Status and biology of harbour seals (*Phoca vitulina*) in Svalbard

Christian Lydersen and Kit M. Kovacs

Norwegian Polar Institute, N-9296 Tromsø, Norway

ABSTRACT

Harbour seals in Svalbard are the northernmost population of this species. This small population is comprised of ca. 1,000 individuals, most of which reside along the west coast of Prins Karls Forland (78°20'N). Satellite tracking studies have shown that adults are resident. Birthing occurs in the latter half of June. Newborns weigh about 11 kg and gain an average of 0.7 kg/d during the nursing period. Haulout patterns in Svalbard harbour seals are influenced by date (season), time of day, tidal cycle and temperature. Moulting takes place in early fall, first among juveniles, then in adult females and finally in adult males. Feeding studies show that polar cod *(Boreogadus saida)* is the dominant prey in terms of numbers, while Atlantic cod *(Gadus morhua)* is the dominant prey based on biomass, at least during the early autumn. Growth curves display significant sexual dimorphism with asymptotic values for standard length and body mass being greater for males. Testosterone levels in males showed an abrupt increase at 6 years of age, while estradiol levels in females increased abruptly from age 4 years. The reproductive rate for adult females was 0.93. Longevity of Svalbard harbour seals is very short compared with populations from other areas.

Lydersen, C. and Kovacs, K. M. 2010. Status and biology of harbour seals (*Phoca vitulina*) in Svalbard. *NAMMCO Sci. Publ.* 8: 47-60.

INTRODUCTION

The harbour seals in Svalbard constitute the northernmost population of this species in the world. The occurrence of this species in Svalbard is mentioned in several accounts from the 1800s (see *e.g.* Brown 1868), but it is evident in some of these records that the authors do not distinguish between harbour and ringed seals (*Pusa hispida*) and that it is the latter species that is described. The first reliable description of this species in Svalbard is from a harbour seal shot in 1898 west of Rossøya (ca 80.83°N, 20.00°E; Fig. 1) described by Römer and Schaudinn (1900). The skull from this specimen has been verified as belonging to a harbour seal by Wiig (1989). The main area

of distribution of this species in Svalbard is off the west coast of Prins Karls Forland (Fig. 1 and 2), and the first trapper diary from this area that distinguished between harbour and ringed seals was from 1907-08 written by Peder Pedersen (Prestrud and Gjertz 1990). In the scientific literature the occurrence of harbour seals in Prins Karls Forland is mentioned by Øynes (1964), and their occurrence is confirmed by observations and specimen collections by Benjaminsen et al. (1973) and Krog and Bjarghov (1973). Since this time, this population has been the focus of several scientific investigations, and the following is a compilation of results from these studies and a general status of knowledge for this unique harbour seal population.

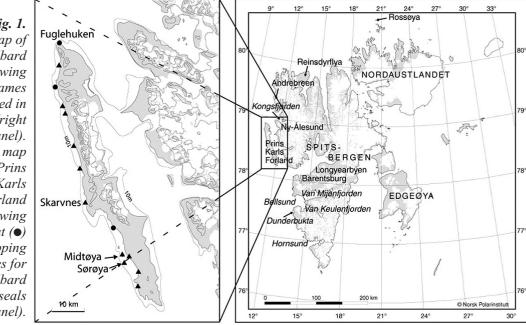
DISTRIBUTION, ABUNDANCE AND MOVEMENTS

The harbour seals in Svalbard are mainly found on the west-coast of Prins Karls Forland (Fig. 1 and 2). This island is 86 km long and is exposed directly to the Greenland Sea; it constitutes the westernmost part of the Svalbard Archipelago. Along the western coastline of this island the northernmost branch of the North Atlantic Current flows northward, making the area warmer than other places at similar latitude. This current is also responsible for keeping the area free of land-fast sea ice during wintertime. During the various studies conducted on harbour seals at Prins Karls Forland many pupping and haulout sites have been registered (see Fig. 1).

Even though the harbour seals in Svalbard are distributed mainly on the west-coast of Prins Karls Forland, observations of this seal species also occur in many other areas. They are regularly found in Kongsfjorden (Hop *et al.* 2002), there is a haulout beach near Andrebreen that is often occupied, and animals are observed at various locations further north, even around the northwest corner of Spitsbergen as far east as Reinsdyrflya. The northernmost record is still the animal shot west of Rossøya in 1898 (see above). South of Prins Karls Forland harbour seals are also sporadically recorded along the west coast of Spitsbergen. A haulout site in Dunderbukta is mentioned by Prestrud and Gjertz (1990). A boat survey for harbour seals in Van Mijenfjorden during summer 2002 recorded 44 animals in July and 31 in August at various haulout sites inside this fjord (Lydersen et al. 2002). Even though Van Mijenfjorden has one of the largest concentrations of harbour seals in Svalbard outside Prins Karls Forland, it is unlikely to be a pupping area since the annual sea-ice normally covers this fjord during the peak pupping time. In addition, a few records of harbour seals from the east coast of Svalbard exist, from the southern parts of Edgeøya (Henriksen et al. 1997).

There is no complete estimate for the size of the population of harbour seals inhabiting Svalbard. A compilation of various opportunistic counts of animals hauled out on Prins Karls Forland from walking, boat, helicopter or snowmobile surveys over several years mainly in the 1980s concluded that the population size was at least 500-600 animals (Prestrud and Gjertz 1990). There was no knowledge available on haulout behaviour of these harbour seals in relation to various environmental, diurnal or seasonal conditions at this time, so no correction was attempted to compensate for animals not hauled out during

Fig. 1. Map of Svalbard showing place names mentioned in the text (right panel). Detailed map of Prins Karls Forland showing *haulout* (•) and pupping (\blacktriangle) sites for Svalbard harbour seals (left panel).



surveys during these various partial estimates. This knowledge is available now (see below: Reder *et al.* 2003) and will be integrated into future surveys for estimation of population size. However, it is clear from the number of seals directly counted in recent years that the population size of harbour seals in Svalbard is at least 1,000 animals.

All harbour seals in Svalbard that have been live-captured for various studies have been equipped with flipper tags (most with one tag in each flipper) resulting in over 400 marked individuals in this small population. Besides recaptures of individuals in the general tagging area during subsequent fieldwork in the same area, only one recapture has been recorded. This was from a young individual that was drowned in a fishing-net at Sommarøya (ca 69.63°N, 18.03°E) west of Tromsø on the Norwegian mainland, approximately 1,000 km south of the tagging site. Young seals of most species undertake long excursions away from their natal sites, and it is noteworthy in this context that the specimen collected on Rossøya, which is the northernmost record of the species, was a pup (Wiig 1989).

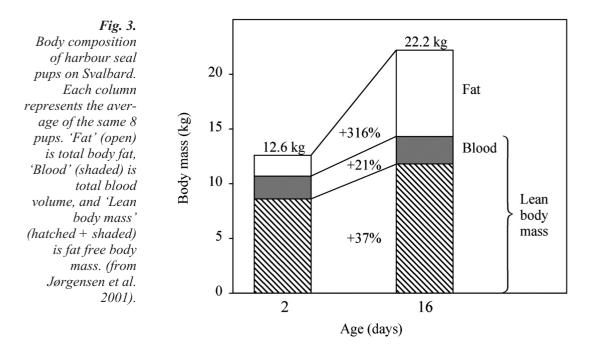
In an attempt to get more information on distribution and movements of the harbour seals in Svalbard, 14 animals were equipped with satellite transmitters during 1992-95 (Gjertz et al. 2001). The study animals included subadult and adult animals of both sexes. The animals were tracked for 110.9 ± 79.9 (SD) days (range 7-313 days). All but 3 of the harbour seals stayed in the Prins Karls Forland area and adjacent offshore waters during the entire tracking period. The 3 animals that moved away (all subadult males) travelled south along the coast of Spitsbergen. One stayed in an offshore area out from Hornsund, while the 2 others moved further south, down to Biørnøva (~74.5°N) and stayed in this general area for the rest of the tracking period. This study concluded that the majority of the harbour seals in Svalbard appear to be stationary and that their local distribution around Prins Karls Forland seems to be little affected by the presence of drifting sea ice.

DIVING

Several studies have been conducted on the harbour seals in Svalbard that shed light on their diving abilities (Gjertz *et al.* 2001, Jørgensen *et al.* 2001, Krafft *et al.* 2002). Jørgensen *et al.* (2001) investigated physiological and behavioural aspects of diving deve lopment of pups, using time-depth recorders (TDRs) and physiological measurements of blood oxygen stores and body composition



Fig. 2. Svalbard harbour seals hauled out at Prins Karls Forland. These harbour seals comprises the northernmost population of this species in the world.



early and late in the nursing period. During the study period (mean age of pups from 2 days to 16 days) the pups almost doubled their body mass, mainly as a result of depositing fat (Fig. 3). All of the dives during this period (N=6,027) were shallow and of short duration (maximum recordings: 30 m and 220 s). Compared with older pups, those less than 5 days of age had an elevated haematocrit and reduced plasma volume. Although both blood and plasma

volume increased in the pups with increasing age, the mass-specific blood oxygen stores fell during this period. At the same time several behavioural indicators of diving ability increased (proportion of time spent in the water, dive depth, dive duration, bottom time, maximum swim speed, and proportion of U-shaped dives). Based on the measured blood oxygen stores, less than 1% of the recorded dives exceeded the aerobic dive limit. It seems that



Fig. 4. Mother and pup harbour seal at Prins Karls Forland. Newborns weigh about 11 kg and gain on average 0.7 kg per day during the nursing period.

Harbour seals in the North Atlantic and the Baltic

neither development in blood oxygen stores or rates of oxygen consumption is restraining the diving development in these young harbour seal pups. Thus, it seems likely that behavioural modifications (*i.e.* experience and learning) are the main rate-limiting factors for ontogeny of diving skills in harbour seal neonates.

Another study of diving in the Svalbard harbour seals involved subadult animals (N=3) during the autumn post-moulting period when the animals are thought to feed intensively (Krafft et al. 2002). The animals spent 82±10% of their time in the water and 18±10% of their time hauled out during the study period. Dives (N= 11,322), collected via TDRs, where classified into one V- and two U-shaped classes using Cluster and Principal Component analyses. The most frequent dive type (U1-dives) was much deeper, lasted longer and had a longer bottom time, in addition to faster descent and ascent rates than the other dive types. The recorded diving occurred mainly in clearly defined bouts. These diving bouts lasted on average 12.5 h during which the seals stayed submerged 74.6% of the time, and the diving consisted almost entirely of U1-dives (97.5%). The shallower dives (V and U2-dives) dominated during the transit from the haul-out site to the area where the diving bout commenced, and during the trip back again to the haul-out site. The maximum recorded values for dive depth and duration recorded during this study were 172 m and 10 min, respectively.

Ten of the previously mentioned 14 satellite transmitters deployed by Gjertz et al. (2001) had dive sensors (Wildlife Computers 0.5 W transmitters) and collected dive information from more than 160,000 dives. The 10 animals studied included subadult and adult individuals of both sexes (males: N=6, body mass range 48-103 kg; females: N=4, body mass range 52-92 kg). More than 50% of the recorded dives were shallower than 40 m and shorter than 2-4 min in duration. A total of 95% of all dives were shallower than 250 m and the deepest recorded dive was 452 m. A total of 97% of all dives were shorter than 10 min in duration, but dives were recorded that lasted longer than 25 min (which was the last data-bin set for sampling prior to deployment). Significantly deeper and longer dives were recorded in the winter months when the seals spent more time offshore away from their terrestrial haulout sites.

DIET

Scats (N=117) were collected from various harbour seals haulout sites on Prins Karls Forland during autumn (September) to get information on their diet (Andersen et al. 2004). Stomach content from specimens that died during handling (N=3), and blubber samples from 22 captured animals (6 juvenile females, 6 juvenile males, 5 adult females, 5 adult males) were also analysed to get further insight into the diets of these seals over a broader time frame. Various species of fish dominated the diet; very few invertebrate parts were identified, but more than 3,000 otoliths were collected. Atlantic cod (Gadus morhua) was found to be the dominant prey in terms of biomass, while polar cod (Boreogadus saida) was the most frequently consumed prey item numerically (Andersen et al. 2004). Hard-part diet analyses produced the same general picture suggested by the fatty acid composition of the blubber regarding the assessment of what the seals ate.

PUPPING

Prins Karls Forland is the only area in Svalbard where harbour seal birthing has been recorded. Peak pupping period for these seals is the second half of June (Gjertz and Børset 1992), which is similar to the timing of pupping on mainland Norway. In a review of timing of pupping for this subspecies of harbour seals (*P. v. vitulina*) no latitudinal variation was found over their whole distributional range from 59°N to 79°N (Temte et al. 1991). Harbour seals pups are normally born in a pelage similar to adult individuals, having moulting their whitish lanugo in utero. However, some few individuals are born with lanugo, and the frequency of this occurrence varies from subspecies to subspecies (Boulva 1975, Shaughnessy and Fay 1977). Krog and Bjargov (1973) speculated as to whether the harbour seals in Svalbard would give birth to more than the average number of white coated pups because of the cold climate of the region. However, several hundred harbour seal pups have been observed in Svalbard (Gjertz and Børseth 1992, Lydersen and Kovacs 2005) and no white coated pups have been recorded.

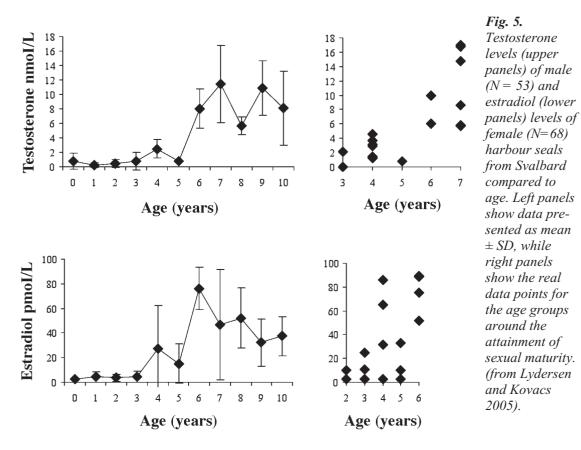
GROWTH

Newborn pups have body masses of ~10-11 kg. Subsequently, they grow at an average rate of 0.7 kg per day throughout lactation (Jørgensen et al. 2001; see also Fig. 3 and 4). Growth curves for older seals based on body masses and standard lengths of live-captured, drugged individuals show that there is sexual size dimorphism in the Svalbard harbour seals (Lydersen and Kovacs 2005). The asymptotic values for both body mass and standard lengths are greater for males than for females (Table 1). Maximum recorded values for standard lengths and masses were 156 cm and 122 kg for males and 147 cm and 111 kg for females. The heaviest female was pregnant; the heaviest non-pregnant female record was 101 kg. A total of 14 males were heavier than 100 kg.

The asymptotic growth values for the harbour seals from Svalbard show that they are somewhat shorter, but heavier than those reported for other populations of this subspecies (P. v. vitulina) from Denmark-Sweden (Härkonen and Heide-Jørgensen 1990) and from southern Norway (Markussen et al. 1989). The comparison of morphometric data for these three populations suggests that the Svalbard harbour seals carry more blubber than animals from the populations further south. All phocid seals go through dramatic seasonal cycles in how much blubber they carry as a consequence of extreme variation in energy intake and expenditure related to breeding and moulting and perhaps also availability of prey. However, the harbour seals from the three studies discussed above were all measured during the same period of the year, so the fact that the Svalbard seals generally are fatter is not due to seasonally biased sampling. One possible reason for Svalbard harbour seals having thicker blubber could be that Svalbard's waters are colder than those in the southern areas where these other populations are found, and that the Svalbard harbour seals therefore need a thicker blubber layer to stay within their thermoneutral zone (for more details: see Lydersen and Kovacs 2005). Colder water could also be an explanatory factor for the size dimorphism between the sexes in the Svalbard harbour seals. In McLaren's (1993) review of pinniped growth there was no reported sex differences in any harbour seal populations from the Atlantic that had been studied at that time, and the review was equivocal regarding whether sexual dimorphism was displayed in harbour seal populations from the Pacific. Large body size in males compared to females in pinnipeds, and more generally in all animals, is thought to occur principally via selection imposed by large size accruing benefits to males during combat for females directly, or for resources that determine mating access to females (e.g. Bartholomew 1970, Emlen and Oring 1977, Clutton-Brock 1988). A low level of sexual dimorphism or monomorphy among aquaticmating pinnipeds has been suggested to be the norm, because manoeuvrability may be more important in aquatic combat than large size (Stirling 1975, 1983). Harbour seals are aquatic breeders. Males use underwater displays including vocalizations to attract females and perhaps to repel competitors at sites along routes used by females between haulout sites and foraging areas (e.g. VanParijs et al. 1997, 2000a, b). In areas where the water is quite cold, large body size is likely beneficial to males at least, because it would permit males to stay onsite at underwater display areas longer without suffering thermal stress. Comparative morphometric data from other harbour seal populations from cold water areas like Hudson Bay or Greenland would be of great interest to pursue this hypothesis further.

REPRODUCTION

Age at sexual maturity in population studies of pinnipeds is normally determined by macroscopic investigations of ovaries and microscopic investigations of testes. These materials were not available from this protected population in Svalbard, so we used levels of circulating sex

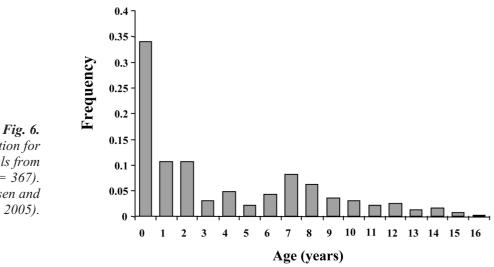


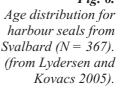
hormones to estimate the time of the onset of sexual maturity for the Svalbard harbour seals (Lydersen and Kovacs 2005).

Testosterone levels in males showed an abrupt increase when the males reached the age of 6 years (Fig. 5 upper panels). For this age group and older males, mean testosterone levels remained above 6 nmol/L. Estradiol levels in females increased abruptly from age 4 (Fig. 5 lower panels). For this and older age groups average estradiol levels were above 20 pmol/L. Females were more variable than males in when their hormones began to rise: one of 3 (33.3%) 3-year olds, 3 of 4 (75%) 4-year olds, 1 of 3 (33.3%) 5-year old and all older females had estradiol levels higher than 20 pmol/L.

Table 1. Calculated parameter estimates for von Bertalanffy's growth curves for harbour seals in Svalbard. L_{∞} and M_{∞} are the asymptotic length (cm) and mass (kg) respectively, *a* determines the rate of approach to the asymptote and *b* determines the curvelinearity of this approach in the model: L_x (or M_x)= L_{∞} (or M_{∞})[$1 - e^{-a(x - x_0)}$]^b. Values are given with SE. (From Lydersen and Kovacs 2005).

		Parameter e	estimate		
Growth parameter	n	L_∞ or M_∞	а	b	r2
Male mass	127	104.0 ± 5.0	0.22 ± 0.05	0.96 ± 0.13	0.88
Female mass	134	83.2 ± 2.7	0.29 ± 0.06	1.02 ± 0.17	0.85
Male length	120	152.9 ± 4.8	0.21 ± 0.04	0.30 ± 0.03	0.90
Female length	129	140.1 ± 2.0	0.26 ± 0.06	0.31 ± 0.04	0.86





A total of 54 females was either captured with a pup, was lactating or was heavily pregnant. Four females that were older than 8 years of age were not reproductively active (pregnant, lactating or captured with a pup). Thus, reproductive rate defined as the proportion of adult females producing a pup (N=54) in relation to the total number of adult females (N=58) is 0.93 for Svalbard harbour seals.

AGE DISTRIBUTION AND LONGEVITY

The age distribution of the captured harbour seals is illustrated in Fig. 6 (Lydersen and Kovacs 2005). Immature seals, other than pups of the year are under-represented in the sample and there is a remarkable lack of older ani-



Fig. 7. Live capture of harbour seals in Svalbard. Here the pup is already onboard and the mother climbs into the Zodiac to access its pup getting herself caught in the process. mals. The age distribution in this study, similar to many other samples from seal populations, clearly under-represents subadult age groups. This is common when most of the sampling occurs in the breeding period at active pupping sites which are mainly occupied by adult animals and pups of the year. However, the lack of older animals in our sample is very different from other studies, where a much higher proportion of the populations is in the 15+ yr age categories (Boulva and McLaren 1979, Burns and Goltsev 1984. Markussen et al. 1989. Härkonen and Heide-Jørgensen 1990. Hauksson 1992), with some individuals living to be older than 30 yr (Härkonen and Heide-Jørgensen 1990, Hauksson 1992). We are convinced that the short longevity measured in our study is not a sampling artefact due to older animals being harder to catch. Svalbard harbour seals are quite naïve (Fig. 7), and we were able to enclose entire groups and get samples that were representative of group composition.

The life span in this population was surprisingly short. This population is on Svalbard's Red List and hence it is protected from hunting. To our knowledge there has been no acute source of mortality such as an epizootic outbreak in recent decades, like those that have affected harbour seals along the coast of Europe (Heide-Jørgensen et al. 1992, Harding et al. 2002) that could explain the absence of older animals. There is little if any surface predation from polar bears Ursus maritimus or other terrestrial carnivores, and there is no reported mortality due to fisheries interactions. Pollution burdens measured thus far are low (Wolkers et al. 2004). Ringed seals from this area of Svalbard have similar levels of organochlorines pollutants to the harbour seals (Wolkers et al. 1998) and they are extremely long-lived with some animals living to ages beyond 40 years (Lydersen and Giertz 1987). It is reasonable to assume that ringed and harbour seals have similar abilities to deal with pollutants, so it seems unlikely that pollution levels are responsible for the short life span observed in Svalbard harbour seals.

Another possible source of mortality for the harbour seals on Svalbard is marine predators like killer whales *Orcinus orca* and Greenland sharks *Somniosus microcephalus*. In the western Atlantic, at Sable Island, shark predation is responsible for up to 45% of harbour seal pup mortality, and in a 5-year period 470 carcasses (241 adults, 23 juveniles and 206 pups) were found that had died due to shark attacks (Lucas and Stobo 2000). This is a minimum estimate of shark-inflicted mortality, since many seals are probably eaten entirely at sea, or at least their bodies do not wash up on shore. Lucas and Stobo (2000) concluded that shark-induced mortality has a significant impact on the Sable Island harbour seal population, possibly to the extent that it has limited its growth and contributed to the recently observed declines (also see Bowen *et al.* 2003).

In the first half of the 1900s there was a large fishery for Greenland sharks in northern Norwegian waters including the Greenland Sea, Svalbard and northern Barents Sea. Oil from shark livers delivered to the marketplace during the 1930s and 1940s corresponds to a harvest of over 10,000 individuals annually (Anon. 1949, Hoel 1949). These fisheries no longer exist, and it is likely that the shark population has increased in recent decades following the cessation of the fishery. Thus, Greenland sharks may be a significant source of mortality for Svalbard's harbour seals. Based on sightings in recent decades and former whaling distribution records for killer whales we also know that the distribution of this species (Øien 1988) overlaps with the Svalbard harbour seals although we do not have any documentation of predation in the area of concern. We can not rule out the possibility that the short life span of Svalbard's harbour seals may be related to extreme seasonality and other harsh environmental conditions that these animals experience at the northern edge of this species' distribution. Long-term, low levels of physiological stress may be induced in arctic populations of this normally temperate species that result in the short longevity observed in this population.

HAULOUT BEHAVIOUR AND MOULTING

Haulout behaviour of the Svalbard harbour seals was studied from June to August 2000 using a combination of counts performed hourly during

12 or 24 hr sessions in addition to telemetric data from 37 VHF-tagged seals (Reder et al. 2003). The largest aggregations of seals were found at Skarvnes (See: Fig. 1), a site where the number of animals increased steadily throughout the summer reaching a peak during the moulting period in August. Season (date), time of day, tidal state and temperature all significantly influenced the number of seals hauled out. Haulout patterns varied by age and sex generally in accordance with the demands of lactation, mating and moult. Not surprisingly,the mother-pup pairs were closely associated during the nursing period, while the mothers left the haulout areas for periods of several days during the post lactation period. The haulout behaviour of adult males suggested that they adjusted their behaviour to follow female distribution and movement patterns during the breeding period. Most juveniles and adults of both sexes stayed ashore for prolonged periods during moulting, which took place first in juveniles, then in adult females and last in adult males. The basic haulout behaviour pattern of the Svalbard harbour seals is similar to what is found for this species at lower latitudes. The data collected in this study can form the basis for making correction factors for population size assessments based on surveys of hauled out animals.

POLLUTION

Levels and patterns of various PCBs and pesticides were measured in adult harbour seal males, females, their pups and in the milk (Wolkers et al. 2004). The levels found of both PCBs and the various pesticides (Table 2) were low compared to harbour seals from populations further south. The seals in Svalbard had contaminant levels 5-10 times lower than that which is detected in harbour seals from the Norwegian mainland. The adult females were found to transfer a modified contaminant mixture to their pups compared to that which was found in their own blubber tissue: for example compounds with higher Kow such as some penta-chlorinated PCBs were selectively transferred into the milk. As a consequence of this selection, the contaminant pattern also differed between adult females and adult males.

In addition, the pups receive a relatively higher amount of the less lipophylic and a lower amount of the more lipophylic compounds via the milk. The contaminant patterns in the milk and in the blubber of the pups are similar, indicating that the pups are unable to metabolize these contaminants which are therefore all deposited.

OTHER STUDIES

Milk from Svalbard harbour seals has been analyzed for various milk sugars (Urashima *et al.* 2003). This study showed that unlike otariid seals, the phocid seals have milk that contains several types of sugars. Some of the acidic oligosaccharides described in this study are the first to have been characterized in the milk of any pinniped species.

Another study documented levels of halogenated dimethyl bipyrroles (HDBPs) in a suite of marine mammals including harbour seals from Svalbard (Tittlemier *et al.* 2002). HDBPs probably have a natural origin rather than being anthropogenic substances, which is further supported by this study since the geographical distribution of these substances is very different from that anthropogenic organohalogens. The study indicates that HDBPs appear to be mainly derived from sources in the North Pacific and then undergo extensive atmospheric and ocean current transport.

MANAGEMENT

Svalbard harbour seals are on the National Red List and thus are totally protected from hunting. There are no commercial fisheries in the area that could have negative impacts on this population in terms of competing for resources or interaction with fishing gear. These seals reside in an area that is rarely visited by humans and are thus very naïve in their behaviour and easy to approach compared with harbour seals from populations elsewhere. Due to their very limited distributional range they are considered vulnerable in relation to any stochastic event, such as an oil spill, a virus outbreak, etc.

ر	Compound	5-PCB	6-PCB	7-PCB	Тох	Tox	Tox	Tox	Σ Τοχ	p,p DDE	HCB	α-HCH
					26	40	44	50				
Males												
(n = 6)	Mean	422.2	1381.5	354.1	59.7	22.0	<pre></pre>	88.5	170.7	1318.1	6.4	16.5
	95 % low	359.8	1044.1	263.3	43.4	14.7		62.7	121.9	1070.5	3.3	5.4
	95 % high	495.5	1828.0	476.0	82.2	32.8		124.8	238.8	1622.9	12.5	50.2
Females												
(n = 4)	Mean	56.8	273.3	121.8	10.2	5.6	<pre>> 4</pre>	7.6	21.2	188.3	2.1	5.9
	95 % low	22.2	133.6	55.1	1.9	1.5		0.8	2.4	86.8	1.2	1.7
	95 % high	145.5	558.9	269.5	54.7	21.3		74.9	188.1	408.3	3.9	20.0
Milk												
(n = 4)	Mean	69.2	161.8	36.2	8.0	5.3	<pre></pre>	4.9	16.3	103.1	2.5	8.5
	95 % low	38.4	96.2	25.5	2.0	1.5		0.7	2.5	48.0	2.0	6.6
	95 % high	124.6	272	51.6	33.0	18.2		32.7	108.0	221.4	3.1	10.8
Pups												
(n = 4)	Mean	94.2	215.8	41.8	4.7	20.2	< 4	5.7	44.5	221.2	4.7	33.9
	95 % low	53.9	107.6	22.8	1.0	12.3		0.8	23.3	101.0	1.0	16.4
	95 % high	164.6	432.8	76.7	21.5	32.9		42.2	84.9	484.5	21.5	70.0

REFERENCES

- Andersen, S.M., Lydersen, C., Grahl-Nielsen, O. and Kovacs, K.M. 2004. Autumn diet of harbour seals (*Phoca vitulina*) at Prins Karls Forland, Svalbard, assessed via scat and fatty-acid analyses. *Can. J. Zool.* 82:1230-1245.
- Anon. 1949. Reports from the sealing, the Greenland shark fisheries and from the overwintering expeditions in 1949. Årsb. Vedrør. *Norges Fisk*. 10. (In Norwegian.)
- Benjaminsen, T., Bergflødt, B. and Øritsland, T. 1973. Selundersøkelser i det nordlige Atlanterhav i 1973. *Fiskets Gang* 48:853-863. (In Norwegian.)
- Bartholomew, G.A. 1970. A model for the evolution of pinniped polygyny. *Evolution* 24:546-559.
- Boulva, J. 1975. Temporal variation in birth period and characteristics of newborn harbour seals. *Rapp. P.-v. Réun. Cons. Int. Explor. Mer* 169:405-408.s
- Boulva, J. and McLaren, I.A. 1979. Biology of the harbour seal, *Phoca vitulina*, in eastern Canada. *Fish. Res. Bd. Can. Bull.* 200.
- Bowen, W.D., Ellis, S. L., Iversen, S.J. and Boness, D. J. 2003. Maternal and newborn life-history traits during periods of contrasting population trends: implications for explaining the decline of harbour seals (*Phoca vitulina*), on Sable Island. *J. Zool.* 261:155-163.
- Brown, R. 1868. Notes on the history and geographical relations of the pinnipedia frequenting the Spitzbergen and Greenland seas. *Proc. Zool. Soc.* 27:405-440.
- Burns, J.J. and Goltsev, V.N. 1984. Comparative biology of harbour seals, *Phoca vitulina* Linnaeus, 1758, of the Commander, Aleutian, and Pribolof Islands. In: Fay, F. H. and Fedoseev, G. A. (eds.); *Soviet-American cooperative research on marine mammals*. Volume 1. Pinnipeds. NOAA Techn Rep NMFS 12, 17-24.
- Clutton-Brock, T.H. (ed.) 1988. Reproductive success. Univ. Chicago Press, Chicago.
- Gjertz, I. and Børset, A. 1992. Pupping in the most northerly harbour seal (*Phoca vitulina*). Mar. Mamm. Sci. 8:103-109.
- Gjertz, I., Lydersen, C. and Wiig, Ø. 2001. Distribution and diving of harbour seals (*Phoca vituli-na*) in Svalbard. *Polar Biol.* 24:209-214.
- Emlen, S.T. and Oring, L.W. 1977. Ecology, sexual selection and the evolution of mating systems. *Science* 197:215-223.
- Harding, K.C., Härkönen, T. and Caswell, H. 2002. The 2002 European seal plague: epidemiology and population consequences. *Ecol. Lett.* 5:727-732.
- Härkönen, T. and Heide-Jørgensen, M.P. 1990. Comparative life histories of east Atlantic and other harbour seal populations. *Ophelia* 32:211-235.
- Hauksson, E. 1992. Biology of Icelandic common seal (*Phoca vitulina* L.) and grey seal (*Halichoerus grypus* Fabr.), length-weight relationships, growth-curves and fecundity. *Hafrannsoknir* 43:23-49.

- Heide-Jørgensen, M.P., Härkönen, T., Dietz, R. and Thompson, P.M. 1992. Retrospective of the 1988 European seal epizootic. *Dis. Aquat. Org.* 13:37-62.
- Henriksen, G., Gjertz, I. and Kondakov, A. 1997. A review of the distribution and abundance of harbour seals, *Phoca vitulina*, on Svalbard, Norway, and in the Barents Sea. *Mar. Mamm. Sci.* 13:157-163.
- Hoel, A. 1949. Håkjerringfisket i Arktiske farvann (Greenland shark fisheries in Arctic waters). In: Strøm, J. (ed.); Særtrykk av Norsk Fiskeri og Fangst Håndbok. Bind I del III. Albert Cammermeyers Forlag, 823-828. (In Norwegian.)
- Hop, H., Pearson, T., Hegseth, E.N., Kovacs, K.M., Wiencke, C., Kwasniewski, S., Eiane, K., Mehlum, F., Gulliksen, B., Wlodarska-Kowalczuk, M., Lydersen, C., Weslawski, J.M., Cochrane, S., Gabrielsen, G.W., Leakey, R., Lønne, O.J., Zajaczkowski, M., Falk-Petersen, S., Kendall, M., Wängberg, S.-Å., Bischof, K., Voronkov, A.Y., Kovaltchouk, N.A., Wiktor, J., Poltermann, M., di Prisco, G., Papucci, C. and S. Gerland. 2002. The marine ecosystem of Kongsfjorden, Svalbard. *Polar Res.* 21:167-208.
- Jørgensen, C., Lydersen, C., Brix, O. and Kovacs, K.M. 2001. Diving development in nursing harbour seals. *J. Exp. Biol.* 204:3993-4004.
- Krafft, B.A., Lydersen, C., Gjertz, I. and Kovacs, K.M. 2002. Diving behaviour of sub-adult harbour seals (*Phoca vitulina*) at Prins Karls Forland, Svalbard. *Polar Biol.* 25:230-234.
- Krog, J. and Bjarghov, R. 1973. Fjordsel på Svalbard. Fauna. 26:217-218. (In Norwegian.)
- Lucas, Z. and Stobo, W.T. 2000. Shark-inflicted mortality on a population of harbour seals (*Phoca vitulina*) at Sable Island, Nova Scotia. *J. Zool.* 252:405-414.
- Lydersen, C. and Gjertz, I. 1987. Population parameters of ringed seals (*Phoca hispida* Schreber, 1775) in the Svalbard area. *Can. J. Zool.* 65:1021-1027.
- Lydersen, C. and Kovacs, K.M. 2005. Growth and population parameters of the world's northernmost harbour seals *Phoca vitulina* residing in Svalbard, Norway. *Polar Biol.* 28:156-163.
- Lydersen, C., Krafft, B.A., Andersen, M. and Kovacs, K.M. 2002. Marine mammals in the Bellsund-Van Mijenfjorden - Van Keulenfjorden area. New investigations and status of knowledge. Norsk Polarinst. *Rapp. Ser.* 121. 36 pp.
- Markussen, N.H., Bjørge, A. and Øritsland, N.A. 1989. Growth in harbour seals (*Phoca vitulina*) on the Norwegian coast. J. Zool. 219:433-440.
- McLaren, I.A. 1993. Growth in pinnipeds. Biol. Rev. 68:1-79.
- Øien, N. 1988. The distribution of killer whales (*Orcinus orca*) in the North Atlantic based on Norwegian catches, 1938-1981, and incidental sightings, 1967-1987. *Rit. Fiskideildar* 11:65-78.
- Øynes, P. 1964. Sel på norskekysten fra Finnmark til Møre. Fisken Hav. 48(5):1-14.
- Prestrud, P. and Gjertz, I. 1990. The most northerly harbour seal, *Phoca vitulina*, at Prins Karls Forland, Svalbard. *Mar. Mamm. Sci.* 6:215-220.

- Reder, S., Lydersen, C., Arnold, W. and Kovacs, K.M. 2003. Haulout behaviour of High Arctic harbour seals (*Phoca vitulina vitulina*) in Svalbard, Norway. *Polar Biol.* 27:6-16.
- Römer, F. and Schaudinn, F. 1900. Enteilungen, Plan des Werkes und Reisebericht. Pp. 1-85 In Römer, F. and Schaudinn, F. (eds.); Eine Zusammenstellung der arktischen Tierformen, mit besonderer Berücksichtigung des Spitzbergen-Gebietes auf Grund der Ergebnisse der Deutschen Expedition in das Nördliche Eismeer im Jahre 1898. *Fauna Arctica I*. Gustav Fisher, Jena. (In German.)
- Shaughnessy, P.D. and Fay, F.H. 1977. A review of the taxonomy and nomenclature of North Pacific harbour seals. *J. Zool.* 192:385-419.
- Stirling, I. 1975. Factors affecting the evolution of social behaviour in the Pinnipedia. Rapp. P.-v. Réun. Cons. Int. l'Explor. *Mer* 169:205-212.
- Stirling, I. 1983. The evolution of mating systems in pinnipeds. *Am. Soc. Mammal. Spec. Publ.* 7:489-527.
- Temte, J.L., Bigg, M.A. and Wiig, Ø. 1991. Clines revisited: the timing of pupping in the harbour seal (*Phoca vitulina*). J. Zool. 224:617-632.
- Tittlemier, S., Borrell, A., Duffe, J., Duignan, P.J., Fair, P., Hall, A., Hoekstra, P., Kovacs, K.M., Krahn, M.M., Lebeuf, M., Lydersen, C., Muir, D., O'Hara, T., Olsson, M., Pransche, J., Ross, P., Siebert, U., Stern, G., Tanabe, S. and Norstrom, R. 2002. Global distribution of halogenated dimetyl bipyrroles in marine mammal blubber. *Arch. Environ. Contam. Toxicol.* 43:244-255.
- Urashima, T., Nakamura, T., Yamaguchi, K., Munakata, J., Arai, I., Saito, T., Lydersen, C. and Kovacs, K.M. 2003. Chemical characterization of the oligosaccharides in milk of high Arctic harbour seal (*Phoca vitulina*). Comp. Biochem. Physiol., A. Mol. Integr. Physiol. 135:549-563.
- VanParijs, S.M., Thompson, P.M., Tollit, D.J. and Mackay, A. 1997. Distribution and activity of male harbour seals during the mating season. *Anim. Behav.* 54:35-53.
- VanParijs, S.M., Hastie, G.D. and Thompson, P.M. 2000a. Individual and geographic variation in display behaviour of male harbour seals in Scotland. *Anim. Behav.* 59:559-568.
- VanParijs, S.M., Janik, V.M. and Thompson, P.M. 2000b. Display-area size, tenure length, and site fidelity in the aquatically mating male harbour seal, *Phoca vitulina. Can. J. Zool.* 78:2209-2217.
- Wiig, Ø. 1989. A description of common seals, *Phoca vitulina* L. 1758, from Svalbard. *Mar. Mamm. Sci.* 5:149-158.
- Wolkers, H., Burkow, I.C., Lydersen, C., Dahle, S., Monshouwer, M. and Witkamp, R.F. 1998. Congener specific PCB and polychlorinated camphene (toxaphene) levels in Svalbard ringed seals (*Phoca hispida*) in relation to sex, age, condition and cytochrome P450 enzyme activity. *Sci. Total Environ.* 216:1-11.
- Wolkers, H., Lydersen, C. and Kovacs, K.M. 2004. Accumulation and lactational transfer of PCBs and pesticides in harbour seals (*Phoca vitulina*) from Svalbard, Norway. *Sci. Total Environ*. 319:137-146.