

Maternal and newborn life-history traits during periods of contrasting population trends: implications for explaining the decline of harbour seals (*Phoca vitulina*), on Sable Island

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Abstract

Annual censuses of the number of harbour seal *Phoca vitulina* pups born on Sable Island Canada showed an increasing trend during the 1980s, but a rapid decline through the 1990s from 625 pups in 1989 to only 32 by 1997. Weekly surveys of the North Beach of the island during the 1991–98 breeding seasons showed that the number of adults and juveniles also declined during the 1990s. Despite the dramatic demographic changes, maternal postpartum mass, pup birth mass, relative birth mass, lactation duration, pup weaning mass and relative weaning mass showed no significant trends during 1987–96. However, two traits did change. The age structure of parturient females increased significantly, indicating reduced recruitment to the breeding population. Mean birth date increased by 7 days during the early 1990s, suggesting nutritional stress of females and later implantation dates. This nutritional stress may in turn have been caused by increased competition from the rapidly increasing grey seal population on Sable Island. Although minimum estimates of shark-inflicted mortality can account for much of the decline, evidence suggests that food shortage arising from interspecific competition may have also played a role in causing the decline of the population through effects on fecundity and juvenile survival.

Key words: pinniped, *Phoca vitulina*, interannual variation, life-history traits, population decline

INTRODUCTION

Understanding the causes and consequences of population change is a fundamental goal of ecology and conservation biology. Population fluctuations result from temporal variation in survival, fecundity, immigration and dispersal. However, determining the relative importance of these factors in marine populations has proved particularly difficult (e.g. Steller sea lions *Eumatopias jubatus*; NRC, 1996). This is because there is usually insufficient information about the temporal trends in age-specific fecundity and sources of mortality to distinguish among competing hypotheses. Although both increasing and decreasing populations are of interest to ecologists and resource managers, decreasing populations are usually of more pressing concern because loss of habitat and depressed fecundity at critically low population density (i.e. Allee effects) may reduce the likelihood of population recovery.

The way in which individuals cope with environmental variability can have important effects on both survival

and reproductive success and thus on the dynamics of populations (Coulson, Milner-Gulland & Clutton-Brock, 2000). For example, food intake can affect maternal growth and condition, which in turn can affect birth mass (Willis & Wilson, 1974; Robinson, 1977; Lunn, Boyd & Croxall, 1994). Similarly, maternal size and age can affect offspring growth and development (Arnborn, Fedak & Boyd, 1997; Mellish, Iverson & Bowen, 1999; Pomeroy *et al.*, 1999; Bowen, Boness, Iverson & Oftedal, 2001). In snow geese *Anser caerulescens*, a long-term decline in quality of foraging habitat led to declines in offspring growth rates, parental body size (Cooch *et al.*, 1991) and female reproductive success (Rockwell *et al.*, 1993). Extreme, short-term environmental events can also have dramatic effects. For example, the strong 1982–83 El Niño resulted in reduced maternal expenditure, milk output and slower pup growth in California sea lions *Zalophus californianus* (Ono, Boness & Oftedal, 1987; Iverson, Oftedal & Boness, 1991) and in failed reproduction and reduced survival in several other species of pinnipeds (Trillmich & Ono, 1991).

The number of harbour seals *Phoca vitulina* born on Sable Island has been monitored by tagging all pups each year since 1978 (Lucas & Stobo, 2000). During a 10-year

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study of maternal effects in harbour seals during lactation (Ellis *et al.*, 2000; Bowen, Boness, Iverson *et al.*, 2001), the demography of the Sable Island population changed dramatically. Beginning in 1991, about halfway through the study period (1987–96), the number of harbour seals born annually dropped 10-fold, from 625 in 1989 to < 50 by 1997 (Lucas & Stobo, 2000). The causes of this dramatic decline in the number of pups born are not fully understood, but are known to include predation by sharks on all age classes (Lucas & Stobo, 2000). Other possible causes include disturbance effects of increased research on this population, competition for food with the large and rapidly increasing population of grey seals *Halichoerus grypus* that also use Sable Island throughout the year (Mohn & Bowen, 1996) and changes in the availability of prey caused, in part, by fluctuations in the physical oceanography on the Scotian Shelf (reviewed in Zwanenburg *et al.*, 2002). Changes in prey availability either through competition or through environmental change may in turn affect maternal condition, which could result in lower fecundity or reduced lactation performance resulting in smaller offspring. Smaller offspring are likely to have reduced survival (Baker & Fowler, 1992; Hall *et al.*, 2001).

Harbour seals are long-lived, iteroparous mammals in the family Phocidae. They are widely distributed along coastal marine habitats throughout much of the Northern Hemisphere. Adult females first give birth between 4 and 6 years of age, but continue to grow until around 10 years of age (Boulva & McLaren, 1979). They give birth on land and like most pinnipeds, bear single, precocial offspring (Bonner, 1984). Offspring usually enter the water with their mothers within hours of birth (Lawson & Renouf, 1985) and spend considerable time at sea throughout lactation (Bowen, Boness & Iverson, 1999). Although lactating females mobilize considerable amounts of fat stored in blubber, unlike the larger-bodied phocid species, harbour seal females also forage intensively during lactation to support the energetic costs of lactation (Boness, Bowen & Oftedal, 1994; Bowen, Boness, Iverson *et al.*, 2001). This means that both maternal and offspring traits might be affected by variation in food supply occurring during the period of offspring provisioning.

Our life-history study provided us with the opportunity to examine whether changes in the number of harbour seals born on Sable Island were associated with changes in maternal and offspring traits. Such changes might provide further insight into the causes of the population decline. Here, data are presented on interannual variation in traits of parturient females (parturition date, maternal postpartum mass (MPPM), duration of lactation) and of pups (birth mass, rate of mass gain during lactation and weaning mass) and two indices of maternal reproductive expenditure, birth mass and weaning mass relative to MPPM. These data, along with survey data on changes in the sex and age composition of the population and updated estimates of pup production, provide a more complete understanding of the causes underlying this rapid decline of harbour seals on Sable Island.

METHODS

The number of harbour seal pups born on Sable Island Nova Scotia, Canada (43°55'N, 60°00'W) was determined by individually tagging all neonates born on the island each year during the breeding season in May–June and accounting for pups that died before they could be tagged (e.g. stillbirths). Annual pup tagging began in 1978. A description of these methods and counts of pup production for the period 1980–96 are reported in Lucas & Stobo (2000). We continued these counts through 2000 using the same tagging methods and through 2002 based on counts of pups. The same observer conducted these counts at the end of the pupping season (i.e. in mid June each year). However, the 2001 and 2002 counts are probably underestimates of total production, as they do not account for stillbirths or pups that might have died or were at sea during the counts. For this reason, they were not included in Fig. 1.

To document trends of different components of the population within the breeding season and among years, weekly counts were conducted in our life-history study area from 1991 to 1998. The study area was a 24-km stretch of North Beach, which covered most of the harbour seal distribution on this side of the Island. Numbered stakes were driven into the sand at 0.5-km intervals at the beginning of each season from a permanent zero marker to determine location of seals on the beach. A comparison of morning and afternoon counts throughout the 1991 season showed that the highest counts were observed in the afternoon (Walker & Bowen, 1993). Therefore, in subsequent years only late afternoon counts were used. With the aid of binoculars, an experienced observer surveyed the study area and counted the number and location of adult males, adult females, juveniles (probably 1- to 3-year-olds based on estimated body length) and pups, as described in Walker & Bowen (1993). Seals in the water were not included in the survey counts, thus our surveys represented a standardized index of numbers and not absolute population size. The average of the 3 highest counts in each demographic category within season was used to examine interannual trends to reduce variability in counts of seals hauled out caused by different weather conditions.

Data on parturient female and newborn harbour seals were collected in May and June each year from 1987 to 1996 and on weaned pups from 1988 to 1996. Each day throughout the pupping season, newborns were sexed, weighed and flipper tagged (Bowen, Oftedal *et al.*, 1994). Most mothers of newborns were also captured and weighed once during the season. Body mass of pups and females taken within 24 h of birth were defined as birth mass and MPPM, respectively (Ellis *et al.*, 2000). Rate of mass gain (mass gained during lactation divided by the number of days between birth and weaning) and weaning mass were also measured on a subset of pups (Bowen, Boness, Iverson *et al.*, 2001).

Parturition dates were converted to day of year. In 1987, observations ended before the end of the pupping season. However, as most pups had been born, the estimated mean

birth date should be reasonably reliable even though the date of last birth and the interval between first and last births are negatively biased. In some years, a few pups had been born before our arrival; however, with few exceptions we were able to estimate the age of these pups based on the mass of the pup and condition of the umbilical cord. To test for effects of changing demography on maternal and pup traits, the data were divided into 2 5-year periods: 1987–91, when pup production was slowly increasing or roughly stable; 1992–96, when pup production was in rapid decline. Maternal age was known for females that were first tagged as pups and that had retained the tags until the time of recapture.

Statistical analyses were performed using SPSS statistical software version 7.0 (SPSS, 1997). Means are reported with standard errors (SE). The significance level for all tests was $P \leq 0.05$.

RESULTS

Interannual trends in numbers

The number of harbour seals born on Sable Island increased from 1978 to 1989 (Fig. 1). Apart from several large annual increases in the late 1970s and early 1980s, which suggest immigration of females to the population, the average annual rate of increase during this period was 5.8%. Between 1992 and 1997, there was a steep decline in pup production and an apparent levelling off at low numbers through 2000 (23–29 pups; Fig. 1). However, minimum counts from 2001 and 2002 indicated a further decline to 12 and 8 pups, respectively (J. McMillan, pers. comm.).

The decline in pup production did not occur uniformly on both the North and South Beaches of Sable Island. Between 1987 and 1990, c. 45% of pups were born on the South Beach (including the brackish water area known as Wallace Lake; Fig. 1). During the period of rapid decline, however, the percentage of pups born on the South Beach steadily declined to c. 25% of total production. Between 1997 and 2000, so few pups were born that the proportion born on the South Beach showed greater variability, but with the exception of 1998, was still only c. 30%. Thus, there was a disproportionate loss of pups on the South Beach.

Our weekly beach surveys showed that all components of the population were affected by this decline, but the trends differed somewhat among age and sex classes (Fig. 2). The index of both adult male and female numbers remained high in 1992 despite the dramatic decline in the pup index and the absolute count of the number of pups born (Fig. 1). However, by 1993 the index of adult males had dropped by half, subsequently stabilized for several years and then dropped once again. In contrast, adult female numbers were relatively stable between 1991 and 1994 and then dropped rapidly through 1996 before levelling off at very low numbers. Of particular interest was the relationship between female and pup counts. Unequal variances of female and pup counts among years,

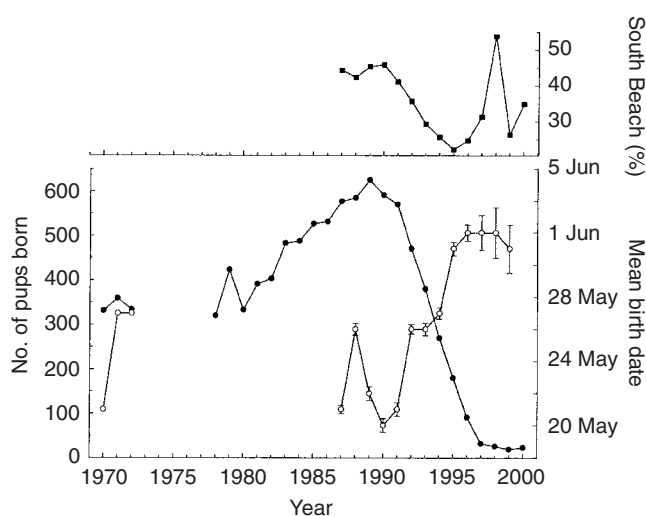


Fig. 1. Number of harbour seal *Phoca vitulina* pups born on Sable Island (closed circles). Data from 1970 to 1972 and from 1978 to 1997 are from Boulva & McLaren (1979), and W. T. Stobo (pers. comm.) and Lucas & Stobo (2000), respectively. Open circles, mean birth dates for 1970–72 (Boulva & McLaren, 1979) and from 1987 to 1999 (this study); solid squares, proportion of pups born on the south side of the Island, outside our study area, from 1987 to 2000.

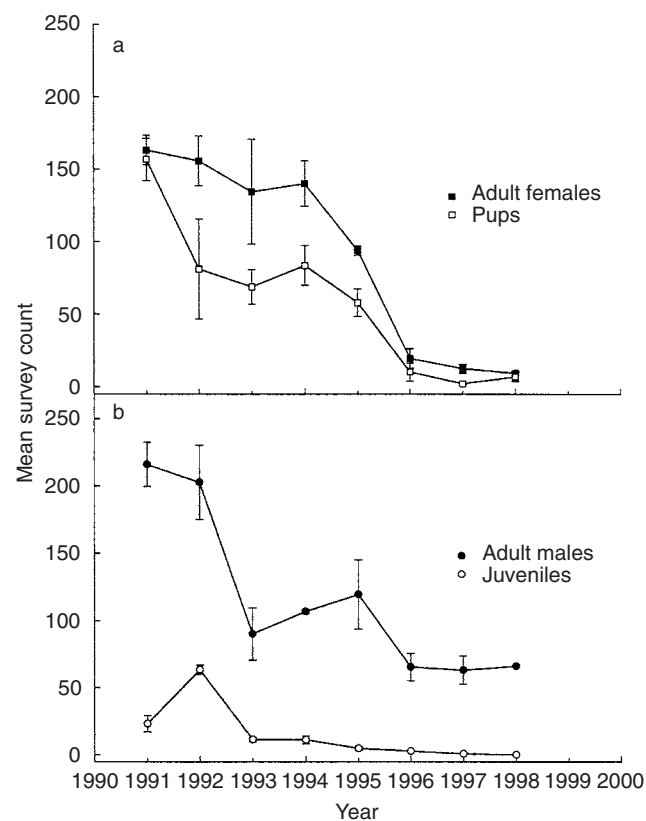


Fig. 2. Mean (\pm SE) number of harbour seal *Phoca vitulina* counted in weekly afternoon surveys of a 24-km section of the North Beach of Sable Island: (a) adult females and pups; (b) adult males and juveniles. Mean based on the three highest counts for each demographic component within each year.

Table 1. Birth dates of harbour seals *Phoca vitulina* on Sable Island 1987–99 ($n = 1341$)

Year	Mean	SE (days)	n	Births		Range (days)
				First	Last	
1987 ^a	21 May	0.26	80	11 May	27 May	17
1988	25 May	0.36	115	18 May	7 June	21
1989	22 May	0.44	108	11 May	6 June	27
1990	20 May	0.43	95	11 May	29 May	19
1991	21 May	0.43	104	11 May	3 June	24
1992	26 May	0.30	177	16 May	7 June	23
1993	26 May	0.38	183	14 May	9 June	27
1994	27 May	0.36	159	16 May	13 June	29
1995	31 May	0.40	173	14 May	16 June	34
1996	1 June	0.52	77	22 May	10 June	20
1997	1 June	1.09	30	18 May	15 June	29
1998	1 June	1.57	22	23 May	14 June	23
1999	31 May	1.51	18	19 May	10 June	23

^a In 1987, sampling was terminated before the end of the pupping season, thus latest date, mean date and range are negatively biased.

even after square root transformation, meant that it was not possible to conduct an analysis using all years. However, the equality of variance assumption was met for the period 1992–94, and during this period counts did not differ by year ($F_{2,26} = 2.0$, $P = 0.15$), but pup counts were significantly lower than those of females ($F_{2,26} = 17.3$, $P < 0.001$). The numbers of juveniles also declined and this group virtually disappeared by 1995 (Fig. 2).

Pup mortality

Lucas & Stobo (2000) reported minimum estimates of the number of pups and other age classes killed throughout the year by sharks on Sable Island between 1980 and 1997. In the 1998, 1999 and 2000 pupping seasons, zero, three and one shark-killed pups were recorded on our North Beach study area.

Interannual variation in parturition dates

Over the 13-year period of our study, births occurred from 11 May to 16 June (Table 1). Mean date of parturition differed significantly among years (one-way general linear model (GLM), $F_{12,1253} = 62.7$, $P < 0.001$) fluctuating between 20 and 22 May from 1987 to 1991, with the exception of 1988 (Fig. 1). Between 1992 and 1996 there was a progressive delay in mean date of parturition, resulting in an overall delay of *c.* 1 week by 1996. This mean remained relatively constant through 1999. Among years in which the entire pupping season was monitored (i.e. excluding, 1987 data, see Methods), the shortest interval between first and last birth was 19 days in 1990 and the longest was 34 days in 1995. Despite the delay in mean parturition dates, however, there was no trend in the interval between first and last births among years

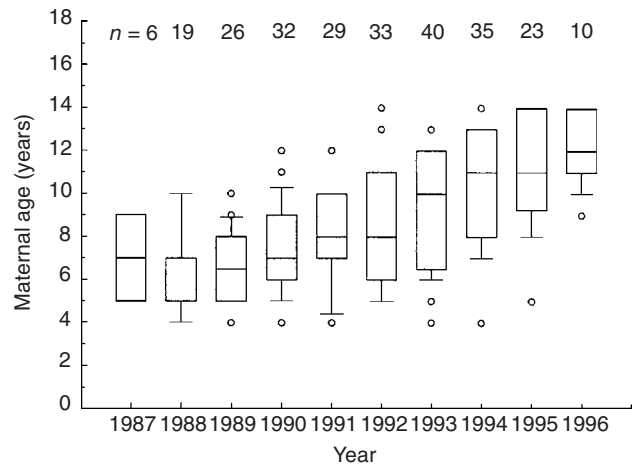


Fig. 3. Trend in median age of known-age female harbour seals *Phoca vitulina* that gave birth on the North Beach of Sable Island between 1987 and 1996. Lines at the bottom, middle and top of each box, 25th, 50th and 75th percentiles, respectively; thin horizontal lines, smallest and largest values that are not outliers; open circles, outliers.

($r = 0.20$, $P = 0.52$), indicating that the entire distribution of births had shifted over time.

Mean parturition date during the period of roughly stable pup production (1987–91) averaged 6 days earlier than during the declining period (1992–96, Table 2). However, mean age of parturient females also increased from 6.4 years during the stable period to 10 years during the declining period. Although some increase in the age of females in the population is expected, the rapid increase during the period of population decline seems to have been driven mainly by lack of recruitment of females 4–6 years of age (Fig. 3). As maternal age was positively correlated with parturition date (Pearson's $r = 0.36$, $n = 91$, $P = 0.001$), an ANCOVA was conducted to determine the influence of time period on parturition dates, once the effect of maternal age had been statistically removed. Having accounted for the change in maternal age between periods, mean parturition date was significantly later during the period of declining pup production than during the stable period (ANCOVA, period $F_{1,88} = 7.1$, $P = 0.009$).

The change in parturition date was further explored using longitudinal data of 27 females of known-age that had given birth to \geq two pups in each time period (stable vs declining pup production). Among these females, mean parturition date was 4 days later during the period of declining production compared with the period of stable production. Again this difference in mean parturition date was owing to time period rather than age (repeated-measures ANCOVA with mean age as a time-varying covariate: period $F = 10.5$, $P = 0.01$; age $F = 2.5$, $P = 0.18$). This corroborates the conclusion drawn from the cross-sectional data that time period was more important than maternal age in determining parturition date.

Table 2. Comparison of life-history traits (mean \pm SE) between periods of stable (1987–91) and declining (1992–96) population of harbour seals *Phoca vitulina* on Sable Island

Trait	1987–91 (n)	1992–96 (n)	P t-test (d.f.)	P ANCOVA (d.f.)
<i>Female</i>				
Parturition date	22 May \pm 0.3 (286)	28 May \pm 0.3 (390)	< 0.001 (674)	< 0.001 ^a (1, 88)
Age (years)	6.4 \pm 0.30 (44)	10.0 \pm 0.52 (47)	< 0.001 (89)	NA
Maternal postpartum mass (kg)	85.3 \pm 0.70 (136)	84.8 \pm 0.84 (108)	0.64 (242)	0.25 ^b (1, 72)
Lactation duration (days)	23.7 \pm 0.33 (87)	24.2 \pm 0.36 (88)	0.31 (173)	NA
Weaning date	June 15 \pm 0.4 (87)	June 21 \pm 0.5 (88)	< 0.001 (173)	< 0.001 ^a (1, 97)
<i>Pup</i>				
Birth mass (kg)	10.8 \pm 0.1 (207)	11.0 \pm 0.9 (168)	0.14 (373)	0.74 ^b (1, 78)
Rate of mass gain (kg/days)	0.62 \pm 0.02 (48)	0.59 \pm 0.01 (68)	0.08 (114)	0.14 ^c (1, 97)
Weaning mass (kg)	24.6 \pm 0.38 (76)	25.1 \pm 0.37 (78)	0.37 (152)	0.68 ^c (1, 97)
Relative birth mass (%)	12.8 \pm 0.13 (136)	13.0 \pm 0.13 (108)	0.40 ^d (242)	0.62 ^e (1, 72)
Relative weaning mass (%)	29.8 \pm 0.48 (47)	29.7 \pm 0.43 (53)	0.91 ^e (98)	N.A.

^a Controlling for maternal age.

^b Log-transformed data, controlling for log maternal age.

^c Log-transformed data, controlling for log maternal postpartum mass.

^d Arcsine-transformed data.

^e Arcsine-transformed data, controlling for log maternal age.

NA No applicable covariates.

Interannual variation in body mass and pup rate of mass gain

Both mean birth mass of pups and mean MPPM varied over the 10-year period, but without evidence of a trend (Fig. 4) and there was no significant correlation between these traits (Spearman $r=0.07$, $n=10$, $P=0.85$). Previously we have shown that birth mass is correlated with maternal age (Ellis *et al.*, 2000). After controlling for the effect of maternal age, there was no significant interannual variation in either pup birth mass (ANCOVA, $F_{9,70}=1.3$, $P=0.25$) or MPPM (ANCOVA, $F_{9,64}=1.7$, $P=0.10$). Mean rate of pup mass gain also did not differ significantly among years (Fig. 4, ANCOVA with log MPPM as covariate, $F_{8,90}=1.8$, $P=0.10$). Weaning mass ranged from 23.7 kg in 1991 to 26.2 kg in 1992, but did not differ significantly among years, once the effect of MPPM had been removed (ANCOVA with log MPPM as covariate, $F_{8,90}=1.7$, $P=0.11$). Mean pup weaning mass and rate of mass gain also did not differ by time period, before or after controlling for maternal postpartum mass (Table 2).

Mean duration of lactation did not vary by time period (Table 2). Mean weaning date was significantly higher in the period of declining numbers, as would be expected from the later mean parturition dates, but similar lactation durations (Table 2). After controlling for effects

of maternal age, neither relative birth mass nor relative weaning mass varied among years or between periods (Table 2).

DISCUSSION

Demographic trends

The rapid decline in the number of harbour seal pups born on Sable Island during the 1990s has not previously been observed in this population. Counts from Boulva & McLaren (1979) in the early 1970s and the first cohort tagging by the Department of Fisheries and Oceans (DFO) in the late 1970s suggest that pup production was roughly stable during this period at *c.* 350 births/year (Fig. 1). An interesting feature of the annual pup production censuses is the three large between-year increases in production (1977–78, 1980–81 and 1982–83; Fig. 1). In each case production increased by > 17% between years. Based on vital rates for harbour seals given in Boulva & McLaren (1979), it is unlikely that these increases were generated from a closed Sable Island population. Thus, there seems to have been several immigration events to Sable Island around 1980. Although the number of pups born on Sable steadily increased during the 1980s, by 1997 pup production had declined

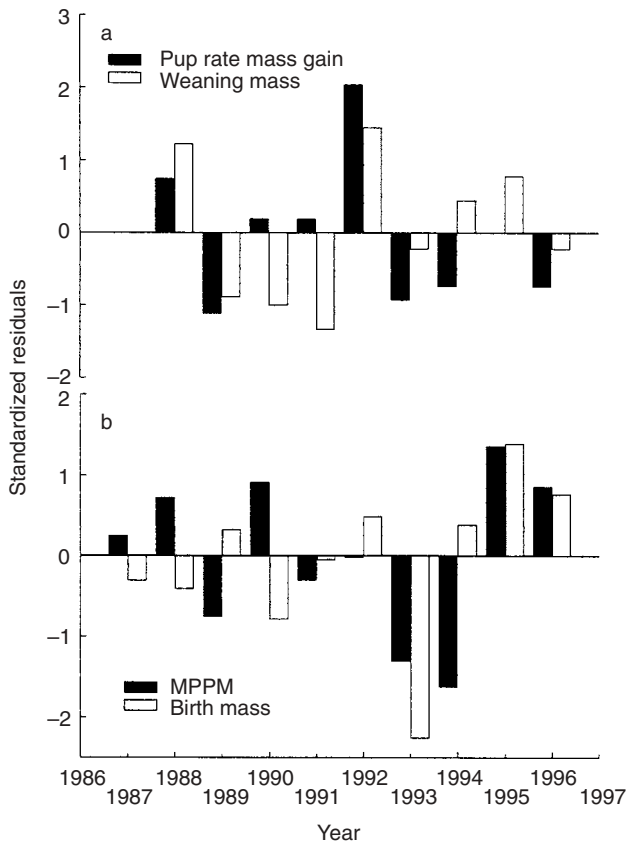


Fig. 4. Interannual variation in standardized residuals (residuals of overall average/SD) of harbour seal maternal postpartum mass (MPPM), pup birth mass, rate of pup mass gain and weaning mass during 1987 to 1996.

by 95%. The numbers of juveniles, adult females and males also declined significantly during the 1990s. Thus, all components of the population were affected. With the further decline in pup production in 2001 and 2002, it seems inevitable that Sable Island will cease to be a breeding colony for harbour seals.

Severe population crashes are common in populations of large mammals (Young, 1993) and dramatic declines in pinniped populations have been observed that cannot be accounted for by direct or indirect exploitation (e.g. Loughlin, Perlov & Vladimirov, 1992). There are also other examples of rapid declines in harbour seal populations. For example, the number of harbour seals at Tugidak Island, Alaska declined by *c.* 85% over a 12-year period, for reasons that were not apparent (Pitcher, 1990). Samples taken in the mid 1970s indicated that pregnancy rates for mature animals were high and thus reproductive failure seemed an unlikely cause. Although disease could have contributed to the decline, there were no reports of unusually large numbers of dead or sick animals on Tugidak Island during that period. The decline was also apparently not the result of emigration to nearby areas (Pitcher, 1990). Thus, substantial mortality must have occurred over these periods to account for the rapid rates of decline. Thompson, van Parijs & Kovacs (2001)

reported declines in harbour seal numbers ranging from 64% to 84% at several sites in Orkney, Scotland. The cause of those declines remains unclear, although, similarly to Sable Island, there was evidence of reduced local recruitment.

Life-history traits

Despite the observed changes in the harbour seal population over the course of our study, there were no significant interannual trends in most life-history traits studied, including MPPM, pup birth mass (Ellis *et al.*, 2000), rate of pup mass gain during of lactation, or pup weaning mass (Bowen, Boness, Iverson *et al.*, 2001). Harbour seal females must forage during lactation to augment body energy stores used for milk production and maternal maintenance metabolism (Bowen, Boness, Iverson *et al.*, 2001). Thus, food shortage just before or during lactation could result in reduced maternal or offspring mass, reduced rates of offspring mass gain and hence weaning mass. The lack of significant interannual variation in these maternal and offspring traits indicates that lactating females were able to compensate for interannual changes in food availability that may have occurred. Thus, it does not seem that food shortage during the breeding season contributed to the population decline.

Food shortage at other times of the year may have contributed to the decline because our sample of females that gave birth may not be representative of those that initially became pregnant. Adult females that were known not to have given birth within a breeding season were rarely seen hauled-out in our study area. As we had little opportunity to sample non-pregnant females, changes in fecundity could have contributed to the decline in pup production. Evidence that this might have occurred comes from our weekly beach surveys and anecdotal observations during the breeding season. During the first year of the surveys, 1991, there was a close correspondence between the counts of pups and females. However, between 1992 and 1994, pup counts were lower than female counts, suggesting a decline in birth rate. It was during this period that females on the beach in the study area that seemed not to have fattened for reproduction were also occasionally noted. Together these observations provide some support for reduced fecundity during some years of the decline.

One life-history trait that changed significantly over the study period was parturition date. In mammals, photoperiod primarily controls the timing of birth (Follett, 1982). In pinnipeds, including harbour seals (Temte *et al.*, 1991; Temte, 1994), photoperiod is thought to initiate embryonic implantation and all females in a population should implant at about the same time to ensure synchronized reproduction (Boyd, 1991). Although photoperiod plays a key role in the timing of these events, parturition date can be influenced by food availability through changes in gestation length. In Antarctic fur seals *Arctocephalus gazella*, parturition dates were delayed

owing to longer pregnancies in years of low food availability (Boyd, 1996). Mean birth date for this species can vary by up to 10 days (Lunn & Boyd, 1993) as a result of variability in food abundance. Also, the number of young born was reduced in years where births were later on average (Lunn & Boyd, 1993), suggesting that nutritional stress changes the timing of birth and reduces the probability that females will carry a foetus to term (Boyd, 1996). The mean birth date of harbour seals on Sable Island in 1996–2000 was 13 days later than in 1990 and at least 6 days later than in the rest of the 1990s and 1980s. This increasing trend in birth dates may indicate decreasing food availability for pregnant females. The apparent reduction in fecundity between 1992 and 1995 (Fig. 1) provides further support for this hypothesis.

What caused the population decline?

Sharks are a documented source of natural mortality on harbour seals in eastern Canada (Boulva & McLaren, 1979; Brodie & Beck, 1983; Bowen, Boness & Iverson, 1999; Lucas & Stobo, 2000; Bowen, Boness, Iverson *et al.*, 2001). The data presented by Lucas & Stobo (2000) provide compelling evidence that shark-inflicted mortality was a major cause of the decline in the Sable Island population. There was a rapid increase in the minimum shark-inflicted mortality rate of pups from < 10% to between 30% and 50% after 1993. Even more significantly, the estimated total mortality from sharks on adults was greater than that of pups during the same period, and adult females were killed disproportionately. Between 1993 and 1997, all adult female harbour seals killed by sharks between March and June (the pre-pupping period), whose reproductive status could be determined, were carrying foetuses at the time of death. Further, the minimum number of females killed in 1994, 1995 and 1996 (i.e. 42, 52 and 32, respectively) can account for about half of the observed decline in the number of pups born in the following years. Thus, there can be no doubt that shark-inflicted mortality accounted for a considerable fraction of the decline of harbour seals on Sable Island (Lucas & Stobo, 2000). These minimum mortality estimates no doubt underestimate the number of harbour seals killed by sharks. However, unless these minimum estimates are substantial underestimates of the actual mortality caused by sharks, there remains a portion of the decline that requires another explanation.

One possibility is that there was emigration of adult females or female recruits (Lucas & Stobo, 2000). Given that there is some evidence for immigration to Sable in the early 1980s, certainly emigration to mainland colonies is possible. Females might have emigrated in response to increased interspecific competition with grey seals (see below). Unfortunately, there are no long-term data from Canadian mainland colonies with which to test this hypothesis. A related explanation is that increased human disturbance, including life-history studies, which began in 1987, may have caused females to abandon Sable Island (Lucas & Stobo, 2000). The duration of research activity

on the North Beach was variable, but without trend, but the number of researchers did increase to eight in some years from four in 1987. Although there was variation and an overall increase in the number of researchers, this had little effect on the number of seals captured in the study area from 1988 to 1991.

There are several lines of evidence that would indicate that disturbance was not a significant cause of the decline. First, the life-history studies were confined to the North Beach and numbers continued to increase for several years after the research began. Second, harbour seal females on Sable Island are quite tame, enabling researchers easily to approach mothers and their pups on foot. After release from capture, females and their pups often stayed in the area apparently little disturbed by the presence of researchers. Finally, during the decline, numbers of pups were lost most rapidly on the South Beach where little research was done (Fig. 1). Thus, although emigration cannot be eliminated as having contributed to the decline, no evidence was found to suggest that human disturbance was a significant factor.

Natural die-offs of carnivores tend to be the result of diseases (Harwood & Hall, 1990; Young, 1993). It is now well known that northern European harbour seal populations were reduced substantially by morbillivirus epizootic in the late 1980s (Heide-Jørgensen *et al.*, 1992). Routine screening for diseases was not conducted; however, during the period of decline on Sable Island there were no unusual signs of disease in this population as judged by the presence of carcasses or moribund animals.

Although food seems not to have been limiting during the breeding season, as noted above, reduced fecundity and increased mortality could have been caused by broader ecosystem changes. Cooling of ocean temperatures on the eastern Scotian Shelf over the study period has been implicated in shifting distributions of fish and invertebrates, with an increased abundance of colder water species (Frank, Simon & Carscadden, 1996; Zwanenburg *et al.*, 2002). Continuous plankton recorder data of phytoplankton colour index, diatoms and *Calanus* sp. show significant decadal scale changes between 1961 and 1998 (Sameoto, 2001), with a significant influx of arctic species during the 1990s. These cooler ocean temperatures may also have resulted in an increase in the numbers of cold-water sharks, such as the Greenland shark *Somniosus microcephalus*, near Sable Island.

Harbour seals consume a variety of small pelagics, such as herring *Clupea harengus* and sandlance *Ammodytes dubius*, gadoids and flatfishes (Bowen & Harrison, 1994). Despite the decrease in some gadoid fishes on the Scotian Shelf during the 1990s (e.g. Mohn & Bowen, 1996), the increases in small pelagic fishes may have resulted in an overall increase in the abundance of harbour seal prey during the period of rapid decline. However, analyses of stomach and scat contents have shown strong dietary overlap between harbour and grey seals, both inshore (Bowen & Harrison, 1996) and on Sable Island (Bowen & Harrison, 1994). The grey seal population on Sable Island has been growing exponentially for some 40 years with a doubling time of about 6 years. Large numbers of grey

seals haul out on and forage in the waters surrounding Sable Island throughout the year. At the beginning of the harbour seal decline, grey seals would have outnumbered harbour seals by > 20: 1 and by the end of the 1990s by > 500: 1. Thus it seems probable that interspecific competition with grey seals for food must have increased during the 1990s. Although we have no direct evidence that there was competition for food, the increasing trend in parturition dates and evidence of reduced fecundity and female recruitment are consistent with this hypothesis.

Thus, it seems probable that the decline in the harbour seal population on Sable Island resulted from the combined effects of shark predation and interspecific competition for food. Although the relative effect of these two factors must remain tentative, they are both linked with the rapidly expanding grey seal population. Grey seals are also a major target of shark predation at Sable Island (pers. obs.) and presumably the sharks frequenting the waters near Sable Island were principally attracted to the island because of the large grey seal population and not because of the 10 times smaller harbour seal population. In fact, the timing of shark predation on grey seal pups may have influenced the effects on harbour seals. Thousands of weaned grey seal pups enter the sea around Sable Island for the first time in February. Undoubtedly, hundreds of grey seal pups are taken at this time by sharks. This is also when sharks killed many adult female harbour seals at Sable Island (Lucas & Stobo, 2000). If our interpretation is correct, these data illustrate the fragile nature of small populations to ecosystem changes.

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