Decreasing Iice Cceoverage Wwill Rreduce the Bbreeding Ssuccess of Baltic Ggrey Sseal (*Halichoerus grypus)* fFemales.

Abstract

Baltic grey seals (*Halichoerus grypus*) alternate between land- and ice breeding, depending on ice conditions. We show that the fitness of grey seal females in terms of pup mortality and quality is reduced when breeding on land as compared with ice. The mMean pre-weaning mortality rate on land was 21.1% (range 0% to 31.6%), and was correlated with birth density (range 0.5 – 5.2 pups /100 m^{-2}). The mMean mortality rate on ice was 1.5%, where the highest density was 0.2 pups /100 m^{-2} in particularly dense breeding groups. Mean weights of pups born on ice were significantly greater (48.3 ± 8.1 kg) at the onset of moult, compared with than those of pups born on land (37.4 ± 7.8 kg). Since Because indices of life-time net reproductive rate (pup survival) and pup quality (weaning weight and health) were more auspicious on ice as compared withthan on land, diminishing ice fields will lower the fitness of Baltic grey seal females and substantially increase the risk for quasi-extinction.

IntroductionINTRODUCTION

Reduction of ice coverage in the Arctic has been predicted to result in a more northern distribution of marine mammals adapted to the habitats provided by ice (1)[1]. Such profound ecosystem changes may hamper limit their possibilities forto foraginge and reproductione (2)[2], but and also may bring into contact species that formerly were mainly primarily separated species into contact(3)[3]. However, the future scenario of more northern distributions of marine mammals (1)[1] adapted to ice is not an option for land-locked species, such as Baikal, Caspian, Ladoga,

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Comment [B1]: I suggest changing "a more northern distribution" to "a northward shift in the distribution".

Comment [B2]: Please confirm whether the edits to this sentence are ok. It may help further clarify this sentence to more substantially reword it, like this (if this meaning is correct): "Such profound ecosystem changes may reduce suitable habitat for foraging and reproduction and promote contact between species that were historically separated from one another."

Saimaa, and Baltic seals.- All of these seals breed mainly or exclusively on ice, and ~~there is currently~~ no data are currently available on the possible consequences of diminishing ice fields for these land-~~-~~locked species.

Model~~l~~ing ~~suggests~~ predicts that the "normal" ice conditions, ~~where~~ under which nearly 50% of the Baltic has been covered by ice over the past 50 years (4)[4], ~~is predicted to develop into a situation where~~will change such that ice fields will be restricted to fractions of the most northerly bay (5)[5]. For facultative land-~~/~~ice breeders, this would imply a shift from mainly ice breeding to land breeding.

In this study, we analyz~~s~~e how the fitness of Baltic grey seal (*Halichoerus grypus*) females is affected by giving birth on land instead of ice. We define female fitness as the number~~s~~ of offspring in the ~~far~~ distant future according to McNamara and Houston (6)[6], which in practice has two major components: life-time net reproductive rate (R_0), measured as number~~s~~ of offspring (7)[7], and the quality of offspring (6)[6]. We argue that pup survival rate and pup weight at weaning are appropriate indices for R_0 and pup quality, respectively, and discuss the implications of our findings with regard to future effects on population growth rates and extinction risk.

MATERIALS AND METHODS~~Materials and methods~~

Study P~~p~~opulation~~.~~

The Baltic Sea was colonized by grey seals only some 9~~,~~000 years ago after the last glaciation-, and- genetic data (8)[8] suggest that the Baltic grey seal~~s~~ can be treated as an isolated population in most contexts. According to archaeological data and hunting statistics, the grey seal was ~~earlier~~ once distributed throughout the ~~entire~~ Baltic, although the highest densities have ~~always~~ been in the central and northern areas ~~ever~~ since the Mesolithic, some 8000 years before present (9)[9].

Population surveys in the 1960s indicated that the Baltic grey seal ~~to be~~is a typical ice-breeding pinniped, giving birth between ~~in~~ February and~~-~~ March on the drift ice in the central and northern Baltic (10)[10]. Births of pups on land have generally not been documented during the latter half of the 20th century (10)[10], although breeding on land ~~has been~~was reported from several regions in the Baltic Sea prior to the 1950s (11)[11].

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Breeding on Iice

Location and extent of pack ice show considerable annual variations. During mean ice conditions, drift ice suitable for breeding can be found in the northern part of the Baltic pProper, with relatively narrow extensions down to Öland on the Baltic Wwest Ceoast and along the Estonian and Latvian coasts in the east (Fig. 1). During mild winters, the ice edge does not reach these areas in the breeding season, and grey seals in the region are confined to breed on land. Historical ice records show that approximately one-~~-~~third of winters provided insufficient ice-~~-~~cover for ice breeding in the southern Baltic (4)[4]. Although~~,~~ mild winters appeared randomly throughout ~~the~~ recorded history from 1720 to ~~-~~2000, a series of mild winters predominated during the study period, 1990~~—~~2001 (4)[4].

Baltic grey seals mainly breed in pack ice formations close to the fast ice edge or on larger ice floes. Seals keep close to natural openings and cracks and are not known to establish systems of breathing- and haulout-holes in the fast ice, as is found in Baltic ringed seals (*Phoca hispida botnica*) (10)[10]. The drift ice used by grey seals for breeding is mostly ~~in~~ sheltered from direct wave action, and the ~~utilized~~ ice floes used are thick and large enough to provide a stable substratum for the whole ~~length~~ duration of the nursing period (10)[10]. The samples for this study were taken from the latter habitat type~~,~~;~~ and due to~~ because of the severe ice conditions, the field work was carried out from icebreakers equipped with helicopters.

The ice data w~~as~~ere collected from the drift -ice in the Baltic p~~P~~roper and the Bothnian Bay ~~in years~~from 1990 -to 1993 (Fig. 1). Sighted pups were caught, measured, and inspected for external pathological changes. Ice breeding was observed ~~to occur~~ in Estonia, and data from 2001 are related to the more extensive sampling in the Central and Northern Baltic.

Land ~~b~~Breeding~~.~~

Surveys carried out since 1990 revealed extensive breeding on land in the west Estonian archipelago in the Eeast Baltic (Fig. 1), ~~the~~ Stockholm Cecounty (Sweden) in the W~~w~~est Baltic, and the Finnish South-western Archipelago (12)[12]. One major breeding group was observed at Allirahu (Fig. 1.), situated in the northern part of the Gulf of Riga, about ~~seven~~7 ~~kilometres~~km from the southern coast of Saaremaa. Here the breeding area consists of several sandy or gravel islets with the maximum elevation at about 1.5 m above the mean sea level. Shapes and sizes of these islets are modified annually by ice and currents. Although there are no tides in the Baltic Sea, the sea level fluctuates with atmospheric conditions such that the islets can be partially flooded, ~~which~~ makinges the area available for breeding variable.

A second major breeding group was found at Innarahu (Fig. 1), which is situated on~~at~~ the western coast of Saaremaa, 800 m from the main island. The maximum elevation of the islet is approximately 3.5 m~~eters~~ above sea level, and the area of the islet is not affected by the sea level~~,~~ because of the steep shore-line consisting of gravel and stones. The area where births took place was restricted to coastal slopes that make up about 75% of the total area of the islet (8000 m^2). The Estonian names of both sites, which refer~~ring~~ to grey seals or to grey seal reproduction, suggest that land breeding of grey seals has occurred at these islets for centuries.

Data on land breeding were collected at the Estonian coast ~~in years~~from 1990 -to 2001 (Fig~~ure~~ 1.). The breeding islets were visited using inflatable boats equipped with outboard

Comment [B3]: Is West Estonian Archipelago an accepted regional name? If so, it should be capitalized as with Finnish Southwestern Archipelago.

engines. In 1994 and 1996, land breeding sites were locked in the ice and were not accessible by boat. However, early visits after break-up of ice cover did not reveal evidence of breeding. In all other years, the land breeding sites were visited twice at~~s~~ a minimum, and up to six~~6~~ times, to ensure that pups from early and late breeders were sampled.

Number~~s~~ of ~~p~~Pups and Pup M~~m~~ortality

From the ice habitat, a sample of 414 pups captured ~~in years~~between 1990- and 1993 in the c~~C~~entral and n~~N~~orthern Baltic, and 200 additional pups in the northern part of the Gulf of Riga in 2001, provided information on mortality and morbidity rates, as well as breeding group size and density. At the breeding islands, pup production was estimated by non-invasive, stage-structured censuses of total numbers observed. ~~The~~ gGrey seal neonates ~~go through~~undergo a sequence of ~~well-~~easily distinguished~~able~~ developmental stages, lasting only a couple of days each. Newborn pups (stage 0) can be distinguished from older pups by a combination of features, such as the presence of blood and~~,~~ birth fluids and a weak response to disturbance. Subsequent age stages (1, 1.5, 2.0, 2.5, and 3.0) are determined from other features, such as the condition of the umbilicus, body contour, and ~~the~~ intact lanugo fur (13, 14)[13, 14]. Stage class 3.5 is defined as the onset of mo~~u~~lt, which always starts on the head and the flippers, whereas pups in stage class 4 share all characteristics of stage class 3.5 except ~~for~~ that more than 50% of the lan~~u~~ago fur is mo~~u~~lted. Stage class 5 denotes fully mo~~u~~lted pups (12)[12]. This non-invasive method is widely used as an indication of the developmental stage of an individual pup~~;~~, ~~and~~ for larger groups of seals, it provides a ~~possibility~~ way to estimate the phase of breeding season and ~~the~~ total pup production (10, 13, 14)[10, 13, 14]. Pup mortality rates are given as the ratio of recorded numbers of dead pups in relation to total numbers of pups observed on ice, and estimated total numbers born on land.

Comment [B4]: You may want to consider the following rewrite for clarity, if it retains the correct meaning: "Pup mortality rates are given as the recorded number of dead pups divided by either the total number of pups observed on ice or the estimated total number born on land."

Innarahu was used for analysis of density-dependent effects. Density is given as numbers of births per 100 m^{-2}, where the total area available for breeding was 6000 m^2. External injuries and pathological changes were noted during years from 1990 to 1993 and in 1995 in live pups, and from external examination of a sample of 46 dead pups collected in 1997 were externally examined. From the ice in the Bothnian Bay, 409 live pups were examined for external injuries.

Mother-pup pairs were scattered in across the drift ice, and we studied the density of births in two ways: as group size on the one hand, and distance to nearest neighbour on the other. We measured the distance to closest neighbour (m) and divided the data into seven categories,: 0-50, 51-100, 101-200, 201-300, 301-400, 401-500, and >500 m;, where we regard the last category as single mother-pup pairs without association with other seals.

Pup Wweaning Mmass

Pups were weighed with using a spring scale with the an accuracy of ± 0.5 kg in years from 1991 to 1993 on land breeding sites, and in 1990 and 1991 on ice in the Bothnian Bay and the Baltic proper. We used the mass of pups in stages 3.5 to 4.0 (corresponding to about 16 to 18 days after birth) as indices of weaning mass since because weaning occurs in the earliest moulting stages (13)[13]. For this analysis we had access to 90 pups from land breeding sites and 89 pups from the ice in the critical stage classes.

We used the mean value for the first stage class pups in stage 0 (12.1 kg), as the mean birth mass, both on ice and at land breeding sites;, this which is expected to be slightly heavier than the true birth mass.

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Comment [B5]: Is this edit correct (making it consistent with previous reference to stages) or should this be stage 1?

RESULTSesults

Pup Mmass on Iice and at Lland Bbreeding Ssites

No significant differences were found betweenin weights of male and female pups for any of the stage classes, when comparing pups from the same habitats. Thus, for pups born on ice, there was no significant difference in weight between the sexes for pups in stage classes 3.5 and 4.0 combined (df = 54, t = 1.996, p = 0.113, Table 2). Also, at the land breeding sites, pup weights were similar for the two sexes in the combined stage classes 3.5 and 4.0 (df = 87, t = 1.99, p = 0.44). Consequently, in the following analyses we pooled data for the sexes, and only compare pup weights as such on ice and at land breeding sites.

Pups in classes younger than stage 3.0 showed similar weights both on land and on ice; this which also suggests that weights also were similar weights at birth. However, for stage classes 3.5 and 4.0 combined, pups born on ice were significantly heavier (48.3 ± 8.1 kg) than land–born pups (37.4 ± 7.8 kg, df = 176, t = 7.997, p < 0.0001,) (Table 2). This significant difference remaineds also when comparingfor comparison of stage 4 pups (about 18 days old) only (df = 63, t = 1.998, p < 0.0001) and, for any other combination of stage classes 3.5 and 4.

Pup Ddensity, Mmortality, and mMorbidity on Iice

Group sizes ranged from single mother-pup pairs and up to 23 pairs, whereasand mean group size was 7.4 pairs (SD = 21.0). The frequency distribution of the group size appeared to be closely described (R^2 = 0.92) by the power function $y = 110*x^{-2.00}$, where y is the numbers of groups and x is the numbers of seals in each of the groups.

Using the mean value of each distance category, we plotted mean distance to closest neighbour, x, against the numbers of seals in the each categoryies, y, and find found that also this distribution also is closely described (R^2 = 0.92) by a power function, $y = 2285.1*x^{-0.945}$ (Fig. 2).

Comment [B6]: If the meaning here is that ice vs. land breeding site pups (but not male vs. female pups) will be compared, this is ok as is, except I think you could delete "as such". But if the meaning is that various comparisons will be made, not limited to ice vs. land breeding pups, but not including a male vs. female comparison, you might want to end the sentence after "sexes".

Comment [B7]: Should "and for any other combination of stage classes 3.5 and 4" be changed to indicate which combinations are possible other than 3.5 alone? It's not clear to me what the other combinations might be.

Comment [B8]: Please confirm whether this edit retains the correct meaning.

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Comment [B9]: In this sentence, should the variables be defined using letters other than x and y, which are used in the previous paragraph to define different variables? Also the power function in Fig. 2 is different. Should it be the same? Or not repeated at all?

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Consequently, 45.6% of ~~the~~ pups were found in the densest category, 0–50 m, where the mean pup density was estimated at 0.20 pups ~~/~~100 m^{-2} (Fig. 2).

The mean mortality rate among 614 ice–born pups was 1.5% (Table 1), and~~,~~ ~~whereas~~ the morbidity rate ~~is indicated~~appears to be very low as none of the ~~investigated~~ 605 live pups investigated showed external signs of infections or septic lesions, although ~~occasional~~ a small number of pups (< 1%) had minor scars.

In the sample of pups born on ice in Estonia in 2001 (n = 200), only four (2%) were found dead, of which two were stillborn~~,~~ and two had died of other ~~reasons~~causes.

Pup D~~d~~ensity, M~~m~~ortality, and M~~m~~orbidity on L~~l~~and

Pup densities at Innarahu varied between 0.46 and 5.2 pups ~~/~~100 m^{-2} over the study period, 1991–~~-~~2000, and the mortality rate was positively correlated ~~to~~with density (df = 10, F = 18.85, p = 0.002, Fig. 3.). Of the 2952 pups estimated to have been born ~~totally~~ at the two land breeding sites combined, 622 (21.1%) were ~~registered dead~~known to have died (Table 1)~~;~~. ~~which~~this is an order of magnitude greater than mortality in the ice habitat. At the land breeding sites, pups showed traumatic injuries, mainly in form of bleeding wounds in the head and ~~-~~neck region and infected wounds on hind flippers. At Innarahu, infected eyes and discharge from nostrils were recorded among 21% of pups (46 out of 216 pups observed) in 1992, ~~while~~whereas ~~less~~ fewer than 5% of pups at Allirahu showed similar symptoms in the same year. Starvation was a common condition among~~st~~ dead pups. Forty-two of the 46 (90%) ~~examined~~ dead pups examined at Innarahu in 1997~~,~~ had died within the first week of ~~their~~ life, and the mean weight of 29 dead pups was 10.8 kg.

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Comment [B10]: This result appears to be repeated in the caption for Fig. 3. It may be better to provide the result in only one place. Also, if this is an ANOVA should there be another degree of freedom?

Comment [B11]: Are the edits to this sentence ok? Also, if this sentence should indicate the time period, such as "known to have died during the study period" or "known to have died in the first week of life", please reword as needed.

Numbers of pups born on land at both ~~study sites~~ Allirahu (df = 10, F = 6.26, p = 0.03) and Innarahu (df = 10, F = 10.06, p = 0.01) showed significantly negative correlations with the annual maximum ice coverage of the Baltic Sea (Fig. 4).

Comment [B12]: Again, it may be better not to repeat the result in the figure caption. And again, should the test have another degree of freedom (if it's an ANOVA)?

DISCUSSION~~iscussion~~

We defined female fitness as the number~~s~~ of offspring in the ~~far~~ distant future, according to McNamara and Houston (6)[6], which in practice has two major components: life-time net reproductive rate (R_0), measured as the number~~s~~ of offspring (7)[7], and the quality of offspring (6)[6]. We compared these ~~aspects~~ components of female fitness of grey seals in two types of breeding habitats and found that indices of life-time net reproductive rate (pup survival) and the quality of offspring (pup weaning weight) were higher on ice ~~compared with~~than on land. We also showed that females chose ~~the~~ ice for breeding~~,~~ when both land and ice habitats were available. We ~~shall~~ discuss and evaluate these findings in the following sections.

Reproductive Eeffort

~~The r~~Reproductive effort, which is ~~a~~ central ~~technical term in~~to life history theory, ~~. It~~ is ~~either~~ measured either as survival cost, where reproducing females could suffer higher mortality, or as a potential fecundity cost, where energy used for present reproduction could lower body growth, resulting in decreased future reproductive output (6, 15)[6, 15]. However, in most studies, confounding factors make it difficult to obtain detailed information on energy allocation and ~~the~~ cost in the form of survival. One way to overcome the problem of measuring energy allocation would be to use model organisms ~~where~~ for which the annual energetic allocation to reproduction is fixed from the attainment of sexual maturity ~~and~~ until death. Thus, in species that reproduce repeatedly and ~~where~~ in which the annual reproductive allocation is delimited to a certain amount of energy, two possibilities emerge: either to reproduce or not. Consequently, such ~~species~~

organisms can, at reproductive size, allocate available energy to either reproduction or growth. Further, there will be no other ~~possibilities~~ ways to affect the R_0 except through ~~from varying~~variation of the age at first parturition (AFP) and the survival rate.

One interesting feature of such a model organism is that ~~the~~ R_0 will be constant if the trade-off between present fecundity and longevity is optimized~~;~~, i.e.~~-~~, under these circumstances, changes in AFP will not affect R_0, whereas the number~~s~~ of offspring in the ~~far~~ distant future will increase with decreasing AFP as a consequence of decreasing generation time. Hence, the use of R_0 as a measure of fitness, as suggested in theoretical and empirical studies (16),[16] would not be ~~futile~~useful in such cases ~~like this~~. The optimal strategy for the organism outlined here is to reproduce as early as possible, ~~and~~ thereby maximizing the number~~s~~ of offspring in the ~~far~~ distant future. However, a force in the opposite direction ~~is given by that early reproduction is indicated to reduce~~will occur through reductions in survival rates or in the quality of offspring (10, 17)[10, 17].

Grey seals possess most features of this model organism. They are long-lived animals that ~~at the most~~ produce no more than one offspring each year~~;~~, ~~i.e.~~ in other words, the energetic investment in the offspring is basically similar ~~at each occasion~~each year. Furthermore, ~~grey seals~~ as is the case with many other true seals, grey seals are capital breeders~~,~~ ~~which~~that rely on stored energy for lactation (18, 19)[18, 19], when ~~average~~ females, on average, use 85% of their reserves (20)[20]. The nursing period is relatively short (2–3 weeks), compared with the long foraging period when ~~the~~ energy is accumulated in the form of a sub-cutaneous blubber layer (21)[21]. Recoveries of marked individuals (10)[10] and satellite telemetry (22)[22] ~~all~~ indicate wide dispersal of individuals ~~in the entire~~throughout the Baltic Sea during the ice-free period. Thus, feeding conditions and feeding areas during the energy accumulation period ~~can be considered~~are probably similar for~~in~~ females giving birth in different habitat types. Consequently, the

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reproductive effort of females can be regarded as similar among ice- and land-breeding females, and ~~the~~ female fitness ~~of a female~~ will be directly linked to pup survival and quality.

Influence of ~~h~~Habitat on C~~c~~ondition ~~-~~ and S~~s~~urvival of P~~p~~ups

Factors affecting breeding success in pinnipeds are ~~found to be~~ dependent on topography (23)[23] and birth density (24)[24]. Ice can be regarded as an unlimited breeding area, ~~while~~ whereas breeding grounds on land are limited to suitable fractions of islands (23)[23]. Births on ice are dispersed over wide areas where interactions among mother–pup pairs are low or non-existen~~ting~~ (25)[25], ~~while~~ whereas on land, limited suitable areas in many cases result in dense colonies (26)[26]. Ice provides a spectrum of substrata, from small, unstable ice floes exposed to wind and wave action, to stable fast ice. Baltic grey seals breed predominantly on large stable ice floes (10)[10]. ~~but e~~Early break-up of ice~~, or~~and ice pressure caused by storms are potential dangers to young pups. ~~H~~however, loss of the breeding platform is not fatal to young seals~~,~~ as they are already capable swimmers ~~already~~ at early ages. Mothers assisting their pups to safe grounds have been observed both by Hook and Johnels (10)[10] and during the expeditions of this study. Also, mothers attend their offspring on ice floes or in close proximity even when ice fields drift long distances at~~in~~ high speeds (10)[10]. Thus, there is no ~~support for assuming~~evidence that ice instability ~~to be~~is an important cause of pup mortality under severe and normal ice conditions.

The land and ice substrata also differ ~~as~~ in the extent to which they are sources ~~for~~ of infectious agents. –The low temperature on ice, which forms annually, ~~will~~ lead~~s~~ to a relatively sterile environment, ~~while~~ whereas the ground is more contaminated and ~~with~~ carries a higher risk~~s~~ for infections (24, 26)[24, 26]. Morbidity rates among ice-born pups are ~~suggested~~ thought to be very low, as very few dead pups have been found during expeditions on ice (10)[10].

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Furthermore, apart from small uninfected wounds, which are probably caused by attacks of large gulls, no signs of infections or septic wounds have been noted.

At land breeding sites, the ground can be a primary source of infection (24)[24], ~~while~~ and interactions between seals and traffic in a breeding colony increase contact rates among individuals. Virological studies of ~~-~~grey seal pups in 1992 and 1993 (at Innarahu) showed that 14 of 15 pups sampled (93%) were infected by Calici virus, and that ~~also~~ Herpes~~-~~ virus and an unidentified Morbilli virus also were common in sampled pups (B. Westerling ~~B~~ and K. Kulonen ~~K~~ pers. ~~com~~comm.). None of these viruses were lethal to grey seal pups, but were considered responsible for weakening the general condition and resistance of the immune system.

~~Also p~~Potential predation and disturbance by birds ~~is~~ also are likely to differ between the habitats. Low attendance rates of birds in the vicinity of ice~~-~~born pups is indicated by the frequent presence of placentas, ~~while~~ whereas on land, only one placenta ~~has been~~was observed during the ~~whole~~ entire study period. ~~Here~~ On land, placentas are probably consumed by the numerous gulls soon after delivery. ~~-~~Throughout the breeding season, white~~-~~tailed eagles (*Haliaetus albicilla*) are present at land breeding sites with a maximum observation of eight birds at ~~a time~~once for both study sites. Eagle attacks on grey seal pups, invoking ~~a defence~~ defense reactions by~~of~~ several grey seal females, have been recorded in both studied land ~~-~~breeding sites. Thus, high pup concentrations in restricted areas of islands probably increase contact rates between large birds and seals.

Pup morbidity and mortality have been found to be closely linked to the type of breeding habitat (24, 26)[24, 26]~~;~~, ~~which~~ this is supported by the findings of this study. In most cases, the primary causes of death remain unknown, but the absence of subcutaneous fat indicate~~s~~d long-term starvation. Pup mortality rates observed on land in this study are similar to major land-

Comment [B13]: Please check whether the virus terms should be all lower case and whether each should be closed up as one word (e.g. herpesvirus).

Comment [B14]: Does this mean that each attack typically results in a response by several females (i.e., more than one female defends a single attacked pup, mobbing the predator)? If so, maybe change sentence to: "Eagle attacks on grey seal pups, each of which invokes defense reactions by several grey seal females, have been recorded in both studied land breeding sites." Or does it mean that females have been observed on several occasions to respond to attacks on pups, with only one female defending a single attacked pup? If so, maybe change sentence to: "Eagle attacks on grey seal pups, each of which invokes a defense reaction by a grey seal female, have been recorded on several occasions in both studied land breeding sites." Or otherwise clarify.

breeding colonies in~~at~~ the British Isles, where mortality rates ranged between 10% and 35% (23, 24, 26)[23, 24, 26].

Quality of ~~o~~Offspring

The growth of grey seal pups is closely linked to the maternal energetic investment during lactation (20)[20]~~,~~ but, as discussed earlier, this allocation is likely to be similar in both studied habitats~~,~~ ~~since~~ because the same females alternate between ice~~-~~ and land breeding. However, two major components contribute to this energy allocation: energy transfer to the pup (23)[23] and energy required by the female for maintenance and activity during the lactation period. The latter component ~~has~~ did not ~~been given~~receive much attention in earlier studies, but is likely to vary substantially among breeding sites. The h~~H~~ighest densities of females ~~are~~ occur in ~~the~~ proximity ~~of~~to pools (27)[27], and lactating Baltic grey seals frequently spend time in the water (12)[12]. This behavio~~u~~ral feature may be linked to thermoregulation, and access to water could therefore reduce the physiological stress of lactating females (27)[27]. Furthermore, movements between the pup and the water may be more costly in dense colonies ~~since~~ because both the distance to water and interactions with other seals ~~is~~are expected to increase with seal density (21, 27)[21, 27]. Therefore, energy expenditure of females, measured as weight loss (20, 21)~~-~~[20, 21], may not be directly linked to mother~~–~~–pup energy transfer.

Similar energetic effects can be expected in pups ~~since~~ because physiological stress and harassment may vary with environmental conditions and density. Therefore, we expect energy transfer efficiency to be higher in areas with "~~"~~favo~~u~~rable~~"~~" environmental conditions and low seal densities. This is corroborated by empirical data from both West and East Atlantic grey seal populations (21, 23, 27)[21, 23, 27]. In areas with low seal densities (Sable Island, Amet Island, and ice), the mean daily weight gain of pups is higher ~~compared with~~than in areas of high seal

densities (e.g., North Rona and our land breeding areas). Although initially lighter, ice-born pups in the Baltic attain ~~similar~~ weaning weights similar to those ~~as~~ found in Atlantic populations. Pups born on ice in the Baltic were also heavier at weaning compared with other East Atlantic populations, ~~while~~ whereas land-born Baltic pups exhibited the lowest weaning weights. Our results confirm that negative effects on pup growth appear at high densities, but such effects are less explicit when density is low.

Comment [B15]: It is not clear what "less explicit" means in this context.

~~There is n~~No evidence suggests that weaning weights differ between land and ice breeding habitats in Canadian seals. However, in the only study (19)[19] ~~where~~ in which data were collected from both habitats, land breeding conditions (e.g., density) were not specified. ~~Since~~ Because the reported breeding area in that study was 6600 m^2~~,~~ and the largest sample of pups was 48, it is possible that the breeding density was too low to affect pup growth. However, a later Canadian study showed that, when compared with land-born seals, ~~that~~ ice~~-~~born seals are nursed during a shorter period (15 days) and grow faster, although the energy received ~~energy wa~~is the same ~~when compared with studies of land breeders~~(21)[21].

Our principal finding ~~wa~~is that pups born on ice were significantly heavier at weaning ~~compared with~~than pups born on land (Table 2). We therefore suggest that this difference in weaning weights is primarily ~~to be~~ a consequence of higher energetic expenditure on land by both pups and females, although the generally poorer health of pups ~~condition~~ at land breeding sites may be a contributing~~ory~~ factor. High weaning weight of pups is correlated with~~to~~ increased chances of survival (28)[28]. Consequently, ~~it could be expected that~~ females may give birth in habitats that maximize~~sing~~ their fitness in terms of pup survival and quality. Baltic grey seal females selected ice over land sites when both were available (Fig. 4).

Consequences

The ~~scenario of~~ retreat~~ing~~ of ice fields (5) will force a great majority of Baltic grey seal females to breed on land, which will reduce their fitness both in terms of life~~-~~time net reproductive rate and pup quality. The ~~M~~major predicted consequences will be a lower~~ed~~ and more variable future mean population growth rate; this~~, a~~ combination of consequences will lead~~ing~~ to dramatically enhanced risks for quasi-extinction (29)[29]. The accepted Helsinki Commission~~HELCOM~~ seal recommendation from 2006 identifies three main long-term management principles: n~~N~~atural distribution, natural abundance, and a health status that secures the long-term persistence of Baltic seal species. ~~-~~Remedial actions can ~~only~~ be taken only when these long-term management principles are no~~'~~t compromised~~;~~; ~~which~~ in ~~practise~~practice, this implies that population growth rates of Baltic seal species and populations should be positive until they level~~l~~ling off for natural reasons. The predicted reduced and more variable population growth rate of Baltic grey seals in the future would entail that the time for reaching the first two ~~first~~ long-term goals will be substantially extended compared with the current situation, and that the risk for rapid declines will be greatly enhanced.

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Comment [B16]: Please confirm whether the acronym "HELCOM" has been correctly defined as "Helsinki Commission". Also, should a reference be cited for this recommendation?

~~Literature Cited~~References and Notes

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31. First submitted 15 May 2007. Accepted for publication 5 July 2007.

Figure captions

Figure 1. Location of land study sites, Allirahu (A) and, Innarahu (B), and ice areas from where data were collected during ice expeditions. The 2001 ice data were collected from the northern part of the Gulf of Riga (Estonia).

Figure 2. Mean distance to closest neighbouring pup on ice. Proportions (squares), and densities (filled circles), given as numbers / 100 m^{-2}) of mother–pup pairs for seven spatial categories, withwhere mean pup distances varied betweenof 1–50m, 51–100m, 101–200m, 201–300m, 301–400m, 401–500m, and > 500m. The last category (open square) would

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represents mother–pup pairs without association. Proportions of pups in different categories fitted to $y = 748x^{-0.946}$, $R^2 = 0.92$. Numbers of pups = 338.

Figure 3. Pup mortality rates and birth densities were positively correlated (ANOVA: F = 18.8, p = 0.002) at Innarahu over the study period.

Figure 4. Birth densities at land breeding sites and the extent of ice cover in the Baltic through years 1991–2001. Negative correlations were shown both at Allirahu (ANOVA: F = 6.26, p = 0.03) and Innarahu (ANOVA: F = 10.05, p = 0.01).

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Table 1~~:~~. Data on Baltic grey seal pups collected on ice and at the two major land breeding ~~s~~Sites, Allirahu and Innarahu, in the Baltic (Fig. 1).

Area ~~/~~year^{-1}	No. of p~~P~~ups	No. d~~D~~ead	Percentage~~rop. Dd~~ead ~~(%)~~	Ice c~~C~~over (km^2*10^3)
Ice				
1990	77	0	0.0	
1991	82	1	1.2	
1992	157	4	2.5	
1993	98	0	0.0	
2001	200	4	2.0	
Total	614	9	1.5	
Allirahu				
1991	21	1	4.8	122
1992	377	119	31.6	66
1993	155	4	2.6	70
1995	175	50	28.6	68
1997	109	2	1.8	128
1998	181	22	12.2	129
2000	488	133	27.3	95
Total	1506	331	22.0	
Innarahu				
1991	41	3	7.3	
1992	328	72	22.0	
1993	141	15	10.6	
1995	188	23	12.2	
1997	238	47	19.8	
1998	181	46	25.4	
1999	26	0	0.0	
2000	303	85	28.1	
Total	1446	291	20.1	
Grand total land	2952	622	21.1	

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Table 2. Weaning weights (Sstage classes 3.5 and 4.0 combined, see text) of Baltic grey seal pups from land breeding sites and ice. Weaners on ice were significantly heavier than pups at land breeding sites.

Habitat	Group	Weaning weight in kg ± SD (n)
Land	Males	38.1 ±7.5 (42)
	Females	36.8 ±7.8 (48)
	Pooled	37.4 ±7.7 (90)
Ice	Males	50.1 ±8.4 (35)
	Females	47.2 ±7.6 (54)
	Pooled	48.3 ±8.1 (89)