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A Review of the Developmental, Behavioural and Physiological Adaptations of the Ringed Seal, *Phoca hispida*, to Life in the Arctic Winter

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ABSTRACT. Ringed seals, *Phoca hispida*, the smallest of the marine arctic pinnipeds, are one of only two seal species in the world adapted to life in the land-fast sea ice. The habitat is characterized by a stable ice platform forming in early winter and lies at latitudes subject to extreme low temperatures. The small body size of adults and semi-altricial pups are an unusual adaptation to cold, allowing ringed seals to use shelters that they construct in the snow overlying their breathing holes. These small subnivean structures act to hide adults and pups from predators, especially polar bears, *Ursus maritimus*, and arctic foxes, *Alopex lagopus*. It appears that dry lanugal pups could withstand the arctic cold without shelter, but pups that have been wetted become hypothermic and require shelter to regain thermoneutrality. Since female seals actively swim away with their pups from attacks on their birth lairs by foxes and bears, both the physical and the thermal protection of alternate subnivean lairs are important for the survival of the neonate. Weddell seals, *Leptonychotes weddelli*, resident in the land-fast ice of the Antarctic, are the ecological counterpart of the ringed seal. Their large body size is typical of the usual cold adaptive strategy of other polar phocid seals.

Key words: ringed seal, behaviour, development, physiology, adaptations, arctic winter, *Phoca hispida*

RÉSUMÉ. Le phoque annelé, *Phoca hispida*, le plus petit des phoques marins de l'Arctique, est l'une des deux seules espèces adaptées à l'hiver dans les habitats côtiers; ces habitats se caractérisent par une plate-forme de glace stable qui se forme au commencement de l'hiver à des latitudes auxquelles sévissent de très basses températures. La petite taille des adultes et l'état de sous-développement relatif des nouveau-nés constituent des adaptations insolites au froid associées à l'utilisation d'abris construits sous la neige. En plus d'aider à l'équilibre thermique, ces terriers sous-nivéens sont une protection contre les prédateurs, surtout les ours blancs, *Ursus maritimus*, et les renards arctiques, *Alopex lagopus*. Il semble que les blanchons pourraient supporter sans abris les froids de l'Arctique lorsque leur pelage est sec; lorsqu'ils sont mouillés, ils entrent en hypothermie et la présence d'un abri est alors nécessaire pour regagner la thermoneutralité. Puisque les femelles, en cas d'attaque par les ours ou les renards, fuient le terrier à la nage avec leur blanchon, la protection physique et thermique de terriers de remplacement est très importante pour la survie des nouveau-nés. Le phoque de Weddell, *Leptonychotes weddelli*, occupant les habitats de glaces côtières en Antarctique, est l'espèce écologiquement analogue au phoque annelé. Ils ont une grande taille qui représente la stratégie typique d'adaptation au froid des autres *Phocidae* des régions polaires.

Mots clés: phoque annelé, comportement, développement, physiologie, adaptations, hiver arctique, *Phoca hispida*

INTRODUCTION

The ringed seal is the smallest of the Arctic Ocean pinnipeds, with a birth weight of 4-5 kg and an adult female asymptotic weight of 65 kg. It is the only one of the seven phocid species in the Arctic Ocean adapted to living throughout the winter in the land-fast ice. Two closely related species, *Phoca caspica* and *Phoca sibirica*, live in the Caspian Sea and Lake Baikal, large areas of semibrackish water cut off from the Arctic Ocean. They are of comparable or smaller size than the ringed seal and show similar adaptations to the winter habitat (King, 1983).

As a winter resident in the coastal areas of annually forming ice up to latitudes of approximately 82°N, the ringed seal has developed adaptations allowing it to maintain thermoneutrality in extreme low temperatures, feed itself in areas of low marine productivity, successfully nurture its slow-growing young and avoid mortality from predation.

The ringed seal is circumpolar in its arctic distribution, occupying areas of ice-covered oceans influenced by diverse meteorological and oceanographic features. It gives birth during the spring to a single lanugal pup in the shelter of a subnivean lair (Smith and Stirling, 1975). We review and examine the developmental, behavioural and physiological adaptations of the ringed seal that have been shaped by the various features of its habitat and relate these to the geographic and climatic factors governing population size and distribution.

THE STUDY AREAS AND TYPES OF ICE

We have studied ringed seals in three different areas of the Canadian Arctic: southeastern Baffin Island (latitudes 62-64°N), the Amundsen Gulf region (latitudes 70-72°N) and the Barrow Strait area (latitudes 74-75°N) (Fig. 1). Recently we have also had the opportunity to examine the areas of western Spitsbergen (latitudes 78-79°N) (Fig. 1). Each area differs somewhat in its climate and its ice and snow cover characteristics (Table 1). Both the duration of the ice cover and the total precipitation are important factors combining to create sufficient snow depth for the building of the subnivean lairs by ringed seals. Features of the surface topography of the ice also play an important part in providing obstacles around which snow can accumulate.

Southeastern Baffin has a complex coastline of deep fiords, which freeze up each year in late autumn and remain stable until break-up in late June. The shoreline fast ice is deformed by large tides, which create persistent cracks across the entrances to bays. Often lairs are associated with these cracks, which are covered by considerable depths of snow (Smith *et al.*, 1979; Smith and Hammill, 1981). Snowfall is sufficient in southeastern Baffin to permit lair construction even where there are no obvious rough ice surface features (Smith and Hammill, 1981).

Amundsen Gulf, bounded by the arctic mainland to the south and Banks and Victoria islands to the north, is a vast area subject to varying ice cover from year to year (Stirling

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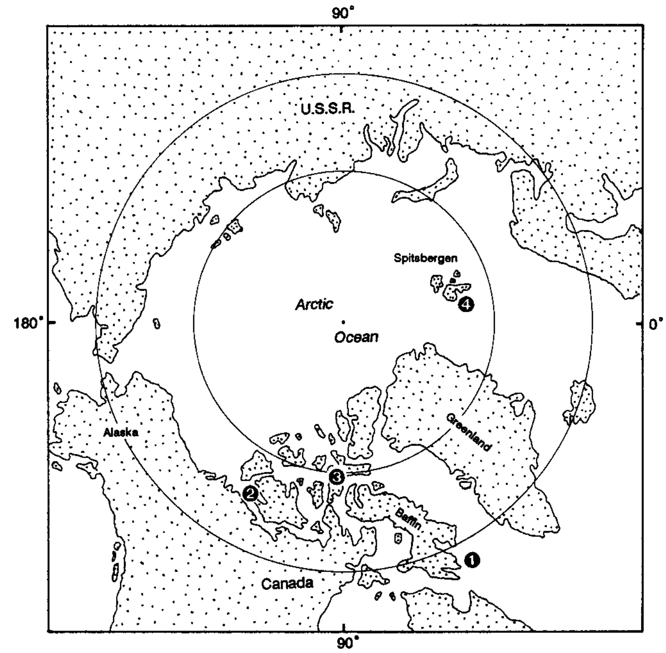

FIG. 1. Map of study areas in the Canadian and Norwegian Arctic: (1) southeast Baffin Island; (2) Amundsen Gulf; (3) Barrow Strait; (4) western Spitsbergen.

et al., 1982; Hammill, 1987a; Kingsley, 1984). In large sea-ice expanses, such as Prince Albert Sound in eastern Amundsen Gulf, where currents and tides are not pronounced, wind appears to be the main factor influencing the surface ice features. Lairs in these areas are found along well-defined pressure ridges or in areas of ice hummocks. Pressure ridges are often in the same general locations each winter and sometimes cross the sounds from one shore to the other. Areas of ice hummocks are less well-defined regions in the ice sheets that have been broken up by wind pressure during the early part of the winter. Ice blocks, about 15-25 cm thick and variable in their height above the ice surface, result in snow drifts of different depths. These areas are very stable and provide a more dispersed and diverse selection of sites for lair construction than do pressure ridges.

Barrow Strait is bounded to the north by Cornwallis and Devon islands and to the south by Prince of Wales and Somerset islands. In the majority of years the fast ice extends from Viscount Melville Sound to Lancaster Sound, but considerable variation is seen in the position of the eastern fast-ice edge (Lindsay, 1975, 1977; Marko, 1982). The anchor points for the land-fast ice in Barrow Strait are quite distant and the ice sheet is subject to considerable influence from both currents and wind. Temperatures are quite low, so that periods of calm result in extensive ice formation and consolidation. Seal lairs are normally found associated with small, low-profile pressure ridges formed where the ice pans meet.

The west coast of Spitsbergen is fiord indented and influenced by the warm Norwegian current (Gulf Stream). Here the annual dates of freeze-up and break-up are extremely variable and are affected by the orientation and topographical characteristics of the different fiords and bays in Svalbard. For example, Kongsfiord over the period 1980-87 only had two years of the eight when the fast ice persisted without breaking up during the winter period. Because of the general instability of the fast-ice platform, snow accumulation for ringed seal lairs also is very uncertain. The ice surface of western Spitsbergen fiords is very flat, with few pressure ridges or ice hummocks. The main areas where snow accumulates to sufficient depths for seal lair formation are in the vicinity of active glaciers, where bergy bits and growlers have frozen into the annual ice (Armstrong *et al.*, 1973; Lydersen and Gjertz, 1986). These areas are subject to disruptions in late winter, when the glaciers begin to calve; when the ice sheet is thin, glacier calving can occasionally break up the whole of the fragile land-fast ice platform (pers. obs., Kongsfiord, April 1984).

METHODS

Surveys of the Breeding Habitat

The subnivean lairs and breathing holes of ringed seals were located by trained survey dogs (Smith and Stirling, 1975). Each structure was then opened and classified as a birth lair, haul-out lair, male haul-out lair, breathing hole or male breathing hole. Structures used by rutting males were distinguished by the lingering odour produced by facial secretions from the underlying secretory sebaceous and apocrine glands (Hardy *et al.*, in press). The relative abundance of structures in these surveys was expressed as the number of lairs or holes found per unit time of searching. Where absolute densities were required, we used a catch per unit effort model called the removal method (Zippin, 1956). This was applied to the number of structures found by the dogs during searches of fixed effort in measured plots of 2.25 or 4.0 km^2 (Hammill and Smith, 1990).

TABLE 1. Temperature, snow depth, tidal amplitude and sea-ice surface topography of study areas in the Canadian and Norwegian Arctic

Area	Latitude (N)	Mean Jan. temp. (°C)	Max. tidal amplitude (m)	Snow accumulation Nov. - 30 April (cm)	Ice topography for subnivean lair construction	Sources
SE Baffin Island, N.W.T.	62-64°	−25	12	106	Stable fiords, tidal ridges	Smith *et al.* (1979); Smith and Hammill (1981)
Amundsen Gulf, N.W.T.	70-72°	−27	1	49	Ice hummocks and large pressure ridges	Smith and Stirling (1975, 1978)
Barrow Strait, N.W.T.	74-75°	−33	2	30	Small pressure ridges, consolidated ice pans	Hammill and Smith (1989)
Western Spitsbergen	78-79°	−12	1	56	Flat fiord ice, bergy bits at glacier foot	Lydersen and Gjertz (1986)

Snow depths were recorded over each seal structure and at several points in the plots where densities were estimated (Hammill and Smith, 1989). Lairs were described by their two maximum horizontal dimensions and the height of the dome in the main chamber (Smith and Stirling, 1975). Evidence of predation by arctic fox (Smith, 1976) or polar bear (Stirling and Archibald, 1977; Smith, 1980) were noted in detail.

A qualitative description of the ice surface was noted in the surveys where relative abundances were measured. In the measured plots the topography was assessed from aerial photographs taken with a 7.0 × 7.0 cm format camera from a helicopter at 300-350 m altitude. Photographs were examined using a 121 grid square per frame overlap, from which the frequency of pressure ridges and rough ice was recorded.

Metabolic Rate Determination

Resting metabolic rate of wet and dry pups exposed to temperatures of +10 to −35°C was determined in seven lanugal and two moulted pups captured at Kongsfiord on Svalbard during March to April in 1979 and 1980. The pups were housed on snow in outdoor cages with access to warm wooden boxes for shelter. They were fed, via a stomach tube, homogenized summer herring fillets, supplemented with vitamins and salt tablets (Taugbøl, 1984). Lanugal pups were fed 850 g of herring per day in 1979 and 550 g of herring per day in 1980. Moulted pups were fed 500-1500 g of herring per day. Metabolic rates were determined by indirect calorimetry. Outside air was pumped through a cylindrical metabolic chamber (0.4 × 0.8 m), then through a moisture-absorbing filter (Kieselgel). CO_2 levels inside the chamber were kept below 0.9%. In 1979, expired air was collected in 200 L Douglas bags during metabolic trials lasting 15-30 min. CO_2 concentration was measured using a Scholander ½ cc chemical gas analyzer (Scholander, 1947). In 1980, CO_2 and O_2 concentrations were monitored continuously (Applied Electronics S-3A O_2 analyzer and Leybold-Heraeus Binos 1 CO_2 analyzer) during 30 min metabolic trials. Metabolic rates were measured 4-5 h after feeding, at least 2 h after exposure to a given temperature and when the metabolic rate had remained constant for 30 min. Skin and rectal temperatures were measured after metabolic trials or after the pups had spent a minimum of ¼ h in air after being immersed in water.

Biological Samples

Surveys of the breeding habitat were supplemented by collections of animals with the help of Inuit hunters. Animals were killed at their breathing holes or after they had hauled out onto the ice during the spring. From these animals we measured total length, maximum girth, axillary girth, sternal blubber thickness, body weight and sculp weight. A lower canine tooth was removed to determine age. Stomach contents and female reproductive tracts were also examined to determine diet and reproductive rates (Smith, 1987; Hammill, 1987b).

RESULTS AND DISCUSSION

Maternal Investment and Pup Development

The small ringed seal resident in the stable land-fast ice has a lactation period of 38-44 days, which is similar to that of the Weddell seal but is much longer than the 4- to 28-day lactation period of seals occupying the pack ice (Table 2). Because of the sensitivity of ringed seals to disturbance on the ice resulting from their exposure to polar bear and arctic fox predation, it has been necessary to use dead specimens collected through the season to study pup development. At birth the pups weigh only 4.5-5 kg (Smith, 1987; Hammill, 1987b), which is smaller than the predicted weight of 7.0 kg for a female ringed seal with an asymptotic weight of 65 kg (Kovacs and Lavigne, 1986). During lactation the pups grow to a length of 91 cm and weigh 20.3 kg (range 11.4-35.9 kg). We likely underestimate weaning weight because we do not know how long the pups have been fasting at the time of collection. Estimating weight at weaning using body length-weight relationships (Usher and Church, 1969) and assuming that little growth occurs after weaning would yield pups of 22.2 kg, for a growth rate of 450 $g \cdot d^{-1}$ and 6.1 $mm \cdot d^{-1}$. This represents a caloric value of approximately 116 000 kcal (Stirling and McEwan, 1975). Weight at weaning expressed as a percentage of the asymptotic weight of the adult female is around 0.30, which is similar to the ratio found in other northern pinnipeds (Table 2). It appears that pups achieve 93% of their first-year growth in body length during the suckling period. They then appear to lose condition during August and September and probably regain their fat stores during the winter months.

During lactation female ringed seals lose approximately 450 $g \cdot d^{-1}$, which is similar to the rate of weight gain seen in the pups but does not take into account the costs of milk production or maintenance costs of the female. In order to meet these costs, it appears that the female is actively supplementing her energy reserves by feeding beneath the ice (Hammill, 1987b). After a lactation period of 44 days, the females have lost close to 27% of their body weight, which is similar to the 20-22% reported in hooded, *Cystophora cristata* (Bowen et al., 1987) and harp seals, *Phoca groenlandica* (Stewart, 1986), but is much less than the 38-46% weight loss reported in grey seals, *Halichoerus grypus* (Fedak

TABLE 2. Weight and development of northern phocid seals

Species	Adult female weight (kg)	Birth weight (kg)	Weaning weight (kg)	% of adult female weight	Lactation period (d)	Weight gain per day (kg)	Sources
Phoca hispida	61	4-5	36.8	27	44	0.76	Smith (1987); Hammill (1987b)
Phoca largha	65	10	28	43	28	0.64	Burns et al. (1972)
Phoca groenlandica	130	9.9	35.0	20	12	2.0	Stewart (1986)
Halichoerus grypus	170	14.6	44.2	38	17	1.8	Anderson and Fedak (1987)
Cystophora cristata	179	22	41	22	4	7.1	Bowen et al. (1987)
Erignathus barbatus	271	33.4	84.6	31	12-18	2.8	Burns and Frost (1988)
Histriophoca fasciata	90	10.5	27-30	32	21-28	0.72	Burns (1970)

and Anderson, 1982), northern Elephant seal, *Mirounga angustirostris* (Costa *et al.*, 1986) and Weddell seals (Tedman and Green, 1987).

Thermoregulation and Metabolism of Pups

The skin temperatures of dry lanugal pups are quite high. At ambient temperatures of +5 to −10°C, skin temperatures of 37°C were measured on seven lanugal pups. These temperatures declined to 29°C when ambient air temperatures were reduced to −35°C, but no change was observed in rectal temperatures, which remained stable at 37.5°C. Rectal temperatures of lanugal pups declined to 35.5°C after immersion in ice water for 15 min and were further reduced to 33°C after immersion for 30 min. After removal from the water, the pups commenced shivering and curled into a fetal posture.

Skin temperatures of moulting pups were 10-20°C cooler than the rectal temperatures of 37.5°C over the ambient air temperature range of +5 to −23°C. Rectal temperatures showed no change in a 20 kg moulted pup immersed for 2 h in ice water, but declined to 36°C in a 13 kg moulted pup with 2 cm of blubber after an equal period of immersion.

Resting metabolic rates were up to three times higher than predicted by Kleiber for BMR (Table 3). In a single lanugal pup measured over the temperature range of 10 to −35°C, metabolic rates increased sharply at −25°C (Fig. 2). We were unable to examine the remaining lanugal pups over the entire temperature range, but higher rates were observed at temperatures below −25°C (Table 3). A lanugal pup immersed in ice water for only a few minutes had metabolic rates 70% higher than thermoneutral rates (Fig. 3). At temperatures >0°C, the wet pup took 4-5 h to return to thermoneutral values, while at temperatures of −8 to −10°C, increasing signs of hypothermia were observed. In dry moulted pups, the lower critical temperature was −10°C based on metabolic trials completed on two pups over the temperature range −25 to +10°C (Fig. 4). Resting metabolic rates of three animals weighing 20-50 kg were 20 ml $O_2 \cdot kg^{-0.75}$, while the small moulted pup weighing 13 kg had a metabolic rate of 27 ml $O_2 \cdot kg^{-0.75}$.

Age Distribution within the Sea Ice

During the ice-free months all age classes of ringed seals are found in the coastal areas of the Canadian and Norwegian Arctic. As ice begins to form, initially in the fiords and large bays and then later in the inter-island channels and straits, seals begin to actively maintain position in the ice by digging open breathing holes and later constructing subnivean lairs.

Knowledge of the distribution of seals in their winter habitat is based primarily on collections of specimens killed by the Inuit in the late spring where seals haul out onto the ice or from dog search surveys of the subnivean lairs. On southeastern Baffin there is an age segregation resulting in the sexually mature seals occupying the stable fiord ice, which provides the best sites for birth lairs (McLaren, 1958; Smith, 1973). Adult males appear to be actively territorial, and parturient females might also maintain territories around a few potential birth-lair sites (Smith and Hammill, 1981). The same general picture pertains to the Prince Albert Sound area in the Amundsen Gulf. There prime birth-lair habitat appears to be in the areas of hummocked ice and large pressure ridges. Subadults are sometimes found adjacent to ice, but they are restricted to occupation of breathing holes along refrozen cracks with little snow cover for lair formation. In those situations subadults often are bitten and actually driven out of the water, evidence of strong intra-specific territoriality (Stirling, 1973; Smith, 1987).

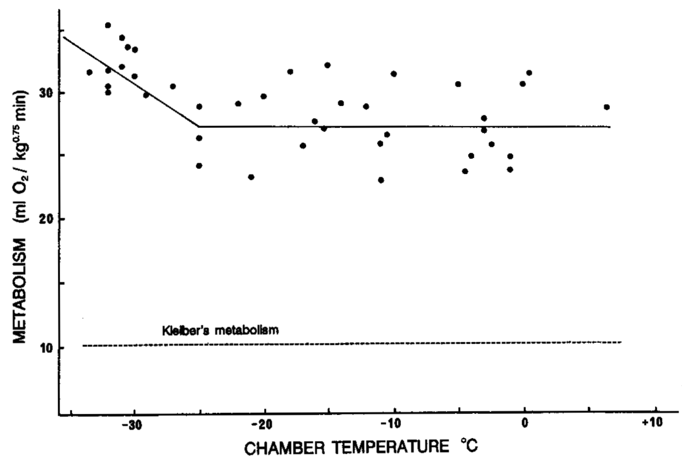

FIG. 2. Resting metabolism of a lanugal ringed seal pup in air temperatures of +10 to −35°C.

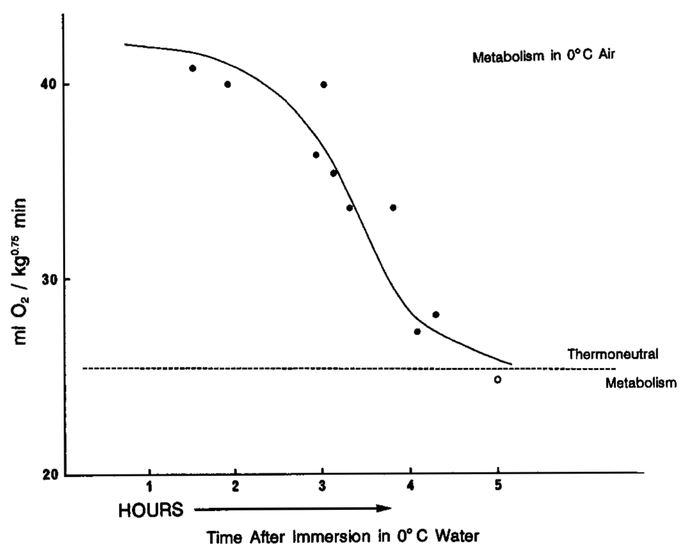

FIG. 3. Metabolism of a wet lanugal ringed seal pup at 0°C.

TABLE 3. Resting metabolism (ml $O_2 \cdot kg^{-0.75}$ min) of lanugal ringed seal pups above and below −25°C

Seal #	Metabolism at above −25°C	No. of tests	Respiratory Quotient	Metabolism at below −25°C	No. of tests	Respiratory Quotient
3	27.0 ± 0.5	28	0.78 ± 0.005	32.2 ± 0.6	14	0.76 ± 0.006
4	22.7 ± 0.8	14	0.74 ± 0.01		0	
5	23.6 ± 0.9	8	0.79 ± 0.001	27.6	1	0.77
6	27.9 ± 1.7	2	0.77 ± 0.01	33.0 ± 0.4	3	0.76 ± 0.003
7	23.0 ± 1.4	3	0.77 ± 0.02	28.4	1	0.74

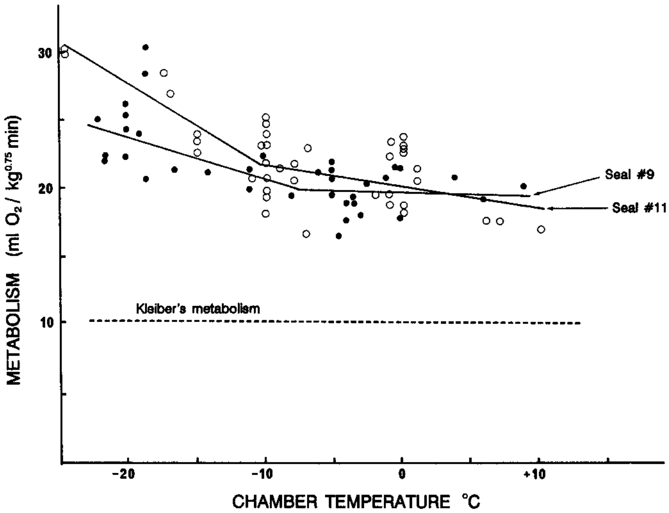

FIG. 4. Resting metabolism of two moulted ringed seal pups in air temperatures of +10 to −20°C.

In the Barrow Strait area of the Canadian High Arctic we have recently examined the large-scale and proximate features of sea-ice habitat influencing the winter distribution of ringed seals. The extent of ice cover and date of ice consolidation is so variable that ringed seals must be adaptable to local habitat features. In this area ringed seals do not necessarily remain in the areas first occupied during the late autumn months. Instead they follow the advancing ice edge, seeking out areas with deep snow in areas of late-consolidating yet stable ice. There is also evidence that ringed seals are able to dig new holes through ice 45-65 cm thick and thus select sites with suitable snow accumulation for the construction of birth lairs. In such areas immature ringed seals are sometimes seen in close proximity to breeding habitat occupied by the mature animals, but they are still restricted to areas of more unstable ice with little snow cover (Hammill and Smith, 1989).

In the Norwegian Arctic, large collections of ringed seal specimens have only been taken in the area of Kongsfiord on western Spitsbergen. In Kongsfiord the mean age of males was 11.3 and that of females was 14.3 years, which is quite old compared to those from other study areas (Lydersen and Gjertz, 1986). Most samples were taken during the March-April period on the stable fiord ice near the glacier feet, and the juvenile age classes are excluded at this time of the year, as in other areas of prime breeding habitat we have examined.

The Subnivean Lair

In autumn the small bays and large sounds that freeze over are often broken open several times by wind and tide before finally consolidating. Ringed seals occupying these areas maintain breathing holes by abrading the forming ice with the strong claws of their foreflippers. The bearded seal, *Erignathus barbatus*, harp seal and grey seal also form or maintain holes in the sea ice in this fashion (TGS and MOH, pers. obs.), but the Weddell seal, the Antarctic counterpart of the ringed seal, maintains its breathing holes by abrading the ice with its canines and incisors (Bertram, 1940; Stirling, 1969).

Breathing holes are initially situated in the last remaining areas of open water, such as cracks in the ice along the edges of ice pans, leads or along pressure cracks. These areas may have a rough or elevated ice surface profile, which causes the accumulation of snow.

Subnivean structures made by ringed seals are of two basic types, the birth lair and the haul-out or resting lair. The lairs are dug into the wind-compacted snow by the seal working initially from within the enlarged breathing hole. Ordinary resting lairs are found as early as January in some areas. The chamber averages approximately 1.5 × 2.0 m, with a ceiling about 30 cm high. These lairs can be occupied by either sex, but those used by rutting males are easily identified by their particular odour. Birth lairs are not found until about mid-March at the earliest. They are located in much larger drifts than haul-out lairs and are distinguished by the small tunnels off the main chamber, which are dug by the pup, or by evidence of the remains of the white natal lanugo of the pup frozen to parts of the walls. The main chamber is approximately 2.5 × 3.0 m, with a 30 cm ceiling, and is found in snow of about 75 cm minimum depth. The birth lair is usually one of two to three similar structures in the area separated by up to 200 m and forms part of a complex belonging to the same female (Smith and Stirling, 1975, 1978; Smith and Hammill, 1981).

The Role of Predation

Ringed seals are hunted in their sea-ice habitat by polar bears, arctic foxes and man.

The Thule Inuit culture entered the Canadian Arctic about 1000 years B.P. Their culture was strongly dependent on the ringed seal for the necessities of life. Living on the land-fast sea ice in domed snow houses for 6-8 months of the year provided them with a constant source of food and fuel close to their dwellings (Stefansson, 1913; McGhee, 1984). Present-day Inuit continue to live on the sea coast and still depend to a certain extent on ringed seals for their food and cash revenue (Smith and Wright, 1989). In Canada as late as 1974 or 1975, certain areas were heavily harvested for ringed seal pelts (Smith and Taylor, 1977). While no direct quantitative estimate is possible on the levels of harvesting mortality, it is probable that in areas such as the Amundsen Gulf the Inuit killed as much as 7% of the neonates annually (Smith, 1987). Recent anti-hunting pressures, which have destroyed the European fur markets for seal pelts, have had a serious impact on the Inuit economy and resulted in a reduced harvest of ringed seals in Canada (Wenzel, 1978; Smith, 1987).

Polar bears depend primarily on ringed seals for their sustenance (Stirling, 1988) and are most successful at hunting them from the sea ice. Bears use a variety of strategies when hunting (Stirling, 1974a; Stirling and Archibald, 1977) and are able to kill ringed seals of any age or size. During the winter months they hunt along ice edges or open leads, sometimes lying in wait for seals at their breathing holes (Kumlein, 1879; Freuchen, 1935). These hunting strategies are not well described or quantitatively evaluated, but the main mortality in these situations is within the juvenile age classes (Stirling and McEwan, 1975; Smith, 1980).

During the months of March through May bears hunt ringed seals in their subnivean lairs. The relative amount of effort expended by bears on hunting in these habitats compared to other situations is not known. Most bear attacks on subnivean lairs are aimed at the birth lairs (Smith *et al.*, 1979; Smith, 1980; Gjertz and Lydersen, 1986), with strong evidence that they selectively avoid taking rutting male seals (Smith, 1980). In areas such as Amundsen Gulf and the fiords of Svalbard and southeastern Baffin Island, bears hunt mainly along defined pressure ridges, in hummocked ice or along refrozen cracks situated at the entrances to bays or fiords. They rarely penetrate deep into fiords, preferring to concentrate hunting efforts between the most productive areas of stable land-fast ice and the offshore ice containing open water areas.

When hunting at birth lairs, polar bears easily kill the newborn pups and attempt to catch the fat mother seal when she returns to rescue her pup (Smith, 1980, 1987; Stirling and McEwan, 1975). Often the carcass of the pup is found only beheaded or almost untouched by the bear, while the whole of the blubber layer of the adult female has been consumed. When hunting in areas containing pups a polar bear will usually open more than one birth lair in its attempt to kill a seal. The abundance of digs in an area and the relatively low success rate (Smith, 1980; Hammill and Smith, 1990) attests to the efficiency of the birth lair complex as a means of protecting ringed seals from bear predation. However, polar bears may still have a significant impact on ringed seal production. In Barrow Strait, pup mortality from bear predation varies from 8 to 44% of the estimated pup production (unpubl. data) and is influenced by local fast-ice conditions, proximity of the fast-ice edge (Ramsay and Stirling, 1986) and snow conditions.

Arctic foxes only recently have been recognized as important predators of ringed seal pups in almost every part of their circumpolar range. In the Amundsen Gulf area large fox populations are subject to marked annual variation in numbers. Mortalities of seal pups vary with the density of foxes in the range of 0.06-0.40 of the total annual pup recruitment (Smith, 1987). In other areas, such as southeastern Baffin Island (Smith *et al.*, 1979), the Beaufort Sea (Burns and Frost, 1988) and western Spitsbergen (Lydersen and Gjertz, 1986), significant fox predation on birth lairs has also been noted.

The diminutive arctic fox, weighing 2-3 kg when mature (Hammill, 1983), appears to be capable of killing newborn pups only in the early stages of their development. Foxes are very efficient at finding lairs and had scent-marked most of the structures that we found in our surveys (Smith, 1987). Foxes are probably able to identify birth lairs, since we find them to be penetrated more frequently than other types of seal structures (Smith, 1976). The small, 10 cm diameter hole dug by the fox allows it entry into the birth lair, where it kills and consumes the pup.

We have made observations at Kongsfiord, on western Spitsbergen, where ringed seal pups are born on the surface of the ice because of insufficient snow cover for lair construction. In these circumstances we have watched single foxes observing the area from vantage points along the nearshore pressure ice zone. When they see a birth taking place they quickly run to the birth site and proceed to bite the pup around the muzzle and eyes until it is incapacitated. The initial reaction of the mother seal is to flee by diving down her exit hole into the water, which gives the fox time to seriously injure the newborn and move it some distance away from the hole. The newborn is usually not able to escape into the water, but we have noted a few exceptions. After her initial flight, the female invariably returns but will not move more than a few metres from her hole to rescue her pup. If given the chance, the female will move the pup by biting the head or neck and swimming with it to another site. The mother–pup bond appears to be quite strong in some pairs and is used to some advantage by Inuit hunters to lure the female back to the hole by lowering the pup attached to a line into the water. When the female returns it is easily harpooned by the waiting hunter.

Avian predators such as glaucous gulls, *Larus hyperboreus*, and ravens, *Corvus corax*, are also known to kill pups born on the surface of the ice (Lydersen and Smith, 1989). This may be an important source of mortality in fast-ice areas adjacent to open water where large numbers of gulls overwinter and may be one of the important factors limiting the southern range of the ringed seal.

CONCLUSION

The earliest phocids that have been found are from the middle Miocene and appear to have dispersed from the North Atlantic basin (Davies, 1958; Repenning *et al.*, 1979; Repenning, 1980). With the subsequent cooling in the Pliocene and ensuing Pleistocene glaciation, a diversity of species appeared. Many became adapted to life in the pack ice since access to land-breeding sites was restricted, especially in the polar regions. Only two species, the arctic ringed seal and the Antarctic Weddell seal, have evolved to occupy the land-fast oceanic coastal ice.

Life in the polar fast ice necessitates adaptations to residence in a habitat characterized by long periods of extreme low temperatures with restricted access to breathing holes. The Phocine seals, which have evolved a streamlined body form for life in the aquatic medium, have lost some of their mobility on solid substrates, making them more vulnerable to terrestrial predators. This selective pressure has forced the ringed seals into a completely different evolutionary strategy for adaptation to the fast ice than its Antarctic counterpart, the Weddell seal. A combination of cold temperatures and heavy predation on all age classes from polar bears and the large periodic mortality of their pups from arctic foxes has forced the small-sized ringed seals to shelter themselves in subnivean lairs. Weddell seals, living in an area free of terrestrial predators, give birth on the sea ice and have retained the more usual cold-adaptive strategy of large adult body size. Their newborn pups are 29 kg, are born exposed on the sea ice, do not enter the water until 8-10 days of age and are weaned at 110 kg, which is 26% of the asymptotic weight of the adult female. Unlike their pack-ice relatives, Weddell seals have a long lactation period of some 6-7 weeks, gaining approximately 1.3 $kg \cdot d^{-1}$ (Testa *et al.*, 1989). It is thought that this long period of development protects the pups by keeping them in an area sheltered from aquatic predators such as killer whales, *Orcinus orca*, and leopard seals, *Hydrurga leptonyx* (Stirling, 1974b).

It appears that all phocid seals have evolved a natal lanugo, providing them with adequate insulation in dry cold (Øritsland and Ronald, 1973, 1978). They also have special energy stores in the form of brown fat (Grav *et al.*, 1974; Grav and Blix, 1976; Blix *et al.*, 1979) to increase heat production if exposed to extreme low temperatures as neonates. In the ringed seal the lower critical temperature of dry pups is −25°C, which would allow pups to survive unsheltered on the surface of the ice in most parts of their range (Fig. 5). However, the lower critical temperature rises

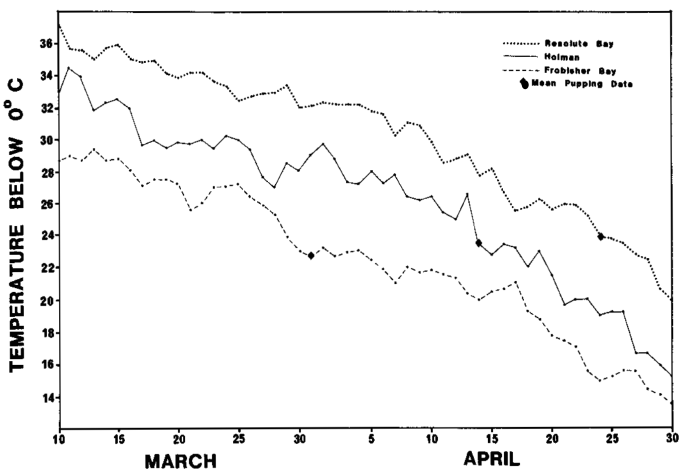

FIG. 5. Mean lowest daily temperature (°C) in three different Canadian arctic locations where ringed seals pup.

dramatically to about 0°C and metabolism remains above the thermoneutral range for a considerable time after the pup has been wetted. Because of the attacks by foxes and bears, neonate seals are forced into the icy water to escape and are therefore greatly dependent on the thermal protection afforded by the subnivean lair to prevent irreversible hypothermia. Lairs occupied by seals have measured temperatures of 0 to +2°C when air temperatures outside were from −15° to −27°C (T.G. Smith, unpubl. data; Kelly and Quakenbush, 1990). The combination of good insulation provided by the snow, the heat from the seals and the seawater result in a relatively warm and efficient thermal shelter.

The small altricial ringed seal pup benefits from the stable fast-ice habitat and thermal shelter to grow slowly during a long lactation period of 6-7 weeks. This increases the total time invested by the mother, but the strategy appears to be adjusted ultimately to her small body size and capacity for blubber storage and possibly to the limited food resources available to her during the arctic winter. The investment of the female in the pup is spread over a longer period by her actively foraging for food during lactation, thereby avoiding high energy costs of building and maintaining a large blubber reserve. This would seem to be a good strategy in view of the high risk of pups being killed by predators prior to weaning.

Much remains to be learned about the behaviour, feeding ecology and physiological adaptations of ringed seals during their occupation of the breeding habitat. Recent developments in technology, including methods of monitoring the movements and diving activity of seals under the ice, will shed new light on how ringed seals have adapted to their specialized niche.

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