition of harp seals which will in turn affect demographic rates such as reproduction and survival.

## Supplementary data

Supplementary material 1 is available at the ICESJMS online version of the manuscript for detailed list of candidate models considered in the model selection procedure performed in this study.

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