Distribution, abundance and biology of ringed seals (*Phoca hispida*): an overview

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ABSTRACT

The ringed seal (*Phoca hispida*) has a circumpolar Arctic distribution. Because of its great importance to northern communities and its role as the primary food of polar bears (*Ursus maritimus*) the ringed seal has been studied extensively in Canada, Alaska, Russia, Svalbard and Greenland as well as in the Baltic Sea and Karelian lakes. No clear-cut boundaries are known to separate ringed seal stocks in marine waters. Adult seals are thought to be relatively sedentary, but sub-adults sometimes disperse over long distances. Stable ice with good snow cover is considered the most productive habitat although production in pack ice has been little studied. Populations appear to be structured so that immature animals and young adults are consigned to sub-optimal habitat during the spring pupping and breeding season. Annual production in ringed seal populations, defined as the pup percentage in the total population after the late winter pupping season, is probably in the order of 18-24%. Most estimates of maximum sustainable yield are in the order of 7%.

The world population of ringed seals is at least a few million. Methods of abundance estimation have included aerial surveys, dog searches and remote sensing of lairs and breathing holes, acoustic monitoring, correlation analysis by reference to sizes of polar bear populations, and inference from estimated energy requirements of bear populations. Aerial strip survey has been the method of choice for estimating seal densities over large areas. Adjustment factors to account for seals not hauled out at the time of the survey, for seals that dove ahead of the aircraft, and for seals on the ice within the surveyed strip but not detected by the observers, are required for estimates of absolute abundance.

Male and female ringed seals are sexually mature by 5-7 years of age (earlier at Svalbard). Pupping usually occurs in March or early April and is followed by 5-7 weeks of lactation. Breeding takes place in mid to late May, and implantation is delayed for about 3 months. In at least some parts of their range, ringed seals feed mainly on schooling gadids from late autumn through early spring and on benthic crustaceans and polar cod (*Boreogadus saida*) from late spring through summer. Little feeding is done during the moult, which takes place in late spring and early summer. Pelagic crustaceans offshore and mysids inshore become important prey in late summer and early autumn in some areas. Ringed seals have several natural predators, the most important of which is the polar bear in most arctic regions. Arctic foxes (*Alopex lagopus*) kill a large percentage of pups in some areas.

From a conservation perspective, the ringed seal appears to be secure. Levels of exploitation of arctic populations have usually been considered sustainable, except in the Okhotsk Sea. Large fluctuations in production of ringed seals in the Beaufort Sea and Amundsen Gulf are thought to be driven by natural variability in environmental conditions. While concern has been expressed about the potential impacts of industrial activity and pollution on ringed seals, such impacts have been documented only in limited areas. Because of their ubiquitous occurrence and availability for sampling, ringed seals are good subjects for monitoring contaminant trends in Arctic marine food chains.

INTRODUCTION

This global review of the ringed seal (*Phoca hispida*) (Fig. 1) was initially prepared for the NAMMCO Scientific Committee meeting in February 1996. The Committee had been asked specifically for advice on (1) stock identity, (2) abundance, (3) the long-term effects of present removals on the ringed seal population in each stock area and (4) the likely effects on ringed seals of recent environmental changes (e.g. disturbance, pollution), changes in food supply and interactions with other living marine resources. To support the committee in developing its advice, I was asked to review published information on status, reproductive rates, possible maximal rates of increase, population size and general biology of ringed seals throughout their range. It was agreed that this review should summarize the status of the species *Phoca hispida* on a global basis but emphasize those populations living in Arctic marine environments, particularly those in the North Atlantic Arctic and adjacent waters.

Relevant literature was identified by reference to major pinniped bibliographies (Ronald *et al.* 1976, 1983, 1991) and on-line database searches carried out at Blacker-Wood Library of Biology, McGill University, Montreal (Zoological Record, Biological Abstracts, BIOSIS, Aquatic Sciences and Fisheries Abstracts). The paper was revised and updated following the February 1996 meeting on the basis of discussions at the meeting, critical advice from colleagues, and additional literature.

TAXONOMIC REVIEW

Scheffer (1958:95) recognized the "plasticity" of the polytypic ringed seal group, which at the time was assigned to the genus *Pusa*:

> It is a plastic group whose members have encircled the Arctic Ocean and have exploited both marine and fresh-water habitats. Wherever seals of the genus *Pusa* occur, however, they have retained a certain delicate structure of skull, and an affinity for ice, both of which set them apart from their nearest relative, the harbor seal *Phoca*.

Scheffer recognized six named forms of the ringed seal, *Pusa hispida Schreber* 1775, as follows: *P. hispida hispida* of the circumpolar Arctic Ocean, *P. hispida ochotensis* of the Okhotsk Sea, *P. hispida krascheninikovi* of the Bering Sea, *P. hispida botnica* of the Baltic Sea including the Gulfs of Bothnia and Finland, *P. hispida ladogensis* of Lake Ladoga in western Russia, and *P. hispida saimensis* of Lake Saimaa in Finland (see Fig. 2 for geographical locations). The Baikal seal (*Pusa sibirica*) and

Fig. 1
A ringed seal killed in Wolstenholme Fjord, northwest Greenland (76°40'N, 68°23'W), where this species is important to the household economy of the Inuit (Polar Eskimos). The characteristic "ringed" pattern on the body explains the common name of the species. (Photo: S. Leatherwood).

Caspian seal (*Pusa caspica*) were considered congeneric with *Pusa hispida*.

The name *Pusa* has been abandoned, and the entire group is now considered part of the inclusive phocid genus *Phoca*, although Burns and Fay (1970) found it useful to recycle the name *Pusa* to denote a subgenus of *Phoca*. Four of the six forms mentioned by Scheffer (1958), excluding only *P. h. krascheninikovi* and *P. h. hispida*, have come to be regarded as "fairly well-defined subspecies" that occur as "geographically isolated peripheral populations" (Rice 1977:4), although King (1983) also gives some credence to *P. h. krascheninikovi* centered in the northern Bering Sea. Frost and Lowry (1981) submerged all of the Arctic circumpolar ringed seals under Scheffer's *P. h. hispida*.

DISTRIBUTION

The northern circumpolar distribution of the species *Phoca hispida* was partially mapped by Frost and Lowry (1981), and McLaren (1990) reproduced maps of distribution in the Bering, Chukchi and Beaufort seas (from Burns 1978) and northern Canada (based on various sources). Ringed seals were observed regularly during a cruise northwards from Bering Strait all the way to the North Pole in August-September (Ramsay and Farley 1997). Also, according to tour operators who run ship cruises from Murmansk to the pole each summer, seals are seen all along that route (M.A. Ramsay pers. comm.).

In Alaska, ringed seals are abundant during winter and early spring in the northern Bering Sea, Norton and Kotzebue sounds and throughout the Chukchi and Beaufort seas (Frost 1985, Kelly 1988). Although they occur as far south as Nunivak Island and Bristol Bay during years of extensive ice coverage, they are generally not abundant south of Norton Sound. An annual migration takes place through Bering Strait as the seals follow the receding pack ice northward in spring, then move southward just ahead of the advancing sea ice in autumn. Some movement by individual seals from the eastern Beaufort Sea westward to the Chukotka Peninsula has been demonstrated by tagging and recapture (Smith 1987).

In the Eurasian Arctic, ringed seals inhabit the gulfs and bays of the Kola Peninsula and the coastal waters of the White and southeastern Barents seas (Lukin and Potelov 1978, Helle 1992; see Belikov and Boltunov, this volume). Popov (1982) specifically noted the following areas where they are apparently relatively common: Cheshsky Gulf, Pechora Sea, southwestern Kara Sea (east coast of Bely Island, Malygin Strait [between Bely Island and the Yamal Peninsula], Baydaratskaya Bay), Tazovskaya and Obskaya bays and along the east coast of Yamal Peninsula, and the Laptev Sea (including Khatangsky, Anabarsky, Oleneksky and Yansky gulfs) (see Fig. 2). He stated that their occurrence in the East Siberian and Chukchi seas was poorly known, although Ognev (1962) described them as common across the entire north coast of Asia. The population of ringed seals in the Okhotsk Sea is probably isolated from those in the Bering Sea. Fedoseev (1971) identified three main pupping areas for Okhotsk Sea ringed seals - the northwest coast from Tauyskaya Bay to Ayan, Shelikhova Bay and off the east coast of Sakhalin.

Ringed seals occur around much of Svalbard (Smith and Lydersen 1991, Lydersen this volume). Pup production in the fast ice bordering this archipelago does not, however, appear to be adequate to support the polar bear (*Ursus maritimus*) population in the Svalbard drift ice. Smith and Lydersen (1991) therefore suggested the need to assess the possibility that an influx of seals from fast ice elsewhere or from the pack ice offshore helps sustain Svalbard's polar bear population. Joiris (1992) confirmed the presence of ringed seals in the pack ice of the Greenland Sea during June.

Ringed seals are found throughout Greenland, in variable densities (see Teilmann and Kapel this volume). In West Greenland they are said to be most abundant north of the Polar Circle (66°32'N) while in East Greenland they are also abundant farther south (Kapel 1975). Their presence in southern Greenland is mainly dependent on the arrival of drift ice in the East Greenland Current during summer (Kapel 1975). Ringed seals are abundant in the Scoresby Sund fjord-complex, where the high-

Fig. 2 *Circumpolar projection showing localities mentioned in text.*

est annual take per hunter in Greenland is reported (Born 1983). Highest densities of breeding ringed seals in East Greenland are in the fjords with productive glaciers, including Scoresby Sund, Dove Bugt and Jøkelbugt (Dietz *et al.* 1985). Ringed seals are locally common all across North Greenland (Dietz and Andersen 1984, Bennike 1991). Large numbers (> 1,000 on one occasion) have been seen in August in the heavy pack ice of southern Kane Basin (Born and Knutsen 1989). The species also inhabits the offshore pack ice of the Greenland Sea, where some pupping may occur (Dietz *et al.* 1985).

Ringed seals have an extensive distribution in northern Canada, as reflected in the geographic extent of ringed seal hunting by Inuit (Freeman 1976, Riewe 1992, see Reeves *et al.* this volume). They occur continuously in marine waters from northern Newfoundland and Labrador, northward to the North Pole and westward throughout Hudson and James bays and the high Arctic archipelago (McLaren 1958a, Mansfield 1967, Kingsley 1990). The ringed seals in Nettilling Lake and the Koukdjuak River on Baffin Island were given a subspecies name, *P. h. soperi*, by Anderson (1943), but this freshwater population has not been studied in detail (see Soper 1944). A "resident" population is also said to inhabit Lake Melville in southeastern Labrador (ca. 54°N) (deGraaf *et al.* 1981).

One or more populations of several thousand ringed seals inhabit the northern and eastern Baltic Sea, centered in the Gulf of Bothnia (also called Bothnian Bay) (Helle 1980a, 1980c, 1980d, 1986; Härkönen and Heide-Jørgensen 1990) and the Gulfs of Riga and Finland (Tormosov and Esipenko 1986, 1989). The occasional occurrence of ringed seals in western Europe to as far south as France and Portugal was summarized by Helle (1992).

As mentioned earlier, two isolated lake populations exist in Europe. One is entirely confined to Lake Ladoga, a brackish lake in Karelia, Russia (Reijnders *et al.* 1993, Sipilä and Hyvärinen this volume), the other to Lake Saimaa in southeastern Finland (Sipilä 1990, Sipilä *et al.* 1990, Sipilä and Hyvärinen this volume).

STOCK IDENTITY

Little progress has been made in identifying stocks of ringed seals. This may be due, in part, to the lack of focused investigations of the problem. Except for those populations that are isolated by land barriers or expanses of unsuitable habitat (cf. Müller-Wille 1969, Hyvärinen and Nieminen 1990), ringed seals appear to have a continuous circumpolar distribution. Some researchers have nevertheless assumed, at least implicitly, that separate stocks exist, regardless of the difficulty of defining the boundaries between them (e.g. McLaren 1962, Kapel and Petersen 1982). McLaren (1962) analyzed the yields of ringed seals in separate areas defined by the trading spheres of Hudson's Bay Company posts, thus treating the seals in these areas as management units.

Although it has sometimes been assumed that adult ringed seals are essentially sedentary (McLaren 1958a), tagged individuals (all subadults) have relocated over straight-line distances of up to 1,300 km in the western North American Arctic (Smith 1987) and 900-1,400 km in western Greenland (Knutsen and Born 1989, Heide-Jørgensen *et al.* 1992, Teilmann and Kapel this volume). Stirling et al. (1982:20) referred to a "large and predictable" annual westward migration by sub-adult ringed seals along the north coast of Alaska during late summer and autumn. Ringed seals that winter in the Bering and southern Chukchi seas apparently migrate northward in late spring and summer (Kelly 1988), but details about this behaviour are not known. Observations in the Baffin Bay region that ringed seals leave some coastal areas in summer, while in other (generally more northerly) areas large influxes of ringed seals occur during the open water period, have been interpreted as suggesting substantial migrations, either north-south or inshore-offshore (Miller *et al.* 1982). The generally cyclonic movement of surface currents in Baffin Bay, with mean velocities in the order of 4-35km/day, has large implications for ringed seals in the pack ice, particularly for mothers with pups (Miller *et al.* 1982). Ringed seals in the offshore pack ice of the Arctic Ocean must move considerable distances against the net flow of the ice; otherwise they would end up in the North Atlantic

Fig. 3
One of four male ringed seals caught in Wolstenholme Fjord, northwest Greenland, and instrumented with satellite-linked radio transmitters. No clear pattern of dispersal emerged, and it was suggested that the seals in northern Baffin Bay and adjoining sounds and embayments are well mixed (see Heide-Jørgensen et al. 1992). (Photo: S. Leatherwood)

in the ice-free zone (M.A. Ramsay pers. comm.).

Satellite radio-tracked ringed seals from NW Greenland (Fig. 3) dispersed widely and rapidly, indicating considerable mixing by seals throughout eastern Baffin Bay (Heide-Jørgensen *et al.* 1992, also see Kapel *et al.* this volume). One seal's movement from Resolute in the Canadian High Arctic in the spring of one year to Narsalik in SW Greenland the following March (a separation distance of 2,272 km) has been documented (NAMMCO 1996:138, Kapel *et al.* this volume).

One individual, thought to have been a locally "dominant" male, was resighted in two successive years at the same locality off SE Baffin Island (Smith and Hammill 1980a, 1981). This was interpreted as indicative of site fidelity.

HABITAT

Ringed seals occur in water of virtually any depth, and their distribution and movements are probably driven mainly by food availability and ice conditions (see below). The preferred breeding habitat has been described as land-fast ice with good snow cover in fjords and island-infested embayments (McLaren 1958a, 1958b, Lukin and Potelov 1978, Furgal *et al.* 1996, Fig. 4). Any assumption about "preferred" or "prime" breeding habitat must be qualified by noting that the vast majority of research on ringed seal pupping and breeding has been done in the fast ice. The potential importance of stable, drifting pack ice as ringed seal breeding habitat, suggested by Finley *et al.* (1983), has never been adequately investigated. According to Smith (1987) snow cover of at least 60-65cm is necessary for "good breeding ice" In Svalbard, the length of time that stable, land-fast ice is available prior to pupping is "the primary factor influencing the quality of ringed seal breeding habitat" (Smith and Lydersen 1991:587).

Areas of prime habitat are generally thought to be used mainly by older adults. Younger animals that are reproductively active are apparently consigned to simpler coastlines where the ice conditions are less predictably suitable (cf. McLaren 1958a). Most sub-adult ringed seals inhabit the shear zones between the land-fast ice and the drifting pack ice, shore lead systems, polynyas and the unconsolidated offshore pack ice (Stirling *et al.* 1981).

The location of prime breeding habitat may differ between the Canadian high Arctic and areas farther south in North America. In the former, the inner reaches of bays generally have smooth ice and relatively little snowdrift; most pupping in the higher latitudes takes place in the rougher ice along island coastlines and in inter-island channels rather than deep inside the bays (Smith *et al.* 1979a, Stirling *et al.* 1983, Smith 1987). The preference for late-consolidating ice at bay entrances and in channels may be due to increased food availability at the ice edge or to increased mobility (Hammill and Smith 1989). Furgal *et al.* (1996) found ringed seal lairs and breathing holes in Admiralty Inlet and Strathcona Sound (northern Baffin Island, Canada) primarily near large, thick ice ridges in areas with deep snow cover. A preference for fast ice with < 40% pressure ridging (deformation) has been noted in several areas of Canada (see Hammill and Smith 1989). In western Svalbard, the prime breeding habitat is at glacier fronts, where glacial debris frozen into the annual ice provides sites for deep snow accumulation (Smith and Lydersen 1991).

Kingsley *et al.* (1985) found that in the Canadian high Arctic during late June and early July densities of ringed seals were higher in annual ice than in multi-year ice. Within the annual ice, densities were highest in cracking ice, lower in unbroken ice, and lowest in floe and rotten ice. This trend in preferences was reflected in the broad-scale relative abundance of seals, with a clear density gradient between the unproductive, sparsely populated strata centered in western Viscount Melville Sound, Hazen Strait and Prince Philip Basin, and the productive areas of Queens Channel, Barrow Strait and eastern Viscount Melville Sound (also see Smith and Hammill 1980b). Kingsley *et al.* (1985) also found a tendency of ringed seals to avoid deep water (> 175m). In the northeastern Beaufort Sea, the density of basking ringed seals was found to be lower over water deeper than 100m, and even lower over water 300-400m deep (Stirling *et al.* 1982).

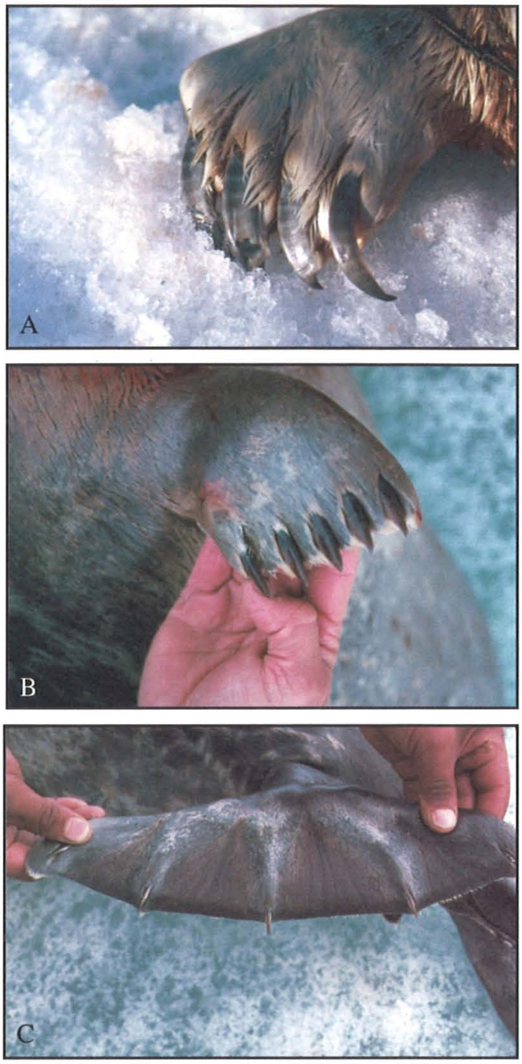

Fig. 4
The strong, sharp foreclaws (A, B) are used by ringed seals to maintain breathing holes in fast ice. The claws on the hind flippers (C) have no obvious function. (Photos: S. Leatherwood, Wolstenholme Fjord, Northwest Greenland)

As mentioned above, the significance of dense, relatively stable pack ice as pupping habitat is uncertain. In most regions, land-fast ice has traditionally been considered much more productive than pack ice for ringed seals (except possibly in the Okhotsk Sea - see Fedoseev 1975). Smith and Stirling (1975:1297), however, citing Lentfer's (1972) observations of many seal dens in the moving heavy pack ice north of Barrow, Alaska, stated that "the far offshore areas of shifting but relatively stable ice are an important part of the breeding habitat." An initial effort was made to investigate lairs in the pack ice of the eastern Chukchi Sea in 1984, but the results were inconclusive (Frost and Burns 1989). A large breeding population centered in the Baffin Bay pack ice was suggested on the basis of aerial survey observations, skull morphometry, age and reproductive status of hunted seals, and intestinal parasite faunas (Finley *et al.* 1983). Without substantial ringed seal production in the pack ice, it is difficult to reconcile the high catches made in West Greenland (Miller *et al.* 1982, see Teilmann and Kapel this volume). The possibility has also been raised that ringed seals pup and breed in the offshore pack ice of the Greenland Sea (Dietz *et al.* 1985). It has been confirmed that ringed seal production occurs in the pack ice of the Barents Sea (Wiig *et al.* 1998). Uncertainty about the quantitative significance of pupping and breeding in the pack ice will remain until appropriate field studies are carried out.

An attempt to predict suitable pupping habitats from underwater vocalization rates yielded ambiguous results, so Calvert and Stirling (1985) concluded that dog searches were the preferred method of assessing winter distribution and the incidence of birth lairs in early spring.

Although construction of sub-nivean (snow-covered) birth lairs is a typical characteristic of ringed seals in most areas (Chapski 1940, Smith and Stirling 1975, Helle *et al.* 1984, Lydersen and Gjertz 1986), those in the Okhotsk Sea regularly give birth on the exposed sea surface (Fedoseev 1971, 1975). Births in the open also occur occasionally in other areas, but with the result that most pups are killed by predators (cf. Lydersen and Smith 1989).

Ringed seals that normally live in marine waters occasionally move up rivers to distances of at least several kilometers (Ognev 1962, Mansfield 1967, Popov 1982). In the Okhotsk Sea ringed seals regularly haul out on land as well as ice (Ognev 1962). They are also said to do so in the southern end of Admiralty Inlet, eastern Canadian Arctic (S. Innes pers. comm.).

REPRODUCTIVE RATES

Defining reproductive rate as the proportion of mature females that are either pregnant (i.e. lactating or with a foetus) or have a corpus luteum of ovulation in any given year, published estimates range from as low as 0.45 (Hammill 1987), 0.54 (Smith 1987), 0.62 (Smith 1987) and 0.63 (Nazarenko 1965), to as high as 0.78 (McLaren's data from southern Baffin Island, *fide* Hammill 1987), 0.81 (Smith *et al.* 1979a) and 0.86 (Johnson *et al.* 1966). The very low reproductive rate in the Bothnian Bay population (0.28; Helle 1980b) was related to uterine pathologies that have not been reported in Arctic ringed seal populations. Hammill (1987) recalculated reproductive rates from several published sources, excluding animals < 8 years old as a way of standardizing the rates for comparison (juveniles were under-represented in his Barrow Strait sample). This gave rates of 0.63 rather than 0.45 for Barrow Strait (Hammill 1987), 0.75 rather than 0.54 for Amundsen Gulf (Smith 1987), 0.77 rather than 0.62 for Home Bay, Baffin Island (Smith 1987) and 0.81 rather than 0.78 for southern Baffin Island (McLaren's data, *fide* Hammill 1987).

Regional production can vary considerably on an annual basis. Years of exceptionally low production (or at least low recruitment) have been attributed to insufficient snow accumulation for lair construction and maintenance (Lukin 1980, Kelly 1988) and to early, unusually heavy ice formation (Smith and Stirling 1978, Stirling *et al.* 1982). Other ecological factors (e.g. food availability, ice surface conditions) undoubtedly play roles as well (Smith 1987).

Confusion exists in the literature about the ovulation rate of ringed seals (Davis *et al.* 1980). Calculations depend partly on what age class is selected as the youngest for mature females. Inclusion of 4- and 5-year-old females causes a substantially lower estimate than if these age classes are excluded. The ovulation rate is both age-specific (females < 7-8 years old are much less fecund than older females; e.g. see age-specific rates provided by Smith 1987:33, Hammill 1987) and year-specific (at least it was found to vary greatly in the eastern Beaufort Sea between 1972 and 1975; Stirling *et al.* 1977, Smith 1987). An exceptionally high ovulation rate of 0.91 at Svalbard was explained as resulting from favourable environmental conditions at the time of sampling (early 1980s; Lydersen and Gjertz 1987).

McLaren (1958b) reduced the pregnancy rates of older females in his hypothetical population, having found that the only female > 30 years old in his sample was senile. Smith (1973a, 1987) found little or no evidence for reduced fecundity with age, whereas Lydersen and Gjertz (1987) reported two females (40 and 45 years old) to be senile (another 40-year-old seal in their sample had normally functioning ovaries). McLaren and Smith (1985), citing Nazarenko

(1965), referred to low pregnancy rates reported for older female ringed seals in the White Sea (specifically Cheshskaya Inlet). They cautioned that the samples were taken in early winter (actually in January) along ice edges, which may have caused an over-representation of non-pregnant animals.

Fedoseev (1975) estimated the average reproductive "capability" of ringed seal populations in the Okhotsk Sea, Bering Strait and Chukchi Sea to be 0.21 (apparently referring to annual percentage of pregnant females in the total population), but his analysis is of limited use because of the lack of details concerning samples and methods. His earlier paper (1965) states that females 15 years or older do not conceive annually.

Miller *et al.* (1982) used available data to make five estimates of production rate (annual pup production as a percentage of the total population). Based on observed sex ratios, these ranged from 14.7-23.5%; once corrected for an assumed 1:1 sex ratio, the range narrowed to 18.2-24.1%. These authors' "best" estimate was 20.4%. Frost's (1985) estimate of somewhat more than 16-18% is not far out of line.

POSSIBLE MAXIMAL RATES OF INCREASE

Stirling and Calvert (1979) gave 0.08 as a rough estimate of maximum sustainable yield. This figure was apparently based mainly on the work of McLaren (1958b, 1962) and Smith (1973a, 1975b). McLaren (1958b, 1962), for example, estimated that removal rates of 0.07-0.10 per year were sustainable for ringed seals along the north coast of Hudson Strait in the 1950s, and he used 0.08 as a sustainable yield rate for other Canadian ringed seal populations. Smith (1973a) used a population projection model to estimate an exponential rate of increase of 0.11 for a stable-age population of ringed seals. Using population estimates from surveys and removal estimates from sealskin trade data for Home Bay, he estimated the maximum sustainable yield rate to be 0.072. This assumed a zero population growth rate and that the total population could have been underestimated. Smith (1975a) used 0.08 to calculate sustainable yields from population estimates in Hudson and James Bays. McLaren and Smith (1985) acknowledged that the assumption of population stationarity made their models circular. It is also not clear how, or if, the roles of predation by polar bears and foxes were taken into account in these authors' calculations.

Fedoseev (1975) used estimates of age-specific mortality (see also Popov 1982:his Table 3) to calculate a maximal annual rate of increase of 0.04-0.05 for ringed seal populations in the Okhotsk Sea, Bering Strait and Chukchi Sea (but see comments above).

The above estimates were critically evaluated by Davis *et al.* (1980) who called attention to the substantial uncertainties underlying them. They estimated a confidence interval of at least ± 30% around Smith's (1973a) sustainable yield estimate of 0.072. Davis *et al.*'s conclusion was that much refinement of the available estimates would be needed if the removal rates of ringed seals in the Canadian Arctic were to increase significantly.

Law (1979) used population parameters from McLaren (1958b) and Smith (1973a) to explore the idea that age-specific and time-of-year-specific harvesting would optimize sustainable yields from ringed seal populations.

ABUNDANCE AND DENSITY ESTIMATES

Methods

Given their extensive and often remote distribution, small body size, solitary habits, and denning behaviour, ringed seals present severe challenges for population estimation. To some extent, the factors in their biology and behaviour that make them cryptic targets of hunters and predators also make them cryptic to researchers. Assessment efforts (see reviews by Davis *et al.* 1980, Kingsley 1990) have included ship-based strip surveys (McLaren 1958b, 1961, Mansfield 1970); land-based counts (McLaren 1958b, Smith 1973a); aerial visual modified line transect surveys (Helle 1980c, 1986); aerial visual strip surveys (McLaren 1966, Johnson *et al.* 1966, Fedoseev 1971, Burns and Harbo 1972, Smith 1973b, 1975a, Stirling *et al.* 1977, 1982, Finley *et al.* 1983,

Table 1. Published estimates of ringed seal density.

In some (most?) cases, area refers to ice area and does not necessarily include open water (cf. Kingsley *et al.* 1985). All estimates (with one exception) were derived from aerial visual strip surveys.

Area	Ice type	Density (seals/km^2)	Source[1]
Belcher Is.[2]	Open water	0.7	1
Amundsen Gulf		0.9-1.1	2
N Amundsen Gulf	Fast and >6/8 cover	1.6-3.1	3,4
Prince Albert Sd		2.12	2
Prince Albert Sd	Fast and >6/8 cover	2.0-3.5	3,4
Prince Albert Sd		1.13	11
Minto Inlet		0.18	2
Minto Inlet		0.25	11
Can. Beaufort Sea	Variable	0.10-0.69	5
Can. Beaufort Sea	Fast; <25 m water depth	0.08-0.41	3
Can. Beaufort Sea	Pack; >25 m water depth	0.20-0.30	3
Can. Beaufort Sea	Fast; 6/8+ cover	0.062-0.408	18
Can. Beaufort Sea	Pack; 6/8+ cover	0.185-0.444	18
Can. high Arctic (73°30'-78°10'N)	6/8+ cover	0.21-1.16	6
Can. central high Arctic		0.58-1.54	6,7
Can. central high Arctic		0.24-0.73	13,6[3]
Can. central high Arctic (75°-76°30'N)		0.29	14,6[4]
Can. central high Arctic (76°30'-78°30'N)		0.49	14,6[4]
Western Coronation Gulf	Fast, polynya edge	0.12-0.74	11
Alaskan Beaufort Sea			8
Baffin Bay	Pack	1.39	9
E Baffin Island	Fast Fjord	0.86-3.2 (mean 1.72)	9
E Baffin Island	Fast shelf	1.31	9
Hudson and James bays	Stable near-shore	1.49[5]	10
Hudson and James bays	Stable off-shore	0.42[5]	10
Hudson and James bays	Unstable off-shore	0.37[5]	10
Wager Bay	Fast	1.03	12
W Hudson Bay	Fast	1.267	19
W Hudson Bay	1/8-5/8 cover	0.402	19
W Hudson Bay	6/8+ cover	1.933	19
SE Beaufort Sea	Mainly open water	0.08-0.42	15
Kong Oscars Fjord, E Greenland	Fast fjord	1.04	16
Davy Sund, E Greenland	Heavy, ridged pack	0.79	16
Scoresby Sund	Fast fjord	2.00	16
Okhotsk Sea	Variable	0.2-3.2	17

[1] 1, McLaren and Mansfield (1960); 2, Smith (1973b); 3, Kingsley (1986); 4, Kingsley (1990); 5, Stirling *et al.* (1982); 6, Kingsley *et al.* (1985); 7, Finley (1976) as reported in Ref. 6; 8, Burns and Harbo (1972); 9, Finley *et al.* (1983); 10, Smith (1975a); 11, Alliston and McLaren (1981); 12, Heard and Donaldson (1981); 13, Smith *et al.* (1979a); 14, Smith *et al.* (1979b); 15, Harwood and Stirling (1992); 16, Born *et al.* this volume; 17, Fedoseev (1971); 18, Kingsley (1984); 19, Lunn *et al.* (1997).

[2] Ship-board survey.

[3] Table 14 in Kingsley *et al.* (1985) includes weighted mean values from Smith *et al.* (1979a).

[4] Table 14 in Kingsley *et al.* (1985) includes weighted mean values from Smith *et al.* (1979b).

[5] Unweighted averages; see Davis *et al.* (1980).

Kingsley *et al.* 1985, Kingsley 1986, Jensen and Knutsen 1987, Frost *et al.* 1988, Lunn *et al.* 1997, Born *et al.* this volume; see Table 1) on at least one occasion supplemented by "spot-photo" techniques (Jensen and Knutsen 1987); extrapolation from observed breathing hole or lair densities derived from dog searches (Smith *et al.* 1979a, Hammill and Smith 1990, Lydersen *et al.* 1990, Smith and Lydersen 1991, Lydersen and Ryg 1991); and aerial photographic counts and mapping of breathing holes in combination with intensive ground-level observations of seal behaviour (Finley 1979). Stirling *et al.* (1983) called attention to the method used by Pastukov (1965) of counting birth lairs of Baikal seals (*Phoca sibirica*) in late spring, after the roofs of the lairs had caved in. The most common recent method of estimating ringed seal densities has been visual strip surveys flown during late spring and early summer when the highest proportion of the seal population is thought to be hauled out and visible.

The timing of surveys intended to sample hauled-out seals is critical. It is well established that the greatest proportion of the total seal population is hauled out during late spring and early summer, just prior to break-up, with the date of this peak varying by latitude (McLaren 1958a, Smith 1973a, 1973b, Kelly and Quakenbush 1990). A diurnal pattern must also be taken into account. Midday has generally been regarded as the peak basking period during the moult (Burns and Harbo 1972, Smith 1973a, Finley 1979, Smith and Hammill 1981). Air temperature, wind speed and cloud cover, however, also affect haul-out behaviour. For example, at Freemans Cove and Aston Bay in the Canadian high Arctic, Finley (1979) concluded that "a combination of bright, warm, and calm conditions during the 'night' will induce seals to remain hauled out, [while] similar conditions at midday may exceed the thermal tolerance of ringed seals and they may escape into the water."

The widths of surveyed strips have differed among studies (Table 2). According to Smith (1973a:29), surveys conducted at 12-30m altitude and a speed of 250-260km/hr allowed two observers to count all seals within 5.6km of either side of the track-line "without significant error." In surveys flown at 20-40m altitude in the Gulf of Bothnia, Helle (1980c, 1980d, 1986) used a modified line transect approach to estimate effective transect half-widths of 700-850m. Stirling *et al.* (1977, 1982), Kingsley *et al.* (1985) and Lunn *et al.* (1997) divided their 400m strips on either side of the aircraft into equal inner and outer portions. Density estimates for the outer portions were consistently higher than those for the inner portions, demonstrating that negative bias was greater near the track-line than away from it. The authors were uncertain of the reason(s) for this result but offered several possible explanations.

Adjustment ("correction") factors have been crudely derived for reducing availability bias. Smith (1975a) doubled his estimates of hauled-out seals to account for those in the water. This procedure was based on a 24 hr count made at one site on 24 June, when the peak number hauled out was 19 and the estimated total of different seals in the area throughout the day was 38. Finley (1979) estimated that under ideal survey conditions up to 70% of the ringed seals in an area would be visible on the ice. Smith and Hammill (1981) found during the latter half of May that 23-80% (average 48%) of the seals in the fast ice of inner Popham Bay, Baffin Island, were on the ice at the diel peak of haul-out. Using a different approach in another area, Hammill and Smith (1990) estimated that true densities were 1.3-1.9 times higher than estimated from aerial surveys. Kelly and Quakenbush (1990) found from radiotelemetry that ringed seals off Alaska spent about 43% of their time out of the water in early June. Most of the calibration data have been collected during the spring moulting period in areas of "prime" breeding habitat where adult seals predominate. Areas of poor or unsuitable breeding habitat, where sub-adults predominate, have been neglected in spite of the fact that sub-adults comprise the largest component of the total population (Stirling and Øritsland 1995). Stirling and Øritsland (1995) reasoned that the correction factors used in previous studies to account for seals in the water during overflights, ranging from about 30% to 90%, were "likely to be conservative when applied universally."

The problem of adjusting for perception (or visibility) bias (e.g. Caughley 1974, Marsh and

Sinclair 1989) has generally not been addressed in surveys of ringed seals although Stirling *et al.* (1977, 1982) and Kingsley *et al.* (1985) demonstrated that it could be substantial. In most studies, it seems to have been assumed that except for seals that dove ahead of the aircraft or were in the narrow blind strip directly beneath the aircraft, all hauled-out seals within the surveyed strip were detected. Front-seat observers detect more seals than rear-seat observers. Estimates of the difference have varied substantially, e.g. between 10-13% and about 50% according to Miller *et al.* (1982, citing Koski and Davis 1979, Koski 1980). According to Finley *et al.* (1983) the front-seat/rear-seat ratio for surveys at 90m altitude was 1.97:1.

McLaren (1958b, 1961, 1962) used the following reasoning to estimate a population of approximately 1 million ringed seals in the eastern Canadian Arctic south of Lancaster Sound and north of Cape Chidley (Labrador) and James Bay (northern Quebec): (1) he assumed that equal areas of shore-fast ice of the same type would contain the same number of animals; (2) he defined three categories of fast ice - < 1.853km (1 nautical mile) from shore and surrounded by further ice, < 1.853km from shore but exposed to open water on its seaward edge and > 1.853km from shore; (3) from a few counts of basking seals in late spring, he estimated that these ice categories would contain 35, 10 and 5 seals (or 7, 2 and 1 birth lairs), respectively, per 3.434km^2 (1 square nautical mile) of ice; and (4) he measured the extent of fast ice from maps and then made population estimates for different areas of coastline. He also provided estimates of ringed seal populations for specific areas defined roughly by the trading zones of certain Hudson's Bay Company posts (McLaren 1962).

Ship-board counting of ringed seals during the open-water season was attempted by McLaren (1958b, 1961; also see Mansfield 1970). He estimated that a ringed seal's head (represented by a paint can in this study!) on a calm sea surface would disappear from view at a distance of 350-610m (0.19-0.33 of a nautical mile). He therefore defined the total strip width for vessel surveys as approximately 1,240m (0.67 of a nautical mile). No explicit reference was made to eye height of observer, but an observer standing on the foredeck of the M/V *Calanus*, the vessel used for McLaren's experiment, would be viewing from approximately 4m above sea level (E.H. Grainger pers. comm., 7 January 1997). Alternatively, the observer could have been situated on the masthead with his eye level approximately 13m above sea level (Grainger, as above). To my knowledge, abundance-estimation surveys of ringed seals from vessels have not been conducted anywhere on a significant scale, except possibly in the Okhotsk Sea.

The problem of calibrating the number of breathing holes or lairs to the number of seals present in an area has been addressed by several authors (e.g. Finley 1979, Smith and Hammill 1980a, 1981, Hammill and Smith 1990, Kelly and Quakenbush 1990, Lydersen and Hammill 1993a). It does not appear that counts of holes or sub-nivean structures can be used reliably to estimate absolute population abundance, especially if a single structure-to-seal ratio is applied on a large geographical scale (cf. Smith and Hammill 1981, Digby 1984). Finley (1979), however, considered the observed ratio of number of holes to maximum number of seals in his Freemans Cove study site to be a useful "first estimate" of this relationship in an area where the population was thought to be stable. The density of seal holes may be regarded as a meaningful index of the overall importance of a particular fast-ice area to overwintering ringed seals (Finley 1979, Alliston and McLaren 1981, Kingsley *et al.* 1985) although spring surveys of nursing lairs using dogs are probably the best method for assessing production.

An indirect approach to estimating the size of a ringed seal population is by reference to the energy requirements or seal-killing rates of the polar bear population that depends on it (Kingsley this volume). A polar bear-based model for the Beaufort Sea gave ringed seal abundance estimates 5-100 times larger than those from aerial surveys (Stacey 1985). Kingsley (1990) made a crude preliminary calculation for the Canadian Arctic. He estimated that a 200kg polar bear had an estimated basal metabolic rate of 3.7Mcal/day and that a 25kg seal had a caloric density of 5Mcal/kg. The seal's yield of 125Mcal would represent about 34 days' maintenance for the bear. He divided 34 days by 4 to account for wastage, assimilation and the difference between average and basal metabolism to give an annual average requirement of 1 seal per 8.5 days to sustain a polar bear. Assuming that the polar bear population in the Canadian Arctic was 15,000-20,000 and that each bear needed 40 ringed seals per year, this implied an annual off-take by bears of 0.7 x 10^6 seals, or an order of magnitude larger than the estimated kill by humans. Assuming an annual production rate for ringed seals of about 20% (see above), the total seal population would need to be close to 4 million to sustain both the polar bear and human populations in the Canadian Arctic, according to this analysis (Kingsley 1990).

The "overall robustness" of the relationship between estimates of ringed seal populations (from aerial strip transect surveys) and corresponding estimates of polar bear populations (mainly from mark-recapture analyses) was interpreted by Stirling and Øritsland (1995) as meaning that "the population size of one may be used to predict an expected population of the other." There is also a correlation between the reproductive output of ringed seals and the natality and body condition of polar bears in the same region (Stirling and Lunn 1996).

Published Abundance Estimates

Worldwide

Reference has been made to an aggregate world population of 6-7 million ringed seals (Stirling and Calvert 1979), but this was an educated guess rather than an actual estimate. Frost and Lowry (1981:33) concluded that it was "unwise at this time to attempt an estimate of the world population ... due to the vast unsurveyed areas and the unknown relationship between observed and total numbers." In spite of the considerable survey efforts in some areas since 1980, this conclusion remains appropriate.

Eastern Russian Waters

Crude estimates of ringed seal populations in eastern Russia in the 1970s were 800,000-plus in the Okhotsk Sea and 70,000-80,000 in the Bering Sea (Popov 1982). Visual aerial surveys in the Okhotsk Sea in 1968 and 1969 produced estimates of 818,000 and 865,000, respectively, referring only to the number of seals hauled out on the ice (Popov 1982).

Svalbard (Norway)

Based on a maximal count of 600 seals hauled out simultaneously on fast ice in Fritjovhamna, southwestern Svalbard, in July 1986, the local population (including Van Mijen and Van Keulen fjords) was estimated as 1,200 ringed seals (Jensen and Knutsen 1987).

Greenland

An estimate of approximately 2 million animals, with an annual pup production of hundreds of thousands, was suggested for Greenland (Kapel and Petersen 1982), but this was a guess, apparently based largely on hunting returns. Miller *et al.* (1982) used density estimates from surveys of the fast ice along the east coast of Baffin Island, together with Marko's (1981) map of fast ice along the Greenland side of Baffin Bay, to estimate at least 98,000 ringed seals in the fast ice south of Kap York. After adjusting for seals missed by the rear observer (adjustment factor 1.32) and for those not hauled out at the time of the surveys (adjustment factor 1.43; see discussions above under Methods), this estimate was raised to 185,000 seals, which is far below the guess by Kapel and Petersen (1982). Even when an estimate for the fast ice from Kap York northward to Kane Basin, derived in the same manner, was added (about 16,000 seals), this did little to change the incongruence between the Miller *et al.* (1982) estimate and that of Kapel and Petersen (1982).

Systematic aerial surveys of Kong Oscars Fjord, Scoresby Sund and adjacent areas of NE Greenland in June 1984 resulted in an aggregate unadjusted estimate of approximately 30,000 ringed seals (Born *et al.* this volume).

Canada

McLaren's estimate of 1 million ringed seals in a portion of the eastern Canadian Arctic during the 1950s is mentioned above. Other published estimates for eastern Canada are summarized in Table 3.

Table 2. Operational characteristics of aerial visual strip surveys of ringed seals based on published descriptions. NS = not stated.

Altitude (m)	Speed (km/hr)	Strip half-width (m)	Source
30	NS	< 1130	McLaren (1966)
91	241-250	800	Johnson *et al.* (1966)
152	213-240	800	Burns and Harbo (1970)
100	NS	100	Fedoseev (1971)
305-365	NS	NS	Smith (1973a)
12-30	250-260	NS	Smith (1973a)
90	NS	NS	Smith (1975a)
152	240	400	Stirling *et al.* (1977)
91	193	800	Smith et al. (1979b)
100	240	500	Alliston and McLaren (1981)
150	220-260	400	Stirling *et al.* (1982)
90	240	800	Finley *et a*l. (1983)
152	240	402	Kingsley *et a*l. (1985)
152	240	400	Kingsley (1984, 1986)
150	NS	300	Tormosov and Esipenko (1986)
90	185	250, 500	Härkönen and Heide-Jørgensen (1990)
100	240	500	Alliston and McLaren (1981)
150	230	500	Heard and Donaldson (1981)
150	220	200	Born *et al.* (this volume)
305	200	400	Harwood and Stirling (1992)
150	260	400	Lunn *et al.* (1997)
90	NS	400	Härkönen and Lunneryd (1992)
200	185	200	Jensen and Knutsen (1987)

Using density estimates calculated separately for three ice types - fjord (1.72/km^2), coastal shelf (1.31/km^2) and pack ice (1.39/km^2) - Finley *et al.* (1983) estimated that there were at least 67,000 seals in the 24,000 km^2 of fast ice between Cape Dyer and Navy Board Inlet and 417,000 in the Baffin Bay pack ice (300,000 km^2) during late June and early July 1979. They suggested that with corrections to account for seals missed, either because they were in the water at the time of the surveys or were overlooked by the rear observer, the pack ice population would be 787,000 seals (a "shared" Greenland-Canada population). Miller *et al.* (1982) suggested that an additional 15,500-plus seals were present in the fast ice along the east coast of Devon Island and north to 80°N.

Lunn *et al.* (1997) estimated that 140,880 (SE 8,100) ringed seals were hauled out on the spring ice of western Hudson Bay in June 1995. These authors suggested that the estimate of visible seals could represent a total population of about 280,000.

Alaska

A minimum of 11,600 ringed seals was estimated for the land-fast ice between Point Lay and Barter Island along the Alaskan north slope in 1970; this figure refers only to seals visible on the ice surface (Burns and Harbo 1972).

Frost and Lowry (1984) extrapolated from a mean density of 0.40 seals per km^2 (7 years of aerial survey data; correction factor of times 2 to ac-

Table 3. Published estimates of ringed seal abundance in the eastern North American Arctic (between Victoria Island and West Greenland). Estimates are uncorrected for visibility bias.

Area	Year(s)	Estimate	Source
Cape Dorset	1950s	68,900	McLaren (1962)
Pond Inlet	1950s	66,300	McLaren (1962)
Belcher Is.	1950s	49,900	McLaren (1962)
Wakeham Bay	1950s	20,400	McLaren (1962)
SW Baffin Is.	1964	70,800	McLaren (1966)
Frobisher Bay	1964	47,200	McLaren (1966)
NW Quebec	1964	5,500	McLaren (1966)
Hudson Bay		227,500[1]	Smith (1975a)
		203,000[2]	Davis *et al.* (1980)
James Bay		30,500[1]	Smith (1975a)
		28,000[2]	Davis *et al* .(1980)
Can. E Arctic	1950s	947,000	McLaren (1958b; sum from Kingsley [1990])
NE Baffin Is. fast ice	1979	67,000+	Finley *et* al. (1983)
Baffin Bay pack ice		417,000+	Finley *et al.* (1983)
W Greenland fast ice	1979	97,800+	Miller *et al.* (1982)
W Hudson Bay	1995	140,880 (SE 8100)	Lunn *et al.* (1997)

[1] From unweighted average densities.

[2] Extrapolations weighted for lengths of transects.

count for availability bias, based on Smith 1973a, 1975a) to estimate 40,000 ringed seals in the Alaskan Beaufort Sea during winter and spring (1 November to 1 July). They guessed that the regional population would double during summer as migrating seals arrived from the west and south, giving an estimate of 80,000 for the Alaskan Beaufort Sea during the open-water season.

Using McLaren's (1958b, 1962) method but with much lower estimates of seal densities from Alaskan surveys, Frost (1985) estimated at least 250,000 ringed seals on the shore-fast ice throughout Alaska. She reasoned, further, that although densities were much lower in the pack ice than in the shore-fast ice, the vastness of the pack ice meant that the absolute number of ringed seals was much greater there than in the more limited shore-fast ice. Thus her estimate for Alaskan waters overall was 1-1.5 million seals, a figure which she considered "probably conservative," given estimated rates of polar bear predation on ringed seals (see below).

Published Indices of Abundance

The expense and logistical difficulties of mounting surveys covering huge expanses of the ringed seal's ice-infested habitat, together with problems of survey design, timing and interpretation, conspire to make indices, rather than estimates of absolute abundance, attractive options for monitoring ringed seal populations (cf. McLaren and Smith 1985). Production (i.e. number of pups born annually) has sometimes been used as a proxy for abundance (e.g. Smith and Lydersen 1991).

Indices have often been used to compare the densities of ringed seals in different types of habitat (cf. Finley 1979) or to compare densities in the same habitat between years (cf. Stirling *et al.* 1977). Such indices have taken the form of: minutes of searching required for a dog to detect a lair or breathing hole (Smith and Stirling 1975, 1978, Smith *et al.* 1979a, Smith 1987, Hammill 1987, Hammill and Smith 1989), ringed seal vocalizations recorded per minute at stations in a grid (Smith and Stirling 1978, Stirling *et al.* 1983, Calvert and Stirling 1985), seals sighted per minute of aerial survey (Braham *et al.* 1984), densities of breathing holes or lairs detected by dog searches (Lydersen *et al.* 1990, Smith and Lydersen 1991), and densities of breathing holes and/or hauled-out seals observed in aerial surveys (Finley 1979, Smith *et al.* 1979b, Alliston 1980, Alliston and McLaren 1981, Kingsley *et al.* 1985). Some densities clearly refer to areas of ice rather than total surface areas (ice and open water, combined; e.g. Stirling *et al.* 1982, Kingsley *et al.* 1985).

Large-scale surveys reported by Harwood and Stirling (1992) were flown during 1982 and 1984-86 over mostly open water, with both whales and seals as target species. This study provided density estimates (seals/100 km^2) and "abundance indices" (annual estimates of relative abundance) for ringed seals in the south-eastern Beaufort Sea. The results suggested a marked decline between 1982 and 1985, and this suggestion was consistent with other evidence pointing to a "substantial failure of recruitment" from 1984 to 1987 (Harwood and Stirling 1992:898; also see Stirling and Lunn 1996).

The drained ice areas around seal breathing holes can be detected using remote sensing techniques (Digby 1984). Such detection is reliable, however, only for undeformed first-year sea ice in the high Arctic, where the ice is thick enough and the temperature low enough to preclude the formation of thaw holes until late in the melt season. Moreover, not all seal holes "drain" (S. Innes pers. comm.). In spite of its potential usefulness for monitoring the winter distribution of seals over large areas, the remote sensing of breathing holes has numerous drawbacks as a method for estimating ringed seal densities (Digby 1984). The same can be said of remote sensing (with infrared) of under-snow lairs (Kingsley *et al.* 1990, Sipilä and Kurlin 1992). Even dog searches, efficient as they may be for limited areas, have their drawbacks, not the least being that they are labour-intensive.

Fig. 5
One-day-old ringed seal pup being nursed. (Photo: K.Kovacs)

GENERAL BIOLOGY

Maturation and Reproduction

Both males and females usually reach full sexual maturity by 5-7 years of age (McLaren 1958a, Frost and Lowry 1981) although seals at Svalbard mature earlier than those in other regions (Lydersen and Gjertz 1987). The mean age at first reproduction, calculated by Smith (1987) using the method of York (1983), is 7-8 years for most Arctic ringed seal populations. The peak breeding season was considered by McLaren (1958a) and Smith (1973a) to be from about mid April to early May on the assumption that ovulation normally occurred shortly after parturition. Smith (1987), however, estimated that it occurs nearer the end of May, with a mean date of ovulation of 21 May in the eastern Beaufort Sea. Implantation is delayed for about 3 to 3.5 months, so foetal development spans perhaps 7-8 months. Most pups are born in late March and April, usually in a sub-nivean birth lair (Smith and Stirling 1975, Lukin and Potelov 1978). There is some geographic variability in mean pupping dates (Smith *et al.* 1991), and ovulation dates would vary accordingly. Lactation lasts 5-7 weeks (Frost and Lowry 1981, Hammill *et al.* 1991, Lydersen and Hammill 1993a, Lydersen 1995, Fig. 5). Nursed pups gain an estimated 350 ± 80g (Lydersen and Hammill 1993b) or 386 ± 104g (Lydersen *et al.* 1992) of body mass per day.

Feeding

The ringed seal has been described as "widely adaptable in its feeding habits" (McLaren 1958a:16), but strong preferences for particular types of prey are evident (McLaren 1958a, Johnson *et al.* 1966, Lowry *et al.* 1980, Popov 1982, Weslawski *et al.* 1994, Siegstad *et al.* this volume). The ringed seals in a given area typically prey on no more than 10-15 prey species, and they tend to focus on only two to four of these (Weslawski *et al.* 1994). Most prey fishes are 5-10cm long; most prey crustaceans, 2-6cm long. The maximal prey size is about 20cm (Weslawski *et al.* 1994).

Pelagic schooling fishes, mainly polar cod (*Boreogadus saida*) and secondarily saffron cod (*Eleginus navaga*) and other gadids, dominate the diet from late autumn through early spring (November-April) in some areas (Lowry *et al.* 1980, Popov 1982, Siegstad *et al.* this volume). Young redfish (*Sebastes* spp.) can be an important component of the diet around Svalbard in spring (Weslawski *et al.* 1994). The spring diet in northwestern Svalbard consists mainly of polar cod, decapods and larger amphipods (Gjertz and Lydersen 1986a); the schizopod *Thysanoessa inermis* ("krill") also contributes significantly to the diet in Kongsfjorden, particularly in summer and autumn (Weslawski *et al.* 1994). In Southwest Greenland capelin (*Mallotus villosus*), redfish (*Sebastes* spp.) and squid (*Gonatus* spp.) are important prey items (Siegstad *et al.* this volume). A wider variety of organisms is taken during late spring and summer, in some areas dominated by benthic crustaceans (mysids, shrimps and gammarid amphipods; Lowry *et al.* 1980) and in others by polar cod (Bradstreet and Cross 1982). During late summer and early autumn, pelagic crustaceans become the main prey in offshore waters (hyperiid amphipods in Arctic regions and euphausiids in areas influenced by subarctic waters), and mysids in some nearshore areas (Lowry *et al.* 1980, Siegstad *et al.* this volume). A small sample of ringed seals killed at Hornsund, Svalbard, in autumn contained polar cod, the pelagic amphipod *Parathemisto libellula* and the mysid *Mysis oculata* (Lydersen *et al.* 1989). Regional differences in diet probably reflect differences in prey availability, prey preferences (possibly related to energy content) and water depth.

Food consumption rates vary seasonally (Ryg *et al.* 1990, Ryg and Øritsland 1991, Siegstad *et al.* this volume). The general pattern is for seals to feed intensively from late summer to early spring and less intensively during late spring and early summer, coincident with the moult (late March to July, peak in June; Frost and Lowry 1981, Smith 1987). Thus, seals are fattest in autumn and winter and leanest in May-July. Females lose mass rapidly during lactation (c. 0.64kg/day) in spite of the fact that they forage under the ice during the lactation period (Hammill *et al.* 1991; also see Lydersen 1995, Kelly and Wartzok 1996).

McLaren (1958a, 1962) interpreted the observation that ringed seals are sometimes scarce in areas where food is abundant, but common in areas of low productivity, to mean that their distribution and abundance were driven less by food resources than by other factors, most notably sea-ice conditions. Lowry *et al.* (1980), in contrast, emphasized the role of food availability and catchability in influencing the movements and productivity of ringed seals. Some authors have considered the density of ringed seals as a useful index of biological productivity. For example, Stirling and Øritsland (1995) cite the fact that the lowest seal densities in Kingsley *et al.*'s (1985) study area occurred in the most northerly strata, where the water would be expected to be nutrient-poor and where multi-year ice would limit light penetration and thus inhibit photosynthesis. They also cite Smith's findings that 40% of 4-year old and 60% of 5-year old female ringed seals were sexually mature in western Baffin Bay (Smith 1973a), while only 20 and 29% of the same age classes, respectively, were mature in the Beaufort Sea (Smith 1987). This wide difference was interpreted as supporting the hypothesis that the Baffin Bay environment is more productive than the Beaufort Sea environment (Stirling and Øritsland 1995; also see Stirling 1997). It is probably also less temporally variable, judging by the comparative infrequency of seal population crashes.

Commercially valuable fish that are eaten by ringed seals in the White and Barents seas include herring (*Clupea harengus*) and navaga (saffron cod) (Popov 1982). In the rivers of the Kola Peninsula, ringed seals reportedly form dense concentrations while feeding on salmon (*Salmo salar*; Popov 1982). This report deserves closer investigation as adult salmon would be outsized prey for ringed seals. In Alaska, ringed seals are viewed as having relatively few conflicts with commercial fisheries (Frost 1985, Kelly 1988), and this is also the case in Canada (Malouf 1986). As consumers of shrimp (*Pandalus borealis*; Gjertz and Lydersen 1986a, Weslawski *et al.* 1994), the ringed seals in Svalbard waters might compete to some extent with the large shrimp fisheries there. In Greenland, the ringed seal's consumption of shrimp and Greenland halibut (*Reinhardtius hippoglossoides*) may be in conflict with fisheries.

Diving and Orientation

Unrestrained ringed seals can dive for well over 20 min, but most dives last less than about 9 min (Elsner *et al.* 1989, Lydersen 1991, Lydersen *et al.*1992, Kelly and Wartzok 1996, Fig. 6). The aerobic dive limit is uncertain. One acoustically tracked seal dove to the bottom in water 222m deep (Kelly and Wartzok 1996). A female instrumented by S. Innes (pers. comm.) dove to 340m. Experimental evidence suggests that vision plays a primary role in under-ice pilotage by ringed seals, followed in importance by audition and vibrissal (tactile) stimuli (Elsner *et al.* 1989). They may also use "spatial memory" to find their way from one breathing hole to another during the dark polar winter (Wartzok *et al.* 1992).

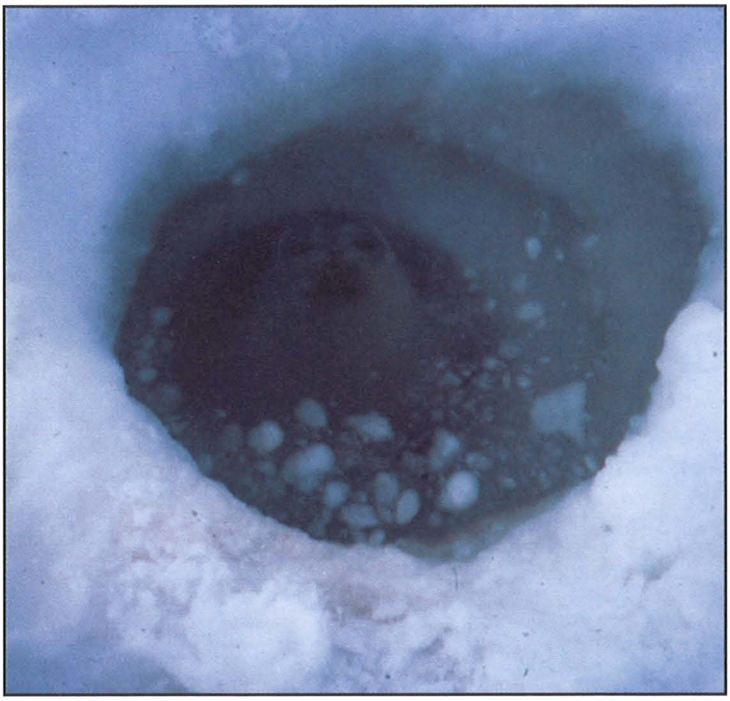

Fig. 6
Adult ringed seal about to surface in a breathing hole. (Photo: C. Lydersen)

Territoriality

Adult male ringed seals are well known by Inuit to enter a condition called "tiggak" during the winter. At this time, the males have a distinctly offensive odour which taints their meat and marks their breathing holes (Chapski 1940, Ognev 1962, Smith and Stirling 1975, Hardy *et al.* 1991, Ryg *et al.* 1992, Furgal *et al.* 1996).

Although the maintenance of underwater territories by adult male ringed seals has not yet been confirmed by direct observation or telemetry, several lines of evidence support the idea that it occurs. Among these are the observed segregation of age classes in the fast ice, the strong odour emitted by adult males, the wounds on the bodies of male and immature seals (indicative of intraspecific fighting) and the "disparate sex ratio in the breeding habitat" (Hammill and Smith 1991:133). Stirling and Øritsland (1995) noted the similarity in densities of ringed seal breathing holes in two areas of prime breeding habitat - the fast ice of western Barrow Strait (Hammill and Smith 1991) and Amundsen Gulf (Kingsley 1986). They inferred from this similarity that "the territorial behavior of resident seals" may regulate the under-ice distribution of ringed seals during winter and spring (until break-up). Acoustic tracking during the spring breeding season revealed that breeding-age males made shallower, shorter dives than females and subadult males (Kelly and Wartzok 1996). This difference is consistent with the hypothesis that the males "were guarding territories or mates near the undersurface of the ice" (Kelly and Wartzok 1996).

Ringed seals that pup and breed in pack ice may behave differently from those that inhabit shore-fast ice. For example, "pack-ice seals can occupy thin ice that continually forms during winter and thus probably need not maintain and defend one breathing hole (or small groups of holes) throughout the winter" (Finley *et al.* 1983:171).

Predation on Ringed Seals

The polar bear (*Ursus maritimus*) is unquestionably the most important predator of Arctic ringed seals in most parts of their range (Smith 1980, Davis *et al.* 1980, Stirling 1988, Stirling and Øritsland 1995, Fig. 7). Polar bears kill pups in birth lairs, usually in offshore areas along large pressure ridges and the edges of rough ice (Stirling and McEwan 1975, Smith 1980). Bears also hunt ringed seals in lairs in the stable land-fast ice (Stirling and Archibald 1977, Smith 1980, Lydersen and Gjertz 1986, Gjertz and Lydersen 1986b, Hammill and Smith 1991) and in ice-free waters at least in some areas (Furnell and Oolooyuk 1980). As surplus killers, polar bears sometimes kill more seals than they can eat (Stirling and Øritsland 1995). Pup carcasses, in particular, are often left uneaten (Stirling and McEwan 1975). Most predation by bears in the flaw zone and in moving ice involves sub-adult seals (1+ to 2+ years old) (Stirling and McEwan 1975). It has been suggested that the annual caloric requirements of bears may differ according to where they live - e.g. those that live on ice during the entire year may kill more seals, particularly during summer and autumn, than those living in areas where open water precludes efficient seal hunting for several months (Stirling and Øritsland 1995).

An adult bear in the Canadian high Arctic kills a ringed seal every 2-6 days (Stirling 1974, Stirling and Latour 1978). In a study of the land-fast ice in Barrow Strait, Hammill and Smith (1991) estimated that, in some years, 44% of the annual pup production of ringed seals was removed by polar bears before weaning. In Admiralty Inlet and Strathcona Sound, bears were found to be less successful in their attempts at predation as snow depth and the thickness of the lair roofs increased (Furgal *et al.* 1996). The predator-prey interactions of polar bears and ringed seals have recently been examined in detail by Stirling and Øritsland (1995) and Stirling and Lunn (1996).

Walruses (*Odobenus rosmarus*) are commonly found to have ingested seals, but it is often not clear whether the walrus has made the kill itself or has eaten the seal as carrion (Lowry and Fay 1984). The finding of fresh hyperiid amphipods in the intact stomach of a ringed seal that had been eaten by a walrus, however, led Fay *et al.* (1990) to conclude that in at least that instance the seal had been killed by the walrus. Elevated levels of organochlorines in the blubber of walruses from eastern Hudson Bay have been interpreted as signaling a regular seal-eating habit, i.e. that walruses there occupy the same trophic status as polar bears (Muir *et al.* 1995). It has frequently been noted that ringed seals keep away from areas where walruses are present, and this has been interpreted as predator avoidance (Kingsley *et al.* 1985; also see Gjertz 1990, Stirling 1997). A large walrus population that is food-stressed may increase its predation on ringed seals and thus have a significant effect on the regional seal population (cf. Lowry and Fay 1984).

Fig. 7
Polar bear feeding on ringed seal. (Photo: A. Derocher)

Killer whales (*Orcinus orca*) are said to prey on ringed seals (e.g. Miller 1955, Stirling and Calvert 1979), and numerous reports refer to the fact that ringed seals and other marine mammals respond dramatically to the presence of these whales (Heide-Jørgensen 1988, Reeves and Mitchell 1988). The stomachs of two killer whales taken at the head of Cumberland Sound contained ringed seal claws (MacLaren Marex Inc. 1979). Presumably, their close association with ice makes ringed seals largely inaccessible to killer whales during most of the year in most areas.

Ringed seal pups are also vulnerable to ravens (*Corvus corax*), glaucus gulls (*Larus hyperboreus*), red foxes (*Vulpes vulpes*), Arctic foxes (*Alopex lagopus*), wolves (*Canis lupus*), dogs (*Canis familiaris*) and wolverines (*Gulo gulo*) in addition to polar bears and walruses (Burns 1970, Smith 1976, Andriashek and Spencer 1989, Lydersen and Smith 1989). In the vicinity of Holman on Victoria Island, central Canadian high Arctic, an estimated average of 26% of ringed seal birth lairs were predated by Arctic foxes (Smith 1976). Fox predation is especially heavy in the near-shore fast ice (also see Lydersen and Gjertz 1986) where polar bear predation is often less severe. Predation by canids can be particularly significant in years when the birth lairs are disrupted by unseasonably warm weather in March and April (Lukin 1980).

Relations with other Species

Burns (1970; also see Braham *et al.* 1984) reviewed the evident partitioning of sea-ice habitat among various phocid species in the Bering and Chukchi seas. Breeding adults, in particular, inhabit near-shore areas from which other seals are largely excluded by the thick land-fast ice. For example, in aerial surveys of the fast ice in the Alaskan Beaufort and Chukchi seas, more than 99% of the marine mammals observed were ringed seals (Frost 1985). The occurrence of sub-adult ringed seals in the flaw zone and shifting pack ice places them in closer proximity to other phocids as well as walruses and cetaceans. Of the ice-associated phocids in the Arctic Basin, the ringed seal is the most widespread and is associated with the greatest variety of ice conditions.

The diverse character of the ringed seal's diet ensures overlap with the diets of several other predators (Lowry *et al.* 1980, Lowry and Frost, 1981). Little overlap is evident, however, in the diets of ringed and bearded seals (Finley and Evans 1983), and these two ice-associated seals are ecologically separate in most respects (Burns 1981). Although ringed seals sometimes form aggregations to feed on dense schools of polar cod (Smith 1987; cf. Harwood and Stirling 1982), they are not often seen to be part of "feeding frenzies" involving other cod predators such as harp seals (*Phoca groenlandica*), narwhals (*Monodon monoceros*) and white whales (*Delphinapterus leucas*) (Bradstreet *et al.* 1986:27). Welch *et al.* (1993) estimated that 60% of the annual diet of ringed seals in the Resolute area consisted of polar cod (also see Welch *et al.* 1992), but they observed few ringed seals associated with cod schools. A notable exception was an occasion in Allen Bay (southern Cornwallis Island) in August when about 500 ringed seals were congregated, feeding on a large school of cod.

Because of the broad seasonal overlap in diet between ringed seals and bowhead whales (*Balaena mysticetus*) (the two species have been seen feeding together in the southeastern Beaufort Sea; Harwood and Stirling 1992), the historic depletion of bowhead stocks could have improved foraging conditions for ringed seals and allowed their populations to increase (Lowry *et al.* 1978). Competition could also have been indirect. For example, if the reduced numbers of bowheads allowed expansion of polar cod populations (potentially major competitors with bowheads for copepods and euphausiids), this could have benefited ringed seals by making more cod available to them (Frost and Lowry 1984). On the other hand, the recent major increase in the western North Atlantic stock of harp seals, which feed heavily on polar cod and other ringed seal prey (e.g. *Parathemisto* and *Mysis*) during the summer open-water season, could be having an impact on the ringed seal stocks currently (Finley *et al.* 1990). Apparently ringed seals in Lancaster Sound and western Baffin Bay consume more polar cod than do all other marine mammal and seabird species, combined (LGL data cited in Bradstreet *et al.* 1986:31).

STATUS OF POPULATIONS

Referring mainly to the Arctic population(s) of ringed seals, Stirling and Calvert (1979) concluded that "levels are probably the same as in the 18th and 19th centuries, though this is not well documented."

Canada

Local overexploitation of ringed seals may have occurred within the hunting radii of communities where exploitation has been intensive (Mansfield 1970, Smith 1973a, Malouf 1986). The Royal Commission on Seals and the Sealing Industry in Canada cautioned that it was "quite possible that the catches made in some areas prior to 1983 ... exceeded the sustainable yield, and the decline in sales of skins apparent in some areas in the mid-1960s [i.e. during a period of increasing sealskin prices] might be a sign of this" (Malouf 1986:161). It warned that the resumption of catching at the levels of the 1970s could cause "the collapse of some of these stocks." The Royal Commission acknowledged, however, that great uncertainty surrounded the status of ringed seal populations in all parts of Canada.

In the absence of unbiased time series of catch data, trends in catch rates in Canada are difficult to characterize and interpret (see Reeves *et al.* this volume). Most published catch estimates have been based on skin sales (e.g. Mansfield 1967, Usher 1975, Malouf 1986) or police reports which are of varying quality and precision (e.g. Riewe and Amsden 1979, Usher and Wenzel 1987). Skin sales are obviously sensitive to market factors, so considerable uncertainty exists about what the trade statistics signify.

After analyzing estimated kill rates and population estimates from surveys of fast-ice habitat, Finley *et al.* (1983) concluded that the hunting by Inuit of eastern Baffin Island was sustained, in part, by seals produced in the offshore pack ice of Baffin Bay ("pulajuraaq" or "pulaniit"). Earlier, both McLaren (1958a) and Smith (1973a) had concluded that settlements on the east and south coasts of Baffin Island depended on recruitment from adjacent, highly productive areas to sustain their local catches of ringed seals.

Extreme annual variation in the density of ringed seals in the eastern Beaufort Sea and Amundsen Gulf, apparently due (at least indirectly) to differences in weather and ice conditions, has been demonstrated by survey and other data (Smith and Stirling 1975, Stirling *et al.* 1977, 1982, Smith 1987, Harwood and Stirling 1992, Stirling and Lunn 1996, Kingsley and Byers this volume). Ringed seal production in other areas is undoubtedly also subject to the effects of environmental variability. Documented long-term unidirectional changes in the natality and body condition of polar bears in western Hudson Bay have led to speculation that the bear population is responding to the reduced availability of seals, possibly caused by climate change (Stirling and Lunn 1996, Lunn *et al.* 1997, Stirling 1997).

Greenland

Although ringed seal populations in Greenland have not been rigorously assessed, Kapel and Petersen (1982:54-55) concluded that they were not threatened by hunting and were "unlikely to become so as long as the present hunting pattern is maintained." These authors assumed that large, remote areas, "to some degree the object[s] of deliberate conservation measures" by Greenland, along with the offshore drift (= pack) ice in Baffin Bay, serve as breeding refugia and thus help replenish the supply of ringed seals available in hunting zones (cf. Vibe 1950, Miller *et al.* 1982). Miller *et al.* (1982) reasoned that a large proportion of the annual kill in West Greenland (perhaps as much as 70%) must come from somewhere other than the coastal fast ice.

Kapel and Petersen (1982) claimed that the population of ringed seals available to Greenlandic hunters had been low in the early 1900s but increased during the 1950s and 1960s to its currently high level (cf. Vibe 1967). Kapel and Petersen (1982) estimated an annual secured catch of about 50,000-70,000 during the 1960s and 1970s, with an increasing trend (see further Teilmann and Kapel this volume).

Eurasian Arctic

Ringed seal populations in most of the Eurasian Arctic have been considered "underexploited" (Popov 1982:368). The only Arctic area where sealing for this species has been regular and intensive is apparently the White Sea, where ringed seals were "important objects of the sealing industry" (Timoshenko 1987) and the Russian annual quota was 3,500 in the late 1970s (Popov 1982). According to Chapski (1940), Soviet State purchasing agencies were obtaining about 7000 ringed seal skins annually from the White and Barents seas in the 1930s. In addition, many skins were used within the hunting communities (each hunter in Novaya Zemlya used about 10 per year for his own needs). Some 17,000 ringed seals were killed in the Barents, Kara and White seas in 1962 (Helle 1992, see Belikov and Boltunov this volume, for details and an update). A recruitment failure similar to that described above for the Beaufort Sea and Amundsen Gulf may have occurred in the White Sea in 1977, when unusually early break-up of the fast ice led to high pup mortality from predation (Lukin 1980).

Okhotsk Sea

Ringed seals in the Okhotsk Sea were over-exploited by commercial sealing, and Popov

(1982) referred to evidence of a recent decrease in the population. Although annual removals as high as 25,000-30,000 from the late 1800s to mid-1900s reportedly did not reduce the population, average annual removals of 72,000 between 1955 and 1965 apparently did (Popov 1982). Ship sealing was subsequently regulated, beginning with a quota of 32,000 in 1969, reduced to 25,000 in 1972 and 18,000 in 1975. Sealing by coastal residents became regulated by quota in 1975, with a limit of 7,000 ringed seals per annum (Popov 1982).

Alaska (Bering, Chukchi and Western Beaufort Seas)

The combined Soviet and American kill was estimated at 12,000-16,000 ringed seals in the 1970s (Stirling and Calvert 1979), but the basis for this estimate was unclear (cf. Kelly 1988). According to Frost (1985), the catch by Alaskan residents between 1962 and 1972 ranged from about 7,000 to 15,000 seals per year, and the combined Soviet and American catch varied between about 9000 and 16,000 per year. A major decline in the number of ringed seals taken in Alaska occurred after the U.S. Marine Mammal Protection Act was implemented in 1972. The estimated annual catch from 1973 to 1977 was 3,000-6,000, and in 1979 only 2,000-3,000 were secured by Alaskan residents (Frost 1985). In 1985 the combined Soviet and American catch was thought to average about 10,000 ringed seals per year (Frost 1985). Based on accurate catch statistics for two villages on St. Lawrence Island, Kelly (1988) concluded that the annual take throughout Alaska in the mid-1980s was more than 3,000.

The total population of ringed seals in Alaskan waters was assumed to be stable (or possibly increasing slightly) in the mid-1980s, with actual numbers in the range of 1-1.5 million or 3.3-3.6 million, depending on the method of estimation (Frost 1985, also see Frost *et al.* 1988).

Baltic Sea

The most recent estimate of about 5,000-8,000 seals in this population (including Bothnian Bay and the gulfs of Finland and Riga, combined) stands in contrast to the annual catch of more than 20,000 (Finland and Sweden, combined) in the early 1900s (Helle and Stenman 1990) and to a crude estimate of the population size as slightly over 300,000 in 1900 (Durant and Harwood 1986). Ringed seals were definitely depleted in the Baltic, and a declining trend was reported until the 1980s (Helle 1986, Härkönen and Heide-Jørgensen 1990). Aerial surveys of the Bothnian Bay component indicated that it was essentially stable from 1975 to 1990 (Härkönen and Lunneryd 1992), and the population(s) in the gulfs of Riga and Finland may have stabilized or increased slightly beginning in the late 1970s (Tormosov and Esipenko 1986, 1989). With the prohibition on hunting since the late 1980s (Helle 1992), some recovery was believed to be occurring in the early 1990s (Reijnders *et al.* 1993).

European (Karelian) Lakes

Of the two European lake populations, that in Lake Ladoga is thought to be stable or increasing (population in the order of 10,500-12,500; Zemsky and Filatov 1984), while that in Lake Saimaa is very small and endangered (< 200 seals) (Helle 1992, Reijnders *et al.* 1993).

EFFECTS OF OIL POLLUTION ON RINGED SEALS

The subject of how oil pollution can affect ringed seals is fraught with hearsay and conjecture. St. Aubin (1990) found only two explicit references to oiled ringed seals in the literature, one event in Repulse Bay, Canada, and the other in Greenland. Some experimental investigation has been done of the potential effects on ringed seals of immersion in and ingestion of oil. However, lethal thresholds were not established from these studies, and the results were not particularly conclusive (St. Aubin 1990).

Geraci and Smith (1976) found no evidence of "mechanical" damage to ringed seals immersed in Norman Wells crude oil for 24 hr. Transient irritation and damage to the seals' eyes was ascribed to volatile components of the oil. This immersion also resulted in generally low concentrations of petroleum residues in tissues (Engelhardt *et al.* 1977, Engelhardt 1983). The uptake of hydrocarbons apparently occurred mainly across the respiratory epithelium (i.e. through inhalation of petroleum vapors).

Although captive seals died within 71 min after being exposed to Norman Wells crude oil introduced to their pool, Geraci and Smith (1976) concluded that the cause of death was the superimposition of oil contamination onto the stress of captivity ("additive stress effects"; Engelhardt 1978).

Captive seals fed oil-contaminated fish exhibited no deleterious effects (Geraci and Smith 1976). Oil ingestion studies reported by Engelhardt (1978, 1983) indicated that petroleum residues accumulated mainly in the blubber and liver, with comparatively lower concentrations in muscle and other tissues.

Engelhardt (1983) concluded, after evaluating the experimental evidence on effects of oil on ringed seals, that apart from the transient eye problems, the renal system was the most likely site of serious impacts. He also noted the tendency of petroleum fractions to be sequestered in the blubber until periods of energetic stress, when the blubber reserves are metabolized and the stored hydrocarbons are released to circulation (also see Engelhardt 1982).

Oil is likely to cause the greatest harm when it spreads into the fast-ice breeding habitat. Exposure of pups to oil immersion and to more-frequent-than-normal immersion in water (due to the mother's need to move the pup) could lead to hypothermia and pup mortality (Smith 1987).

Oil contamination could also affect the food resources of ringed seals. The seriousness of any impact would obviously depend on the scale, timing and location of the spill (see McLaren 1990 for a discussion of population-level effects of oil on ringed seals and other pinnipeds).

EFFECTS OF VESSEL TRAFFIC AND NOISE ASSOCIATED WITH OTHER HUMAN ACTIVITY

Ringed seals have been killed by ice-breakers moving through the fast-ice breeding habitat (S. Innes pers. comm.), and the destabilization of ice edges by the passage of large vessels could have "an even more widespread effect" (Smith 1987:60). In one field study, the density of seal holes was higher in the re-frozen track of an icebreaker than in the surrounding ice (Alliston 1980). Mansfield (1983), however, noted that on this occasion only two tracks were made, and that more intensive ice-breaker activity in an area might have a negative impact on seals. Three tagged seals in Strathcona Sound, northern Baffin Island (Fig. 8), showed no visible reaction as an icebreaker passed them (S. Innes pers. comm.).

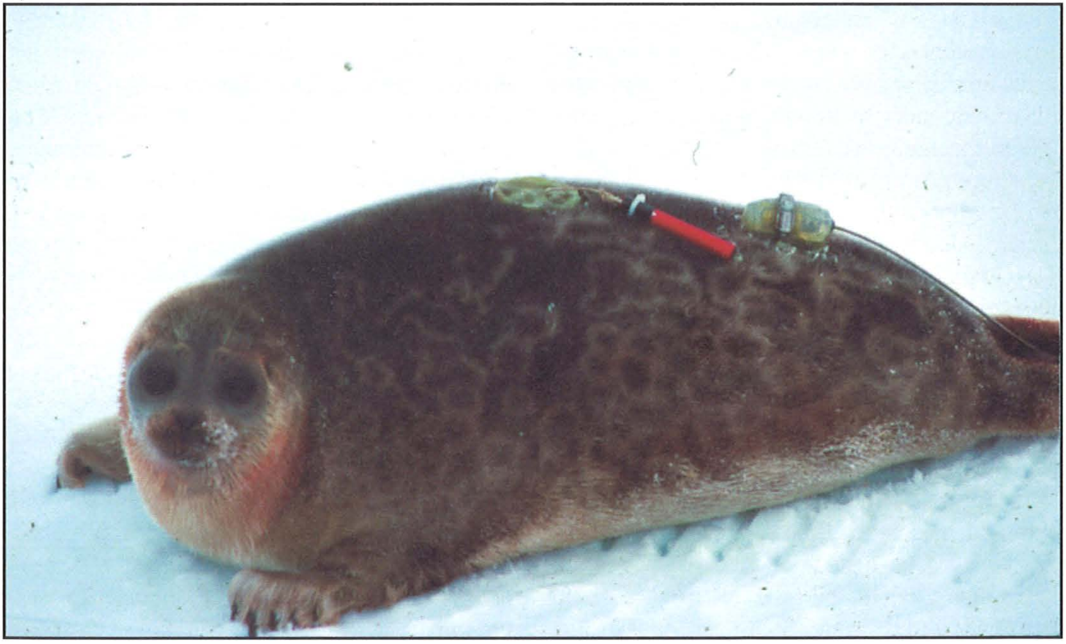

Fig. 8
An adult female ringed seal captured in Strathcona Sound, northern Baffin Island in May 1992, and instrumented to study the effects of ice-breaking traffic. The orange cylinder is a depth-sensitive acoustic tag; the tag with the antenna is a VHF radio tag. (Photo: S. Innes)

Seismic activity along the north coast of Alaska was suspected of causing a reduction in ringed seal abundance, and this led to management actions to regulate the timing, distribution and nature of seismic testing there (Stirling and Calvert 1983). It also stimulated field studies of the effects of various types of industrial noise (e.g. machinery used in seismic operations, helicopters, snow machines, people walking or skiing on the ice) on ringed seals (Burns and Kelly 1982, Kelly *et al.* 1986, 1988, Frost and Burns 1989). Responses showed considerable variability with respect to the behaviour of radio-tagged seals and the rates of abandonment of seal structures at different distances from human activities. In general, it was concluded that seals abandon breathing holes and lairs at significantly higher rates in disturbed than in undisturbed conditions (4% in undisturbed shore-fast ice vs. 13.5% in areas of shore-fast ice subjected to industrial noise) (Kelly *et al.*1988). The impacts are probably most serious from late March through June when the seals are spending more time out of water and the movements of mothers and pups, in particular, are limited to small areas. On-ice vibrational seismic profiling (Vibroseis) displaced seals from breathing holes and lairs, but the effects were considered local and judged to be of little significance at the population scale (cf. Kelly 1988, Davis *et al.* 1991).

The effects of underwater noise, especially from ice-breakers and tankers, in masking vocalizations or otherwise disturbing ringed seals have been widely acknowledged but little studied. Such effects are thus uncertain and controversial (e.g. Mansfield 1983, Smith 1987, Kelly *et al.* 1988, Davis *et al.* 1991).

ORGANOCHLORINE BODY BURDENS

The relatively high consumption of lipid-rich wildlife foods, including ringed seal tissues, places Arctic residents at high risk of exposure to lipophilic organochlorine contaminants (Dewailly *et al.* 1989, 1993, 1996, Jensen 1991, Cameron and Weis 1993). The bio-accumulation of organochlorine compounds by polar bears is closely linked to levels in ringed seal tissue (Zhu and Norstrom 1993). Much of the documentation of contaminant levels in ringed seal (and other marine mammal) tissues has been undertaken as a way of monitoring global patterns of dispersal of these compounds (e.g. Luckas *et al.* 1990, Muir and Norstrom 1991). The main sources of these pollutants are in agricultural and industrial centers outside the Arctic. Transport pathways can be through airflow and precipitation or through freshwater drainage. The most abundant residues detected in the tissues of Arctic marine mammals are toxaphene, chlordane and PCBs (Wagemann and Muir 1984, Jensen 1991).

A decline was documented both in PCBs and the DDT-group in ringed seals from the Holman area of the western Canadian Arctic between 1972 and 1981. Of the two, PCB levels had declined much faster (average PCB/DDE ratio 3.34 in 1972, 1.71 in 1981) (Addison *et al.* 1986). An opposite trend was found at Svalbard, where the PCB/DDE ratio in ringed seal blubber almost doubled between 1984 and 1986 (0.96 to 1.73) (Daelemans *et al.* 1993). By 1989, the blubber concentrations of PCBs in ringed seals at Holman had declined to about 20% of their 1972 level (Addison 1992). A continuing supply of DDT to the western North American Arctic was inferred from the less dramatic decline of DDT-group residues (*Ibid.*).

Organochlorine residues in ringed seal blubber from the central Canadian high Arctic (Barrow Strait, Admiralty Inlet, Jones Sound) consisted of approximately equal portions of chlordane, PCB and DDT isomers (Muir *et al.* 1988). Chlorinated cyclodeine compounds in ringed seals, polar bears and people in northern Quebec were investigated by Zhu *et al.* (1995). Levels of polychlorinated compounds in ringed seals at Svalbard have been reported in numerous publications (e.g. Oehme *et al.* 1988, 1990).

Pathological changes in uterine physiology, attributed to high concentrations of chlorinated hydrocarbons, were documented in Baltic Sea ringed seals during the 1960s and 1970s (Helle *et al.* 1976, Helle 1980b; see McLaren and Smith 1985:69 for a "note of caution"). Comparisons of dieldrin, DDT-group and PCB levels in ringed seals from the Arctic (Canadian and Norwegian) vs. other phocids in northern temperate latitudes revealed consistently less contamination in the Arctic ringed seals (Holden 1972). In contrast, levels of toxaphene (polychlorinated camphenes, PCCs) in ringed seals from Svalbard were found to be similar to those of seals from the Baltic and Caspian seas (Andersson *et al.* 1988).

BODY BURDENS OF HEAVY METALS

Concerns similar to those mentioned above in relation to organochlorines, potential health effects on seals and on human consumers of seal tissues, apply to heavy metals (e.g. Smith and Armstrong 1978, Hansen 1981, Dietz *et al.* 1990, 1996, this volume, Muir *et al.* 1992). Besides being delivered locally as a result of normal geological processes, these substances are carried in the atmospheric airflow from southern sources and delivered to the Arctic marine system through precipitation (Muir *et al.* 1992). Mercury, cadmium, lead, selenium, arsenic and nickel are the most commonly reported heavy metals in Arctic marine mammals (Wagemann and Muir 1984). Concentrations of heavy metals are usually highest in the enzyme organs (especially liver) and muscle. Toxic and mutagenic effects have not been unequivocally demonstrated in marine mammals (Melnikov 1991).

It has been suggested that ringed seals may have some protection from mercury poisoning because of an ability to de-methylate mercury and store it in a less toxic form (Koeman *et al.* 1975). Selenium may be involved in the process of mercury detoxification in ringed seals (Koeman *et al.* 1975, Smith and Armstrong 1978, Holden 1978). One freshwater ringed seal, however, with a relatively high concentration of mercury (210mg/kg in its liver) showed behavioral symptoms of methyl mercury poisoning (Tillander *et al.* 1972, Kelly 1988).

Adult ringed seals from Greenland had significantly higher concentrations of organic mercury (in muscle, liver and kidney tissues) than those of "yearlings" (Dietz *et al.* 1990). Most of the mercury in the muscle tissue of ringed seals was organic mercury. Much higher levels of mercury and selenium were found in the tissues of ringed and harp seals than in those of harbour and grey seals killed in Norwegian coastal waters (Skaare *et al.* 1994).

Wagemann (1989) studied relative body burdens of seven metals (lead, mercury, cadmium, copper, zinc, selenium and arsenic) in two groups of ringed seals, one ("exposed") group from Strathcona Sound near a lead-zinc mine and the other ("reference") group from the larger, adjacent Admiralty Inlet. The exposed group had significantly higher mean concentrations of lead in liver and selenium in muscle than the reference group, and nearly half of the exposed individuals had higher mercury, lead or cadmium levels than the reference group. Seals from both groups had high cadmium concentrations. Cadmium levels were about twice as high in the liver of ringed seals from the eastern Canadian Arctic than in that of ringed seals from the western Canadian Arctic (Wagemann *et al.* 1996).

The finding of higher mercury levels in ringed seals from the western than the eastern Canadian Arctic has been interpreted as the result of a difference in natural background concentrations (Wagemann *et al.* 1995, 1996). However, mercury levels in the livers of ringed seals from the western Canadian Arctic were significantly higher in animals sampled in 1987-93 than in ones sampled in 1972-73, indicating a temporal increase in rate of accumulation over the past 20 years within that region (Wagemann *et al.* 1996).

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