

Ecology of ringed seals (*Phoca hispida*) in western Hudson Bay, Canada

by

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Abstract

Recently, Hudson Bay experienced unidirectional trends in temperature, sea-ice extent, time of break-up, and length of the open-water season. Predicted impacts on population dynamics of ice-associated species include habitat loss and shift in prey availability. The ringed seal (*Phoca hispida*) depends on a stable ice platform with sufficient snow depth and a productive open-water season for reproduction and survival. Evidence of ringed seal sensitivity to environmental variations has been reported, but mechanisms involved were poorly understood. In western Hudson Bay, density, life-history traits, and diet of ringed seals were monitored over two decades, providing an opportunity to understand the effects of climatic variations on the population dynamics of this long-lived carnivore. Ringed seal density was estimated through strip-transect analyses after aerial surveys were flown in western Hudson Bay in late spring during the annual moult in the 1990s and 2000s. During these periods, ringed seals were also sampled from Inuit subsistence fall harvests in Arviat, NU, and ages, reproductive status, percentage of pups in the harvest, body condition, and diet were assessed. Strong inter-annual variations in these parameters were observed, and a decadal cycle was suggested and related to variations in the sea-ice regime. The cold and heavy ice conditions that prevailed in western Hudson Bay in 1991-92 likely induced a decrease in pelagic productivity, reducing the availability to ringed seals of sand lances (*Ammodytes* sp.), their major prey. The nutritional stress endured, combined with a strong predation pressure, led to a decrease in ringed seal reproductive performances, pup survival, and density during the 1990s. The

recovery of ringed seal demographic parameters and number in the 2000s was associated with the immigration of pups, juveniles, and young adults into western Hudson Bay. Impact of current climatic trends on ringed seal population dynamics was not apparent, but considering the limited range of environmental variations tolerated by ringed seals, the response of this species to climate warming might be of a catastrophic type. Ringed seals were found to be good indicators of ecosystem changes, and long-term monitoring of the species in Hudson Bay should be a priority.

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Dedication

To my late grand-mother, my mom, and my partner, Sebastián Luque, who believe in me and give me the love, strength and support to succeed in all my life endeavours.

C'est le temps que tu as perdu pour ta rose qui fait ta rose si importante.

Antoine de Saint-Exupéry

He, who can no longer pause to wonder and stand rapt in awe, is as good as dead; his eyes are closed.

Albert Einstein

Y sobre todo, sean siempre capaces de sentir en lo más hondo cualquier injusticia cometida contra cualquiera en cualquier parte del mundo. Es la cualidad más linda de un revolucionario.

Ernesto Guevara

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Ga: gastropod; Hy: Hyperiidae; Ca: *Calanus* sp.; Eu: Euphasiidae; Mu: mussel (Bivalvia); Amp: amphipods (Amphipoda); Ech: starfish (Asteroidea); Gam: Gammaridae; Mys: Mysidae; SL: sand lances (*Ammodytes* sp.); Li: *Liparis* sp.; Ph: Pholidae; Sq: squid (Teuthida); Shr: shrimps (Decapoda); Sti: Stichidae; Cap: capelin (*Mallotus villosus*); Cot: Cottidae; Zo: Zoarcidae; Ag: Agonidae; Og: Greenland cod (*Gadus ogac*); AC: arctic cod (*Boreogadus saida*).

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Chapter 1

Introduction



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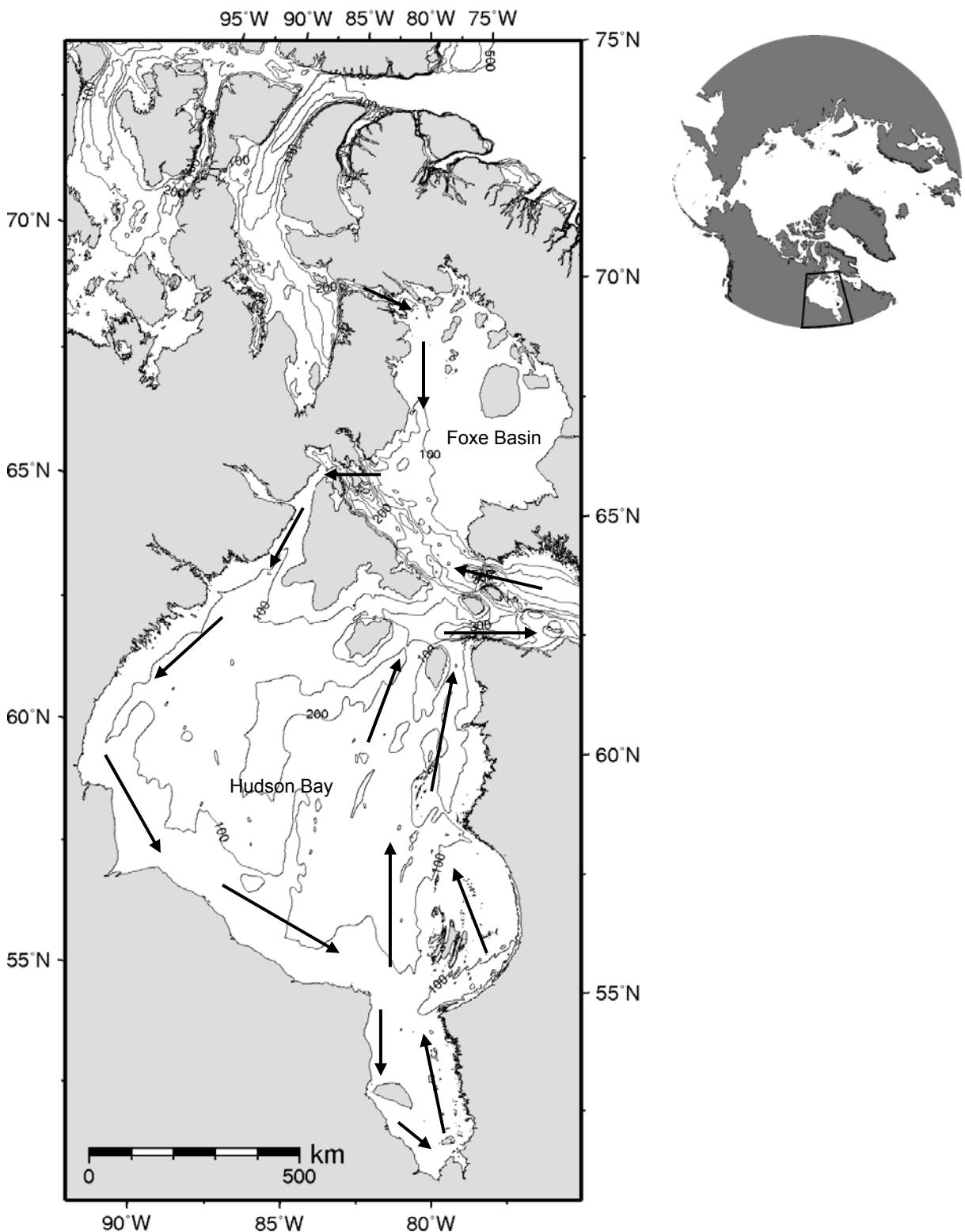
Depending on environmental conditions, individuals must adopt a reproductive strategy that will maximize their fitness through trade-offs in resource allocation to growth/maintenance and reproduction, thus shaping the population structure and dynamics (Stearns 1992). Population dynamics are the result of variations in life-history parameters such as juvenile survival, age at first reproduction, reproductive rates, adult survival, and dispersal (Fowler and Smith 1978, Caughley 1980, Hindell 1991). Changes in population dynamics could reflect large-scale changes in the ecosystem. In large, long-lived vertebrates, a decrease in resource abundance has been shown to affect early survival first, followed by a reduced growth rate leading to an increase of age at first reproduction, and possibly to a decline in reproductive parameters. Adult survival shows the highest degree of elasticity to environmental variations, but a decline in adult survival, and particularly female survival, has the greatest impact on population growth (Hanks 1978, Gaillard et al. 1998, Eberhardt 2002). Identifying factors and mechanisms involved in the variation of these life-history traits is thus a major concern in ecology and has significant implications for management and conservation (Caughley 1980, Gaillard et al. 1998).

Climatic changes have been found to have a strong influence on inter-annual variations in life-history parameters of both terrestrial and marine long-lived vertebrate species (e.g., Trillmich and Ono 1991, Barbraud and Weimerskirch 2001, Forchhammer et al. 2001, Stenseth et al. 2002). Over the last 100 years, the global average surface temperature of the earth has increased by about 0.7 °C (IPCC (Intergovernmental Panel on Climate Change) 2007), and impacts of

climate warming on ecosystems and species have been widely reported (e.g., Walther et al. 2002, Root et al. 2003, Post et al. 2009). Northern polar regions are warming at about twice the global rate due to snow and ice albedo feedbacks (Manabe and Stouffer 1980, IPCC 2007). In the Arctic, the unidirectional warming is likely responsible for the reduction of sea-ice extent and snow cover, the thinning of multi-year ice, and the lengthening of the ice-free season (Comiso 2002, Gagnon and Gough 2005a, IPCC 2007, Comiso et al. 2008, Parkinson and Cavalieri 2008). Similar patterns have been reported for Hudson Bay, a sub-Arctic large Canadian inland sea.

Hudson Bay is a shallow basin (mean depth 125m; maximum depth 370m) with a coastal shelf extending to 80m deep, from 20 to 100km from the coast (Prinsenberg 1986, see also review by Stewart and Lockhart 2005; Figure 1). Hudson Bay receives Arctic waters from the Fury and Hecla Strait via Foxe Basin and Roes Welcome Sound and, through a cyclonic water circulation, exchanges waters with the Atlantic ocean via Hudson Strait (Prinsenberg 1986). Hudson Bay is ice-covered from November to June when sea-ice break-up occurs, and is completely free of ice in late summer and early autumn (Markham 1986, Prinsenberg 1986, Saucier et al. 2004). Open-water leads adjacent to the coast are present throughout the ice-covered season, especially in western Hudson Bay (Markham 1986, Prinsenberg 1986, Stirling 1997).

Figure 1: Map of the Hudson Bay ecosystem showing the water cyclonic circulation (arrows; from Prinsenberg 1986).



Despite its low-latitude position, the incursion of Arctic waters confers to the Hudson Bay ecosystem an Arctic climate and biota. Marine mammals, year-round inhabitants or seasonal visitors, are represented by five species of pinnipeds: the Atlantic walrus (*Odobenus rosmarus rosmarus*), the ringed (*Phoca hispida*), bearded (*Erignathus barbatus*), harbour (*Phoca vitulina*) and harp (*Phoca groenlandica*) seals; four species of cetaceans: the bowhead whale (*Balaena mysticetus*), the narwhal (*Monodon monoceros*), the beluga (*Delphinapterus leucas*), and the killer whale (*Orcinus orca*); and the polar bear (*Ursus maritimus*).

Recently, sea-ice extent and snow depth have decreased in Hudson Bay, whereas surface air temperature has increased, leading to the lengthening of the open-water season, partly due to the spring sea-ice break-up now occurring earlier than it did in the 1970s at a rate of about 10 days per decade (Skinner et al. 1998, Parkinson et al. 1999, Stirling et al. 1999, Gough et al. 2004, Stirling et al. 2004, Ferguson et al. 2005, Gagnon and Gough 2005a, Stirling and Parkinson 2006, Parkinson and Cavalieri 2008). General circulation models for Hudson Bay under different climate change scenarios predicted that the observed trends will continue, with dramatic consequences for the annual cryogenic cycle (Gough and Wolfe 2001, Gagnon and Gough 2005b). By affecting the atmospheric-ice-ocean coupling, these changes are predicted to influence ocean primary productivity with cascading effects through the marine food web (Hansen et al. 2003). On top of possible shift in prey distribution and availability, sea-ice dependent species will be impacted by habitat loss and a possible increase in

predation and competition pressures with temperate species (Gaston and Woo 2008, Post et al. 2009), likely resulting in changes in distribution, nutrition, reproduction, and ultimately survival and abundance (Tynan and DeMaster 1997, Laidre et al. 2008).

Evidence of such changes has been reported in Hudson Bay for ice-associated species. An earlier laying date and a decrease in chick growth rates and adult body mass was described for thick-billed murres (*Uria lomvia*) in northern Hudson Bay at the end of the 1990s (Gaston et al. 2005). During the same period, a shift toward less arctic cod (*Boreogadus saida*), a typical Arctic species, and more capelin (*Mallotus villosus*), a sub-Arctic species, was reported in prey murres brought back to their nestlings, and was related to a reduction in the mid-July sea-ice cover (Gaston et al. 2003). Since the 1980s, polar bear abundance, body condition, reproductive rate, and cub survival have declined in western Hudson Bay, most likely as a response to earlier dates of ice break-up in the spring (Stirling et al. 1999, Regehr et al. 2007). In addition, as the sea-ice broke-up earlier in the late 1990s in western Hudson Bay, polar bear diet, as represented by biomarkers, consisted of a greater proportion of harbour and harp seals concurrent with a decrease in bearded seals (McKinney et al. 2009) or ringed seals (Iverson et al. 2006; but see Thiemann et al. 2008).

The ringed seal (Order Carnivora; Family Phocidae; Picture 1) has a northern circumpolar distribution and is the most abundant pinniped in the Arctic (Mansfield 1967, Frost and Lowry 1981). The ringed seal is among the smallest phocids (McLaren 1993), can live up to 40+ years of age (McLaren 1958,

Lydersen and Gjertz 1987) and reaches sexual maturity around the age of 5-7 years (McLaren 1958, Smith 1973, 1987, Breton-Provencher 1979, Lydersen and Gjertz 1987, Holst et al. 1999, Krafft et al. 2006, Chambellant 2010). A year-round inhabitant of the Arctic, the ringed seal keeps breathing holes open through the ice throughout the winter (Picture 2), enabling the occupation of land-fast and high ice cover areas (Smith and Stirling 1975). Sexually mature ringed seals use primarily stable and consolidated ice with ice deformations where drifted snow can accumulate to build sub-nivean lairs to rest and give birth (McLaren 1958, Smith and Stirling 1975, Smith 1987, Hammill and Smith 1989, Furgal et al. 1996). A single pup is born in early spring, after a gestation of 10-11 months, including a period of suspended development of 2-3 months (McLaren 1958, Smith 1973, 1987, Lydersen 1995). Birth lairs (Picture 3) with a thick and strong snow roof are critical to protect ringed seal pups from cold and predators, including polar bears, arctic foxes (*Alopex lagopus*), and humans (McLaren 1958, Smith and Stirling 1975, Smith 1976, 1980, Lydersen and Smith 1989, Hammill and Smith 1991, Smith et al. 1991, Furgal et al. 1996). Females maintain a complex of several lairs that provide alternate sites to move their pups to escape a predator attack (Smith and Hammill 1981, Smith 1987). Pups are weaned before the spring ice break-up, after a six-week lactation period (Hammill et al. 1991), during which mothers rely on both fat reserves and feeding (Lydersen 1995, Kelly and Wartzok 1996, Simpkins et al. 2001). Although pups enter the water shortly after birth and spend a substantial amount of time in the water during lactation (Lydersen and Hammill 1993), after weaning occurs ringed seal

Picture 1: Ringed seal in its winter habitat



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Picture 2: Ringed seal breathing holes in a) land fast ice and b) newly formed ice (arrows)



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Picture 3: Ringed seal lair with crashed snow roof



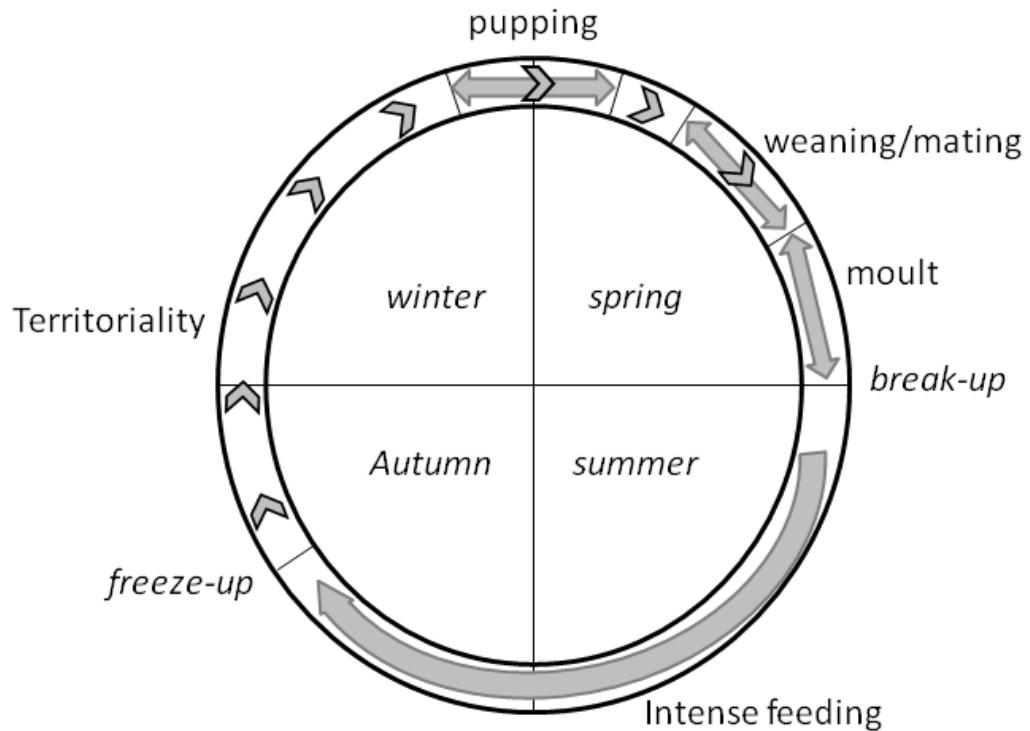
pups may still, like some other phocids, use the ice as a platform to rest while developing foraging skills (Bowen 1991, Stirling 2005). Mating is thought to occur underwater around the time of weaning (Smith 1987, Lydersen 1995) and precedes the annual moult in June, when ringed seals haul-out on ice to bask in the sun (McLaren 1958, Smith 1973). The ringed seal is only slightly sexually size-dimorphic (McLaren 1993, Chambellant 2010) and is thought to have a weakly polygynous, resource-defence mating system (Smith and Hammill 1981, Krafft et al. 2007, Yurkowski et al. 2010). Adult ringed seals show signs of site fidelity during the winter and spring months (McLaren 1958, Smith and Hammill 1981, Kelly and Quakenbush 1990, Krafft et al. 2007, Kelly et al. 2010).

Ringed seals are the leanest after the breeding and moulting seasons and engage in an intensive feeding period in summer and fall to replenish their fat reserves in anticipation of the next winter (McLaren 1958, Breton-Provencher 1979, Smith 1987, Ryg et al. 1990, Goodyear 1999). Ringed seals consume a large variety of prey species across their range but generally only 2-4 prey taxa dominate the diet in a specific time or location (McLaren 1958, Weslawski et al. 1994, Siegstad et al. 1998). Arctic cod and invertebrates such as mysids (Mysidae), hyperiidae amphipods (Amphipoda), and euphausiids (Euphausiacea) are recurrent prey of ringed seals, but diet composition varies greatly with geographical location, season, life-stage, and/or sex (McLaren 1958, Breton-Provencher 1979, Lowry et al. 1980, Bradstreet and Finley 1983, Gjertz and Lydersen 1986, Smith 1987, Weslawski et al. 1994, Siegstad et al. 1998, Wathne et al. 2000, Holst et al. 2001, Labansen et al. 2007). During the open-water

season, ringed seals of all ages have been described to mix offshore to feed in sometimes large aggregations (McLaren 1958, Smith 1973, 1987, Harwood and Stirling 1992). When the ice starts to form in late fall, adults move toward prime breeding habitats where they are thought to establish territories from which they exclude younger age classes that will spend the winter and spring at the ice edge or in leads and polynyas (McLaren 1958, Smith 1973, 1987, Smith and Hammill 1981, Stirling et al. 1981, Holst et al. 1999, Born et al. 2004, Krafft et al. 2007; Figure 2).

Considering its position near the top of the Arctic food web and its high degree of adaptation to exploit the sea-ice habitat for reproduction and survival, the ringed seal is predicted to be particularly vulnerable to variations in its environment under current and predicted climatic changes (Kovacs and Lydersen 2008, Laidre et al. 2008, Post et al. 2009). Ringed seals could therefore be good indicators of ecosystem changes. In fact, a decrease in the relative abundance of ringed seals during warming/light-ice events have been reported by archaeological and historical studies (Vibe 1967, Woollett et al. 2000, Harrington 2008). More contemporaneously, early/late ice break-up, *i.e.*, light /heavy ice conditions, have been found to negatively affect ringed seal body condition, reproduction and/or survival in the Arctic (Stirling et al. 1982, Smith 1987, Kingsley and Byers 1998, Harwood et al. 2000, Smith and Harwood 2001). Recent findings also revealed that ringed seal pup survival was

Figure 2: Schematic representation of the ringed seal annual life-cycle. The sequence of small arrows indicates that territoriality likely takes place from freeze-up to mating.



negatively impacted by unusual warm and/or rain events (Stirling and Smith 2004) and insufficient snow depth (Hammill and Smith 1991, Ferguson et al. 2005) in the spring.

Several authors have suggested that ice-adapted marine mammals occurring at the southern limit of their range will likely experience first the effects of climate change (e.g., Kovacs and Lydersen 2008, Laidre et al. 2008). The ringed seal occurs at the southern limit of the species range in Hudson Bay (Mansfield 1967, Frost and Lowry 1981) and, in the 1990s, low reproductive rates and survival of pups (Holst et al. 1999, Ferguson et al. 2005, Stirling 2005) concurrent with a decline in ringed seal density (Chambellant et al. 2010) have been reported in western Hudson Bay. Decreasing snow depth and earlier break-up dates were evoked as possible factors involved in the observed changes, but mechanisms through which they would impact ringed seal population dynamics are still poorly understood. Considering the recent climatic trends in Hudson Bay, studying ringed seals in this ecosystem could represent a good opportunity to better understand the mechanisms and effects of environmental variations on their life-history traits and ultimately population dynamics.

Effects of climatic changes on population dynamics of a long-lived carnivore require long time series to assess and differentiate climate-induced changes from contemporaneous natural variations (Tynan and DeMaster 1997, Laidre et al. 2008). For my research project, I compiled ringed seal data collected in western Hudson Bay during the 1990s by Environment Canada and the 2000s by

Fisheries and Oceans Canada, and obtained the first long-time series for ringed seals in Hudson Bay.

The objectives of my research project were to explore ringed seal

1. density and distribution (Chapter 2)
2. life-history traits and body condition (Chapter 3)
3. feeding habits (Chapter 4)

and assess the role of environmental variables in the variability of these parameters over a 15 year-period, in order to enhance our understanding of ringed seal population dynamics in the Hudson Bay ecosystem.

Ultimately, this knowledge may allow us to forecast future ringed seal responses to climate change and adopt conservation measures required to maintain ringed seal numbers at a level sufficient to provide food for polar bears, cultural and economic resource for Inuit, and a genetic reservoir for the circumpolar species in the Arctic.

Chapter 2

Distribution and density of ice-obligated seals in western Hudson Bay over a 14-year period, 1995-2008.



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**Distribution and density of ice-obligated seals in western Hudson Bay over
a 14-year period, 1995-2008.**

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Abstract

We conducted strip-transect surveys at the end of May in 1995-97, 1999-2000 and 2007-2008 to estimate distribution, density and abundance of ringed (*Phoca hispida*) and bearded (*Erignathus barbatus*) seals in western Hudson Bay, Canada. When hauled out, ringed seals preferred land-fast ice and consolidated pack ice, whereas bearded seals chose preferentially unconsolidated pack ice. Bearded seal and ringed seal density estimates varied from 0.0036 to 0.0229 seals/km² and from 0.46 to 1.60 seals/km² of ice, respectively, over the study period. Strong inter-annual variations were recorded in the density and abundance estimates of both ice-obligated seal species, with the largest number of seals encountered in 1995 (104,162 and 1,494 ringed and bearded seals, respectively) and the lowest in 2008 for ringed seals (33,701) and in 1997 for bearded seals (278). Estimated densities of ringed and bearded seals were negatively correlated with mean ice cover in western Hudson Bay at the end of May-beginning of June. A sine function with an 11 year-period was fitted to seal density estimates in western Hudson Bay and suggested a decadal cycle, with low densities in the 1990s and an increase in the 2000s. Our results were supported by studies of ringed seal demographic parameters that reported low pregnancy rates and pup survival in the 1990s and a recovery in the 2000s. We propose that the heavy ice conditions that prevailed in western Hudson Bay in the early 1990s resulted in the decline in ringed and bearded seal density estimates observed in the 1990s. We examined the limitations of the data, commented the reliability of density estimates obtained from aerial surveys, and

discussed our results in the context of climate warming. We concluded that long-term monitoring of ice-obligated seal populations is critical for the conservation and management of these species, especially in sub-Arctic regions where they occur at the southern limit of their range and where effects of climatic changes impacts are occurring first.

Keywords: abundance, aerial survey, Arctic, bearded seal, decadal cycle, sea ice cover, land-fast ice, marine mammals, ringed seal, spring break-up, strip-transects.

Introduction

Over the last four decades, the extent of Arctic sea ice has been decreasing as a result of global warming (Johannessen et al. 1999, Comiso 2002, 2003, Johannessen et al. 2004, IPCC (Intergovernmental Panel on Climate Change) 2007, Comiso et al. 2008). In Hudson Bay, surface air temperature and length of the ice-free period have increased significantly, whereas sea-ice extent and snow depth have decreased (Skinner et al. 1998, Parkinson et al. 1999, Gough et al. 2004, Ferguson et al. 2005, Gagnon and Gough 2005a, Parkinson and Cavalieri 2008, Hochheim et al. 2010). As a consequence of rising temperatures, spring sea ice break-up in western Hudson Bay is now occurring earlier at a rate of about 10 days per decade since the 1970s (Stirling et al. 1999, Stirling et al. 2004, Gagnon and Gough 2005a, Stirling and Parkinson 2006). Climate change scenarios for the Hudson Bay ecosystem predict that trends observed in recent years will continue and amplify, and may result in dramatic modifications in the cryogenic cycle (Gough and Wolfe 2001, Gagnon and Gough 2005b).

Distribution, nutrition, reproduction, and ultimately survival and abundance of sea-ice dependent species will be impacted by sea ice reduction through habitat loss, shifts in the distribution and availability of their prey, and a possible increase in predation and competition pressures with temperate species (Tynan and DeMaster 1997, Gaston and Woo 2008, Laidre et al. 2008, Post et al. 2009). Evidence for impacts of climate warming on top marine predator populations has already been documented in Hudson Bay for thick-billed murres (*Uria lomvia*;

Gaston et al. 2003, Gaston et al. 2005) and polar bears (*Ursus maritimus*; Stirling et al. 1999, Regehr et al. 2007).

The ringed seal (*Phoca hispida*), an ice-dependent phocid, has a northern circumpolar distribution and is the most abundant pinniped in the Arctic (Mansfield 1967, Frost and Lowry 1981). Ringed seal pups are born in early spring (McLaren 1958, Smith 1973, 1987, Hammill et al. 1991) and sexually mature ringed seals prefer stable and consolidated ice with ice deformations where drifted snow can accumulate to build sub-nivean birth lairs that are critical for pup survival (McLaren 1958, Smith and Stirling 1975, Hammill and Smith 1989, 1991, Smith et al. 1991). After the breeding season in late spring, ringed seals undergo an annual moult and use the ice as a platform to haul out and bask in the sun (McLaren 1958, Smith 1973), which heat facilitates epidermal regeneration (Feltz and Fay 1966) and allows the maintenance of the epidermis thermal requirement at limited energetic costs (Boily 1995).

As a species that has evolved to exploit the sea ice habitat for reproduction and survival, the ringed seal may face critical challenges should unidirectional climate warming continue as predicted by the IPCC (2007). Previous studies have documented sensitivity of ringed seals to variations in their sea-ice habitat. Early or late ice break-up, light/heavy ice conditions (Stirling et al. 1982, Smith 1987, Kingsley and Byers 1998, Harwood et al. 2000, Smith and Harwood 2001), unusual warm and/or rain events in the spring (Stirling and Smith 2004) and insufficient snow depth (Hammill and Smith 1991, Ferguson et al. 2005) have been shown to negatively affect ringed seal body condition, reproduction and/or

survival. Archaeological and historical studies also reported a decline in ringed seal relative abundance during warmer periods (Vibe 1967, Woollett et al. 2000, Harrington 2008). Effects on population size require long-term studies to assess and differentiate climate-induced changes from natural variation (Tynan and DeMaster 1997, Laidre et al. 2008). However, current published information on density and abundance of ringed seals in Hudson Bay is limited to estimates obtained by aerial surveys in 1974 (Smith 1975) and 1994-95 (Lunn et al. 1997).

We conducted aerial surveys in western Hudson Bay in 2007 and 2008 and combined these data with those collected over the period 1995-2000 by Environment Canada to 1) provide density and abundance estimates of ice-adapted seals (ringed and bearded seals, *Erignathus barbatus*) in western Hudson Bay; 2) assess potential inter-annual variations in seal density in relation to the sea-ice regime; and 3) identify and interpret trends in ringed seal density in the context of the current climatic warming trend.

Material and Methods

Study area

Surveys were flown in western Hudson Bay, Canada (Fig. 1) in an area bounded by the communities of Churchill, Manitoba ($58^{\circ}47'N$; $94^{\circ}10'W$) in the south and, Arviat, Nunavut ($61^{\circ}6'N$; $94^{\circ}4'W$) in the north, the western Hudson Bay coastline to the west, and the $89^{\circ}W$ longitude to the east (transects 7 to 16 of surveys flown by Lunn et al. (1997). Initially, the study area was defined to match winter

and spring hunting habitat of western Hudson Bay polar bears for which long-term data was collected (Lunn et al. 1997).

Survey design

The survey was designed as a systematic, strip-transect survey following Lunn et al. (1997). Ten transects were set perpendicular to the shoreline at intervals of 15' of latitude between Churchill, MB and Arviat, NU (Fig. 1). Out of the 22 transects originally flown by Lunn et al. (1997), only ten were retained in subsequent years (Lunn et al. 2000). Surveys were flown in late spring (Table 1) during the annual moult, when ringed seals haul out on the ice (McLaren 1958, Smith 1973) for more than 55% of their time (Kelly et al. 2010), and thereby when the largest proportion of the population is visually available to be counted from the air. A Cessna 337 “Skymaster” was used to fly at a targeted altitude of 152m and speed of 260km/h. Transect width was 400m on each side of the plane and was divided into two intervals of 200m, an inner strip and an outer strip. Bubble windows were not available, so a strip underneath the plane was not accessible to observers. Two observers sat at the rear of the airplane and each was assigned one side of the plane for the whole survey duration. To assist observers in assigning observed seals to either the inner or outer strip, wing struts and windows were marked on the ground using the following formula:

$$y = Xa / A \quad (1)$$

where y is the projected transect width on the ground, X is the desired transect width (400m) at 152m of altitude, A is the flying altitude and a is the specific height of observer eye level in the plane from the ground.

Figure 1: Study area and transects flown during seven aerial surveys in western Hudson Bay, 1995-2008. Transect numbers (7 to 16) refer to survey protocol described in Lunn et al. (1997).

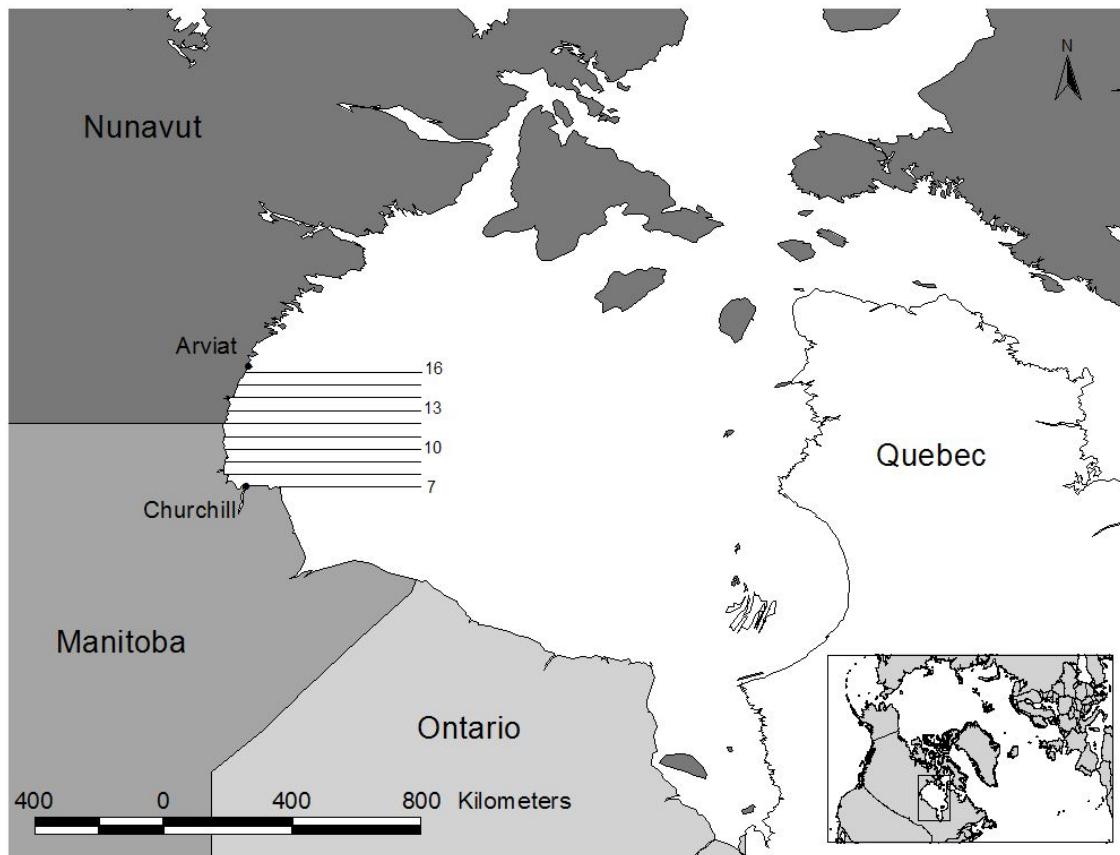


Table 1: Mean wind speed and temperature during aerial surveys in western Hudson Bay, 1995-2008. Means for the entire survey period are indicated in bold and italic.

Date	Line flown	Start time	End time	Wind speed km/h			Temperature °C		
				Churchill	Arviat	mean	Churchill	Arviat	mean
01-Jun-95	7, 8, 9, 10	10:28	15:35	14.60	18.50	16.55	3.00	1.70	2.35
02-Jun-95	15, 16	17:11	19:26	18.80	/	18.80	3.30	/	3.30
03-Jun-95	11, 12, 13, 14	10:12	17:22	20.10	/	20.10	10.10	/	10.10
				17.83	18.50	18.17	5.47	1.70	3.58
05-Jun-96	9, 10, 11, 12	10:04	16:50	18.30	4.40	11.35	6.00	4.80	5.40
06-Jun-96	7, 8, 13, 14	9:20	14:54	14.86	16.90	15.88	7.69	5.80	6.75
				16.58	10.65	13.62	6.85	5.30	6.07
30-May-97	7, 8, 9, 10	10:14	16:24	18.10	19.30	18.70	2.60	0.08	1.34
31-May-97	13, 14, 15, 16	9:42	16:50	31.00	/	31.00	8.50	/	8.50
01-Jun-97	11, 12	9:28	12:04	24.00	/	24.00	5.70	/	5.70
				24.37	19.30	21.83	5.60	0.08	2.84
30-May-99	13, 14, 15, 16	9:27	17:59	10.60	25.30	17.95	3.20	-0.30	1.45
31-May-99	7, 8, 9, 10, 11, 12	8:42	20:02	13.30	12.20	12.75	14.20	1.50	7.85
				11.95	18.75	15.35	8.70	0.60	4.65
01-Jun-00	13, 14, 15, 16	12:18	19:54	25.00	42.10	33.55	-1.30	-4.90	-3.10
02-Jun-00	7, 8, 9, 10, 11, 12	8:36	19:07	22.90	30.80	26.85	-2.50	-4.60	-3.55
				23.95	36.45	30.20	-1.90	-4.75	-3.33
26-May-07	12, 13, 15, 16	12:37	19:46	24.30	21.80	23.05	18.40	3.10	10.75
27-May-07	7, 8	11:11	13:47	21.00	8.80	14.90	16.30	0.40	8.35
29-May-07	9, 10, 11, 14	12:04	19:16	19.40	21.60	20.50	1.50	0.30	0.90
				21.57	17.40	19.48	12.07	1.27	6.67
28-May-08	7, 8, 9, 10, 11	10:22	20:16	23.70	36.50	30.10	4.40	2.80	3.60
29-May-08	15, 16	13:35	16:42	18.60	15.00	16.80	8.90	1.10	5.00
31-May-08	12, 13, 14	10:17	15:43	18.10	43.90	31.00	10.40	3.10	6.75
				20.13	31.80	25.97	7.90	2.33	5.12

Data presented in this paper were collected in 1995-97 and 1999-2000 (1990s) by one author (NJL), and in 2007-2008 (2000s) by the other authors (SHF and MC). Survey design and protocol over the two time periods were identical. In the 1990s, the right observer remained the same (NJL) whereas four different individuals were designated as left observers; in the 2000s, observers remained the same during the two years of the study. In the 1990s, data were collected in 2-min intervals, whereas data were recorded continuously on mini-disc recorders in the 2000s. Observers did not communicate real-time results while on survey. Waypoints and start and end times of each transect were recorded with the aid of a GPS. Observers surveyed the 400m transect width and recorded sightings by strips (inner or outer). Sightings beyond transect (*i.e.*, > 400m) were recorded as “off” data and were not included in the estimates of density and abundance. Although ringed seals were the target species, bearded seals and other marine mammals were also recorded. Group size of ringed seals and seal structures (holes and lairs) were also recorded in 2007 and 2008. A group consisted of two or more seals around the same hole or along a crack; if seals along a crack were forming sub-aggregations of two or more animals less than one body length apart, then multiple groups were defined. Ringed seals in water were recorded but not accounted for in the analysis due to different visibility biases relative to seals on ice (Kingsley et al. 1985). Physical variables such as ice cover (in eighths), ice type (land-fast, floe size) and color, percent cloud cover and visibility were recorded for each 2-min intervals (1990s) or when they changed (2000s).

Length of each of the ten transects was calculated by the great circle distance method (<http://www.movable-type.co.uk/scripts/latlong-vincenty.html>) using starting and ending coordinates. Effective ground speed was then computed by dividing the length of each transect by the time elapsed during flight. Transect length was reduced to account for missing effort due to technical (e.g., recorder malfunction) and/or null visibility (e.g., fog) issues. Total study area and ice area within the study area were calculated by multiplying total effort (sum of transect lengths) and effort over ice (sum of transect lengths flown over ice), respectively, by the distance between each transect (*i.e.*, 27.795 km corresponding to 15' of latitude).

Environmental data

Weather information from airport weather stations in Churchill, MB and Arviat, NU, were obtained from Environment Canada:

http://www.climate.weatheroffice.ec.gc.ca/climateData/canada_e.html

Wind speed (km/h) and temperature (degree Celsius) were obtained for Churchill and Arviat, and averaged over the time the survey was flown for each day.

Break-up dates in western Hudson Bay were calculated for the survey period (1995-2008) following Stirling et al. (1999) and compared to the long-time average 1971-2008. For each survey year, ice cover of western Hudson Bay (Canadian Ice Service: <http://ice-glaces.ec.gc.ca/>) for 21 and 28 May, and 4 June were averaged to provide a mean ice cover for the period 'end of May-beginning

of June'. Mean ice cover anomalies (difference from mean) were computed for each survey year, using the average ice cover for the period 1971-2008.

Seal density and abundance estimates

Data from the 1990s were re-analysed for consistency with data collected on the two more recent surveys (2007 and 2008).

Density of ringed seals per km² of ice, \hat{D} , was estimated per year, by observer, by strip and for observers and strips combined, following the standard ratio estimate (Buckland et al. 2001):

$$\hat{D} = \sum_{i=1}^k n_i / \omega \sum_{i=1}^k l_i \quad (2)$$

where k is the number of transects, n_i is the number of ringed seal counted on the i^{th} transect, ω is the strip width and l_i is the length of the i^{th} transect flown over the ice.

Strip-transect analysis assumes detection of all animals present on transect and could produce negatively biased density and abundance estimates compared to line-transect analysis (Burnham and Anderson 1984, Burnham et al. 1985, Hone 1988). Chambellant and Ferguson (2009) compared results from the 2007 and 2008 surveys using both line- and strip-transect analyses and concluded that, despite being slightly biased low, strip-transect analysis was sufficiently robust for our survey conditions and design. Density and abundance estimates were not corrected for availability bias (*i.e.*, for seals not on top of ice at the time of survey and therefore not available for visual observation) and are expected to be biased

low (Moulton et al. 2002, Frost et al. 2004, Carlens et al. 2006, Kelly et al. 2006, Krafft et al. 2006); they should therefore be considered indices.

Variance of \hat{D} ($\sigma^2(\hat{D})$) was obtained following Kingsley and Smith (1981) for systematic survey:

$$\sigma^2(\hat{D}) = k * \frac{\sum_{i=1}^{k-1} (d_i - d_{i+1})^2}{2(k-1) * \left(\omega \sum_{i=1}^k l_i \right)^2} \quad (3)$$

where

$$d_i = n_i - \hat{D} * \omega l_i \quad (4)$$

Log-based confidence intervals were estimated following Buckland et al. (2001).

Lower and upper 95% bounds were obtained by:

$$\hat{D}_L = \hat{D} / C \quad (5)$$

and

$$\hat{D}_U = \hat{D} * C \quad (6)$$

with

$$C = \exp \left\{ 1.96 * \sqrt{\log_e \left(1 + [cv(\hat{D})]^2 \right)} \right\} \quad (7)$$

where $cv(\hat{D})$ is the coefficient of variation of estimated density.

Abundance of ringed seals in the study area (\hat{N}) was estimated by multiplying the estimated density (\hat{D}) by the ice area (IA). The standard error of \hat{N} ($se(\hat{N})$) was computed as described in Stirling et al. (1982):

$$se(\hat{N}) = \hat{N} * cv(\hat{D}) \quad (8)$$

Data analysis

A Mann-Whitney *U*-test was used to compare differences between group sizes in 2007 and 2008. We used a components-of-variance model to test for differences in seal density estimates between observers and between strips in order to control for the error variance between transects (σ_a^2), as described in Stirling et al. (1982) and Kingsley et al. (1985). Briefly, the error variance of density estimates over the entire transect strip (800m; V_w) was calculated using equation 3. V_s was computed as the mean of error variances of density estimates calculated for left and right observers, and inner and outer strips. The component of the error variance due to variation between-strips/observers (within transect and between parts of the strip), σ_b^2 , was then obtained using:

$$\sigma_b^2 = 2(V_s - V_w) \quad (9)$$

A Student's *t*-test, using σ_b^2 as the error variance was used to compare density estimates between observers and between strips. An ANOVA with a Games-Howell post-hoc test was performed to compare seal density on the different ice types. Extent of land-fast ice was compared between years using a Kruskal-

Wallis test. Pearson correlation matrices were used to explore the importance of environmental variables in explaining inter-annual variation of ringed seal density estimates. Graphs and statistical analyses were performed using Systat 12 (Systat Software Inc. 2007), SigmaPlot 11 (Systat Software Inc. 2008) and Excel 2007 (Microsoft Office 2007).

All tests were two-tailed and differences considered significant at $p < 0.05$.

Unless otherwise stated, results are provided as mean \pm standard error (se).

Results

Survey

In all years, the ten survey transects were flown during either the last week of May or the first week of June (Table 1). Average flying speed was 251 km/h and ranged from 226 km/h in 1999 to 266 km/h in 1995. It took on average 11.6 hours to fly the 10 transects.

Fog precluded flying transects 15 and 16 in 1996, some parts of transects 7 and 8 in 1996 and 1999, 7 to 10 and 15 and 16 in 2000, and 15 in 2008. Together with logistic problems, effort missed (km of lines not flown) ranged from 4% in 1999 to 25% in 1996, whereas all transects were flown in their entirety in 1995 and 1997.

Environmental variables

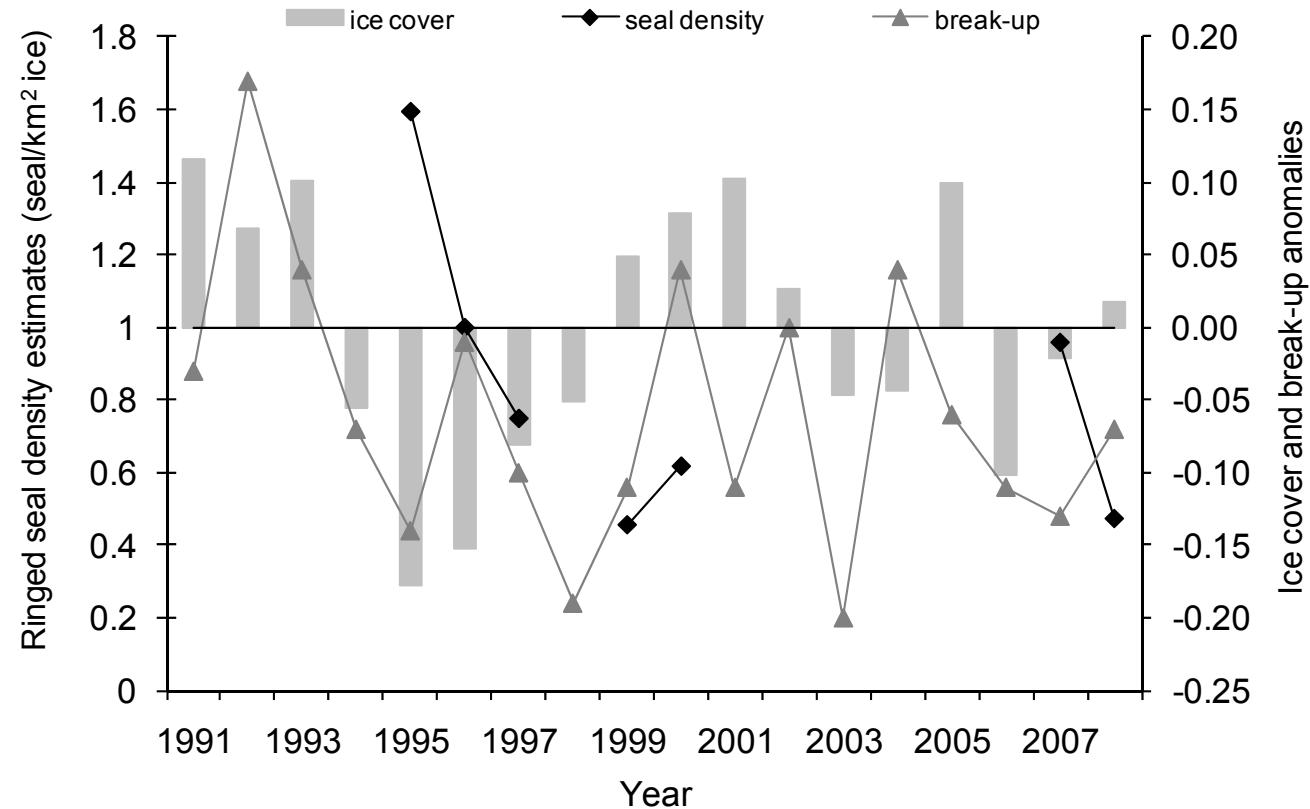
Temperature during the surveys varied between years and ranged from an average of -3.3 °C in 2000 to +6.7 °C in 2007 (Table 1). Winds were generally moderate (< 30 km/h), except in 2000 and 2008 when winds superior to 40 km/h were recorded by the Arviat weather station (Table 1). Over the area surveyed, cloud cover was less than 50% for all years other than 2008, which was predominantly cloudy. Among survey years, break-up occurred later than average in 2000 (7 July) and earlier than average in all other years, particularly in 1995 and 2007 (20 and 21 June, respectively; Fig. 2). Mean ice cover anomalies for the end of May to beginning of June showed that 1999, 2000, and 2008 were years of above normal ice cover whereas the remaining survey years had below normal ice cover, especially 1995 and 1996 (Fig. 2).

When flying eastward from the coast out into the bay, the surveyed area typically consisted of a band of land-fast ice, a lead, and a predominant area of pack ice composed of ice floes of different sizes, separated by cracks and minor leads. Extent of land-fast ice was under 10 km and remained relatively constant among years (Table 3; $KW = 7.97$, $p = 0.24$). In 1995 and 1999, land-fast ice was absent from 5 (7, 10, 12, 13, 15) and 3 (8, 9, 10) transects, respectively. The maximum land-fast ice width, 18 km, was recorded on transect 8 in 1995.

Width of the major open-water lead along the coast varied greatly among transects and years (Table 2) but was generally greater toward the northern part of the study area (transects 12-16). There was no lead present between transects 7 to 11 in 1995, 1997 and 1999, or in 2000 between transects 8 to 11.

Figure 2: Ringed seal density estimated by strip-transect analysis (black filled diamond), break-up dates (grey filled triangles) and ice cover for the end of May to beginning of June (light grey bars) anomalies (departure from the mean) in western Hudson Bay over the period 1995-2008. The solid line denotes averaged break-up and ice cover conditions over the period 1971-2008.

cc



In the two most recent years, a lead was present on all transects, except on transect 7 in 2008.

The pack ice was dominated by consolidated ice (ice cover 6-8/8) in all years but 1999, when high and low (1-5/8) ice cover areas were in equal proportions (Table 2). Areas of low ice cover (*i.e.*, unconsolidated ice) in 2000 and 2007-08 were greatly reduced relative to values recorded in the period 1995-99 (Table 2). The ice surveyed was a mix of blue and grey ice but tended to be greyer in 1995 and 1997. Presence of rotten ice (grey/black, drainage patterns, pools on top of ice) was only recorded for 2007 and 2008 and was 5.5 times greater in 2008 than 2007.

Seal distribution

Ringed seal density estimates differed according to the different ice types ($F_{(2, 18)} = 22.08, p < 0.0001$) and were consistently greater on land-fast than on pack ice ($p < 0.01$ for both consolidated and unconsolidated pack ice) despite high error variance (coefficient of variation ranged from 32% to 71%; Fig. 3). On pack ice, ringed seal density estimates tended to be higher on consolidated (6-8/8) than on unconsolidated (1-5/8) ice ($p = 0.08$), except in 2007 and 2008 when no difference was observed (Fig. 3). In 2007, ringed seals hauled out in groups of 2 or more individuals represented 44% of the sightings and average group size was $\bar{x} = 2.04 \pm 0.07$ ($n = 1035$). Groups of 10 seals or more were rare (1.4%), and the largest group recorded on transect was of 32 ringed seals along a crack perpendicular to the flight path. In 2008, ringed seals were seen as lone

Table 2: Annual survey effort (distance flown), mean width and percentage of land-fast ice (LFI), percentage of unconsolidated and consolidated pack ice (ice cover 1-5/8 and 6-8/8, respectively), and percentage of open water in the study area during seven ringed seal aerial surveys in western Hudson Bay, 1995-2008. (mean \pm standard error).

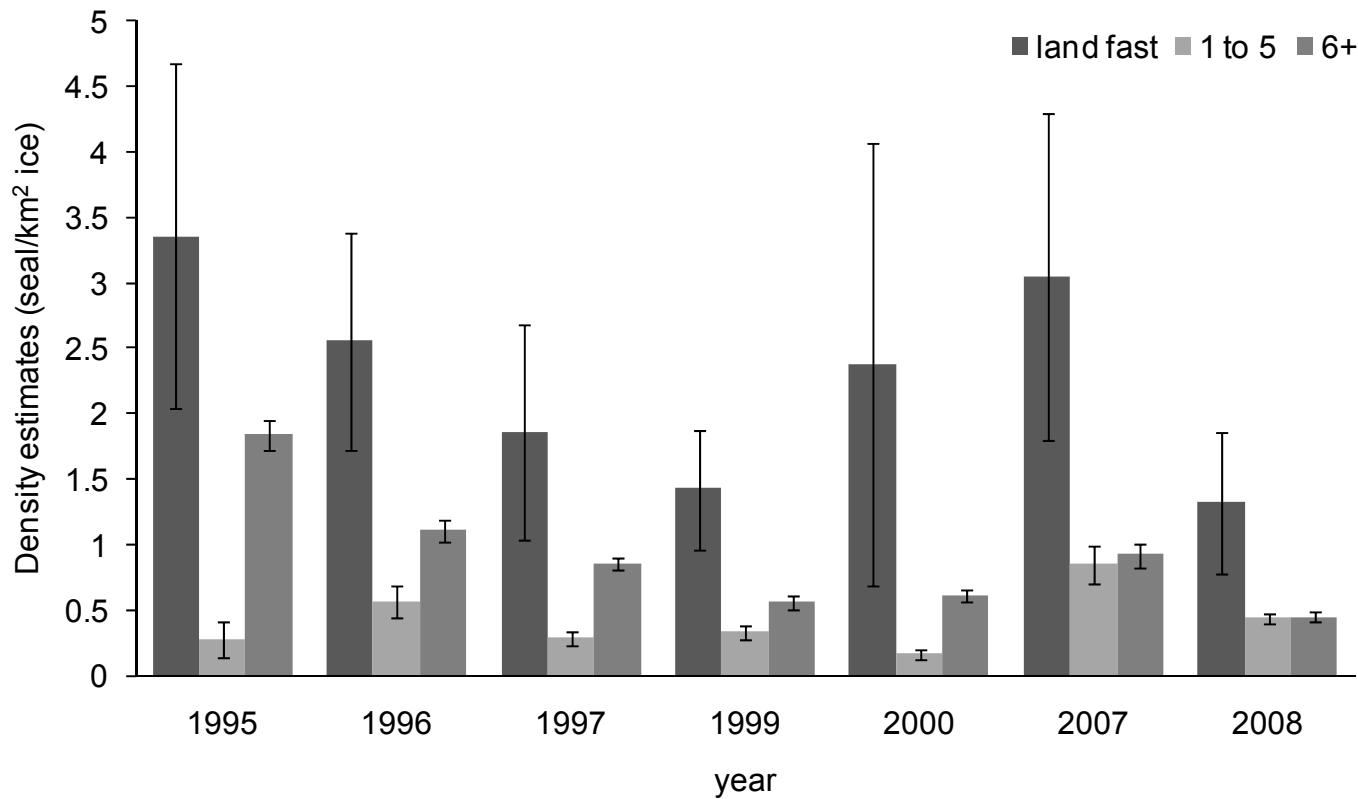
	Total effort (km)	LFI in km (# transects)	% LFI	% 1 to 5	% 6-8	% open water
1995	3074.6	5.0 \pm 1.99 (10)	1.6	13.7	61.1	23.6
1996	2298.0	7.1 \pm 1.2 (8)	2.5	27.1	69.7	0.8 [§]
1997	3074.5	5.9 \pm 1.41 (10)	1.9	20.6	68.0	9.5
1999	2951.4	4.3 \pm 1.36 (10)	1.5	49.7	46.4	2.4
2000	2630.0	5.3 \pm 1.15 (10)	2.0	7.4	88.8	1.8
2007	2869.5	5.8 \pm 0.66 (9)	1.8 [¶]	8.3	85.6	4.3
2008	2764.8	8.0 \pm 0.95 (9)	2.6	5.4	84.7	7.3 [§]

[§]underestimated. Transects 15 and 16, and part of transect 15, which typically presented a large amount of open water ($\bar{x} = 75.8 \pm 21.2$ km), were not flown in 1996 and 2008, respectively.

[¶]underestimated. Transect 8, which usually presented a long band of land-fast ice ($\bar{x} = 12.4 \pm 2.6$ km), was not flown in 2007.

Figure 3: Distribution of ringed seals in relation to ice type during seven aerial surveys flown in western Hudson Bay between 1995 and 2008. Land-fast = land-fast ice; 1 to 5 = unconsolidated pack ice (ice cover 1-5/8); 6+ = consolidated pack ice (ice cover 6-8/8). Density estimates \pm standard error.

98



individuals 64.5% of the time and average group size was significantly lower than in 2007 ($\bar{x} = 1.70 \pm 0.05$, $n = 572$; $U = 320969.5$, $p < 0.005$). Ten ringed seals along a crack represented the largest and only group of ten or more individuals observed in 2008 (0.17%).

No bearded seals were observed on land-fast ice. Bearded seals density estimates on consolidated and unconsolidated pack ice were not statistically different ($F_{(1, 12)} = 0.36$, $p = 0.56$) but bearded seals were more numerous on unconsolidated ice (1-5/8) for four of the seven study years, and especially in 2007 and 2008 (Table 3). In 2007 and 2008, bearded seals were hauled out as single individuals on all occasions but one in 2007, where two individuals were seen hauled out close to each other.

Seal density and abundance estimates

Ringed seal density estimates on ice varied considerably from year-to-year with a maximum of 1.60 seals/km² of ice in 1995, and a minimum of 0.46 seals/km² of ice in 1999 (Table 4). A similar pattern was found when ringed seal density estimates were calculated over the entire survey area (ice and water) or over land-fast ice (Fig. 4). Therefore, only the density estimates on ice were used in the analyses.

The declining trend in ringed seal density estimates suggested by surveys in the 1990s ($r = -0.87$, $S_{Y,X} = 0.26$, $n = 5$, $p = 0.058$) was not apparent across the whole study period ($r = -0.47$, $S_{Y,X} = 0.39$, $n = 7$, $p = 0.29$). An eleven-year period sine function was fitted to the data (Residual Sum of Squares (RSS)_{sine} = 0.08;

Table 3: Bearded seal density estimates (seals/km² ice) for the different types of ice encountered during seven aerial surveys over western Hudson Bay, 1995-2008.

	LFI	Ice cover (/8)	
		1 to 5	6-8
1995	0	0.012 (47.7) [0.005-0.029]	0.026 (39.1) [0.012-0.054]
1996	0	0.020 (43) [0.009-0.045]	0.020 (42.7) [0.009-0.044]
1997	0	0.006 (104.1) [0.001-0.032]	0.003 (59.2) [0.001-0.009]
1999	0	0.005 (40.3) [0.002-0.011]	0.003 (47.2) [0.001-0.007]
2000	0	0.006 (94.8) [0.001-0.031]	0.007 (48.9) [0.003-0.017]
2007	0	0.021 (53.9) [0.008-0.057]	0.007 (35.3) [0.003-0.013]
2008	0	0.017 (35.3) [0.009-0.033]	0.004 (31.4) [0.002-0.008]

Note: LFI = land-fast ice. Ice cover is expressed in eighths. Density estimates (percent coefficient of variation) [95% confidence interval].

Table 4: Ringed and bearded seal density (\hat{D} ; seals/km² ice) and abundance (\hat{N}) estimates, total effort over ice and ice area for each year of seven aerial surveys conducted in western Hudson Bay, 1995-2008.

	Effort over ice (km)	Ice area (km ²)	Ringed seal					Bearded seal				
			\hat{D}	95% CI	\hat{N}	95% CI	% CV	\hat{D}	95% CI	\hat{N}	95% CI	% CV
1995	2349.7	65310.3	1.595	1.401-1.815	104162	91521-118549	6.6	0.0229	0.0132-0.0396	1494	862-2589	28.6
1996	2280.5	63385.8	0.999	0.842-1.186	63338	53369-75170	8.8	0.0192	0.0098-0.0377	1216	618-2392	35.6
1997	2781.3	77307.0	0.749	0.663-0.845	57883	51279-65337	6.2	0.0036	0.0013-0.0101	278	99-783	56.7
1999	2881.4	80087.4	0.456	0.371-0.559	36481	29732-44762	10.5	0.0039	0.0022-0.0069	313	178-549	29.4
2000	2582.6	71782.1	0.617	0.541-0.704	44298	38841-50523	6.7	0.0068	0.0030-0.0155	486	212-1114	44.3
2007	2746.4	76337.1	0.959	0.826-1.113	73170	63039-84930	7.6	0.0077	0.0044-0.0136	591	336-1039	29.4
2008	2564.4	71277.7	0.473	0.403-0.555	33701	28709-39562	8.2	0.0049	0.0031-0.0077	347	219-551	23.8

Note: %CV: percent coefficient of variation; 95% CI: 95% confidence interval.

Figure 4: Ringed seal densities estimated from aerial surveys in western Hudson Bay over the entire study area (ice and water; light grey filled squares), on the ice area (dark grey filled triangles) and on land-fast ice (black filled circle) for the period 1995-2008.

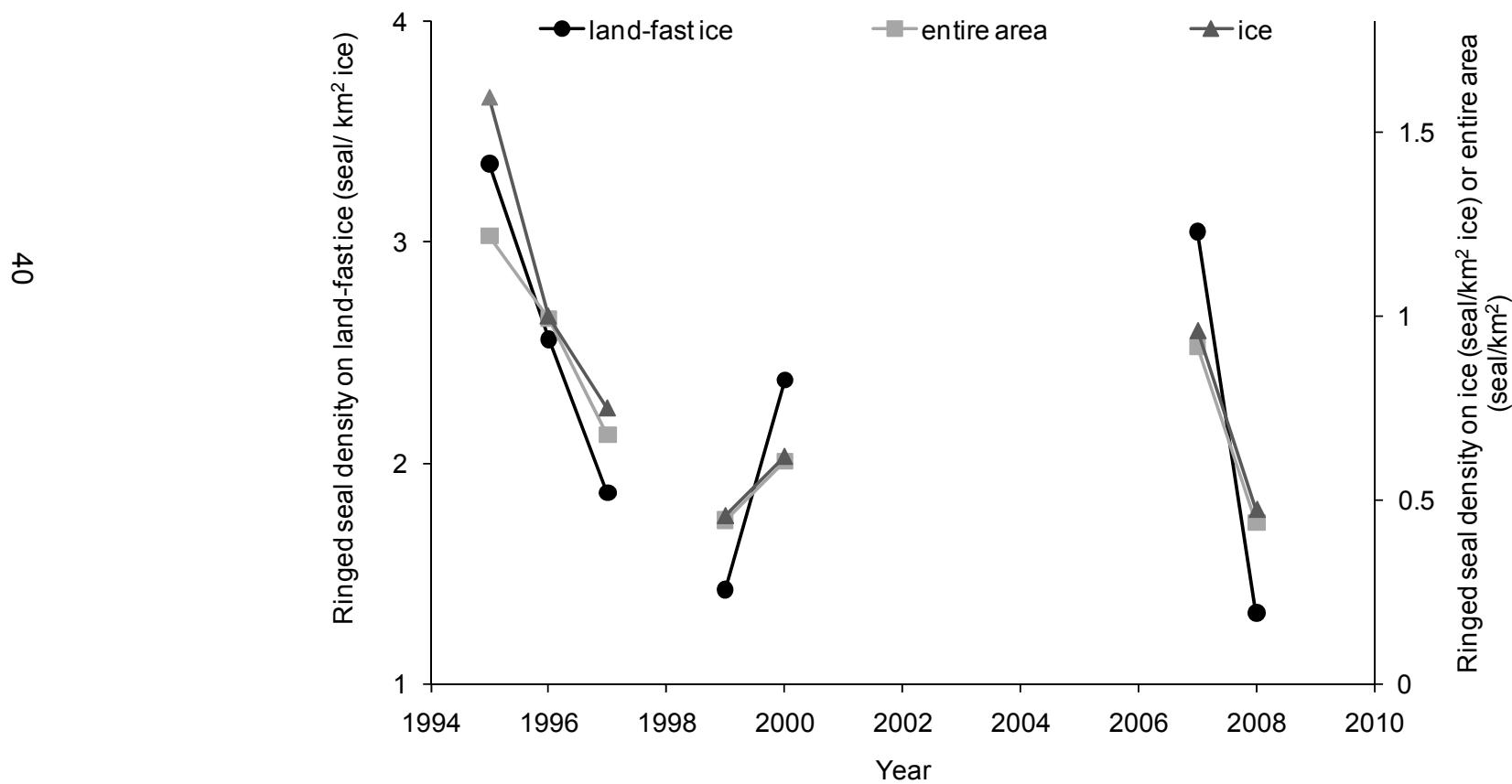


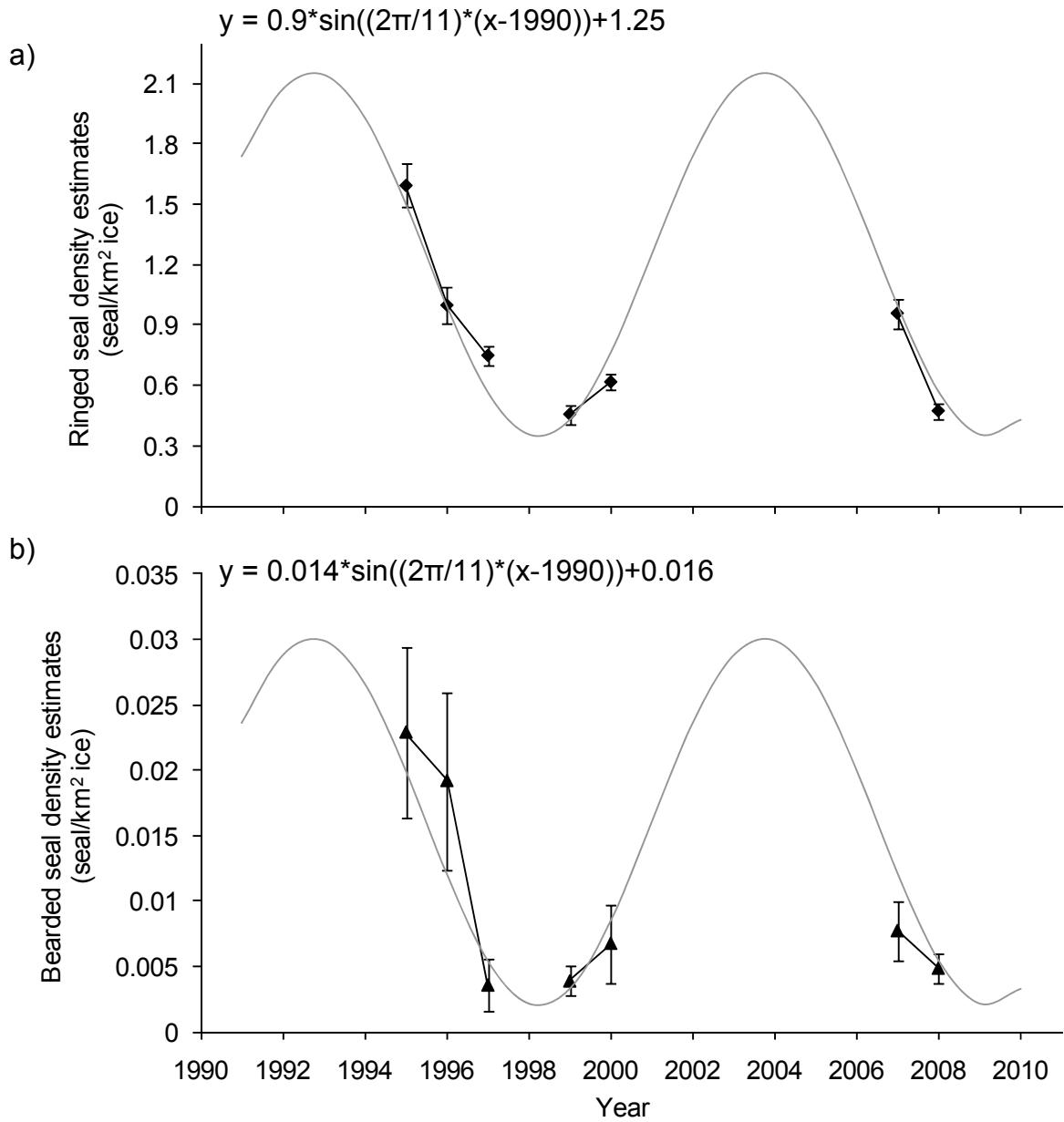
Fig. 5a). Ringed seal density estimates were not correlated with the total ice area (IA) in the study area ($r = -0.62$, $n = 7$, $p = 0.14$) but were negatively correlated with the average ice cover in western Hudson Bay for the end of May-beginning of June ($r = -0.84$, $n = 7$, $p = 0.02$; Fig. 2). Break-up dates were not correlated with ringed seal density estimates ($r = -0.36$, $n = 7$, $p = 0.43$; Fig. 2). Ringed seal abundance varied from a high of 104,162 animals estimated in the study area in 1995 to a low of 33,701 seals in 2008 (Table 4).

Bearded seal density estimates showed a pattern of inter-annual variation similar to what we observed for ringed seals ($r = 0.88$, $n = 7$, $p = 0.01$) and the best fitted sine function had also an 11-year period ($RSS_{\text{sine}} = 0.00009$; Fig. 5b). Bearded seal density estimates were negatively correlated with both the ice area in the study area ($r = -0.87$, $n = 7$, $p = 0.012$) and the average ice cover in western Hudson Bay for the end of May-beginning of June ($r = -0.82$, $n = 7$, $p = 0.03$). Abundance estimates of bearded seals ranged from a high of 1,494 in 1995 to a low of 278 in 1997 (Table 4).

Ringed and bearded seal density estimates were not significantly correlated with temperature, wind, or with the median date of survey.

The difference between the number of animals sighted by the left and right observers was statistically significant and ranged from 10 to 64% for ringed seals and from 50 to 367% for bearded seals (Table 5). The percent difference between ringed seals detected in inner and outer strips was relatively low, except

Figure 5: Ringed (a) and bearded (b) seal densities estimated from aerial survey in western Hudson Bay over the period 1995-2008 and fitted with a sine function with an eleven-year period. Seal density estimates \pm standard error.



in 1999 when it reached 45%, with a tendency to detect more animals in the outer strip (Table 5).

Incidental sightings

A total of 58 polar bears, including eight adult females accompanied by cubs (19 individuals), were recorded during the seven survey years (Table 6). Only solitary animals were sighted in 1999 and 2008. On two occasions (in 2007 and 2008) a polar bear was observed eating on a seal carcass. Polar bears were distributed across the area surveyed, except on transect 16, but 72% of observations occurred between transects 9 and 13. We also counted a total of 162 polar bear tracks and evidence of 29 recent seal kills by polar bears in 2007 and 2008 (Table 6).

We sighted 253 beluga whales (Table 6) distributed over the entire area of the survey, although 61% were found between transects 9 and 13. In years of relatively late break-up (1996 and 2000) beluga tended to be scarce, whereas more than 80 animals were seen in 1995 and in 2007, when break-up occurred about 15 days earlier than average. Except for 1995, numbers of beluga observed in the 1990s were relatively low and 50% of the sightings occurred in 2007 and 2008 (Table 6).

In 1995, two bowhead whales were seen northeast of Arviat. In 1997, a walrus was recorded on transect 7 on pack ice, in an area of high ice cover (Table 6). In 2007 and 2008, seal structures were recorded. Crashed (*i.e.*, broken into by polar bears) or melted seal lairs were observed 68 times. Holes with no seal associated were counted consistently by the left observer only and totalled 1038

Table 5: Comparisons of ringed and bearded seals density estimates (seal/km² ice) between right and left observers and inner (0-200m) and outer (200-400m) strips estimated from seven aerial surveys in western Hudson Bay, 1995-2008.

Year	Density estimates				Error variances (10 ⁻³)			% difference [§]		Student's <i>t</i>	
	Left	Right	Outer	Inner	V _w	V _s	σ _b ²	Left-right	Inner-outer	Left-right	Inner-outer
Ringed seals											
1995	1.507	1.683	1.702	1.487	7.364	11.438	8.148	11.7	14.4	4.375*	5.323*
1996	0.953	1.046	0.967	1.032	7.969	10.155	4.372	9.8	6.7	2.816*	1.957
1997	0.573	0.924	0.791	0.706	2.046	3.836	3.579	61.1	12.0	13.099*	3.158*
1999	0.392	0.519	0.540	0.371	2.120	2.301	0.361	32.3	45.3	14.919*	19.817*
2000	0.531	0.703	0.644	0.591	1.784	3.879	4.190	32.2	9.0	3.876*	1.838
2007	0.726	1.191	0.942	0.975	5.413	9.651	8.475	63.9	3.5	11.275*	0.797
2008	0.404	0.542	0.444	0.502	2.156	3.748	3.184	34.3	13.2	5.485*	2.319*
Bearded seals											
1995	0.034	0.012			0.043	0.057	0.027	190.9		9.589*	
1996	0.027	0.011			0.047	0.073	0.051	150.0		4.556*	
1997	0.003	0.004			0.004	0.006	0.004	66.7		2.012 ^a	
1999	0.002	0.006			0.001	0.002	0.002	250.0		7.568*	
2000	0.004	0.010			0.009	0.016	0.015	150.0		3.325*	
2007	0.003	0.013			0.005	0.010	0.010	366.7		6.988*	
2008	0.004	0.006			0.001	0.003	0.004	50.0		2.124 ^a	

Note: V_w is the error variance of the density estimates over the all transect strip (right and left = 2*400 = 800m). V_s is the mean of error variances of density estimates calculated for left and right observers, and inner and outer strips. $\sigma_b^2 = 2(V_s - V_w)$ is the component of the error variance due to variation between-strips/observers. * $p < 0.05$; ^a marginally significant ($p \sim 0.05$); [§] percentage of the smaller value.

sightings. More than twice the number of holes was counted in 2007 compared to 2008 (Table 6). The density of holes on transect was higher on land-fast ice (0.53 holes/km² ice) compared to pack ice (0.26 holes/km² ice) in 2007 but the difference was reduced in 2008 (0.70 vs. 0.63 holes/km² ice for land-fast and pack ice, respectively).

Discussion

During their annual moult, ringed seals in western Hudson Bay were found at higher densities on land-fast ice (1.32-3.36 seals/km²). On pack ice, ringed seals tended to favour consolidated (ice cover 6-8/10; 0.45-1.84 seals/km²) over unconsolidated, *i.e.*, ice consisting of small and scattered floes, pack ice (ice cover 1-5/8; 0.17-0.85 seals/km²; Fig. 3). These results agree with previous studies documenting that ringed seals prefer consolidated, stable ice with evidence of cracks (land-fast ice: range 0.21-10.44, pack ice: range 0.19-1.47; (Burns and Harbo Jr. 1972, Smith 1973, 1975, Stirling et al. 1977, Breton-Provencher 1979, Finley 1979, Heard and Donaldson 1981, Stirling et al. 1982, Finley et al. 1983, Kingsley 1984, Kingsley et al. 1985, Smith 1987, Kingsley 1990, Born et al. 1998, Simpkins et al. 2003, Frost et al. 2004, Bengtson et al. 2005, Krafft et al. 2006). Ringed seals were observed hauled-out around holes and along narrow cracks but never on the floe edge of big leads. Kingsley et al. (1985) found a similar pattern for ringed seals in the high Arctic. Bearded seals however were typically observed basking on the edge of leads in the pack ice

Table 6: Incidental sightings of marine mammals, ringed seal structures (holes and lairs), and polar bear (PB) tracks and kills detected on and off transect during seven aerial surveys in western Hudson Bay, 1995-2008.

	Polar bear	Beluga	Walrus	Bowhead whale	Seal structures		Polar bears	
					Hole [¶]	Lair	Track	Kill
1995	4 (1)	84		2	n/a	n/a	n/a	n/a
1996	15 (3)	10			n/a	n/a	n/a	n/a
1997	8 (1)	17	1		n/a	n/a	n/a	n/a
1999	3 (0)	14			n/a	n/a	n/a	n/a
2000	10 (2)	2			n/a	n/a	n/a	n/a
2007	10 (1)	81			330	39	92	15
2008	8 (0)	45			708	29	70	14

Note: The number of polar bear family groups (females accompanied by cubs) observed is indicated in brackets.

[¶] holes were only recorded by the left observer

and were absent from land-fast ice. Preference of bearded seals for more open and broken ice has been reported in other regions of the Arctic: Bering-Chukchi Seas (Burns 1981, Simpkins et al. 2003, Bengtson et al. 2005); high Arctic (Kingsley et al. 1985); and eastern Beaufort Sea (Stirling et al. 1982). Density estimates of bearded seals were low compared to ringed seals (0.004-0.023) but were in the range found in previous studies in the Canadian Arctic (Heard and Donaldson 1981: 0.011; Stirling et al. 1982: 0.013-0.025; Lunn et al. 1997: 0.122).

Density estimates of ringed seals varied greatly from year to year in western Hudson Bay. Inter-annual variations of ringed seals hauled out on the ice have been reported in the literature (Stirling et al. 1982, Kingsley et al. 1985, Smith 1987, Hammill and Smith 1990, Frost et al. 2004) and, other than an actual change of seal numbers, have been explained by several factors. Ice type and conditions, water depth, temperature, wind speed, cloud cover, time of day and period of the year have all been found to potentially affect ringed seal presence (emigration/immigration), haul out activity and detectability in aerial survey areas (Finley 1979, Smith and Hammill 1981, Stirling et al. 1982, Kingsley et al. 1985, Kelly and Quakenbush 1990, Lunn et al. 1997, Moulton et al. 2002, Frost et al. 2004, Bengtson et al. 2005, Carlens et al. 2006, Kelly et al. 2006, Krafft et al. 2006).

In our study, a decline of 51% was observed in ringed seal density estimates between the 2007 and 2008 surveys, which were flown over 3 days at the same period of the year (end of May) and same time of the day. Percentages of the

different ice types were relatively similar during both years surveyed. However, the pack ice in 2008 was perceived to have fewer cracks and leads than in 2007, which was supported by the overall ice cover in western Hudson Bay that presented a positive anomaly and a late break-up in 2008 compared to 2007. The ice available for hauling out in 2008 was in a more decayed condition than what was recorded for 2007, with considerably more rotten ice. The weather was also colder, windier and cloudier at the time of survey in 2008. In 2008, ringed seals were observed hauled out as individuals more often and group sizes were significantly smaller than in 2007 and the number of holes with no seals associated more than doubled in 2008 compared with 2007.

These findings suggest that the relatively low number of ringed seals detected in 2008 could reflect a low number of ringed seals present in the area (*i.e.*, animals left/did not move in the area), and/or a low number of seals hauled out on the ice at the time of survey (*i.e.*, animals in water, under ice or still in snow lairs), likely due to unsuitable ice and climatic conditions in the survey area. Kelly et al. 2006) suggested that the optimum survey window (*i.e.*, when the highest proportion of seals present in the survey area would be visible) could be after ringed seals emerged from their lairs and before the ice conditions deteriorates, suggesting that the survey in 2008 might have been flown after the optimum window of detectability. Similar results were found by Lunn et al. (1997) for the survey flown in 1994.

Although both the highest estimate of ringed seal density and the largest amount of open water occurred in 1995, we did not find a significant relationship between

the amount of available ice in the survey area and ringed seal density estimates. When estimated over the entire area (water and ice included) and over land-fast ice only (which area did not differ over the years; Table 3), the density of ringed seals in 1995 decreased but was still the highest density recorded throughout the study period and the overall temporal pattern in density estimates remained similar (Fig. 4). We found a negative relationship between ringed seal density estimates and ice coverage in western Hudson Bay around the time of our survey, suggesting that in years of low ice concentration, seals may move to areas where suitable ice to haul out remains. Finley (1979) and Carlens et al. (2006) also noted an influx of ringed seals, abandoning unsuitable ice conditions, in their survey area during the moulting period.

Changes in the environmental conditions at the time of survey may have influenced observed ringed seal density estimates, but changes in demographic parameters of ringed seals recorded in western Hudson Bay over the last 2 decades could be a predominant factor. The decline of ringed seal density estimates from 1995 to 1999 is likely the result of reduced ringed seal recruitment in the 1990s. Indeed, low pregnancy rates (56.5%) and percent of pups in the fall harvest (5.5%) were reported in western Hudson Bay in the 1990s (Holst et al. 1999, Stirling 2005, Chambellant et al. 2010b). Ferguson et al. (2005) confirmed low pup survival in the 1990s compared to the 1980s and suggested a decadal pattern in ringed seal recruitment in western Hudson Bay. In the 2000s (2000-2006), pregnancy rates and percent pups in the fall harvest increased (84% and 17.8%, respectively; Chambellant et al. 2010b) suggesting

that better production and recruitment occurred in the 2000s. Although seal counts in western Hudson Bay were not available from 2001 to 2006, previous findings on ringed seal demographic parameters support the approximate 11-year period cycle of ringed seal density estimates in western Hudson Bay suggested in this study, with a decline in density in the 1990s and an apparent recovery in the 2000s.

Decadal fluctuations, especially in the sea-ice regime through atmospheric forcing (e.g., North Atlantic Oscillation), have been previously described in the Arctic environment (Mysak and Manak 1989, Wang et al. 1994, Hurrell 1995, Mysak et al. 1996, Mysak and Venegas 1998, Johannessen et al. 1999, Marshall et al. 2001, Gagnon and Gough 2005a) and fluctuations in life-history parameters and/or abundance of several Arctic species have been linked to variations in environmental conditions (Skinner et al. 1998, Ottersen et al. 2001, Post and Forchhammer 2002, Stirling 2002, Derocher 2005, Ferguson et al. 2005, Regehr et al. 2007, Irons et al. 2008, Post et al. 2009). Our results suggest that environmental conditions were not favourable for ice-obligated seals in the 1990s in western Hudson Bay, but were more favourable in the 2000s.

In 1991-92, colder than normal conditions were recorded in the eastern Arctic and were attributed to the simultaneous occurrence of a strong positive phase of the North Atlantic Oscillation, a strong El Niño event and the eruption of Mount Pinatubo in June 1991 (Graf et al. 1993, McCormick et al. 1995, Mysak et al. 1996, Gough et al. 2004). In western Hudson Bay, we found that the early 1990s were characterized by heavy ice conditions and late dates of spring break-up.

Similar conditions in the western Arctic in the mid-1970s and 1980s were linked to major ringed seal reproductive failures (Smith 1987, Kingsley and Byers 1998, Stirling 2002) and decline in abundance (Stirling et al. 1982). We suggest that the decline in ringed and bearded seal density estimates observed in the 1990s in western Hudson Bay could have been triggered by the exceptionally cold and heavy ice conditions that prevailed earlier in the decade. Mechanisms involved may include a difficulty or impossibility for seals to maintain breathing holes open in heavy ice (Vibe 1967, Stirling et al. 1982), a increased predation pressure by polar bears which spring hunting season is prolonged in years with late break-up (Stirling 1997, Stirling and Lunn 1997, Stirling et al. 1999), and a decrease in the overall Hudson Bay productivity due to the reduced extent of leads and polynyas in the winter and of the open-water season, creating a nutritional stress in seals. Chambellant et al. (2010a) found that in the early 1990s, late break-up dates induced a reduction in sand lance (*Ammodytes* sp.) availability to ringed seals, resulting in a decrease in ringed seal food consumption and energy acquired, which impacted ringed seal demographic parameters during the entire decade.

In conclusion, this study presented the first time-series data of ringed and bearded seal density estimates in Hudson Bay. Ice-associated seal density estimates in western Hudson Bay may follow a decadal cycle reflecting environmental fluctuations, particularly in the ice regime. Demographic parameters previously reported in the literature showed a similar cycling pattern and strongly supported our interpretation. The natural cycle in seal density estimates is more likely to present a period and amplitude that fluctuate over time

rather than fixed ones, as represented by the sine curve in this study. The sine function was applied to provide a simple graphical representation of the cycling pattern that may occur in seal population dynamics. Since the 1980s, a decline in abundance, body condition, reproductive rates and cub survival of polar bears have been documented in western Hudson Bay (Stirling et al. 1999, Regehr et al. 2007). An earlier laying date and a decrease in chick growth rates and adult body mass was described for thick-billed murres in northern Hudson Bay at the end of the 1990s (Gaston et al. 2005), concurrent with a diet shift toward less arctic cod (*Boreogadus saida*) and more capelin (*Mallotus villosus*; Gaston et al. 2003). Recent, unidirectional climatic trends and changes in polar bear and murre population ecology suggest that long-term modifications may be happening in the Hudson Bay ecosystem. Effects of such long-term changes on ringed seal population dynamics are also expected and previous studies have reported negative effects on pup survival of reduced snow depth, increased rain and early break-up in the spring (Smith and Harwood 2001, Stirling and Smith 2004, Ferguson et al. 2005). A decline in ringed seal density and abundance in western Hudson Bay should therefore not be excluded in the near future, as an underlying trend to the possible natural cycle.

Our ability to examine and interpret trends in seal densities in western Hudson Bay was limited by the absence of survey data over a 6-year period (2001-2006) and strong inter-annual variations. Long-term monitoring of ice-obligated seal density should be considered critical to acquire a better understanding of seal population dynamics, especially in sub-Arctic regions where these species occur

at the southern limit of their range and where impacts of global climatic changes are occurring first (Walsh 2008).

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References

- Bengtson, J.L., Hiruki-Raring, L.M., Simpkins, M.A., and Boveng, P.L. 2005. Ringed and bearded seal densities in the eastern Chukchi Sea, 1999-2000. *Polar Biology* 28: 833-845.
- Boily, P. 1995. Theoretical heat flux in water and habitat selection of phocid seals and beluga whales during annual molt. *Journal of Theoretical Biology* 172: 235-244.
- Born, E.W., Teilmann, J., and Riget, F. 1998. Abundance of ringed seals (*Phoca hispida*) in the Kong Oscars Fjord, Scoresby Sound and adjacent areas in eastern Greenland. In *Ringed seals in the North Atlantic*. Edited by M.P. Heide-Jorgensen and C. Lydersen. The North Atlantic Marine Mammal Commission. Tromso. pp.152-166.
- Breton-Provencher, M. 1979. Etude de la population de phoques annelés (*Phoca hispida*) et des autres pinnipèdes de la région de Poste-de-la-baleine (Nouveau-Québec). GIROQ, Rapport à l'hydro-Québec, Projet Grande-Baleine (Mandat d'avant-projet préliminaire OGB/76-1). 148 pp.
- Buckland, S.T., Anderson, D.R., Burnham, K.P., Laake, J.L., Borchers, D.L., and Thomas, L. 2001. *Introduction to distance sampling, estimating abundance of biological populations*. Oxford University Press. New York.
- Burnham, K.P. and Anderson, D.R. 1984. The need for distance data in transect counts. *Journal of Wildlife Management* 48(4): 1248-1254.

Burnham, K.P., Anderson, D.R., and Laake, J.L. 1985. Efficiency and bias in strip- and line-transect sampling. *Journal of Wildlife Management* 49(4): 1012-1018.

Burns, J.J. 1981. Bearded seal *Erignathus barbatus* Erxleben, 1777. In *Handbook of marine mammals. Edited by S.H. Ridgway and R.J. F. R. S. Harrison*. Academic Press. London, New-York, Toronto, Sydney, Dan Francisco. pp.145-170.

Burns, J.J. and Harbo Jr., S.J. 1972. An aerial census of ringed seals, northern coast of Alaska. *Arctic* 25(4): 279-290.

Carlens, H., Lydersen, C., Krafft, B.A., and Kovacs, K.M. 2006. Spring haul-out behavior of ringed seals (*Pusa hispida*) in Kongsfjorden, Svalbard. *Marine Mammal Science* 22(2): 379-393.

Chambellant, M. and Ferguson, S.H. 2009. Comparison of strip- and line-transect sampling to estimate density and abundance of ringed seals (*Phoca hispida*) in western Hudson Bay, 2007 and 2008. *Can. Sci. Advis. Sec., Res. Doc.* 2009/002. iv + 19 pp.

Chambellant, M., Stirling, I., and Ferguson, S.H. 2010a. Temporal variation in western Hudson Bay ringed seal (*Phoca hispida*) diet as an indicator of ecosystem changes. *Marine Ecology Progress Series* Submitted in August 2010.

- Chambellant, M., Stirling, I., Gough, W.A., and Ferguson, S.H. 2010b. Temporal variations in Hudson Bay ringed seal (*Phoca hispida*) life-history parameters in relation to environment. *Journal of Mammalogy* Submitted in July 2010.
- Comiso, J.C. 2002. A rapidly declining perennial sea ice cover in the Arctic. *Geophysical Research Letters* 29(20): 171-174.
- Comiso, J.C. 2003. Warming trends in the Arctic from clear sky satellite observations. *Journal of Climate* 16: 3498-3510.
- Comiso, J.C., Parkinson, C.L., Gersten, R., and Stock, L. 2008. Accelerated decline in the Arctic sea ice cover. *Geophysical Research Letters* 35: L01703.
- Derocher, A.E. 2005. Population ecology of polar bears at Svalbard, Norway. *Population Ecology* 47: 267-275.
- Feltz, E.T. and Fay, F.H. 1966. Thermal requirements *in vitro* of epidermal cells from seals. *Cryobiology* 3: 261-264.
- Ferguson, S.H., Stirling, I., and McLoughlin, P. 2005. Climate change and ringed seal (*Phoca hispida*) recruitment in western Hudson Bay. *Marine Mammal Science* 21(1): 121-135.
- Finley, K.J. 1979. Haul-out behaviour and densities of ringed seals (*Phoca hispida*) in the Barrow Strait area, N.W.T. *Canadian Journal of Zoology* 57: 1985-1997.

Finley, K.J., Miller, G.W., Davis, R.A., and Koski, W.R. 1983. A distinctive large breeding population of ringed seals (*Phoca hispida*) inhabiting the Baffin Bay pack ice. *Arctic* 36(2): 162-173.

Frost, K.J. and Lowry, L.F. 1981. Ringed, Baikal and Caspian seals *Phoca hispida* Schreber, 1775; *Phoca sibirica* Gmelin, 1788 and *Phoca caspica* Gmelin, 1788. In *Handbook of marine mammals*. Edited by S.H. Ridgway and R.J. Harrison F.R.S. Academic Press. London, New York, Toronto, Sydney, San Francisco. pp.29-53.

Frost, K.J., Lowry, L.F., Pendleton, G., and R., N.H. 2004. Factors affecting the observed densities of ringed seals, *Phoca hispida*, in the Alaskan Beaufort Sea, 1996-99. *Arctic* 57(2): 115-128.

Gagnon, A.S. and Gough, W.A. 2005a. Trends in the dates of ice freeze-up and break-up over Hudson Bay, Canada. *Arctic* 58(4): 370-382.

Gagnon, A.S. and Gough, W.A. 2005b. Climate change scenarios for the Hudson Bay region: an intermodel comparison. *Climatic Change* 69: 269-297.

Gaston, A.J. and Woo, K. 2008. Razorbills (*Alca torda*) follow subarctic prey into the Canadian Arctic: colonization results from climate change? *The Auk* 125(4): 939-942.

Gaston, A.J., Woo, K., and Hipfner, J.M. 2003. Trends in forage fish populations in northern Hudson bay since 1981, as determined from the diet of nestling thick-billed murres, *Uria lomvia*. *Arctic* 56(3): 227-233.

- Gaston, A.J., Gilchrist, H.G., and Hipfner, J.M. 2005. Climate change, ice conditions and reproduction in an Arctic marine bird: Brunnich's guillemot (*Uria lomvia* L.). *Journal of Animal Ecology* 74: 832-841.
- Gough, W.A. and Wolfe, E. 2001. Climate change scenarios for Hudson bay, Canada, from general circulation models. *Arctic* 54(2): 142-148.
- Gough, W.A., Cornwell, A.R., and Tsuji, L.J.S. 2004. Trends in seasonal sea ice duration in southwestern Hudson Bay. *Arctic* 57(3): 299-305.
- Graf, H.-F., Kirchner, I., Robock, A., and Schult, I. 1993. Pinatubo eruption winter climate effects: model versus observations. *Climate Dynamics* 9: 81-93.
- Hammill, M.O. and Smith, T.G. 1989. Factors affecting the distribution and abundance of ringed seal structures in Barrow Strait, Northwest Territories. *Canadian Journal of Zoology* 67: 2212-2219.
- Hammill, M.O. and Smith, T.G. 1990. Application of removal sampling to estimate the density of ringed seals (*Phoca hispida*) in Barrow Strait, Northwest Territories. *Canadian Journal of Fisheries and Aquatic Sciences* 47: 244-250.
- Hammill, M.O. and Smith, T.G. 1991. The role of predation in the ecology of ringed seal in Barrow strait, Northwest Territories, Canada. *Marine Mammal Science* 7(2): 123-135.
- Hammill, M.O., Lydersen, C., Ryg, M., and Smith, T.G. 1991. Lactation in the ringed seal (*Phoca hispida*). *Canadian Journal of Fisheries and Aquatic Sciences* 48: 2471-2476.

Harington, C.R. 2008. The evolution of Arctic marine mammals. Ecological Applications 18 Supplement(2): S23-S40.

Harwood, L.A., Smith, T.G., and Melling, H. 2000. Variation in reproduction and body condition of the ringed seal (*Phoca hispida*) in the western Prince Albert Sound, NT, Canada, as assessed through a harvest-based sampling program. Arctic 53(4): 422-431.

Heard, D.C. and Donaldson, J.L. 1981. Distribution and abundance of ringed and bearded seals in Wager Bay, N.W.T. N.W.T. Wildlife Service. File Report #12. 20 pp.

Hochheim, K., Barber, D.G., and Lukovich, J.V. 2010. Changing sea ice conditions in Hudson Bay, 1980-2005. In A little less Arctic: Top predators in the world's largest northern inland sea, Hudson Bay. Edited by S.H. Ferguson, L.L. Loseto and M.L. Mallory. Springer. Dordrecht, Heidelberg, London, New York. pp.39-51.

Holst, M., Stirling, I., and Calvert, W. 1999. Age structure and reproductive rates of ringed seals (*Phoca hispida*) on the northwestern coast of Hudson Bay in 1991 and 1992. Marine Mammal Science 15(4): 1357-1364.

Hone, J. 1988. A test of the accuracy of line- and strip-transect estimators in aerial survey. Australian Wildlife Research 15: 493-497.

Hurrell, J.W. 1995. Decadal trends in the North Atlantic oscillation: regional temperatures and precipitation. Science 269: 676-679.

IPCC (Intergovernmental Panel on Climate Change) 2007. Climate Change
2007: Synthesis Report. Edited by R.K. Pachauri and A. Reisinger. 104 pp.

<http://www.ipcc.ch/ipccreports/ar4-syr.htm>

Irons, D.B., Anker-Nilssen, T., Gaston, A.J., Byrd, G.V., Falk, K., Gilchrist, G.,
Hario, M., Hjernquist, M., Krasnov, Y.V., Mosbech, A., Olsen, B., Petersen, A.,
Reid, J.B., Robertson, G.J., Strom, H., and Wohl, K.D. 2008. Fluctuations in
circumpolar seabird populations linked to climate oscillations. Global Change
Biology 14: 1455-1463.

Johannessen, O.M., Shalina, E.V., and Miles, M.W. 1999. Satellite evidence for
an Arctic sea ice cover in transformation. Science 286(3): 1937-1939.

Johannessen, O.M., Bengtsson, L., Miles, M.W., Kuzmina, S.I., Semenov, V.A.,
Alekseev, G.V., Nagurnyi, A.P., Zakharov, V.F., Bobylev, L.P., Pettersson,
L.H., Hasselmann, K., and Cattle, H.P. 2004. Arctic climate change: observed
and modelled temperature and sea-ice variability. Tellus 56A: 328-341.

Kelly, B.P. and Quakenbush, L.T. 1990. Spatiotemporal use of lairs by ringed
seals (*Phoca hispida*). Canadian Journal of Zoology 68: 2503-2512.

Kelly, B.P., Badajos, O.H., Kunnsranta, M., and Moran, J. 2006. Timing and re-
interpretation of ringed seal surveys. School of Fisheries and Oceans
Sciences. Final Report. OCS Study MMS 2006-013. University of Alaska
Fairbanks. 60 pp.

Kelly, B.P., Badajos, O.H., Kunnasranta, M., Moran, J.R., Martinez-Bakker, M., Wartzok, D., and Boveng, P. 2010. Seasonal home ranges and fidelity to breeding sites among ringed seals. *Polar Biology* 33: 1095-1109.

Kingsley, M.C.S. 1984. The abundance of ringed seals in the Beaufort Sea and Amundsen Gulf, 1983. Canadian Manuscript Report of Fisheries and Aquatic Sciences 1778: 1-8.

Kingsley, M.C.S. 1990. Status of the ringed seal, *Phoca hispida*, in Canada. *Canadian Field Naturalist* 104(1): 138-145.

Kingsley, M.C.S. and Smith, G.E.J. 1981. Analysis of data arising from systematic transect surveys. In *Symposium on census and inventory methods for populations and habitats*. Edited by F.L. Miller and A. Gunn. Forest, Wildlife and Range Experiment Station, University of Idaho. Moscow, Idaho. pp.40-48.

Kingsley, M.C.S. and Byers, T.J. 1998. Failure in reproduction of ringed seals (*Phoca hispida*) in Amundsen Gulf, Northwest Territories in 1984-1987. In *Ringed seals in the North Atlantic*. Edited by M.P. Heide-Jorgensen and C. Lydersen. The North Atlantic Marine Mammal Commission. Tromso. pp.197-210.

Kingsley, M.C.S., Stirling, I., and Calvert, W. 1985. The distribution and abundance of seals in the Canadian high Arctic, 1980-82. *Canadian Journal of Fisheries and Aquatic Sciences* 42: 1189-1210.

- Krafft, B.A., Kovacs, K.M., Andersen, M., Aars, J., Lydersen, C., Ergon, T., and Haug, T. 2006. Abundance of ringed seals (*Pusa hispida*) in the fjords of Spitsbergen, Svalbard, during the peak molting period. *Marine Mammal Science* 22(2): 394-412.
- Laidre, K.L., Stirling, I., Lowry, L.F., Wiig, O., Heide-Jorgensen, M.P., and Ferguson, S.H. 2008. Quantifying the sensitivity of Arctic marine mammals to climate-induced habitat change. *Ecological Applications* 18(2 Supplement): S97-S125.
- Lunn, N.J., Stirling, I., and Nowicki, S.N. 1997. Distribution and abundance of ringed (*Phoca hispida*) and bearded seals (*Erignathus barbatus*) in western Hudson Bay. *Canadian Journal of Fisheries and Aquatic Sciences* 54: 914-921.
- Lunn, N.J., Stirling, I., and Davis, C. 2000. Distribution and abundance of seals in western Hudson Bay. Annual progress report for Manitoba Hydro. 19 pp.
- Mansfield, A.W. 1967. Seals of Arctic and eastern Canada. *Fisheries Research Board of Canada, Bulletin* 137, 35 pp.
- Marshall, J., Kushnir, Y., Battisti, D., Chang, P., Czaja, A., Dickson, R., Hurrell, J., McCartney, M., Saravanan, R., and Visbeck, M. 2001. North Atlantic climate variability: phenomena, impacts and mechanisms. *International Journal of Climatology* 21: 1863-1898.

McCormick, M.P., Thomason, L.W., and Trepte, C.R. 1995. Atmospheric effects of the Mt Pinatubo eruption. *Nature* 373: 399-404.

McLaren, I.A. 1958. The biology of the ringed seal (*Phoca hispida* Schreber) in the eastern Canadian Arctic97 pp.

Moulton, V.D., Richardson, W.J., McDonald, T.L., Elliott, R.E., and Williams, M.T. 2002. Factors influencing local abundance and haul-out behaviour of ringed seals (*Phoca hispida*) on land fast ice in the Alaskan Beaufort Sea. *Canadian Journal of Zoology* 80: 1900-1917.

Mysak, L.A. and Manak, D.K. 1989. Arctic sea-ice extent and anomalies, 1953-1984. *Atmosphere-Ocean* 27(2): 376-405.

Mysak, L.A. and Venegas, S.A. 1998. Decadal climate oscillations in the Arctic: a new feedback loop for atmosphere-ice-ocean interactions. *Geophysical Research Letters* 25(19): 3607-3610.

Mysak, L.A., Ingram, R.G., Wang, J., and Van der Baaren, A. 1996. The anomalous sea-ice extent in Hudson Bay, Baffin Bay and the Labrador sea during three simultaneous NAO and ENSO episodes. *Atmosphere-Ocean* 34(2): 313-343.

Ottersen, G., Planque, B., Belgrano, A., Post, E., Reid, P.C., and Stenseth, N.C. 2001. Ecological effects of the North Atlantic Oscillation. *Oecologia* 128: 1-14.

Parkinson, C.L. and Cavalieri, D.J. 2008. Arctic sea ice variability and trends, 1979-2006. *Journal of Geophysical Research* 113: C07003.

Parkinson, C.L., Cavalieri, D.J., Gloerson, P., Zwally, H.J., and Comiso, J.C.

1999. Arctic sea ice extents, areas, and trends, 1978-1996. *Journal of Geophysical Research* 104(C9): 20837-20856.

Post, E. and Forchhammer, M.C. 2002. Synchronization of animal population dynamics by large-scale climate. *Nature* 420: 168-171.

Post, E., Forchhammer, M.C., Bret-Harte, M.S., Callaghan, T.V., Christensen, T.R., Elberling, B., Fox, A.D., Gilg, O., Hik, D.S., Hoye, T.T., Ims, R.A., Jeppesen, E., Klein, D.R., Madsen, J., McGuire, A.D., Rysgaard, S., Schindler, D.E., Stirling, I., Tamstorf, M.P., Tyler, N.J.C., van der Wal, R., Welker, J., Wookey, P.A., Schmidt, N.M., and Aastrup, P. 2009. Ecological dynamics across the Arctic associated with recent climate change. *Science* 325: 1355-1358.

Regehr, E.V., Lunn, N.J., Amstrup, S.C., and Stirling, I. 2007. Effects of earlier sea ice break-up on survival and population size of polar bears in western Hudson Bay. *Journal of Wildlife Management* 71(8): 2673-2683.

Simpkins, M.A., Hiruki-Raring, L.M., Sheffield, G.G., Grebmeier, J.M., and Bengtson, J.L. 2003. Habitat selection by ice-associated pinnipeds near St. Lawrence Island, Alaska in March 2001. *Polar Biology* 26: 577-586.

Skinner, W.R., Jefferies, R.L., Carleton, T.J., Rockwell, R.F., and Abraham, K.F. 1998. Prediction of reproductive success and failure in lesser geese based on early season climatic variables. *Global Change Biology* 4: 3-16.

Smith, T.G. 1973. Population dynamics of the ringed seal in the Canadian eastern Arctic 55 pp.

Smith, T.G. 1975. Ringed seals in James Bay and Hudson Bay: Population estimates and catch statistics. Arctic 28: 170-182.

Smith, T.G. 1987. The ringed seal, *Phoca hispida*, of the Canadian western Arctic 81 pp.

Smith, T.G. and Stirling, I. 1975. The breeding habitat of the ringed seal (*Phoca hispida*). The birth lair and associated structures. Canadian Journal of Zoology 53: 1297-1305.

Smith, T.G. and Hammill, M.O. 1981. Ecology of the ringed seal, *Phoca hispida*, in its fast ice breeding habitat. Canadian Journal of Zoology 59: 966-981.

Smith, T.G. and Harwood, L.A. 2001. Observations of neonate ringed seals, *Phoca hispida*, after early break-up of the sea ice in Prince Albert Sound, Northwest Territories, Canada, Spring 1998. Polar Biology 24: 215-219.

Smith, T.G., Hammill, M.O., and Taugbol, G. 1991. A review of the developmental, behavioral and physiological adaptations of the ringed seal, *Phoca hispida*, to life in the Arctic winter. Arctic 44(2): 124-131.

Stirling, I. 1997. The importance of polynyas, ice edges, and leads to marine mammals and birds. Journal of Marine Systems 10: 9-21.

Stirling, I. 2002. Polar bears and seals in the eastern Beaufort Sea and Amundsen Gulf: a synthesis of population trends and ecological relationships over three decades. *Arctic* 55(supp.1): 59-76.

Stirling, I. 2005. Reproductive rates of ringed seals and survival of pups in northwestern Hudson Bay, Canada, 1991-2000. *Polar Biology* 28: 381-387.

Stirling, I. and Lunn, N.J. 1997. Environmental fluctuations in Arctic marine ecosystems as reflected by variability in reproduction of polar bears and ringed seals. *In Ecology of Arctic environments. Edited by S.J. Woodin and M. Marquiss. Blackwell Science.* pp.167-181.

Stirling, I. and Smith, T.G. 2004. Implications of warm temperatures and an unusual rain event for the survival of ringed seals on the coast of southeastern Baffin Island. *Arctic* 57(1): 59-67.

Stirling, I. and Parkinson, C.L. 2006. Possible effects of climate warming on selected populations of polar bears (*Ursus maritimus*) in the Canadian Arctic. *Arctic* 59(3): 261-275.

Stirling, I., Archibald, W.R., and DeMaster, D. 1977. Distribution and abundance of seals in the Eastern Beaufort Sea. *Fisheries Research Board of Canada* 34: 976-988.

Stirling, I., Kingsley, M.C.S., and Calvert, W. 1982. The distribution and abundance of seals in the eastern Beaufort Sea, 1974-79. *Canadian Bulletin of Fisheries and Aquatic Sciences. Occasional paper* 47. 23 pp.

Stirling, I., Lunn, N.J., and Iacozza, J. 1999. Long-term trends in the population ecology of polar bears in western Hudson Bay in relation to climatic change. *Arctic* 52(3): 294-306.

Stirling, I., Lunn, N.J., Iacozza, J., Elliott, C., and Obbard, M. 2004. Polar bear distribution and abundance on the southwestern Hudson Bay coast during open-water season, in relation to population trends and annual ice pattern. *Arctic* 57(1): 15-26.

Tynan, C.T. and DeMaster, D.P. 1997. Observations and predictions of Arctic climatic change: potential effects on marine mammals. *Arctic* 50(4): 308-322.

Vibe, C. 1967. Arctic animals in relation to climatic fluctuations. C.A. Reitzels Forlag. Kobenhavn.

Walsh, J.E. 2008. Climate of the Arctic marine environment. *Ecological Applications* 18(2 Supplement): S3-S22.

Wang, J., Mysak, L.A., and Ingram, R.G. 1994. Inter-annual variability of sea-ice cover in Hudson Bay, Baffin Bay and the Labrador Sea. *Atmosphere-Ocean* 32(2): 421-447.

Woollett, J.M., Henshaw, A.S., and Wake, C.P. 2000. Palaeoecological implications of Archaeological seal bone assemblages: case studies from Labrador and Baffin Island. *Arctic* 53(4): 395-413.

Chapter 3

Temporal variations in Hudson Bay
ringed seal (*Phoca hispida*) life-history
parameters in relation to environment.



Temporal variations in Hudson Bay ringed seal (*Phoca hispida*) life-history parameters in relation to environment.

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Abstract

Climatic changes could have a strong influence on the inter-annual variations in demographic parameters of long-lived vertebrates. The ringed seal (*Phoca hispida*), an ice-dependent phocid, has been reported to be sensitive to changes in ice conditions and snow depth. We related temporal variation of environmental variables to demographic parameters of ringed seals in Hudson Bay, where they occur at the southern limit of the geographic range of the species. Ringed seals were measured and sampled from fall subsistence harvests in the Inuit community of Arviat, Nunavut, located on the western Hudson Bay coast over the period 1991-2006. Ringed seal pupping dates extended over a 44 days period, with a peak at the beginning of March. Ringed seal ovulation rate did not change over time, but pregnancy rate and percent pups in the fall harvest increased in the 2000s compared to low values in the 1990s. Age at maturity and age at first parturition for female ringed seals decreased from 5.4 and 7.3 years in the 1990s to 3.8 and 5.5 years in the 2000s, respectively. Ringed seals grew faster, adult females were longer and the age structure shifted to younger age-classes in the 2000s compared to the 1990s. A survivorship curve suggested strong cohorts in the 1980s and possibly 2000s, and weak cohorts in the 1970s and 1990s. The body condition index (BCI) of adult females tended to decrease over the years surveyed, but no significant trend was detected for juvenile or pup BCI. A polynomial regression best described the relationship between 1) percent pups in the harvest and snow depth; and 2) pup and adult female body condition index and date of spring break-up, suggesting that ringed seals are adapted to a limited

range of environmental variations. Ringed seal demographic parameters were characteristic of a population in decline in the 1990s and a growing population in the 2000s. We propose that the decline of ringed seal reproductive parameters in the 1990s could have been triggered by cold winters and heavier ice conditions that prevailed in Hudson Bay at the beginning of the 1990s, through nutritional stress and increased predation pressure. The recovery in the 2000s may have been augmented by the immigration of pups, juveniles, and young adult ringed seals into the study area. We discuss the possibility of a decadal-scale biological cycle that reflects fluctuations in climatic variables, and especially in the sea-ice regime.

Key words: age at maturity, body condition, decadal cycle, foetus, immigration, pregnancy rate, pup survival, reproduction, sea-ice spring break-up, snow depth.

Introduction

Depending on environmental conditions, individuals must adopt a reproductive strategy that will maximize their fitness through trade-offs in resource allocation to growth/maintenance and reproduction, thus shaping the population structure and dynamics (Stearns 1992). Changes in population dynamics could reflect large-scale changes in the ecosystem and result from variations in life-history parameters such as juvenile survival, age at first reproduction, reproductive rates, adult survival, and dispersal (Fowler and Smith 1978, Caughley 1980, Hindell 1991). In large, long-lived vertebrates, a decrease in resource availability has been shown to affect early survival first, followed by a reduced growth rates leading to an increase in the age at first reproduction, and possibly to a decline in reproductive parameters. Adult survival shows the highest degree of elasticity to environmental variations, but a decline in adult survival, and particularly female survival, has the greatest impact on population growth (Hanks 1978, Gaillard et al. 1998, Eberhardt 2002). Growing populations typically exhibit low juvenile mortality, early sexual maturity, and high reproductive rates and adult survival (Hanks 1978). Identifying the factors and mechanisms involved in the variation of these life-history traits is thus a major concern in ecology and has significant implications for management and conservation (Caughley 1980, Gaillard et al. 1998).

Climatic changes could have a strong influence on the inter-annual variations in demographic parameters of both terrestrial and marine long-lived vertebrate species (e.g., Trillmich and Ono 1991, Barbraud and Weimerskirch 2001,

Forchhammer et al. 2001, Stenseth et al. 2002). Hudson Bay, a large Canadian inland sea, ice-covered from November to June (Markham 1986, Saucier et al. 2004), has seen a reduction of the sea-ice-extent and snow depth, whereas the surface air temperature increased, leading to earlier dates of spring sea ice break-up (about 10 days per decade) and lengthening of the open-water season (Skinner et al. 1998, Parkinson et al. 1999, Stirling et al. 1999, Gough et al. 2004, Stirling et al. 2004, Ferguson et al. 2005, Gagnon and Gough 2005b, Stirling and Parkinson 2006, Parkinson and Cavalieri 2008). General circulation models for Hudson Bay under different climate change scenarios predict that the observed trends will continue, with dramatic consequences for the annual cryogenic cycle (Gough and Wolfe 2001, Gagnon and Gough 2005a). On top of possible shifts in prey distribution and availability, Arctic species dependent on the sea-ice platform for most of their life-cycle, such as polar bears (*Ursus maritimus*) and seals, will also be impacted by sea ice habitat loss, likely resulting in changes of distribution, nutrition, reproduction, and ultimately survival and abundance of these species (Tynan and DeMaster 1997, Laidre et al. 2008).

Such changes in life-history traits of ice-associated species have already been observed in the Hudson Bay ecosystem. An earlier laying date and a decrease in chick growth rate and adult body mass were described for thick-billed murres (*Uria lomvia*) in northern Hudson Bay at the end of the 1990s (Gaston et al. 2005). During the same period, a shift toward less arctic cod (*Boreogadus saida*), a typical ice-associated species, and more capelin (*Mallotus villosus*), an open-water sub-Arctic species, was reported in the prey murres brought back to their

nestlings and was related to a reduction in the mid-July sea-ice cover, suggesting a regime transition may have occurred at the end of the 1990s (Gaston et al. 2003). Polar bear abundance, body condition, reproductive rate, and cub survival have declined in western Hudson Bay since the 1980s, and the earlier dates of ice break-up in the spring were suggested to be responsible for the observed patterns (Stirling et al. 1999, Regehr et al. 2007). In addition, as the sea-ice broke-up earlier in the late 1990s in western Hudson Bay, polar bear diet, as represented by biomarkers, consisted of a greater proportion of harbour (*Phoca vitulina*) and harp (*Pagophilus groenlandicus*) seals concurrent with a decrease in ringed seals (*Phoca hispida*; Iverson et al. 2006) or bearded seals (*Erignathus barbatus*; McKinney et al. 2009).

Ringed seals have a circumpolar distribution and are the most numerous of the Arctic pinnipeds (Mansfield 1967, Frost and Lowry 1981). Ringed seals are among the smallest phocids (McLaren 1993), can live up to 40+ years of age and mature around the age of 6 years (McLaren 1958, Smith 1973, Breton-Provencher 1979, Lydersen and Gjertz 1987, Smith 1987, Holst et al. 1999, Krafft et al. 2006, Chambellant 2010). After a gestation of 10-11 months, including a period of suspended development of 2-3 months, a single pup is born in early spring inside a sub-nivean lair built by adult females on stable ice with sufficient snow cover (McLaren 1958, Smith 1973, Smith and Stirling 1975, Smith 1987, Hammill and Smith 1989). Birth lairs with thick and strong snow roofs are critical to ensure pup protection from cold and predators, like polar bears, arctic foxes (*Alopex lagopus*) and humans (McLaren 1958, Smith and Stirling 1975,

Smith 1976, 1980, Hammill and Smith 1991, Smith et al. 1991, Furgal et al. 1996). Pups are weaned before the spring ice break-up, after a six-week lactation period (Hammill et al. 1991), during which mothers rely on both fat reserves and feeding (Lydersen 1995, Kelly and Wartzok 1996, Simpkins et al. 2001). Like other phocids (Bowen 1991), after weaning ringed seal pups may use the ice as a platform to rest while developing foraging skills (Stirling 2005). Mating is thought to occur underwater around the time of weaning (Smith 1987, Lydersen 1995) and precedes the annual moult in June, when ringed seals haul out on ice to bask in the sun (McLaren 1958, Smith 1973). The open water season represents an intense feeding period for ringed seals that replenish their fat reserves after the breeding and moulting seasons, and in anticipation of the upcoming winter (McLaren 1958, Breton-Provencher 1979, Smith 1987, Ryg and Ortsland 1991). When the ice starts to form in late fall, adult ringed seals move toward prime breeding habitats where they are thought to establish territories from which they exclude younger age-classes, that will spend the winter and spring at the ice edge or in leads and polynyas (McLaren 1958, Smith 1973, Smith and Hammill 1981, Stirling et al. 1981, Smith 1987, Holst et al. 1999, Born et al. 2004, Krafft et al. 2007). The ringed seal is only slightly sexually size-dimorphic (McLaren 1993, Chambellant 2010) and is thought to have a weakly polygynous, resource-defence mating system (Smith and Hammill 1981, Krafft et al. 2007, Yurkowski et al. 2010; but see Kelly et al. 2010). During the winter and spring months, adult ringed seals show signs of site fidelity (McLaren 1958,

Smith and Hammill 1981, Kelly and Quakenbush 1990, Krafft et al. 2007, Kelly et al. 2010).

Sufficient snow depth and a stable ice platform in the spring, and a highly productive summer and fall are therefore essential to ringed seal reproductive success and survival. As such, ringed seals are expected to be particularly vulnerable to variations in their sea-ice habitat under the current and predicted climatic changes. In fact, a decrease in the relative abundance of ringed seals during warming/light ice periods has been reported by archaeological and historical studies (Vibe 1967, Woollett et al. 2000, Harrington 2008). More recently, early/late ice break-up, light/heavy ice conditions (Stirling et al. 1982, Smith 1987, Kingsley and Byers 1998, Harwood et al. 2000, Smith and Harwood 2001), unusual warm and/or rain events in the spring (Stirling and Smith 2004), and insufficient snow depth (Hammill and Smith 1991, Ferguson et al. 2005) have been found to negatively affect ringed seal body condition, reproduction and/or survival in the Arctic.

Considering its high degree of adaptation to exploit the sea-ice habitat for reproduction and survival, the ringed seal represents a good model to understand the effect of ecosystem changes on life-history traits and ultimately population dynamics of marine carnivores.

In this study, we assess ringed seal demographic parameters and body condition in western Hudson Bay over 9 sampling years spanning 1991-2006 to test for temporal trends in relation to environmental variation. Our goal is to improve our

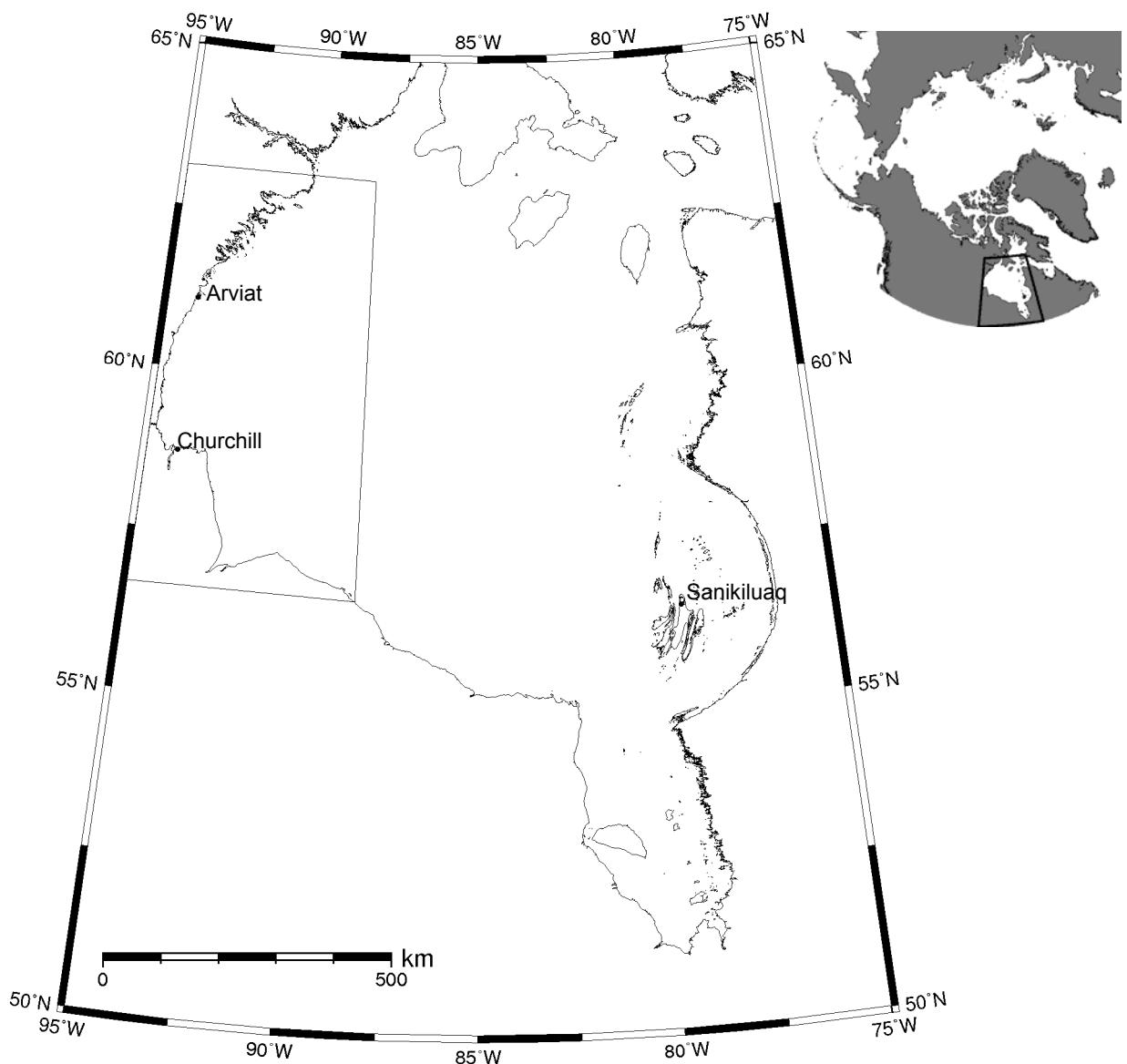
understanding on ringed seal population dynamics in the Hudson Bay ecosystem, that may permit to forecast future responses to climate change and adopt conservation measures required to maintain ringed seal numbers at a level sufficient to provide food for polar bears, cultural and economic resource for Inuit, and a genetic reservoir for the circumpolar species in the Arctic.

Material and Methods

Seal collection

Ringed seals were sampled in 1991, 1992, and 1998-2000 by Canada Wildlife Service and in 2003-2006 by Fisheries and Oceans Canada, from Inuit subsistence fall harvest in the Hudson Bay community of Arviat, Nunavut, Canada (Fig. 1). Ringed seals were hunted non-selectively from September into early November. Seals of all age- and sex-classes are mixed before freeze-up, and thus provide a sample representative of the seals available in Arviat waters at that time of the year (Smith 1973). Inuit hunters were asked to provide basic information (species, sex, date, and location of kill), measurements (standard length, L, axillary girth, and fat depth at the sternum, Committee on marine mammals 1967), the lower jaw, and reproductive organs for all seals. Samples were frozen in the field and sent to Canadian Wildlife Service in Edmonton or Fisheries and Oceans Canada in Winnipeg for analysis.

Figure 1: The study was located in the Inuit community of Arviat, Nunavut, in the western Hudson Bay area (rectangle), Canada.



Age determination

Ringed seal lower jaws were simmered in hot water for 2-3 hours and right canine teeth extracted and preserved in 70% ethanol. When the right canine tooth was not available, another tooth was extracted in the order of preference as follow: 1) the left canine tooth, 2) the right or left first post-canine tooth, 3) a post-canine double-rooted tooth (Chambellant and Ferguson 2009). The periodontal ligament was not cleaned from teeth to prevent potential damage to the most recently deposited annual growth layer group (GLG). Ages were determined by interpreting and counting the GLGs in the cementum of decalcified, stained, longitudinal thin tooth sections (Stirling et al. 1977, Bernt et al. 1996, Stewart et al. 1996). GLGs were counted in 2 to 3 blind replicates for each tooth and final ages were estimated using 2 identical readings or the median of 3 different readings.

Animals born in the spring and harvested in the fall of the same year were referred to as pups. Seals from 1 to 5 years of age were considered juveniles and seals of 6 years of age and older were categorized as adults (Holst et al. 1999).

Reproduction

We examined 230 ringed seal female reproductive tracts. Complete ringed seal female reproductive tracts (uterus and ovaries) were not always provided. When the uterus was provided, we recorded the presence/absence of embryo/foetus, horns measurements, and the parity status based on the size and aspect of uterine horns. Ovaries were detached from oviducts, measured, and weighed

fresh before being soaked in 10% buffered formalin for 2 weeks. Ovaries were then sectioned at 2-3 mm intervals using a razor blade and examined macroscopically for the presence and number of follicles, *corpora lutea*, and *corpora albicantia*.

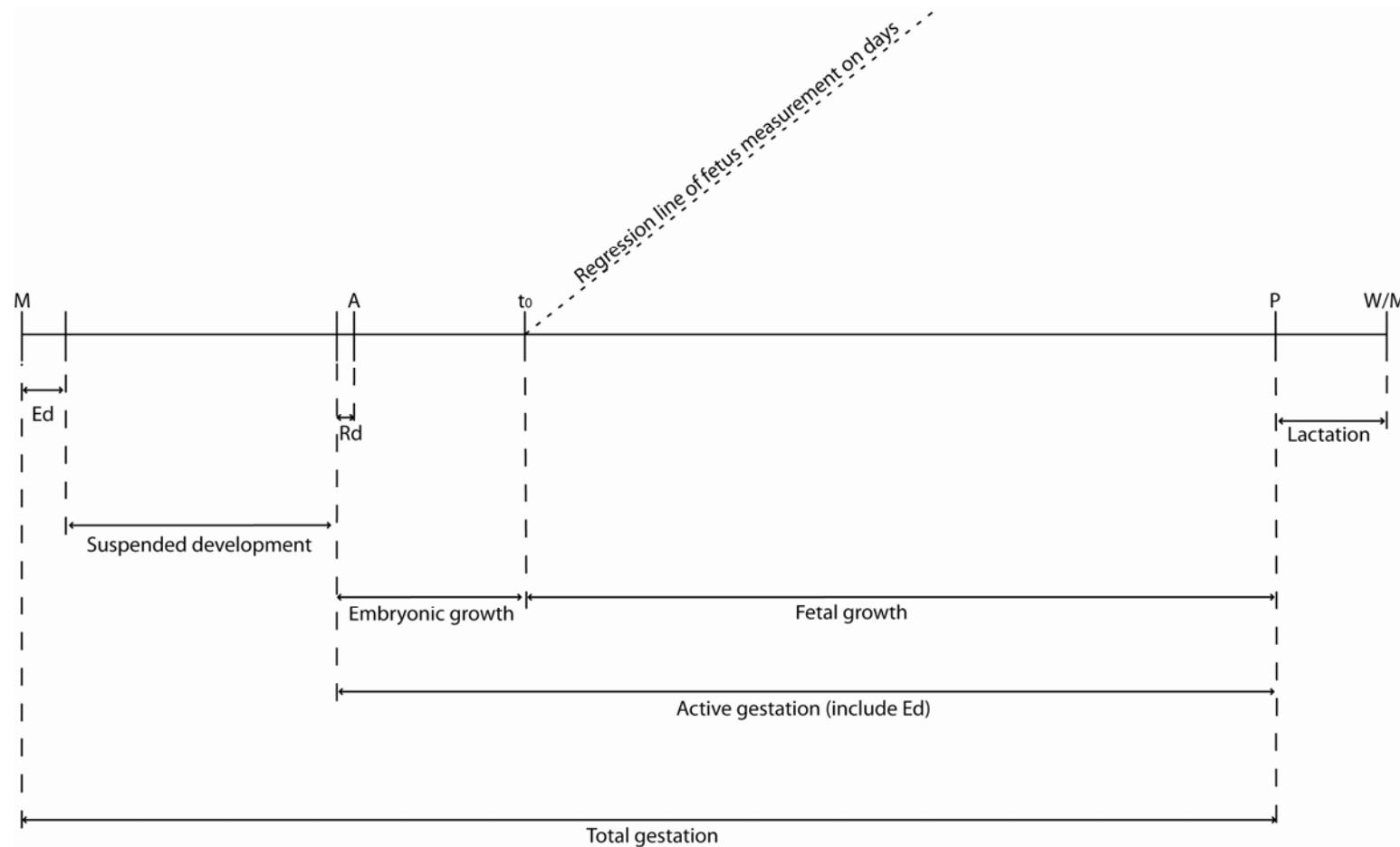
Pregnancy was defined by the presence/absence of a foetus. Ovulation status was determined by the presence or absence of a *corpus luteum* in one of the ovaries of non-pregnant adult females, by the presence of a *corpus luteum* in the ovary of pregnancy, or by the presence of a foetus when no ovaries were collected. The average age of sexual maturity (first ovulation) and at first parturition were computed from the data collected in the 1990s and in the 2000s (year 2000 excluded because only the reproductive tracts of adult seals were processed) by bootstrapping 1000 times with replacement following the algorithm of DeMaster (1981). However, contrary to DeMaster (1981), we chose not to assume that females ovulate every year after sexual maturity, nor that a female that did not ovulate at age x had never ovulated before and used the same algorithm for both age at maturity and at first parturition. Our choice was motivated by the fact that, out of the 136 adult females for which an ovulation status was assessed, eight aged 6 to 17 did not ovulate in the year they were collected although 4 of them exhibited signs of previous gestations as confirmed by the presence of a *corpora albicantia* and/or because of being classified as multiparous following examination of the uterine horns.

Foetal growth rate was estimated by regressing the mass^{1/3} and the standard length of foetuses on the Julian day of collection. Four foetuses collected in

Sanikiluaq, Nunavut, Canada, a Inuit community located on the Belcher Islands in southeastern Hudson Bay (Fig. 1), in early September ($n = 2$), November ($n = 1$) and January ($n = 1$) 2006 were added to the Arviat collection to augment sample sizes. Using a birth mass of 5.4 ± 0.3 kg and standard length of 63.4 ± 1.3 cm (Hammill et al. 1991), we extrapolated the regression line to determine a date of parturition for ringed seal in Hudson Bay. We then calculated a weaning date by adding the 39 days of lactation (Hammill et al. 1991) to the parturition date. We assumed ovulation and mating to be concurrent with weaning date (Smith 1987, Lydersen 1995). Duration of total gestation (G_T) was determined as the time between mating and parturition (Fig. 2). Duration of active gestation (G_A) and suspended development or embryonic diapause (D) and date of attachment (A) of the blastocyst to the uterus wall were determined following a modified method of Huggett and Widdas (1951) and Hewer (1964; Fig. 2). We did not use the regression of days of collection on foetus mass $^{1/3}$ /length to calculate t_0 (intercept of the regression line on the date of collection axis) as suggested in Huggett and Widdas (1951) and Hewer (1964), but used the regression of foetus mass $^{1/3}$ /length on days of collection instead and applied the inverse prediction algorithm to calculate the 95% confidence interval (CI) of the x-intercept as described in Sokal and Rohlf (1995; see also Laws et al. 2003). Time period of the different reproductive cycle events was estimated by calculating regression

Figure 2: Schematic representation of a ringed seal female annual reproductive cycle from mating (M) to weaning of its pup (W). Ed: early development; Rd: recommencement of development; A: attachment; t_0 : start of foetus growth; P: parturition. Adapted from Hewer and Backhouse (1968)

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lines of similar slopes but passing through the extreme data points (McLaren 1958).

Growth

Changes in female standard length with age during the 1990s and the 2000s were described using a sigmoid curve with 3 parameters of the form:

$$y = \frac{a}{1 + e^{-\left(\frac{x-x_0}{b}\right)}} \quad (1)$$

where a is the asymptote, x_0 is the inflection point and b is the slope.

Recruitment

Using the ages of ringed seals collected during the study period to determine the year of birth, recruitment was estimated by the number of ringed seals born in any given year. Survivorship was then modelled by fitting the data with an exponential regression of the form:

$$y = ae^{bx} \quad (2)$$

with y , the number of seals predicted to be in the sample, x , the year of birth, e the base of the natural logarithm, and a and b , constants.

Body condition

Ringed seal body condition was estimated using the general prolate spheroid model described in Goodyear (1999). Briefly, ringed seal body shape was approximated to 2 prolate spheroids: one for the total body shape (total body

volume, TBV) and one for the skeleto-muscular inner core (Fig. 3). The fat volume (FV) was then estimated by a 2-step algorithm:

$$TBV = 4/3 * \pi * 1/2 L * (G/2\pi)^2 \quad (3)$$

where L is the standard length in cm and G the axillary girth in cm, and

$$FV = TBV - 4/3 * \pi * 1/2 L * ((G/2\pi) - F)^2 \quad (4)$$

where F is the fat depth at sternum in cm.

The body condition index (BCI) was then computed by dividing the fat volume by the cubic standard length.

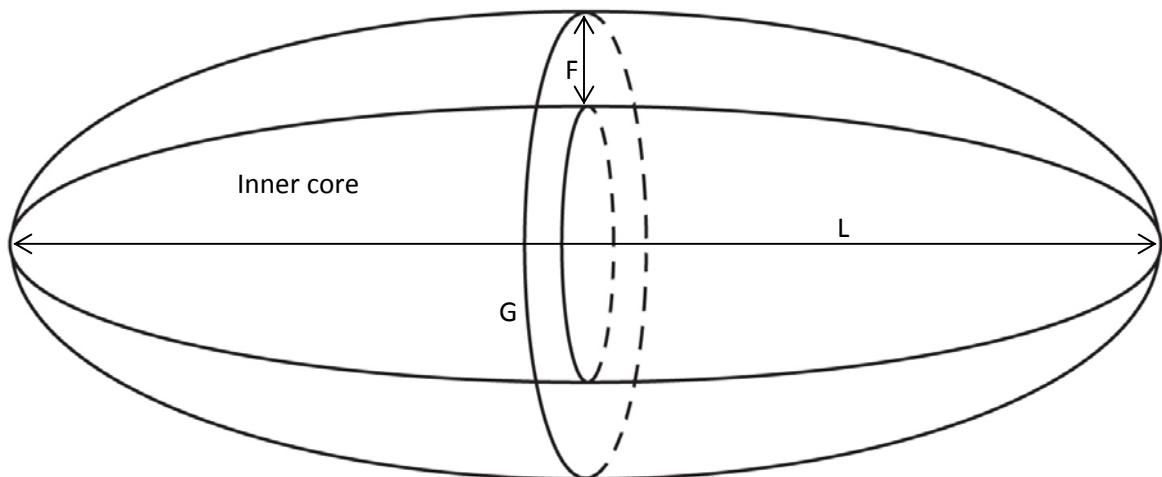
Environmental variables

Daily temperatures, snow depth, and rain in Arviat, NU, were obtained from the airport weather station from 1973 (1985 for snow) to 2007 through Environment Canada: http://www.climate.weatheroffice.ec.gc.ca/climateData/canada_e.html

Temperatures (in °C) were averaged for each year of the study period (1991-2006) per season as follow: 1) winter: 1 January to 31 March; 2) spring: 1 April to 30 June; 3) summer: 1 July to 30 September; and, 4) autumn: 1 October to 31 December. The mean of each season for all years available (1973-75 and 1985-2007) was also computed.

We calculated the maximum snow depth (in cm) for the period February-May for each study year, as well as the average maximum snow depth for all years available (1985-2007).

Figure 3: Sketch of the prolate spheroid model. Ringed seals are modelled as two prolate spheroids inserted in one another, one representing the whole seal body (total volume) and the other one the inner body (inner volume). Fat volume is obtained by subtracting the inner volume to the total volume. Fat depth at sternum (F), standard length (L) and axillary girth (G) are used to compute volumes. Adapted from Goodyear (1999).



The sum of rain fall (in mm) for the months April, May and June was computed from the daily values for each study year and averaged over all years available (1973-75 and 1985-2007).

The percent ice cover of northwest Hudson Bay for 21 May, 28 May, and 4 June (Canadian Ice Service: <http://ice-glaces.ec.gc.ca/>) were averaged to provide a mean ice cover for the period ‘end of May-beginning of June’ for each study year and for all years available (1971-2008).

Break-up and freeze-up dates in western Hudson Bay (as defined in Stirling et al. 1999; Fig. 1) were calculated for 1991 through 2006, following the method described in Gagnon and Gough (2005b). The western Hudson Bay region was divided into a grid 0.5° Latitude $\times 1.5^{\circ}$ Longitude. Weekly ice concentration maps of Hudson Bay were retrieved from the Canadian Ice Service and used to obtain the ice concentration at the 42 center points defined by the grid. The break-up date (± 1 week) at each point was then defined as the earliest date with an ice concentration of 50% or less, if this condition was maintained for the next 2 weeks. Freeze-up dates were obtained when the ice concentration at each point reached 50% over the period October-December, and maintained this condition for the next 2 weeks. Break-up and freeze-up dates for the entire western Hudson Bay region were then computed by taking the median of the 42 center points of the grid.

The sea surface chlorophyll a concentration (mg/m^3) in the western Hudson Bay region during the open water seasons (June to October) of 1998 to 2006 was

obtained from the Sea-viewing Wide Field-of-view Sensor (SeaWiFS) Level 3 monthly composite images at 9 km resolution, distributed by the Ocean Color Group at NASA (Feldman and McClain 2009). A new composite was created for the time period available (1998-2006) using SEADAS software (Baith et al. 2001; Fig. 4). The mean chlorophyll a concentration of the 11,658 cells of the western Hudson Bay region was used as an index of primary productivity.

Statistical analyses

Normality was assessed using the Anderson-Darling test and determined whether parametric or nonparametric tests were employed.

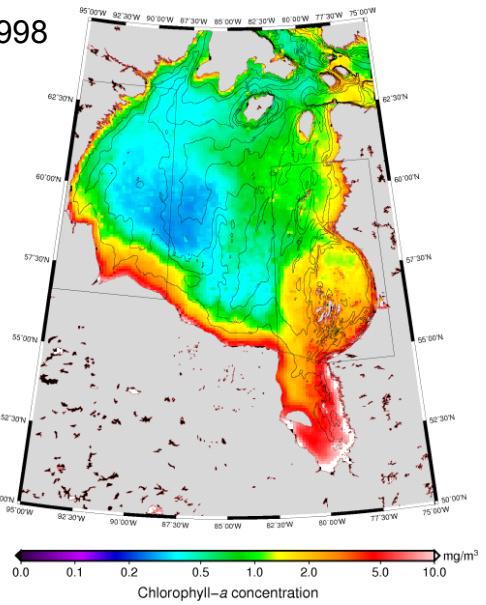
The sex-ratio was assessed for unity departure using a G-test goodness-of-fit with Williams's correction (Sokal and Rohlf 1995). Percent of pups in the harvest, ovulation, and pregnancy rates in the 1990s and 2000s were compared using a G-test of independence with Williams's correction (Sokal and Rohlf 1995).

The mean age at maturity and first parturition, the mean BCI, the mean length of open water period, sum of rain fall, spring temperatures, and percent ice cover between 1990s and 2000s were compared using a *t*-test with Welch correction to account for different standard deviations (Zar 1996), when necessary. The median age and adult female length and the median date of spring break-up and maximum snow depth between the 2 decades were compared using a Mann-Whitney test corrected for tied and large samples since normality of residuals was not reached.

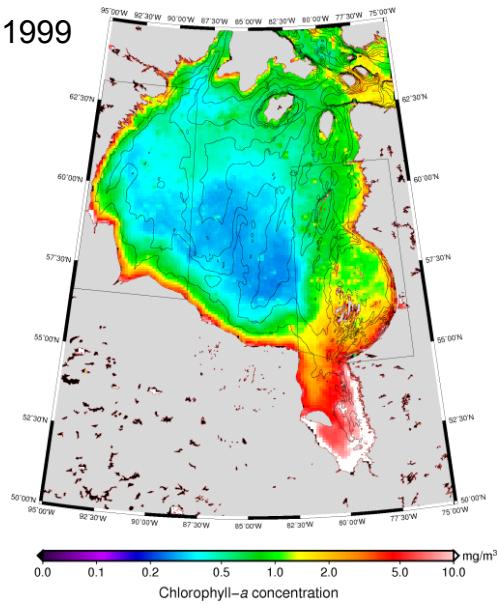
Figure 4: Sea-surface chlorophyll a concentration (mg/cm^3) during the open-water season in Hudson Bay from 1998 to 2006. Rectangles indicate the western and eastern Hudson Bay regions.

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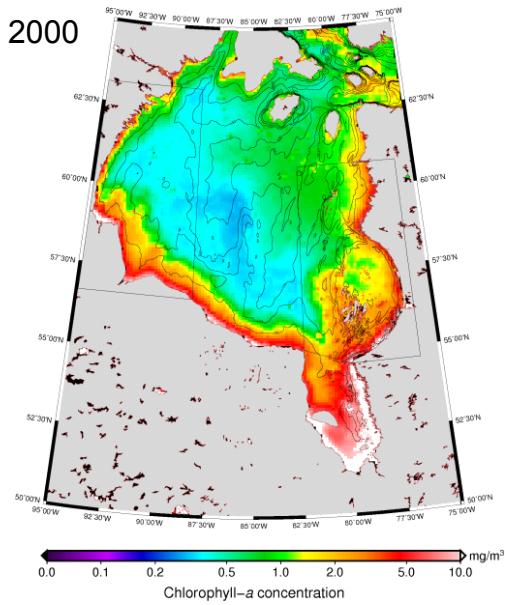
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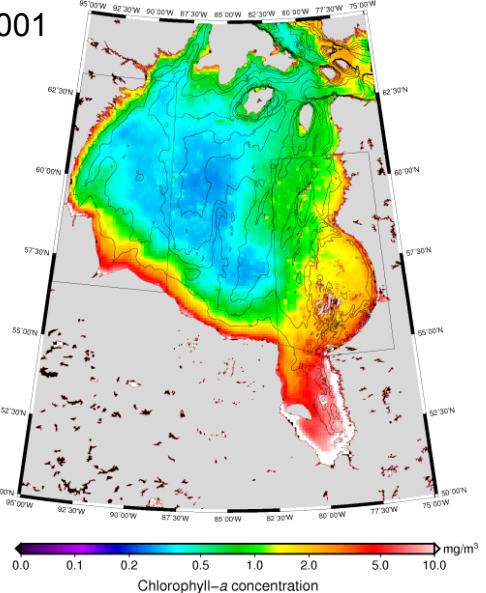
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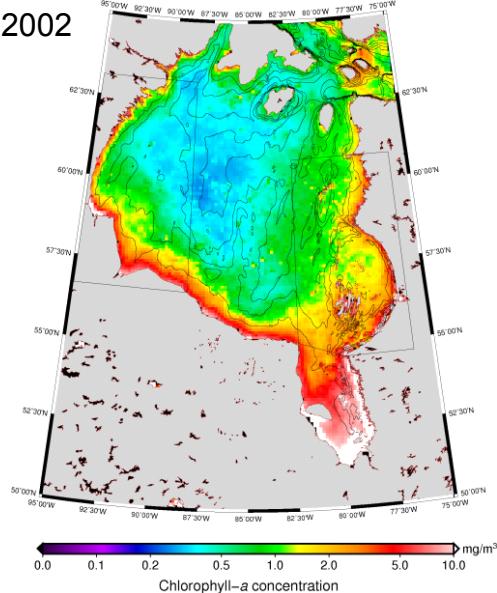
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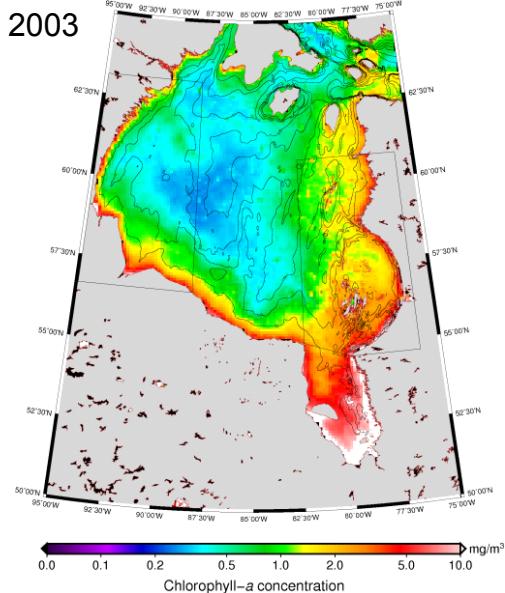
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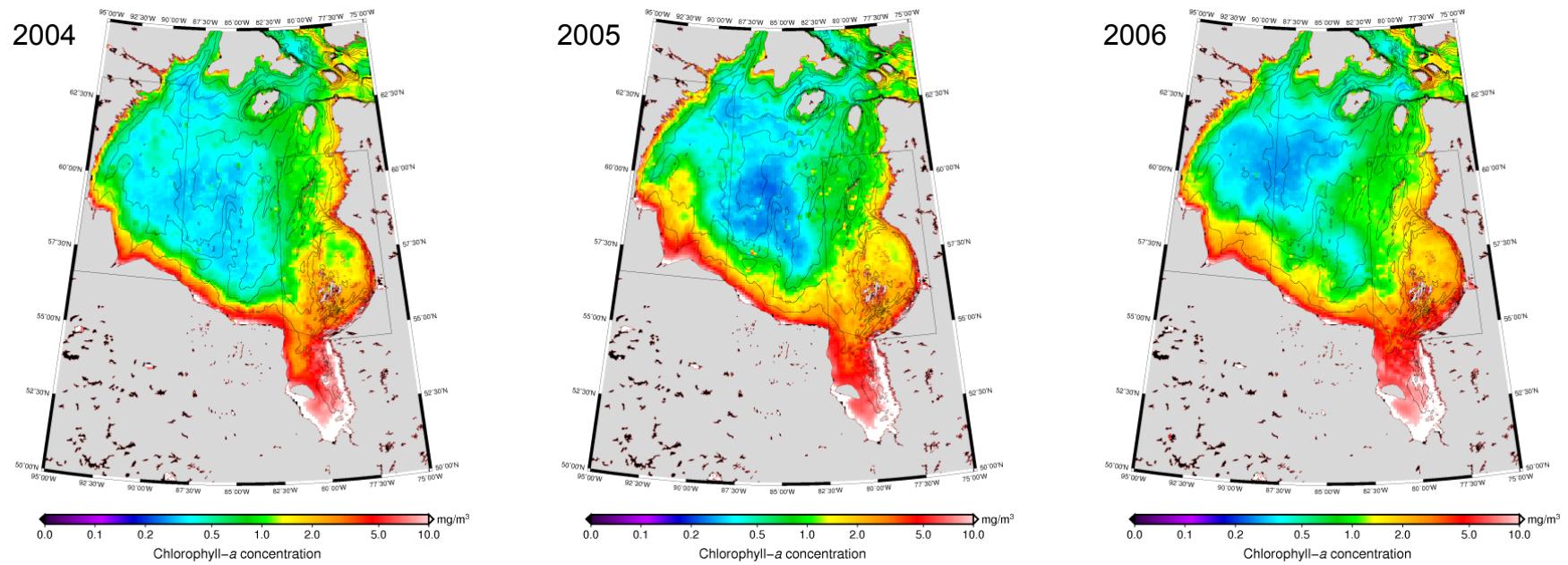
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Correlations between percent pups in the harvest, ovulation and pregnancy rates, and BCI were investigated using Spearman rank order correlation (r_s).

Correlations between environmental variables were explored using Pearson product moment correlation analyses (r_P).

To remove the year effect in the analyses, residuals of the linear regression of ringed seal demographic and body condition parameters over years were used to explore relationships (linear or polynomial) with environmental variables.

Statistical analyses were performed using Systat 12 (Systat Software Inc. 2007), SigmaPlot 11 (Systat Software Inc. 2008) and the GNU R system (R Development Core Team 2004). Unless otherwise stated, results are provided as mean \pm standard deviation (SD) or median [1st-3rd quartile]. All tests were 2-tailed and differences considered significant at $p < 0.05$.

Results

A total of 672 ringed seals were sampled through the study period. Median dates of collection were fairly constant over the years (mid- to late October), with the exception of 2006 when 69% (33/48) of the sample was collected in early November (Table 1).

The global sex-ratio of adults was not different from 1:1 ($G_{corr} = 2.66$, $n = 338$, $p > 0.1$) but was significantly male biased in 2000 ($G_{corr} = 10.95$, $n = 54$, $p < 0.001$) and female biased in 2005 ($G_{corr} = 4.61$, $n = 22$, $p < 0.05$; Table 1). The adult

Table 1: Date of sampling, sample size of collection, percentage of adults, and sex-ratio of ringed seals sampled during the fall subsistence harvest in Arviat, NU, from 1991 to 2006. An asterisk denotes a statistical difference. ns: non-significant; n: sample size.

Year	Median date (range)	n	% adults	% Females		% adult Females
1991	19 Oct. 1991 (2-21 Oct.)	41	48.78 (20/41)	53.66 (22/41)		55.00 (11/20)
1992	24 Oct. 1992 (17-29 Oct.)	71	56.34 (40/71)	56.34 (40/71)	45.87	47.50 (19/40)
1998	12 Oct. 1998 (21 Sept.-12 Oct.)	93	72.5 (58/80)	44.57 (41/92)		48.28 (28/58)
1999	12 Oct. 1999 (4-14 Oct.)	99	79.59 (78/98)	36.36 (36/99) *		39.74 (31/78)
2000	25 Oct. 2000 (13 Oct.-2 Nov.)	97	56.84 (54/95)	36.08 (35/97) *		27.78 (15/54) *
2003	18 Oct. 2003 (22 Sept.-28 Oct.)	101	52.08 (50/96)	50.50 (51/101)		54.00 (27/50)
2004	21 Oct. 2004 (30 Sept.-31 Oct.)	31	16.13 (5/31)	41.23	39.29 (11/28)	45.33
2005	20 Oct. 2005 (12-23 Oct.)	91	24.72 (22/89)	48.35 (44/91)		72.73 (16/22) *
2006	05 Nov. 2006 (23 Oct.-8 Nov.)	48	35.42 (17/48)	51.06 (24/47)		43.75 (7/16)
		672	53.00	*	45.58 *	ns
					45.56	ns

sex-ratio was similar in the 1990s and 2000s ($G_{corr} = 0.004$, $n = 338$, $p > 0.9$; Table 1).

The regressions of foetus mass^{1/3} and standard length on days were significant ($t = 11.4$, $n = 50$, $p < 0.0001$ and $t = 13.1$, $n = 99$, $p < 0.0001$, respectively; Fig. 5).

Dates of birth and weaning/mating are presented in Table 2. Mean spread of the breeding season was 44 days. The duration of total gestation for ringed seals was estimated at 326 days. The regression line of foetus mass^{1/3} and standard length on days intercepted the X-axis at $t_0 = 222$ (95% CI = 194-245) and at $t_0 = 235$ (95% CI = 212-255), respectively. Date of attachment and duration of active gestation and suspended development extrapolated from t_0 are presented in Table 2.

The number of pups in the harvest and the pregnancy rate were significantly lower in the 1990s than in the 2000s ($G_{corr} = 24.11$, $n = 649$, $p < 0.001$ and $G_{corr} = 11.32$, $n = 135$, $p < 0.001$, respectively; Table 3). The ovulation rate, however, did not differ between the 2 periods ($G_{corr} = 0.52$, $n = 135$, $p > 0.1$; Table 3). Adult females up to 37 years of age were showing signs of a recent ovulation (including pregnancy), suggesting that no senescence was apparent in the females of our collection. Ovulation and pregnancy rates were correlated ($r_s = 0.81$, $n = 8$, $p = 0.01$) but the percent pups in the harvest was not correlated with the pregnancy rate the year before ($r_s = 0.41$, $n = 5$, $p = 0.45$). Since the percentage pups in the fall harvest increased significantly over the years, we took the residuals of the linear regression on years to explore the correlation with the BCI, in order to control for the effect of the year. Residuals of the percentage

Figure 5: Foetal growth rate in a) standard length ($n = 99$) and b) mass ($n = 50$) of ringed seals sampled in Arviat, NU, during the falls 1991 to 2006. Dashed lines are linear regressions passing by the upper and lower extreme points of each data set. Four foetuses sampled in Sanikiluaq, NU, were added to the Arviat sample.

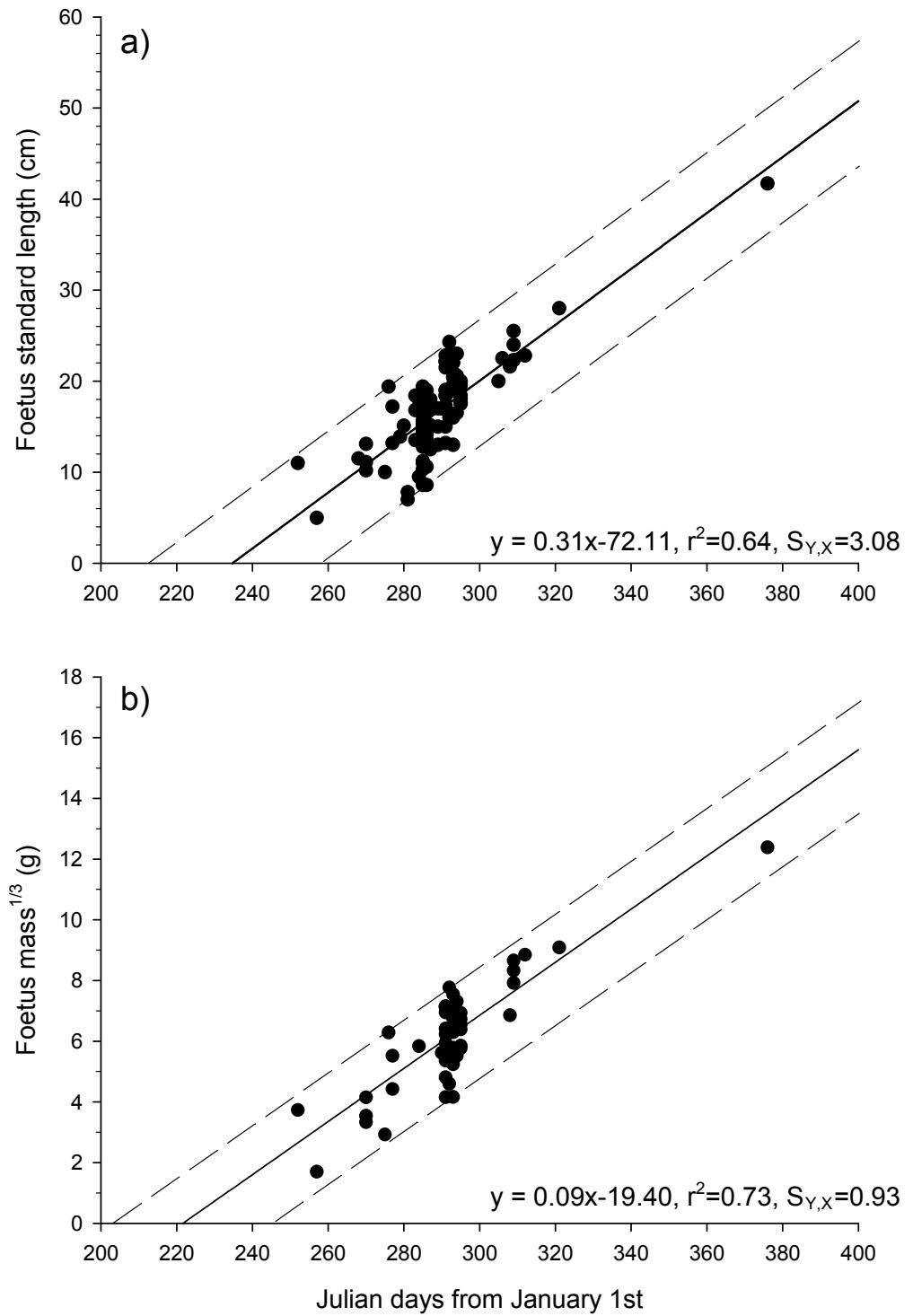


Table 2: Date and length of different life-cycle events of ringed seals sampled in Arviat, NU, in the falls 1991 to 2006, determined by the regression of foetus standard (STD) length and foetus mass^{1/3} on time. Date (range) and length (95% confidence interval).

	Foetus STD length	Foetus mass ^{1/3}
Parturition	17-Mar (23 Feb-10 Apr)	26-Feb (8 Feb-22 Mar)
Weaning/Mating	25-Apr (3 Apr-19 May)	06-Apr (19 Mar-30 Apr)
Attachment	13-Jul (21 Jun-6 Aug)	02-Jul (14 Jun-26 Jul)
Active gestation	258 (233-286)	250 (221-285)
Suspended development	69 (40-94)	76 (41-105)

Table 3: Percentage of pups in the fall subsistence harvest and adult female ovulation and pregnancy rates of ringed seals sampled in Arviat, NU, from 1991 to 2006. An asterisk denotes a statistical difference. ns: non-significant.

	% pup	% ovulation		% pregnancy	
1991	4.88 (2/41)		100 (11/11)		90.91 (10/11)
1992	4.23 (3/71)	5.52	83.33 (15/18)	92.94	0 (0/18) 56.47
1998	7.50 (6/80)		100 (25/25)		64.00 (16/25)
1999	5.10 (5/98)		90.32 (28/31)		70.97 (22/31)
2000	22.11 (21/95)		86.67 (13/15)		46.67 (7/15)
2003	13.54 (13/96)		100 (17/17)		100 (17/17)
2004	22.58 (7/31)	17.83	/	95.56	/ 84.00
2005	14.61 (13/89)		100 (13/13)		100 (13/13)
2006	20.83 (10/48)		100 (5/5)		100 (5/5)
<i>G-test</i>		*		ns	*

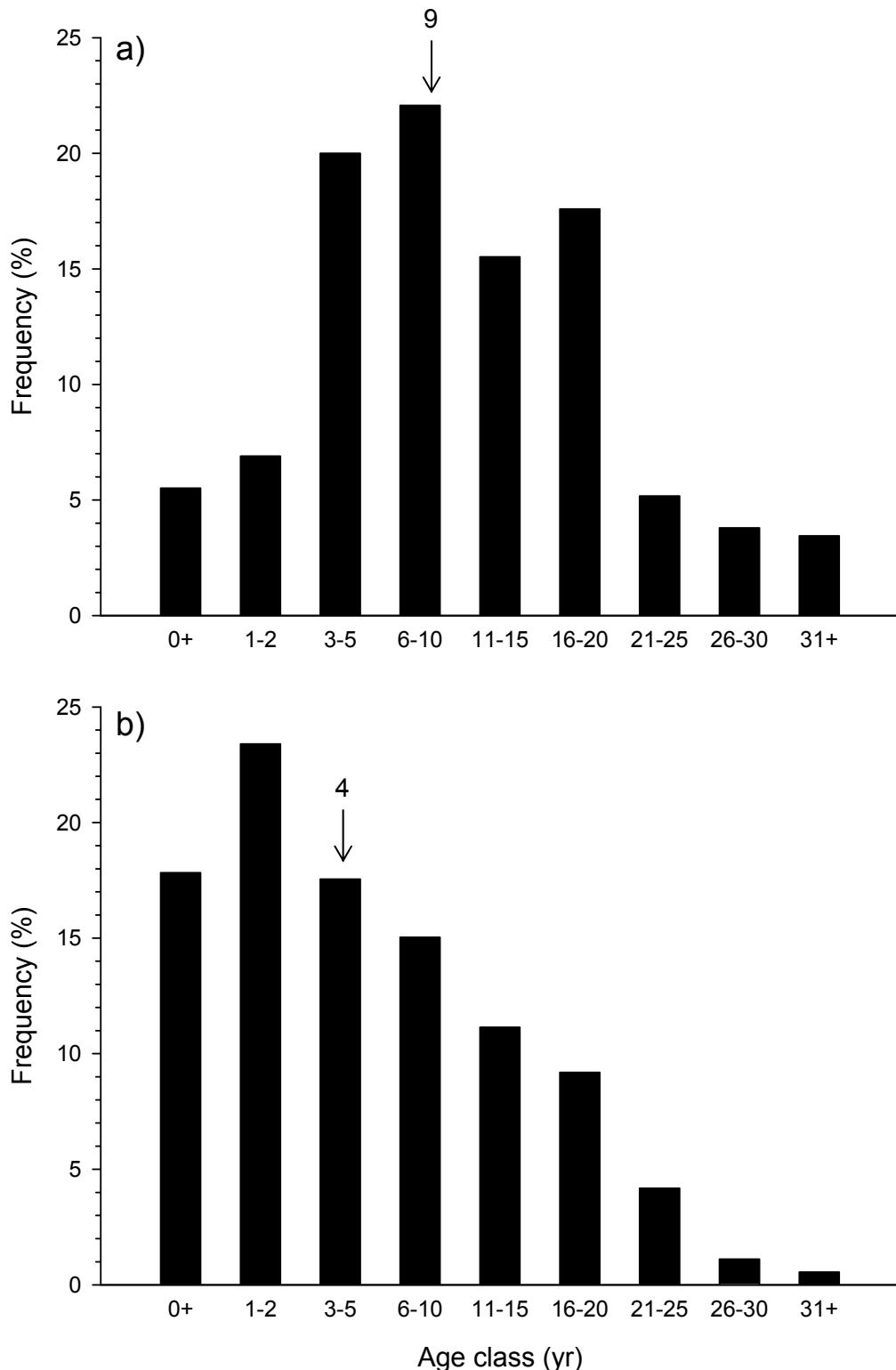
pups were not correlated with the pup BCI ($r_s = 0.43, n = 9, p = 0.25$) nor with the female BCI ($r_s = 0.24, n = 8, p = 0.58$) or the female BCI the year before ($r_s = 0.00, n = 5, p = 1$). Ovulation and pregnancy rates were not correlated with the female BCI ($r_s = -0.44, n = 8, p = 0.26$ and $r_s = -0.37, n = 8, p = 0.35$, respectively).

The age structure of ringed seals collected in the 1990s was skewed toward older age classes with very few seals 2 years of age or younger (Fig. 6a). In the 2000s, however, the age structure was largely skewed toward younger age classes with animals younger than 6 years having the highest frequency of occurrence (Fig. 6b). The younger age-structure in the 2000s was reflected in the percent of adults ($G_{corr} = 45.32, n = 649, p < 0.001$; Table 1) and the median age ($x_{1990s} = 9$ [5-16] years vs. $x_{2000s} = 4$ [1-11] years, $U = 70,722, p < 0.0001$) of ringed seals in the collection that were higher in the 1990s than in the 2000s. The median age of adult females, however, stayed constant over the 2 periods ($x_{1990s} = 15$ [10-20] years vs. $x_{2000s} = 16$ [12-20] years, $U = 3158.5, p = 0.42$).

The average age at sexual maturity of ringed seals collected in the 1990s ($x = 5.4 \pm 0.3$ years) was significantly higher than of seals collected in the 2000s ($x = 3.8 \pm 0.2$ years, $t_{0.05,1721} = 150.2, p < 0.0001$). Similarly, the age of first parturition of ringed seals in the 1990s ($x = 7.3 \pm 0.6$ years) was greater than in the 2000s ($x = 5.5 \pm 0.5$ years, $t_{0.05,1849} = 73.4, p < 0.001$).

The standard length of adult females was significantly lower in the 1990s ($x = 113.5$ [108.8-119.4] cm) than in the 2000s ($x = 123$ [115.8-128.4] cm, $U =$

Figure 6: Age structure of ringed seals sampled in the fall in Arviat, NU, in the a) 1900s ($n = 290$) and b) 2000s ($n = 359$). Arrows indicate the median age of the collection. 0+: pups.



4222.5, $p < 0.0001$). Ringed seal females sampled in the 2000s grew faster and were longer than females sampled in the 1990s (Fig. 7). The sigmoid model fitted to the 1990s data poorly due to the lack of young age classes, particularly pups ($n = 5$) and 1 year-olds (none). The survivorship curve showed strong cohorts in the 1980s and early 2000s, but weak cohorts in the 1970s and 1990s, with the exception of 1992 and 1994 (Fig. 8).

Adult female BCI tended to decrease over the study period (Fig. 9), whereas juvenile and pup BCI did not change over the years (juveniles: $y = -0.0001x + 0.26$, $r^2 = 0.11$, $p = 0.38$, $S_{Y,X} = 0.002$, $n = 9$; pups: $y = 0.0002x - 0.42$, $r^2 = 0.20$, $p = 0.23$, $S_{Y,X} = 0.0025$, $n = 9$; Fig. 9). When the 2 decades were compared, adult females tended to be in better condition in the 1990s ($x_{1990s} = 0.0230 \pm 0.0059$, $n = 88$ vs. $x_{2000s} = 0.0210 \pm 0.0060$, $n = 62$, $t_{0.05,148} = 1.98$, $p = 0.049$), there was no difference in juvenile BCI and pups tended to be in better condition in the 2000s ($x_{1990s} = 0.0192 \pm 0.0034$, $n = 16$ vs. $x_{2000s} = 0.0213 \pm 0.0054$, $n = 57$, $t_{0.05,38.8} = -1.91$, $p = 0.06$). Only 2 and 3 pups were collected in 1991 and 1992, respectively, suggesting caution in interpreting pup BCI trend over the years. For adults and juveniles, the highest BCI was recorded for the years 1991 and 2004, respectively, and in 2004 for pups. Among adult females, pregnant females had a higher body condition than non-pregnant females in the 1990s ($x_{preg} = 0.0244 \pm 0.0061$ vs. $x_{non-preg} = 0.0209 \pm 0.0049$; ANCOVA controlled for age and year: $F_{1, 81} = 13.02$, $p = 0.0005$), but not in the 2000s ($x_{preg} = 0.0209 \pm 0.0049$ vs. $x_{non-preg} = 0.0236 \pm 0.0044$; ANCOVA controlled for age and year: $F_{1, 45} = 0.67$, $p = 0.42$).

Figure 7: Growth of ringed seal adult females sampled in the fall in Arviat, NU, modelled by a sigmoid function with three parameters in the a) 1990s ($r^2 = 0.29$, n = 131) and b) 2000s ($r^2 = 0.45$, n = 158).

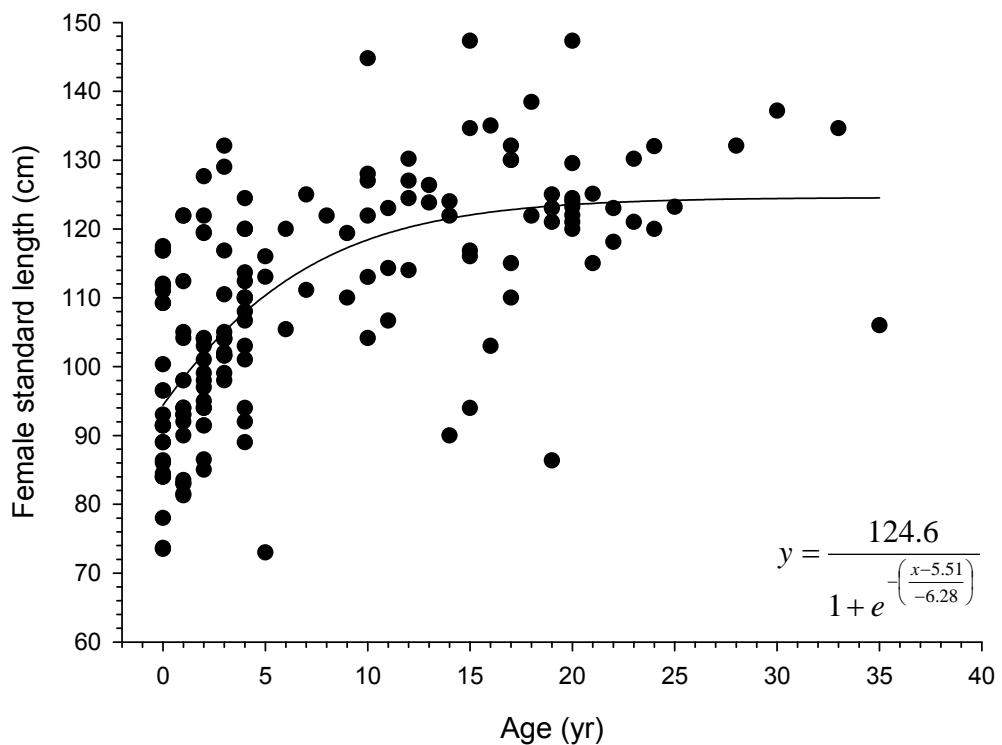
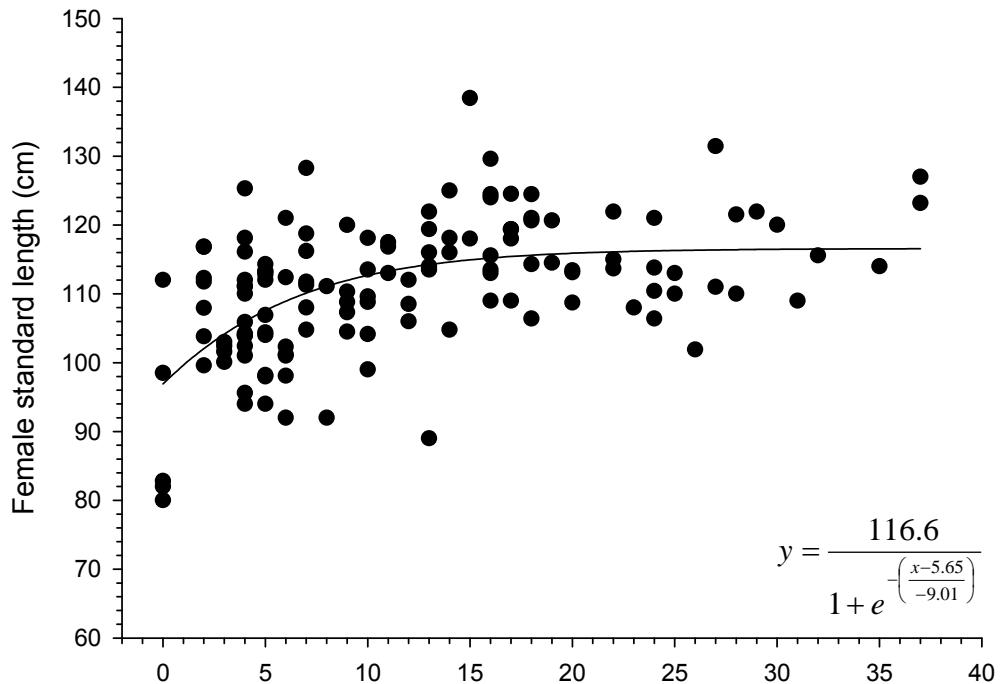


Figure 8: Recruitment of ringed seals sampled in Arviat, NU, in the falls 1991 to 2006. Bars represent a cohort, *i.e.*, the number of seals born in a particular year that were found in our collection. Survivorship is modelled by an exponential regression of the form: $y = ae^{bx}$, with $a = 3.88E-38$ and $b = 0.045$ ($r^2 = 0.53$, $n = 588$).

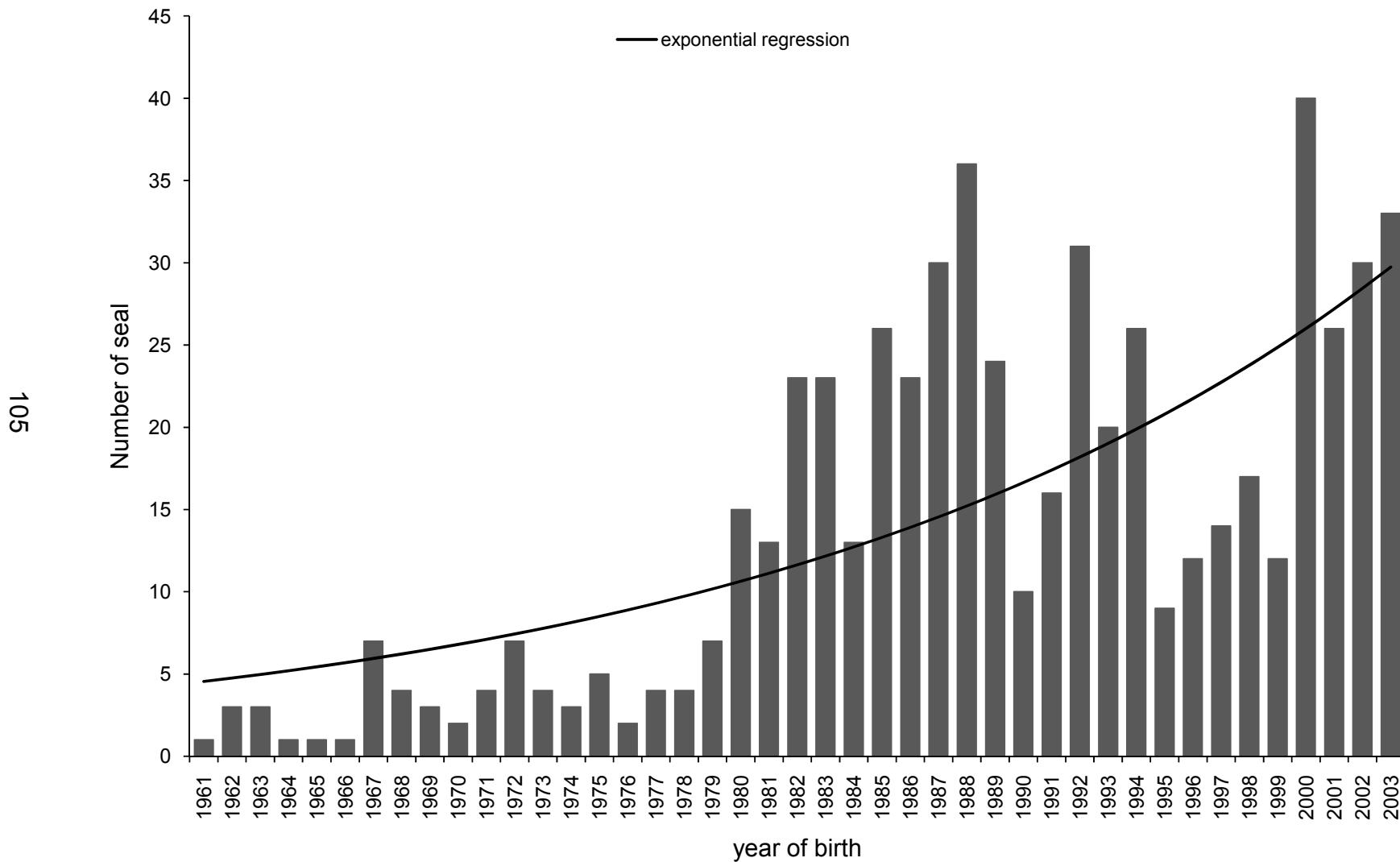
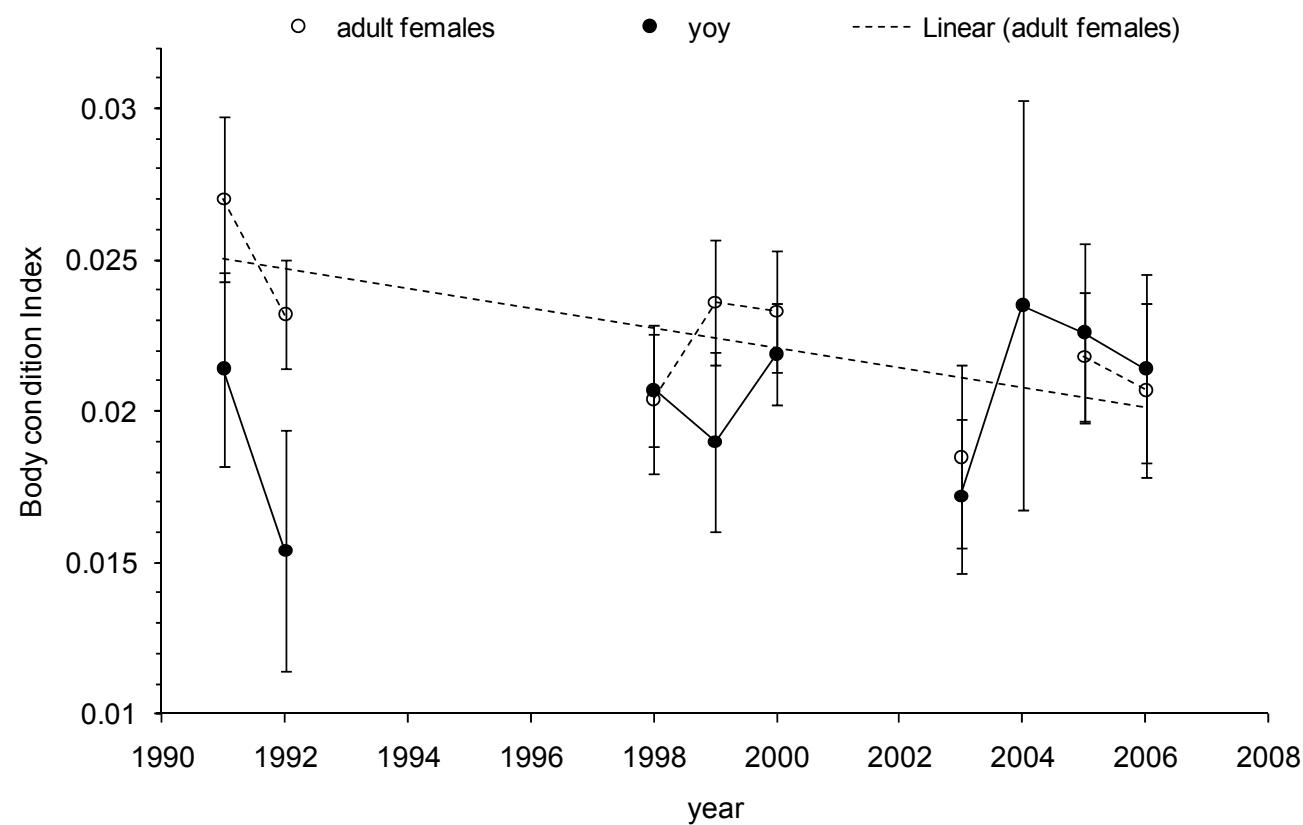


Figure 9: Mean body condition index (BCI) of ringed seal adult females (open circle) and pups (close circle) sampled in Arviat, NU, in the falls 1991-2006. The dotted line is the linear regression of female BCI over time: $BCI = -0.0003\text{year} + 0.68$, $r^2 = 0.50$, $p = 0.05$, $S_{Y,X} = 0.002$, $n = 8$. Mean $\pm 1.96 \times \text{standard error}$.



Of the 7 environmental variables tested over our study period (1991-2006), only the sum of rain from April to June presented a significant positive trend, and the length of the open water period showed a marginally significant increase (Fig. 10). When the environmental variable means were compared between the 1990s and the 2000s, none of the differences observed were statistically significant (Table 4). The date of break-up was negatively correlated to the length of the open water period, the spring temperatures and the sum of rain in the spring, and was positively correlated to the ice cover in May-June (Table 5). The sum of rain in the spring increased with increasing winter and spring temperatures, which were positively correlated to winter, summer, and fall temperatures (Table 5). Summer and fall temperatures were also positively correlated ($r_P = 0.61$, $n = 22$, $p = 0.03$).

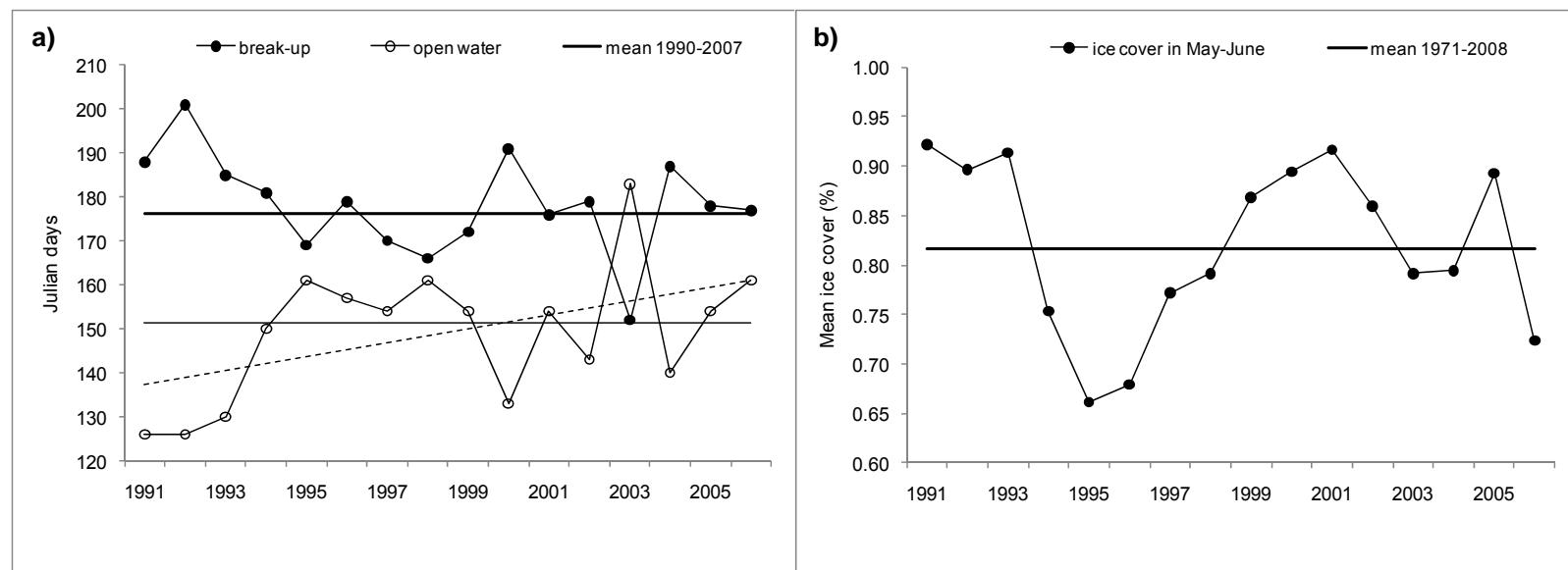
The residuals of the linear regression of percentage of pups in the harvest over years increased linearly as the spring temperature decreased (Fig. 11b), but was related to the maximum snow depth in the spring by a polynomial relationship (Fig. 11a). A polynomial function was also the best model to describe the relationship between residuals of pup and female BCI over years and date of spring break-up (Fig. 11c, d).

Discussion

Despite the lack of significance in the differences of the environmental variables between the 2 decades, an interesting pattern occurred (Fig. 10). The beginning

Figure 10: Trends in a) break-up date (closed circle) and length of the open-water (LOW) season (open circle). The dotted line is the linear regression: $LOW = 1.60\text{year}-3039$, $r^2 = 0.24$, $p = 0.05$, $S_{Y,X} = 13.8$, $n = 16$; b) mean ice cover for the last 2 weeks of May and first week of June; c) maximum snow depth for February-May; d) mean spring temperatures; e) sum of rain fall for April-June. The solid line is the linear regression: sum of rain fall = $2.35\text{year}-4671$, $r^2 = 0.38$, $p = 0.01$, $S_{Y,X} = 14.6$, $n = 16$; f) Chlorophyll a concentration in western Hudson Bay for the period 1991-2006. Horizontal lines are the average value for 1991-2006.

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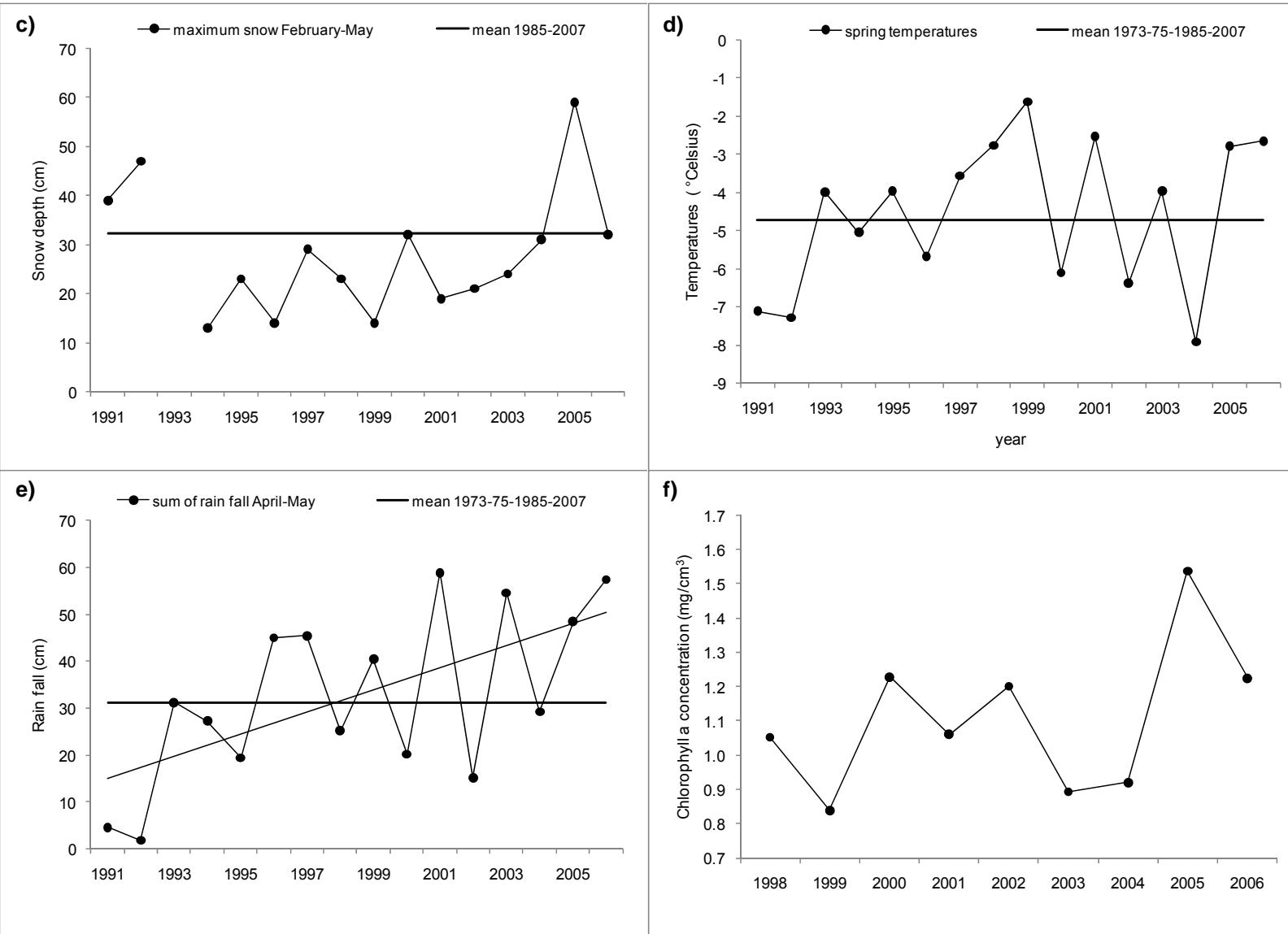


Table 4: Comparison of environmental variables obtained for western Hudson Bay, Nunavut, between the two decades: 1990s and 2000s. p : p-value from a two-tailed *t-test*. Mean \pm SD (n) [range] or median {1st-3rd quartile} (n) [range].

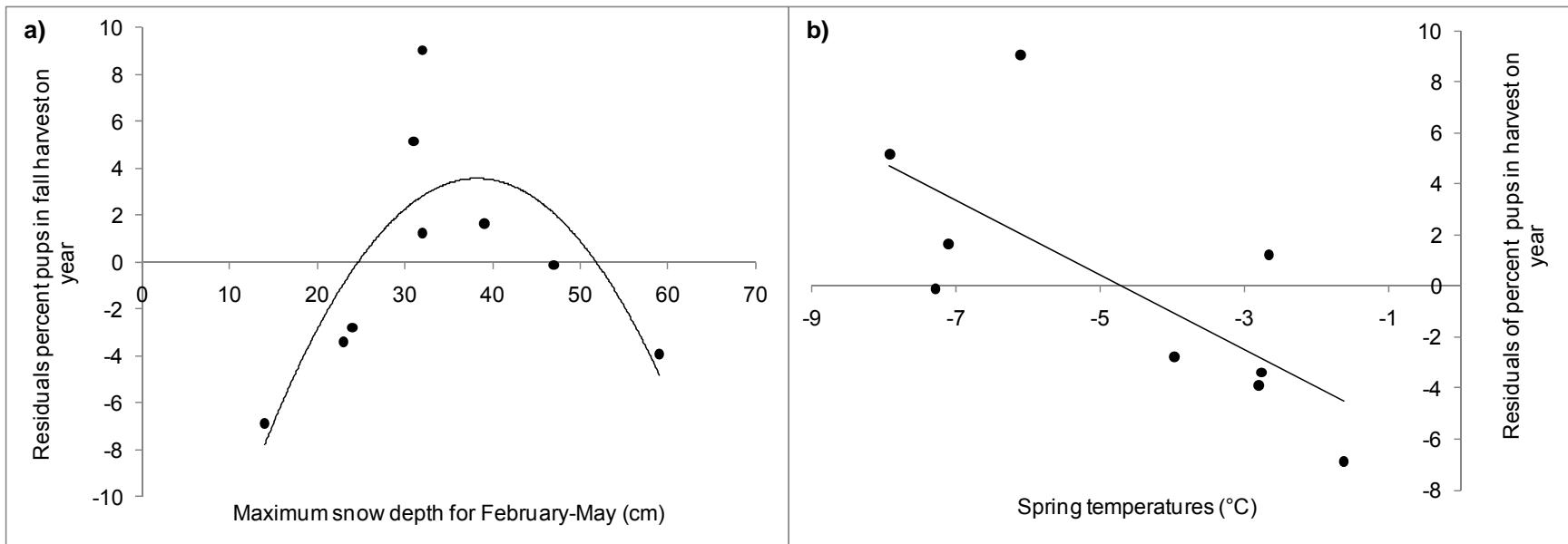
	1990s	2000s	p
Break-up date (Julian day)	179 {170-185} (9) [166-201]	178 {176.5-183} (7) [152-191]	0.96 [§]
Length of open water period (day)	146.6 \pm 14.9 (9) [126-161]	152.6 \pm 16.5 (7) [133-183]	0.46
Maximum snow depth Feb-May (cm)	23 {14-31.5} (8) [13-47]	31 {22.5-32} (7) [19-59]	0.34 [§]
Sum of rain fall April-May (cm)	26.7 \pm 16.0 (9) [1.8-45.4]	40.5 \pm 18.5 (7) [15.2-58.8]	0.13
Spring temperatures (°C)	-4.6 \pm 1.9 (9) [-7.3--1.6]	-4.6 \pm 2.2 (7) [-7.9--2.5]	0.95
Ice cover MayJune (%)	0.81 \pm 0.1 (9) [0.66-0.92]	0.84 \pm 0.07 (7) [0.72-0.92]	0.48

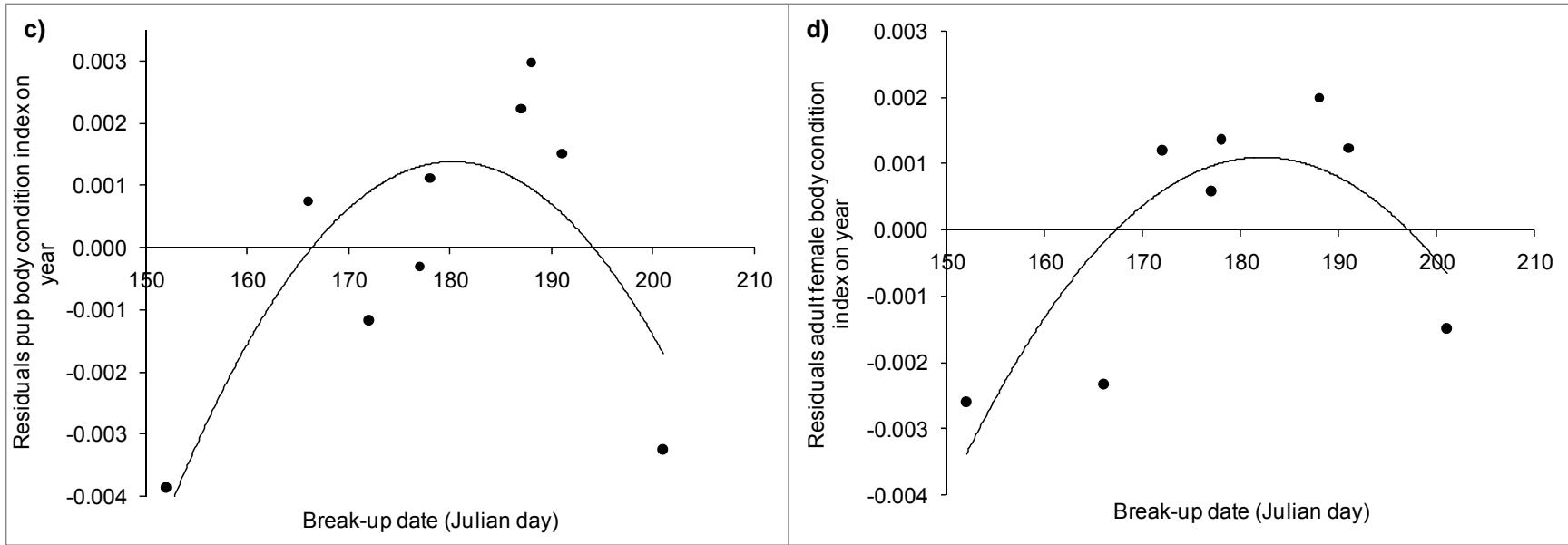
[§] p from a Mann-Whitney test

Table 5: Pearson product moment correlation matrix for environmental variables obtained in western Hudson Bay, NU, 1991- 2006. Bold and italic values indicate statistical significance. r_P = Pearson correlation coefficient; p : p-value; n : sample size. Open water: length of the open-water season; [Chl. A]: concentration of chlorophyll a; max. snow: maximum snow depth for February-May; sum of rain: total rain fall in April-May; temp.: temperature; ice cover: ice cover in May-June.

		open water	[Chl. a]	max. snow	sum of rain	winter temp.	spring temp.	ice cover
Break-up date	r_P	-0.93	0.37	0.34	-0.51	-0.07	-0.56	0.48
	p	0.00	0.30	0.19	0.03	0.78	0.02	0.05
	n	18	10	17	18	18	18	18
[Chl. a]	r_P			0.79	-0.01	0.03	0.04	0.24
	p			0.01	0.98	0.94	0.91	0.49
	n			10	10	10	10	11
max. snow	r_P				-0.15	-0.12	-0.26	0.29
	p				0.51	0.62	0.26	0.24
	n				22	21	21	19
sum of rain	r_P					0.43	0.56	-0.23
	p					0.046	0.01	0.32
	n					22	22	20
winter temp.	r_P						0.44	0.02
	p						0.04	0.93
	n						22	20
spring temp.	r_P							-0.05
	p							0.82
	n							20
summer temp.	r_P						0.47	
	p						0.0275	
	n						22	
fall temp.	r_P						0.645	
	p						0.0012	
	n						22	

Figure 11: Relationship between a) residuals of the linear regression of percent pups in the harvest over years and maximum snow depth ($y = -0.019x^2 + 1.48x - 24.72$, $r^2 = 0.64$, $p = 0.047$, $n = 9$, $x_1 = 24.7\text{cm}$ and $x_2 = 51.6\text{cm}$); b) residuals of the linear regression of percent pups in the harvest over years and spring temperatures ($y = -1.46x - 6.84$, $r^2 = 0.51$, $p = 0.03$, $S_{Y,X} = 3.70$, $n = 9$); c) residuals of the linear regression of pup body condition index over years and date of break-up ($y = -7E-6x^2 + 0.0026x - 0.2306$, $r^2 = 0.63$, $p = 0.051$, $n = 9$, $x_1 = 166$ Julian day and $x_2 = 194$ Julian day); and d) residuals of the linear regression of female body condition index over years and date of break-up ($y = -4.9E-6x^2 + 0.0018x - 0.162$, $r^2 = 0.66$, $p = 0.066$, $n = 9$, $x_1 = 167$ Julian day and $x_2 = 197$ Julian day) of ringed seals sampled in Arviat, Nunavut, in the falls 1991 to 2006.





of the 1990s were characterized by late dates of break-up (e.g., 21 July in 1992, 25 days later than average) and short open water periods (126 days in 1992 and 1993), cold temperatures, and a high ice cover in late spring, suggesting heavy ice conditions. Similar conditions were also observed in 2000. The combined effect of a strong positive phase of the North Atlantic Oscillation and a strong El Niño event in 1991/92, and the eruption of Mount Pinatubo in June 1991, created colder than average conditions in the eastern Arctic, including Hudson Bay, in the earlier 1990s (Graf et al. 1993, McCormick et al. 1995, Mysak et al. 1996, Gough et al. 2004). In the western Arctic, heavy ice conditions in the mid-1970s and 1980s were proposed as the major cause of ringed seal reproductive failures and abundance decline (Smith 1987, Kingsley and Byers 1998, Harwood et al. 2000, Stirling 2002).

In western Hudson Bay, the percent of ringed seal pups in the fall harvest more than tripled in the 2000s and pups tended to be fatter compared to the 1990s, suggesting that conditions were less favourable for pups in the 1990s than in the 2000s. Even so, the proportion of pups in the fall harvest in western Hudson Bay in the 2000s (18%) was still a relatively low percentage compared to that reported from other locations around the Arctic with similar ovulation/pregnancy rates (McLaren 1958, Smith 1973, Stirling et al. 1977, Breton-Provencher 1979, Stirling et al. 1982, Smith 1987, Kingsley and Byers 1998, Teilmann and Kapel 1998, Stirling 2002).

We believe that differences in our results from the different sampling periods reflect biologically significant events for ringed seals in western Hudson Bay and

that the variation of the percent pups over the years in the harvest was not an artefact of our sampling program. Stirling (2005) discussed this issue in a previous paper regarding ringed seals collected in 1991-92 and 1998-2000 in the same community, at the same time of the year, and by several of the same hunters than the ringed seal collection from 2003 to 2006, and concluded no support for sexual or age-class segregation that might bias the collection. In Arviat, the fall subsistence hunt is non-selective since hunters have no incentive to shoot ringed seals of a particular age-class and hunt them generally from shore, from long distances, thus precluding visual evaluation of the size of the animal prior to shooting.

Adult ringed seal ovulation rate was not different between the 2 decades and varied little, being 100% for 5 of the 8 years with data and never under 80%, even for the lowest rates in 1992 and 2000. This result fits in the range of rates previously reported in the literature for different locations across the Arctic (39-100%; Smith 1973, Stirling et al. 1977, Stirling et al. 1982, Lydersen and Gjertz 1987, Harwood et al. 2000, Holst and Stirling 2002, Krafft et al. 2006) and agree with the fact that, in pinnipeds, ovulation and implantation are less sensitive to stress than later gestation stages (see review by Trites and Donnelly 2003). The pregnancy rate was significantly lower in the 1990s than in the 2000s, particularly in 1992 when none of the 18 adult females collected were pregnant and 2000 when less than 50% of the females were gestating. Both these years were characterised by later than average break-up and heavy ice conditions. The pregnancy rate in the 1990s was not sufficiently low to account for the low

percent of pups in the harvest at the same period (Stirling 2005), suggesting that either late intra-uterine and/or newborn mortality occurred, or pups did not survive well through the summer and/or left the Arviat area before the fall harvest.

The age structure, the percent of adults, and the median age of the collection in the 1990s and the 2000s indicated that ringed seals collected in the latter decade were significantly younger. Considering the low pregnancy rates and percent pups in the harvest in the late 1990s, the high frequency of the age classes 0+, 1-2 and 3-5 in the 2000s suggested that not only pup production, survival and site-fidelity (*i.e.*, seals born in the Arviat area remained in this area until fall) increased, but pup and juvenile seals from other area(s) likely have immigrated to the Arviat area. Particularly supporting this hypothesis is the low pregnancy rates in 1999 while the percent pups in the harvest was the second highest of the study period and the 2000 cohort was over represented in the harvest. Albeit a similar median age, adults females collected in the 2000s were characteristically longer than in the 1990s.

Ringed seal females also attained sexual maturity at a younger age in the 2000s, suggesting a faster growth (Laws 1956) confirmed in this study by the growth curves, possibly under conditions more favourable than may have prevailed in the Arviat area during the 1990s. Therefore, these results may indicate that not only non-mature animals immigrated into the Arviat area in the 2000s, but also adult females. Supporting the adult immigration to the study site in the 2000s is the Figure 8. The survivorship curve highlighted the presence of strong (1980s

and 2000s) and weak (1970s and 1990s) cohorts, as already indicated by Ferguson et al. (2005). During the 1990s, where fewer animals than expected survived most of the years, ringed seals born in 1992 were over represented in the harvest (Fig. 8). From Table 3 and Fig. 10a, we found that 1992 was unique in having the latest date of spring break-up (25 days later than average), the lowest ovulation and pregnancy rates, and the lowest percentage of pups in the harvest of the entire study period, suggesting poor conditions for ringed seals that year. The 1992 cohort was nearly absent from the collection in 1992 and 1998 but reappeared in 1999 and 2000, when seals were 7 and 8 years old. The fact that the 1992 cohort was overrepresented in our collection despite the low percent pups in the harvest recorded and the poor environmental conditions that year therefore suggests that most ringed seals born in 1992 found in our collection were either 1) born around the Arviat area, left as pups to find more suitable conditions and returned as young adults, and/or 2) were not born in Arviat and settled in western Hudson Bay at the end of the 1990s as young adults. The recovery of population number and demographic parameters through the immigration of immature and young adult seals have already been suggested for ringed seals (Stirling et al. 1982, Kingsley and Byers 1998) and Weddell seals (*Leptonychotes weddellii*; Testa and Siniff 1987), the ecological counterpart of ringed seals in the southern polar regions (Stirling 1969). Cameron et al. (2007) reported an increase in site fidelity with age up to 12 years and an increased fidelity to sites where successful breeding events occurred in Weddell seals. Our results suggest that in Hudson Bay ringed seals might follow a pattern similar to

Weddell seals, *i.e.*, moving among different sites at the beginning of their reproductive life.

Ringed seal adult females carrying a foetus were in better condition than non-pregnant females. Although this result was only significant for the 1990s, the fact that only 8 non-pregnant females were collected in the 2000s might explain the lack of significance in the difference between pregnant and non-pregnant female BCI in the 2000s. Pup survival, and ovulation and pregnancy rates were not affected by pup or female body condition, respectively. Contrasting with previous studies (e.g., Guinet et al. 1998, Harwood et al. 2000, Chambellant et al. 2003, see review by Trites and Donnelly 2003), these results suggest the possibility that nutritional stress may not be an important factor determining the demographic differences reported in this study. However, all the parameters studied (age at maturity/first parturition, growth and length of adult females, pregnancy rate, percent pups in the harvest, females being in better condition more likely to be pregnant) suggested poor nutritional state in the 1990s (e.g., Laws 1956, Eberhardt 1977, Trites and Donnelly 2003).

Several non- exclusive hypotheses could be proposed to clarify this apparent paradox: 1) our time series and sample sizes might not be long/large enough to find a significant correlation between BCI and demographic parameters; 2) our body condition index might not be sensitive enough to significantly detect small but biologically significant changes in ringed seal nutritional conditions. The BCI of all age-classes declined in 1992, a year with extreme climatic conditions and a severe reduction in food consumption (Chambellant et al. 2010), indicating that

major stresses are reflected by our BCI but minor stresses may be not; 3) the fall might not be relevant to assess variations in female BCI since they are the fattest at this period. Female BCI in the spring could be more appropriate to relate to pup survival; 4) previous studies have reported that, in pinnipeds, ovulation and implantation are more resistant to stress than late gestation stages (see review by Trites and Donnelly 2003). Our pregnancy rates might then be overestimated since abortion might have taken place later in the gestation and would not be recorded; 5) the percentage of pups in the fall harvest may not be a good representation of pup survival since emigration and immigration are confounded factors; and 6) adult ringed seals might have evolved behavioural or physiological responses to provide compensatory physiology to reoccurring high variability stress of poor nutritional conditions (Trites and Donnelly 2003).

Ringed seal pupping in western Hudson Bay peaked at the beginning of March, a month earlier than previously described in the literature (McLaren 1958, Smith 1973, 1987, Hammill et al. 1991, Lydersen 1995). Our sample size of foetuses from early and late gestation stage was small, which might have biased the relationships and dates we found and thus reduce the strength of our interpretation. However, this result is corroborated by traditional knowledge (McDonald et al. 1997, Cleator 2001, M. Chambellant, personal observation) and supports the hypothesis of a latitudinal gradient of pupping suggested by McLaren (1958) and Smith (1987). Similar to McLaren (1958) and Smith (1973, 1987), our results indicated a relatively long breeding season (44 days), also in agreement with the range of male sexual activity reported by the same authors

and Breton-Provencher (1979). The estimated weaning date was found to be around mid-April, with the latest weaning date on May 19. Such an early date of pup independence might be an advantage and could be an adaptation of ringed seals living at lower latitudes, where spring break-up occurs earlier. This finding could be particularly relevant in the current climate warming context: in Hudson Bay, where the ice is now breaking-up about 4 weeks earlier than in the 1970s, ringed seal pups might be temporarily sheltered from the detrimental effect on survival of a premature separation from their mother (Thomas and DeMaster 1983, Harwood et al. 2000).

Over the study period, environmental variables, except for rain fall and, to a lesser extent length of the open-water season, did not show a particular trend. However, previous studies have reported significant long-term trends for date of break-up, length of the open water period, rain fall, snow depth and air temperature in Hudson Bay (Parkinson et al. 1999, Stirling et al. 1999, Gough et al. 2004, Stirling et al. 2004, Ferguson et al. 2005, Gagnon and Gough 2005b, Stirling and Parkinson 2006, Parkinson and Cavalieri 2008), emphasizing that comparison of different time periods and sub-regions may provide different results (Higdon and Ferguson 2009), particularly in such a variable environment.

Pups seemed to prefer cold conditions in the spring and by extension later break-up dates and heavy ice years. Although colder springs might enhance pups pre-weaning survival by ensuring lairs integrity, pups post-weaning survival might be compromised. As for most mammal young-of-the-years, the first months/years of independence represent a challenging time for ringed seals that have to learn

how to forage and avoid predators on their own (Reiter et al. 1978, Trites and Donnelly 2003). Indeed, while a very late break-up date would provide a platform for pups to rest, feed under, and learn to survive on their own for a longer time, it would also mean being exposed to polar bear predation for a longer period (Stirling 1997, Stirling and Lunn 1997, Stirling et al. 1999), as well as a very short open-water season, which may not be optimal for pup survival during their first summer.

The open-water period represents the most productive phase of the Arctic ocean annual cycle (Arrigo et al. 2008) and a short open-water season might reduce the overall productivity in Hudson Bay. For ringed seals, the open-water season is a period of intense feeding, necessary to replenish their fat reserves following the breeding and moulting period, in anticipation of the coming winter. A decline in productivity could therefore be detrimental for ringed seals, especially for inexperienced pups. In fact, heavy ice years have been previously associated with reproductive failures in ringed seals (Smith 1987, Kingsley and Byers 1998, Stirling 2002). We propose that, rather than a linear regression, a range of spring temperatures should provide optimal conditions for pup pre- and post-weaning survival, *i.e.*, break-up not too early to disrupt lactation, and not too late to provide enough time for feeding by pups during their first summer. We indeed found that ringed seal pups' and, to a lesser extent, adult females', BCI were optimized when break-up occurred around the end of June (180 Julian days) and within a range mid-June-Mid-July (Fig. 11).

Our results also suggested a window of snow depths on the ground (25-52cm; peak around 38 cm; Fig. 11) that optimized pup survival in the spring. This is in agreement with optimal snow depth for ringed seal recruitment suggested by Ferguson et al. (2005) and previously reported snow depths on the ground in ringed seal habitat (Smith and Stirling 1975, Furgal et al. 1996). It is important to keep in mind that measurements of snow depth correspond to measurements on the ground, next to weather stations, and not on the ice. Snow depth on sea-ice is highly variable because of winds and ice deformations. Smooth ice platform will typically have less snow than highly deformed areas, where snow accumulates along ice structures and which constitute ringed seal preferred birth lair sites (McLaren 1958, Smith and Stirling 1975, Lydersen and Gjertz 1986, Smith 1987, Hammill and Smith 1989). Consequently, snow depths reported at ringed seal lairs in the literature (Lydersen and Gjertz 1986, Hammill and Smith 1989) are greater relative to the values reported in this study. The detrimental effect on pup survival of a snow layer deeper than 52 cm, and by extension of a thicker lair snow roof, could include an altered air circulation inside the lair, forcing pups to leave lairs on regular basis to replenish the oxygen supply (Kelly and Quakenbush 1990).

Ringed seal life-history traits varied between the 2 decades, with the 2000s presenting younger seals that grew faster, matured earlier and produced more pups that survived better. Such a configuration in life-history traits suggested a growing population, whereas figures in the 1990s suggested a declining population (Stearns 1976, Hanks 1978, Oli and Dobson 1999). Evidence for the

alternation of strong and weak ringed seal recruitment since the 1970s and the change in life-history traits during the 2 study periods, supports the hypothesis that ringed seal population dynamics in western Hudson Bay may follow a decadal cycle, as previously suggested by Ferguson et al. (2005) in Hudson Bay and Stirling (1997, 2002) in the western Arctic. Our hypothesis is consistent with results found by Chambellant (2010) on ringed seal density in western Hudson Bay, where a sine function with an 11-year period was the best fit for the aerial survey data, showing a decrease in ringed seal density in the 1990s (peak in 1993) and an increase in the 2000s (peak in 2004).

In the Arctic, decadal fluctuations of the sea-ice regime through atmospheric forcing (e.g., North Atlantic Oscillation) have been reported (Mysak and Manak 1989, Wang et al. 1994, Hurrell 1995, Mysak et al. 1996, Mysak and Venegas 1998, Johannessen et al. 1999, Marshall et al. 2001, Gagnon and Gough 2005b), and climatic variations have been linked to variations in life-history parameters of several Arctic species (Skinner et al. 1998, Ottersen et al. 2001, Post and Forchhammer 2002, Stirling 2002, Derocher 2005, Ferguson et al. 2005, Regehr et al. 2007, Irons et al. 2008). We suggest that the decline in ringed seal reproductive parameters in the 1990s could have been triggered by the cold and heavy ice conditions that prevailed in western Hudson Bay at the beginning of the decade, through nutritional stress and increased predation pressure. Heavy ice conditions could have prevented ringed seals from maintaining breathing holes over the winter (Vibe 1967, Stirling et al. 1982). The short open water seasons and reduced number and/or extent of leads and polynyas in the winter

resulting from cold and heavy ice conditions, may have generated a decrease in the overall productivity of the area (Stirling et al. 1982, Stirling 1997, Stirling and Lunn 1997), creating a nutritional stress in ringed seals. Chambellant et al. (2010) found that ringed seal food consumption was reduced in the early 1990s compared to the 2000s. The negative effect of nutritional stress on reproduction, survival and growth of pinnipeds have been widely reported in the literature (Laws 1956 and see review from Trites and Donnelly 2003). The poor conditions in western Hudson Bay in the early 1990s might also have generated an emigration of young animals to more productive and suitable areas, as has been suggested for ringed seals (Vibe 1967, Smith and Stirling 1978) and Weddell seals (Cameron and Siniff 2004).

Polar bear condition and natality increased in western Hudson Bay in the early 1990s and were associated with later break-up dates and consequently longer hunting seasons on ringed seal pups on the ice in the spring (Stirling 1997, Stirling and Lunn 1997, Stirling et al. 1999). Roth (2003) found that arctic foxes increased their consumption of ringed seals during low lemming years. In the Arviat area, the lemming population was in a trough in 1991 and 1992 (Krebs et al. 2002). These results indicate that, on top of a possible nutritional stress, ringed seals, and particularly ringed seal pups, were under high predation pressure by both polar bears and arctic foxes at the beginning of the 1990s.

In conclusion, our results support the paradigm enounced by Eberhardt (2002) by which early survival and age at parturition are the first life-history traits to be

affected by a decrease in resources. We propose that ringed seal population dynamics follows a decadal cycle that relates to fluctuations in the environment and particularly in the sea-ice regime, through changes in ocean productivity and predation pressure. At the low phase of the cycle, we emphasize the important role of immigration of pups, juveniles, and young adult animals in the recovery of ringed seals in western Hudson Bay. Our results suggested that ringed seals are adapted to a specific but limited range of environmental variations (e.g., Gaden et al. 2009). If current trends continue in Hudson Bay, as projected (Gough and Wolfe 2001, Gagnon and Gough 2005a), environmental conditions may exceed ringed seal tolerance thresholds, possibly triggering a long-term decline that could underlay or override the natural cycle. Further research exploring the mechanisms involved in the coupling environment/ringed seals demography, and in particular testing the nutritional stress hypothesis, would contribute to our understanding of the Hudson Bay ecosystem. Although our study presents the first time-series of life-history parameters of ringed seals in Hudson Bay over an extended time period, in such a highly variable environment, our ability to draw conclusions about factors influencing long-term trends was influenced by temporal gaps in data collection and low numbers in some samples. Long-time series, with larger sample sizes, are essential for assessing demographic parameters in different parts of the Hudson Bay eco-region to gain a more comprehensive understanding of ringed seal population dynamics, particularly to project ringed seal responses to the effects of climate change in Hudson Bay.

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References

- Arrigo, K.R., van Dijken, G., and Pabi, S. 2008. Impact of a shrinking Arctic ice cover on marine primary production. *Geophysical Research Letters* 35: 1-6.
- Baith, K., Lindsay, R., Fu, G., and McClain, C.R. 2001. SeaDAS, a data analysis system for ocean-color satellite sensors. *EOS Trans. Amer. Geophys. U.* 82: 202.
- Barbraud, C. and Weimerskirch, H. 2001. Emperor penguins and climate change. *Nature* 411: 183-186.
- Bernt, K.E., Hammill, M.O., and Kovacs, K.M. 1996. Age estimation of grey seals (*Halichoerus grypus*) using incisors. *Marine Mammal Science* 12(3): 476-482.
- Born, E.W., Teilmann, J., Acquarone, M., and Riget, F.F. 2004. Habitat use of ringed seals (*Phoca hispida*) in the north water area (North Baffin Bay). *Arctic* 57(2): 129-142.
- Bowen, W.D. 1991. Behavioural ecology of pinniped neonates. In *The behaviour of pinnipeds*. Edited by D. Renouf. Chapman and Hall. London, New York, Tokyo, Melbourne, Madras. pp.66-127.
- Breton-Provencher, M. 1979. Etude de la population de phoques annelés (*Phoca hispida*) et des autres pinnipèdes de la région de Poste-de-la-baleine (Nouveau-Québec). GIROQ, Rapport à l'hydro-Québec, Projet Grande-Baleine (Mandat d'avant-projet préliminaire OGB/76-1). 148 pp.
- Cameron, M.F. and Siniff, D.B. 2004. Age-specific survival, abundance and immigration rates of Weddell seal (*Leptonychotes weddelli*) population in McMurdo sound, Antarctica. *Canadian Journal of Zoology* 82: 601-615.

- Cameron, M.F., Siniff, D.B., Proffitt, K.M., and Garrott, R.A. 2007. Site fidelity of Weddell seals: the effects of sex and age. *Antarctic Science* 19(2): 149-155.
- Caughley, G. 1980. Analysis of vertebrate populations. The Blackburn Press. Chichester, New York, Brisbane, Toronto.
- Chambellant, M. 2010. Hudson Bay ringed seal: ecology in a warming climate. In A little less Arctic: top predators in the world's largest northern inland sea, Hudson Bay. Edited by S.H. Ferguson, L.L. Loseto and M.L. Mallory. Springer. Dordrecht, Heidelberg, London, New York. pp.137-158.
- Chambellant, M. and Ferguson, S.H. 2009. Ageing live ringed seals (*Phoca hispida*): which tooth to pull? *Marine Mammal Science* 25(2): 478-486.
- Chambellant, M., Stirling, I., and Ferguson, S.H. 2010. Temporal variation in western Hudson Bay ringed seal (*Phoca hispida*) diet as an indicator of ecosystem changes. *Marine Ecology Progress Series* Submitted in August 2010.
- Chambellant, M., Beauplet, G., Guinet, C., and Georges, J.-Y. 2003. Long-term evaluation of pup growth and preweaning survival rates in subantarctic fur seals, *Arctocephalus tropicalis*, on Amsterdam Island. *Canadian Journal of Zoology* 81: 1222-1232.
- Cleator, H. 2001. Traditional knowledge study of ringed seals: a transcript of interviews with hunters from Chesterfield Inlet, Nunavut. Fisheries and Oceans Canada, Central and Arctic Region, Winnipeg, MB, R3T 2N6. 108 pp.
- Committee on marine mammals, -. 1967. Standard measurements of seals. *Journal of Mammalogy* 48(3): 459-462.

- DeMaster, D.P. 1981. Estimating the average age at first birth in marine mammals. Canadian Journal of Fisheries and Aquatic Science 38: 237-239.
- Derocher, A.E. 2005. Population ecology of polar bears at Svalbard, Norway. Population Ecology 47: 267-275.
- Eberhardt, L.L. 1977. Optimal policies for conservation of large mammals with special reference to marine ecosystems. Environmental Conservation 4: 205-212.
- Eberhardt, L.L. 2002. A paradigm for population analysis of long-lived vertebrates. Ecology 83(10): 2841-2854.
- Feldman, G.C. and McClain, C.R. 2009. Ocean Color Web, SeaWiFS. *Edited by* N. Kuring and S.W. Bailey. pp.
- Ferguson, S.H., Stirling, I., and McLoughlin, P. 2005. Climate change and ringed seal (*Phoca hispida*) recruitment in western Hudson Bay. Marine Mammal Science 21(1): 121-135.
- Forchhammer, M.C., Clutton-Brock, T.H., Lindstrom, J., and Albon, S.D. 2001. Climate and population density induce long-term cohort variation in a northern ungulate. Journal of Animal Ecology 70: 721-729.
- Fowler, C.W. and Smith, T.D. 1978. Dynamics of large populations. John Wiley & Sons. New York, Chichester, Brisbane, Toronto, Singapore.
- Frost, K.J. and Lowry, L.F. 1981. Ringed, Baikal and Caspian seals *Phoca hispida* Schreber, 1775; *Phoca sibirica* Gmelin, 1788 and *Phoca caspica* Gmelin, 1788. In Handbook of marine mammals. *Edited by* S.H. Ridgway and

R.J. Harrison F.R.S. Academic Press. London, New York, Toronto, Sydney, San Francisco. pp.29-53.

Furgal, C.M., Innes, S., and Kovacs, K.M. 1996. Characteristics of ringed seal, *Phoca hispida*, subnivean structures and breeding habitat and their effect on predation. Canadian Journal of Zoology 74: 858-874.

Gaden, A., Ferguson, S.H., Harwood, L., Melling, H., and Stern, G.A. 2009. Mercury trends in ringed seals (*Phoca hispida*) from the Western Canadian Arctic since 1973: associations with length of ice-free season. Environmental Science and Technology 43: 3646-3651.

Gagnon, A.S. and Gough, W.A. 2005a. Climate change scenarios for the Hudson Bay region: an intermodel comparison. Climatic Change 69: 269-297.

Gagnon, A.S. and Gough, W.A. 2005b. Trends in the dates of ice freeze-up and break-up over Hudson Bay, Canada. Arctic 58(4): 370-382.

Gaillard, J.-M., Festa-Bianchet, M., and Yoccoz, N.G. 1998. Population dynamics of large herbivores: variable recruitment with constant adult survival. Trends in Ecology and Evolution 13(2): 58-63.

Gaston, A.J., Woo, K., and Hipfner, J.M. 2003. Trends in forage fish populations in northern Hudson bay since 1981, as determined from the diet of nestling thick-billed murres, *Uria lomvia*. Arctic 56(3): 227-233.

Gaston, A.J., Gilchrist, H.G., and Hipfner, J.M. 2005. Climate change, ice conditions and reproduction in an Arctic marine bird: Brunnich's guillemot (*Uria lomvia* L.). Journal of Animal Ecology 74: 832-841.

- Goodyear, M.A. 1999. Variation in growth and seasonal condition of ringed seal, *Phoca hispida*, from the Canadian Arctic. MSc, Department of Zoology, University of Manitoba, Winnipeg, MB, R3T 2N2.
- Gough, W.A. and Wolfe, E. 2001. Climate change scenarios for Hudson bay, Canada, from general circulation models. Arctic 54(2): 142-148.
- Gough, W.A., Cornwell, A.R., and Tsuji, L.J.S. 2004. Trends in seasonal sea ice duration in southwestern Hudson Bay. Arctic 57(3): 299-305.
- Graf, H.-F., Kirchner, I., Robock, A., and Schult, I. 1993. Pinatubo eruption winter climate effects: model versus observations. Climate Dynamics 9: 81-93.
- Guinet, C., Roux, J.-P., Bonnet, M., and Mison, V. 1998. Effect of body size, body mass, and body condition on reproduction of female South African fur seals (*Arctocephalus pusillus*) in Namibia. Canadian Journal of Zoology 76: 1418-1424.
- Hammill, M.O. and Smith, T.G. 1989. Factors affecting the distribution and abundance of ringed seal structures in Barrow Strait, Northwest Territories. Canadian Journal of Zoology 67: 2212-2219.
- Hammill, M.O. and Smith, T.G. 1991. The role of predation in the ecology of ringed seal in Barrow strait, Northwest Territories, Canada. Marine Mammal Science 7(2): 123-135.
- Hammill, M.O., Lydersen, C., Ryg, M., and Smith, T.G. 1991. Lactation in the ringed seal (*Phoca hispida*). Canadian Journal of Fisheries and Aquatic Sciences 48: 2471-2476.

- Hanks, J. 1978. Characterization of population condition. In Dynamics of large mammal populations. Edited by C.W. Fowler and T.D. Smith. John Wiley & Sons. New York, Chichester, Brisbane, Toronto, Singapore. pp.47-73.
- Harington, C.R. 2008. The evolution of Arctic marine mammals. Ecological Applications 18 Supplement(2): S23-S40.
- Harwood, L.A., Smith, T.G., and Melling, H. 2000. Variation in reproduction and body condition of the ringed seal (*Phoca hispida*) in the western Prince Albert Sound, NT, Canada, as assessed through a harvest-based sampling program. Arctic 53(4): 422-431.
- Hewer, H.R. 1964. The determination of age, sexual maturity, Longevity and a life-table in the grey seal (*Halichoerus grypus*). Proceedings of the Royal Society of London 142(4): 593-624.
- Hewer, H.R. and Backhouse, K.M. 1968. Embryology and foetal growth of the grey seal, *Halichoerus grypus*. Journal of Zoology 155: 507-533.
- Higdon, J.W. and Ferguson, S.H. 2009. Loss of Arctic sea ice causing punctuated change in sightings of killer whales (*Orcinus orca*) over the past century. Ecological Applications 19(5): 1365-1375.
- Hindell, M.A. 1991. Some life-history parameters of a declining population of Southern elephant seals, *Mirounga leonina*. Journal of Animal Ecology 60(1): 119-134.
- Holst, M. and Stirling, I. 2002. A comparison of ringed seal (*Phoca hispida*) biology on the east and west sides of the North water Polynya, Baffin Bay. Aquatic Mammals 28(3): 221-230.

- Holst, M., Stirling, I., and Calvert, W. 1999. Age structure and reproductive rates of ringed seals (*Phoca hispida*) on the northwestern coast of Hudson Bay in 1991 and 1992. *Marine Mammal Science* 15(4): 1357-1364.
- Huggett, A.S.G. and Widdas, W.F. 1951. The relationship between mammalian foetal weight and conception age. *Journal of Physiology* 114: 306-317.
- Hurrell, J.W. 1995. Decadal trends in the North Atlantic oscillation: regional temperatures and precipitation. *Science* 269: 676-679.
- Irons, D.B., Anker-Nilssen, T., Gaston, A.J., Byrd, G.V., Falk, K., Gilchrist, G., Hario, M., Hjernquist, M., Krasnov, Y.V., Mosbech, A., Olsen, B., Petersen, A., Reid, J.B., Robertson, G.J., Strom, H., and Wohl, K.D. 2008. Fluctuations in circumpolar seabird populations linked to climate oscillations. *Global Change Biology* 14: 1455-1463.
- Iverson, S.J., Stirling, I., and Lang, S.L.C. 2006. Spatial and temporal variation in the diets of polar bears across the Canadian Arctic: indicators of changes in prey populations and environment. In *Top predators in marine ecosystems: their role in monitoring and management*. Edited by I.L. Boyd, S. Wanless and C.J. Camphuysen. Cambridge University Press. pp.98-117.
- Johannessen, O.M., Shalina, E.V., and Miles, M.W. 1999. Satellite evidence for an Arctic sea ice cover in transformation. *Science* 286(3): 1937-1939.
- Kelly, B.P. and Quakenbush, L.T. 1990. Spatiotemporal use of lairs by ringed seals (*Phoca hispida*). *Canadian Journal of Zoology* 68: 2503-2512.
- Kelly, B.P. and Wartzok, D. 1996. Ringed seal diving behavior in the breeding season. *Canadian Journal of Zoology* 74: 1547-1555.

- Kelly, B.P., Badajos, O.H., Kunnasranta, M., Moran, J.R., Martinez-Bakker, M., Wartzok, D., and Boveng, P. 2010. Seasonal home ranges and fidelity to breeding sites among ringed seals. *Polar Biology* 33: 1095-1109.
- Kingsley, M.C.S. and Byers, T.J. 1998. Failure in reproduction of ringed seals (*Phoca hispida*) in Amundsen Gulf, Northwest Territories in 1984-1987. In *Ringed seals in the North Atlantic*. Edited by M.P. Heide-Jorgensen and C. Lydersen. The North Atlantic Marine Mammal Commission. Tromso. pp.197-210.
- Krafft, B.A., Kovacs, K.M., and Lydersen, C. 2007. Distribution of sex and age groups of ringed seals *Pusa hispida* in the fast-ice breeding habitat of Kongsfjorden, Svalbard. *Marine Ecology Progress Series* 335: 199-206.
- Krafft, B.A., Kovacs, K.M., Frie, A.K., Haug, T., and Lydersen, C. 2006. Growth and population parameters of ringed seals (*Pusa hispida*) from Svalbard, Norway, 2002-2004. *ICES Journal of Marine Science* 63: 1136-1144.
- Krebs, C.J., Kenney, A.J., Gilbert, S., Danell, K., Angerbjorn, A., Erlinge, S., Bromley, R.G., Shank, C., and Carriere, S. 2002. Synchrony in lemming and vole populations in the Canadian Arctic. *Canadian Journal of Zoology* 80: 1323-1333.
- Laidre, K.L., Stirling, I., Lowry, L.F., Wiig, O., Heide-Jorgensen, M.P., and Ferguson, S.H. 2008. Quantifying the sensitivity of Arctic marine mammals to climate-induced habitat change. *Ecological Applications* 18(2 Supplement): S97-S125.

- Laws, R.M. 1956. Growth and sexual maturity in aquatic mammals. *Nature* 178: 193-194.
- Laws, R.M., Baird, A., and Bryden, M.M. 2003. Breeding season and embryonic diapause in crabeater seals (*Lobodon carcinophagus*). *Reproduction* 126: 365-370.
- Lydersen, C. 1995. Energetics of pregnancy, lactation and neonatal development in ringed seals (*Phoca hispida*). In *Whales, seals, fish and man*. Edited by A.S. Blix, L. Walloe and O. Ultang. Elsevier. Amsterdam, Lausanne, New York, Oxford, Shannon, Tokyo. pp.319-327.
- Lydersen, C. and Gjertz, I. 1986. Studies of the ringed seal (*Phoca hispida* Schreber 1775) in its breeding habitat in Kongsfjorden, Svalbard. *Polar Research* 4: 57-63.
- Lydersen, C. and Gjertz, I. 1987. Population parameters of ringed seals (*Phoca hispida* Schreber, 1775) in the Svalbard area. *Canadian Journal of Zoology* 65: 1021-1027.
- Mansfield, A.W. 1967. Seals of Arctic and eastern Canada. *Fisheries Research Board of Canada, Bulletin* 137, 35 pp.
- Markham, W.E. 1986. The ice cover. In *Canadian Inland Seas*. Edited by I.P. Martini. Elsevier. Amsterdam, Oxford, New-York, Tokyo. pp.101-116.
- Marshall, J., Kushnir, Y., Battisti, D., Chang, P., Czaja, A., Dickson, R., Hurrell, J., McCartney, M., Saravanan, R., and Visbeck, M. 2001. North Atlantic climate variability: phenomena, impacts and mechanisms. *International Journal of Climatology* 21: 1863-1898.

- McCormick, M.P., Thomason, L.W., and Trepte, C.R. 1995. Atmospheric effects of the Mt Pinatubo eruption. *Nature* 373: 399-404.
- McDonald, M., Arragutainaq, L., and Novalinga, Z. 1997. Voices from the Bay: traditional ecological knowledge of Inuit and Cree in the Hudson Bay bioregion. Canadian Arctic Resources Committee, Environmental Committee of the municipality of Sanikiluaq.
- McKinney, M.A., Peacock, E., and Letcher, R.J. 2009. Sea ice-associated diet change increases the levels of chlorinated and brominated contaminants in polar bears. *Environmental Science and Technology* 43: 4334-4339.
- McLaren, I.A. 1958. The biology of the ringed seal (*Phoca hispida* Schreber) in the eastern Canadian Arctic 97 pp.
- McLaren, I.A. 1993. Growth in pinnipeds. *Biological Reviews* 68: 1-79.
- Mysak, L.A. and Manak, D.K. 1989. Arctic sea-ice extent and anomalies, 1953-1984. *Atmosphere-Ocean* 27(2): 376-405.
- Mysak, L.A. and Venegas, S.A. 1998. Decadal climate oscillations in the Arctic: a new feedback loop for atmosphere-ice-ocean interactions. *Geophysical Research Letters* 25(19): 3607-3610.
- Mysak, L.A., Ingram, R.G., Wang, J., and Van der Baaren, A. 1996. The anomalous sea-ice extent in Hudson Bay, Baffin Bay and the Labrador sea during three simultaneous NAO and ENSO episodes. *Atmosphere-Ocean* 34(2): 313-343.
- Oli, M.K. and Dobson, F.S. 1999. Population cycles in small mammals: the role of age at sexual maturity. *Oikos* 86: 557-565.

- Ottersen, G., Planque, B., Belgrano, A., Post, E., Reid, P.C., and Stenseth, N.C. 2001. Ecological effects of the North Atlantic Oscillation. *Oecologia* 128: 1-14.
- Parkinson, C.L. and Cavalieri, D.J. 2008. Arctic sea ice variability and trends, 1979-2006. *Journal of Geophysical Research* 113: C07003.
- Parkinson, C.L., Cavalieri, D.J., Gloerson, P., Zwally, H.J., and Comiso, J.C. 1999. Arctic sea ice extents, areas, and trends, 1978-1996. *Journal of Geophysical Research* 104(C9): 20837-20856.
- Post, E. and Forchhammer, M.C. 2002. Synchronization of animal population dynamics by large-scale climate. *Nature* 420: 168-171.
- Regehr, E.V., Lunn, N.J., Amstrup, S.C., and Stirling, I. 2007. Effects of earlier sea ice break-up on survival and population size of polar bears in western Hudson Bay. *Journal of Wildlife Management* 71(8): 2673-2683.
- Reiter, J., Stinson, N.L., and LeBoeuf, B.J. 1978. Northern elephant seal development: the transition from weaning to nutritional independence. *Behavioral Ecology and Sociobiology* 3: 337-367.
- Roth, J.D. 2003. Variability in marine resources affects Arctic fox population dynamics. *Journal of Animal Ecology* 72: 668-676.
- Ryg, M. and Ortsland, N.A. 1991. Estimates of energy expenditure and energy consumption of ringed seals (*Phoca hispida*) throughout the year. *Polar Research* 10(2): 595-602.
- Saucier, F.J., Senneville, S., Prinsenberg, S., Roy, F., Smith, G., Gachon, P., Caya, D., and Laprise, R. 2004. Modelling the sea ice-ocean seasonal cycle in

- Hudson Bay, Foxe Basin and Hudson strait, Canada. Climate Dynamics 23: 303-326.
- Simpkins, M.A., Kelly, B.P., and Wartzok, D. 2001. Three-dimensional analysis of search behaviour by ringed seals. Animal Behaviour 62: 67-72.
- Skinner, W.R., Jefferies, R.L., Carleton, T.J., Rockwell, R.F., and Abraham, K.F. 1998. Prediction of reproductive success and failure in lesser geese based on early season climatic variables. Global Change Biology 4: 3-16.
- Smith, T.G. 1973. Population dynamics of the ringed seal in the Canadian eastern Arctic 55 pp.
- Smith, T.G. 1976. Predation of ringed seal pups (*Phoca hispida*) by the arctic fox (*Alopex lagopus*). Canadian Journal of Zoology 54: 1610-1616.
- Smith, T.G. 1980. Polar bear predation of ringed and bearded seals in the land-fast ice habitat. Canadian Journal of Zoology 58: 2201-2209.
- Smith, T.G. 1987. The ringed seal, *Phoca hispida*, of the Canadian western Arctic 81 pp.
- Smith, T.G. and Stirling, I. 1975. The breeding habitat of the ringed seal (*Phoca hispida*). The birth lair and associated structures. Canadian Journal of Zoology 53: 1297-1305.
- Smith, T.G. and Stirling, I. 1978. Variation in the density of ringed seal (*Phoca hispida*) birth lairs in the Amundsen Gulf, Northwest Territories. Canadian Journal of Zoology 56: 1066-1070.
- Smith, T.G. and Hammill, M.O. 1981. Ecology of the ringed seal, *Phoca hispida*, in its fast ice breeding habitat. Canadian Journal of Zoology 59: 966-981.

- Smith, T.G. and Harwood, L.A. 2001. Observations of neonate ringed seals, *Phoca hispida*, after early break-up of the sea ice in Prince Albert Sound, Northwest Territories, Canada, Spring 1998. *Polar Biology* 24: 215-219.
- Smith, T.G., Hammill, M.O., and Taugbol, G. 1991. A review of the developmental, behavioral and physiological adaptations of the ringed seal, *Phoca hispida*, to life in the Arctic winter. *Arctic* 44(2): 124-131.
- Sokal, R.R. and Rohlf, F.J. 1995. *Biometry: The principles and practice of statistics in biological research*. Freeman, W.H. and Company. New York.
- Stearns, S.C. 1976. Life-history tactics: a review of the ideas. *The Quarterly Review of Biology* 51(1): 3-47.
- Stearns, S.C. 1992. *The evolution of life-histories*. Oxford University Press. Oxford.
- Stenseth, N.C., Mysterud, A., Ottersen, G., Hurrell, J.W., Chan, K.-S., and Lima, M. 2002. Ecological effects of climate fluctuations. *Science* 297: 1292-1296.
- Stewart, R.E.A., Stewart, B.E., Stirling, I., and Street, E. 1996. Counts of growth layer groups in cementum and dentine in ringed seals (*Phoca hispida*). *Marine Mammal Science* 12(3): 383-401.
- Stirling, I. 1969. Ecology of the Weddell seal in McMurdo Sound, Antarctica. *Ecology* 50(4): 573-586.
- Stirling, I. 1997. The importance of polynyas, ice edges, and leads to marine mammals and birds. *Journal of Marine Systems* 10: 9-21.

- Stirling, I. 2002. Polar bears and seals in the eastern Beaufort Sea and Amundsen Gulf: a synthesis of population trends and ecological relationships over three decades. *Arctic* 55(supp.1): 59-76.
- Stirling, I. 2005. Reproductive rates of ringed seals and survival of pups in northwestern Hudson Bay, Canada, 1991-2000. *Polar Biology* 28: 381-387.
- Stirling, I. and Lunn, N.J. 1997. Environmental fluctuations in Arctic marine ecosystems as reflected by variability in reproduction of polar bears and ringed seals. *In Ecology of Arctic environments. Edited by S.J. Woodin and M. Marquiss. Blackwell Science.* pp.167-181.
- Stirling, I. and Smith, T.G. 2004. Implications of warm temperatures and an unusual rain event for the survival of ringed seals on the coast of southeastern Baffin Island. *Arctic* 57(1): 59-67.
- Stirling, I. and Parkinson, C.L. 2006. Possible effects of climate warming on selected populations of polar bears (*Ursus maritimus*) in the Canadian Arctic. *Arctic* 59(3): 261-275.
- Stirling, I., Archibald, W.R., and DeMaster, D. 1977. Distribution and abundance of seals in the Eastern Beaufort Sea. *Fisheries Research Board of Canada* 34: 976-988.
- Stirling, I., Cleator, H., and Smith, T.G. 1981. Marine mammals. *In Polynyas in the Canadian Arctic. Occasional paper Number 45. Edited by I. stirling and H. Cleator. Canadian Wildlife Service.* pp.45-58.

- Stirling, I., Kingsley, M.C.S., and Calvert, W. 1982. The distribution and abundance of seals in the eastern Beaufort Sea, 1974-79. Canadian Bulletin of Fisheries and Aquatic Sciences. Occasional paper 47. 23 pp.
- Stirling, I., Lunn, N.J., and Iacozza, J. 1999. Long-term trends in the population ecology of polar bears in western Hudson Bay in relation to climatic change. *Arctic* 52(3): 294-306.
- Stirling, I., Lunn, N.J., Iacozza, J., Elliott, C., and Obbard, M. 2004. Polar bear distribution and abundance on the southwestern Hudson Bay coast during open-water season, in relation to population trends and annual ice pattern. *Arctic* 57(1): 15-26.
- Teilmann, J. and Kapel, F.O. 1998. Exploitation of ringed seals (*Phoca hispida*) in Greenland. In *Ringed seals in the North Atlantic*. Edited by M.P. Heide-Jørgensen and C. Lydersen. The North Atlantic Marine Mammal Commission. Tromso. pp.130-151.
- Testa, J.W. and Siniff, D.B. 1987. Population dynamics of Weddell seals (*Leptonychotes weddelli*) in McMurdo Sound, Antarctica. *Ecological Monographs* 57(2): 149-165.
- Thomas, J.A. and DeMaster, D.P. 1983. Parameters affecting survival of Weddell seal pups (*Leptonychotes weddelli*) to weaning. *Canadian Journal of Zoology* 61: 2078-2083.
- Trillmich, F. and Ono, K.A. 1991. Pinnipeds and El Niño: Responses to environmental stress. Springer-Verlag. Berlin, Heidelberg, New York, London, Paris, Tokyo, Hong Kong, Barcelona, Budapest.

- Trites, A.W. and Donnelly, C.P. 2003. The decline of Steller sea lion *Eumetopias jubatus* in Alaska: a review of the nutritional stress hypothesis. *Mammal Review* 33: 3-28.
- Tynan, C.T. and DeMaster, D.P. 1997. Observations and predictions of Arctic climatic change: potential effects on marine mammals. *Arctic* 50(4): 308-322.
- Vibe, C. 1967. Arctic animals in relation to climatic fluctuations. Reitzels Forlag, C.A.
- Wang, J., Mysak, L.A., and Ingram, R.G. 1994. Inter-annual variability of sea-ice cover in Hudson Bay, Baffin Bay and the Labrador Sea. *Atmosphere-Ocean* 32(2): 421-447.
- Woollett, J.M., Henshaw, A.S., and Wake, C.P. 2000. Palaeoecological implications of Archaeological seal bone assemblages: case studies from Labrador and Baffin Island. *Arctic* 53(4): 395-413.
- Yurkowski, D.J., Chambellant, M., and Ferguson, S.H. 2010. Evidence of polygyny from baculum and testicle growth in the aquatic-mating ringed seal (*Phoca hispida*). *Journal of Mammalogy* (submitted).
- Zar, J.H. 1996. Biostatistical analysis. Prentice-Hall.

Chapter 4

Temporal variation in western Hudson Bay ringed seal (*Phoca hispida*) diet as an indicator of ecosystem changes.



**Temporal variation in western Hudson Bay ringed seal (*Phoca hispida*) diet
as an indicator of ecosystem changes.**

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Abstract

During the last 40 years, the Hudson Bay ecosystem has experienced major climatic changes that have affected ice-dependent species. Because of their position near the top of the Arctic food web and their dependence on sea-ice for reproduction and survival, ringed seals (*Phoca hispida*) are expected to be good indicators of ecosystem change under current and predicted climatic trends, particularly in Hudson Bay where they occur at the southern limit of the species range. We collected ringed seal samples during the Inuit subsistence harvest in Arviat, NU, over a period spanning 1991-2006, and present the first detailed study of ringed seal feeding habits in western Hudson Bay. Ringed seals of all ages fed predominantly on sand lances (*Ammodytes* sp.), particularly during the open-water season. Prior to break-up of the sea ice in spring, ringed seal diet was dominated by other fish than sand lances: arctic cod (*Boreogadus saida*) in the 1990s and capelin (*Mallotus villosus*) in the 2000s. The diet was also more diverse and the importance of invertebrates increased relative to the open-water season. Adult ringed seals exploited a more benthic and/or inshore habitat and fed on a slightly higher trophic level than younger age-classes. Secondary fish consumed by ringed seals changed at the end of the 1990s, with arctic cod becoming less important and capelin and rainbow smelt (*Osmerux mordax*) appearing in the diet, perhaps in response to a rise in water temperature as part of the current trend of climate warming. Cold and heavy ice conditions that prevailed in the early 1990s in western Hudson Bay could have produced a shift from pelagic to benthic dominated food web, reducing the availability of sand

lances to ringed seals which fed more on benthically, leading to reduced food and energy consumption. We suggest that ringed seals in western Hudson Bay are strongly regulated by bottom-up processes since timing of break-up was found to be critical for sand lance recruitment and adult abundance, distribution, and /or availability to ringed seals, with consequences to ringed seal energy budget and hence to their reproductive success and abundance.

Keywords: *Ammodytes* sp., Arctic, *Boreogadus*, bottom-up regulation, ecosystem change, feeding habits, *Mallotus*, northward shift, parasite, stable isotope, stomach content.

Introduction

Over the last 40 years, Hudson Bay, a large Canadian sub-Arctic inland sea, ice-covered from November to June (Markham 1986, Saucier et al. 2004), has experienced major climatic changes that reflect the unidirectional warming occurring on a global scale (IPCC (Intergovernmental Panel on Climate Change) 2007). Break-up of the sea ice in spring in western Hudson Bay is now occurring earlier than it did in the 1970s, at a rate of about 10 days by decade, and is accompanied by an increase in the length of the open-water season and a reduction of sea-ice extent and snow depth, likely a result of increasing surface air temperature (Skinner et al. 1998, Parkinson et al. 1999, Stirling et al. 1999, Gough et al. 2004, Stirling et al. 2004, Ferguson et al. 2005, Gagnon and Gough 2005, Stirling and Parkinson 2006, Parkinson and Cavalieri 2008, Hochheim et al. 2010).

By affecting the atmospheric-ice-ocean coupling, these changes are expected to influence ocean primary productivity with cascading effects through the marine food web (Hansen et al. 2003). As well as possible shifts in prey distribution and availability, loss of sea-ice habitat will likely result in changes in distribution, reproduction, and ultimately survival and abundance of sea-ice dependent Arctic species (Tynan and DeMaster 1997, Laidre et al. 2008). Evidence of such changes have been reported in Hudson Bay for ice-associated species, such as thick-billed murre (*Uria lomvia*; Gaston et al. 2003, Gaston et al. 2005) and polar bear (*Ursus maritimus*; Stirling et al. 1999, Iverson et al. 2006, Regehr et al. 2007, McKinney et al. 2009).

The ringed seal (*Phoca hispida*) is among the smallest phocids (McLaren 1993), is distributed throughout the ice-covered waters of the circumpolar Arctic, and is the most abundant pinniped species of the northern polar regions (Mansfield 1967, Frost and Lowry 1981). Sexually mature ringed seals depend on stable ice with sufficient snow cover for females to build sub-nivean birth lairs that are critical to protect newborn pups from cold and predators, like polar bears, arctic foxes (*Alopex lagopus*) and humans (McLaren 1958, Smith and Stirling 1975, Smith 1976, Hammill and Smith 1991, Smith et al. 1991, Furgal et al. 1996). Ringed seals feed year-round under the ice but especially intensively during the open-water season in late summer and fall, as is apparent from the pattern of seasonal variations in fat depth measurements (McLaren 1958, Breton-Provencher 1979, Ryg et al. 1990). Ringed seals consume a large variety of prey species across their range but generally only a few prey taxa (2-4) dominate the diet in a specific location (McLaren 1958, Weslawski et al. 1994, Siegstad et al. 1998). Arctic cod and invertebrates such as mysids (Mysidae), hyperiid amphipods (Amphipoda) and euphausiids (Euphausiacea) are consistent prey of ringed seals, but diet composition varies with geographical location, season, life-stage and/or sex (McLaren 1958, Breton-Provencher 1979, Lowry et al. 1980b, Bradstreet and Finley 1983, Gjertz and Lydersen 1986, Smith 1987, Weslawski et al. 1994, Siegstad et al. 1998, Wathne et al. 2000, Holst et al. 2001, Labansen et al. 2007).

Considering their position near the top of the Arctic food web and high degree of adaptation to exploit sea-ice habitat for reproduction and survival, ringed seals

could be good indicators of ecosystem changes. In Hudson Bay, ringed seals occur at the southern limit of the species range (Mansfield 1967, Frost and Lowry 1981). Considering the current trends in the Hudson Bay ecosystem, a shift in prey species in ringed seal diet might be predicted, potentially affecting ringed seal energy budget, body condition, reproduction and survival. Low reproductive rates and pup survival (Holst et al. 1999, Ferguson et al. 2005, Stirling 2005, Chambellant et al. 2010b) concurrent with a decline in ringed seal numbers (Chambellant et al. 2010a) have been reported in the 1990s in western Hudson Bay and a nutritional stress was proposed as a possible explanation (Chambellant et al. 2010b). However, ringed seal feeding habits in Hudson Bay have been poorly addressed (McLaren 1958, Breton-Provencher 1979, Stirling 2005).

Traditionally, diet studies of pinnipeds have depended upon recovery of hard parts in stomachs/gastro-intestinal tracts or faeces, providing both qualitative and quantitative information on prey consumed. However, there are also several limitations associated with this technique which may bias and/or compromise diet determination. Differential digestion rates of large and small, hard and soft prey or rapid transit rate are examples of such limitations (Murie and Lavigne 1986, Tollit et al. 1997, Bowen 2000, Hammill et al. 2005). Furthermore, stomach contents provide information on prey ingested shortly before collection and may not be representative of species diet over time and space (Andersen et al. 2004, Hammill et al. 2005). Consequently, indirect methods have recently been developed to determine marine predator diets, including analyses of stable

isotope ratios (Hobson et al. 1996, Lawson and Hobson 2000), and fatty acids in their tissues (Iverson et al. 2004, Thiemann et al. 2008).

Stable isotope (SI) analysis is based on the natural occurrence of different isotopes of the same element and their differential fractionation during biological processes (Kendall et al. 1995, Kendall and Caldwell 1998). During photosynthesis, differential fractionation of carbon (C) SI (^{13}C and ^{12}C) creates a unique carbon-isotopic signature in phytoplankton that is passed on to consumers with minimum enrichment (DeNiro and Epstein 1978, Hobson and Welch 1992, Lesage et al. 2001). In marine mammal studies, carbon SI ratio ($^{13}\text{C}/^{12}\text{C}$, labelled $\delta^{13}\text{C}$) informs on feeding habitat (*i.e.*, benthic/ pelagic, freshwater/marine, inshore/offshore) and general geographic locations (water masses of different isotopic signatures; Smith et al. 1996, Kelly 2000, Rubenstein and Hobson 2004, Newsome et al. 2010). Differential fractionation of nitrogen (N) SI, ^{15}N and ^{14}N , occurs in consumers that preferentially excrete the lighter isotope through urea, resulting in an enrichment of 2-5‰ of the heavier isotope from diet to consumer tissues (*e.g.*, DeNiro and Epstein 1981, Hobson and Welch 1992, Hobson et al. 1996, Kelly 2000, Kurle 2002). In food web studies, nitrogen SI ratio ($^{15}\text{N}/^{14}\text{N}$, labelled $\delta^{15}\text{N}$) indicates the relative trophic level of an organism, and trophic relationships between organisms in an ecosystem (Hobson and Welch 1992, Kelly 2000, Newsome et al. 2010). Due to the specific protein turn-over rate of each tissue, the isotopic signature of different tissues in the same animal provides information on prey assimilated over a range of time scales (Tieszen et al. 1983, Kurle and Worthy 2002, Crawford et al. 2008) and

places (Hobson 1999, Rubenstein and Hobson 2004). Tissues with a high turn-over rate (liver, kidney, serum) represent food ingested days or weeks before collection, tissues with a lower turn-over rate (muscle, red blood cells) represent food ingested months before and inert tissues (whisker, fur, tooth) integrate prey consumed over months or entire lifetime. Although models have been developed to estimate the contribution of different a-priori potential prey species to predator diet using C and N SI ratios (Phillips 2001, Phillips and Gregg 2003, Hall-Aspland et al. 2005, Moore and Semmens 2008), several limitations (e.g., prey need to have a different isotopic signature) hinder assessment of species composition in diet using SI analysis, especially for diversified diets. Using SI analysis is thus a complementary method to more traditional hard-part reconstruction techniques, and this combination has been successively used to explore pinnipeds feeding habits (e.g., Burns et al. 1998, Holst et al. 2001, Dehn et al. 2007).

In this study, we examined the diet of ringed seals in western Hudson Bay over nine sampling years between 1991 and 2006, using both stomach contents and carbon and nitrogen stable isotope ratios in muscle and liver tissues. Our objectives were to 1) quantify a baseline for ringed seal diet against which comparison could be made in future studies; 2) evaluate age-related and seasonal variability; 3) assess and interpret inter-annual variability of ringed seal diet over time in relation to changes in the sea ice regime; and 4) test the nutritional stress hypothesis proposed to explain the decline in ringed seal reproductive performances and densities in western Hudson Bay in the 1990s.

Material and Methods

Sample collection

Ringed seals were collected in 1991, 1992, and in 1998- 2000 by Canadian Wildlife Service, and in 2003-2006 by Fisheries and Oceans Canada, Winnipeg, in the Hudson Bay community of Arviat, Nunavut, Canada (Fig. 1) from the Inuit fall subsistence harvest (September through November), when ringed seals feed in open water. In 1991, 1992, 2004, and 2005, samples were also collected from the spring subsistence harvest, when ringed seals are hauled-out on the ice to moult. After collection, stomachs, muscle and liver tissues, and lower jaws were labelled, put in individual bags and kept frozen at -20° C. Muscle and liver tissues were not collected from 1998 to 2000.

Fish and invertebrate species potentially consumed by ringed seals were collected from 2004 to 2007 at different locations in Hudson Bay, including Coats Island (see Elliott and Gaston 2008), sample sites from the ArcticNet leg 2 cruise transect (see Pazerniuk 2007), and opportunistic collections from Arviat, Churchill and Sanikiluaq, Nunavut. Some prey items were also recovered from seal stomachs if they were in fresh enough condition.

Age determination

Ringed seal lower jaws were simmered in hot water for two to three hours to soften tissues. Right canine teeth were extracted and preserved in 70% ethanol. When the right canine tooth was not available, the left canine tooth, right or left first post-canine tooth, or a double-rooted post-canine tooth was used, in this

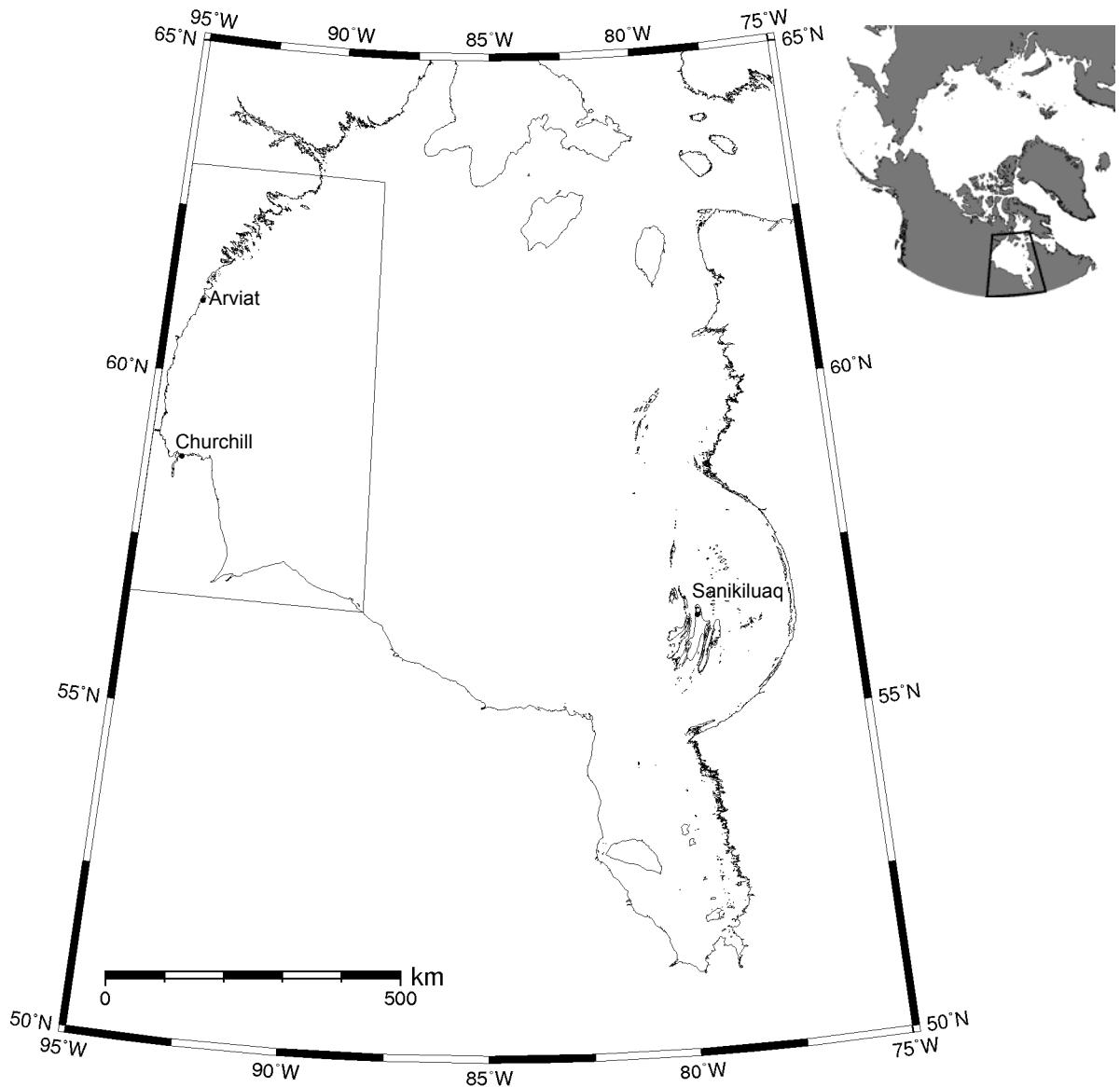
order of preference (Chambellant and Ferguson 2009). The periodontal ligament was not cleaned from tooth roots to prevent potential damage to the most recently deposited annual growth layer group (GLG). Ages were determined by interpreting and counting GLGs in cementum of decalcified, stained, longitudinal thin tooth sections following the technique described by Stirling et al. (1977), Bernt et al. (1996) and Stewart et al. (1996). GLGs were counted in two to three blind replicates for each tooth and final ages were estimated using two identical readings or the median of three different readings.

Ringed seals were grouped according to three age-classes. Seals born in spring and harvested during the same year were referred to as pups; seals of 1 to 5 years of age were considered juveniles; and seals of 6 years of age and older were categorized as adults (Holst et al. 1999).

Stomach processing

Thawed stomachs were weighted to the nearest 0.1g using an A&D electronic balance. Each stomach was emptied into a glass tray and wet weight of content was recorded. Large or whole food items were removed, identified to species, weighed to the nearest 0.1g, and measured when possible, to the nearest 1mm (total/fork length for fish and carapace length for crustaceans). Remaining content was washed through graduated, nested sieves of 4.75, 2 and 1mm. Sagittal otoliths and invertebrate remains, including carapaces, claws, and eye lenses of crustaceans, were sorted, counted and identified to the lowest taxonomic level possible using Fisheries and Oceans Canada reference

Figure 1: Map of Hudson Bay showing the study site, the community of Arviat on the western coast of Hudson Bay, Nunavut, and the area defined as western Hudson Bay according to Stirling et al. (1999).



collections and published guides (Campana 2004). Otoliths too eroded for a positive identification were classified as unidentified fish and not measured.

Paired otoliths retrieved from fish skulls were kept separately. If possible, otoliths were paired and the largest structure measured to the nearest 0.01mm using a Mitutoyo digimatic calliper (> 5mm) or an image analysis software (< 5mm; ImagePro[©] Plus v. 6.0, Media Cybernetics, Inc., <http://www.mediacy.com/>).

When the number of otoliths was greater than 30, a random sample of 30 otoliths was measured, and mean otolith length was assumed for remaining unmeasured otoliths. For otoliths too eroded to be measured but identifiable, we used mean otolith length of the particular prey in the same stomach, or in the same year if no other specimen of the same prey was present in that stomach. If otoliths retrieved from skulls were present, only these measurements were used to determine mean otolith length. For invertebrate species with no measured weight, we took the mean weight of that species for the year or over all years, depending on available sample sizes.

The minimum number of individuals (MNI) present in a given stomach was determined by adding the number of whole individuals, the number of unique structures (e.g., shrimp telson), the number of otolith pairs and, when paired structures could not be identified as a pair (e.g., eye lenses, loose otoliths), the number of such structures divided by two. When only bones were present, a single individual was recorded.

Stomachs from the 1990s (1991-2000), particularly from 1991 and 1992, were processed in a different lab, by different individuals and on two different

occasions likely resulting in loss of comparability and reduced quality of some information. Stomach content reconstruction was done meticulously using all material and information available to provide the best estimate possible. However, the number of items is likely underestimated. Whole individuals and hard-parts identification and measurement were done as stated above and concurrently to the rest of the collection, assuring consistency.

Body length (Fork or total length depending of species; cm) and wet mass (g) of fish were estimated from regressions with otolith measurements (mm) taken from published and unpublished data (Tables 1 and 2), and were used to estimate total biomass of prey ingested for each stomach. Total energy consumed was estimated by summing the products of total biomass of each prey species by its energy density (kJ/g wet mass) taken from literature and unpublished data (Table 2).

Stable isotope analysis

Muscle and liver tissues from ringed seals, and muscle tissues from fish and whole invertebrates (head and telson were removed from shrimps; shell was removed from bivalves) were freeze-dried and homogenized. Lipids were removed with chloroform:methanol (2:1 v/v) using a modified liquid-liquid Folch method (Folch et al. 1956).

Carbon and nitrogen isotopic analyses on muscle and liver samples were accomplished by continuous flow ion ratio mass spectrometry (CF-IRMS) using a GV-Instruments® IsoPrime attached to a peripheral temperature controlled

Table 1: Regression equations used to estimate the body length (BL, cm) from the otolith length (OL, mm) of fish recovered from ringed seal stomachs collected in Arviat, NU, over the period 1991-2006.

Prey taxa	Body Length (cm)	r^2	n	[range OL]	source
	Equation (OL, mm)				
<i>Ammodytes</i> sp.	BL=(76.454*OL-13.547)/10	0.92	486	[1.04-3.07]	1
<i>Clupea harengus</i>	BL=(15.627+57.86*OL)/10	0.98	477	[0.87-3.02]	1
Cottidae [§]	BL=0.5445*OL^2+1.1569*OL+2.9606	0.91	33	[1.14-3.81]	2
<i>Artemiellus</i> sp.	BL=-0.1261*OL^2+2.9693*OL	0.84	31	[1.98-4.93]	2
<i>Gymnoanthus tricuspidis</i> [§]	BL=0.5445*OL^2+1.1569*OL+2.9606	0.91	33	[1.14-3.81]	2
<i>Myoxocephalus scorpioides</i> [¶]	BL=2.2271*OL^1.2493	0.83	19	[4.38-7]	2
<i>Myoxocephalus scorpius</i>	BL=2.2271*OL^1.2493	0.83	19	[4.38-7]	2
<i>Myoxocephalus</i> sp. [¶]	BL=2.2271*OL^1.2493	0.83	19	[4.38-7]	2
<i>Triglops murrayi</i>	BL=0.5445*OL^2+1.1569*OL+2.9606	0.91	33	[1.14-3.81]	2
Gadidae [¶]	BL=4.4986+0.1184*OL+0.1997*OL^2	0.96	502	[1.81-17.95]	3
<i>Boreogadus saida</i>	BL=(19.433+(18.612*OL)+0.546*(OL)^2)/10	0.81	270	[1.08-11.55]	1
<i>Gadus morhua</i>	BL=4.4986+0.1184*OL+0.1997*OL^2	0.96	502	[1.81-17.95]	3
<i>Gadus ogac</i>	BL=0.1001*OL^2+0.9985*OL+2.6473	0.95	330	[4.2-17.9]	2
<i>Liparis</i> sp.	BL=5.7414*OL^1.3634	0.83	43	[0.97-2.69]	2
<i>Mallotus villosus</i>	BL=((215.741*OL)-(176.657*OL^2)+(71.062*OL^3)-(9.449*OL^4)-23.151)/10	0.98	407	[0.64-3.42]	1
<i>Eumesogrammus praecisus</i>	BL=3.4394*OL^0.982	0.91	40	[2.2-6.39]	2
<i>Lumpenus lampretaeformis</i> [¶]	BL=9.2666*OL^0.6212	0.87	62	[1.05-2.56]	2
<i>Lumpenus fabricii</i> [¶]	BL=9.2666*OL^0.6212	0.87	62	[1.05-2.56]	2
<i>Leptoclinus maculatus</i>	BL=9.2666*OL^0.6212	0.87	62	[1.05-2.56]	2
<i>Osmerus mordax</i>	BL=2.8571*OL^1.131	0.88	57	[3.71-6.35]	2
<i>Pungitius pungitius</i>	BL=7.21*OL	n/a	35	[1.5-5.8]	4

¹Lidster et al. 1994; ²Stenson and McKinnon, unpublished data; ³B. Healey, unpublished data; ⁴Leopold et al. 1991

[§]Equation from *Triglops murrayi*; [¶]Equation from *Myoxocephalus scorpius*; [¶]Equation from *Gadus morhua*; [¶]Equation from *Leptoclinus maculatus*

Table 2: Energy density (kJ/g wet mass) and regression equations used to estimate wet mass (WM, g) from otolith length (OL, mm) or body length (BL, cm) of prey recovered from ringed seal stomachs collected in Arviat, NU, 1991-2006.

Prey taxa	Wet mass (g)		r^2	n	source	Energy (kJ/g wet mass)	source
	Equation (OL, mm)						
Fish							
<i>Ammodytes</i> sp.	WM=2.26*(BL/10) ^{2.86}		0.79	87	1	5.06	1
<i>Clupea harengus</i>	WM=1.48*OL ^{3.08}				2	7.18	6
<i>Cottidae</i> ^a	WM=7.37*(BL/10) ^{2.57}		0.87	252	1	4.57	7
<i>Arctozenus</i> sp. ^a	WM=7.37*(BL/10) ^{2.57}		0.87	252	1	3.69	8
<i>Gymnophantherus tricuspidis</i>	WM=11.11*(BL/10) ^{4.03}		0.92	17	1	4.57	7
<i>Myoxocephalus scorpioides</i>	WM=9.54*(BL/10) ^{2.64}		0.96	10	1	4.43	8
<i>Myoxocephalus scorpius</i>	WM=9.54*(BL/10) ^{2.64}		0.96	10	1	4.43	8
<i>Myoxocephalus</i> sp.	WM=9.54*(BL/10) ^{2.64}		0.96	10	1	4.43	8
<i>Triglops murrayi</i>	WM=6.48*(BL/10) ^{2.96}		0.81	113	1	4.33	1
<i>Gadidae</i> ^b	WM=(10 ^{(-5.2106+3.0879*\log_{10}(BL))} *1000			502	4	4.7	8
<i>Boreogadus saida</i>	WM=6.24*(BL/10) ^{2.98}		0.86	354	1	4.7	1
<i>Gadus morhua</i>	WM=(10 ^{(-5.2106+3.0879*\log_{10}(BL))} *1000			502	4	4.52	9
<i>Gadus ogac</i>	WM=0.0101*OL ^{4.0995}		0.96	239	3	4.7	8
<i>Liparis</i> sp.	WM=0.0065*BL ^{3.1802}		0.96	39	3	2.84 ^d	8
<i>Mallotus villosus</i>	WM=4.21*(BL/10) ^{3.74}		0.85	187	1	4.9	1
<i>Eumesogrammus praecisus</i>	WM=6.70*(BL/10) ^{3.29}		0.96	109	1	3.22	1
<i>Lumpenus lampretaeformis</i> ^c	WM=3.04*(BL/10) ^{2.16}		0.87	70	1	5.57	11
<i>Lumpenus fabricii</i> ^c	WM=3.04*(BL/10) ^{2.16}		0.87	70	1	4.51	11
<i>Leptoclinus maculatus</i>	WM=3.04*(BL/10) ^{2.16}		0.87	70	1	4.97	1
<i>Osmerus mordax</i>	WM=0.0026*BL ^{3.3001}			59	3	4.2	11
<i>Pungitius pungitius</i>	WM=1.54*OL ^{2.62}			35	5	7.26	12

Invertebrates

Copepoda	4.12	8
Cumacea	3.63 ^ψ	13
<i>Atylus carinatus</i>	3.88	7
<i>Onisimus litoralis</i>	8.24	14
Hyperiidae	4.18	1
<i>Themisto libellula</i>	4.18	1
Gammaridae	3.88	7
Mysidae	3.63	13
Decapoda	3.48	1
<i>Eualus fabricii</i>	4.87	8
<i>Lebbeus groenlandicus</i>	4.81	8
<i>Lebbeus polaris</i>	5.46	8
<i>Spirontocaris phippsi</i>	4.37 ^β	15
Dendrobranchiata	3.48	1
Mollusca	4 [§]	10
Bivalvia	3.03 [¶]	10
Polychaeta	2.78	8
Echinoidea	1.33 [‡]	10

¹Elliott and Gaston 2008; ²Ross 1993; ³Stenson and McKinnon, unpublished data; ⁴B. Healey, unpublished data; ⁵Leopold et al. 1991; ⁶mean of values from D. Chabot, unpublished data (5.61kJ/g), Anthony et al. 2000, Lawson et al. 1998, Arrhenius and Hansson 1993 and Steimle and Terranova 1985; ⁷mean of values from D. Chabot, unpublished data (4.47kJ/g) and Bradstreet and Finley 1983; ⁸D. Chabot, unpublished data; ⁹mean of values from D. Chabot, unpublished data (5.04kJ/g), Lawson et al. 1998, Steimle and Terranova 1985 and Holdway and Beamish 1984; ¹⁰Steimle and Terranova 1985; ¹¹Hammill et al., unpublished data; ¹²mean of values from D. Chabot, unpublished data (9.71kJ/g) and Ball et al. 2007; ¹³mean of values from D. Chabot, unpublished data (*Boreomysis arctica*: 3.76kJ/g and *Mysis mixta*: 3.14 kJ/g), Bradstreet and Finley 1983 and Tyler 1973; ¹⁴Bradstreet and Finley 1983; ¹⁵Tyler 1973.

^ψEquation from “all sculpins”; ^θEquation from *Gadus morhua*; ^εEquation from *Leptoclinus maculatus*; ^δmean of three species; ^ψvalue from Mysidae; ^βvalue from *Spirontocaris* sp.; [§]mean of 21 species; [¶]mean of 11 species; [‡]mean of four species

EuroVector® elemental analyzer (EA) (University of Winnipeg Isotope Laboratory, *UWIL*). One mg samples were loaded into tin capsules and placed in the EA auto-sampler along with internally calibrated carbon/nitrogen standards (Pharma and Casein proteins: $\delta^{13}\text{C} = -22.95$ and -26.98 ‰ VPDB; $\delta^{15}\text{N} = 5.00$ and 5.94 ‰ AIR, respectively). Carbon and nitrogen isotope results are expressed using standard delta (δ notation in units of *per mil* (‰)). Delta values of carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) represent deviations from a standard, such that:

$$\delta_{\text{sample}} (\text{‰}) = [(R_{\text{sample}}/R_{\text{standard}})-1]*1000 \quad (1)$$

where R is the $^{13}\text{C}/^{12}\text{C}$ or $^{15}\text{N}/^{14}\text{N}$ ratio in the sample and the standard. Standards used for carbon and nitrogen isotopic analyses are Vienna PeeDee Belemnite (VPDB) and IAEA-N-1 (IAEA, Vienna), respectively. Accuracy was obtained through analysis of laboratory standards used for calibration of results. Analytical precision, determined from duplicate measurements of laboratory standards run at the same time than samples, was $\pm 0.18\text{ ‰}$ for $\delta^{13}\text{C}$ and $\pm 0.19\text{ ‰}$ for $\delta^{15}\text{N}$.

Carbon stable isotope ratios were corrected for 1) the oceanic Suess effect by adding -0.019 ‰ per year (Quay et al. 2003) using year 1991 as our starting point; and 2) for presence of carbonates in invertebrates by adding -0.3 ‰ (Bunn et al. 1995).

Time of spring break-up

Annual break-up dates in western Hudson Bay (as defined in Stirling et al. 1999; Fig. 1) were calculated for the period 1991-2006. Following the method described

in Gagnon and Gough (2005), the western Hudson Bay region was divided into a grid of 0.5 Latitude x1.5 Longitude. Weekly ice concentration maps of Hudson Bay were retrieved from Canadian Ice Service (Canadian Ice Service: <http://ice-glaces.ec.gc.ca/>) and ice concentration at 42 points defined by the grid was determined. Break-up date (± 1 week) at each center point was defined as the earliest date with an ice concentration of 50% or less, that was maintained for at least three weeks. Annual break-up dates for the entire western Hudson Bay region were calculated by taking the median of the 42 values from the grid. Average date of break-up over the entire period was also calculated.

Data analyses

In the spring, the proportion of adult ringed seals with identified prey items in their stomach was 83% (15/18), so only adult diet was considered for this period.

Prey grouping was performed so that each group was present in at least 10 stomachs when all years were pooled, resulting in nine prey groups in the fall and eight in the spring.

Diet composition and importance of prey taxa were assessed using 1) percentage abundance of prey ($\%P = \text{number of prey } i / \text{total number of prey} * 100$), 2) frequency of occurrence ($FO = \text{number of stomach with prey } i / \text{total number of stomach} * 100$), 3) percentage biomass contribution ($\%B = \text{wet mass of prey } i / \text{total wet mass} * 100$), 4) percentage energy contribution ($\%E = \text{energy from prey } i / \text{total energy from prey} * 100$) and 5) index of global importance (IG; Moreno and Castro 1995) defined as:

$$IG = \frac{(IN + IW)}{2} \quad (2)$$

with IN and IW, indices of importance by number and by wet mass, respectively, computed as:

$$IN = (\% P * FO)^{1/2} \quad (3)$$

$$IW = (\% B * FO)^{1/2} \quad (4)$$

Use of multiple measures to describe ringed seal diet provides information on different aspects of its feeding habits (Cortes 1997), but each has limitations (e.g., %P over-emphasizes the contribution of small prey eaten in large numbers and %B of single heavy prey to the diet (Hyslop 1980, Joy et al. 2006, Tollit et al. 2007). IG was computed to integrate the different information into one single measure, and by averaging IN and IW, to mitigate their limitations (Moreno and Castro 1995).

Variation in diet composition between age-classes and years was assessed using the Bray-Curtis similarity index (S) on IG. S varies from 0 to 1, S = 1 indicating a total similarity in prey consumed. A non-metric multidimensional scaling (MDS) was produced based on S to visualize the multivariate data and a $S \geq 0.8$ was set to indicate similarity between two groups (*i.e.*, age-class or year).

Simpson's diversity index ($D' = 1-D$), the probability that two randomly selected prey items are from different species, and Renyi's entropy of order two $1/D$ (N_2), the number of species that would have been found in the diet if all were equally

common (a measure of evenness or niche breadth), were computed on the number of prey (P), using all prey taxa (Hammer et al. 2001, Magurran 2003).

Statistical analyses

Normality was assessed using the Anderson-Darling test (Stephens 1974).

Frequency of empty stomachs, gastroliths and parasites were compared between seasons, age-class and years using a G-test of independence with William's correction (Sokal and Rohlf 1995).

Means or medians were compared using a t-test with Welch correction to account for different standard deviations (Zar 1996) when necessary, or a Mann-Whitney/Kruskal-Wallis test corrected for tie and large samples with Dunn's multiple comparisons test, when normality of residuals was not reached.

Relationships between sand lance IG and total number of prey per stomach, total biomass, and total energy were explored using sigmoid functions, whereas the Pearson product moment correlation (r_p) was used to describe relationships with the diversity index, the percentage of empty stomachs and the timing of spring sea-ice break-up.

An analysis of similarity (ANOSIM) was performed on the Bray-Curtis similarity matrix on IG to test for difference between season, age-classes and years.

Difference of D' between seasons, years and age-classes was assessed pairwise by bootstrapping 1000 times with replacement (Hammer et al. 2001).

Graphs and statistical analyses were performed using Systat 12 (Systat Software Inc. 2007) and SigmaPlot 11 (Systat Software Inc. 2008). The free statistics package PAST 1.97 (Hammer et al. 2001) was used to perform similarity and diversity analyses. Unless otherwise stated, results are presented as mean \pm standard deviation (SD) or median [1st-3rd percentiles]. All tests were two-tailed and differences considered significant at $p < 0.05$.

Results

A total of 889 ringed seal stomachs were processed over the 9 years of study, most collected during the fall open-water period (Table 3). Adult ringed seals made up more than 80% of the collection in the spring. In the fall, percentage of adults in the harvest varied over the years, with a lower representation in the 2000s than in the 1990s ($G_{corr} = 46.1$, $df = 1$, $p < 0.001$), and averaged about 50% (Table 3). The average sex-ratio was slightly male biased in both seasons (Table 3) but sexes were pooled for analyses.

Results from ringed seal liver and muscle C and N SI analyses were similar; we therefore decided to present results for muscle tissues only.

Stomachs with no prey, and non-prey items and parasite occurrence

Annual percentages of stomachs without prey (i.e., empty and only containing non-prey items) did not vary in the spring ($G_{corr} = 0.28$, $df = 3$, $p > 0.9$), but were significantly different in the fall ($G_{corr} = 38.48$, $df = 8$, $p < 0.001$), with the highest fall percentages in 1992 and 1991 and the lowest in 2006 (Table 3). Overall, less

than half of stomachs contained prey items in the fall whereas in the spring, prey items were found in only about 10% of stomachs ($G_{corr} = 44.02$, $df = 1$, $p < 0.001$; Table 3). This seasonal difference was significant for all years but 1992, where stomachs without prey represented more than 80% of the collection in both fall and spring (Table 3). Percentage of stomachs without prey was not statistically different among age classes (spring: $G_{corr} = 1.14$, $df = 2$, $p > 0.5$; fall: $G_{corr} = 3.02$, $df = 2$, $p > 0.1$) despite inter-annual variations.

Non-prey items included seaweed, sand and stones. Fewer than 10% of stomachs contained gastroliths (stomach stones) and the percentage did not differ between seasons ($G_{corr} = 0.08$, $df = 1$, $p > 0.5$) but showed inter-annual ($G_{corr} = 26.11$, $df = 8$, $p < 0.005$) and age-class ($G_{corr} = 6.98$, $df = 2$, $p < 0.05$) variations. Gastroliths were recovered from more stomachs during the period 1992 to 2000 and pups had a higher occurrence of gastroliths compared to adults and juveniles (Table 3). In the fall, 33% of stomachs with gastroliths contained no prey, and in the spring this percentage reached 84%. Sand was only found in three stomachs collected in the fall of 2004 ($n = 1$) and 2005 ($n = 2$). Seaweeds were not found in spring collections and composed only a small percentage (< 5%) of fall collections (Table 3).

Parasite occurrence was not recorded for the 2003 to 2006 stomach collections. Percentage of ringed seal stomachs parasitized was higher in the spring than in the fall ($G_{corr} = 6.32$, $df = 1$, $p < 0.025$; Table 3). There was no annual difference in parasite loads in the spring ($G_{corr} = 0.004$, $df = 1$, $p > 0.9$) but ringed seals sampled in the fall were more parasitized in the late 1990s compared to 1991

and 1992 ($G_{corr} = 21.43$, $df = 4$, $p < 0.001$). Percentage of stomachs with parasites was not statistically different between age-classes (spring: $G_{corr} = 1.42$, $df = 2$, $p > 0.1$ and fall: $G_{corr} = 3.96$, $df = 2$, $p > 0.1$), although adults tended to be less parasitized in both seasons (Table 3). Parasite load (number of parasites per stomach) was greater in the spring than in the fall ($x_{spring} = 7.5$ [5-20], $n = 20$ vs. $x_{fall} = 3$ [2-5], $n = 46$, $U = 208.5$, $p = 0.0004$). In the fall, annual parasite loads did not vary significantly ($KW = 8.2$, $df = 4$, $p = 0.084$) but sample sizes in 1991 ($n = 2$), 1992 ($n = 3$) and 2000 ($n = 2$) were small. Ringed seal pups tended to have a greater parasite load ($x_{pup} = 10$ [2-21], $n = 6$) than juveniles ($x_{juvenile} = 3$ [1.75-5], $n = 13$) and adults ($x_{adult} = 3.5$ [1-5], $n = 24$) but the difference was not statistically significant ($KW = 1.55$, $df = 2$, $p = 0.46$). In the spring, parasite load was not different between years ($U = 45.5$, $p = 0.75$, $n = 2$) or age-classes ($KW = 2.5$, $df = 2$, $p = 0.29$) but sample sizes were small for pups ($n = 1$) and juveniles ($n = 4$). Of parasitized stomachs, 84% and 38.5% had no prey items in spring and fall, respectively.

Diet composition and seasonal variations

A total of 35 prey types (nine groups) in the fall and 13 prey types (eight groups) in the spring were found in ringed seal stomachs. Mean number of prey groups per stomach was 1.61 ± 1.03 ($n = 200$; maximum = 6) in the fall, with 63.5% of seals with only one prey group in their stomachs, and 1.14 ± 0.36 ($n = 14$; maximum = 2) in the spring, with 12 out of 14 seals that had ingested only one prey group.

Table 3: Characteristics of ringed seal stomach spring (May-June) and fall (September-November) collections from Arviat, NU, 1991-2006 and frequency of occurrence of non-prey items and stomachs without prey. n is the total number of stomachs collected; n prey is the number of stomachs collected that contained prey items.

	Fall							Spring							
					Frequency of occurrence (%)							Frequency of occurrence (%)			
	n	n prey	age class (%)	sex- ratio	Stomach without prey	stone	seaweed	parasite	n	n prey	age class (%)	sex- ratio	Stomach without prey	stone	parasite
1991	41	10		0.86	75.6	2.4	0	7.3	81	8		1.19	88.9	4.9	16.05
Adult	20	5	48.8		75	5		5	74	6	91.4		90.5	2.7	12.2
Juvenile	19	4	46.3		79	0		10.5	6	1	7.4		83.3	16.7	16.7
Pup	2	1	4.9		50	0		0	1	1	1.2		0	100	0
1992	70	11		0.79	84.3	2.9	0	5.7	73	7		1.35	90.4	19.2	16.4
Adult	39	5	55.7		87.2	5.1		0	56	6	76.7		89.3	19.6	12.5
Juvenile	28	6	40		78.6	0		10.7	10	0	13.7		100	20	30
Pup	3	0	4.3		100	0		33.3	7	1	9.6		85.7	14.3	25.6
1998	91	46		1.28	48.4	16.5	9.9	26.4							
Adult	58	31	73.4		44.8	17.2	8.6	20.7							
Juvenile	15	7	19		53.3	13.3	13.3	40							
Pup	6	2	7.6		66.7	33.3	16.7	33.3							
1999	97	37		1.69	61.9	9.3	0	23.7							
Adult	77	30	79.4		61	11.7		20.8							
Juvenile	15	6	15.5		60	0		26.7							
Pup	5	1	5.1		80	0		60							
2000	97	46		1.77	52.6	11.3	7.2	11.3							

<i>Adult</i>	54	27	56.8	50	9.3	5.6	7.4						
<i>Juvenile</i>	20	11	21.1	45	10	20	20						
<i>Pup</i>	21	8	22.1	61.9	19	0	14.3						
2003	84	30		0.95	60.7	3.6	2.4	n/a					
<i>Adult</i>	41	11	51.9	73.2	0	2.4							
<i>Juvenile</i>	25	11	31.6	48	4	0							
<i>Pup</i>	13	6	16.5	53.8	15.4	7.7							
2004	31	15		1.55	51.6	6.5	2.2	n/a	15	2	0.36	86.7	0
<i>Adult</i>	5	3	16.1	40	0	0			13	2	86.6	84.6	
<i>Juvenile</i>	19	8	61.3	57.9	5.3	5.3			1	0	6.7	100	
<i>Pup</i>	7	4	22.6	42.9	14.3	0			1	0	6.7	100	
2005	91	44		1.07	49.5	3.3	2.2	n/a	70	6	1.5	90	1.4286
<i>Adult</i>	22	5	24.7	72.7	4.5	0			62	5	92.5	90.3	1.613
<i>Juvenile</i>	53	28	59.6	47.2	1.9	1.9			5	1	7.5	80	0
<i>Pup</i>	14	10	15.7	21.4	7.1	7.1			0	0	0	0	0
2006	48	26		0.96	45.8	4.2	2.1	n/a					
<i>Adult</i>	17	8	35.4	52.9	5.9	0							
<i>Juvenile</i>	21	13	43.8	38.1	7.8	4.8							
<i>Pup</i>	10	5	20.8	50	0	0							
All years	650	265		1.2	58.3	7.4	3.4	n/a	239	23	1.23	89.5	7.9
<i>Adult</i>	333	125	52.9	61.9	8.7	2.7			205	19	86.9	89.8	6.8
<i>Juvenile</i>	215	94	34.2	55.3	3.7	4.2			22	2	9.3	90.9	13.6
<i>Pup</i>	81	37	12.9	53.1	12.3	3.7			9	2	3.8	77.8	22.2

[†]Age classes defined following Holst et al. 1999 (Adult: ≥6 years; Pup: <1 year; Juvenile: 1-5 years)

Ringed seals in western Hudson Bay fed predominantly on fish, and sand lances were the most important prey species, both in fall and spring when it represented approximately 80% and 45% of energy acquired, respectively (Tables 4 and 5). During the fall, sculpins were the second most important prey for ringed seals ($IG = 10.68$), although their energy contribution to diet was slightly under that of other Gadidae (6.71% vs. 10.35%; Table 4). In the spring, ringed seals fed secondarily on capelin ($IG = 26.88$), followed by other invertebrates (*i.e.*, Decapoda and Mysidae; Table 5). Arctic cod was not an important part of ringed seal diet, contributing less than 1% and 4% of the overall energy ingested in fall and spring, respectively (Tables 4 and 5). Hyperiid amphipods were an important invertebrate prey for ringed seals in both seasons, but shrimps were more important in the spring, when invertebrates were more than twice as important in ringed seal diet than in the fall ($IG = 12.87$ vs. 5.36; Tables 4 and 5). Overall, only 15% of ringed seal stomachs contained invertebrates in the fall, whereas they were found in 40% of stomachs collected in the spring (Tables 4 and 5). The energy contribution of invertebrates was negligible in both seasons.

Adult ringed seal spring diet was more diversified than the fall diet (spring: $D' = 0.55$, $N_2 = 2.22$ and fall: $D' = 0.20$, $N_2 = 1.26$; Bootstrap $p = 0.00$), in agreement with observed pattern that one species dominated the diet in the fall (sand lances) and two in the spring (sand lances and capelin/arctic cod). Number of prey per adult ringed seal stomach was lower in the spring (22.4) than in the fall (46.5).

Table 4: Overall number of identified prey (n prey), number of stomachs in which a particular prey was found (n stomach), frequency of occurrence (FO), percentage prey (%P), percentage biomass (%B), percentage energy (%E), and index of global importance (IG) of identified prey found in ringed seal stomachs (n = 232) collected in Arviat, NU, during falls (September-November) 1991-2006. Taxa in bold represents the nine key groups used in the analyses.

Prey taxon	n prey	n stomach	FO	%P	%B	%E	IG
<u>Fish</u>							
Sand lances (Ammodytidae)							
<i>Ammodytes</i> sp.[§]	10307	203	87.50	87.99	79.64	81.20	85.61
Cods (Gadidae)							
Arctic cod (<i>Boreogadus saida</i>)	16	14	6.03	0.14	0.26	0.25	1.08
Other Gadidae	31	13	5.60	0.26	10.35	9.76	4.42
Unidentified gadids	5	4	1.72	0.04	0.03	0.03	0.25
Atlantic cod (<i>Gadus morhua</i>)	1	1	0.43	0.01	1.15	1.04	0.38
Greenland cod (<i>Gadus Ogac</i>)	25	9	3.88	0.21	9.17	8.68	3.44
Smelts (Osmeridae)							
Capelin (<i>Mallotus villosus</i>)	35	16	6.90	0.30	0.31	0.31	1.45
Rainbow smelt (<i>Osmerus mordax</i>)	188	12	5.17	1.60	2.18	1.84	3.12
Sculpins (Cottidae)							
<i>Artediellus</i> sp.	378	55	23.71	3.23	6.71	6.10	10.68
	3	2	0.86	0.03	<0.01	<0.01	0.12

	Arctic staghorn sculpin (<i>Gymnocanthus tricuspidis</i>)	42	10	4.31	0.36	2.07	1.91	2.12
	Moustache sculpin (<i>Triglops murrayi</i>)	27	6	2.59	0.23	0.66	0.58	1.04
	Arctic sculpin (<i>Myoxocephalus scorpioides</i>)	5	4	1.72	0.04	0.06	0.05	0.30
	Shorthorn sculpin (<i>Myoxocephalus scorpius</i>)	104	20	8.62	0.89	1.33	1.19	3.08
	<i>Myoxocephalus</i> sp.	8	1	0.43	0.07	0.18	0.17	0.23
	Unidentified sculpins	189	35	15.09	1.61	2.39	2.20	5.47
	Other Fish	94	24	10.34	0.80	0.43	0.44	2.49
	Herrings (Clupeidae)							
	Atlantic herring (<i>Clupea harengus</i>)	3	1	0.43	0.03	0.05	0.07	0.12
	Snailfishes (Liparidae)							
	<i>Liparis</i> sp.	10	6	2.59	0.09	0.02	0.01	0.36
	Sticklebacks (Gasterosteidae)							
	Ninespine stickleback (<i>Pungitius pungitius</i>)	60	9	3.88	0.51	0.04	0.06	0.90
	Shannies (Stichaeidae)							
	Fourline snakeblenny (<i>Eumesogrammus praecisus</i>)	4	3	1.29	0.03	0.06	0.04	0.24
	Daubed shanny (<i>Leptoclinus maculatus</i>)	4	4	1.72	0.03	0.02	0.02	0.22
	Slender eelblenny (<i>Lumpenus fabricii</i>)	8	1	0.43	0.07	0.12	0.11	0.20
	Snakeblenny (<i>Lumpenus lampretaeformis</i>)	5	1	0.43	0.04	0.12	0.13	0.18
	<u>Invertebrates</u>							
	Amphipoda	471	24	10.34	4.02	0.10	0.08	3.73
	Dexaminiidae							
	<i>Atylus carinatus</i>	3	1	0.43	0.03	<0.01	<0.01	0.07
	Uristidae							
	<i>Onisimus litoralis</i>	30	3	1.29	0.26	<0.01	<0.01	0.31
	Gammaridae							
	Unidentified gammarids	14	6	2.59	0.12	<0.01	<0.01	0.30

Hyperiidae		424	15	6.47	3.62	0.09	0.08	2.81
	Unidentified hyperiids	197	14	6.03	1.68	0.02	0.02	1.78
	<i>Themisto libellula</i>	227	1	0.43	1.94	0.07	0.06	0.54
Other Invertebrates		194	17	7.33	1.66	0.02	0.01	1.92
Decapoda		12	5	2.16	0.10	0.01	<0.01	0.32
	Unidentified shrimps	2	2	0.86	0.02	<0.01	<0.01	0.11
	Dendrobranchiata	10	3	1.29	0.09	<0.01	<0.01	0.19
Mysidae		175	8	3.45	1.49	<0.01	<0.01	1.20
	Unidentified mysids	167	7	3.02	1.43	<0.01	<0.01	1.10
	<i>Mysis litoralis</i>	8	1	0.43	0.07	<0.01	<0.01	0.09
Copepoda		1	1	0.43	<0.01			
Echinoidea		1	1	0.43	<0.01			
Mollusca								
	Unidentified Mollusca	1	1	0.43	<0.01			
	Bivalvia	3	2	0.86	0.03	<0.01	<0.01	0.08
Polychaeta		1	1	0.43	<0.01			
Fish total		11049	221	95.26	94.32	99.88	99.90	96.17
Invertebrates total		665	36	15.52	5.68	0.12	0.10	5.36
Other [‡]		6	4	1.51	0.05			
Unidentified Fish		290	56	21.13	2.41			
Unidentified Invertebrates		37	9	3.40	0.31			
Grand total		12047	265					

[§]Ammodytes dubius and Ammodytes hexapterus are found in Hudson Bay (Coad and Reist 2004)

[‡]includes fish eggs, stomach of a fish and an unknown prey item

Table 5: Overall number of identified prey (n prey), number of stomachs in which a particular prey was found (n stomach), frequency of occurrence (FO), percentage prey (%P), percentage biomass (%B), percentage energy (%E), and index of global importance (IG) of identified prey found in adult ringed seal stomachs (n = 15) collected in Arviat, NU, during springs (May-June) 1991, 1992, 2004 and 2005. Taxa in bold represents the eight groups used in the analyses.

Prey taxon	n prey	n stomach	FO	%P	%B	%E	IG
<u>Fish</u>							
Sand lances (Ammodytidae) Ammodytes sp.[§]	178	4	26.67	61.38	43.20	44.64	37.20
Cods (Gadidae)							
Arctic cod (<i>Boreogadus saida</i>)	5	1	6.67	1.72	4.14	3.97	4.32
Unidentified gadids [¶]	2	1	6.67	0.69	20.81	19.98	6.96
Smelts (Osmeridae)							
Capelin (<i>Mallotus villosus</i>)	77	4	26.67	26.55	27.65	27.67	26.88
Sculpins (Cottidae)							
Arctic staghorn sculpin (<i>Gymnocanthus tricuspidis</i>)	2	1	6.67	0.69	2.89	2.55	3.27
Sticklebacks (Gasterosteidae)							
Ninespine stickleback (<i>Pungitius pungitius</i>)	1	1	6.67	0.34	0.02	0.03	0.93
<u>Invertebrates</u>							

Amphipoda	15	2	13.33	5.17	0.08	0.07	4.68
Hyperiidae							
Unidentified hyperiids	2	1	6.67	0.69	<0.01	<0.01	1.20
<i>Themisto libellula</i>	13	1	6.67	4.48	0.07	0.06	3.09
Other Invertebrates	10	4	26.67	3.45	1.20	1.09	7.63
Decapoda (Hippolytidae)	8	3	20.00	2.76	1.20	1.09	6.16
Arctic eualid (<i>Eualus fabricii</i>)	1	1	6.67	0.34	0.12	0.03	1.21
Spiny lebbeid (<i>Lebbeus groenlandicus</i>)	5	1	6.67	1.72	0.77	0.75	2.83
Polar lebbeid (<i>Lebbeus polaris</i>)	1	1	6.67	0.34	0.15	0.17	1.26
Punctate blade shrimp (<i>Spirontocaris phippsii</i>)	1	1	6.67	0.34	0.15	0.14	1.26
Mysidae							
<i>Mysis litoralis</i>	2	1	6.67	0.69	<0.01	<0.01	1.13
Fish Total	265	10	66.67	91.38	98.71	98.83	79.59
Invertebrates total	25	6	40.00	8.62	1.29	1.17	12.87
Unidentified Fish	133	7	36.84	31.22			
Unidentified Invertebrates	3	2	10.53	0.70			
Grand Total	426	19					

[§]*Ammodytes dubius* and *Ammodytes hexapterus* are found in Hudson Bay (Coad and Reist 2004)

[¶]likely *Gadus ogac* (personal observations; Coad and Reist 2004)

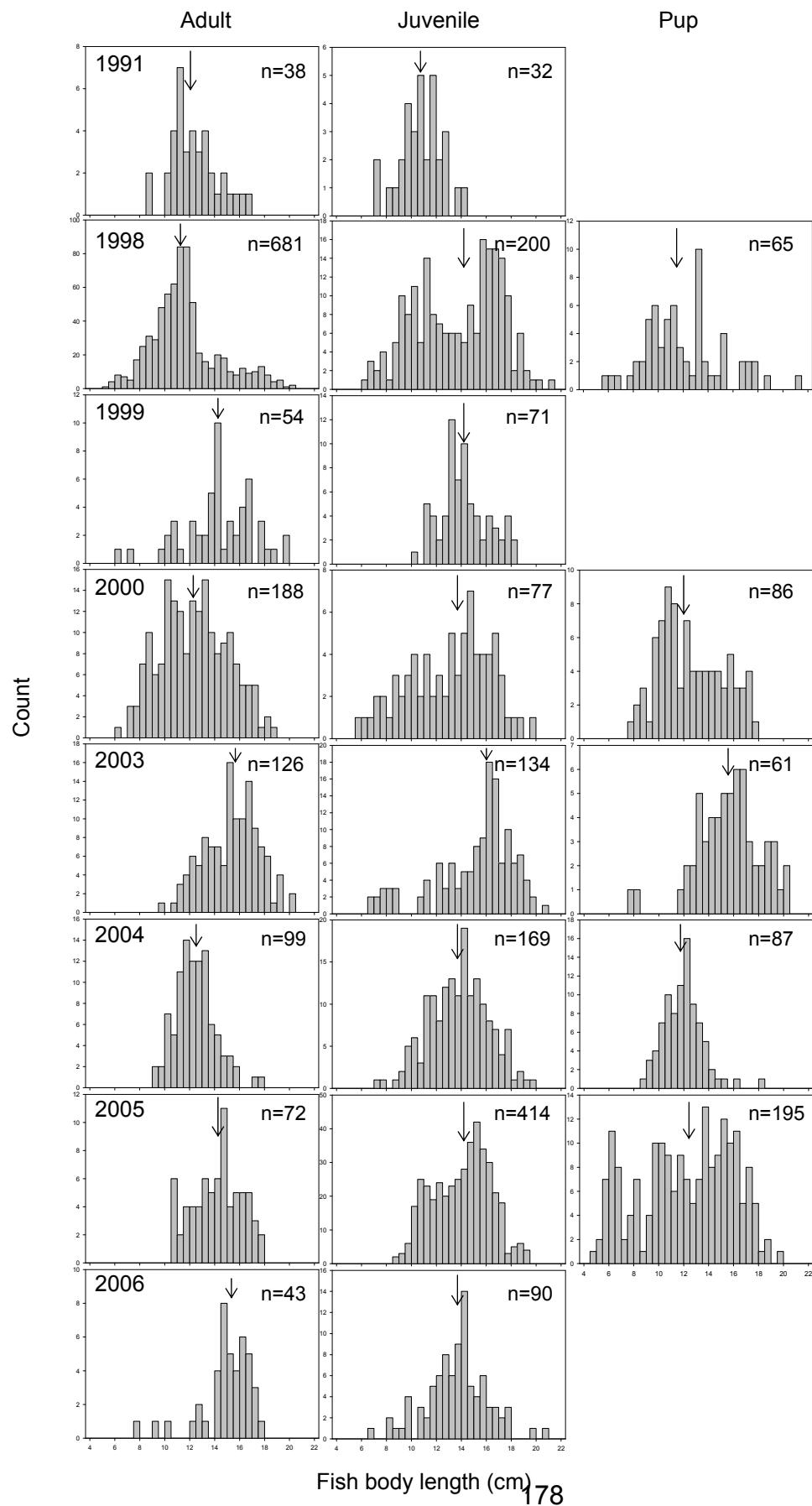
No statistical difference between spring and fall diets was found using carbon ($\delta^{13}\text{C}_{\text{spring}} = -19.13$ [-19.60--18.76], n = 30 and $\delta^{13}\text{C}_{\text{fall}} = -19.33$ [-20.20--19.02], n = 20; U = 222, p = 0.13) and nitrogen ($\delta^{15}\text{N}_{\text{spring}} = 14.64$ [14.28-14.94], n = 30 and $\delta^{15}\text{N}_{\text{fall}} = 15.07$ [14.42-15.55], n = 20; U = 215.5, p = 0.10) stable isotope ratios in ringed seal muscle tissues.

Sand Lance body length

The estimated body length of sand lances found in ringed seal stomachs varied from 4.84cm to 21.43cm. We found no seasonal difference in sand lance body length over the study period ($x_{\text{spring}} = 12.48$ [11.26-14.43], n = 127 vs. $x_{\text{fall}} = 13.10$ [11.03-15.47], n = 3050, U = 207807.5, p = 0.16). Overall, juvenile ringed seals consumed larger sand lances than adults and pups (KW = 162.03, p = 0.0000) but the difference was not apparent for all years studied (Fig. 2). Sand lance body length showed strong inter-annual variations (KW = 433.19, p = 0.0000), with adult, juvenile and pup ringed seals consuming the largest sand lances in 2003 ($x_A = 15.51$ [13.78-16.91], n = 126; $x_J = 16.06$ [13.40-17.20], n = 134 and $x_P = 15.77$ [14.01-17.07], n = 61; Fig. 2). The body length of sand lances consumed by ringed seals of all ages in the 2000s was significantly larger than fish consumed in the 1990s ($x_{1990s} = 11.87$ [10.34-14.43], n = 1620; $x_{2000s} = 13.86$ [11.64-15.77], n = 1557; U = 891735.5, p = 0.0000).

Figure 2: Distribution of body length of sand lances recovered from adult, juvenile and pup ringed seal stomachs collected in western Hudson Bay over 1991-2006.

Sample sizes in 1992 and for pups in 1999 and 2006 were too small to provide a relevant fish size distribution. Arrows denote median fish length.



Age-class variations in the fall diet

In the spring, only three out of the 18 seals collected that had prey items in their stomachs were not adult, too small a number to facilitate comparisons between different age-classes.

There was no difference in the diet of ringed seals of different age-classes (ANOSIM: $r = -0.0029$ and $p = 0.46$). However, the number of prey groups in adult ringed seal stomachs was significantly lower than number found in juveniles and pups ($n_A = 1.36 \pm 0.83$, $n_J = 1.74 \pm 1.02$, $n_P = 2.06 \pm 1.39$; $KW = 15.5$, $p = 0.0004$). Simpson diversity index D' was significantly different between age-classes when all years were pooled, with juveniles showing the most diverse diet (Table 6, bootstrap $p=0.000$ for all combinations).

Adult ringed seals fed on a higher trophic level than pups according to their nitrogen stable isotope muscle signature ($\delta^{15}\text{N}_{\text{adult}} = 15.56$ [14.79-16.34], $n = 64$ and $\delta^{15}\text{N}_{\text{pup}} = 14.88$ [14.05-15.57], $n = 32$; $KW = 6.67$, $p = 0.036$) and were showing more benthic and/or inshore feeding habits than both younger age-classes as indicated by the ^{13}C enriched signal from their muscle tissues collected in the fall ($\delta^{13}\text{C}_{\text{adult}} = -19.33$ [-19.77--18.99], $n = 64$; $\delta^{13}\text{C}_{\text{juvenile}} = -19.82$ [-20.42--19.26], $n = 86$ and $\delta^{13}\text{C}_{\text{pup}} = -20.16$ [-20.42--19.64], $n = 32$; $KW = 18.72$, $p = 0.0001$).

Table 6: Total number of prey (n prey) and identified prey (n IDed prey), number of prey per stomach, total biomass (kg) and energy (MJ) of identified prey, and Simpson diversity index (D'), Renyi's entropy of order two (N_2) and number of taxa found in ringed seal stomachs collected in falls (September-November) 1991-2006 in Arviat, NU, per year and age-class. n stomach and n stomach with IDed prey are the total number of stomach collected containing prey items and the number of stomachs with identified prey, respectively. * and # indicate a similarity in Simpson diversity index between years and italicized values of Simpson diversity index indicate similarity between age-classes.

180	n prey	n stomach	n prey/stomach	n IDed prey	n stomach with IDed prey	Biomass of IDed prey (kg)	Energy of IDed prey (MJ)	n taxa present	D'	N_2
1991	275	10	27.5	84	7	0.24	1.24	6	0.5*	1.99
Adult	241	5	48.2	66	4	0.18	0.92	5	0.52	2.10
Juvenile	18	4	4.5	2	2	<0.01	<0.01	1		
Pups	16	1	16.0	16	1	0.06	0.32	2	0.12	1.13
1992	63	11	5.7	27	8	0.14	0.68	7	0.78	4.59
Adult	43	5	8.6	12	4	0.03	0.13	2	0.44	1.80
Juvenile	20	6	3.3	15	4	0.12	0.55	6	0.72	3.57
Pups		0			0					
1998	4107	46	89.3	4066	42	16.11	81.25	11	0.02	1.02
Adult	3415	31	110.2	3375	27	12.24	61.71	10	0.02	1.02
Juvenile	383	7	54.7	383	7	2.21	11.15	3	0.02	1.02

	Pups	141	2	70.5	140	2	0.70	3.55	2	0.01	1.01
	1999	492	37	13.3	484	29	1.53	7.60	8	0.60	2.48
	Adult	333	30	11.1	325	22	0.57	2.77	6	0.47	1.88
	Juvenile	157	6	26.2	157	6	0.96	4.82	5	0.14	1.17
	Pups	2	1	2.0	2	1	<0.01	<0.01	1		
	2000	954	46	20.7	932	38	8.66	41.25	12	0.36	1.56
	Adult	462	27	17.1	453	22	4.15	19.87	7	0.28	1.40
	Juvenile	218	11	19.8	208	9	2.87	13.48	9	0.63	2.67
	Pups	274	8	34.3	271	7	1.63	7.9	8	0.21	1.26
→ 81	2003	1477	30	49.2	1465	26	11.28	56.93	7	0.26#	1.35
	Adult	686	11	62.4	683	8	4.69	23.71	5	0.36	1.57
	Juvenile	436	11	39.6	434	10	4.00	20.20	6	0.09	1.10
	Pups	231	6	38.5	231	6	1.58	8.00	3	0.11	1.13
	2004	1490	15	99.3	1486	15	11.29	55.54	15	0.18	1.23
	Adult	348	3	116.0	348	3	2.92	14.08	9	0.10	1.11
	Juvenile	737	8	92.1	733	8	6.84	33.71	10	0.25	1.34
	Pups	405	4	101.3	405	4	1.53	7.74	5	0.12	1.14
	2005	2905	44	66.0	2897	44	16.49	81.95	14	0.24#	1.32
	Adult	224	5	44.8	224	5	1.64	8.26	4	0.06	1.07
	Juvenile	1727	28	61.7	1726	28	10.35	50.92	11	0.34	1.50
	Pups	905	10	90.5	904	10	4.49	22.69	9	0.03	1.03
	2006	284	26	10.9	273	23	1.68	8.17	12	0.54*	2.15

Adult	62	8	7.8	58	6	0.38	1.93	4	0.30	1.43
Juvenile	147	13	11.3	142	12	0.85	4.17	11	0.31	1.44
Pups	75	5	15.0	73	5	0.45	2.07	8	0.80	4.89
All years	12047	265	45.5	11714	232	67.42	334.6	35	0.22	1.29
Adult	5814	125	46.5	5544	101	26.79	133.37	25	0.20	1.26
Juvenile	3843	94	40.9	3800	86	28.21	139.02	25	0.29	1.40
Pups	2049	37	55.4	2042	36	10.45	52.27	19	0.14	1.16

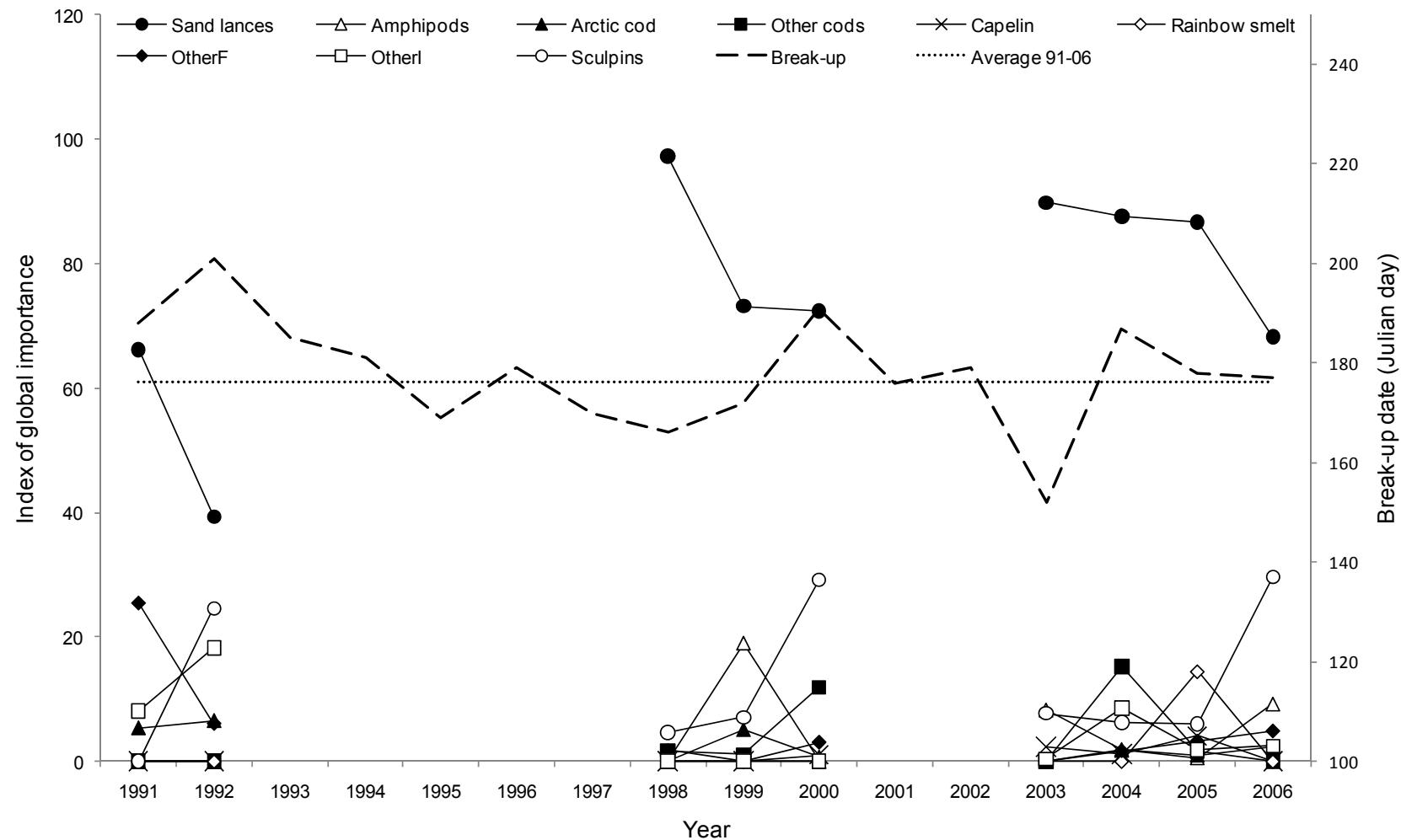
Inter-annual variation of the diet

Fall

The number of prey groups per stomach varied over the years ($KW = 33.29, p = 0.0001$) with a maximum of 2.5 ± 1.45 prey groups per stomach in 2004 and a minimum of 1.13 ± 0.35 in 1991-92. Number of prey groups per stomach was below 1.5 until 2003 and around 2 thereafter.

The Bray-Curtis similarity index matrix indicated that 1991 and 1992 were different from the other study years ($S < 0.80$), which was confirmed by an ANOSIM between groups 1991-92 and 1998-06 ($R = 0.9, p = 0.029$). Three other groups emerged from the similarity matrix: 1999, 2000/2006 and 1998/2003/2004/2005. Inter-annual variations of the different prey groups IG are presented in Figure 3. Diets in 1991 and 1992 were characterized by their relatively low representation of sand lances ($IG < 70$) and relatively high representation of benthic species such as arctic cod, other fish (exclusively represented by ninespine sticklebacks (*Pungitius pungitius*) in these two years) and other invertebrates (mostly decapods and Mysidea; Table 7; Fig. 3). In 1992, sculpins were second in importance after sand lances but contributed to the total energy consumed twice as much than sand lances (64.7% vs. 29.6%, respectively). In 1999, 2000 and 2006, sand lance IG was also relatively low (~70). Sculpins were the second most important prey item in term of IG and percentage energy consumed for 2000 and 2006, while in 1999, amphipods had the second highest IG but the energy contribution of sculpins was greater (2.9%

Figure 3: Variation of the index of global Importance (IG) of the nine prey groups identified in ringed seal stomachs collected in falls (September-November) 1991-2006 in Arviat, NU, and of dates of spring sea-ice break-up in western Hudson Bay. Sand lances: *Ammodytes* sp.; arctic cod: *Boreogadus saida*; Other cods: Gadidae; capelin: *Mallotus villosus*; rainbow smelt: *Osmerus mordax*; sculpins: Cottidae; OtherF: other fish; OtherI: other invertebrates; Average 91-06: average date of sea ice spring break-up over 1991-2006.



vs. 7.4%, respectively). Arctic cod IG was relatively high in 1999. The last group, composed by years 1998 and 2003-05, showed a diet where sand lances largely dominated ($IG > 85$), especially in 1998 ($IG = 97.26$). The second most consumed prey item of ringed seals in 2005 was rainbow smelt (*Osmerus mordax*; $IG = 14.45$), a fish that was part of the diet exclusively that year. Importance of capelin in the diet was also the highest in 2005 ($IG = 4.06$; Table 7; Fig. 3). Capelin was not part of ringed seal diet before 2000 (Table 7).

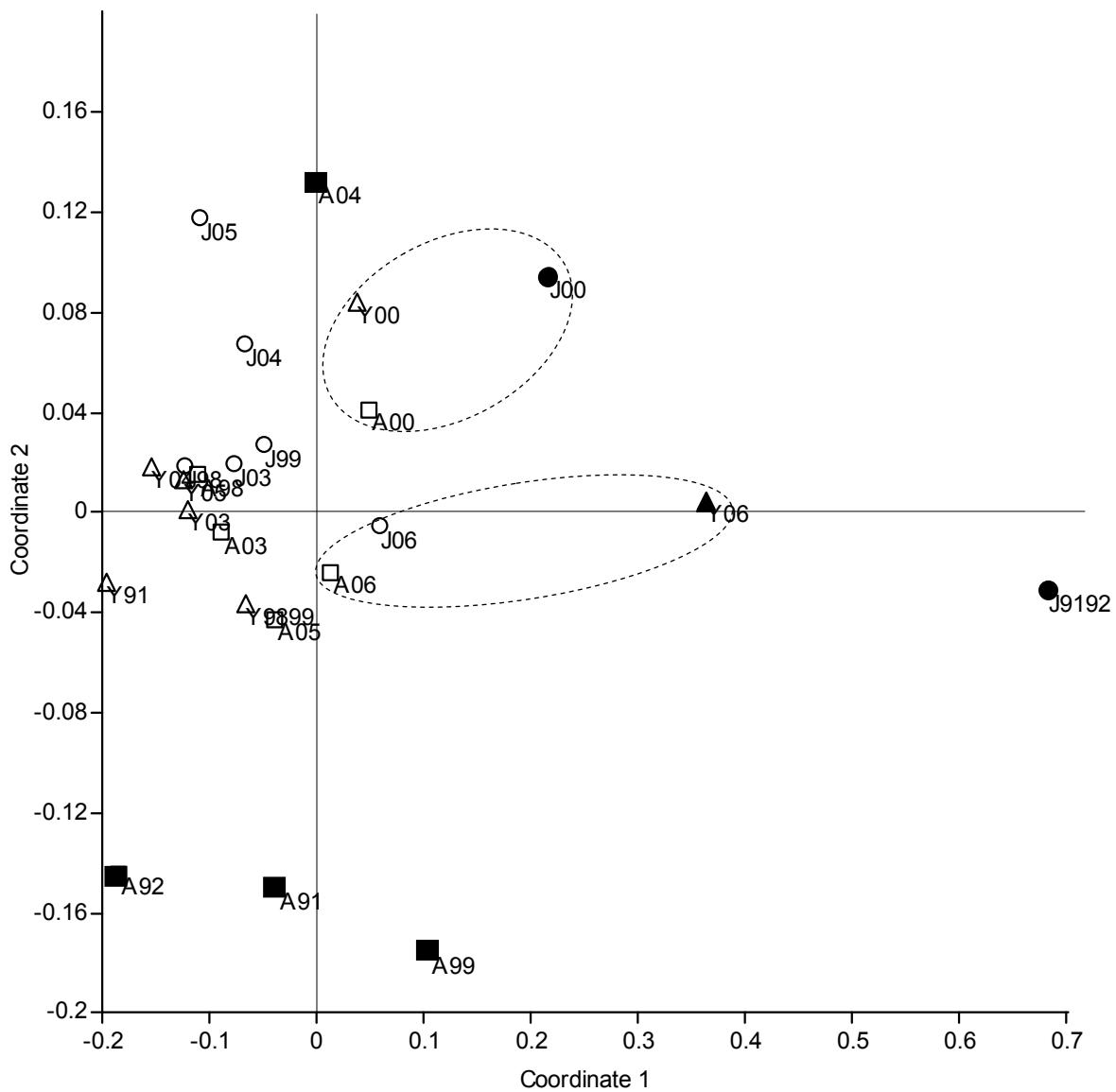
A non-metric multidimensional scaling (MDS) based on the Bray-Curtis similarity matrix on IG for age-class and year (Fig. 4) provided more information on inter-annual variations in ringed seal diet. The Bray-Curtis similarity index was higher than 0.80 for three or less pair wise comparisons in the distance matrix for juveniles in 2000, pups in 2006, juveniles in 1991-92 and adults in 1991, 1992, 1999 and 2004 (Fig. 4). The relatively low importance of sand lances in ringed seal diet in 1991 and 1992 was largely due to juveniles that ingested very few, particularly in 1992 when none were consumed (Table 7). In 2000 and 2006, it was in juvenile and pup diets, respectively, that the importance of sand lances was reduced while sculpin IG were the two highest recorded (Table 7). However, all age-classes showed the same trends in these two years, as can been seen from their position on the MDS (Fig. 4). Patterns observed for 1999 were due to adult diet. Adult ringed seal diet in 2004 was unique due to relatively high importance of other Gadidae ($IG = 33.62$), that represented the second most important item after sand lances (Table 7).

Table 7: Index of global importance (IG) per year and age-class for the different prey groups identified in ringed seal stomachs collected in falls (September-November) 1991-2006 in Arviat, NU. A: adults; J: juveniles and P: pups.

	Sand lances	Arctic cod	Gadidae	Capelin	Rainbow smelt	Sculpins	Other fish	Amphipod	Other invertebrates
	Age class/year								
A91	74.01	8.21	0	0	0	0	21.22	0	0
A92	68.16	0	0	0	0	0	0	0	22.43
A98	96.43	0	1.36	0	0	5.21	2.48	0	0
A99	60.59	6.94	0	0	0	5.10	0	25.24	0
A00	73.87	0	10.95	0	0	20.95	0.93	0	0
A03	87.54	0	0	2.27	0	2.75	0	9.26	0
A04	83.47	4.30	33.62	0	0	10.49	4.93	1.72	0
A05	76.41	0	0	0	8.09	5.67	1.89	0	0
A06	76.45	4.76	0	0	0	15.62	0	8.51	0
J9192	19.76	8.95	0	0	0	33.17	21.17	0	8.29
J98	98.37	0	5.30	0	0	2.56	0.00	0	0
J99	88.15	0	3.45	0	0	12.92	0	3.57	0
J00	58.91	0	9.38	4.11	0	44.80	6.09	0	0
J03	87.75	0	0	4.34	0	8.14	0	2.05	1.15
J04	86.21	1.76	12.43	0	0	5.79	0	2.73	11.93
J05	83.17	0	1.72	5.55	19.78	6.19	3.90	0.97	1.74
J06	73.73	2.20	0	0	0	22.35	6.03	5.30	4.81
Y91	97.15	0	0	0	0	0	0	0	23.67
Y9899	81.17	4.69	0	0	0	0	0	2.77	0
Y00	84.18	3.52	16.37	0	0	26.70	2.81	0	0
Y03	98.41	0	0	0	0	2.18	0	5.27	0
Y04	98.07	0	0	5.21	0	2.34	2.75	0	9.05
Y05	99.24	4.04	0.85	1.87	1.35	2.77	2.01	0	0

Y06	41.79	0	0	0	0	35.97	7.36	16.16	0
Year									
1991	66.13	5.38	0	0	0	0	25.35	0	8.12
1992	39.36	6.55	0	0	0	24.62	6.10	0	18.25
1998	97.26	0	1.74	0	0	4.65	1.76	0.14	0
1999	73.11	5.11	1.08	0	0	7.11	0	18.99	0
2000	72.36	0.71	11.92	1.04	0	29.17	3.10	0	0
2003	89.82	0	0	2.37	0	7.71	0	8.26	0.39
2004	87.59	1.92	15.22	1.19	0	6.25	1.75	1.79	8.59
2005	86.67	1.03	1.62	4.06	14.45	6.03	3.27	0.60	1.86
2006	68.26	2.28	0	0	0	29.58	4.90	9.22	2.50
Age									
Adult	86.94	1.09	4.37	0.25	0.40	8.17	2.18	4.52	0.41
Juvenile	80.30	0.59	4.91	2.95	7.20	12.86	3.17	1.59	3.47
Pup	89.27	2.55	3.18	1.23	0.42	11.41	2.29	2.01	2.54

Figure 4: Non-metric multidimensional scaling based on the Bray-Curtis distance matrix computed from the index of global importance of the nine prey groups identified in adult (A; open square), juvenile (J; open circle) and pup (Y; open triangle) ringed seal stomachs collected in the fall in Arviat, NU, over 1991-2006. Closed symbols indicate that the Bray-Curtis similarity index of the group age-class/year was higher than 0.8 for three or less pair wise comparisons in the distance matrix. Dashed circles indicate year grouping.



The total number of prey per stomach showed strong inter-annual variations, from less than 6 prey per stomach in 1992 to nearly 100 in 2004, and was generally lower in the 1990s (Table 6). The number of prey per stomach was positively correlated with total biomass ($r_p = -0.83, p = 0.006$). Over the years, sand lance IG was negatively related to percentage of empty stomachs ($r_p = -0.74, p = 0.022$) and a sigmoid function best described the relationship between sand lance IG and total number of prey per stomach ($r^2 = 0.80$), total biomass ($r^2 = 0.86$) and total energy consumed ($r^2 = 0.86$ 2; Fig. 5).

Simpson diversity index, D', varied from 0.02 in 1998 to 4.59 in 1992 (Table 6) and was different between years, except for 1991/2006 and 2003/2005, years that were similar (bootstrap $p = 0.61$ and $p = 0.37$, respectively; Table 6). Apart from 1998, D' was generally higher in the 1990s compared to the 2000s. D' was negatively correlated with the number of prey per stomach ($r_p = -0.89, p = 0.0013$) and with sand lance IG ($r_p = -0.93, p = 0.0002$; Fig. 6), indicating a diversification of ringed seal diet when the importance of sand lances decreased.

Sand lance IG in ringed seal diet was negatively correlated with time of break-up in western Hudson Bay ($r_p = -0.72, p = 0.028$; Fig. 7).

Carbon and nitrogen stable isotope ratios were significantly lower in the 2000s (2003-06) than in the 1990s (1991-92), with $\delta^{13}\text{C}_{90\text{s}} = -19.29$ [-19.73--18.99], $n = 52$ and $\delta^{13}\text{C}_{00\text{s}} = -19.87$ [-20.39--19.29], $n = 132$ ($U = 2047.5, p < 0.0001$) and $\delta^{15}\text{N}_{90\text{s}} = 16.27$ [15.75-17.14], $n = 52$ and $\delta^{15}\text{N}_{00\text{s}} = 15.02$ [14.15-15.76], $n = 132$ ($U = 1433.5, p < 0.0001$; Fig. 8).

Figure 5: The relationship between sand lance index of global importance (IG) in the diet of ringed seals and the total energy consumed by ringed seals in western Hudson Bay during the falls 1991, 1992, 1998-2000 and 2003-06 was best described by a Gompertz model with 3 parameters.

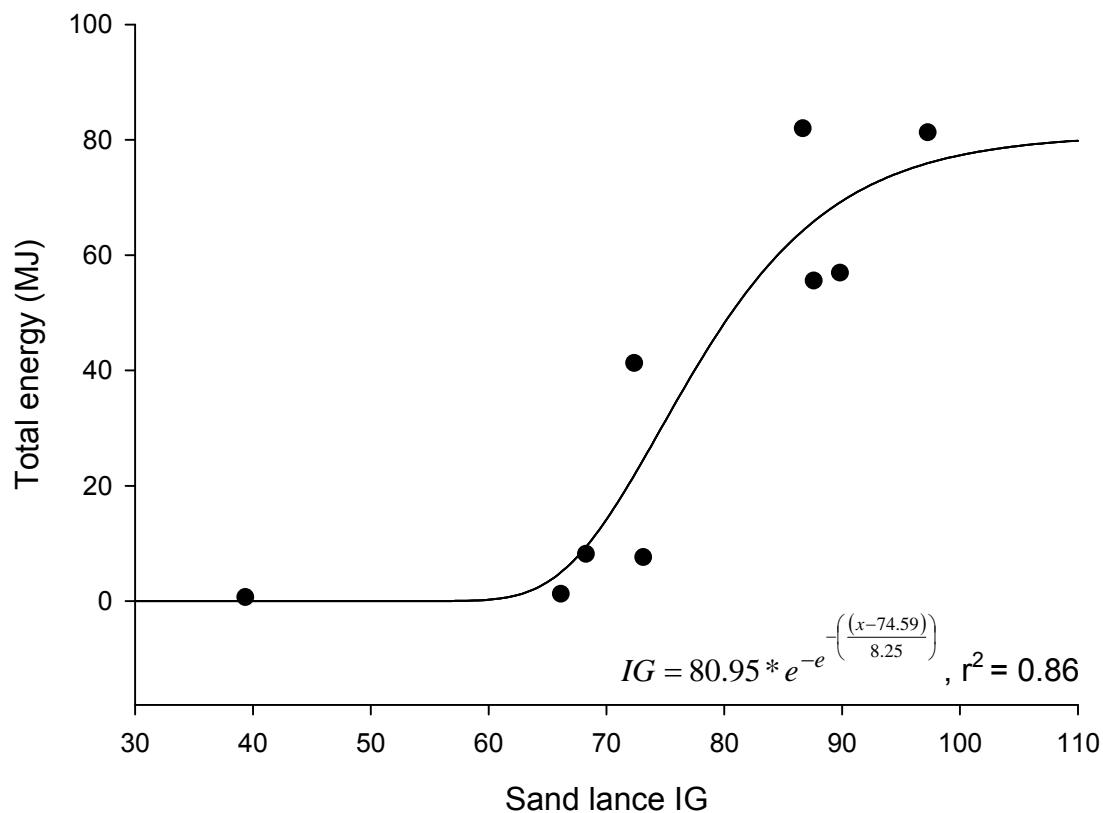


Figure 6: Linear regression of Simpson diversity index (D') and sand lance index of global importance (IG) in the fall diet of ringed seals sampled in western Hudson Bay, NU, over 1991-2006. Dashed lines represent the 95% confidence interval.

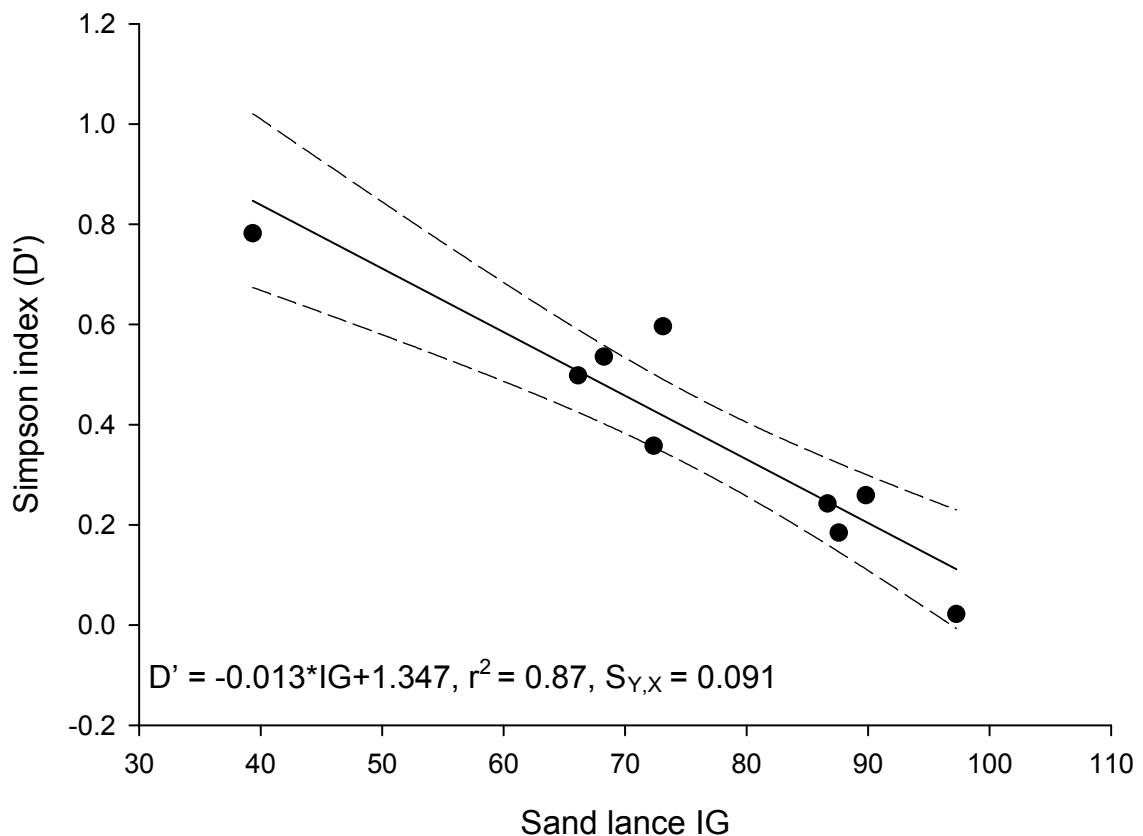
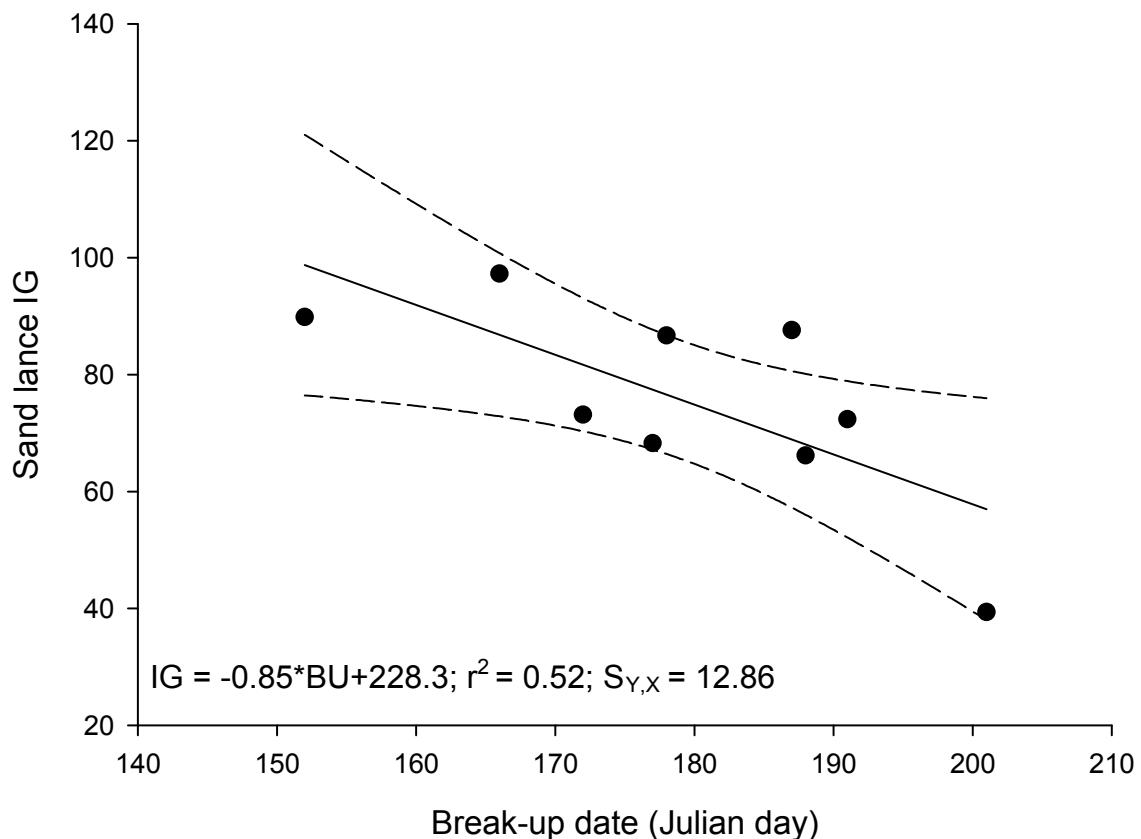


Figure 7: Linear regression of Sand lance index of global importance (IG) in the fall diet of ringed seals collected in Arviat, NU, over 1991-2006, on time of spring break-up (BU) in western Hudson Bay. Dashed lines represent the 95% confidence interval.



Mean carbon and nitrogen stable isotope ratios of fish and invertebrate species potentially consumed by ringed seals, and of seal muscle tissues collected in the 1990s and 2000s are presented in Figure 9.

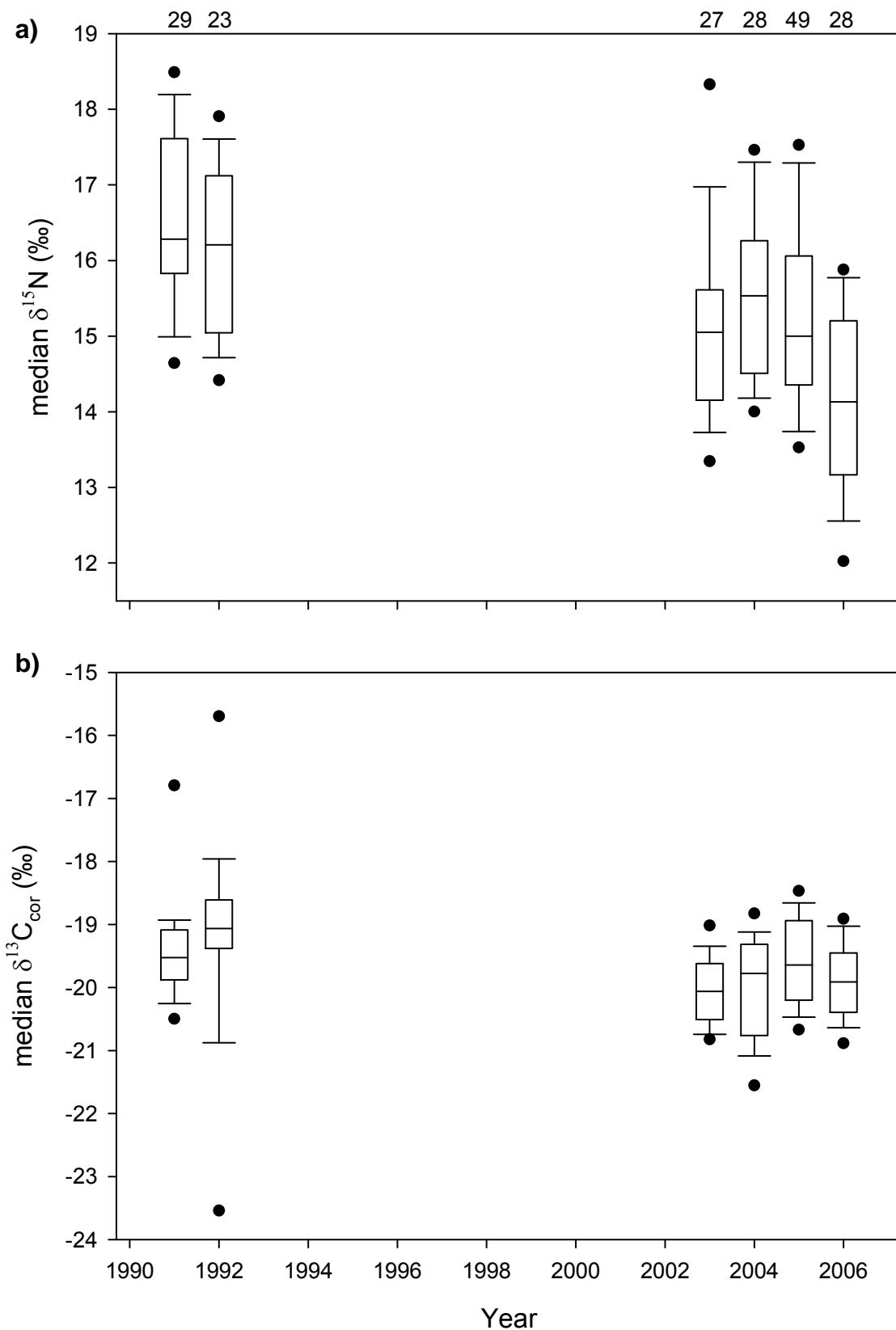
Using fractionation values of +2.4‰ and +1.3‰ from prey to seal muscle tissues for $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$, respectively (Hobson et al. 1996), isotope signature of seal muscle collected in the 1990s is consistent with a pattern of a mixed diet of sand lances and cods (Gadidae) and/or benthic species, whereas in the 2000s, seal muscle isotopic signature indicated a diet strongly focused on sand lances.

Spring

Ringed seal adult spring and fall diets had a different composition in 1991 and 2005 ($S < 0.80$) but were similar in both seasons in 1992 ($S = 0.84$), when other invertebrates ($IG_{\text{spring}} = 45.78$ and $IG_{\text{fall}} = 22.43$) were the second most important and only other prey item after sand lances ($IG_{\text{spring}} = 60.00$ and $IG_{\text{fall}} = 68.16$). In 1991 and 2005, sand lances did not dominate the spring diet, and its importance was reduced ($IG < 35$) compared to the fall ($IG > 70$). This was particularly the case in 1991 when sand lances were 4th in importance out of five prey groups in the diet ($IG = 17.65$). Arctic cod ($IG = 29.25$), followed by sculpins ($IG = 22.11$) and amphipods ($IG = 20.8$), were the most important. In 2005, however, the most important prey in ringed seal spring diet was capelin ($IG = 35.5$). No arctic cod were recorded in 2005 spring diet.

In the spring, D' was significantly higher in the period 1991-92 ($D' = 0.72$, $N_2 = 3.62$) than in 2004-05 ($D' = 0.62$, $N_2 = 2.61$; bootstrap $p = 0.018$).

Figure 8: Median a) nitrogen ($\delta^{15}\text{N}$) and b) carbon ($\delta^{13}\text{C}$) stable isotope ratios in ringed seal muscle tissues collected in the fall (September-November) in Arviat, NU, in the 1990s (1991 and 1992) and the 2000s (2003-2006). Sample size for each year is indicated on top of the graph. Carbon isotope ratios were corrected for the oceanic Suess effect (C_{cor}). Box: median, 1st and 3rd quartiles; error bar: 10th and 90th percentiles; dot: 5th and 95th percentiles.



SI ratios in the spring were only available for 2004 and 2005.

Discussion

Diet composition

Although a variety of prey taxa were found in the stomachs of ringed seals, their diet in western Hudson Bay was dominated by sand lances, especially during the open-water season. It has been previously reported that ringed seal diet usually comprised of a few dominant taxa and could be specialized in time and space (Lowry et al. 1980b, Weslawski et al. 1994). Arctic cod is typically reported as the primary prey of ringed seals (Northern Foxe Basin and south western Baffin Island: McLaren 1958; western Canadian Arctic: Smith 1987; high Canadian Arctic: Bradstreet and Finley 1983; Barents Sea: Wathne et al. 2000; northern Greenland: Siegstad et al. 1998; northern Baffin Island: Holst et al. 2001; Svalbard: Gjertz and Lydersen 1986, Weslawski et al. 1994, Labansen et al. 2007). However, studies on ringed seals collected at lower latitudes (Ungava Bay and northern Labrador: McLaren 1958 and southeastern Hudson Bay: Breton-Provencher 1979, Chambellant 2010) revealed that sand lances were the main fish prey, while records of arctic cod were anecdotal or absent. Ours results, from similar low latitudes, support the suggestion of a latitudinal gradient in ringed seal feeding habits based on preference and/or availability of fish, as has been suggested by McLaren (1958) and Siegstad et al. (1998). Previous studies suggested that ringed seals preferentially feed on prey forming large swarms or shoals (McLaren 1958, Lowry et al. 1980b, Siegstad et al. 1998). Of schooling

fish that are both common in Hudson Bay (Coad and Reist 2004), and found in ringed seal stomachs (*i.e.*, sand lances, capelin, arctic cod and rainbow smelt), sand lances have the highest energy density in summer (Table 2). In years when the importance of sand lances in the diet was lower, ringed seals diversified their diet but did not seem able to fully compensate for the energy loss by consumption of alternate prey taxa. This result, together with the overall low diversity index, suggested that ringed seals in western Hudson Bay are sand lance specialists, which could have important implications for their body condition, and possibly reproductive performances in years when availability of sand lances is low. In general, specialists are more vulnerable to rapid, long-term and unidirectional environmental changes, such as is currently occurring with warming and loss of sea ice in the Arctic (Bluhm and Gradinger 2008, Kovacs and Lydersen 2008, Laidre et al. 2008, Post et al. 2009).

Sculpins were the second most important food resource for ringed seals in western Hudson Bay. Previous studies have reported sculpins to be an important fish prey for ringed seals (McLaren 1958, Gjertz and Lydersen 1986, Siegstad et al. 1998), but only in west Greenland were they the second most important prey taxon (Siegstad et al. 1998). The importance of sculpins was particularly high in years when the energy contribution of sand lances was low, suggesting that ringed seals may have attempted to compensate for a shortage of sand lances by foraging more benthically on sculpins. Hudson Bay is a relatively shallow basin with depths not exceeding 250m, and with an extended coastal shelf (Stewart and Lockhart 2005). Since ringed seals are capable of diving deeper

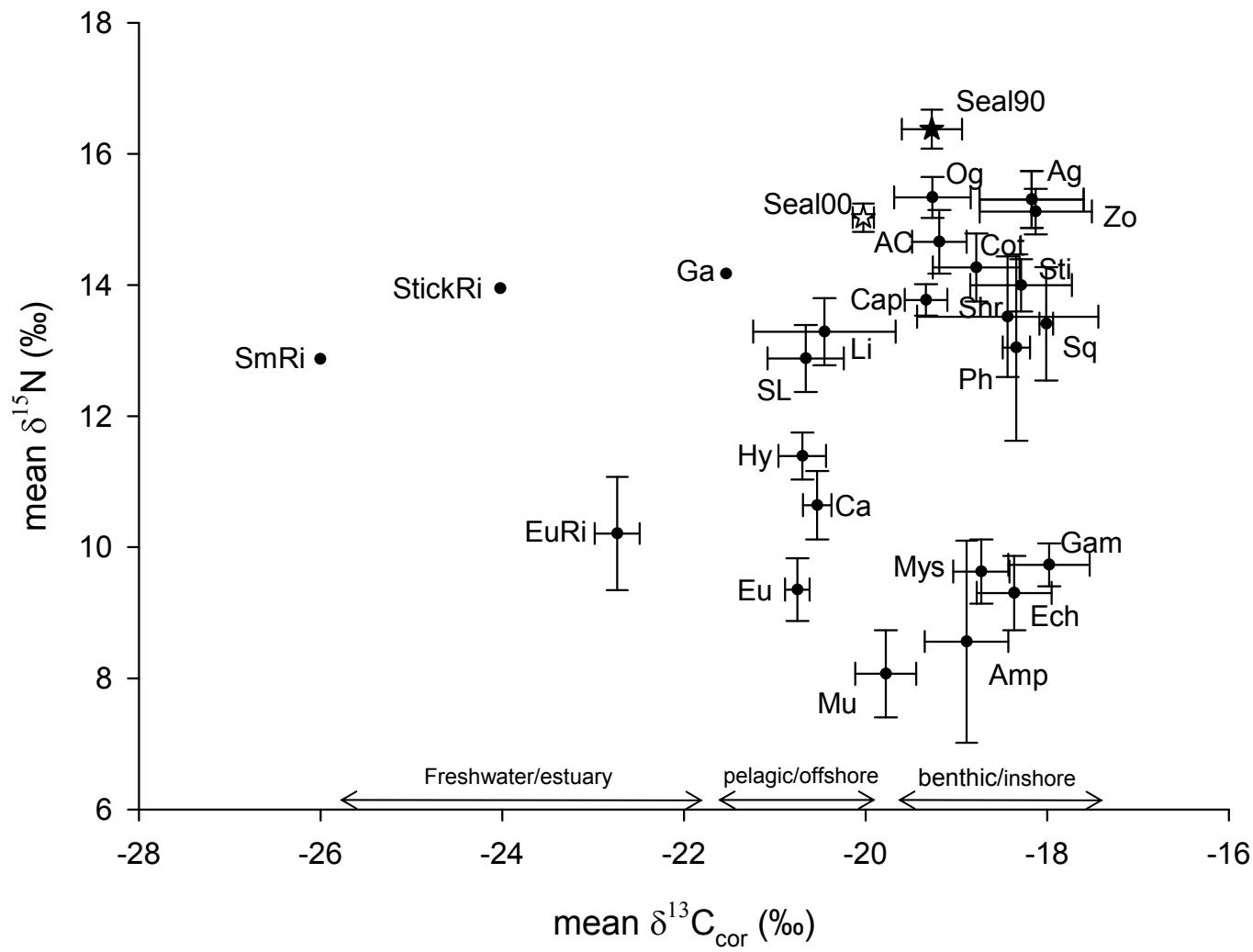
than 250m (Teilmann et al. 1999), it appears that benthic prey are readily available to ringed seals in Hudson Bay. Acquiring energy from sculpins when the availability of sand lances is low might constitute a trade-off for ringed seals between travelling long distances (horizontally) in search of pelagic, schooling sand lances that can be caught in large quantity near the surface with a minimum effort, and foraging vertically by diving locally to catch dispersed prey on the seafloor.

Invertebrates did not represent an important food resource for ringed seals in western Hudson Bay. This result is similar to Labansen et al. (2007) but contrasted with most of previous studies that found invertebrates, and particularly hyperiid amphipods and mysids, to be major contributors to ringed seals diet (McLaren 1958, Breton-Provencher 1979, Lowry et al. 1980b, Bradstreet and Finley 1983, Gjertz and Lydersen 1986, Smith 1987, Lydersen et al. 1989, Weslawski et al. 1994, Siegstad et al. 1998, Holst and Stirling 2002, Chambellant 2010). Invertebrates can be underestimated in diet reconstructed from stomach contents because of their usually small size and the fact that they leave few identifiable and quantifiable remains (Bowen and Harrison 1994, Lawson et al. 1995, McKenzie and Wynne 2008). Therefore, the importance of invertebrates in ringed seal diet in Hudson Bay may be greater than indicated in our analysis. However, we think it is not likely to be a major source of bias in our study because, when using fractionation values of 2.4‰ for $\delta^{15}\text{N}$ and 1.3‰ on $\delta^{13}\text{C}$ on ringed seal muscle (Hobson et al. 1996), the value obtained is consistent with a

Figure 9: Mean nitrogen ($\delta^{15}\text{N}$) and carbon ($\delta^{13}\text{C}$) stable isotope ratios in ringed seal muscle tissues collected in the fall (September-November) in Arviat, NU, in the 1990s (closed star; Seal90, n = 52) and in the 2000s (open star; Seal00, n = 132) and of potential prey taxa collected in Hudson Bay over the period 2004-2007. Carbon isotope ratios were corrected for the oceanic Suess effect and the presence of carbonates for invertebrates (C_{cor}). Mean \pm 1.96*standard error.

SmRi: smelt (*Osmerus mordax*) from river; StickRi: nine-spine stickleback (*Pungitius pungitius*) from river; EuRi: Euphasiidae from river; Ga: gastropod; Hy: Hyperiidae; Ca: *Calanus* sp.; Eu: Euphasiidae; Mu: mussel (Bivalvia); Amp: amphipods (Amphipoda); Ech: starfish (Asteroidea); Gam: Gammaridae; Mys: Mysidae; SL: sand lances (*Ammodytes* sp.); Li: *Liparis* sp.; Ph: Pholidae; Sq: squid (Teuthida); Shr: shrimps (Decapoda); Sti: Stichidae; Cap: capelin (*Mallotus villosus*); Cot: Cottidae; Zo: Zoarcidae; Ag: Agonidae; Og: Greenland cod (*Gadus ogac*); AC: arctic cod (*Boreogadus saida*).

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diet where invertebrates did not constitute an important food resource for ringed seals, at least during the open-water season (see Fig. 9).

Seasonal variation

Both the number of stomachs containing prey and the number of prey per stomach were lower in the spring than in fall. These results may indicate a decrease in food consumption by ringed seals in the spring, during periods when they are nursing, mating, and moulting. Similar conclusions were previously reported for ringed seals based on energetic/body condition (McLaren 1958, Breton-Provencher 1979, Ryg et al. 1990, Goodyear 1999), feeding (McLaren 1958, Lowry et al. 1980a, Bradstreet and Finley 1983, Smith 1987) and behavioural (Smith and Hammill 1981) studies. However, results could be confounded by the fact that the digestion rate of ringed seals is extremely rapid (Helm 1983, Murie and Lavigne 1986). The probability of having an empty stomach is therefore increased for ringed seals collected on ice during the moulting season when they spend a large proportion of time basking on ice (McLaren 1958, Smith 1973, Kelly et al. 2010), relative to the fall when ringed seals are collected in open-water.

Ringed seal diet was more diverse in the spring and presented a lower importance of sand lances than in the fall, but overall sand lances were still the dominant prey. Capelin, Gadidae, including arctic cod, and invertebrates, particularly decapods and hyperiid amphipods, were more important in the spring compared to fall diet. However, when spring diets were compared between years, it was apparent that the diet in 1992 was different from 1991 and 2005.

1992 was also atypical in terms of climatic conditions since the combined effect of a strong positive phase of the North Atlantic Oscillation, a strong El Niño event and the eruption of Mount Pinatubo in 1991-92, created colder than normal conditions over the eastern Arctic (Graf et al. 1993, McCormick et al. 1995, Mysak et al. 1996, Gough et al. 2004). In Hudson Bay, in 1992 the spring sea-ice break-up occurred 25 days later than the average 1991-2006. Sand lances and decapods dominated the diet of ringed seal in the spring 1992, whereas arctic cod and capelin were the most important prey species consumed by ringed seals in the springs 1991 and 2005, respectively. In interpreting our results from the spring collection, it should be taken into consideration that sample size of stomachs with identified prey was small ($n = 4$ for 1991 and for 1992 and $n = 7$ for 2005), and only 3 years were available. Previous studies reporting seasonal variations indicated an increase or dominance of invertebrates consumed during the ice-free season (Lowry et al. 1980b, Bradstreet and Finley 1983, Smith 1987), while fish dominated the ice-covered season (Holst et al. 2001, Labansen et al. 2007). Seasonal life-cycle of the different prey, and thus variations in their availability, was evoked to explain differences observed between spring and fall diet. However, the availability of prey may not be the only explanation to dominance of fish in ringed seals diet; preference/selectivity could also play an important part in its composition. Wathne et al. (2000) showed that ringed seals in the Barents Sea fed predominantly on arctic cod, even though it represented only 1% of the biomass available, because their size, energy density and digestibility were higher than those of invertebrates. Our results showed that in

western Hudson Bay, fish are available and/or preferentially selected by ringed seals from spring to late fall.

Age variation

In our study, reconstruction of stomach contents did not show any age-related difference in ringed seal fall diet in western Hudson Bay, although adult ringed seals tended to rely less on capelin, invertebrates (particularly Mysidae) other than amphipods, and sculpins, than younger age-classes (Table 7), and pups more on sand lances. In late summer however, C and N SI ratios showed that adult ringed seals fed at a slightly higher trophic level than pups and foraged more benthically/inshore compared to the two younger age-classes.

A possible explanation for the lack of age-related differences between age-classes when diet was estimated through stomach content compared to SI analysis is that there may be a difference in diet of the different age-classes between late summer and fall. To examine this aspect, we evaluated the C and N SI signature in ringed seal liver tissues collected in the fall. Liver has a higher protein turn-over rate than muscle and would therefore represent food ingested over a shorter time period, likely of the order of 1-2 weeks (Kurle and Worthy 2002). Results from liver tissues were similar to those found for muscle tissues, with adult ringed seals presenting a statistically higher $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ than the younger age-classes, giving support to an age-related difference in diet in the fall.

The fact that the two methods gave different results could be due to limitations of the stomach content reconstruction technique, and particularly the possible underrepresentation of invertebrates (Bowen and Harrison 1994, Lawson et al. 1995, McKenzie and Wynne 2008), of otoliths of small fish like seasnails (*Liparis* sp.), or some species of Stichidae, that would be digested faster or be more degraded by digestion relative to otoliths from bigger fish (Harvey 1989, Tollit et al. 1997, Bowen 2000), and the fact that diet estimated through stomach reconstruction represents only the last meal and not an integration of food ingested over the entire study period.

Previous studies have reported either no age-related differences in ringed seal diet (McLaren 1958, Gjertz and Lydersen 1986, Siegstad et al. 1998, Holst et al. 2001) or that pups fed more on invertebrates and less on fish than adults (Lowry et al. 1980b, Bradstreet and Finley 1983, Smith 1987, Siegstad et al. 1998, Holst et al. 2001). When age differences were found in ringed seal diet, the limited foraging experience and diving capabilities of pups and/or the spatial segregation of the different age-classes at different times of the year were proposed as possible, but non-exclusive, explanations.

During the open-water season, ringed seals of all ages have been observed feeding offshore together, sometimes in large aggregations (McLaren 1958, Smith 1973, 1987, Harwood and Stirling 1992), whereas when the ice starts to form in the fall, adults move toward the prime breeding habitat to possibly establish territories from which they would exclude younger age-classes (McLaren 1958, Smith 1973, Smith and Hammill 1981, Stirling et al. 1981, Smith

1987, Holst et al. 1999, Born et al. 2004, Krafft et al. 2007). Our SI results could therefore suggest the possibility that, in western Hudson Bay, spatial segregation of younger age-classes might be taking place in late summer. Segregation of young seals during the spring breeding time was confirmed by the high percentage of adults (86%) in our spring collection. However, in the fall, the percentage of adult ringed seals collected showed great inter-annual variations and was overall approximately 50%, which is not consistent with spatial segregation. Physiological and behavioural constraints due to their smaller body size and inexperience, respectively, limit the diving capacities and abilities of immature seals (Kelly and Wartzok 1996, Burns 1999, Jorgensen et al. 2001). Although ringed seal pups were found to dive down to the sea floor as deep as 90m and remain under water for up to 12min, mean dive duration was close to a minute (Lydersen and Hammill 1993, Kelly and Wartzok 1996). Adult and sub-adult ringed seals were found to dive deeper than 250m, for durations of more than 39min (Kelly and Wartzok 1996, Teilmann et al. 1999), which would enable them to exploit the benthic community more efficiently than younger age-classes.

Inter-annual variation

Stomach content and stable isotope analyses indicated that the diets of ringed seals in western Hudson Bay were different in the early 1990s relative to the 2000s. Despite challenges encountered in reconstructing ringed seal diet from the early 1990s, the composition of diet estimated through stomach contents was consistent with SI signatures from ringed seal muscle tissues, and therefore provided an accurate representation of taxa preyed upon by ringed seal at that

time. Higher N SI ratios in the early 1990s suggested more benthic/inshore feeding habits by ringed seals relative to the 2000s, but could also indicate a nutritional stress, *i.e.*, the catabolism of protein from ringed seal muscle tissues (see Newsome et al. 2010).

In comparison to the 1990s, the importance of arctic cod in the diet of ringed seals in western Hudson Bay was reduced in the 2000s. This trend was more apparent in the spring where arctic cod was the most important prey in 1991 but was not present in the diet in 2005, having been replaced by capelin. Capelin did not appear in the diet of ringed seals prior to 2000 and was then consumed every year with the exception of 2006. Rainbow smelt was present in ringed seal diet in 2005 only and was mostly consumed by juveniles, although adults and pups did prey on this species as well. These changes in prey composition of ringed seal diet over the years are likely to reflect changes in availability, distribution and/or abundance of these secondary prey items in the western Hudson Bay ecosystem. The typical Arctic water, ice-adapted arctic cod seems to have been replaced by more sub-Arctic species in the 2000s. Similar observations and interpretation have been reported by Gaston et al. (2003), who found that thick-billed murres brought back more capelin and sand lances than arctic cod and benthic prey items to their chicks in northern Hudson Bay, a switch that occurred at the end of the 1990s. They concluded that a change in fish community likely occurred at the end of the 1990s, due to changes in oceanographic conditions driven by the current warming trend in water temperatures. Inuit also reported a recent decline of arctic cod in southeastern and northwestern Hudson Bay

(McDonald et al. 1997). Occurrence of capelin in ringed seal stomachs have been described in southeastern Hudson Bay in the late 1970s (Breton-Provencher 1979). Dunbar (1983) also reported large numbers of capelin in the same region, and suggested they could belong to a relict population from a warmer period. Capelin is known to be very sensitive to water temperature and important changes in their abundance, distribution, growth and spawning time have been observed and linked to changes in water temperatures (Carscadden et al. 2001). Rainbow smelt was illegally introduced into the Hudson Bay water drainage in the early 1990s and, starting in 2002, expanded their distribution from river systems to the western Hudson Bay coast (see Stewart and Lockhart 2005). Both species may therefore profit from the warming trend in water temperature to expand their range northward in the Hudson Bay ecosystem, while arctic cod distribution might have shifted to higher latitudes.

Benthic/inshore feeding habits dominated in the early 1990s, with ninespine stickleback, Mysidae, shrimps, sculpins and arctic cod having their highest or one of their highest IG, and importance of sand lances was reduced relative to the other years of the study period, particularly in 1992. Cold and heavy ice conditions were recorded over the eastern Arctic at the beginning of the 1990s (McCormick et al. 1995, Mysak et al. 1996, Gough et al. 2004), which was confirmed by particularly late spring break-ups in western Hudson Bay during the same period (Fig. 3). In this study, we found that the importance of sand lances in ringed seal diet was low in years with a late spring sea-ice break-up. This was particularly the case in 1992, when the ice broke up 25 days later than average

(Fig. 3). Sand lances are zooplanktivores that feed in pelagic waters in large schools (see Nelson and Ross 1991, McKenzie and Wynne 2008). In Hudson Bay, sand lances spawn in the spring before the break-up of the sea ice and larvae start feeding shortly after break-up on earlier stages of copepods, associated with the phytoplankton bloom triggered by the ice break-up (Drolet et al. 1991). Thus, variability in sand lances recruitment has been found to be affected by variability in the timing of ice break-up, with late break-up delaying the phytoplankton bloom and leading to starvation of sand lance larvae (Drolet et al. 1991). However, sculpins and other benthic species will be less affected by the timing of break-up since their larvae emerge after the break-up and thus during the phytoplankton bloom (Drolet et al. 1991). Moreover, during cold and heavy ice years, the herbivorous zooplankton community is less abundant, and reduced ice algae grazing allows transfer of primary productivity to the benthos, leading to a benthic-dominated food web (see Tynan and DeMaster 1997, Bluhm and Gradinger 2008). These differences in ecology between benthic and pelagic prey and in the cryo-pelagic-benthic coupling could be important in understanding the pattern observed in ringed seals that increased the importance of benthic species, and particularly sculpins, in their diet in cold years when the importance of sand lances was reduced. A similar pattern was described by Smith (1987) in the western Arctic, where ringed seals switched from arctic cod to benthic species in 1974, a year of heavy ice and late break-up (Harwood et al. 2000).

From body length of sand lances consumed, ringed seals appeared to target principally the sub-adult and young adult age-classes (*i.e.*, 1-2 years-old; Winters 1989, Nelson and Ross 1991). This result suggested that, by affecting the timing of the phytoplankton bloom and so growth and abundance of zooplankton (Drolet et al. 1991), the timing of ice break-up could also affect the abundance, distribution and/or availability of adult sand lances to ringed seals in the fall. Effects of a late break-up on sand lance populations are likely to have repercussions on years following a cold year, since growth, recruitment and possibly adult survival are affected. In years of late break-up and therefore low availability of sand lances, ringed seals food consumption was reduced, as shown by a higher percentage of empty stomachs, a lower number of prey per stomach, and a lower biomass and energy ingested. Reduced energy consumption by ringed seals is expected to be reflected in their body condition, reproduction and possibly abundance and/or distribution. No significant annual variations were found in ringed seal fall body condition but poor reproductive performances, low recruitment and a decline in ringed seal density occurred in western Hudson Bay in the 1990s (Holst et al. 1999, Ferguson et al. 2005, Stirling 2005, Chambellant et al. 2010a, Chambellant et al. 2010b), supporting the nutritional stress hypothesis proposed by Chambellant et al. (2010b). These findings provides evidence that, on top of top-down processes associated with polar bear and arctic fox predation (Smith 1976, Hammill and Smith 1991, Chambellant et al. 2010b), ringed seals in western Hudson Bay are strongly regulated by bottom-up processes driven by variations in the sea-ice regime.

In conclusion, the feeding habits of ringed seals differed under varied environmental conditions and therefore appeared to be good indicators of environmental changes in the ecosystem. Our results also facilitated inferences to be made on the dynamics of marine fish communities, as well as on regulatory mechanisms for ringed seals in the western Hudson Bay ecosystem. However, strong inter-annual variations and gaps in the data limited our interpretations and emphasize the need for continued long-term monitoring of feeding habits to better understand how this pinniped species interacts with the different elements of the food web within the marine ecosystem. Carbon and nitrogen stable isotope ratios provided a more integrative perspective of ringed seal diet and a good temporal complement to the traditional stomach content diet reconstructions, by reducing some of biases and permitting a better understanding and interpretation of results. Future studies exploring marine mammal feeding habits would gain in combining traditional and biomarker techniques, including stable isotopes of different elements, fatty acid and/or mercury in multiple tissues.

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References

- Andersen, S.M., Lydersen, C., Grahl-Nielsen, O., and Kovacs, K.M. 2004. Autumn diet of harbour seals (*Phoca vitulina*) at Prins Karls Forland, Svalbard, assessed via scat and fatty-acid analyses. Canadian Journal of Zoology 82: 1230-1245.
- Anthony, J.A., Roby, D.D., and Turco, K.R. 2000. Lipid content and energy density of forage fishes from the northern Gulf of Alaska. Journal of Experimental Marine Biology and Ecology 248: 53-78.
- Arrhenius, f. and Hansson, S. 1993. Food consumption of larval, young and adult herring and sprat in the Baltic Sea. Marine Ecology Progress Series 96: 125-137.
- Ball, J.R., Esler, D., and Schmutz, J.A. 2007. Proximate composition, energetic value, and relative abundance of prey fish from the inshore eastern Bering Sea: implications for piscivorous predators. Polar Biology 30: 699-708.
- Bernt, K.E., Hammill, M.O., and Kovacs, K.M. 1996. Age estimation of grey seals (*Halichoerus grypus*) using incisors. Marine Mammal Science 12(3): 476-482.
- Bluhm, B.A. and Gradinger, R. 2008. Regional variability in food availability for Arctic marine mammals. Ecological Applications 18 Supplement(2): S77-S96.
- Born, E.W., Teilmann, J., Acquarone, M., and Riget, F.F. 2004. Habitat use of ringed seals (*Phoca hispida*) in the north water area (North Baffin Bay). Arctic 57(2): 129-142.

- Bowen, W.D. 2000. Reconstruction of pinniped diets: accounting for complete digestion of otoliths and cephalopod beaks. Canadian Journal of Fisheries and Aquatic Science 57: 898-905.
- Bowen, W.D. and Harrison, G.D. 1994. Offshore diet of grey seals *Halichoerus grypus* near Sable Island, Canada. Marine Ecology Progress Series 112: 1-11.
- Bradstreet, M.S.W. and Finley, K.J. 1983. Diet of ringed seals (*Phoca hispida*) in the Canadian high Arctic. LGL Limited, Environmental Research Associates, 44 Eglinton Ave. W., Toronto, Ontario, M4R 1A1. 36 pp.
- Breton-Provencher, M. 1979. Etude de la population de phoques annelés (*Phoca hispida*) et des autres pinnipèdes de la région de Poste-de-la-baleine (Nouveau-Québec). GIROQ, Rapport à l'hydro-Québec, Projet Grande-Baleine (Mandat d'avant-projet préliminaire OGB/76-1). 148 pp.
- Bunn, S.E., Loneragan, N.R., and Kempster, M.A. 1995. Effects of acid washing on stable isotope ratios of C and N in penaeid shrimp and seagrass: implications for food-web studies using multiple stable isotopes. Limnology and Oceanography 40(3): 622-625.
- Burns, J.M. 1999. The development of diving behavior in juvenile Weddell seals: pushing physiological limits in order to survive. Canadian Journal of Zoology 77: 737-747.
- Burns, J.M., Trumble, S.J., Castellini, M.A., and Testa, J.W. 1998. The diet of Weddell seals in McMurdo Sound, Antarctica as determined from scat collections and stable isotope analysis. Polar Biology 19: 272-282.

- Campana, S.E. 2004. Photographic Atlas of Fish Otoliths of the Northwest Atlantic Ocean. NRC Research Press. Ottawa, Ontario.
- Carscadden, J.E., Frank, K.T., and Leggett, W.C. 2001. Ecosystem changes and the effects on capelin (*Mallotus villosus*), a major forage species. Canadian Journal of Fisheries and Aquatic Sciences 58: 73-85.
- Chambellant, M. 2010. Hudson Bay ringed seal: ecology in a warming climate. In A little less Arctic: top predators in the world's largest northern inland sea, Hudson Bay. Edited by S.H. Ferguson, L.L. Loseto and M.L. Mallory. Springer. Dordrecht, Heidelberg, London, New York. pp.137-158.
- Chambellant, M. and Ferguson, S.H. 2009. Ageing live ringed seals (*Phoca hispida*): which tooth to pull? Marine Mammal Science 25(2): 478-486.
- Chambellant, M., Lunn, N.J., and Ferguson, S.H. 2010a. Distribution and density of ice-obligated seals in western Hudson Bay over a 14-year period, 1995-2008 Polar Biology Submitted in August 2010.
- Chambellant, M., Stirling, I., Gough, W.A., and Ferguson, S.H. 2010b. Temporal variations in Hudson Bay ringed seal (*Phoca hispida*) life-history parameters in relation to environment. Journal of Mammalogy Submitted in July 2010.
- Coad, B.W. and Reist, J.D. 2004. Annotated list of the Arctic marine fishes of Canada. Canadian Manuscript Report of Fisheries and Aquatic Sciences 2674: iv + 112 p.
- Cortes, E. 1997. A critical review of methods of studying fish feeding based on analysis of stomach contents: application to elasmobranch fishes. Canadian Journal of Fisheries and Aquatic Sciences 54: 726-738.

- Crawford, K., McDonald, R.A., and Bearshop, S. 2008. Applications of stable isotope techniques to the ecology of mammals. *Mammalian Reviews* 38(1): 87-107.
- Dehn, L.-A., Sheffield, G.G., Follmann, E.H., Duffy, L.K., Thomas, D.L., and O'Hara, T.M. 2007. Feeding ecology of phocid seals and some walrus in the Alaskan and Canadian Arctic as determined by stomach contents and stable isotope analysis. *Polar Biology* 30: 167-181.
- DeNiro, M.J. and Epstein, S. 1978. Influence of diet on the distribution of carbon isotopes in animals. *Geochimica et Cosmochimica Acta* 42: 495-506.
- DeNiro, M.J. and Epstein, S. 1981. Influence of diet on the distribution of nitrogen isotopes in animals. *Geochimica et Cosmochimica Acta* 45: 341-351.
- Drolet, R., Fortier, L., Ponton, D., and Gilbert, M. 1991. Production of fish larvae and their prey in subarctic southeastern Hudson Bay. *Marine Ecology Progress Series* 77: 105-118.
- Dunbar, M.J. 1983. A unique international polar year contribution: Lucien Turner, Capelin, and climatic change. *Arctic* 36(2): 204-205.
- Elliott, K.H. and Gaston, A.J. 2008. Mass-length relationships and energy content of fishes and invertebrates delivered to nestling thick-billed murres *Uria lomvia* in the Canadian Arctic, 1981-2007. *Marine Ornithology* 36: 25-34.
- Ferguson, S.H., Stirling, I., and McLoughlin, P. 2005. Climate change and ringed seal (*Phoca hispida*) recruitment in western Hudson Bay. *Marine Mammal Science* 21(1): 121-135.

- Folch, J., Lees, M., and Sloane Stanley, G.H. 1956. A simple method for the isolation and purification of total lipids from animal tissues. *Journal of Biological Chemistry* 226: 497-509.
- Frost, K.J. and Lowry, L.F. 1981. Ringed, Baikal and Caspian seals *Phoca hispida* Schreber, 1775; *Phoca sibirica* Gmelin, 1788 and *Phoca caspica* Gmelin, 1788. In *Handbook of marine mammals*. Edited by S.H. Ridgway and R.J. Harrison F.R.S. Academic Press. London, New York, Toronto, Sydney, San Francisco. pp.29-53.
- Furgal, C.M., Innes, S., and Kovacs, K.M. 1996. Characteristics of ringed seal, *Phoca hispida*, subnivean structures and breeding habitat and their effect on predation. *Canadian Journal of Zoology* 74: 858-874.
- Gagnon, A.S. and Gough, W.A. 2005. Trends in the dates of ice freeze-up and break-up over Hudson Bay, Canada. *Arctic* 58(4): 370-382.
- Gaston, A.J., Woo, K., and Hipfner, J.M. 2003. Trends in forage fish populations in northern Hudson bay since 1981, as determined from the diet of nestling thick-billed murres, *Uria lomvia*. *Arctic* 56(3): 227-233.
- Gaston, A.J., Gilchrist, H.G., and Hipfner, J.M. 2005. Climate change, ice conditions and reproduction in an Arctic marine bird: Brunnich's guillemot (*Uria lomvia* L.). *Journal of Animal Ecology* 74: 832-841.
- Gjertz, I. and Lydersen, C. 1986. The ringed seal (*Phoca hispida*) spring diet in northwestern Spitsbergen, Svalbard. *Polar Research* 4: 53-56.

- Goodyear, M.A. 1999. Variation in growth and seasonal condition of ringed seal, *Phoca hispida*, from the Canadian Arctic. MSc, Department of Zoology, University of Manitoba, Winnipeg, MB, R3T 2N2.
- Gough, W.A., Cornwell, A.R., and Tsuji, L.J.S. 2004. Trends in seasonal sea ice duration in southwestern Hudson Bay. *Arctic* 57(3): 299-305.
- Graf, H.-F., Kirchner, I., Robock, A., and Schult, I. 1993. Pinatubo eruption winter climate effects: model versus observations. *Climate Dynamics* 9: 81-93.
- Hall-Aspland, S.A., Hall, A.P., and Rogers, T.L. 2005. A new approach to the solution of the linear mixing model for a single isotope: application to the case of an opportunistic predator. *Oecologia* 143(1): 143-147.
- Hammer, O., Harper, D.A.T., and Ryan, P.D. 2001. PAST: paleontological statistics software package for education and data analysis. *Palaeontologia Electronica* 4(1): 9pp.
- Hammill, M.O. and Smith, T.G. 1991. The role of predation in the ecology of ringed seal in Barrow strait, Northwest Territories, Canada. *Marine Mammal Science* 7(2): 123-135.
- Hammill, M.O., Lesage, V., and Carter, P. 2005. What do harp seals eat? Comparing diet composition from different compartments of the digestive tract with diet estimated from stable-isotope ratios. *Canadian Journal of Zoology* 83: 1365-1372.
- Hansen, A.S., Nielsen, T.G., Levinsen, H., Madsen, S.D., Thingstad, T.F., and Hansen, B.W. 2003. Impact of changing ice cover on pelagic productivity and

- food web structure in Disko Bay, West Greenland: a dynamic model approach. Deep-Sea Research I 50: 171-187.
- Harvey, J.T. 1989. Assessment of errors associated with harbour seal (*Phoca vitulina*) faecal sampling. Journal of Zoology (London) 219(1): 101-111.
- Harwood, L.A. and Stirling, I. 1992. Distribution of ringed seals in the southeastern Beaufort sea during late summer. Canadian Journal of Zoology 70: 891-900.
- Harwood, L.A., Smith, T.G., and Melling, H. 2000. Variation in reproduction and body condition of the ringed seal (*Phoca hispida*) in the western Prince Albert Sound, NT, Canada, as assessed through a harvest-based sampling program. Arctic 53(4): 422-431.
- Helm, R.C. 1983. Rate of digestion in three species of pinnipeds. Canadian Journal of Zoology 62: 1751-1756.
- Hobson, K.A. 1999. Tracing origins and migration of wildlife using stable isotopes: a review. Oecologia 120: 314-326.
- Hobson, K.A. and Welch, H.E. 1992. Determination of trophic relationships within a high Arctic marine food web using $d^{13}\text{C}$ and $d^{15}\text{N}$ analysis. Marine Ecology Progress Series 84: 9-18.
- Hobson, K.A., Schell, D.M., Renouf, D., and Noseworthy, E. 1996. Stable carbon and nitrogen isotopic fractionation between diet and tissues of captive seals: implications for dietary reconstructions involving marine mammals. Canadian Journal of Fisheries and Aquatic Sciences 53: 528-533.

- Hochheim, K., Barber, D.G., and Lukovich, J.V. 2010. Changing sea ice conditions in Hudson Bay, 1980-2005. In *A little less Arctic: Top predators in the world's largest northern inland sea, Hudson Bay*. Edited by S.H. Ferguson, L.L. Loseto and M.L. Mallory. Springer. Dordrecht, Heidelberg, London, New York. pp.39-51.
- Holdway, D.A. and Beamish, F.W.H. 1984. Specific growth rate and proximate body composition of Atlantic Cod (*Gadus morhua* L.). *Journal of Experimental Marine Biology and Ecology* 81: 147-170.
- Holst, M. and Stirling, I. 2002. A comparison of ringed seal (*Phoca hispida*) biology on the east and west sides of the North water Polynya, Baffin Bay. *Aquatic Mammals* 28(3): 221-230.
- Holst, M., Stirling, I., and Calvert, W. 1999. Age structure and reproductive rates of ringed seals (*Phoca hispida*) on the northwestern coast of Hudson Bay in 1991 and 1992. *Marine Mammal Science* 15(4): 1357-1364.
- Holst, M., Stirling, I., and Hobson, K.A. 2001. Diet of ringed seals (*Phoca hispida*) on the east and west sides of the North Water Polynya, northern Baffin Bay. *Marine Mammal Science* 17(4): 888-908.
- Hyslop, E.J. 1980. Stomach contents analysis-a review of methods and their application. *Journal of Fish Biology* 17: 411-429.
- IPCC (Intergovernmental Panel on Climate Change) 2007. Climate Change 2007: Synthesis Report. Edited by R.K. Pachauri and A. Reisinger. 104 pp.
<http://www.ipcc.ch/ipccreports/ar4-syr.htm>

- Iverson, S.J., Stirling, I., and Lang, S.L.C. 2006. Spatial and temporal variation in the diets of polar bears across the Canadian Arctic: indicators of changes in prey populations and environment. *In* Top predators in marine ecosystems: their role in monitoring and management. *Edited by* I.L. Boyd, S. Wanless and C.J. Camphuysen. Cambridge University Press. pp.98-117.
- Iverson, S.J., Field, C., Bowen, W.D., and Blanchard, W. 2004. Quantitative fatty acid signature analysis: a new method of estimating predator diets. *Ecological Monographs* 72(2): 211-235.
- Jorgensen, C., Lydersen, C., Brix, O., and Kovacs, K.M. 2001. Diving development in nursing harbour seal pups. *The Journal of Experimental Biology* 204(3993-4004).
- Joy, R., Tollit, D.J., Laake, J.L., and Trites, A.W. 2006. Using simulations to evaluate reconstructions of sea lion diet from scat. *In* Sea Lions of the world. *Edited by* A.W. Trites, S.K. Atkinson, D.P. DeMaster, L.W. Fritz, T.S. Gellat, L.D. Rea and K.M. Wynne. Alaska Sea Grant College Program, University of Alaska Fairbanks. pp.205-221.
- Kelly, B.P. and Wartzok, D. 1996. Ringed seal diving behavior in the breeding season. *Canadian Journal of Zoology* 74: 1547-1555.
- Kelly, B.P., Badajos, O.H., Kunnsranta, M., Moran, J.R., Martinez-Bakker, M., Wartzok, D., and Boveng, P. 2010. Seasonal home ranges and fidelity to breeding sites among ringed seals. *Polar Biology* 33: 1095-1109.
- Kelly, J.F. 2000. Stable isotopes of carbon and nitrogen in the study of avian and mammalian trophic ecology. *Canadian Journal of Zoology* 78: 1-27.

- Kendall, C. and Caldwell, E.A. 1998. Fundamentals of isotope geochemistry. In Isotope tracers in catchment hydrology. Edited by C. Kendall and J.J. McDonnell. Elsevier Science. Amsterdam. pp.51-86.
- Kendall, C., Sklash, M.G., and Bullen, T.D. 1995. Isotopes tracers of water and solute sources in catchments. In Solute modelling in catchment systems. Edited by S.T. Trudgill. John Wiley and Sons Ltd. New-York. pp.261-303.
- Kovacs, K.M. and Lydersen, C. 2008. Climate change impacts on seals and whales in the North Atlantic Arctic and adjacent shelf seas. *Science Progress* 91(2): 117-150.
- Krafft, B.A., Kovacs, K.M., and Lydersen, C. 2007. Distribution of sex and age groups of ringed seals *Pusa hispida* in the fast-ice breeding habitat of Kongsfjorden, Svalbard. *Marine Ecology Progress Series* 335: 199-206.
- Kurle, C.M. 2002. Stable-isotope ratios of blood components from captive northern fur seals (*Callorhinus ursinus*) and their diet: applications for studying the foraging ecology of wild otariids. *Canadian Journal of Zoology* 80: 902-909.
- Kurle, C.M. and Worthy, G.A.J. 2002. Stable nitrogen and carbon isotope ratios in multiple tissues of the northern fur seal *Callorhinus ursinus*: implications for dietary and migratory reconstructions. *Marine Ecology Progress Series* 236: 289-300.
- Labansen, A.L., Lydersen, C., Haug, T., and Kovacs, K.M. 2007. Spring diet of ringed seals (*Phoca hispida*) from northwestern Spitsbergen, Norway. *ICES Journal of Marine Science* 64(6): 1246-1256.

- Laidre, K.L., Stirling, I., Lowry, L.F., Wiig, O., Heide-Jorgensen, M.P., and Ferguson, S.H. 2008. Quantifying the sensitivity of Arctic marine mammals to climate-induced habitat change. *Ecological Applications* 18(2 Supplement): S97-S125.
- Lawson, J.W. and Hobson, K.A. 2000. Diet of Harp seals (*Pagophilus groenlandica*) in nearshore northeast Newfoundland: inferences from stable-carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) isotope analyses. *Marine Mammal Science* 16(3): 578-591.
- Lawson, J.W., Stenson, G.B., and McKinnon, D.G. 1995. Diet of harp seals (*Phoca groenlandica*) in nearshore waters of the northwest Atlantic during 1990-1993. *Canadian Journal of Zoology* 73: 1805-1818.
- Lawson, J.W., Magalhaes, A.M., and Miller, E.H. 1998. Important prey species of marine vertebrate predators in the northwest Atlantic: proximate composition and energy density. *Marine Ecology Progress Series* 164: 13-20.
- Leopold, M.F., van Damme, C.J.G., Philippart, C.J.M., and Winter, C.J.N. 1991. Otoliths of North Sea fish - Fish identification key by means of otoliths and other hard parts. World Biodiversity Database CD-Rom Series: ETI-Bioinformatics, Amsterdam, Netherlands. <http://www.eti.uva.nl/>.
- Lesage, V., Hammill, M.O., and Kovacs, K.M. 2001. Marine mammals and the community structure of the estuary and Gulf of St Lawrence, Canada: evidence from stable isotope analysis. *Marine Ecology Progress Series* 210: 203-221.

- Lidster, W.W., Lilly, G.R., and Dawe, E.G. 1994. Otoliths of Arctic Cod (*Boreogadus saida*), small Atlantic Cod (*Gadus morhua*), and three other fish species from Newfoundland waters: description and relationship of body length to otolith length. *Journal of Northwest Atlantic Fishery Science* 16: 33-40.
- Lowry, L.F., Frost, K.J., and Burns, J.J. 1980a. Feeding of bearded seals in the Bering and Chukchi Seas and trophic interaction with Pacific Walruses. *Arctic* 33(2): 330-342.
- Lowry, L.F.K., Frost, j., and Burns, J.J. 1980b. Variability in the diet of ringed seals, *Phoca hispida*, in Alaska. *Canadian Journal of Fisheries and Aquatic Sciences* 37: 2254-2261.
- Lydersen, C. and Hammill, M.O. 1993. Diving in ringed seal (*Phoca hispida*) pups during the nursing period. *Canadian Journal of Zoology* 71: 991-996.
- Lydersen, C., Gjertz, I., and Weslawski, J.M. 1989. Stomach contents of autumn-feeding marine vertebrates from Hornsund, Svalbard. *Polar Record* 25: 107-114.
- Magurran, A.E. 2003. Measuring biological diversity. Blackwell Publishing.
- Mansfield, A.W. 1967. Seals of Arctic and eastern Canada. *Fisheries Research Board of Canada, Bulletin* 137, 35 pp.
- Markham, W.E. 1986. The ice cover. In *Canadian Inland Seas*. Edited by I.P. Martini. Elsevier. Amsterdam, Oxford, New-York, Tokyo. pp.101-116.
- McCormick, M.P., Thomason, L.W., and Trepte, C.R. 1995. Atmospheric effects of the Mt Pinatubo eruption. *Nature* 373: 399-404.

- McDonald, M., Arragutainaq, L., and Novalinga, Z. 1997. Voices from the Bay: traditional ecological knowledge of Inuit and Cree in the Hudson Bay bioregion. Canadian Arctic Resources Committee, Environmental Committee of the municipality of Sanikiluaq.
- McKenzie, J. and Wynne, K.M. 2008. Spatial and temporal variation in the diet of Steller sea lions in the Kodiak Archipelago, 1999 to 2005. *Marine Ecology Progress Series* 360: 265-283.
- McKinney, M.A., Peacock, E., and Letcher, R.J. 2009. Sea ice-associated diet change increases the levels of chlorinated and brominated contaminants in polar bears. *Environmental Science and Technology* 43: 4334-4339.
- McLaren, I.A. 1958. The biology of the ringed seal (*Phoca hispida* Schreber) in the eastern Canadian Arctic 97 pp.
- McLaren, I.A. 1993. Growth in pinnipeds. *Biological Reviews* 68: 1-79.
- Moore, J.W. and Semmens, B.X. 2008. Incorporating uncertainty and prior information into stable isotope mixing models. *Ecology Letters* 11: 470-480.
- Moreno, T. and Castro, J.J. 1995. Community structure of the juvenile of coastal pelagic fish species in the Canary Islands waters. *Scientia Marina* 59: 405-413.
- Murie, D.J. and Lavigne, D.M. 1986. Interpretation of otoliths in stomach content analyses of phocid seals: quantifying fish consumption. *Canadian Journal of Zoology* 64: 1152-1157.
- Mysak, L.A., Ingram, R.G., Wang, J., and Van der Baaren, A. 1996. The anomalous sea-ice extent in Hudson Bay, Baffin Bay and the Labrador sea

- during three simultaneous NAO and ENSO episodes. *Atmosphere-Ocean* 34(2): 313-343.
- Nelson, G.A. and Ross, M.R. 1991. Biology and population changes of Northern Sand Lance (*Ammodytes dubius*) from the gulf of Maine to the middle Atlantic bight. *Journal of Northwest Atlantic Fishery Science* 11: 11-27.
- Newsome, S.D., Clementz, M.T., and Koch, P.L. 2010. Using stable isotope biogeochemistry to study marine mammal ecology. *Marine Mammal Science*.
- Parkinson, C.L. and Cavalieri, D.J. 2008. Arctic sea ice variability and trends, 1979-2006. *Journal of Geophysical Research* 113: C07003.
- Parkinson, C.L., Cavalieri, D.J., Gloerson, P., Zwally, H.J., and Comiso, J.C. 1999. Arctic sea ice extents, areas, and trends, 1978-1996. *Journal of Geophysical Research* 104(C9): 20837-20856.
- Pazerniuk, M.A. 2007. Mercury and Stable isotopes in the pelagic food web of Hudson Bay, *Environment and Geography*, University of Manitoba, Winnipeg.
- Phillips, D.L. 2001. Mixing models in analyses of diet using multiple stable isotopes: a critique. *Oecologia* 127: 166-170.
- Phillips, D.L. and Gregg, J.W. 2003. Source partitioning using stable isotopes: coping with too many sources. *Oecologia* 136: 261-269.
- Post, E., Forchhammer, M.C., Bret-Harte, M.S., Callaghan, T.V., Christensen, T.R., Elberling, B., Fox, A.D., Gilg, O., Hik, D.S., Hoye, T.T., Ims, R.A., Jeppesen, E., Klein, D.R., Madsen, J., McGuire, A.D., Rysgaard, S., Schindler, D.E., Stirling, I., Tamstorf, M.P., Tyler, N.J.C., van der Wal, R., Welker, J., Wookey, P.A., Schmidt, N.M., and Aastrup, P. 2009. Ecological dynamics

- across the Arctic associated with recent climate change. *Science* 325: 1355-1358.
- Quay, P., Sonnerup, R., Westby, T., Stutsman, J., and McNichol, A. 2003. Changes in the $^{13}\text{C}/^{12}\text{C}$ of dissolved inorganic carbon in the ocean as a tracer of anthropogenic CO₂ uptake. *Global Biogeochemical Cycles* 17(1): 1-20.
- Regehr, E.V., Lunn, N.J., Amstrup, S.C., and Stirling, I. 2007. Effects of earlier sea ice break-up on survival and population size of polar bears in western Hudson Bay. *Journal of Wildlife Management* 71(8): 2673-2683.
- Ross, S. 1993. Food and feeding of the hooded seal in Newfoundland, Memorial University, St John's, NL.
- Rubenstein, D.R. and Hobson, K.A. 2004. From birds to butterflies: animal movement patterns and stable isotopes. *Trends in Ecology and Evolution* 19(5): 256-263.
- Ryg, M., Smith, T.G., and Ortsland, N.A. 1990. Seasonal changes in body mass and composition of ringed seals (*Phoca hispida*) on Svalbard. *Canadian Journal of Zoology* 68: 470-475.
- Saucier, F.J., Senneville, S., Prinsenberg, S., Roy, F., Smith, G., Gachon, P., Caya, D., and Laprise, R. 2004. Modelling the sea ice-ocean seasonal cycle in Hudson Bay, Foxe Basin and Hudson strait, Canada. *Climate Dynamics* 23: 303-326.
- Siegstad, H., Neve, P.B., Heide-Jorgensen, M.P., and Harkonen, T. 1998. Diet of the ringed seal (*Phoca hispida*) in Greenland. In *Ringed seals in the North*

- Atlantic. Edited by M.P. Heide-Jorgensen and C. Lydersen. The North Atlantic Marine Mammal Commission. Tromso. pp.229-241.
- Skinner, W.R., Jefferies, R.L., Carleton, T.J., Rockwell, R.F., and Abraham, K.F. 1998. Prediction of reproductive success and failure in lesser geese based on early season climatic variables. Global Change Biology 4: 3-16.
- Smith, R.J., Hobson, K.A., Koopman, H.N., and Lavigne, D.M. 1996. Distinguishing between populations of fresh- and salt-water harbour seals (*Phoca vitulina*) using stable-isotope ratios and fatty acid profiles. Canadian Journal of Fisheries and Aquatic Sciences 53: 272-279.
- Smith, T.G. 1973. Population dynamics of the ringed seal in the Canadian eastern Arctic 55 pp.
- Smith, T.G. 1976. Predation of ringed seal pups (*Phoca hispida*) by the arctic fox (*Alopex lagopus*). Canadian Journal of Zoology 54: 1610-1616.
- Smith, T.G. 1987. The ringed seal, *Phoca hispida*, of the Canadian western Arctic 81 pp.
- Smith, T.G. and Stirling, I. 1975. The breeding habitat of the ringed seal (*Phoca hispida*). The birth lair and associated structures. Canadian Journal of Zoology 53: 1297-1305.
- Smith, T.G. and Hammill, M.O. 1981. Ecology of the ringed seal, *Phoca hispida*, in its fast ice breeding habitat. Canadian Journal of Zoology 59: 966-981.
- Smith, T.G., Hammill, M.O., and Taugbol, G. 1991. A review of the developmental, behavioral and physiological adaptations of the ringed seal, *Phoca hispida*, to life in the Arctic winter. Arctic 44(2): 124-131.

- Sokal, R.R. and Rohlf, F.J. 1995. Biometry: The principles and practice of statistics in biological research. Freeman, W.H. and Company. New York.
- Steimle, F.W. and Terranova, R.J. 1985. Energy equivalents of marine organisms from the continental shelf of the temperate northwest Atlantic. *J. Northw. Atl. Fish. Sci.* 6: 117-124.
- Stephens, M.A. 1974. EDF statistics for goodness of fit and some comparisons. *Journal of the American Statistical Association* 69: 730-737.
- Stewart, D.B. and Lockhart, W.L. 2005. An overview of the Hudson Bay marine ecosystem. Canadian Technical Report of Fisheries and Aquatic Science(2586): vi+487pp.
- Stewart, R.E.A., Stewart, B.E., Stirling, I., and Street, E. 1996. Counts of growth layer groups in cementum and dentine in ringed seals (*Phoca hispida*). *Marine Mammal Science* 12(3): 383-401.
- Stirling, I. 2005. Reproductive rates of ringed seals and survival of pups in northwestern Hudson Bay, Canada, 1991-2000. *Polar Biology* 28: 381-387.
- Stirling, I. and Parkinson, C.L. 2006. Possible effects of climate warming on selected populations of polar bears (*Ursus maritimus*) in the Canadian Arctic. *Arctic* 59(3): 261-275.
- Stirling, I., Archibald, W.R., and DeMaster, D. 1977. Distribution and abundance of seals in the Eastern Beaufort Sea. *Fisheries Research Board of Canada* 34: 976-988.

- Stirling, I., Cleator, H., and Smith, T.G. 1981. Marine mammals. In Polynyas in the Canadian Arctic. Occasional paper Number 45. Edited by I. stirling and H. Cleator. Canadian Wildlife Service. pp.45-58.
- Stirling, I., Lunn, N.J., and Iacozza, J. 1999. Long-term trends in the population ecology of polar bears in western Hudson Bay in relation to climatic change. *Arctic* 52(3): 294-306.
- Stirling, I., Lunn, N.J., Iacozza, J., Elliott, C., and Obbard, M. 2004. Polar bear distribution and abundance on the southwestern Hudson Bay coast during open-water season, in relation to population trends and annual ice pattern. *Arctic* 57(1): 15-26.
- Teilmann, J., Born, E.W., and Acquarone, M. 1999. Behaviour of ringed seals tagged with satellite transmitters in the North Water polynya during fast-ice formation. *Canadian Journal of Zoology* 77: 1934-1946.
- Thiemann, G.W., Iverson, S.J., and Stirling, I. 2008. Polar bear diets and Arctic marine food webs: insights from fatty acid analysis. *Ecological Monographs* 78(4): 591-613.
- Tieszen, L.L., Boutton, T.W., Tesdahl, K.G., and Slade, N.G. 1983. Fractionation and turnover of stable carbon isotopes in animal tissues: implications for $\delta^{13}\text{C}$ analysis of diet. *Oecologia* 57: 32-37.
- Tollit, D.J., Heaslip, S.G., Barrick, R.L., and Trites, A.W. 2007. Impact of diet-index selection and the digestion of prey hard remains on determining the diet of the Steller sea lion (*Eumetopias jubatus*). *Canadian Journal of Zoology* 85: 1-15.

- Tollit, D.J., Stewart, M.J., Thompson, P.M., Pierce, G.J., Santos, M.B., and Hughes, S. 1997. Species and size differences in the digestion of otoliths and beaks: implications for estimates of pinniped diet composition. Canadian Journal of Fisheries and Aquatic Sciences 54: 105-119.
- Tyler, A.V. 1973. Caloric values of some north Atlantic invertebrates. Marine Biology 19: 258-261.
- Tynan, C.T. and DeMaster, D.P. 1997. Observations and predictions of Arctic climatic change: potential effects on marine mammals. Arctic 50(4): 308-322.
- Wathne, J.A., Haug, T., and Lydersen, C. 2000. Prey preference and niche overlap of ringed seals *Phoca hispida* and harp seals *Pagophilus groenlandica* in the Barents Sea. Marine Ecology Progress Series 194: 233-239.
- Weslawski, J.M., Ryg, M., Smith, T.G., and Ortsland, N.A. 1994. Diet of ringed seals (*Phoca hispida*) in a Fjord of West Svalbard. Arctic 47(2): 109-114.
- Winters, G.H. 1989. Life history parameters of Sand Lances (Ammodytes spp.) from the coastal waters of eastern Newfoundland. Journal of Northwest Atlantic Fishery Science 9: 5-11.
- Zar, J.H. 1996. Biostatistical analysis. Prentice-Hall.

Chapter 5

Conclusion



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Despite its ecological, economical, and cultural significance, the ringed seal has seldom been studied in the Hudson Bay ecosystem. In this research project, I presented the first time series data on ringed seal population dynamics in western Hudson Bay. My objectives were to describe ringed seal density, life-history traits and feeding habits, and assess the role of environment in the inter-annual variations of these parameters.

The major results of my research could be summarized as follow:

1. In chapter two, I found that ringed seal density estimates were in the range of previously reported estimates for the species in the Arctic and varied greatly from year to year. A sine function with an eleven-year period was fitted to the variation of ringed seal density estimates over the 14-year period and I proposed that ringed seal density in western Hudson Bay may follow a decadal cycle, with a decline in the 1990s and a recovery in the 2000s. A similar pattern was observed for ringed seal demographic parameters and pup survival in western Hudson Bay, supporting my interpretation. I hypothesized that the exceptionally cold and heavy ice conditions that prevailed in the eastern Arctic at the beginning of the 1990s may have triggered the observed decline in ringed seal density during the decade. I discussed briefly the possibility of a decline in ringed seal density that may be concurrent to the natural cycle due to the detrimental effect on ringed seal pups of early dates of ice break-up, decreasing snow depth and increasing warm/rain events in the spring,

trends that have been reported in western Hudson Bay over the last 30 years.

2. In chapter three, I found that the peak pupping date for ringed seals in western Hudson Bay occurred early March, *i.e.*, about a month earlier than previously reported in the literature. I suggested that an earlier pupping date, and consequently weaning date, might be an adaptation to earlier spring ice break-up dates at lower latitudes, therefore preventing the possibility of a premature separation between an un-weaned pup and its mother. I found that ringed seal life-history traits varied between the two decades of the study period, with the 2000s presenting younger seals that grew faster, matured earlier and produced more pups that survived better than the 1990s, suggesting a decadal cycle in demographic parameters. Although no significant trends were found in the variation of body condition of ringed seal adult females and pups, pregnant females were in better condition than non pregnant females in the 1990s. These results suggested that conditions in the 1990s were not favourable for ringed seals in western Hudson Bay. I hypothesized that the cold and heavy ice conditions that prevailed at the beginning of the 1990s may have impacted ringed seals indirectly and directly by 1) reducing the productivity in western Hudson Bay thus creating a nutritional stress in ringed seals, through reduced abundance/availability of prey; and 2) increasing the predation pressure by polar bears and arctic foxes that had the possibility to stay on the ice platform to hunt for a longer period due to late dates of

break-up, respectively. I proposed that immigration of pups, juveniles, and young adults played a critical role in the recovery of ringed seal demographic parameters in western Hudson Bay in the 2000s. I found that in western Hudson Bay, ringed seals tolerated a wide but nonetheless limited range of environmental variations. In the context of the current unidirectional warming, I suggested that values of environmental variables might reach and/or exceed ringed seal tolerance thresholds with potential negative impacts on population dynamics.

3. In chapter four, I found that, during the open-water season, ringed seals in western Hudson Bay were sand lance specialists. I reported that a shift in ringed seal feeding habits occurred in the 2000s relative to the 1990s, with fewer benthic prey items and more sub-Arctic fish species appearing in the diet. I proposed the current warming trend in western Hudson Bay to be associated with the observed shift by redistributing the fish community northward. I found that, when the spring ice break-up occurred later than average, the importance of sand lances in ringed seal diet was low, which was associated with a decrease in ringed seal food consumption. I suggested that the cold and heavy ice conditions that prevailed in the early 1990s shifted the Hudson Bay ecosystem productivity from pelagic to benthic, negatively impacting the recruitment and abundance, distribution and/or availability of sand lances to ringed seals that were not able to compensate for the energy loss from sand lances by diversifying their diet and foraging benthically. A nutritional stress hypothesis was

evoked and linked to previously described low ringed seal demographic parameters in western Hudson Bay in the 1990s.

I described patterns of density, life-history traits and feeding habits of ringed seals in western Hudson Bay over two decades and showed that strong inter-annual variations that could be linked to variations in environmental variables, particularly in the sea-ice regime, occurred. Similar patterns were observed in the western Arctic (Stirling et al. 1982, Smith 1987, Kingsley and Byers 1998, Harwood et al. 2000).

By combining results of chapters two, three and four, it is possible to highlight some of the mechanisms that could have been involved in the variations of the studied parameters. In particular, the exceptionally cold and heavy ice conditions that prevailed at the beginning of the 1990s in the eastern Arctic (Graf et al. 1993, McCormick et al. 1995, Mysak et al. 1996, Gough et al. 2004) likely induced a shift in the Hudson Bay ecosystem productivity from pelagic to benthic, that negatively impacted the recruitment and availability of sand lances to ringed seals, which were not able to compensate for the energy loss by feeding benthically. The nutritional stress incurred resulted in a decrease in ringed seal reproductive output, pup survival, and density, suggesting that bottom-up processes were strongly regulating ringed seal population dynamics in western Hudson Bay in the early 1990s. Top-down processes, through predation pressure by polar bears and arctic foxes, were concurrently at play in western Hudson Bay in the early 1990s. Ringed seal demographic parameters and density remained low throughout the decade emphasizing the long-lasting effect

on the Hudson Bay ecosystem of the extreme climatic conditions that occurred in 1991-92.

The negative effect of nutritional stress on pinniped reproduction and survival has been widely reported in the literature (e.g., Laws 1956, Lunn et al. 1994, Guinet et al. 1998 and see review from Trites and Donnelly 2003), but I presented the first evidence that such a mechanism was operating on ringed seal population dynamics. Reduced productivity due to heavy ice conditions was suggested as a possible cause of ringed seal reproductive failures in the western Arctic but data was lacking to support the hypothesis, although Smith (1987) presented limited dietary data suggesting a more benthic and reduced food consumption in 1974, a particularly heavy ice year in the western Arctic.

Evidence for an important role of immigration by pups, juveniles, and young adults was presented as a mechanism involved in the recovery of ringed seal demographic parameters and density in the 2000s in western Hudson Bay. Dispersal and movements of immature ringed seals away from areas of unsuitable conditions or in suitable areas have been documented (McLaren 1958, Vibe 1967, Smith 1973, Stirling et al. 1982, Smith 1987) but adult, breeding seals were previously reported to show signs of site fidelity (McLaren 1958, Smith and Hammill 1981, Kelly and Quakenbush 1990, Krafft et al. 2007, Kelly et al. 2010). Cameron et al. (2007) reported an increase in site fidelity with age up to 12 years and an increased fidelity to sites where successful breeding events occurred in Weddell seals, the Antarctic ecological counterpart of ringed seals. Our results suggested that, in Hudson Bay, ringed seals might follow a pattern

similar to Weddell seals, *i.e.*, moving among different sites at the beginning of their reproductive life.

Variations in ringed seal density, demographic parameters and above all, feeding habits reflected changes in the sea-ice regime and productivity of western Hudson Bay, confirming that the ringed seal is a good indicator species of ecosystem changes. Particularly, through variations in ringed seal feeding habits, I highlighted a possible shift in fish community in western Hudson Bay in the 2000s, supporting the conclusions of Gaston et al. (2003). Oceanographic expeditions to monitor fish community are expensive, time consuming and not always successful. Comparatively, monitoring top predator diets and population dynamics is logically and monetarily affordable and has the potential to provide information on the ecosystem all year-round. Long-term monitoring of long-lived top predators in Hudson Bay should be a high priority, especially in the current context of major climatic changes.

The response of ringed seals to the unidirectional environmental warming occurring in Hudson Bay (*e.g.*, Gagnon and Gough 2005a, Parkinson and Cavalieri 2008) was not apparent in the data set I analysed. In western Hudson Bay, I found that pupping, and consequently weaning, occurred earlier than previously reported at higher latitudes (McLaren 1958, Smith 1973, 1987, Hammill et al. 1991, Lydersen 1995), which might temporarily shelter pups from the negative effects of climatic changes and in particular, of the trend in earlier dates of spring ice break-up. However, ringed seals appeared to tolerate a limited range of environmental variations. With the current and projected trends

in early date of break-up, decreasing snow depth and increasing spring temperature and rain falls in Hudson Bay, values of these environmental variables will likely reach and exceed ringed seal tolerance thresholds in the near future, exposing pups to premature weaning, and increased risks of hypothermia and predation (Hammill and Smith 1991, Harwood et al. 2000, Smith and Harwood 2001, Stirling and Smith 2004). In the Arctic, the projected climatic changes are expected to favour pelagic over benthic productivity (Bluhm and Gradinger 2008), which might benefit ringed seals during the open-water season, as found by Harwood et al. (2000). However, effects of such a change on ringed seals feeding habits during the ice-covered, breeding season is more difficult to assess. The effects on ringed seal population dynamics of increased competition (e.g., with the harbour seal; Stirling 2005) and predation (e.g., by killer whales; Higdon and Ferguson 2009) pressures with temperate species in a warming Hudson Bay have yet to be explored. Therefore, if ringed seals are not able to adapt their breeding and feeding behaviours to the projected reduced ice-cover season in Hudson Bay (Gagnon and Gough 2005b), I propose that ringed seal response to climate warming in Hudson Bay might be of a catastrophic type, with no, reduced or positive effects in the short- and medium-term, and a collapse in the long-term.

My research project was based on the first time-series of density, life-history parameters and feeding habits of ringed seals in Hudson Bay over almost two decades. Results found may be used as input in ecosystem models in future research. However, gaps in the data collection, and sometimes small sample

sizes, hindered our ability to draw conclusions about factors influencing long-term trends, particularly in the highly variable Arctic environment. Long-term monitoring with large sample sizes of ringed seal density, demographic parameters and diet should be considered critical to better appreciate the role of environmental variables in ringed seal population dynamics, and to project ringed seal response to effects of climatic changes, particularly in the sub-Arctic Hudson Bay ecosystem, where climate changes are expected to occur first and faster (Walsh 2008), and where the ringed seal occur at the southern limit of the species range.

Bibliography

- Barbraud, C. and Weimerskirch, H. 2001. Emperor penguins and climate change. *Nature* 411: 183-186.
- Bluhm, B.A. and Gradinger, R. 2008. Regional variability in food availability for Arctic marine mammals. *Ecological Applications* 18 Supplement(2): S77-S96.
- Born, E.W., Teilmann, J., Acquarone, M., and Riget, F.F. 2004. Habitat use of ringed seals (*Phoca hispida*) in the north water area (North Baffin Bay). *Arctic* 57(2): 129-142.
- Bowen, W.D. 1991. Behavioural ecology of pinniped neonates. In *The behaviour of pinnipeds*. Edited by D. Renouf. Chapman and Hall. London, New York, Tokyo, Melbourne, Madras. pp.66-127.
- Bradstreet, M.S.W. and Finley, K.J. 1983. Diet of ringed seals (*Phoca hispida*) in the Canadian high Arctic. LGL Limited, Environmental Research Associates, 44 Eglinton Ave. W., Toronto, Ontario, M4R 1A1, Calgary, Alberta, 36pp.
- Breton-Provencher, M. 1979. Etude de la population de phoques annelés (*Phoca hispida*) et des autres pinnipèdes de la région de Poste-de-la-baleine (Nouveau-Québec). GIROQ, Rapport à l'hydro-Québec, Projet Grande-Baleine (Mandat d'avant-projet préliminaire OGB/76-1), 148pp.
- Cameron, M.F., Siniff, D.B., Proffitt, K.M., and Garrott, R.A. 2007. Site fidelity of Weddell seals: the effects of sex and age. *Antarctic Science* 19(2): 149-155.
- Caughley, G. 1980. Analysis of vertebrate populations. The Blackburn Press. Chichester, New York, Brisbane, Toronto.

Bibliography

- Chambellant, M. 2010. Hudson Bay ringed seal: ecology in a warming climate. In A little less Arctic: top predators in the world's largest northern inland sea, Hudson Bay. Edited by S.H. Ferguson, L.L. Loseto and M.L. Mallory. Springer. Dordrecht, Heidelberg, London, New York. pp.137-158.
- Chambellant, M., Lunn, N.J., and Ferguson, S.H. 2010. Distribution and density of ice-obligated seals in western Hudson Bay over a 14-year period, 1995-2008. Polar Biology (submitted).
- Comiso, J.C. 2002. A rapidly declining perennial sea ice cover in the Arctic. Geophysical Research Letters 29(20): 171-174.
- Comiso, J.C., Parkinson, C.L., Gersten, R., and Stock, L. 2008. Accelerated decline in the Arctic sea ice cover. Geophysical Research Letters 35: L01703.
- Eberhardt, L.L. 2002. A paradigm for population analysis of long-lived vertebrates. Ecology 83(10): 2841-2854.
- Ferguson, S.H., Stirling, I., and McLoughlin, P. 2005. Climate change and ringed seal (*Phoca hispida*) recruitment in western Hudson Bay. Marine Mammal Science 21(1): 121-135.
- Forchhammer, M.C., Clutton-Brock, T.H., Lindstrom, J., and Albon, S.D. 2001. Climate and population density induce long-term cohort variation in a northern ungulate. Journal of Animal Ecology 70: 721-729.
- Fowler, C.W. and Smith, T.D. 1978. Dynamics of large populations. John Wiley & Sons. New York, Chichester, Brisbane, Toronto, Singapore.
- Frost, K.J. and Lowry, L.F. 1981. Ringed, Baikal and Caspian seals *Phoca hispida* Schreber, 1775; *Phoca sibirica* Gmelin, 1788 and *Phoca caspica*

Bibliography

- Gmelin, 1788. In *Handbook of marine mammals*. Edited by S.H. Ridgway and R.J. Harrison F.R.S. Academic Press. London, New York, Toronto, Sydney, San Francisco. pp.29-53.
- Furgal, C.M., Innes, S., and Kovacs, K.M. 1996. Characteristics of ringed seal, *Phoca hispida*, subnivean structures and breeding habitat and their effect on predation. Canadian Journal of Zoology 74: 858-874.
- Gagnon, A.S. and Gough, W.A. 2005a. Trends in the dates of ice freeze-up and break-up over Hudson Bay, Canada. Arctic 58(4): 370-382.
- Gagnon, A.S. and Gough, W.A. 2005b. Climate change scenarios for the Hudson Bay region: an intermodel comparison. Climatic Change 69: 269-297.
- Gaillard, J.-M., Festa-Bianchet, M., and Yoccoz, N.G. 1998. Population dynamics of large herbivores: variable recruitment with constant adult survival. Trends in Ecology and Evolution 13(2): 58-63.
- Gaston, A.J. and Woo, K. 2008. Razorbills (*Alca torda*) follow subarctic prey into the Canadian Arctic: colonization results from climate change? The Auk 125(4): 939-942.
- Gaston, A.J., Woo, K., and Hipfner, J.M. 2003. Trends in forage fish populations in northern Hudson bay since 1981, as determined from the diet of nestling thick-billed murres, *Uria lomvia*. Arctic 56(3): 227-233.
- Gaston, A.J., Gilchrist, H.G., and Hipfner, J.M. 2005. Climate change, ice conditions and reproduction in an Arctic marine bird: Brunnich's guillemot (*Uria lomvia* L.). Journal of Animal Ecology 74: 832-841.

Bibliography

- Gjertz, I. and Lydersen, C. 1986. The ringed seal (*Phoca hispida*) spring diet in northwestern Spitsbergen, Svalbard. *Polar Research* 4: 53-56.
- Goodyear, M.A. 1999. Variation in growth and seasonal condition of ringed seal, *Phoca hispida*, from the Canadian Arctic. MSc, Department of Zoology, University of Manitoba, Winnipeg, MB, R3T 2N2.
- Gough, W.A. and Wolfe, E. 2001. Climate change scenarios for Hudson bay, Canada, from general circulation models. *Arctic* 54(2): 142-148.
- Gough, W.A., Cornwell, A.R., and Tsuji, L.J.S. 2004. Trends in seasonal sea ice duration in southwestern Hudson Bay. *Arctic* 57(3): 299-305.
- Graf, H.-F., Kirchner, I., Robock, A., and Schult, I. 1993. Pinatubo eruption winter climate effects: model versus observations. *Climate Dynamics* 9: 81-93.
- Guinet, C., Roux, J.-P., Bonnet, M., and Mison, V. 1998. Effect of body size, body mass, and body condition on reproduction of female South African fur seals (*Arctocephalus pusillus*) in Namibia. *Canadian Journal of Zoology* 76: 1418-1424.
- Hammill, M.O. and Smith, T.G. 1989. Factors affecting the distribution and abundance of ringed seal structures in Barrow Strait, Northwest Territories. *Canadian Journal of Zoology* 67: 2212-2219.
- Hammill, M.O. and Smith, T.G. 1991. The role of predation in the ecology of ringed seal in Barrow strait, Northwest Territories, Canada. *Marine Mammal Science* 7(2): 123-135.

Bibliography

- Hammill, M.O., Lydersen, C., Ryg, M., and Smith, T.G. 1991. Lactation in the ringed seal (*Phoca hispida*). Canadian Journal of Fisheries and Aquatic Sciences 48: 2471-2476.
- Hanks, J. 1978. Characterization of population condition. In Dynamics of large mammal populations. Edited by C.W. Fowler and T.D. Smith. John Wiley & Sons. New York, Chichester, Brisbane, Toronto, Singapore. pp.47-73.
- Hansen, A.S., Nielsen, T.G., Levinsen, H., Madsen, S.D., Thingstad, T.F., and Hansen, B.W. 2003. Impact of changing ice cover on pelagic productivity and food web structure in Disko Bay, West Greenland: a dynamic model approach. Deep-Sea Research I 50: 171-187.
- Harington, C.R. 2008. The evolution of Arctic marine mammals. Ecological Applications 18 Supplement(2): S23-S40.
- Harwood, L.A. and Stirling, I. 1992. Distribution of ringed seals in the southeastern Beaufort sea during late summer. Canadian Journal of Zoology 70: 891-900.
- Harwood, L.A., Smith, T.G., and Melling, H. 2000. Variation in reproduction and body condition of the ringed seal (*Phoca hispida*) in the western Prince Albert Sound, NT, Canada, as assessed through a harvest-based sampling program. Arctic 53(4): 422-431.
- Higdon, J.W. and Ferguson, S.H. 2009. Loss of Arctic sea ice causing punctuated change in sightings of killer whales (*Orcinus orca*) over the past century. Ecological Applications 19(5): 1365-1375.

Bibliography

- Hindell, M.A. 1991. Some life-history parameters of a declining population of Southern elephant seals, *Mirounga leonina*. *Journal of Animal Ecology* 60(1): 119-134.
- Holst, M., Stirling, I., and Calvert, W. 1999. Age structure and reproductive rates of ringed seals (*Phoca hispida*) on the northwestern coast of Hudson Bay in 1991 and 1992. *Marine Mammal Science* 15(4): 1357-1364.
- Holst, M., Stirling, I., and Hobson, K.A. 2001. Diet of ringed seals (*Phoca hispida*) on the east and west sides of the North Water Polynya, northern Baffin Bay. *Marine Mammal Science* 17(4): 888-908.
- IPCC (Intergovernmental Panel on Climate Change) 2007. Climate Change 2007: Synthesis Report. *Edited by* R.K. Pachauri and A. Reisinger. 104 pp.
<http://www.ipcc.ch/ipccreports/ar4-syr.htm>
- Iverson, S.J., Stirling, I., and Lang, S.L.C. 2006. Spatial and temporal variation in the diets of polar bears across the Canadian Arctic: indicators of changes in prey populations and environment. *In* Top predators in marine ecosystems: their role in monitoring and management. *Edited by* I.L. Boyd, S. Wanless and C.J. Camphuysen. Cambridge University Press. pp.98-117.
- Kelly, B.P. and Quakenbush, L.T. 1990. Spatiotemporal use of lairs by ringed seals (*Phoca hispida*). *Canadian Journal of Zoology* 68: 2503-2512.
- Kelly, B.P. and Wartzok, D. 1996. Ringed seal diving behavior in the breeding season. *Canadian Journal of Zoology* 74: 1547-1555.

Bibliography

- Kelly, B.P., Badajos, O.H., Kunnasranta, M., Moran, J.R., Martinez-Bakker, M., Wartzok, D., and Boveng, P. 2010. Seasonal home ranges and fidelity to breeding sites among ringed seals. *Polar Biology* 33: 1095-1109.
- Kingsley, M.C.S. and Byers, T.J. 1998. Failure in reproduction of ringed seals (*Phoca hispida*) in Amundsen Gulf, Northwest Territories in 1984-1987. In *Ringed seals in the North Atlantic*. Edited by M.P. Heide-Jorgensen and C. Lydersen. The North Atlantic Marine Mammal Commission. Tromso. pp.197-210.
- Kovacs, K.M. and Lydersen, C. 2008. Climate change impacts on seals and whales in the North Atlantic Arctic and adjacent shelf seas. *Science Progress* 91(2): 117-150.
- Krafft, B.A., Kovacs, K.M., and Lydersen, C. 2007. Distribution of sex and age groups of ringed seals *Pusa hispida* in the fast-ice breeding habitat of Kongsfjorden, Svalbard. *Marine Ecology Progress Series* 335: 199-206.
- Krafft, B.A., Kovacs, K.M., Frie, A.K., Haug, T., and Lydersen, C. 2006. Growth and population parameters of ringed seals (*Pusa hispida*) from Svalbard, Norway, 2002-2004. *ICES Journal of Marine Science* 63: 1136-1144.
- Labansen, A.L., Lydersen, C., Haug, T., and Kovacs, K.M. 2007. Spring diet of ringed seals (*Phoca hispida*) from northwestern Spitsbergen, Norway. *ICES Journal of Marine Science* 64(6): 1246-1256.
- Laidre, K.L., Stirling, I., Lowry, L.F., Wiig, O., Heide-Jorgensen, M.P., and Ferguson, S.H. 2008. Quantifying the sensitivity of Arctic marine mammals to

Bibliography

- climate-induced habitat change. Ecological Applications 18(2 Supplement): S97-S125.
- Laws, R.M. 1956. Growth and sexual maturity in aquatic mammals. Nature 178: 193-194.
- Lowry, L.F.K., Frost, J., and Burns, J.J. 1980. Variability in the diet of ringed seals, *Phoca hispida*, in Alaska. Canadian Journal of Fisheries and Aquatic Sciences 37: 2254-2261.
- Lunn, N.J., Boyd, I.L., and J.P., C. 1994. Reproductive performance of female Antarctic fur seals: the influence of age, breeding experience, environmental variation and individual quality. Journal of Animal Ecology 63(4): 827-840.
- Lydersen, C. 1995. Energetics of pregnancy, lactation and neonatal development in ringed seals (*Phoca hispida*). In Whales, seals, fish and man. Edited by A.S. Blix, L. Walloe and O. Ultang. Elsevier. Amsterdam, Lausanne, New York, Oxford, Shannon, Tokyo. pp.319-327.
- Lydersen, C. and Gjertz, I. 1987. Population parameters of ringed seals (*Phoca hispida* Schreber, 1775) in the Svalbard area. Canadian Journal of Zoology 65: 1021-1027.
- Lydersen, C. and Smith, T.G. 1989. Avian predation on ringed seal *Phoca hispida* pups. Polar Biology 9: 489-490.
- Lydersen, C. and Hammill, M.O. 1993. Diving in ringed seal (*Phoca hispida*) pups during the nursing period. Canadian Journal of Zoology 71: 991-996.

Bibliography

- Manabe, S. and Stouffer, R.J. 1980. Sensitivity of a global climate model to an increase of CO₂ concentration in the atmosphere. *Journal of Geophysical Research* 85(C10): 5529-5554.
- Mansfield, A.W. 1967. Seals of Arctic and eastern Canada. *Fisheries Research Board of Canada, Bulletin* 137, 35 pp.
- Markham, W.E. 1986. The ice cover. *In Canadian Inland Seas. Edited by I.P. Martini.* Elsevier. Amsterdam, Oxford, New-York, Tokyo. pp.101-116.
- McCormick, M.P., Thomason, L.W., and Trepte, C.R. 1995. Atmospheric effects of the Mt Pinatubo eruption. *Nature* 373: 399-404.
- McKinney, M.A., Peacock, E., and Letcher, R.J. 2009. Sea ice-associated diet change increases the levels of chlorinated and brominated contaminants in polar bears. *Environmental Science and Technology* 43: 4334-4339.
- McLaren, I.A. 1958. The biology of the ringed seal (*Phoca hispida* Schreber) in the eastern Canadian Arctic. *Fisheries Research Board of Canada, Bulletin* 118, 97 pp.
- McLaren, I.A. 1993. Growth in pinnipeds. *Biological Reviews* 68: 1-79.
- Mysak, L.A., Ingram, R.G., Wang, J., and Van der Baaren, A. 1996. The anomalous sea-ice extent in Hudson Bay, Baffin Bay and the Labrador sea during three simultaneous NAO and ENSO episodes. *Atmosphere-Ocean* 34(2): 313-343.
- Parkinson, C.L. and Cavalieri, D.J. 2008. Arctic sea ice variability and trends, 1979-2006. *Journal of Geophysical Research* 113: C07003.

Bibliography

- Parkinson, C.L., Cavalieri, D.J., Gloerson, P., Zwally, H.J., and Comiso, J.C. 1999. Arctic sea ice extents, areas, and trends, 1978-1996. *Journal of Geophysical Research* 104(C9): 20837-20856.
- Post, E., Forchhammer, M.C., Bret-Harte, M.S., Callaghan, T.V., Christensen, T.R., Elberling, B., Fox, A.D., Gilg, O., Hik, D.S., Hoye, T.T., Ims, R.A., Jeppesen, E., Klein, D.R., Madsen, J., McGuire, A.D., Rysgaard, S., Schindler, D.E., Stirling, I., Tamstorf, M.P., Tyler, N.J.C., van der Wal, R., Welker, J., Wookey, P.A., Schmidt, N.M., and Aastrup, P. 2009. Ecological dynamics across the Arctic associated with recent climate change. *Science* 325: 1355-1358.
- Prinsenberg, S.J. 1986. The circulation pattern and current structure of Hudson Bay. In *Canadian inland seas*. Edited by I.P. Martini. Elsevier. Amsterdam, Oxford, New-York, Tokyo. pp.187-204.
- Regehr, E.V., Lunn, N.J., Amstrup, S.C., and Stirling, I. 2007. Effects of earlier sea ice break-up on survival and population size of polar bears in western Hudson Bay. *Journal of Wildlife Management* 71(8): 2673-2683.
- Root, T.L., Price, J.T., Hall, K.R., Schneider, S.H., Rosenzweig, C., and Pounds, J.A. 2003. Fingerprints of global warming on wild animals and plants. *Nature* 421: 57-60.
- Ryg, M., Smith, T.G., and Ortsland, N.A. 1990. Seasonal changes in body mass and composition of ringed seals (*Phoca hispida*) on Svalbard. *Canadian Journal of Zoology* 68: 470-475.

Bibliography

- Saucier, F.J., Senneville, S., Prinsenberg, S., Roy, F., Smith, G., Gachon, P., Caya, D., and Laprise, R. 2004. Modelling the sea ice-ocean seasonal cycle in Hudson Bay, Foxe Basin and Hudson strait, Canada. *Climate Dynamics* 23: 303-326.
- Siegstad, H., Neve, P.B., Heide-Jorgensen, M.P., and Harkonen, T. 1998. Diet of the ringed seal (*Phoca hispida*) in Greenland. In *Ringed seals in the North Atlantic*. Edited by M.P. Heide-Jorgensen and C. Lydersen. The North Atlantic Marine Mammal Commission. Tromso. pp.229-241.
- Simpkins, M.A., Kelly, B.P., and Wartzok, D. 2001. Three-dimensional analysis of search behaviour by ringed seals. *Animal Behaviour* 62: 67-72.
- Skinner, W.R., Jefferies, R.L., Carleton, T.J., Rockwell, R.F., and Abraham, K.F. 1998. Prediction of reproductive success and failure in lesser geese based on early season climatic variables. *Global Change Biology* 4: 3-16.
- Smith, T.G. 1973. Population dynamics of the ringed seal in the Canadian eastern Arctic. *Fisheries Research Board of Canada, Bulletin* 181, 55 pp.
- Smith, T.G. 1976. Predation of ringed seal pups (*Phoca hispida*) by the arctic fox (*Alopex lagopus*). *Canadian Journal of Zoology* 54: 1610-1616.
- Smith, T.G. 1980. Polar bear predation of ringed and bearded seals in the land-fast ice habitat. *Canadian Journal of Zoology* 58: 2201-2209.
- Smith, T.G. 1987. The ringed seal, *Phoca hispida*, of the Canadian western Arctic. *Canadian Bulletin of Fisheries and Aquatic Sciences* 216, 81 pp.

Bibliography

- Smith, T.G. and Stirling, I. 1975. The breeding habitat of the ringed seal (*Phoca hispida*). The birth lair and associated structures. Canadian Journal of Zoology 53: 1297-1305.
- Smith, T.G. and Hammill, M.O. 1981. Ecology of the ringed seal, *Phoca hispida*, in its fast ice breeding habitat. Canadian Journal of Zoology 59: 966-981.
- Smith, T.G. and Harwood, L.A. 2001. Observations of neonate ringed seals, *Phoca hispida*, after early break-up of the sea ice in Prince Albert Sound, Northwest Territories, Canada, Spring 1998. Polar Biology 24: 215-219.
- Smith, T.G., Hammill, M.O., and Taugbol, G. 1991. A review of the developmental, behavioral and physiological adaptations of the ringed seal, *Phoca hispida*, to life in the Arctic winter. Arctic 44(2): 124-131.
- Stearns, S.C. 1992. The evolution of life-histories. Oxford University Press. Oxford.
- Stenseth, N.C., Mysterud, A., Ottersen, G., Hurrell, J.W., Chan, K.-S., and Lima, M. 2002. Ecological effects of climate fluctuations. Science 297: 1292-1296.
- Stewart, D.B. and Lockhart, W.L. 2005. An overview of the Hudson Bay marine ecosystem. Canadian Technical Report of Fisheries and Aquatic Science(2586): vi+487pp.
- Stirling, I. 1997. The importance of polynyas, ice edges, and leads to marine mammals and birds. Journal of Marine Systems 10: 9-21.
- Stirling, I. 2005. Reproductive rates of ringed seals and survival of pups in northwestern Hudson Bay, Canada, 1991-2000. Polar Biology 28: 381-387.

Bibliography

- Stirling, I. and Smith, T.G. 2004. Implications of warm temperatures and an unusual rain event for the survival of ringed seals on the coast of southeastern Baffin Island. *Arctic* 57(1): 59-67.
- Stirling, I. and Parkinson, C.L. 2006. Possible effects of climate warming on selected populations of polar bears (*Ursus maritimus*) in the Canadian Arctic. *Arctic* 59(3): 261-275.
- Stirling, I., Cleator, H., and Smith, T.G. 1981. Marine mammals. In *Polynyas in the Canadian Arctic*. Occasional paper Number 45. Edited by I. stirling and H. Cleator. Canadian Wildlife Service. pp.45-58.
- Stirling, I., Kingsley, M.C.S., and Calvert, W. 1982. The distribution and abundance of seals in the eastern Beaufort Sea, 1974-79. Occasional paper 47, 23pp.
- Stirling, I., Lunn, N.J., and Iacozza, J. 1999. Long-term trends in the population ecology of polar bears in western Hudson Bay in relation to climatic change. *Arctic* 52(3): 294-306.
- Stirling, I., Lunn, N.J., Iacozza, J., Elliott, C., and Obbard, M. 2004. Polar bear distribution and abundance on the southwestern Hudson Bay coast during open-water season, in relation to population trends and annual ice pattern. *Arctic* 57(1): 15-26.
- Thiemann, G.W., Iverson, S.J., and Stirling, I. 2008. Polar bear diets and Arctic marine food webs: insights from fatty acid analysis. *Ecological Monographs* 78(4): 591-613.

Bibliography

- Trillmich, F. and Ono, K.A. 1991. Pinnipeds and El Niño: Responses to environmental stress. Springer-Verlag. Berlin, Heidelberg, New York, London, Paris, Tokyo, Hong Kong, Barcelona, Budapest.
- Trites, A.W. and Donnelly, C.P. 2003. The decline of Steller sea lion *Eumetopias jubatus* in Alaska: a review of the nutritional stress hypothesis. *Mammal Review* 33: 3-28.
- Tynan, C.T. and DeMaster, D.P. 1997. Observations and predictions of Arctic climatic change: potential effects on marine mammals. *Arctic* 50(4): 308-322.
- Vibe, C. 1967. Arctic animals in relation to climatic fluctuations. Reitzels Forlag, C.A.
- Walsh, J.E. 2008. Climate of the Arctic marine environment. *Ecological Applications* 18(2 Supplement): S3-S22.
- Walther, G.-R., Post, E., Convey, P., Menzel, A., Parmesan, C., Beebee, T.J.C., Fromentin, J.-M., Hoegh-Guldberg, O., and Bairlein, F. 2002. Ecological responses to recent climate change. *Nature* 416: 389-395.
- Wathne, J.A., Haug, T., and Lydersen, C. 2000. Prey preference and niche overlap of ringed seals *Phoca hispida* and harp seals *Pagophilus groenlandica* in the Barents Sea. *Marine Ecology Progress Series* 194: 233-239.
- Weslawski, J.M., Ryg, M., Smith, T.G., and Ortsland, N.A. 1994. Diet of ringed seals (*Phoca hispida*) in a Fjord of West Svalbard. *Arctic* 47(2): 109-114.
- Woollett, J.M., Henshaw, A.S., and Wake, C.P. 2000. Palaeoecological implications of Archaeological seal bone assemblages: case studies from Labrador and Baffin Island. *Arctic* 53(4): 395-413.

Bibliography

Yurkowski, D.J., Chambellant, M., and Ferguson, S.H. 2010. Evidence of polygyny from baculum and testicle growth in the aquatic-mating ringed seal (*Phoca hispida*). *Journal of Mammalogy* (submitted).