Shark-inflicted mortality on a population of harbour seals (*Phoca vitulina*) at Sable Island, Nova Scotia

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Abstract

Shark-inflicted mortality on harbour seals *Phoca vitulina* on Sable Island, Nova Scotia, was studied from 1980 to 1997, based on carcasses washed up on shore. During this period, pup production declined dramatically from over 600 in 1989 to 40 in 1997. Between 1980 and 1992, pup deaths only were recorded, and only during the May–June pupping period, while deaths in all age groups were recorded year-round between 1993 and 1997: 458 pups, 23 juveniles and 241 adults were found. Shark-inflicted mortality in pups, as a proportion of total production, was under 10% during 1980–93, roughly 25% in 1994–95, and increased to 45% in 1996. Shark-inflicted mortality occurred in all months except December, January and February, with c. 80% of the pups killed during the pupping period, and 97% of the adults killed outside the pupping period. The decline in pup production was not only a result of reduced recruitment owing to pup mortality. A greater proportion of reproductive females than males was killed. We estimate that shark-inflicted mortality on pups and adult females reduced pup production on Sable Island by 43 to 154 pups annually between 1993 and 1997. Our results indicate that sharks are having an impact on Sable Island harbour seals, possibly to the extent of limiting population growth, or contributing to the observed population decline. Potential reasons for this increased mortality are discussed.

Key words: sharks, predation, mortality, *Phoca vitulina*

INTRODUCTION

Factors influencing at-sea mortality of marine mammals are difficult to assess. LeBoeuf & Crocker (1996) reported that an average of 46% of young-of-the-year northern elephant seals *Mirounga angustirostris* from the Ano Nuevo rookery die at sea, but were unable to determine the cause(s) of this mortality. Influences and assumptions on mortality, based on sampling that is spatially and temporally limited, and potentially biased, are often used in attempts at modelling the dynamics of the populations of pinnipeds (McLaren & Smith, 1985) and other marine mammals. The estimation of predation, as a component of mortality, has been difficult to achieve because of even greater limitations of data. Estes *et al.* (1998) have suggested that the decline in western Alaska sea otters *Enhydra lutris* is the result of predation by killer whales *Orcinus orca*. Their provocative analysis was heavily dependent on assumptions relating to population size, the caloric requirements of killer whales and the caloric content of sea otters. Shark predation on pinnipeds is a well-documented phenomenon (Riedman, 1990), with early reports of shark predation on harbour seals *Phoca vitulina* in the northeast Pacific being given by Scheffer & Slipp (1944), based on shark stomach contents. Although shark predation may exert significant regulation on population growth, there are few quantifiable data available to test the impact at either the cohort or population level.

Shark-inflicted mortality has been suggested as a significant factor in the population dynamics of the Hawaiian monk seal *Monachus schauinslandi* (Kenyon, 1981; Hiruki, Gilmartin *et al.*, 1993). Hiruki, Stirling *et al.* (1993) concluded that such injuries to female Hawaiian monk seals adversely affected reproductive success by reducing offspring survival, but they did not comment on the impact on cohort size or overall population abundance. Recent studies at French Frigate Shoals, Hawaii (1995–98), suggested that shark-inflicted injuries were responsible for 20% of the deaths or disappearance of nursing and weaning monk seal pups. Most of the predation occurred near one pupping area where c. 60% of the French Frigate Shoals monk seals...
Sharks may have a pervasive influence on the behaviour and biology of many pinniped species. Shark-inflicted mortality has been suggested as a factor in the evolution of pinniped behaviour such as prolonged suckling in the Galapagos fur seal Arctocephalus galapagoensis (Bonner, 1984). The abnormal timing of the breeding season in northern elephant seals on the Farallon Islands (Ainley, Henderson et al., 1985), and their diving patterns (LeBoeuf & Crocker, 1996) may be, in part, adaptations to reduce encounters with near-surface predators. Shark predation on breeding harbour seals is known to be common at the South Farallon Islands, California (Ainley, Strong et al., 1981; LeBoeuf, Riedman & Keyes, 1982; Stewart & Yochem, 1985; Long et al., 1996), but the interactions are not well understood. Ainley, Henderson et al. (1985), suggested increases in white shark Carcharodon carcharias sightings around the Farallon Islands were more probably the result of increases in the numbers of northern elephant seals in that area than increases in white sharks or environmental change; more recently Long et al. (1996) have reaffirmed that suggestion. But as McLaren & Smith (1985) suggest, shark predation as an agent of population regulation, needs more exploration. As support for this contention, they refer to the suggestion of Boulva & McLaren (1979) that harbour seal population growth on Sable Island may have been constrained by shark predation and the counter suggestion by Brodie & Beck (1983) that the reduced shark abundance in that area at the same time allowed the Sable Island grey seal population to expand.

Grey seals Halichoerus grypus and harbour seals breed on Sable Island, Nova Scotia, and are year-round residents (Mansfield & Beck, 1977; Boulva & McLaren, 1979; Stobo & Zwanenburg, 1990). The island (44°N, 60°W) is a 40-km-long sand bar in the north-west Atlantic, located 170 km south-east of mainland Nova Scotia, and 40 km north of the edge of the continental shelf. Between December and April, we have seen a few mostly immature ringed seals Phoca hispida, harp seals Phoca groenlandica and hooded seals Cystophora cristata resting on the beaches of the island. Although we and others (Boulva & McLaren, 1979; Brodie & Beck, 1983) have observed shark predation on all five species in the Sable Island area, the harbour seal population has the greatest proportion of observed shark-inflicted mortality on pups and adults.

Earlier studies indicated that shark predation on Sable Island harbour seals was only occasionally high, and primarily on pups (Boulva & McLaren, 1979; Brodie & Beck, 1983). Boulva & McLaren (1979) reported that wounded and dead seals, severely mutilated by shark bites, were seen most frequently on the island between late July and late October. In this study, we report the incidence of shark attacks on harbour seal pups on Sable Island during the last 17 years, and on all age classes during 1993–97. We also report on a dramatic increase in predation on adult harbour seals during 1993–97. The long sand beaches and the lack of terrestrial scavengers or predators on the island facilitate the finding of carcasses of dead seals and provide an opportunity to report minimum mortality levels by season and seal age. This, in conjunction with long-term monitoring of pup production, allows us to comment on the impact of shark predation on the harbour seal population.

**METHODS**

This study was based on shoreline surveys of carcasses washed ashore on Sable Island. It is probable that some carcasses were not found because the animals were consumed entirely, were not washed ashore, or were buried by windblown sand soon after beaching. The numbers presented in this paper are therefore minimum estimates of shark-inflicted mortality.

Data on shark-inflicted mortality of harbour seal pups were collected during the pupping season from 1980 to 1996, and between 1993 and 1997, data for all ages were collected year-round. Data on pups were collected primarily during annual tagging programmes. During the pupping season (May–June) between 1978 and 1996, almost all harbour seal pups born on Sable Island were marked by applying Jumbo Rototags (Dalton Supplies Ltd, Henley-on-Thames, Oxfordshire, UK) to the interdigital web on the hind flipper. The tags were numbered on one side, with a ‘reward’ notice and mailing address printed on the other side. Different coloured tags were used each year to facilitate visual identification of cohorts in subsequent years. Harbour seal pups are mobile, frequently enter the water within a few hours of birth, and attempt to escape into the water when approached. Thus we used sequentially numbered tags to mark each pup on initial capture to facilitate complete monitoring of pup production and eliminate the possibility of double-counting.

During the 1980–82 pupping seasons, the island’s perimeter was usually surveyed every other day, and during the 1983–96 seasons usually once a day, using all-terrain vehicles. The long uninterrupted beaches of Sable Island and the speed of these vehicles allowed capture of pups before they could escape into the water. The naïve young (usually <2 days old when tagged) were relatively easy to capture; all dead pups were counted and marked with paint to avoid duplicate counting. As a result of the frequency of circuits over the pupping beaches, probably few pups were missed. The occurrence of only 1 or 2 newborn during the last several days of the annual field trips suggests few pups would have been born afterwards. The 1997 pup production was estimated from visual counts made during surveys conducted on several consecutive days at the end of the pupping seasons.

Causes of mortality for 1978 and 1979 were not recorded. The data from 1980 to 1983 were obtained from the onset of pupping until roughly the end of the pupping period. Between 1983 and 1993, observations...
were progressively extended into the post-pupping period, until by 1993 the full period from birth to completion of weaning for each pup cohort was monitored.

The frequency of the surveys around the island differed during, and following, the pupping season, and the duration of the field seasons during the pupping periods varied between years. Values are provided for total mortality observed, but for a common reference period for all years, the mortality values from the start of pupping inclusive of 11 days after the median pupping date for each year (the duration of the shortest field season) are also provided.

Collection of data on shark-inflicted mortality for all age groups of harbour seals on Sable Island began in 1993 when year-round surveys were carried out in addition to the ongoing pup-tagging programme of May–June. From January 1993 to December 1997, the beaches were surveyed for pups, immatures, and adults killed by sharks, on average once every 5 days, except for 2–3 periods each year of 2–4 weeks, when no surveys were carried out. Survey effort was roughly equal in all 5 years, with little seasonal bias. Information on time of kill, location, age, sex, condition, reproductive status and presence/absence of tags, was collected. Carcasses were marked, or removed from the beach, to prevent duplicate records. Carcasses were found in various states, from very fresh (bleeding and with a core temperature warm to the bare hand), to partly decomposed and scavenged at sea. For decomposed and scavenged carcasses found during the 1993–97 period death was assumed to have occurred in the previous month (e.g. a partly decomposed carcass washed ashore on 6 June would be considered as a May kill). This adjustment allows for monthly values of total numbers over the 5 years of the study even though there were several 2- to 4-week periods during each year when surveys were not carried out.

Shark-killed seals examined between 1993 and 1997 were divided into 3 age groups (pups, juveniles, adults), with age being assigned on the basis of the calendar year. For example, a seal born in May 1993 and killed before the end of December 1993 would be assigned age 0; if killed between January and the end of December it would be assigned age 1. Seals killed during their second (age 1) and third (age 2) calendar year of life were considered juveniles, and seals killed during or after their fourth (age 3 and older) calendar year were considered adult. For untagged seals, age group was estimated using body size. While there could have been some difficulty in accurately assigning age group to small untagged individuals, all but 2 of the 23 juveniles were tagged, and thus of known age (see Tables 3 and 4). For the untagged animals, we compared their size and length to known-age animals. The 2 untagged animals classed as juveniles were, in size and length, clearly 1 or 2 years old. All of the untagged animals that we classed as adults had body sizes and lengths that indicated they were older than age 3.

**RESULTS**

Our examination of shark predation at Sable Island is based on data collected until 1997. Although beach surveys continued throughout 1998, only 10 shark-
killed harbour seals were found: nine adults (seven male, one female, and one of unknown sex), all between April and August, and one 1998 pup, in June.

Total observed annual pup production and mortality due to sharks and other causes are given in Table 1. During 1980–97, 458 shark-killed pups were found. The 1980 value for pupping period mortality is abnormally high because of deaths caused by a domestic dog before its removal from the island. Of the 77 that died in this year, 15 were known dog kills, and 25 of the remainder were attributed to sharks, but the shark-inflicted mortality may be biased upwards because of insufficient diligence in ascertaining the cause of mortality; the remainder could not be assigned to a specific cause.

Total observed mortality and the mortality observed during the common reference period (from the start of pupping inclusive of 11 days after the median pupping date) show similar trends (Fig. 1), indicating that most of the observed shark-inflicted pup mortality occurred during the pupping period. We therefore decided to present our analyses based on total observed annual mortality.

Between 1980 and 1989, pup production increased to a peak of 625 pups (Table 1), and subsequently decreased to low levels in 1997. Total observed annual mortality, as a percentage of total production, from all causes was 23% in 1980, then decreased to < 15% before 1994 (Fig. 2); subsequently it increased to 50%. Much of the increase in recent years was owing to sharks, from <10% of total observed annual production between 1980 and 1993 to 27.8% and 23.9% in 1994 and 1995, respectively (Fig. 2). In 1996, sharks killed > 45% of all pups born. Shark-inflicted pup mortality, as a percentage of total mortality ranged from 27% to 60% during 1984–92, increasing between 1993 and 1996 to c. 90% annually. Shark-inflicted mortality was, however, not proportional to pup production. Predation on pups did not increase as pup production increased, but when pup production declined by almost 100 pups per year between 1991 and 1996, shark predation increased for most of that period (Table 1).

Between 1993 and 1997, 470 harbour seals of all ages were killed by sharks (Table 2). The trends in mortality over that period (Fig. 3) differed by age group. While pup mortality during the 5 years of observation peaked in 1994 and declined subsequently, total adult mortality
increased from 1993 to 1995, then declined. Relatively little juvenile mortality was observed, which corresponds with our observations that few juvenile harbour seals are on the beaches around Sable Island throughout the year. Total adult mortality from sharks was greater than that of pups during the 1993–97 period (Table 2).

Of the total shark-killed seals, sex could be identified in 80.6%. There was no selective mortality of pups by sex in any year between 1993 and 1997 ($\chi^2 = 0.14$, 0.08, 0.64, 0.02 and 1.30; d.f. = 1, $P = 0.05$) with almost equal numbers of male and female pups killed (50.8% and 49.2%, respectively). More male than female juveniles were killed (70.0% and 30.0%, respectively), but the numbers were too few to warrant a statistical examination of vulnerability by sex. For adults, there seemed to be a selection for females (Fig. 3), although a significant difference occurred only in 1994 and 1995 ($\chi^2 = 29.1$ and 9.5, respectively; d.f. = 1, $P = 0.05$). Overall more adult females than males were killed (64.6% compared to 34.4%), and in each year adult female mortality exceeded that of males. Since the sex of some of the seals could not be determined, it is possible that this difference could occur if males tended to be over-represented in the ‘unknown sex’ category. However, even if all adults of unknown sex were assumed to be males, in every year except 1993 a positive bias towards females would remain.

There were 264 adults and juveniles (Table 2) killed; of these, 33 were too damaged or decomposed to determine tagging status; 36 bore no evidence of having been tagged; 43 showed tag loss, demonstrated by a neat round tag hole in hind flipper tissue; and 152 bore tags, parts of broken tags, or brands, that showed they had been marked, either as pups or adults, on Sable Island during various studies carried out by Fisheries & Oceans Canada. Of these animals, 58 could be identified as having been tagged or branded as pups (before weaning) on Sable Island, and thus the age of this subset of animals could be established (Table 3). Over 70% of the mortality of animals aged 1 year or older was represented by animals <10 years of age. The oldest males killed were 9 years old, and the oldest females were 16 years old. In the age 1 year and older female group, most deaths (65.5%) were females that were fully recruited to the reproductive component of the population (age 7 years and older).

Data from the 1993–97 survey show that harbour seals were killed by sharks during all months except December, January and February (Fig. 4). Most of the shark-inflicted pup mortality occurred during the May–June pupping season, with a cumulative mortality of 167 pups (81.1%) during this period over the 5 years (Table 4). The lack of pup mortality for March–April is an artifact of our ageing criterion; pups were designated 1-year-old (i.e. juveniles) as of 1 January following their birth year. Three of the five juveniles killed in March or April were actually <12 months old. Most juvenile mortality occurred during late summer and autumn (73.9%); <5% of juvenile mortality occurred during the pupping period. Adult mortality exhibited a pattern similar to that for juveniles. Almost all the adult mortality (97%) occurred outside of the pupping period, mostly during the post-pupping period (75%); among these adults, 93.6% of the males, and 98.0% of the females were killed during this period (Table 4).

### Table 2. Harbour seals killed on Sable Island by sharks between 1993 and 1997. M, males; F, females; U, animals too mutilated for sex to be determined (unknown)

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<tbody>
<tr>
<td>Pups</td>
<td>6</td>
<td>10</td>
<td>34</td>
<td>38</td>
<td>70</td>
</tr>
<tr>
<td>Juveniles</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>7</td>
<td>4</td>
</tr>
<tr>
<td>Adults</td>
<td>3</td>
<td>6</td>
<td>7</td>
<td>5</td>
<td>4</td>
</tr>
<tr>
<td>Totals</td>
<td>6</td>
<td>10</td>
<td>34</td>
<td>38</td>
<td>70</td>
</tr>
</tbody>
</table>

Fig. 3. Numbers of harbour seal pups (age 0), juveniles (ages 1–2) and adults (ages 3 and older), by sex, killed annually by sharks between 1993 and 1997.
During the last 5 years of the study, of the 34 adult females killed during March–June (pre-pupping and pupping periods), 12 carcasses were extensively damaged, and reproductive status could not be determined. The remaining 22 carried foetuses. The reproductive status of females killed between July and November was not examined since pregnancy could not be assessed because of the potential effect of delayed implantation.

**DISCUSSION**

All the data presented here are based on seals killed by sharks and washed ashore, and thus represent minimum estimates of shark-inflicted mortality. Some seals may have been killed far enough offshore that carcasses were not beached, and a proportion of smaller (i.e. younger) seals may have been consumed entirely, but we cannot provide estimates of numbers. Long et al. (1996) suggested that northern elephant seal and harbour seal pups may be ingested whole by great white sharks based on the observations of LeBoeuf et al. (1982) that the stomach contents of white sharks often included large portions of pinniped bodies. But we observed many harbour seal pup carcasses washed ashore with largely intact vertebral columns, suggesting that many were not entirely, or even largely, consumed. We are still investigating the species of shark(s) involved. Sable Island is a large sand bar with very gradual sloping beaches with an intertidal zone, which often extends for 30–40 m. Usually when harbour seal pups are observed in the water, they are in the zone between high and low tide levels. Consequently, most of the shark attacks on pups would occur in these shallow water areas. Recent studies (e.g. Osborne & Greenwood, 1992) suggest that incident waves associated with shallow water areas, during the generally fairweather conditions of summer, tend to cause shoreward transport of sediment near the seabed. Since pup carcasses sink to the bottom, this phenomenon could also result in them being washed ashore. Also, tidal currents around Sable Island are semi-diurnal ellipses rotating 360° in a clockwise direction over a tidal cycle (Anon, 1983), thus keeping the carcasses in the vicinity of the island. These physical and environmental features might cause the carcasses to

<table>
<thead>
<tr>
<th>Age Group</th>
<th>March–April</th>
<th>May–June</th>
<th>July–Nov.</th>
<th>Total no.</th>
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<tbody>
<tr>
<td>Pups</td>
<td>n/a a</td>
<td>167</td>
<td>39</td>
<td>206</td>
</tr>
<tr>
<td>Juveniles</td>
<td>5</td>
<td>21.7</td>
<td>4.4</td>
<td>17</td>
</tr>
<tr>
<td>Adults</td>
<td>54</td>
<td>22.4</td>
<td>8</td>
<td>179</td>
</tr>
<tr>
<td>Totals</td>
<td>59</td>
<td>12.6</td>
<td>37.4</td>
<td>235</td>
</tr>
</tbody>
</table>

* a Ages based on calendar year. Since pupping commences in May, no pups (age 0) exist between January and May.

![Fig. 4. Seasonal distribution of shark-inflicted mortality on harbour seal pups (age 0), juveniles (ages 1–2) and adults (ages 3 and older) between March and November. No shark-inflicted mortality was observed during December, January and February.](image-url)
wash ashore to a greater extent than in many other island rookeries.

Harbour seals killed by sharks have been observed on Sable Island since the 1970s (Boulva & McLaren, 1979; Brodie & Beck, 1983). The predation reported in these studies was primarily on pups, but this may have been a result of most observations being made during the harbour seal pupping period. While shark predation on pups increased from <10% in 1993 to >45% in 1996, adult mortality exceeded pup mortality overall (241 vs. 206), and annually, in 3 of the 5 years of full-year observations. These observations are in contrast with those of Ainley, Henderson et al. (1985) and Long et al. (1996), who reported a greater vulnerability of pups. In agreement with these authors, our observations do, however, show a season effect. Most of the Sable Island harbour seal pup mortality occurred during the pupping and weaning period (mid-summer), with that of adults primarily occurring outside the pupping period. This shift in prey size seasonally suggests that the decline in pup mortality outside of mid-summer may be the result of a shift in pup distribution rather than a change in the abundance of sharks in the area.

Pup production of Sable Island harbour seals exhibited a gradual and consistent increase between 1980 and 1989, followed by a dramatic decline between 1989 and 1997. Shark-inflicted pup mortality, however, was much more variable (Table 1), with a decline during the peak pup production years (1985–89) and an increase during the subsequent decline. This pattern suggests that shark-inflicted pup mortality was also influenced by factors other than harbour seal pup availability (i.e. production). We do not have the data to attempt correlations with environmental factors or shark abundance. However, pup production by the grey seal population breeding on Sable Island was increasing at over 12% annually during the same period (Stobo & Zwanenburg, 1990; Mohn & Bowen, 1996). Ainley, Henderson et al. (1985) did not find a correlation with environmental variables. However, Ainley, Henderson et al. (1985) and Long et al. (1996) reported an increase in shark attacks with increased abundance of pinnipeds, the overall increase being due to one of several cohabiting species. But although Long et al. (1996) concluded that an increase in white sharks had occurred, Ainley, Henderson et al. (1985) suggested that only a few sharks may have been responsible and that the increase in attacks was related to availability of prey and an increase in the size of the individual predators over time. They suggested that a few young white sharks may have found the growing food source and continued to use it as they grew larger. In a somewhat similar manner, Estes et al. (1999) suggested that a few apex predators (killer whales) might have been the cause of a large decline in the abundance of sea otters in Alaska.

It is probable that the continued presence of sharks in the Sable Island area is not the result of harbour seal abundance. Predation on the combined age groups of harbour seals was highest in 1994, but pups killed as a proportion of total mortality of all age groups declined each year since 1994. This is consistent with the decrease in pup production, beginning in the early 1990s. But while predation on adult harbour seals increased in 1994 and remained high for 2 years, adult mortality declined in 1997, and in 1998 we observed only nine adults killed. During the same period, however, we observed consistently high predation on grey seals. The diminishing numbers of shark-killed harbour seals found is therefore more probably the result of a decline in the numbers of harbour seals in the area than to a decline in shark activity. It is possible that the adult harbour seals remaining are those that are more wary of sharks and thus able to avoid attacks, but Ellis (1998) reported declines in the numbers of males, juveniles and pups in the Sable Island population between 1991 and 1996, and in females from 1993 to 1996. These observations were based on weekly counts of males, females and pups observed on, or near, a 24-km section of beach on the north side of Sable Island during the pupping season. Although this study was restricted spatially and temporally, and the data did not include shark kill counts, the observations of reduced numbers are consistent with our study.

Brodie & Beck (1983) suggested that depletion of the shark population because of commercial fishing may have been a factor in the increased production observed for Sable Island grey seals. Cessation of those fisheries in the mid-1970s may have resulted in a recovery of the shark populations in the area, leading to the increased predation observed on harbour seals, but there are no quantitative estimates of shark abundance, or information on the species of sharks involved, to assess that possibility. The inter-annual variation and the lack of an increasing trend in shark-inflicted pup mortality between 1980 and 1989 suggest that a complex interaction exists between the sharks and their harbour seal prey. Boulva & McLaren (1979) reported that wounded and dead seals, severely mutilated by shark bites, were most frequent on Sable Island during the post-pupping period, between late July and late October. The difference between their observations and ours suggests some shift in the timing of shark presence around the island. The greater proportion of pups killed during the May–June pupping season in our study suggests that pups are more vulnerable during the mid-summer period. The small number of adult and juvenile kills during the pupping period suggests that sharks may select pups during the time when the pups are likely to be concentrated in the waters adjacent to the island pupping areas.

The decline in harbour seal pup production cannot be explained entirely by a reduction in per capita recruitment resulting from shark-inflicted mortality. If the problem was limited to new recruitment, one would expect to have observed a stabilizing of production near the peak reached in 1989 with a gradual decline as a result of adult female mortality. All adult females for which pregnancy status could be determined, killed during March–June of the 5 years of our study, were pregnant. Boulva & McLaren (1979) found pregnancy
rates for mature harbour seal females (6 years of age and older) of 95%, similar to our observations. Thus, the observed decline has to be at least partly related to a reduction in the numbers of adult females in the population.

A greater proportion of reproductive females than males was killed. Among mature seals of known age and sex, six (25.0%) males and 19 (65.5%) females were at least 6 years old when killed. We do not have an explanation for this differential adult mortality for age within sex, or by sex. Mature males may be less vulnerable to shark attack, because of their slightly larger size or their behaviour, than young males or females. Since mature male harbour seals (5+ years) generally experience higher mortality rates than females (see Heide-Jorgenson & Harkonen, 1988), the greater proportion of older females represented in the shark-kills could also reflect a greater proportion of older females in the population. If the differential mortality were related to differing abundances, then one would expect the proportional mortalities to have stayed roughly the same throughout the study. Our data show that 67–90% of the adult mortality was of females in the early years of the study (1993–95), but only 50–54% of the adult deaths were of females in 1996–97. This change in the mortalities from predominantly adult female could be interpreted as indicating that mortality was proportional to abundance, with the 1:1 ratio being approached as abundances were equalized. Alternatively, if sharks select for adult females, the ratio observed in 1996–97 could indicate that the abundance of adult females had been reduced below that of adult males.

Our observations during the pupping and immediate post-pupping period suggest a high incidence of shark-inflicted pup mortality since the mid-1980s, which would have limited the number of females recruiting to the reproductive group. Ellis (1998) found that, concurrent with the steady decline in the number of harbour seal pups born on Sable Island after 1991, the age distribution of live, known-age, sexually mature females shifted to older ages. She suggested that the trend reflected a lack of recruitment of young females to the breeding population, possibly as a result of higher mortality or emigration of young females.

We examined the potential impact of the deaths of adult females on pup production by estimating the potential reproductive output of those adult females killed by sharks. Juveniles were excluded from this procedure because of the small number involved and the likelihood of the higher, but unknown, mortality of juveniles compared to adults. Five assumptions were made in estimating the reproductive output: (1) the ratio of adult females to males in Table 2 was representative of the ratio in the ‘unknown sex’ category; (2) the proportions of females at ages 3, 4, 5 and ‘6 or older’ from Table 3 were representative of the age structure of the shark-killed animals and was used to derive numbers at age for each year; (3) because of the small sample size and the tendency for more females than males to be taken over time, the proportion for age 5 animals was assumed to be the same as for age 4; (4) the rates for Sable Island female harbour seals reaching reproductive age, calculated by Boulva & McLaren (1979) for ages 3, 4, 5 and ‘6 and older’ of 0.27, 0.55, 0.79 and 0.95, still apply; (5) an annual mortality rate of 10% was chosen to account for non-shark-related deaths. We chose this estimate of non-shark-related mortality based on a total annual mortality estimate made by Boulva & McLaren (1979), as we had no direct measure of overall mortality, and the literature (see Heide-Jorgensen & Harkonen, 1988) provides only broad ranges without distinguishing between shark-related and other causes. Boulva & McLaren (1979) provided an annual mortality rate estimate of 17.5% for a harbour seal population in eastern Nova Scotia but at a near stationary stable-age distribution by an active bounty hunt; again this estimate did not distinguish between sources of natural mortality. Using the first three assumptions, the proportions of adult females killed at ages 3, 4, 5 and ‘6 and older’ were estimated to be 0.13, 0.043, 0.043 and 0.784, respectively (Table 5). Summing progressively along the diagonals (i.e. following cohorts) to obtain the incremental loss of reproductive potential, and applying the adjustments for mortality and partial recruitment, we estimated a loss in potential pup production for the study period increasing from 10 pups in 1994 to 127 pups in 1997.

These estimates of potential reproductive loss resulting from adult female mortality, combined with observed pup mortality between 1994 and 1997 (see Table 1), suggest that sharks reduced production on Sable Island by 43, 124, 134, 154 and 141 pups, respectively, for the years 1993–97. These observations and estimates of pup loss account for < 50% of the decline that was observed annually during 1993–97 from the peak production in 1989. However, we have not attempted to estimate the numbers of pups that would have been completely consumed by sharks and thus not observed by us, nor have we tried to account for the potential reproductive loss to the population of the shark-killed female pups that never reached reproductive age. It is generally accepted that juveniles experience higher mortality rates than adults, but we have been unable to find estimates of juvenile mortality that we could use in this treatment. Therefore no attempt was made to account for losses of juveniles, although inclusion of such potential losses would more closely approach the observed reductions in pup numbers.

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<tr>
<th>Year</th>
<th>Total females</th>
<th>Age composition</th>
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<tr>
<td></td>
<td>killed</td>
<td>3</td>
</tr>
<tr>
<td>1993</td>
<td>11</td>
<td>1</td>
</tr>
<tr>
<td>1994</td>
<td>47</td>
<td>6</td>
</tr>
<tr>
<td>1995</td>
<td>53</td>
<td>7</td>
</tr>
<tr>
<td>1996</td>
<td>32</td>
<td>4</td>
</tr>
<tr>
<td>1997</td>
<td>18</td>
<td>2</td>
</tr>
</tbody>
</table>

Table 5. Estimated number of adult females killed by sharks between 1993 and 1997, in total and by age
Several other factors may have played a part in both the reduced total numbers and the diminishing numbers of pups born on Sable Island. Harbour seals may be shifting their distribution southward, associated with changing environmental conditions. Drinkwater, Colburne & Gilbert (1995) have shown a reduction in water temperatures throughout the east coast of Canada during the early 1990s. Frank, Carscadden & Simon (1996) have documented the recent appearance and increase in the abundance of a cold-water species, capelin, in the area; and we have observed an increase in the occurrence of harp and hooded seals on Sable Island in recent years. The grey seal population on Sable Island has been increasing by >12% annually since the early 1960s (Stobo & Zwanenburg, 1990) to an estimated 40,000+ animals by the late 1980s (Zwanenburg & Bowen, 1990), and >85,000 by 1994 (Mohn & Bowen, 1996). Coincident with this population increase, we have observed increased use of the beaches throughout the year by grey seals, now extending into areas previously used only by harbour seals for pupping, moulting and haul-out. The increased grey seal numbers may have contributed to the reduced abundance of harbour seals by passive interference or resource competition. Scientific investigations of harbour seals on Sable Island also increased dramatically in the late 1980s, and that research continued into the mid-1990s (e.g. Ross, 1990; Muelbert, 1991; Boness, Bowen & Oftedal, 1991, 1994; Bowen, Oftedal & Boness, 1992; Walker, 1992; Bowen, Oftedal, Boness & Iverson, 1994; Coltman, 1997; Bowen, Boness & Iverson, 1998; Ellis, 1998). Harbour seal pups may have been sufficiently disturbed by the combined impact of the long-term tagging programme and the increased intensity of research activities, beginning in the late 1980s, to spend more time in the water, increasing their vulnerability to predation. Adult females may have responded by abandoning Sable Island as a reproductive area. Unfortunately, there are few data on harbour seal abundance elsewhere in Atlantic Canada, and thus if they are shifting to other areas, these movements are not documented.

This study shows that sharks are having an impact on Sable Island harbour seals, possibly to the extent of 40,000+ animals by the late 1980s (Zwanenburg & Bowen, 1990), and >85,000 by 1994 (Mohn & Bowen, 1996). Coincident with this population increase, we have observed increased use of the beaches throughout the year by grey seals, now extending into areas previously used only by harbour seals for pupping, moulting and haul-out. The increased grey seal numbers may have contributed to the reduced abundance of harbour seals by passive interference or resource competition. Scientific investigations of harbour seals on Sable Island also increased dramatically in the late 1980s, and that research continued into the mid-1990s (e.g. Ross, 1990; Muelbert, 1991; Boness, Bowen & Oftedal, 1991, 1994; Bowen, Oftedal & Boness, 1992; Walker, 1992; Bowen, Oftedal, Boness & Iverson, 1994; Coltman, 1997; Bowen, Boness & Iverson, 1998; Ellis, 1998). Harbour seal pups may have been sufficiently disturbed by the combined impact of the long-term tagging programme and the increased intensity of research activities, beginning in the late 1980s, to spend more time in the water, increasing their vulnerability to predation. Adult females may have responded by abandoning Sable Island as a reproductive area. Unfortunately, there are few data on harbour seal abundance elsewhere in Atlantic Canada, and thus if they are shifting to other areas, these movements are not documented.

This study shows that sharks are having an impact on Sable Island harbour seals, possibly to the extent of limiting population growth, or causing population decline. The abundance and species composition of sharks in the area are not known, although examination of wounds on harbour seals suggests that only a few species are involved. Additional research is required on factors affecting the vulnerability of seal populations to shark attacks and on the abundance of sharks necessary to affect such population control.

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