

Demographic, ecological and physiological responses of ringed seals to an abrupt decline in sea ice availability

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To assess whether demographic declines of Arctic species at the southern limit of their range will be gradual or punctuated, we compared large-scale environmental patterns including sea ice dynamics to ringed seal (*Pusa hispida*) reproduction, body condition, recruitment, and stress in Hudson Bay from 2003-2013. Aerial surveys suggested a gradual decline in seal density from 1995-2013, with the lowest density occurring in 2013. Body condition decreased and stress (cortisol) increased over time in relation to longer open water periods. The 2010 open water period in Hudson Bay coincided with extremes in large-scale atmospheric patterns (NAO, AO, ENSO) resulting in the earliest spring breakup and the latest ice formation on record. The warming event was coincident with the highest stress levels and the lowest recorded ovulation rate and low pregnancy rate, few pups in the Inuit harvest, and observations of sick seals. We conclude that although negative demographic responses of Hudson Bay seals are occurring gradually with diminishing sea ice, a recent episodic environmental event played a significant role in a punctuated population decline.

14 ABSTRACT

15 To assess whether demographic declines of Arctic species at the southern limit of their
16 range will be gradual or punctuated, we compared large-scale environmental patterns
17 including sea ice dynamics to ringed seal (*Pusa hispida*) reproduction, body condition,
18 recruitment, and stress in Hudson Bay from 2003-2013. Aerial surveys suggested a gradual
19 decline in seal density from 1995-2013, with the lowest density occurring in 2013. Body
20 condition decreased and stress (cortisol) increased over time in relation to longer open
21 water periods. The 2010 open water period in Hudson Bay coincided with extremes in
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24 stress levels and the lowest recorded ovulation rate and low pregnancy rate, few pups in
25 the Inuit harvest, and observations of sick seals. We conclude that although negative
26 demographic responses of Hudson Bay seals are occurring gradually with diminishing sea
27 ice, a recent episodic environmental event played a significant role in a punctuated
28 population decline.

29 Subjects: Animal population, Climate change

30 Keywords: abundance, body condition, disease, Hudson Bay, *Pusa hispida*, sea ice

31

32 BACKGROUND

33 Organisms evolve specific adaptations to their habitats through natural selection (Mayr
34 1963) and when their habitats change gradually, organisms can adjust phenotypically
35 within an evolved range of flexibility (Levins 1968). However, this evolved adaptation has
36 limitations and in extreme situations, organisms may not be able to adapt to particular
37 habitats and environmental conditions above an evolved threshold (Southwood 1977).
38 Under these circumstances, populations suffer demographic mortality of individuals
39 and/or immigrate to new habitats that may allow increased demographic success
40 (MacArthur and Wilson 1966). The result is a shift in species distribution (Guisan and
41 Thuiller 2005) and understanding this process by identifying thresholds to adaptability
42 and the demographic mechanism of population decline are both critical to species
43 conservation.

44 Predicting how climate warming will result in retraction of an Arctic species range
45 northward requires knowledge of demographic changes and their ecological plasticity in
46 response to environmental change. Few studies have linked marine mammal demographic
47 responses to climate change (Poloczanska et al. 2007) with the notable exception of
48 ringed seals (Meier et al. 2004, Post et al. 2009), where the majority of research results
49 reflect changes in foraging behaviour (Young and Ferguson 2014, Hamilton et al. 2015).
50 Ringed seals (*Pusa hispida*) have a circumpolar distribution and show high variability in the
51 relative importance of predation from polar bears (*Ursus maritimus*) (Thiemann et al.
52 2008) and to varying food habits (Yurkowski et al. 2016a). However, key habitat attributes
53 are linked to survival and successful reproduction. In particular, ringed seals require sea

54 ice during the critical spring period when reproduction and molting occurs (Smith &
55 Stirling 1975) and a seasonal pulse in food availability in the summer ice-free season
56 (Young & Ferguson 2013). Evolved life history characteristics that match these high-
57 latitude environmental features include relative small body size for a pinniped and a life
58 history characterized by early age of maturation, annual birthing, short lactation duration,
59 widely varying but high pup mortality, relatively low adult mortality, and greater fitness
60 investment in long life (Ferguson & Higdon 2006).

61 High latitude species are characterized by a strong seasonal cycle of feast and fast
62 with both periods critical to reproduction and survival. Ringed seals are adapted to cycle
63 annually from intensive foraging during the open water season to accumulate fat reserves
64 to sustain them over winter and during the birthing, nursing, and mating periods when
65 adults are restricted to small home ranges with depleted food resources. In spring, pups
66 are independent and adults undergo molting with little feeding opportunities and
67 increased risk of predation (Young and Ferguson 2015). During periods of deteriorating
68 environmental conditions, the phenology of ringed seals can be interrupted leading to
69 inadequate energy reserves prior to the next year's reproduction. Ringed seal populations
70 can also be negatively affected by infrequent, annual, extreme climatic conditions that exert
71 pressure on their demographics.

72 Endemic Arctic species are challenged by the rapid pace of sea ice declines and
73 resulting changes in ecological dynamics of the marine ecosystem (Post et al. 2013).
74 Southern Hudson Bay represents one of the most southerly distributions of ringed seals
75 and therefore, as an ice-obligate marine mammal, the prediction is for a retraction

76 northward in range from the southern edges of their distribution (Kovacs & Lydersen
77 2008). The initial characteristics of population and demographic changes may already be
78 occurring with a decrease in ringed seal density observed in western Hudson Bay between
79 the two recent aerial surveys in spring 2010 and 2013 (0.78 to 0.20/km²) (Young et al.
80 2015).

81 Here, we assess whether a 2010 extreme climatic event was another year in a long-
82 term declining trend for Hudson Bay or an infrequent episodic event that impacted ringed
83 seal demography, body condition, and reproduction. Our objective was to compare annual
84 trends in sea ice breakup and formation and the influence of major climatic indices to
85 biological data from seal collections, 2003-13 that include (1) body fat from seals harvested
86 by Inuit, (2) reproduction from examination of reproductive tracts, (3) recruitment from
87 hunter harvest statistics, and (4) stress from blubber cortisol levels. We hypothesize that
88 gradual deteriorating change in sea ice characteristics will correlate with a gradual
89 decrease in ringed seal body condition, ovulation rate and pup recruitment, whereas an
90 abrupt decline in sea ice availability in 2010 will result in dramatic negative demographic,
91 ecological and physiological responses by ringed seals.

92 METHODS

93 Sea ice breakup and freeze-up dates were determined from weekly data obtained from the
94 Canadian Ice Service using Icegraph 2.0 (<http://iceweb1.cis.ec.gc.ca/IceGraph/>), for
95 eastern Hudson Bay, 1979-2014. For a given region, ice breakup date was defined as the
96 date on which the sea ice concentration decreased and remained below 50% (Stirling et al.
97 1999). Conversely, freeze-up date was defined as the date on which sea ice concentration

98 increased and remained above 50%. Major climatic indices were obtained from the Climate
99 Prediction Center (<http://www.cpc.ncep.noaa.gov/>), including the Arctic Oscillation (AO),
100 the North Atlantic Oscillation (NAO), and El Nino-Southern Oscillation (ENSO) for the
101 December to February monthly mean estimates from 1971-2014. We included ENSO due to
102 its significant climatic influence in North America and due to its effect on ecological
103 relationships in several ecosystems across the globe (Wang et al. 2010; Nye et al. 2014;
104 Rustic et al. 2015). The longer time frame available for environmental data provided a
105 background to the 2003-2013 period with available ringed seal biological data.

106 Morphological measurements and tissue samples were collected from 926 Hudson Bay
107 ringed seals harvested during the Inuit subsistence hunt from Sanikiluaq, NU, Canada
108 ($56^{\circ}32'34''$ N, $79^{\circ} 13' 30''$ W) and Arviat, NU ($61^{\circ} 6' 29''$ N, $94^{\circ} 3' 25''$ W) from 2003-2013
109 in autumn when age/sex composition is considered representative of the population (Holst
110 et al. 1999). Permits to collect samples as part of the Inuit subsistence hunts were acquired
111 from Fisheries and Oceans Canada. Canine teeth were extracted from the lower jaw for age
112 determination using annual growth layer groups in the cementum (Chambellant and
113 Ferguson 2009). Reproductive tracts were stored frozen before being examined. After
114 gross examination of reproductive tracts, ovaries were excised, formalin-fixed and
115 sectioned at 2-mm intervals, and examined macroscopically for the presence of a corpus
116 luteum (ovulation in the year of collection) and corpora albicantia (previous pregnancies)
117 (Laws 1956). Pup survival was defined as the percentage of pups (i.e., <1 year) in the
118 autumn subsistence hunt and is considered a good measure of 0-6 month survival
119 (Chambellant et al. 2012). An extraction method for ringed seal blubber samples was used

120 in conjunction with radioimmunoassay to measure cortisol levels representing stress
121 (Trana et al. 2014).

122 Four separate general linear models were used to investigate relationships between
123 environmental (i.e. duration of the open water period, ENSO, NAO and AO indices) and
124 biological variables (i.e. percentage of ovulating females, percentage of pups in the harvest,
125 body condition and cortisol levels) over time using R v 3.2.3 (R Core Team 2015).
126 Continuous predictor variables were screened for collinearity and removed when a
127 Pearson's correlation coefficient was ≥ 0.6 and a variance inflation factor (VIF) was > 3.0 .
128 NAO was highly correlated with AO (0.8), thus was removed from all analyses. Prior to
129 analysis, percentage of ovulating females, percentage of pups in harvest, and body
130 condition were normally distributed upon visual examination of histograms and quantile-
131 quantile plots. Cortisol levels were log-transformed before analysis to improve normality.

132 RESULTS

133 Results support a gradual pattern of earlier spring ice breakup and later autumn freeze-up
134 in Hudson Bay; where from 2003-2013, sea ice breakup has varied more widely than
135 freeze-up. No relationship occurred with any climate variability index over 1979-2014, but
136 the NAO and AO have been more positive from 1999-2015 (Fig. 1). The longest ice-free
137 season on record for eastern Hudson Bay occurred in 2010, with the earliest spring
138 breakup (May) and latest freeze-up (January 2011) and an anomalous negative NAO and
139 AO, and a high ENSO index (Fig. 1).

140 Body condition significantly decreased over time ($t = -8.2$, $p < 0.001$), from about
141 55% blubber mass in 2004 to approximately 45% in 2011 (Fig. 2). In addition, body

142 condition significantly decreased with increasing open water period ($t = -2.0$, $p < 0.05$),
143 ENSO index ($t = -2.3$, $p = 0.02$) and NAO index ($t = -2.0$, $p < 0.05$; Table 1; Fig. 3). Ovulation
144 rate varied considerably among years from 100% in 2008 to 56% in 2011, albeit with no
145 relationship with year, open water duration, or climatic indices. Percentage of pups in the
146 harvest, as an estimate of pup survival, exhibited a marginal decline from 2003-2013 ($t = -$
147 2.09 , $p = 0.08$) from about 40% of the harvest to about 20% (Table 1; Fig. 2). Stress, as
148 measured by cortisol concentration (ng/g), significantly increased over time ($t = 8.0$, $p <$
149 0.001) from about 0.1 to 0.6ng/g over the 2003-12 period (Table 1; Fig. 2). A significant
150 decrease in cortisol level occurred with NAO index ($t = -2.6$, $p = 0.01$), whereas a marginally
151 significant increase occurred with ENSO index ($t = 1.93$, $p = 0.05$; Fig. 3). In 2010, cortisol
152 levels in ringed seals had the highest amount of variability (standard deviation = 1.84)
153 compared to other years (Fig. 2). The highest stress levels occurred in 2010, and the lowest
154 recorded ovulation rates occurred in 2011 which supports the pattern of a decrease in
155 ovulation rate after the record high stress levels.

156 DISCUSSION

157 We predicted demographic change occurring at the southern limit of the ringed seal
158 distribution with both gradual changes in environmental variables and episodic events
159 associated with extreme lows in sea ice concentration. Our results suggest both patterns
160 have occurred in southern Hudson Bay over the past decade. Previous research has
161 indicated that Hudson Bay ringed seals (Chambellant et al. 2012) and polar bears
162 (Derocher et al. 2004) have shown gradual reductions in body condition and survival over
163 the past decades which are concurrent with negative consequences of continued

164 environmental change (Holst et al. 1999; Ferguson et al. 2005). We provide additional
165 evidence for a continuation of these progressive patterns for ringed seals with decreasing
166 body condition and increasing stress over 2003-2013. However, no research results have
167 suggested short-temporal pulses in condition and abundance for either seals or polar bears
168 in the Hudson Bay ecosystem, although a regime shift likely occurred in late 1990s (Gaston
169 et al. 2012). Here, we document for the first time, a relationship with ringed seal
170 demographics and the 2010 climatic event that resulted in a punctuated decrease in
171 ovulation, reduced body condition, reduced seal pups in the following autumn harvest, and
172 increased cortisol levels.

173 Gradual reduction in body condition could be associated with the recent changes in
174 Hudson Bay prey resource abundance and availability. The prevalence of capelin (*Mallotus*
175 *villosus*) and sand lance (*Ammodytes spp.*) and decrease in Arctic cod (*Boreogadus saida*)
176 abundance in Hudson Bay since 2000 has caused dietary shifts from endemic Arctic cod to
177 sub-Arctic capelin and sand lance in Arctic marine megafauna including sea birds (Gaston
178 et al. 2003) and ringed seals (Chambellant et al. 2012). In addition, the isotopic niche size
179 of Hudson Bay ringed seals is significantly larger than individuals from higher latitudes
180 which principally consume Arctic cod, indicating a more diverse and omnivorous diet
181 (Young and Ferguson 2013; Yurkowski et al. 2016a, b). Among ringed seal prey items,
182 Arctic cod represent the highest energy content compared to other fish and invertebrate
183 species (Weslawski et al. 1994; Hedeholm et al. 2011) where its decreased consumption in
184 Hudson Bay ringed seal diet and temporal shifts in forage fish availability and abundance
185 may negatively impact ringed seal energetic demands and body condition.

186 Assessing the causes of an episodic event is more difficult. The extremely low extent
187 and duration of the 2010 ice-covered period in Hudson Bay may have adversely affected
188 the abundance, availability and distribution of prey resources but it is unlikely to have,
189 triggered a punctuated decrease in their physiological and energetic demands. We
190 summarized anecdotal evidence for an episodic event affecting the abundance and body
191 condition of ringed seals in Hudson Bay related in 2010-11 (see supplementary material).
192 Anecdotal observations in 2010 are suggestive of a hitherto never before seen event
193 causing impaired biological responses in ringed seal behaviour including unusual
194 approachability, lethargy, and increased tendency for hauling out on land, possibly due to
195 associated respiratory problems that were first seen during that autumn season. Polar
196 bears are thought to have benefited from this behavior since affected seals were easily
197 captured but no estimate of predation over and above normal could be calculated. Evidence
198 for a biological response to an episodic environmental event comes from the low ringed
199 seal density observed between spring 2010 and 2013 surveys and the unusual
200 environmental patterns that suggest a possible shift in seal condition after 2010 (Table 1).

201 An Unusual Mortality Event was declared in 2011 by the US government due to a
202 'new' ulcerative-dermatitis-disease-syndrome of unknown etiology observed in Alaskan ice
203 seals and Pacific walrus (Atwood et al. 2015). A large scale, trans-boundary,
204 interdisciplinary, disease-investigative team from Alaska, Chukotka, Northwest Territories
205 (NWT) and scientists (USA and internationally) found significant pathology of the lung,
206 liver, immune system, and skin of the seals (Barbosa et al. 2015, Bowen et al. 2015).
207 Hundreds of ice seals of all ages had been reported in Alaska (ringed, bearded (*Erignathus*
208 *barbatus*), spotted (*Phoca largha*), ribbon (*Histiophoca fasciata*) and Pacific walrus

209 (*Odobenus rosmarus*)), Chukotka (RU) (ice seals and walrus) and NWT (CA) (ice seals)
210 displaying a variety of skin associated lesions distributed around the eyes, snout, hind
211 flippers, tail, and trunk. As observed in Hudson Bay, the affected ice seals displayed
212 uncommon behaviours such as unusual approachability, lethargy, and increased tendency
213 for hauling out on land, as well as respiratory problems. There was some mortality
214 associated with the disease syndrome; however reliable baseline abundance estimates
215 were not available to assess its significance. Alaskans also reported seeing polar bears
216 preying upon affected seals, suggesting that this additional predation is widespread and
217 represent a significant cause of seal mortality. As of the summer of 2016 no cause of the
218 syndrome has yet been identified.

219 Potential repercussions of a gradual sea ice decline and punctuated decreases in
220 some years include a continual reduction in ringed seal body condition and greater stress
221 leading to implications on their demographics. The years marked by extremes in climatic
222 indices (Fig. 1) are associated at higher latitudes with excessive sea ice extremes; whereas
223 our results at the southern range of ringed seals indicate a lack of sea ice may have
224 attributed to decreased body condition, increased stress, and low ovulation rates and pup
225 recruitment. Spring 2010 recorded an unusually early ice breakup that may have
226 predisposed seals to a delayed molt. In the fall of 2010, numerous (100's) moribund seals
227 were found in distress along the shore of western Hudson Bay. Rising temperatures,
228 reduction of sea ice, reduction in body condition and the resulting stress are known to
229 increase the likelihood of disease outbreaks (Burek et al. 2008). Severity of enzootic
230 diseases can increase and new disease presentations are also likely (Burge et al. 2014) as
231 was seen in Hudson Bay ringed seals in 2010.

232 Numerous examples of episodic events causing major ecological shifts include
233 regime shifts (Hughes et al. 2013), continental growth (Santosh 2013), drought (Ireland et
234 al. 2012), disease (Pickles et al. 2013), and range shifts due to climate (Baker et al. 2008,
235 Seppä et al. 2009, Chen et al. 2011). For ringed seals, the literature suggests periods of
236 ringed seal crashes in abundance associated with poor reproduction during significant
237 heavy ice years. Variation in ringed seal density associated with ENSO events include 1973
238 (Smith and Stirling 1978), 1992 (Ferguson et al. 2005), 1998 (Smith and Harwood 2001),
239 and in 2010 (Fig. 1). Evidence of high latitude regime shifts include 1977 and 1989 (Hare
240 and Mantua 2000), 1998-99 (Litzow 2006, Benson and Trites 2002). Synchronous
241 fluctuations of seabird species across the entire Arctic and sub-Arctic regions were
242 associated with changes in sea surface temperatures that were linked to two climate shifts,
243 in 1977 and again in 1989 (Irons et al. 2008), and 1998 (Flint 2013), including Hudson Bay
244 in 1998 (Gaston et al. 2012). Major atmospheric patterns suggest that we can expect
245 episodic events occurring once every 10-15 years and that they are largely unpredictable in
246 timing but have major consequences on ecosystem structure and function (Ottersen et al.
247 2004).

248 CONCLUSIONS

249 Considerable uncertainties exist with deciphering past patterns to determine possible
250 cause and effect relationships among environmental variation, body condition, and their
251 demographic responses. However, mounting evidence indicates endemic Arctic species,
252 such as ringed seals, are under immense pressure from climate change and complex spatio-
253 temporal shifts in ecology have subsequently resulted in decreased abundance as a
254 harbinger of range shift. Managers need to be wary of climate change culminating in both a

255 gradual decline in condition and unpredictable episodic events that when combined can
256 have major abundance and distribution consequences.

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268 Competing Interests

269 The author's declare there are no competing interests.

270 Author Contributions

271 Steven H. Ferguson conceived and secured the funding for the project and wrote the first
272 draft. All authors contributed to the writing process. David J. Yurkowski and Brent G. Young
273 ran the statistical analysis and developed the figures. Randi Anderson ran the cortisol

274 experiment. Cornelia Willing conducted the reproductive assessments. Ole Nielsen worked
275 on the disease studies.

276 Animal Ethics

277 Permits to collect samples as part of the Inuit subsistence hunts were acquired from
278 Fisheries and Oceans Canada.

279 Data availability

280 Raw environmental data and a summary of observations associated with unusual seal
281 behaviour in 2010-11 is available as electronic supplementary material.

282 Supplemental Information

283 Supplemental information for this article can be found online at:

284 REFERENCES

285 Atwood, T., Peacock, E., Burek-Huntington, K., Shearn-Bochsler, V., Bodenstein, B., Beckmen,
286 K. and Durner, G., 2015. Prevalence and spatio-temporal variation of an alopecia
287 syndrome in polar bears (*Ursus maritimus*) of the southern Beaufort Sea. *Journal of*
288 *wildlife diseases*, 51(1), pp.48-59.

289 Baker, A.C., Glynn, P.W. and Riegl, B., 2008. Climate change and coral reef bleaching: An
290 ecological assessment of long-term impacts, recovery trends and future outlook.
291 *Estuarine, coastal and shelf science*, 80(4), pp.435-471.

292 Barbosa, L., Johnson, C.K., Lambourn, D.M., Gibson, A.K., Haman, K.H., Huggins, J.L., Sweeny,
293 A.R., Sundar, N., Raverty, S.A. and Grigg, M.E., 2015. A novel *Sarcocystis neurona*

- 294 genotype XIII is associated with severe encephalitis in an unexpectedly broad range
295 of marine mammals from the northeastern Pacific Ocean. *International journal for*
296 *parasitology*, 45(9), pp.595-603.
- 297 Benson, A.J. and Trites, A.W., 2002. Ecological effects of regime shifts in the Bering Sea and
298 eastern North Pacific Ocean. *Fish and Fisheries*, 3(2), pp.95-113.
- 299 Bowen, L., Miles, A.K., Stott, J., Waters, S. and Atwood, T., 2015. Enhanced biological
300 processes associated with alopecia in polar bears (*Ursus maritimus*). *Science of The*
301 *Total Environment*, 529, pp.114-120.
- 302 Burek KA, Gulland FM, O'Hara T. 2008 Effects of climate change on Arctic marine mammal
303 health. *Ecolog. Appl.* **18**(sp2): S126-34. (doi: 10.1890/06-0553.1)
- 304 Burge CA, Eakin CM, Friedman CS, Froelich B, Hershberger PK, Hofmann EE, Petes LE,
305 Prager KC, Weil E, Willis BL, Ford SE, C. Drew Harvell. 2014 Climate change
306 influences on marine infectious diseases: implications for management and society.
307 *Ann. Rev. Mar. Sci.* **6**: 249-277. (doi:10.1146/annurev-marine-010213-135029)
- 308 Chambellant, M. and S.H. Ferguson. 2009. Ageing live ringed seals (*Phoca hispida*): which 1
309 tooth to pull? *Marine Mammal Science* 25: 478-486. DOI: 10.1111/j.1748-
310 7692.2008.00269.x
- 311 Chambellant M, Stirling I, Gough WA, Ferguson SH. 2012 Temporal variations in Hudson
312 Bay ringed seal (*Phoca hispida*) life-history parameters in relation to environment. *J.*
313 *Mammal.* **93**, 267-281. (doi:10.1644/10-MAMM-A-253.1)

- 314 Chen, I.C., Hill, J.K., Ohlemüller, R., Roy, D.B. and Thomas, C.D., 2011. Rapid range shifts of
315 species associated with high levels of climate warming. *Science*, 333(6045),
316 pp.1024-1026.
- 317 Derocher AE, Lunn NJ, Stirling I. 2004 Polar bears in a warming climate. *Integr. Comp. Biol.*,
318 **44**, 163-176. (doi:10.1093/icb/44.2.163)
- 319 Ferguson SH, Stirling I, McLoughlin P. 2005 Climate change and ringed seal (*Phoca hispida*)
320 recruitment in western Hudson Bay. *Mar. Mamm. Sci.* **21**, 121 – 135.
321 (doi:10.1111/j.1748-7692.2005.tb01212.x)
- 322 Ferguson SH and Higdon JW. 2006 How seals divide up the world: environment, life-
323 history, and conservation. *Oecologia* **150**, 318-329. (doi:10.1007/s00442-006-0489-
324 x)
- 325 Flint, P.L., 2013. Changes in size and trends of North American sea duck populations
326 associated with North Pacific oceanic regime shifts. *Marine Biology*, 160(1), pp.59-
327 65.
- 328 Gaston, A.J., Woo, K. and Hipfner, J.M., 2003. Trends in forage fish populations in northern
329 Hudson Bay since 1981, as determined from the diet of nestling thick-billed murre
330 *Uria lomvia*. *Arctic*, pp.227-233.
- 331 Gaston AJ, Smith PA, Provencher JF. 2012 Discontinuous change in ice cover in Hudson Bay
332 in the 1990s and some consequences for marine birds and their prey. *ICES J. Mar.*
333 *Sci.* **69**, 1218 – 1225. (doi :10.1093/icesjms/fss040)
- 334 Guisan A. and W. Thuiller. 2005. Predicting species distribution: offering more than simple
335 habitat models. *Ecology Letters* 8: 993-1009.

- 336 Hamilton, C.D., Lydersen, C., Ims, R.A. and Kovacs, K.M., 2015. Predictions replaced by facts:
337 a keystone species' behavioural responses to declining arctic sea-ice. *Biology*
338 *Letters*, 11(11), p.20150803.
- 339 Hare SR, Mantua NJ. 2000 Empirical evidence for North Pacific regime shifts in 1977 and
340 1989. *Prog. Oceanog.* **47**, 103-145. (doi:10.1016/S0079-6611(00)00033-1)
- 341 Hedeholm, R., Grønkjær, P. and Rysgaard, S., 2011. Energy content and fecundity of capelin
342 (*Mallotus villosus*) along a 1,500-km latitudinal gradient. *Marine biology*, 158(6),
343 pp.1319-1330.
- 344 Holst M, Stirling I, Calvert W. 1999 Age structure and reproductive rates of ringed seals
345 (*Phoca hispida*) on the northwestern coast of Hudson Bay in 1991 and 1992. *Mar.*
346 *Mamm. Sci.* **15**, 1357–1364. (doi:10.1111/j.1748-7692.1999.tb00898.x)
- 347 Hughes, T.P., Linares, C., Dakos, V., van de Leemput, I.A. and van Nes, E.H., 2013. Living
348 dangerously on borrowed time during slow, unrecognized regime shifts. *Trends in*
349 *ecology & evolution*, 28(3), pp.149-155.
- 350 Ireland, A.W., Booth, R.K., Hotchkiss, S.C. and Schmitz, J.E., 2012. Drought as a trigger for
351 rapid state shifts in kettle ecosystems: Implications for ecosystem responses to
352 climate change. *Wetlands*, 32(6), pp.989-1000.
- 353 Irons, D.B., Anker-Nilssen, T.Y.C.H.O., Gaston, A.J., Byrd, G.V., Falk, K., Gilchrist, G., Hario, M.,
354 Hjernquist, M., Krasnov, Y.V., Mosbech, A. and Olsen, B., 2008. Fluctuations in
355 circumpolar seabird populations linked to climate oscillations. *Global Change*
356 *Biology*, 14(7), pp.1455-1463.

- 357 Kovacs KM, Lydersen C, 2008 Climate change impacts on seals and whales in the North
358 Atlantic Arctic and adjacent shelf seas. *Sci. Prog.* **91**, 117–150.
- 359 Laws RM. 1956 Growth and sexual maturity in aquatic mammals. *Nat.* **178**, 193–194.
360 (doi:10.1038/178193a0)
- 361 Levins, R., 1962. Theory of fitness in a heterogeneous environment - I. The fitness set and
362 adaptive function. *Am. Nat.* **96**, 361–373.
- 363 Litzow MA. 2006 Climate regime shifts and community reorganization in the Gulf of Alaska:
364 how do recent shifts compare with 1976/1977? *ICES J. Mar. Sci.* **63**, 1386-1396. (doi:
365 10.1016/j.icesjms.2006.06.003)
- 366 MacArthur, R. H. & Wilson, E. O. 1967. *The Theory of Island Biogeography*. Princeton Univ.
367 Press, Princeton.
- 368 Mayr, E. 1963. *Animal species and evolution*. Belknap Press, Harvard Univ. Press,
369 Cambridge, Mass.
- 370 Meier, H.E.M., Döscher, R. and Halkka, A., 2004. Simulated distributions of Baltic Sea-ice in
371 warming climate and consequences for the winter habitat of the Baltic ringed seal.
372 *AMBIO: A Journal of the Human Environment*, **33**(4), pp.249-256.
- 373 Nye, J.A., Baker, M.R., Bell, R., Kenny, A., Kilbourne, K.H., Friedland, K.D., Martino, E.,
374 Stachura, M.M., Van Houtan, K.S. and Wood, R., 2014. Ecosystem effects of the
375 atlantic multidecadal oscillation. *Journal of Marine Systems*, **133**, pp.103-116.

- 376 Ottersen, G., Stenseth, N.C. and Hurrell, J.W., 2004. Climatic fluctuations and marine
377 systems: a general introduction to the ecological effects. *Marine ecosystems and*
378 *climate variation*, pp.3-14.
- 379 Pickles, R.S., Thornton, D., Feldman, R., Marques, A. and Murray, D.L., 2013. Predicting shifts
380 in parasite distribution with climate change: a multitrophic level approach. *Global*
381 *change biology*, 19(9), pp.2645-2654.
- 382 Poloczanska, E.S., Babcock, R.C., Butler, A., Hobday, A.J., Hoegh-Guldberg, O., Kunz, T.J.,
383 Matear, R., Milton, D., Okey, T.A. and Richardson, A.J., 2007. Climate change and
384 Australian marine life. *Oceanography and marine biology*, 45, p.407.
- 385 Post, E., Forchhammer, M.C., Bret-Harte, M.S., Callaghan, T.V., Christensen, T.R., Elberling, B.,
386 Fox, A.D., Gilg, O., Hik, D.S., Høye, T.T. and Ims, R.A., 2009. Ecological dynamics across
387 the Arctic associated with recent climate change. *Science*, 325(5946), pp.1355-1358.
- 388 Post E, Bhatt US, Bitz CM, Brodie JF, Fulton TL, Hebblewhite M, Kerby J, Kutz SJ, Stirling I,
389 Walker DA. 2013 Ecological consequences of sea-ice decline. *Science* **341**, 519-24.
390 (doi:10.1126/science.1235225)
- 391 Rustic, G.T., Koutavas, A., Marchitto, T.M. and Linsley, B.K., 2015. Dynamical excitation of
392 the tropical Pacific Ocean and ENSO variability by Little Ice Age cooling. *Science*,
393 350(6267), pp.1537-1541.
- 394 Santosh, M., 2013. Evolution of continents, cratons and supercontinents: building the
395 habitable Earth. *Current Science(Bangalore)*, 104(7), pp.871-879.

- 396 Seppä, H., Alenius, T., Bradshaw, R.H., Giesecke, T., Heikkilä, M. and Muukkonen, P., 2009.
397 Invasion of Norway spruce (*Picea abies*) and the rise of the boreal ecosystem in
398 Fennoscandia. *Journal of Ecology*, 97(4), pp.629-640.
- 399 Smith TG, Harwood LA. 2001 Observations of neonate ringed seals, *Phoca hispida*, after
400 early break-up of the sea ice in Prince Albert Sound, Northwest Territories, Canada,
401 spring 1998. *Pol. Biol.* **24**, 215-219. (doi:10.1007/s003000000198)
- 402 Smith TJ, Stirling I. 1975 The breeding habitat of the ringed seal (*Phoca hispida*). The birth
403 lair and associated structures. *Can. J. Zool.* **53**, 1297-1305. (doi:10.1139/cjz-2012-
404 0137)
- 405 Smith TG, Stirling I. 1978 Variation in the density of ringed seal (*Phoca hispida*) birth lairs
406 in the Amundsen Gulf, Northwest Territories. *Can. J. Zool.*, **56**, 1066-1070.
407 (doi:10.1139/z78-149)
- 408 Southwood, T.R.E. 1977. Habitat, the templet for ecological strategies? *J Anim Ecol* 46:337-
409 365
- 410 Stirling, I., N. J. Lunn and J. Iacozza. 1999. Long-term trends in the population ecology of
411 polar bears in western Hudson Bay in relation to climatic change. *Arctic* 52:294-
412 306.
- 413 Thiemann GW, Iverson SJ, Stirling I. 2008 Polar bear diets and arctic marine food webs:
414 insights from fatty acid analysis. *Ecolog. Monogr.* **78**, 591-613. (doi:10.1890/07-
415 1050.1)

- 416 Trana MR, Roth JD, Tomy GT, Anderson WG, Ferguson SH. 2014 Influence of sample
417 degradation and tissue depth on blubber cortisol in beluga whales. *J. Exper. Mar.*
418 *Biol. Ecol.* **462**, 8-13. (doi:10.1016/j.jembe.2014.10.010)
- 419 Wang, J., Bai, X., Leshkevich, G., Colton, M., Clites, A. and Lofgren, B., 2010. Severe ice cover
420 on Great Lakes during winter 2008–2009. *Eos*, 91(5), pp.41-42.
- 421 Weslawski, J.M., 1994. Diet of ringed seals (*Phoca hispida*) in a fjord of West Svalbard.
422 *Arctic*, 47(2), p.109.
- 423 Young BG, Ferguson SH. 2013 Seasons of the ringed seal: pelagic open-water hyperphagy,
424 benthic feeding over winter and spring fasting during molt. *Wildl. Res.* **40**, 52-60.
425 (doi:10.1071/WR12168)
- 426 Young, B.G. and Ferguson, S.H., 2014. Using stable isotopes to understand changes in ringed
427 seal foraging ecology as a response to a warming environment. *Marine Mammal*
428 *Science*, 30(2), pp.706-725.
- 429 Young BG, Ferguson SH, Lunn NJ. 2015 Variation in indices of ringed seal density and
430 abundance in western Hudson Bay determined from aerial surveys, 1995 to 2013.
431 *Arctic* **68**, 301-309. (doi:10.1111/j.1748-7692.2005.tb01212.x)
- 432 Yurkowski DJ, Ferguson SH, Semeniuk CAD, Brown TM, Muir DC, Fisk AT. 2016a. Spatial
433 and temporal variation of an ice-adapted predator's feeding ecology in a changing
434 Arctic marine ecosystem. *Oecologia* 180:631-644. (doi:10.1007/s00442-015-3384-
435 5)
- 436 Yurkowski DJ, Ferguson SH, Choy E, Loseto L, Brown TM, Muir DCG, Semeniuk CAD, Fisk
437 AT. 2016b. Latitudinal variation in ecological opportunity and intra-specific competition

438 indicates differences in niche variability and diet specialization of Arctic marine
439 predators. Ecology and Evolution 6:1666-1678
440

441 Table 1. Relationships between Hudson Bay ringed seal biological parameters and
 442 environmental correlates assessed using general linear models, 2003-2013.

Covariates	Ovulation rate (%)	Pup recruitment (%)	Seal condition (blubber %)	Cortisol (ng/g)
Intercept	-48.00 ± 69.51	60.03 ± 28.56 ^a	23.82 ± 2.85***	-34.90 ± 43.48***
Year	0.02 ± 0.03	-0.03 ± 0.01 ^a	-0.01 ± 0.001***	0.002 ± 0.0002***
Ice-free period (days)	0.0003 ± 0.006	0.0008 ± 0.002	-0.0004 ± 0.0002*	0.00003 ± 0.0005
El-Niño Southern Oscillation	0.004 ± 0.01	-0.02 ± 0.05	-0.009 ± 0.004*	0.001 ± 0.006 ^b
North Atlantic Oscillation	0.011 ± 0.012	-0.0008 ± 0.05	-0.009 ± 0.005*	-0.02 ± 0.007 *

^a = 0.08; ^b = 0.055; * P < 0.05; ** P < 0.01; *** P < 0.001

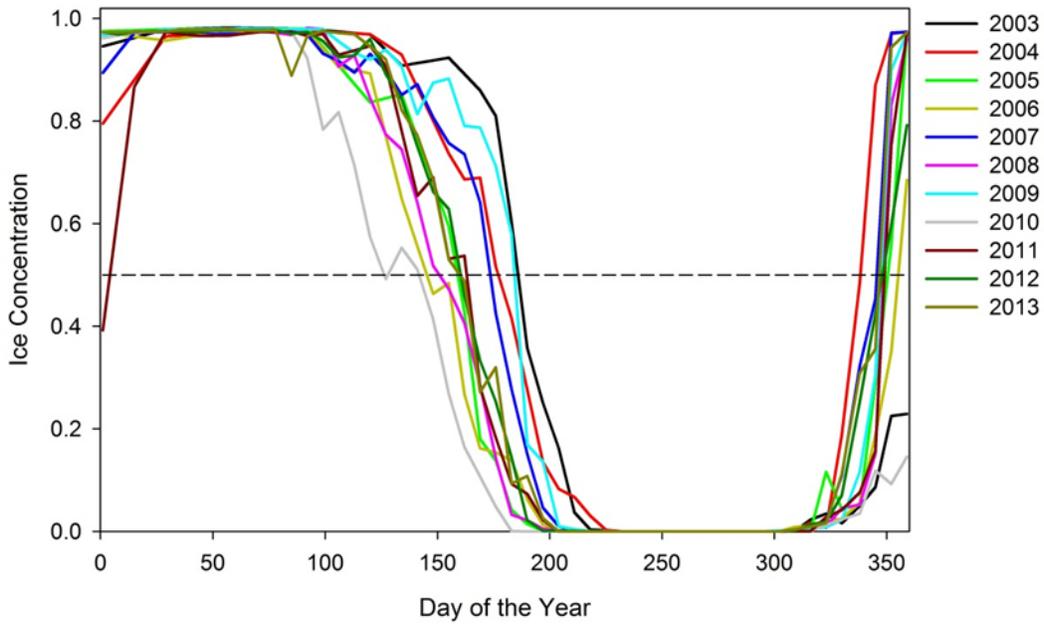
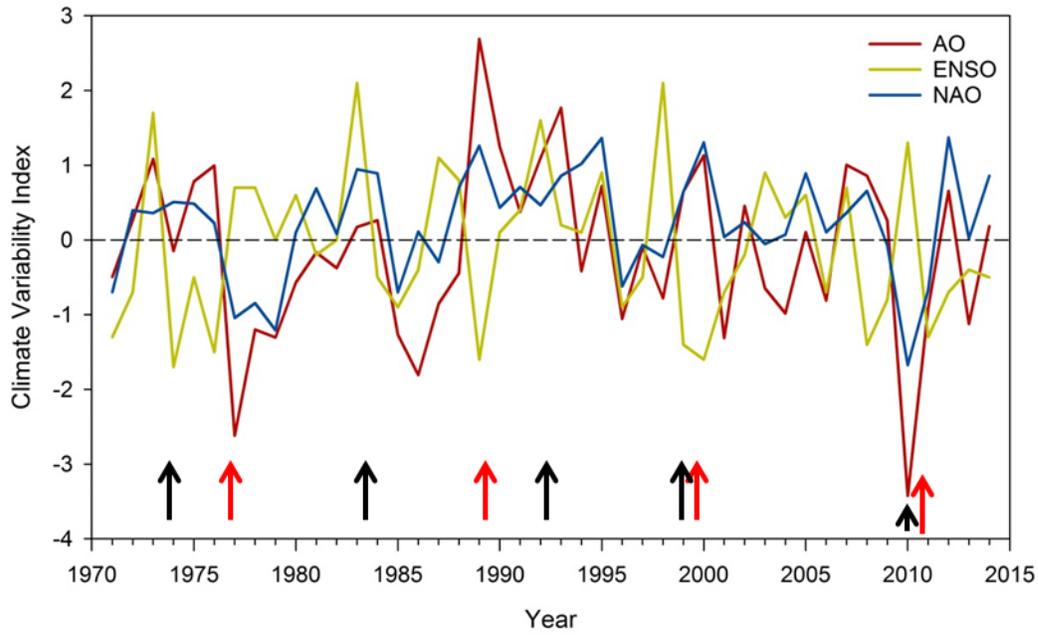
R² was 0.40 for ovulation rate model, 0.46 for pup recruitment model, 0.09 for body condition model, and 0.21 for cortisol level model.

443

444

445 Figure 1. Top: Annual winter (December to February) North Atlantic Oscillation index
446 (NAO), Arctic Oscillation (AO), and El Nino-Southern Oscillation (ENSO), 1971-2014. Note
447 red arrows indicate possible regime shifts (1977, 1989, 1989/99, 2010) and black arrows
448 possible years with poor ringed seal condition: 1973/74, 1983, 1992, 1998, 2010. Bottom:
449 Sea ice patterns over the day of the year showing inter-annual variation in timing of spring
450 breakup, duration of open water season, and time of freeze-up, 2003-2013. Note that
451 autumn 2010 freeze-up did not occur until January 2011.

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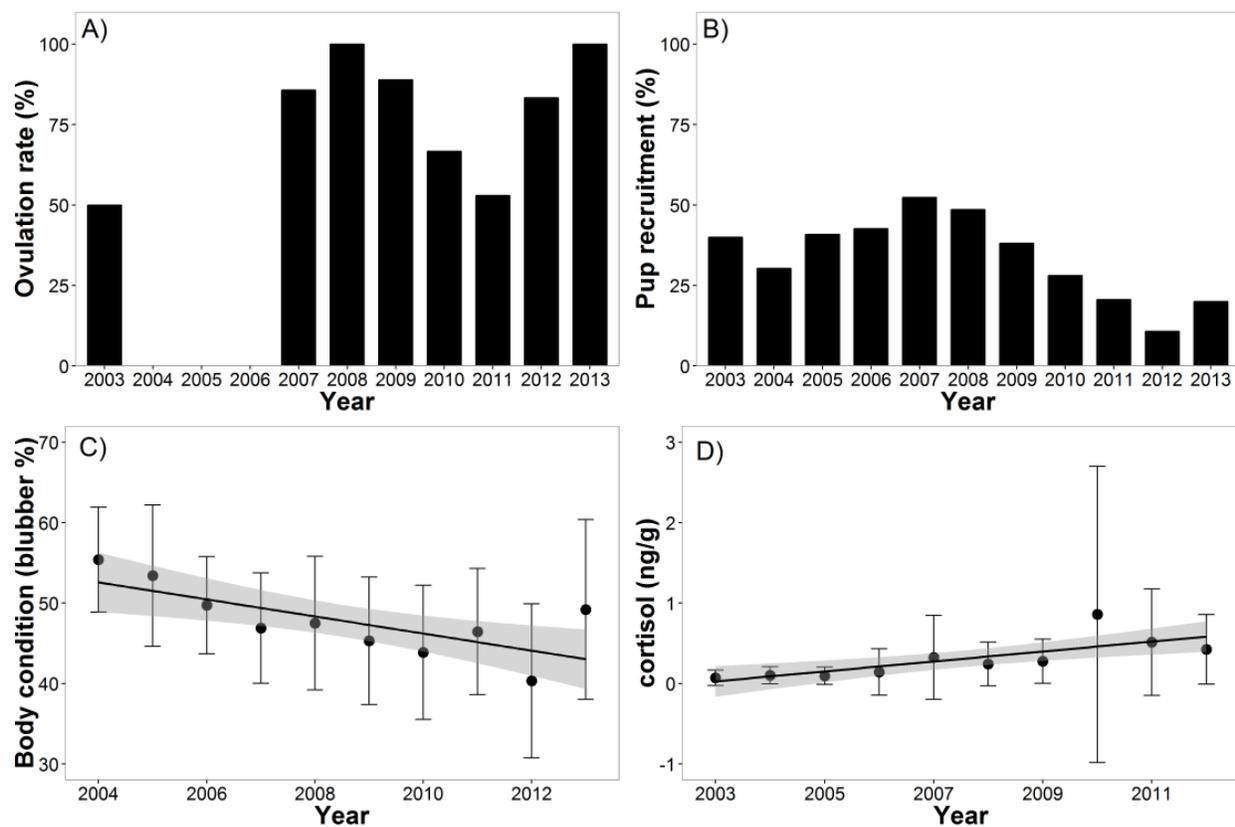


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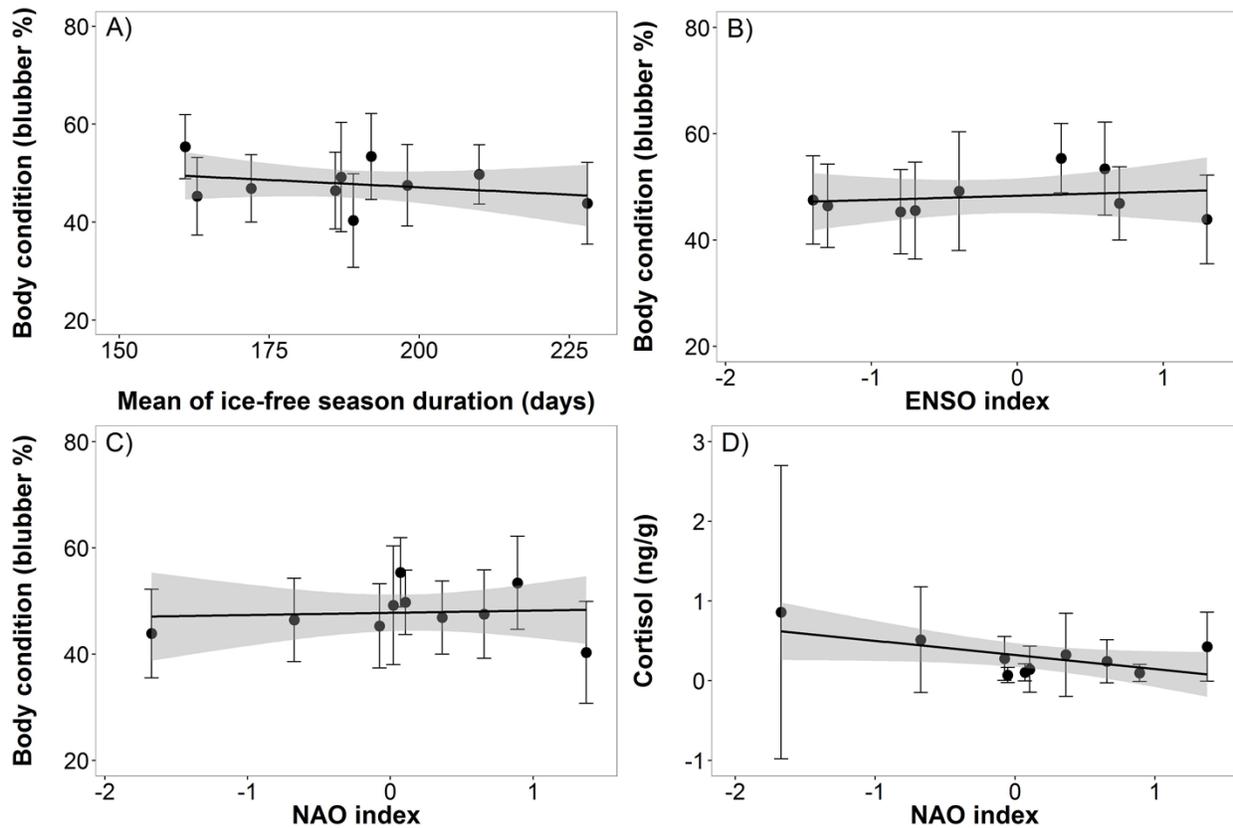
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456 Figure 2. Barplots (A and B) of annual ovulation rates (%) from adult females and annual
457 percentage of pups in the harvest. Linear regressions between ringed seal body condition
458 and harvest year (C; slope = -0.01, $t = -8.2$, $p < 0.001$), and cortisol level and harvest year (D;
459 slope = 0.02, $t = 8.0$, $p < 0.001$). Sample sizes (n) by year: 2003 (115), 2004 (56), 2005 (88),
460 2006 (82), 2007 (126), 2008 (105), 2009 (51), 2010 (96), 2011 (97), 2012 (65) and 2013
461 (45).



462

463 Figure 3. Linear regressions between ringed seal body condition and ice-free duration (A;
464 slope = -0.0004, $t = -2.0$, $p < 0.05$), body condition and El-Nino Southern Oscillation (ENSO)
465 index (B; slope = -0.009, $t = -2.32$, $p = 0.02$), body condition and North Atlantic Oscillation
466 (NAO) index (C; slope = -0.009, $t = 2.0$, $p < 0.05$), and cortisol and NAO index (D; slope = -
467 0.02, $t = 2.6$, $p = 0.01$).



468

469

470 Supplementary Table1. 1971-2014 NAO, AO, ENSO, and eastern Hudson Bay breakup and
 471 freeze-up from 1979 to 2014.

Year	AO	ENSO	NAO	Breakup	Freeze-up	
1971	-0.49459		-1.3	-0.69667		
1972	0.264983		-0.7	0.396667		
1973	1.08517		1.7	0.36		
1974	-0.1462		-1.7	0.506667		
1975	0.781803		-0.5	0.486667		
1976	0.993478		-1.5	0.226667		
1977	-2.6173		0.7	-1.04333		
1978	-1.20007		0.7	-0.84667		
1979	-1.30322		0	-1.20667	166	340
1980	-0.56821		0.6	0.1	163	335
1981	-0.16841		-0.2	0.69	191	337
1982	-0.37507		0	0.08	164	334
1983	0.17346		2.1	0.946667	171	339
1984	0.262857		-0.5	0.89	156	328
1985	-1.2665		-0.9	-0.7	151	333
1986	-1.80645		-0.4	0.11	185	326
1987	-0.85368		1.1	-0.29667	180	345
1988	-0.44515		0.8	0.7	154	342
1989	2.688033		-1.6	1.26	180	334
1990	1.252883		0.1	0.433333	180	335
1991	0.374647		0.4	0.706667	174	336
1992	1.094977		1.6	0.466667	181	329

1993	1.768833	0.2	0.856667	169	328
1994	-0.41784	0.1	1.02	180	348
1995	0.722987	0.9	1.363333	173	334
1996	-1.05476	-0.9	-0.62	184	357
1997	-0.09629	-0.5	-0.06667	164	330
1998	-0.7783	2.1	-0.22667	159	352
1999	0.648627	-1.4	0.643333	146	350
2000	1.1297	-1.6	1.303333	157	351
2001	-1.31188	-0.7	0.04	150	361
2002	0.454133	-0.2	0.236667	171	338
2003	-0.64532	0.9	-0.05333	185	362
2004	-0.98303	0.3	0.07	177	338
2005	0.105223	0.6	0.89	158	350
2006	-0.81005	-0.7	0.104837	145	355
2007	1.002867	0.7	0.36307	173	345
2008	0.859387	-1.4	0.6561	150	348
2009	0.25841	-0.8	-0.07584	184	347
2010	-3.42177	1.3	-1.67293	141	369
2011	-0.9129	-1.3	-0.67427	163	349
2012	0.654935	-0.7	1.371767	159	348
2013	-1.12184	-0.4	0.02096	159	346
2014	0.183305	-0.5	0.85704	168	341

473 Supplementary Table2. Chronology of unusual ringed seal and polar bear observations
 474 gathered from Hudson Bay communities related to a warming event in 2010.

Date	Comment	Reporter
4 Nov. 2010	I've only seen about 3 kills in the 11 years I've worked for you guys and now 7 in a month?	Marc Hebert, Manitoba Conservation Officer
14 Nov. 2010	He has also seen quite a few seals and seal kills by Polar Bears. He also flew over Button Bay and saw a number of seal kills that hadn't been consumed.	Mike Macri (Sea North Tours, Churchill)
16 Nov. 2010	He states that seals are venturing inland than normal. Bears are eating seals. The only physical problems or abnormalities he notes he has seen is one seal that appeared to be bleeding from the anus. Sick seals -- showing evidence of hair loss.	Amanda Currie (DFO) conversation with Donnie (Great White Bear tours).
16 Nov. 2010	Recently found a seal that was still alive but crawling over land near the Rx road just out of the Town of Churchill.	LeeAnn Fishback (CNSC) with Manitoba Conservation
17 Nov. 2010	First Vince had heard of dead seals. But noted Darryl Hedman flew coast and saw over 300 bears - saw 18 dead seals that had been killed so he says by bears - when I	Ole Nielson (DFO Science) with Vince Crichton (Manitoba

asked him how the bears were catching seals he said they Conservation
 are likely getting caught on the flats when tide goes out Manager, Game Fur &
 and bears just taking advantage of easy meal - maybe Problem Wildlife)
 something wrong with seals that they are getting caught
 like this.

18 Nov. They both confirm they've have been no reports of any Tara Bortoluzzi (DFO
 2010 killer whale sightings in the area, as its too late in the Science) spoke with
 seasons for Killer Whales. Also the local polar bears are Mike Macri and Bob
 also very fat, and several appear to be 'stock piling' the Windsor
 seals they catch (i.e. some people have witness and (Conservation Officer
 photographed the bears stock piling or buried seals in Churchill)
 inland instead of eating them). Mike was on a flight a
 week ago and saw a fat polar bear kill a seal, walk away
 and kill another seal on the shore, drag it back to the first,
 and then walk away without eating either. And another
 sow with cubs had a dead seal and was not eating it.
 Another seal was seen moving along RX road about 1-2
 km from shore. Received two pictures of this from Mike
 Macri.

24 Nov. I met two hunters from Chesterfield Inlet and Whale Cove Ole Nielsen (DFO)
 2010 in the Iqaluit airport on Monday that were also very
 concerned with the 'behavior' of ringed seals near their

communities this fall. I'm following up with them and several other HTOs. They reported that they are catching more adult seals this year which are really large, and very few pups. The seals are also very easy to catch, in many cases they said 'too easy'. One hunter caught 30 seals in one day trip. The seals are also coming inland and hanging around the shoreline for extended periods of time. Of course, it's great for hunting, but they were really concerned as this is very unusual.

- 26 Nov. 2010 Some of the Hunters and Trappers Organizations in the Kivalliq region have recently reported concerns with 'odd behaviour' of ringed seals near the communities (i.e. seals coming close to shore and hanging around, and hauling out on shore), as well as some seals that appears to be sick (i.e. molting and loss of hair, seal pocks, low fat content, etc.). Tara Bortoluzzi (DFO) Region communities
- 26 Nov. 2010 She has heard the same concerns from hunters: "After discussion with my board of directors, they have reported some hunters catching seals on shore, and far away from shore with loss of hair (like bald patches) but nobody took pictures and the seals were used as dog food." Leah Muckpah (Arviat HTO Manager)

- 27 Nov. 2010 He hasn't seen any more seals on shore, neither have the helicopters or tundra buggy camps. Also notes another odd thing, the zodiacs, for the first time ever, are covered with scratches from bearded seals who were hauling up into them in September. email from Mike Macri (Sea North Tours)
- 17 Dec. 2010 "A couple weeks ago while he was out of town, Lucassie Takatak, found 6 dead seals on the beach, their heads seem to be craving for air like their heads up back." Lucassie Arragutainaq (Secretary Manager Sanikiluaq HTO)
- 06 Jan. 2011 They observed a very few number of seals were shedding and that even a few number of them were sinking after being shot. The seal harvest in Arviat is usually done when the first ice forms in the salt water, usually late October to Late November. During that time, it is unheard of that seals would be shedding fur and that they would sink after being shot. reports from local hunters of Arviat
- 26 Jan. 2011 Ringed seals usually molt in the spring but locals noted seals molting in the fall. The local Conservation Officer sent seal parts to DFO showing the unusual molt. During fall large numbers (100s) of seals were observed along shorelines. Other communities including Repulse Bay also noted the same unusual conditions. Coral Harbour Ferguson phone conversation with Noah Nakoolak of Coral Harbour HTO

seldom sees seals near town but this past fall large numbers were in the Harbour and some went on land in the harbour (very unusual).

His own personal experience - he was traveling along shoreline in August and found a seal on the beach. The ringed seal kept traveling up the shore - unusual behaviour. Three weeks later he was in a different area and saw a harp seal on land - about ¼ mile inland. It was a late freeze up this autumn and a very warm fall. The ice formed along the shoreline twice in mid-November but drifted off with winds both times before it finally formed fast in December. In December rain fell.