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Distribution of sex and age groups of ringed seals *Pusa hispida* in the fast-ice breeding habitat of Kongsfjorden, Svalbard

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ABSTRACT: Spatial distribution of various age- and sex groups of ringed seals (N = 94; 19 adult males, 33 adult females and 42 subadults) was studied in their fast-ice breeding habitat in Kongsfjorden, Svalbard, during May 2004. Adult females occupied the inner, most stable ice area, while subadults were found predominantly in the outer parts of the fast-ice, where the ice conditions are more unstable. Adult males were scattered across these 2 areas; some were intermingled with breeding females while others were found further out towards the ice edge in areas mainly dominated by subadults. This pattern suggests territorial behaviour with competitive exclusion of the subadults and adult males that cannot compete for territories in the prime breeding areas. The size of adult males was correlated with their testosterone levels, but it was not necessarily the largest males that had the most adult female neighbors. The adult males that had the most adult female neighbors were however significantly older than the adult males with fewer female neighbors (18 ± 1 vs. 12 ± 1 yr). This suggests that experience (age) likely plays a strong role in achieving reproductive success for male ringed seals. A male:female sex ratio of 1:2.4 was found in the prime breeding area, which suggests a slightly polygynous mating system.

KEY WORDS: Ringed seal · *Pusa hispida* · Ice-breeding seals · Mating systems · Sexual segregation

INTRODUCTION

Most mammalian mating systems represent various forms of mate guarding adapted to the spatial and temporal distribution of breeding females (Clutton-Brock 1989). Female distribution is, in turn, dependent on factors such as resource distribution and predation pressure. Pinnipeds exhibit a wide range of mating strategies but most are polygynous to some degree (see for reviews Stirling 1975, 1983, Boness 1991, LeBoeuf 1991). The degree of polygyny achieved by males is mainly determined by how tightly breeding females are aggregated in space and time. The most extreme cases of polygyny are found in terrestrial breeding pinnipeds where space is a limited resource. In otariid seals, sexual size dimorphism is taken to an extreme, and harems of over 100 females are encountered in some species (Gentry 1998). For pinnipeds that breed on ice, space is not as limited as for the terrestrial breeders, and most ice-breeding species mate in the water where males are not able to restrict a female's mobility (Boness et al. 1993). Since the females are more spatially dispersed and free to move at will in the water, males have fewer possibilities to defend and mate with large numbers of females. As a consequence, aquatic mating pinnipeds are generally less polygynous and exhibit less size dimorphism compared to those that mate on land (Stirling 1983, but also see Kovacs 1990, Tinker et al. 1995).

Ringed seals *Pusa hispida* are monomorphic (Lydersen & Gjertz 1987), ice-breeding phocids that mate in the water (Stirling 1975, 1983). The preferred breeding habitat of ringed seals is stable land-fast ice, where ringed seal densities are usually higher inshore than offshore (Smith & Stirling 1975, Lydersen & Gjertz 1986). However, some ringed seals do breed in free-floating pack-ice in several locations (Fedoseev & Yablokov 1964, Fedoseev 1975, Finley et al. 1983, Wiig et al. 1999). Ringed seals build subnivean lairs excavated on top of

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*Corresponding author. Email: kit.kovacs@npolar.no breathing holes in the ice where they spend time resting during the inclement winter months (e.g. Smith & Stirling 1975, 1978). Females give birth in a lair, which is often part of a complex of several similar structures in an area, separated by up to 200 m (Smith & Hammill 1981). Males also use several lairs, spread through an area that contains the lairs of several females (Kelly & Quakenbush 1990). Lairs provide protection from harsh environmental conditions and also provide a degree of protection against predation (Smith & Stirling 1975, Smith 1976, 1980, Lydersen & Gjertz 1986, Lydersen & Smith 1989, Smith et al. 1991, Furgal et al. 1996). A female will move a young pup between lairs within her complex if it is attacked by polar bears *Ursus maritimus* or arctic foxes *Alopex lagopus*. Older pups are able to shift between structures independently (Lydersen & Hammill 1993a). The small ringed seal neonates that weigh 4 to 5 kg (Lydersen et al. 1992) are born with a white lanugo coat that insulates well enough to keep the pups thermoneutral without the shelter of the lair if the fur stays dry (Smith et al. 1991). However, wet pups require the shelter of lairs in order to regain thermoneutrality (Smith et al. 1991). Thus, both the physical and thermal protection provided by these lairs is particularly important for the survival of ringed seal neonates.

Ringed seals have the longest nursing period of the ice-breeding northern phocids with an average duration of 39 d (Hammill et al. 1991). The pups are able to swim and dive shortly after birth and they develop foraging skills prior to weaning (Lydersen & Hammill 1993a). Weaning is less abrupt than for most phocid pups where the mothers simply abandon their pups before they have entered the water for the first time (Bowen 1991, Lydersen & Kovacs 1999).

Many of the larger phocid species are so-called 'capital breeders', which means that they cover the energetic costs of lactation entirely from stored energy reserves (see Costa & Williams 1999). This is however not the case for all phocids, ringed seals rely heavily on energy obtained from foraging to cover the cost of lactation (Lydersen & Hammill 1993b, Lydersen 1995, Lydersen & Kovacs 1999).

Ringed seal females should thus maximize their fitness by ensuring pup survival via choosing stable ice platforms for breeding. The ideal sea-ice platform must be formed well before breeding to ensure enough snow accumulation for lair construction (Smith & Lydersen 1991, Furgal et al. 1996). The sea ice must in addition be stable throughout the entire lactation period so that mother–pup pairs do not get prematurely separated. In addition, the ice habitat must be large enough to contain sufficient amounts of prey to support the resident animals during the relatively long lactation period. In coastal areas with fjords and bays the preferred breeding habitats tend to be inshore areas, which are most stable, and the size of the areas females occupy are probably determined to some degree by the availability of structures in the ice around which snow accumulate for lair construction, and by the density of available prey organisms in the area (Smith & Lydersen 1991, Smith et al. 1991).

Adult male ringed seals maximize their fitness by mating with as many females as possible (e.g. Stirling 1975, 1983). Little is known about the behavior of adult males during this time of the year, but there are reports of aggressive behaviour and fresh bite marks during the breeding season as well as heavy scarring on the hind-flippers of old males (e.g. Smith & Hammill 1981, Krafft et al. 2006a) that are taken as evidence of territorial fighting. In addition, during the breeding period adult ringed seal males secrete a very strong-smelling oily substance produced by facial sebaceous glands (Ryg et al. 1992). The function of this secretion is likely related to marking of territories (Smith 1987), and the most logical places to mark would be the breathing holes or lairs, since the seals are unlikely to be able to smell under water. Since the breeding females are quite dispersed it has been suggested that males defend territories that overlap with several females, or that they defend individual females serially or simply rove in search of receptive females (Smith & Hammill 1981, Kelly & Quakenbush 1990, Boness et al. 2002). Based on direct observations of haul-out behaviour of a few recognizable individual ringed seals, Smith & Hammill (1981) suggested that breeding units were made up of several adult females that occupied an area defended by a territorial male. This study also suggested that the adult females excluded the resident male from the vicinity of their birth-lair complexes until close to the time pups were weaned.

When the various pieces of evidence about ringed seal breeding behaviour are compiled, it seems reasonable to expect that the various sex and age groups would be spatially segregated during the breeding period, with adult animals occupying the most stable ice areas, while younger animals would be excluded to more unstable ice areas (e.g. McLaren 1958, Smith 1987). The purpose of this study was to examine spatial arrangements of ringed seals in detail to shed light on the mating system of this species. The study was conducted in a fjord where the stability of the sea ice varies substantially from the inner to the outer parts, and our working hypothesis was that the adult females should be found in the innermost areas, while subadult animals should be in the outer unstable ice areas. Adult males should be broadly spread with successful territory holders being distributed close to the adult females, while the adult males that are unable to hold prime territories would be located toward the outside edges of the breeding habitat.

MATERIALS AND METHODS

This study was conducted in Kongsfjorden (78° 55′ N, 12° 30′ E, Fig. 1), Svalbard, from 5 to 21 May 2004. Kongsfjorden is a westward pointing fjord where the outer areas are exposed to wind and waves coming in from the Greenland Sea. The inner parts of Kongsfjorden contain a north to south string of small islands and skerries that protect the innermost basin of the fjord from wind and wave action (Fig. 1). As a consequence, the ice conditions in the outer parts of Kongsfjorden are much more variable and unstable compared to the innermost parts east of the protecting islands that experience much more stable ice conditions and a longer season of ice coverage. Kongsfjorden is known to be a good breeding area for ringed seals, with one of the highest lair densities in Svalbard (Lydersen & Gjertz 1986, 1987). For this study, Kongsfjorden was divided into an unstable-ice area (Area A, Fig. 1) and a stable-ice area (Area B, Fig. 1). The dividing line between these 2 areas (Fig. 1) follows the string of islands and shallow water from north to south until the last small skerry, which is located at the point in the map where this line breaks off to the east. The whole area of Kongsfjorden south of this point lacks islands and skerries and is thus exposed to wind and wave action from the west. In addition, the glacier located in the southeastern part of the fjord is actively calving and is thus constantly creating wave action that interferes with the formation of fast-ice. In some years this southern part of Kongsfjorden does not have fast-ice at all. During the study period the fast-ice situation in Kongsfjorden was as depicted in Fig. 1, with Area A consisting of about 50 km^2 of sea ice and Area B about 38 km^2 of fast-ice.

As part of a larger collection program for population studies of ringed seals in Svalbard (see Krafft et al. 2006b for details), 94 animals were shot while hauled out on the fast-ice in Kongsfjorden. Permits to conduct this collection were provided by the Governor of Svalbard (Sysselmannen), and the programme in its entirety was reviewed via the granting process of the National Research Council of Norway. Data on collection point (GPS position), sex, body mass (Salter scale: 100 ± 0.5 kg) and standard length (± 1 cm) were collected from each seal. Blubber thickness was measured mid-dorsally at a point approximately 60 % of the length of the animal from the cranial end, following Ryg et al. (1990a). The lower jaw with teeth was collected; age was determined in the laboratory by counting cementum layers in decalcified, stained longitudinal sections of the canine teeth, following Lydersen & Gjertz (1987). Teeth were read serially, by multiple readers and any significant differences in age were explored further until consensus was reached. The genitals were frozen (–20°C) for later analysis (see below). Blood samples of about 50 ml were collected from the extradural intravertebral vein. Plasma was separated by centrifugation within 4 h, at 3000 rpm for 10 min, and stored frozen (–20°C) until analyses (hormonal; other tissues were also collected for additional studies, e.g. Krafft et al. 2006b, Tryland et al. 2006, Labansen et al. 2007). Hunting effort was spread evenly across the study area. Initially, from 5 to 19 May, hunting was focused on subadults and adult males; the latter recognizable via their size, the penile opening and the dark facial region. Adult females were targeted after 20 May, when the general hunting season opened on Svalbard, in order to avoid potential separation of mother–pup pairs. Kongsfjorden was thought to contain a minimum of ~500 seals (Krafft et al. 2006c) at this time of year, so a maximum *a priori* take was set at 100 animals.

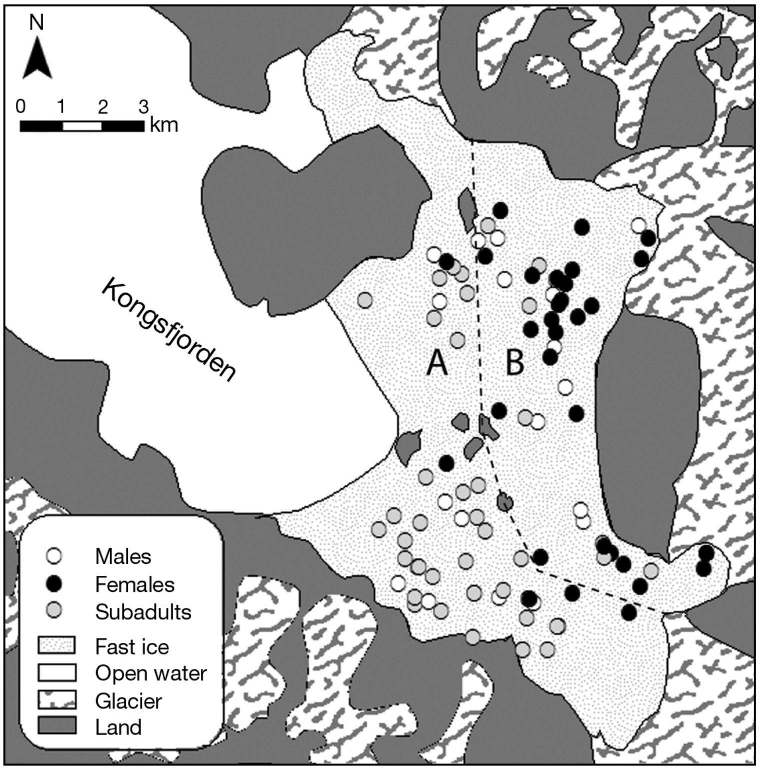

Fig. 1. Study area in Kongsfjorden with the locations of each adult ringed seal *Pusa hispida* male, female and subadult, collected on the fast-ice during May 2004. Area A covers 50 km^2 of land-fast sea ice and Area B covers 38 km^2 of sea ice

In the laboratory both ovaries from each female (N = 45) were analyzed macroscopically by making 2 mm thick longitudinal sections in each ovary with a scalpel. Females were defined as adult females (N = 33) based on occurrence of corpora lutea or corpora albicantia or mature follicles (follicles > 6 mm). Males were defined as adults, potentially participating actively in breeding, when they were >7 yr of age and spermatozoa were found in epididymis or spermatogenesis were detected in the seminiferous tubules (see Krafft et al. 2006b for details). Younger males were defined as juveniles. No pups of the year were collected.

A condition index (CI) was calculated as described in Krafft et al. (2006a). Briefly, $CI = BlM/M^{0.75}$, where BlM is blubber mass and M is body mass and $M^{0.75}$ is the metabolic body mass of the individual, according to Kleiber (1975). BlM was calculated based on a formula developed by Ryg et al. (1990a): $B = 4.44 + 5693 (L/M)^{0.5} \times D$, where B is blubber content (%), L is standard length (m), M is body mass (kg), and D is dorsal blubber thickness (m). This formula estimates the blubber content of phocid seals with less than 3% error. The resulting B was multiplied by M/100 to get the blubber mass (BlM) of the animal.

Testosterone levels in the blood plasma of adult males were measured using a commercially available kit (Spectria Testosterone, RIA, Orion Diagnostica).

GPS positions were programmed into ArcGIS software (ESRI ArcView, v8.3) for analyses of the ringed seal distribution. In one analysis, the adult males in the fast-ice area were split into 2 groups according to the number of neighboring adult females. This was done based on GPS position for each individual and simply counting the 6 closest neighbors for each adult male.

Most statistical analyses were done with STATISTICA v6.1 (StatSoft). Normality was confirmed by Kolmogorov Smirnov with the Lilliefors option test. Differences between groups with normally distributed data were determined using ANOVA (type III). To determine which group(s) differed significantly from each other, a post hoc Tukey's Honest Significant Difference test (HSD for Unequal N) was employed. Differences in the proportions of males, females and subadults in Areas A and B were tested using a χ^2 test. The statistical software SAS/STAT v6 (SAS Institute) was used for the regression analyses. Values are presented as means ± SE.

RESULTS

The ringed seals in this study (N = 94) consisted of 19 adult males (age range: 8–30 yr), 33 adult females (age range: 6–27 yr) and 42 subadults (age range: 1–7 yr) (Table 1). When measuring the distance from the collection point of each seal in a straight east to west line to the shore (bottom of the fjord), a significant difference was found between these 3 groups of seals (ANOVA type III, $F = 19.09$, $p < 0.01$) (Fig. 1). The positions of adult males in relation to the shore (3.3 ± 0.5 km) differed from adult females (1.9 ± 0.2 km, post hoc Tukey, $p = 0.02$) and subadults (4.4 ± 0.3 km) (post hoc Tukey, $p = 0.045$). Adult females also differed with respect to their distance to the shore compared to subadults (post hoc Tukey, $p < 0.01$).

If we consider the distribution of the various age and sex groups in relation to the stability of the ice, more adult females (82%), more adult males (58%) and fewer subadults (19%) were located in the inner stable ice area compared to the outer, more unstable ice area ($\chi^2 = 151.50$, df = 93, $p < 0.01$). Area B was occupied by 11 adult males and 26 adult females, giving an adult sex ratio in the prime breeding habitat of 1:2.4.

No differences were found between adult males in Area A versus Area B with respect to age, standard length, body mass, CI or testosterone levels (Table 2). A Multiple Regression Model examining the effects of testosterone levels of adult males showed no significant effect of age, standard length, CI or their distance to shore ($p > 0.05$); however, testosterone was found to

Table 1. *Pusa hispida*. Data on age and sex groups of ringed seals collected on the fast-ice of Kongsfjorden in May 2004. SL: standard length, BM: body mass, CI: condition index, DFS: distance from shore

Animal category	N	Age ± SE (range) yr	SL ± SE (range) cm	BM ± SE (range) kg	CI ± SE (range)	DFS ± SE (range) km
Adult males	19	15.0 ± 1.2 (8–30)	128.4 ± 1.8 (112–140)	73.1 ± 3.2 (47–89)	1.08 ± 0.04 (0.82–1.41)	3.3 ± 0.5 (0.5–8.1)
Adult females	33	12.9 ± 1.0 (6–27)	126.2 ± 1.2 (111–140)	70.3 ± 1.8 (52–90)	1.32 ± 0.03 (0.74–1.68)	1.9 ± 0.2 (0.2–4.9)
Subadults	42	3.3 ± 0.4 (1–7)	113.0 ± 1.8 (80–135)	51.6 ± 2.2 (20–84)	1.15 ± 0.02 (0.82–1.48)	4.4 ± 0.3 (0.7–7.5)

Table 2. ANOVA (type III) between adult male ringed seals collected in the unstable (Area A) and stable (Area B) parts of the fast-ice in Kongsfjorden in May 2004, using age, SL: standard length, BM: body mass, CI: condition index and testosterone levels as dependent variables

Dependent variables	Area A N = 8	Area B N = 11	F	df (residual)	p
Age ± SE (range) yr	15.9 ± 2.6 (8–30)	14.3 ± 1.1 (9–21)	0.35	1 (17)	0.6
SL ± SE (range) cm	128.3 ± 2.8 (119–139)	128.5 ± 2.5 (112–140)	0.01	1 (17)	0.9
BM ± SE (range) kg	71.1 ± 4.7 (54–89)	74.5 ± 4.5 (47–89)	0.26	1 (17)	0.6
CI ± SE (range)	1.01 ± 0.06 (0.82–1.33)	1.12 ± 0.15 (0.95–1.41)	2.23	1 (17)	0.2
Testosterone ± SE (range) nmol l^{-1}	1.9 ± 0.7 (0.4–7.0)	2.2 ± 0.6 (0.1–7.1)	0.10	1 (17)	0.8

Table 3. ANOVA (type III) between adult male ringed seals with 0–3 neighboring adult females (Group 1) and 5–6 neighboring adult females (Group 2) collected in the inner Area (B) of the fast-ice in Kongsfjorden during May 2004, using age, SL: standard length, BM: body mass, CI: condition index, DFS: distance from shore and testosterone levels as dependent variables

Dependent variables	Group 1 N = 7	Group 2 N = 4	F	df (residual)	p
Age ± SE (range) yr	12.3 ± 0.9 (9–15)	18.0 ± 1.2 (15–21)	14.00	1 (9)	<0.01
SL ± SE (range) cm	128.6 ± 3.2 (112–135)	128.5 ± 4.7 (117–140)	0.00	1 (9)	1.0
BM ± SE (range) kg	72.6 ± 5.3 (47–87)	78.0 ± 9.0 (51–89)	0.31	1 (9)	0.6
CI ± SE (range)	1.16 ± 0.07 (0.98–1.41)	1.06 ± 0.04 (0.95–1.15)	1.23	1 (9)	0.3
DFS ± SE (range) km	1.7 ± 0.5 (0.7–4.0)	1.6 ± 0.5) (0.4–2.8	0.04	1 (9)	0.8
Testosterone ± SE (range) nmol l^{-1}	1.8 ± 0.5 (0.5–4.7)	2.87 ± 1.49 (0.1–7.07)	0.64	1 (9)	0.4

interact significantly in a positive manner with body mass ($F = 18.89$, $p = 0.03$).

The division of adult males in the stable, fast-ice area into 2 groups according to numbers of neighboring adult females resulted in 7 males in Group 1 (0–3 adult neighboring females) and 4 males in Group 2 (5–6 neighboring adult females). There were no significant differences related to standard length, body mass, CI, distance to shore or testosterone levels between adult males from these 2 groups (ANOVA type III, $p > 0.05$). However, the males with more female neighbors were significantly older (18 ± 1 yr) than the males with few female neighbors (12 ± 1 yr) (ANOVA type III, $F = 14.00$, $p < 0.01$) (Table 3).

DISCUSSION

This study has shown that breeding ringed seal females occupy the innermost, stable ice areas, while subadults are found on the outer areas of fast-ice where the ice conditions are more unstable. Adult males are scattered in between these 2 groups, with some intermingled with breeding females, while others are found further out towards the ice edge in areas dominated by subadults. This pattern strongly suggests territorial behavior with competitive exclusion of subadults and those adult males that cannot compete for territories in the prime breeding areas. These observations support earlier suggestions that have been made regarding the social structure of ringed seals, based on Inuit traditional knowledge, small-scale tracking studies and opportunistic observations of natural markings etc. (see below).

The 94 ringed seals in this study were collected by shooting from distances between 100 and 200 m. At this relatively long distance, there were no indications that some age or sex groups were harder to approach than others. Additionally, because the sampling was performed over a short time period, and a standard, expected sex ratio of close to 1:1 (45:49) was achieved, we are quite confident that the spatial distribution pattern emerging from the sample is representative of the spatial distribution for all ringed seals that were present during the breeding season in May 2004. The temporal distribution of hunting was sex-skewed for adults, with the focus of the hunt being initially on males, with a switch to females in the latter part of sampling. However, total hunting effort was quite balanced between the sexes over the sampling interval.

Size differences in seals occupying different areas of pack-ice (adults vs. subadults) is a well known phenomenon among Inuit people (Furgal et al. 2002). The findings of this study confirm the general knowledge that younger, smaller animals occupy the outer, less stable land-fast ice areas, while older, larger animals occupy the inner, more stable areas of ice. The sex ratio found for adult ringed seals in the prime breeding area of Kongsfjorden of 2.4 females per male supports the suggestion of a slightly polygynous mating system, which has been suggested in earlier studies (Smith & Hammill 1981, Stirling 1975, 1977, 1983, Kelly & Quakenbush 1990). It is also similar to the ratio of 1:2.09 reported by Smith (1987). Unlike for terrestrial breeding seals, where large size of males seems to be an important factor for reproductive success, other factors seem more important for aquatically breeding seals, especially in cases where the breeding females are as widely distributed as in the case with ringed seals (Stirling 1975, 1983). The present study found that the larger ringed seal males had the highest levels of testosterone, but that these individuals were not the ones that had most adult female neighbors. The adult males with the most adult female neighbors were significantly older than adult males with fewer female neighbors, suggesting that experience is perhaps more important than size (and high testosterone levels) in determining reproductive success for male ringed seals. It is, however, worth noting that the 2 oldest males in this study (22 and 30 yr old, respectively) were found in Area A (Fig. 1), outside the prime breeding ground, suggesting that there may be an optimal age interval for reproductive success among males.

Female spacing in ringed seals is set in part by the physical nature of the habitat. Lairs must be built where there is sufficient snow, and in Svalbard this occurs primarily where glacier ice pieces are frozen into the land-fast annually formed fjord ice (Lydersen & Gjertz 1986, Smith & Lydersen 1991). Ringed seals are aggressive with one another and appear to defend lair structures (Smith & Hammill 1981). But their dispersed distribution is also likely to be a response to predation pressure from polar bears and arctic foxes (Stirling 1977). The spacing of adult females and males in the innermost part of the fjord is similar to what would have been expected, based on the nature of the lairs, as described 20 yr ago in this fjord (Lydersen & Gjertz 1986).

More subadult males than females were collected in this study, but this is due to the fact that females mature at a significantly younger age (Krafft et al. 2006b). Additionally, our definition of sexual maturity for the 2 sexes differed somewhat, resulting in some physically mature males being classified as subadults (<7 yr of age). However, we think our classification probably reflects a reasonable approximation of social maturity, given the fact that most male pinnipeds are several years beyond sexual maturity when they enter the breeding population (e.g. Fay 1982, Kovacs 1990).

A few adult females were found in the outer, less stable areas in this study (Area A, Fig. 1); these individuals might be mothers whose pups were killed early in the season, and hence mated early and left the fast-ice areas. The outer parts of Kongsfjorden are more productive than the inner area (Hop et al. 2002) and there is no specific reason for females without pups to stay in the inner area. Many females lose their pups to arctic fox predation early in the nursing period, and a variable number of polar bear visits are responsible for additional pup mortality throughout the remaining part of the nursing period (Lydersen & Gjertz 1986).

The inner parts of Kongsfjorden (Area B, Fig. 1) have predictably stable ice-conditions each spring, mainly due to the many small islands that protect this area from wind and wave action. In addition, this area usually has a significant number of icebergs calved into the fjord from several active glaciers, which get fixed in a somewhat annually variable pattern in the inner fjord when the ice forms in early winter. Drifting snow accumulates around these icebergs and these are the prime areas for ringed seal lairs in Kongsfjorden, similar to the other fjords in Svalbard (Smith & Lydersen 1991). Sufficient snow accumulation on the sea ice is likely a limiting resource in Svalbard, as this arctic desert gets quite limited amounts of annual precipitation. Thus, the inner part of Kongsfjorden is a predictably good breeding area for ringed seals with respect to ice-stability and possibilities for lair construction. Food availability may be another factor determining the quality of ringed seal habitat. Even if ringed seal females rely on blubber stores to cover some of the costs of lactation (Ryg et al. 1990b), a large proportion of this energetically demanding process must depend on relatively heavy foraging (Lydersen 1995). The main prey items for ringed seals in this area are polar cod *Boreogadus saida* and crustaceans (Gjertz & Lydersen 1986, Weslawski et al. 1994, Labansen 2005). The Kongsfjorden area is generally considered to be very productive, supporting ringed seals and many other species of marine mammals as well as numerous species of seabirds that forage at the edge of the fast-ice and beyond (Hop et al. 2002). Previous investigations have shown that there is a high density of birth lairs in this area (Lydersen & Gjertz 1986). Since this area is usually very predictable with respect to ice stability, opportunities to construct lairs, and food availability, it could be expected that adult animals return annually to Kongsfjorden to breed. There are a few mark-recapture events supporting this assumption; adult animals have been marked and then recaptured in the next year or after several years some few 100 m from where they were marked (C. Lydersen & K. Kovacs unpubl. data). This means that some adult males may mate with the same females in successive years. Small amounts of data suggesting both intra-annual and inter-annual site fidelity have also been reported previously for breeding ringed seals in other studies (McLaren 1958, Smith & Hammill 1981, Kelly & Quakenbush 1990). But there is also information from other areas strongly suggesting that there is considerable mobility among ringed seals in some areas.

Harvests of ringed seals by humans or polar bears well above sustainable levels are sustained in some locales for long periods of time via recolonization from the broader range of the population (Smith 1973, Hammill & Smith 1991). Currently, little is known about the structure of ringed seal populations, the degree of natural mobility between breeding areas, or the levels of exchange that take place across subpopulation or population boundaries.

Studying social behaviour of ringed seals is challenging, but mounting evidence from a diverse array of sources, including this study, supports a mating system based on territorial defense by males, that results in low-level polygyny. Integration of a variety of new tracking and observational technology may provide more in-depth analyses of ringed seal social behaviour via longitudinal studies of individual animals in the water as well as on the ice surface in the not-to-distant future (e.g. Simpkins et al. 2001, Davis et al. 2003, Mitani et al. 2004).

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