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Distribution of Hauled-Out Ladoga Ringed Seals (*Pusa hispida ladogensis*) in Spring 2012

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ABSTRACT. The spatial distribution and habitat selection of the Ladoga ringed seal (*Pusa hispida ladogensis*), an endangered freshwater seal, are poorly understood, particularly for the ice-covered period. A fixed-wing, strip-transect aerial survey conducted in early April 2012, before the Lake Ladoga breakup, provided data on seal density and distribution throughout the lake in relation to several environmental covariates: depth, distance to shore, recreational ice-fishing activity, and ice type. A predictive model was applied to combinations of covariates to estimate the total number of seals hauled out on ice of Lake Ladoga. The model estimate was 5068 (95% CI: 4026–7086) seals over an area of 16 827 km^2. The mean observed seal density was 0.29 seals/km^2 (SD = 0.351, range from 0 to 8.61), and density was highest (> 1 seal/km^2) in regions that were relatively shallow (< 50 m). Densities appeared to increase with distance from shore but dropped off again at the longest distances. The average density was lower in fast ice habitats (0.13 seals/km^2) than in drifting pack ice habitats (0.44 seals/km^2). Relatively high seal densities observed in "ice edge" zones (0.26 seals/km^2) could be explained by the ice formation pattern of large ridged and hummocked areas in the transition zone between shorefast ice and secondary ice. The presence of fishermen had a highly significant negative effect on seal presence ($\beta = -7.8$, $p = 0.0014$), resulting in a nearly twofold decrease in seal density in shorefast ice habitats (0.09 seals/km^2 in fishing areas and 0.15 seals/km^2 in areas without fishing activity). An extensive winter recreational fishery, in combination with potential negative trends in ice conditions on the lake, might reduce the amount of suitable habitat for the Ladoga ringed seal in the near future.

Key words: Ladoga ringed seal, ice associated seals, distribution, fisheries, ecological factors, modeling

RÉSUMÉ. La répartition spatiale et la sélection de l'habitat du phoque marbré de Ladoga (*Pusa hispida ladogensis*), phoque d'eau douce en voie de disparition, ne sont pas bien comprises, surtout en ce qui a trait à la période d'englacement. Un levé aérien à base de transects en bandes effectué au début du mois d'avril 2012, avant la débâcle du lac Ladoga, a permis d'obtenir des données sur la densité et la répartition du phoque à l'échelle du lac par rapport à plusieurs covariables environnementales : la profondeur, la distance jusqu'au rivage, la pêche récréative sous la glace et le type de glace. Un modèle prédictif a été appliqué à des combinaisons de covariables afin d'estimer le nombre total de phoques qui se hissent sur la glace du lac Ladoga. Le modèle a permis d'obtenir une estimation de 5 068 (IC de 95 % : 4026-7086) phoques dans une aire de 16 827 km^2. La densité moyenne des phoques observés était de 0,29 phoque/km^2 (écart-type = 0,351, écart allant de 0 à 8,61), et la densité était plus élevée (> 1 phoque/km^2) dans les régions relativement peu profondes (< 50 m). Les densités semblaient augmenter en fonction de la distance du rivage, mais elles baissaient de nouveau lorsque les distances étaient plus longues. La densité moyenne était moins élevée dans les habitats à glace rapide (0,13 phoque/km^2) que dans les habitats à banquises en dérive (0,44 phoque/km^2). Les densités de phoques relativement élevées qui ont été observées dans les zones de « lisières de glaces » (0,26 phoque/km^2) pouvaient s'expliquer par le modèle de la formation de glace des grandes zones de glaces tourmentées et moutonnées faisant partie de la zone de transition entre la banquise côtière et la glace secondaire. La présence de pêcheurs avait un effet considérablement négatif sur la présence des phoques ($\beta = -7{,}8$, $p = 0{,}0014$), ce qui se traduisait par une diminution de presque la moitié de la densité de phoques dans les habitats à banquise côtière (0,09 phoque/km^2 dans les zones de pêche et 0,15 phoque/km^2 dans les zones où il n'y avait pas de pêche). L'intensité de la pêche récréative en hiver, alliée aux tendances potentiellement négatives en matière d'état des glaces du lac, pourrait avoir pour effet de rapetisser la quantité d'habitat habitable par le phoque marbré de Ladoga dans un avenir rapproché.

Mots clés : phoque marbré de Ladoga, phoques en fonction des glaces, répartition, pêcheries, facteurs écologiques, modélisation

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Резюме. Распределение ладожской кольчатой нерпы (Pusa hispida ladogensis), пресноводного эндемика, находящегося под угрозой исчезновения, а также выбор нерпой местообитания во время ледового периода крайне мало изучены. Авиаучет на линейных трансектах, проведенный в начале апреля 2012 года с борта самолета перед вскрытием Ладожского озера, предоставил данные о плотности и распределении нерпы на всей акватории озера во взаимосвязи с несколькими факторами окружающей среды, включая глубину, расстояние до берега, тип льда и использование льда рыбаками-любителями. Прогнозирующая модель была применена к комбинации переменных для оценки количества тюленей, находившихся на льду Ладожского озера, которое составило 5 068 (95% CI: 4026 – 7086) особей на 16 827 км2. Средняя наблюдаемая плотность залегания тюленей составила 0.29 особи/км2 (SD=0.351, диапазон от 0 до 8.61), а наибольшая (>1 особи/км2) - в относительно мелководных районах (< 50 м). Выяснилось, что плотность возрастает по мере удаления от берега, но затем вновь падает при наибольших значениях расстояния. Плотность оказалась ниже на припайном льду (0.13 особей/км2), чем на ломаном паковом льду (0.44 особи/км2). Сравнительно высокая плотность залегания на краевых участках льда (0.26 особей/км2) объясняется характером формирования ледового покрова на озере, в частности, образованием обширной зоны торосов на границе берегового припая и вторичного приносимого льда. Присутствие рыбаков на льду имело статистически значимый отрицательный эффект (β=-7.8, p=0.0014), приводящий к сокращению плотности залегания тюленей на припайном льду почти вдвое (0.09 особей/км2 и 0.15 особей/км2 в районах используемых и неиспользуемых рыбаками, соответственно). Экстенсивный зимний любительский лов рыбы в совокупности с возможными негативными тенденциями в ледовых условиях могут привести в ближайшем будущем к уменьшению площади местообитаний, пригодных для ладожской кольчатой нерпы.

Ключевые слова: ладожская кольчатая нерпа, ледовые формы тюленей, распределение, рыболовство, экологические факторы, моделирование

INTRODUCTION

The Ladoga ringed seal (*Pusa hispida ladogensis*, Nordquist, 1899) is an endemic ringed seal subspecies inhabiting Lake Ladoga in northwestern Russia (Fig. 1). Its population has been isolated from the Baltic Sea population for more than 8000 years (Muller-Wille, 1969; Hyvärinen and Nieminen, 1990), and during this time it has successfully adapted to a freshwater environment atypical for most marine mammals. Intensive harvesting during the 20th century caused a severe decline of the Ladoga ringed seal population (Tormosov and Philatov, 1973; Sipilä et al., 2002), which decreased dramatically from an estimated 20 000 in the 1930s (Chapskiy, 1932) to estimates of 3000 – 5000 in the mid-1970s (Zheglov and Chapskiy, 1971; Antonuk, 1975) and 3000 in 2001 (Verevkin, 2003). Harvest of the Ladoga ringed seal was banned in Russia in 1980 as a conservation measure (Sipilä and Hyvärinen, 1998) and the subspecies was included in the Red Data Book (Danilov-Danil'yan et al., 2000). The international scientific community's concern about the future of the Ladoga ringed seal led the International Union for Conservation of Nature to declare it an endangered subspecies (Kovacs et al., 2012).

There is concern about the interaction of ringed seal with fisheries in the area; high by-catch of seals is considered to be one of the major threats to the survival of this subspecies. Conflicts between seals and commercial fishermen are increasing because the seals cause significant damage to fishing gear and hauls, which makes fishing unprofitable in most areas of the lake (Trukhanova et al., 2012). Furthermore, a large portion of the coastal fast ice is used by

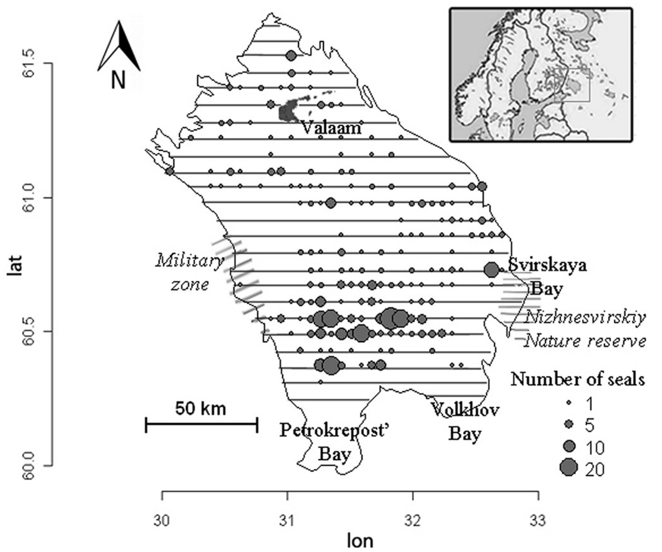

FIG. 1. Survey transects in Lake Ladoga, April 2012. Dots represent seal sightings.

recreational ice fishermen during the seal pupping period, which may indirectly affect pup survival.

Aside from fishing-related effects, key features of Ladoga seals' behavior and seasonal movements are influenced by their freshwater environment. The Ladoga ringed seal and the Saimaa ringed seal (*P. h. saimensis*) are the only two subspecies of ringed seal that inhabit freshwater lakes year-round, which has led to marked differences from marine subspecies in habitat preferences and movements (Berta and Churchill, 2011). The marine breeding habitats of ringed seals are associated with landfast ice and pack ice areas (e.g., McLaren, 1958; Finley et al., 1983; Lydersen and Gjertz, 1986; Kunnasranta, 2001), while Saimaa ringed seals give birth in snowdrifts on the shorelines of islands or islets close to the shore (Sipilä, 1990). The Ladoga ringed seal is thought to breed in hummocked areas located along the fast ice band or, more seldom, in snowdrifts in the northern part of the lake (Antonuk, 1975; Sipilä et al., 1996; Kunnasranta, 2001). Because the entire lake does not freeze completely every year, variations in ice extent affect seal distribution from season to season (Antonuk, 1975; Philatov, 1990). Both Lake Saimaa and Lake Ladoga are relatively shallow water basins (Kuusisto, 1999; Kuderskiy, 2009) but regional differences in depth and temperature regimes influence seasonal fish migrations (Kuderskiy, 2009), which then influence seal distribution (Harkönen et al., 2006).

The Ladoga ringed seal, like all subspecies of the ringed seal, is pagophilic, using ice for pupping, pup nursing, resting, and the annual molt. The breeding behavior of the Ladoga seal has not been documented, but most likely the pupping season lasts from March to the beginning of April (Agafonova et al., 2007). It is thought that lactation lasts 1.5–2 months and that mating takes place during the mid to late stages of lactation (Chapskiy, 1932). In early April, seals begin to molt and tend to bask on the ice surface or rockeries until mid-May, ensuring better insulation for their skin (Feltz and Fay, 1966; Kelly, 1988). These facts suggest that the ringed seals, especially breeding animals, are likely to be sedentary during the ice season and tend to stay near their lairs, while continuously maintaining breathing holes in the ice and nursing pups. Subadult seals tend to travel much greater distances during winter (Smith, 1987; Gjertz et al., 2000; Freitas et al., 2008) since they are not constrained by establishing and maintaining birth lairs. During periods of severe ice conditions, however, they also depend on permanent breathing holes.

The seasonal activities of Ladoga seals are affected by anthropogenic and environmental factors that influence birth and survival rates, distribution, and abundance of the subspecies (Agafonova et al., 2007). The factors that are most influential in determining the spatial use, distribution, and ultimately, the abundance of the Ladoga ringed seals remain largely unknown. In this paper, we use results of an aerial survey of ice seals performed in Lake Ladoga in April 2012 to model densities and habitat selection of the Ladoga ringed seal on spring ice throughout the lake with respect to bathymetry, proximity to the shoreline, ice type, and use of the area by recreational fisheries in winter. Our specific goals are to identify and interpret the physical features of the lake environment that are most directly related to space use by seals, to generate density maps over the entire lake, and to quantify the effect, if any, of recreational fisheries. We also discuss implications for the management of this population.

MATERIAL AND METHODS

Aerial Survey

The Ladoga ringed seal aerial survey, conducted on 4, 5, 6, and 14 April 2012, encompassed ice-covered areas of Lake Ladoga at the beginning of the annual molt, using standard line transect methods (see, e.g., Skalski et al., 2005). Flights took place primarily between 1000 and 1500 (local time) under sunny or mainly clear weather conditions. Three observers collected the data from a fixed-wing, low-noise aircraft (Cessna-182T) flying along strictly east–west oriented linear transects. Observations were made from both sides of the aircraft to 413 m distance on either side, i.e., along a strip 826 m wide. Observers maintained a consistent strip width by aligning markers placed on the windows and the wing struts of the aircraft. The flight altitude and ground speed were controlled by the onboard navigation system and maintained as consistently as possible at 90 m and 190 km/h. In total, 24 survey transects (Fig. 1) covered 1748 km^2 (10.4%) of ice surface and 109 km^2 of water surface (the water surface was excluded from the analysis). Each seal detected on ice was photographed, and its coordinates were determined using hand-held Garmin cs62 GPS units attached to the cameras. For the purpose of the analysis, we used a set of waypoints, each of which marked individual animals seen within transects.

Physical Covariates

Lake Ladoga (Fig. 1) is a large (17 872 km^2), relatively shallow subarctic lake in northwestern Russia. Its maximum extent is 125 km (E-W) and 219 km (N-S); mean depth is 48 m and maximum depth is 228 m. The coastline is represented by flat, sandy beaches and wetlands except on the northern shore, referred to as the "skerries region," which is marked by fjord-like inlets and rocky cliffs. Typically, ice forms on the lake in early December and reaches its maximum extent in February, usually covering the entire lake.

We subdivided Lake Ladoga into a grid of equal blocks (5 km^2 each), 491 of which were included in transect coverage. Three physical factors (depth, distance to the shore, and ice type) and the presence or absence of recreational fishermen were covariates chosen for the analysis and modeling of seal distribution. Depth for each individual block in Lake Ladoga was obtained from Garmin BlueChart map (ver. 3.01© 2011 Garmin Ltd). Distance to the shore (proximity) was measured as the shortest straight line from the block center point to the nearest lakeshore, using Garmin BaseCamp (ver. 3.3.2© 2008–12 Garmin Ltd).

We determined several ice types for the analysis on the basis of satellite imagery AERONET_Helsinki (for 5 April 2012) with 250 m resolution provided by NASA and downloaded in the 7-2-1 frequency band for easier interpretation (http://rapidfire.sci.gsfc.nasa.gov). We assumed that the total ice area was constant over the survey period and that the ice did not move significantly. In winter 2011 – 12, ice began to form on the lake in late January, when a narrow (5 – 10 km) fast ice band appeared along the shoreline. Ice coverage was 100% by the beginning of March, and breakup began about a week later. When the survey started, the central part of the lake was covered with extensive ice floes or groups of ice floes frozen together (hereafter referred to as "drifting pack ice"). During the winter, this area had stable ice that was associated with fast ice zones. However, it was the first area to break up in early spring. The fast ice band still remained untouched along the western, eastern, and southern shores and completely covered the northern skerries region of the lake (to the north of Valaam Archipelago). Fast and drifting pack ice areas were divided by open water areas. Another specific habitat type was the ice edge. Any block that covered both ice and water areas was classified as "ice edge," and the area covered by ice in this category was averaged to be 2.5 km^2.

Twelve main winter fishing areas were defined on the basis of interviews with recreational and commercial fishermen and through data from an aerial survey that photographed and mapped concentrations of fishermen on the ice. This covariate was entered in the model as "true" if there was any ice fishing activity in a given block, and "false" in the opposite case.

ANALYSIS

Analysis and modeling included specifying and fitting a negative binomial generalized linear model (NBGLM) of seal count data as a function of several covariates in various combinations. The model is written as:

$$N_i = \text{NB}(\mu_i, k)$$
$$\log(\mu_i) = f(\cdot)$$

where NB refers to the negative binomial distribution with fitted dispersion parameter k and mean μ_i is the expected number of seals in a given block, modeled as the exponential of a linear combination $f(\cdot)$ of the covariates. The NBGLM was chosen over standard Poisson GLM in order to account for over-dispersion in the count data (Zuur et al., 2009), and preferred over a quasi-Poisson model because a well-defined likelihood for the negative binomial facilitated comparison of models, and because a diagnostic plot of means against variances suggested a squared relationship more appropriate to a negative binomial model (VerHoef and Boveng, 2007).

The response variable in the fitted models was the number of seals in the blocks. Explanatory variables were the factors listed above: depth and proximity to the shore were computed at all locations of the seal sightings and included as continuous covariates. Because of observed non-linear responses of seal counts to depth and distance from shore (Fig. 2A, 2C), we also added square root terms, $\text{depth}^{0.5}$(d2) and $\text{proximity}^{0.5}$(p2), to the set of fitted models. Ice type was a categorical covariate. The models we fitted ranged from the null model (M0) of a constant linear predictor to the most complex model (M36), which included linear and square root terms of depth and proximity, as well as their interaction with each other and with the ice-type covariate [in formula notation: $(\text{depth} + \text{depth}^{0.5})*(\text{proximity} + \text{proximity}^{0.5})*\text{ice-type}$]. Note that we used the square root term (rather than, e.g., a square term) to capture non-linear structure because the square root transformation has the property of keeping predictions from increasing unrealistically at higher values of depth or distance from shore. We chose to use non-linear terms in the GLM over a generalized additive model (GAM) because the GLM provided a good fit without the additional levels of complexity and decisions required for fitting a GAM.

We compared all 37 models using Akaike's Information Criterion (Burnham and Anderson, 2002). As a measure of goodness of fit, we used proportion deviance explained (PDE), which is analogous to an adjusted R^2 measure (Wood, 2006):

$$\text{PDE} = 100 \times (1 - \text{residual deviance} / \text{null deviance}).$$

Because ice type was a highly significant interaction factor (see RESULTS), we modeled the seal densities in each different habitat separately and selected models as described above, comparing negative binomial GLMs that included various combinations of the depth, proximity, and non-linear terms. Because fishery activities were identified almost exclusively in the shorefast ice type, we additionally added fisheries presence as an explanatory covariate in that ice habitat.

We obtained an uncorrected estimate of total seal abundance by subdividing the lake into a grid of blocks of the same size as the transect blocks used in the modeling and obtaining a model prediction using a hybrid combination of the most parsimonious models in each habitat as selected by AIC. Confidence intervals around the point estimate were obtained by using a bootstrap method (Manly, 1997), whereby we resampled our observed data with replacement and re-estimated the total abundance 1000 times. We report the 2.5% and 97.5% quartiles of the bootstrapped distribution. The predicted abundance was converted into densities and mapped in order to compare the structure of relative densities across the lake region.

For all analyses, we used the R statistical programming language (R Development Core Team, 2008), including the "MASS" package (Venables and Ripley, 2002) for negative binomial generalized linear modeling and the "maps" and "mapdata" packages (Becker and Wilks, 1993) for mapping.

RESULTS

Lake Ladoga is characterized roughly by two regions: a shallow, sandy-bottomed zone in the southern part of the lake (mean depth ca. 30 m), and a deepwater zone in the

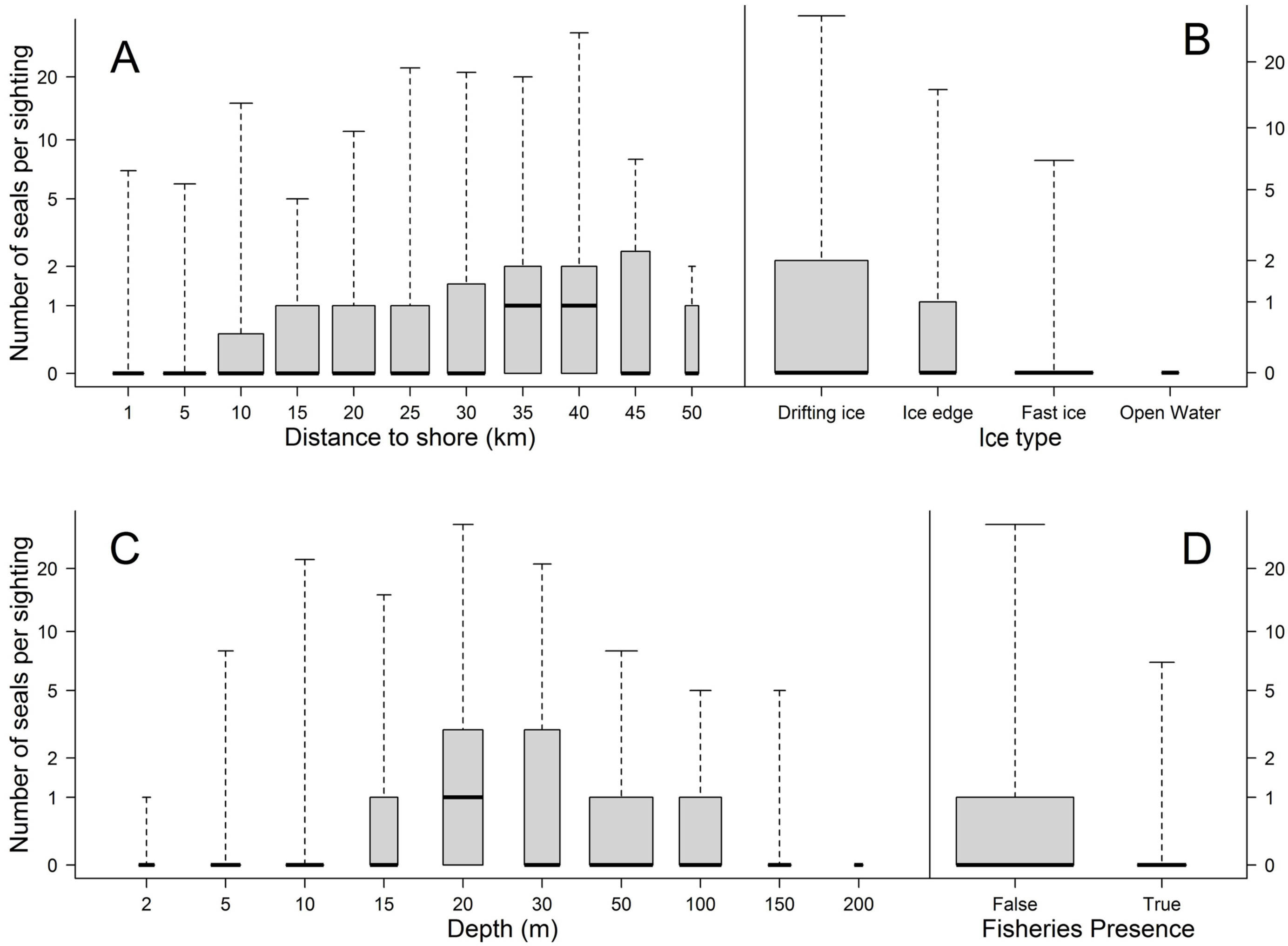

FIG. 2. Seal distribution (number of seals per block) plotted against environmental covariates (A, B, and C) and fisheries factor (D). The width of the boxes is proportional to the number of observations in each group. Bold horizontal lines in boxes indicate median number of seals.

northwest, characterized by reefs and skerries (mean depth ca. 130 m). For the purposes of modeling and fitting, we subdivided the lake into 3460 blocks of 5 km^2 and determined depths, proximity to shore, ice type, and presence of fisheries for each block. Mean depth measurements ranged from 2 m along the shoreline to 200 m in the deepest area (mean 43.4 m, SD = 37.9 m, Fig. 2C). Distance to shore for each block was determined at 5 km resolution and ranged from 0 to 50 km in the central part of the lake. At the beginning of April 2012, out of a total area of 17 872 km^2, the lake had only 1045 km^2 (5.9%) of open water. The ice-covered portion had somewhat more drifting pack ice (8860 km^2, 49.6% of total area) than fast ice (7367 km^2, 41.2%). The remaining 600 km^2 (3.6%) was classified as ice edge. We estimated that around 2800 km^2 of fast ice was actively used for ice fishing in April 2012 (defining "use" as the presence of fishery activity within a 5 km^2 block).

The seal survey data used for modeling consisted of 491 blocks, each with an area of 5 km^2. Seals were sighted in 179 (36.4%) of these blocks. Sightings ranged from 1 seal (81 blocks) to 32 seals (1 block), with a total of 558 individual seals sighted. The mean observed seal density was 0.29 seals/km^2 (SD = 0.351, ranging from 0 to 8.61). We identified patterns in the relationship of the sightings to environmental covariates (Figs. 2, 3). In particular, densities appeared to increase with distance to shore but dropped off again at the longest distances (Fig. 2A), and similarly, densities were highest at intermediate depths (Fig. 2C). Finally, densities tended to be higher on the drifting ice (mean 0.44 seals/km^2, Fig. 2B) than on the fast ice (mean 0.13 seals/km^2).

We fitted 37 NBGLMs and report the AIC, ΔAIC, and proportion deviance explained in Table 1. Most of the best models were among the more complex models. The model with the lowest AIC was:

M36: seal number~ ((depth + d2) + (proximity + p2))
* ice-type

which explained 24% of the total variance. The most complex model, M37, ranked 5th, accounting for the absolute maximum of 26% of the PDE. Note that all of the top 10 models included a square root term for either proximity or depth. Further, all of the top six models included an

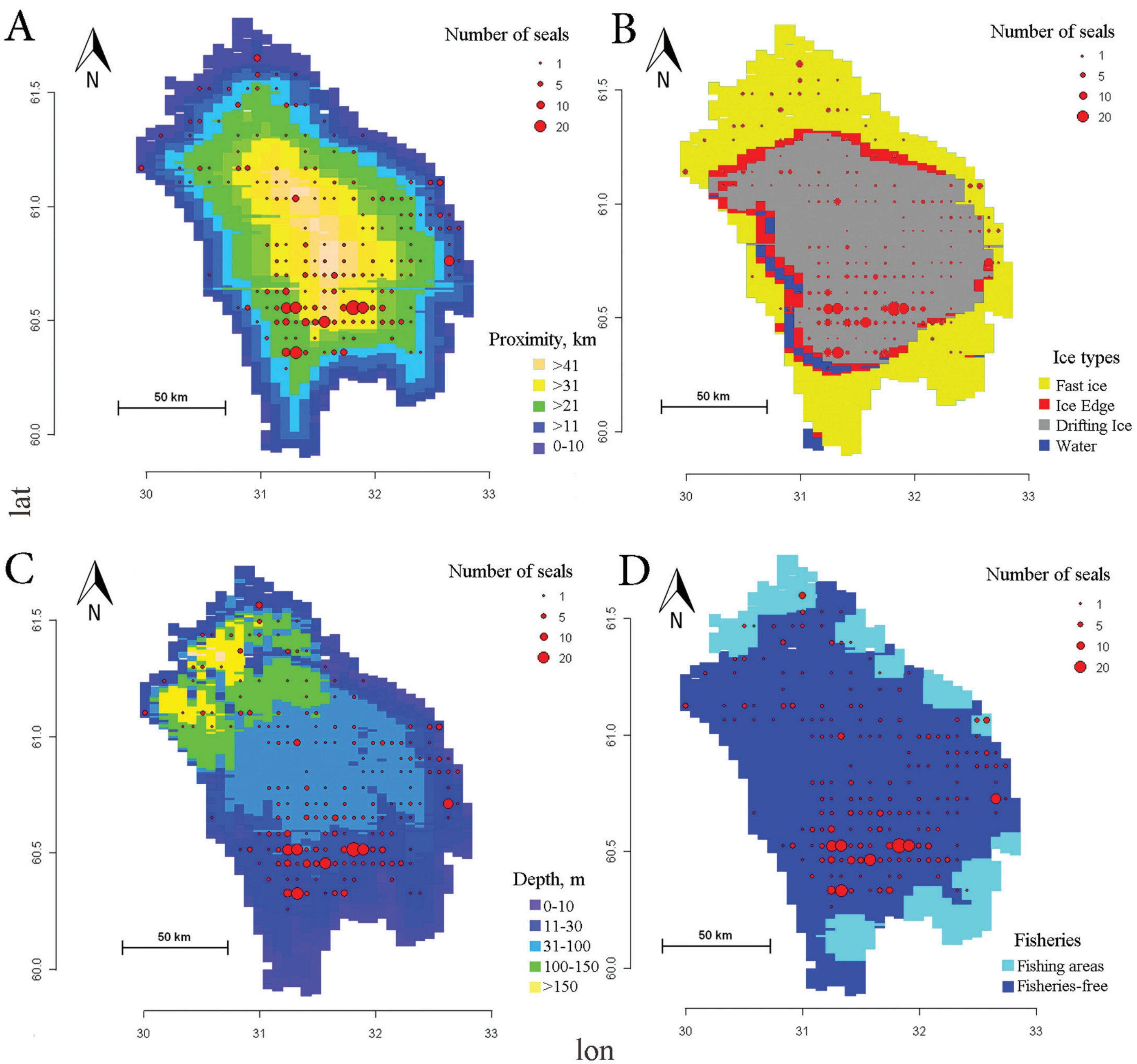

FIG. 3. Maps of observed seal distribution in relation to covariates (A – distance to shore, B – ice type, C – depth, D – fishing areas). Red dots symbolize actual group size (seals per block).

interaction with ice type, suggesting that a unique set of parameters modeled the number of seals in each ice type.

Because the ice-type interaction was clearly an important one, we fitted the complete additive model (depth + depth$^{0.5}$ + proximity + proximity$^{0.5}$) to the seal sightings in each of the three ice types. The values for the coefficients and their respective p-values (using Type III ANOVA, i.e., sequential chi-squared likelihood ratio tests after removing each of the terms) are displayed in Table 2. All the slope coefficients for the drifting pack ice are significantly different from zero, suggesting that there are strong, structural relationships between seal abundance and these physical covariates. There is a preference for shallower waters in the drift ice (negative first-order slope) that is exaggerated by a positive square root term. In contrast, there is a weaker positive relationship with distance to shore, which is attenuated by a negative square root term. Interestingly, the signs on the slope coefficients for the shorefast ice are exactly inverted compared to the drift ice. In particular, there is a negative first-order relationship with distance from shore, but a gradual increase with depth, though these effects are less significant (p-values between 0.05 and 0.10). The edge habitat displayed the highest magnitude of response to distance from shore, but no effects were significant, in part because of small sample sizes in this transitional category.

TABLE 1. Model selection table for the Ladoga ringed seal count data (April 2012) with all possible combinations of distance to shore (proximity) and depth and their squares (p2 and d2, respectively), the three ice types, and all interactions considered as explanatory variables. Models are sorted by increasing ΔAIC, and the lowest AIC and highest partial deviance explained (PDE) models are shown in bold type.

Model	Formula	K	AIC	ΔAIC	PDE
36	**~ ((depth + d2) + (proximity + p2)) * ice-type**	**15**	**1254.0**	**0.0**	**0.23**
31	~ ((depth + d2) + proximity) * ice-type	12	1259.7	5.7	0.21
32	~ ((depth + d2) * proximity) * ice-type	18	1263.5	9.5	0.23
34	~ (depth + (proximity + p2)) * ice-type	12	1264.2	10.2	0.2
37	**~ ((depth + d2) * (proximity + p2)) * ice-type**	**27**	**1264.5**	**10.4**	**0.26**
30	~ (depth + d2) * ice-type	9	1265.1	11.1	0.18
20	~ ((depth + d2) * proximity) + ice-type	8	1265.4	11.4	0.18
25	~ ((depth + d2) * (proximity + p2)) + ice-type	11	1266.9	12.8	0.19
8	~ ((depth + d2) * proximity)	6	1267.1	13.1	0.16
35	~ (depth * (proximity + p2)) * ice-type	18	1267.1	13.1	0.22
28	~ (depth + proximity) * ice-type	9	1269.0	15.0	0.17
26	~ depth * ice-type	6	1269.7	15.7	0.16
17	~ (depth * proximity) + ice-type	6	1269.8	15.8	0.16
13	~ ((depth + d2) * (proximity + p2))	9	1271.0	17.0	0.17
29	~ (depth * proximity) * ice-type	12	1271.7	17.7	0.18
23	~ (depth * (proximity + p2)) + ice-type	8	1272.3	18.3	0.16
5	~ (depth * proximity)	4	1273.1	19.1	0.14
11	~ (depth * (proximity + p2))	6	1275.5	21.5	0.14
19	~ ((depth + d2) + proximity) + ice-type	6	1284.9	30.9	0.12
24	~ ((depth + d2) + (proximity + p2)) + ice-type	7	1286.3	32.3	0.12
12	~ ((depth + d2) + (proximity + p2))	5	1287.2	33.2	0.11
16	~ (depth + proximity) + ice-type	5	1287.9	33.9	0.11
18	~ (depth + d2) + ice-type	5	1287.9	33.9	0.11
7	~ ((depth + d2) + proximity)	4	1288.4	34.4	0.1
10	~ (depth + (proximity + p2))	4	1288.9	34.9	0.1
14	~ depth + ice-type	4	1289.0	35.0	0.1
22	~ (depth + (proximity + p2)) + ice-type	6	1289.1	35.1	0.11
4	~ (depth + proximity)	3	1290.1	36.0	0.09
33	~ (proximity + p2) * ice-type	9	1291.8	37.8	0.12
15	~ proximity + ice-type	4	1293.7	39.7	0.09
27	~ proximity * ice-type	6	1294.1	40.1	0.1
21	~ (proximity + p2) + ice-type	5	1295.5	41.5	0.09
9	~ (proximity + p2)	3	1299.8	45.8	0.07
3	~ proximity	2	1299.9	45.9	0.06
2	~ depth	2	1313.1	59.1	0.03
6	~ (depth + d2)	3	1314.9	60.8	0.03
1	~ 1	1	1321.7	67.7	0

Mean seal density for fishermen-free areas was 0.15 seals/km^2 (SD = 0.32), compared to 0.09 seals/km^2 (SD = 0.33) for the areas occupied by the fishermen. We modeled the effect of fisheries separately in the fast ice habitat where the fisheries occur by adding the fisheries presence categorical variable to the depth and proximity first- and second-order terms and guiding model selection with AIC as before. Again, there were 37 models to compare, of which the top 10 are presented in Table 3. Four of the five best models included the presence of fisheries, and the best model included both depth covariates, but not distance to shore (M30: seal number ~ (depth + d2) * Fisheries). The coefficients and Type III ANOVA results for this model are presented in Table 4.

The fisheries main effect was highly negative (β = −7.8) and highly significant (Type III ANOVA, $p = 0.0014$), indicating that seals were avoiding the presence of fishermen on the fast ice. While the main effects of depth and square root of depth were weak and insignificant, the fisheries interaction with both of these covariates was highly significant, with coefficients suggesting an overall preference for deeper waters, especially in the presence of fishery activities.

TABLE 2. Estimated regression coefficients, including the mean and square-root effects of distance to shore (proximity) and depth on seal abundance, for each of the three ice types. *P*-values (in parentheses) are obtained from sequential chi-squared comparisons of likelihoods (Type III ANOVA). Marginally significant values ($p < 0.10$) are italicized, significant values ($p < 0.05$) are in bold type, and highly significant values ($p < 0.01$) are italic and bold.

	Shorefast ice	Edge (transitional)	Drifting pack ice
N	186	41	264
depth (m)	*−0.04* (0.075)	0.051 (0.359)	***0.064*** (0.009)
depth$^{0.5}$	**0.67** (0.042)	−0.96 (0.221)	***−1.3*** (<0.001)
proximity (km)	*0.213* (0.096)	0.254 (0.632)	**−0.19** (0.024)
proximity$^{0.5}$	−1.3 (0.108)	−2.4 (0.574)	***2.5*** (0.006)

An analogous analysis for the edge ice type suggested a best model with depth and square root of depth effects (PDE 17%, Type III ANOVA $p = 0.06$ and 0.04 for depth and depth$^{0.5}$ respectively) and no significant distance to shore effects.

TABLE 3. Model selection table for Ladoga ringed seal abundance (top 10 models) in the shorefast ice with additional fisheries presence variable (Fisheries). Models are sorted by increasing ΔAIC, and the lowest AIC and highest partial deviance explained (PDE) models are in bold.

Model	Formula	K	AIC	ΔAIC	PDE
30	**~ (depth + d2) * Fisheries**	**6**	**307.9**	**0.0**	**0.148**
31	~ ((depth + d2) + proximity) * Fisheries	8	309.3	1.4	0.170
36	**~ ((depth + d2) + (proximity + p2)) * Fisheries**	**10**	**311.5**	**3.6**	**0.186**
6	~ (depth + d2)	3	312.5	4.6	0.047
18	~ (depth + d2) + Fisheries	4	312.8	4.8	0.064
1	~ 1	1	313.1	5.2	0.000
12	~ ((depth + d2) + (proximity + p2))	5	313.8	5.9	0.073
3	~ proximity	2	314.3	6.4	0.009
7	~ ((depth + d2) + proximity)	4	314.4	6.5	0.048
2	~ depth	2	314.6	6.7	0.006

TABLE 4. ANOVA table for model of seal abundance in the shorefast ice. Significant values ($p < 0.05$) are in bold, and highly significant ($p < 0.01$) are italic and bold.

Factor	β	Likelihood ratio chi-square	Df	p (> chi-square)
depth	−0.008	0.1	1	0.7553
d2	0.131	0.11	1	0.7351
Fisheries	**−7.780**	10.27	1	***0.0014***
depth:Fisheries	**−0.159**	7.36	1	***0.0067***
d2:Fisheries	**2.482**	8.46	1	***0.0036***

We used these results to develop three different prediction models, one for each of the three ice types. The models can be written as:

$$N_s(d_i, f_i \mid \text{fast ice}) = NB[\alpha_0 + (1 - f_i)(\alpha_2\, d_i + \alpha_3\, \mathrm{sqrt}(d_i)) + f_i\, (\alpha_3\, d_i + \alpha_4\, \mathrm{sqrt}(d_i)))]$$

$$N_s(d_i \mid \text{edge ice}) = NB[\beta_0 + \beta_2\, d_i + \beta_3\, \mathrm{sqrt}(d_i)]$$

$$N_s(d_i\, p_i \mid \text{drift ice}) = NB[\gamma_0 + \gamma_2\, d_i + \gamma_3\, \mathrm{sqrt}(d_i) + \gamma_4\, p_i + \gamma_5\, \mathrm{sqrt}(p_i)]$$

where N_s represents the number of seals in a block at depth d_i, distance from shore $p_{i,}$ and fishery presence (0 or 1) denoted f_i. The coefficients of the linear predictors are α, β, and γ. We applied the prediction model to the combinations of covariates in each of 3640 blocks covering the area of the lake and plotted the distribution of predicted densities (Fig. 4).

Maximum seal densities were predicted to be in the central part of the lake with a distinct spike (> 1.0 seal/km^2) in the zone with depths of less than 50 m (see Fig. 4). That prediction corresponds well with actual sighting data: most sightings were in the 20–30 m depth range (see Fig. 2). Density decreased to 0.4–0.6 seals/km^2 in deeper areas (50–100 m). The northern deepwater skerries area covered with fast ice and the southernmost bays had the lowest seal density.

Estimation of total seal abundance was not possible because we do not have the necessary data on detection and seal hauling-out probabilities in a given time. However, the final model did allow estimation of the expected number of hauled-out seals based on a combination of covariates. The estimate of hauled-out seals for early April 2012 was 5068 seals (95% CI: 4026–7086) and to our understanding was likely to be biased low.

DISCUSSION

The survey was performed before the spring breakup of ice, so that the ice cover was stable during the survey period. We therefore consider our predicted density map to be a reasonable representation of ringed seal distribution throughout the lake during the ice season in 2012. There is, however, a possibility that seal counts in the skerries region were biased downward as lairs located close to the shoreline were still partly covered with snow at the time of the survey and therefore harder to detect.

Despite the fact that our density map corresponds well with the general location of seal sightings made during the survey, the model explains less than 25% of the count deviance. This fact suggests that other factors, which we did not observe or include in the model, were affecting seal distribution. One possible candidate is behavioral aggregation of individuals leading to unaccounted spatial auto-correlation (Dormann et al., 2007). Possible reasons for seals to aggregate in springtime include a preference for leads in the ice vs. breathing holes, food availability in specific areas, or avoidance of sources of disturbance. Also, male seals may aggregate close to mature females nursing their pups and wait until mating occurs; such a reproductive behavior strategy has been demonstrated, for example, for the Caspian seal (*Phoca caspica*; Wilson et al., 2012).

Landlocked seal populations have stricter constraints on their spatial distribution than most seals in marine environments. These constraints make them more susceptible to random variations in the environment, such as lack of suitable habitat arising from ice formation patterns in a given year, or trends in fish stock availability. The GLM framework we used for our habitat-based distribution modeling assumes to some extent that the entire lake area is accessible to the seals, without taking into account any constraints on the availability of those areas or the residual effect of movement from the ice-free period. In early winter when

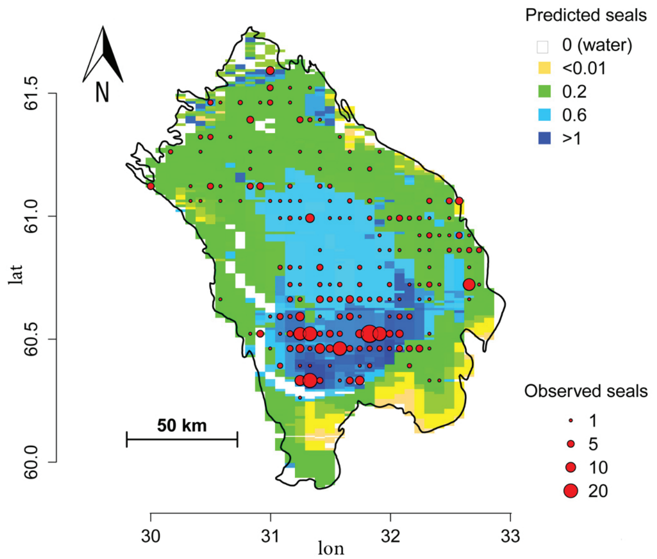

FIG. 4. Map of seal density distribution predicted for the 2012 ice season (density gradient – seals per km^2).

ice forms, the seals choose appropriate habitat on the basis of obvious ice characteristics and possibly other factors, such as prey availability. Fast ice zones have traditionally been considered the habitat most actively used by ringed seals for making lairs and pupping (Sipilä et al., 1996; Kunnasranta et al., 2001). However, 38% of the fast ice area in Lake Ladoga is actively used for recreational ice fishing, which makes these areas less suitable for breeding seals. From early winter until late spring, thousands of recreational fishermen and some commercial fishermen use the fast ice for ice fishing, a traditional winter recreation in the region. Fishermen use skis, snowmobiles, and cars to reach remote areas and sometimes spend several days living in tents on thick ice. Winter fishing areas may vary from season to season depending on ice conditions, although in general, traditional fishing sites remain consistent. Even under ideal ice conditions, a seal is unlikely to breed close to high concentrations of fishermen or intense transport traffic on ice. This assertion is supported by our data and modeling results: very few seals were detected in these areas during the aerial survey, and the NBGLM suggested a strong avoidance of ice-fisherman areas, even controlling for distance to shore effects.

Local fishermen have told us that some seals use ice-fishing holes as breathing holes and even occasionally feed from the nets set under the ice. These behaviors are more likely typical of non-breeding seals, since breeding females tend to remain in their territories throughout the winter to maintain their lairs and breathing holes, while breeding males tend to concentrate near females during the lactation period until mating occurs. These hypotheses are based on observations and more detailed documentation of Caspian seal breeding behavior (Wilson et al., 2012).

Thus, we conclude that disturbance caused by humans has become a major factor influencing seal distribution and has likely shifted the core area of seal pupping from the shorefast ice to the central part of the lake. In combination with an apparently increased population size (compared to the previous aerial survey estimates of Verevkin, 2003), this shift could lead to higher seal densities in the central part of the lake, outside the fast ice zone and more distant from the shore. A number of pups detected during the survey in the central part of the lake demonstrate that the seals do breed in remote areas away from shore without a high level of dependence on fast ice, though it should be kept in mind that the ice cover, wherever it is formed, must be stable enough during the pupping season to provide a platform for pup rearing.

Relatively high seal densities observed in ice edge zones (0.26 seals/km^2) in our opinion could be well explained by ice formation patterns. In early winter, after formation of shorefast ice, new ice floes are brought by the wind to the ice edge, where the ice breaks, freezes together, and forms hummocked zones suitable for lair construction. When the breakup process starts in spring, it begins in the boundary zone between primary and secondary ice, where seal density is originally high. As snow melts and a polynya appears in this particular area, we can expect high numbers of animals to stay along the ice edge.

Unfortunately, very little historical information is available on seal winter distribution patterns. Several aerial surveys conducted on the lake in the 1950s, 1970s, and 1980s either did not report registered seal locations at all or had rather poor coverage because of early ice melt or limited survey extent (Sorokin, 1957; Zheglov and Chapskiy, 1971; Antonuk, 1975; Philatov, 1990). In March – April 1973, a series of aerial surveys (Antonuk, 1975) showed that the majority of the seals were hauling out in the Svirskaya Bay area (0.33 – 0.76 seals/km^2), while another dense grouping (0.14 – 0.20 seals/km^2) was found in the far northeastern part of the lake, either on ice fields or on fast ice. Such high densities might have been a result of poor ice coverage, since less than 30% of the Lake Ladoga surface was frozen in that winter. Later, Bychkov and Antonyuk (1975) published a ringed seal spring-winter haul-out map identifying the eastern part of the lake (to the east of 32.0˚ E) as an area commonly used by the seals in the ice-bound season. Similar results were achieved by Zheglov and Chapskiy (1971), although they also reported occasional seal sightings in the skerries region (0.028 seals/km^2) and on broken fast ice along the western shore (0.19 seals/km^2). Although the ice coverage during their survey period was close to 80%, their survey transects did not include the central part of the lake, which left a gap in their seal density data. The only brief note on females and pups occupying the central part of the lake in severe winters is found in Philatov (1990), but without any further clarification. Hence we can see a significant data deficiency that does not allow a comparison of the modeled density distribution for winter-spring 2012 with density distributions of previous years. We assume that in mild winters, incomplete ice coverage makes seals concentrate in all available habitat types regardless of distance to shore or bathymetry, since the low ice coverage facilitates

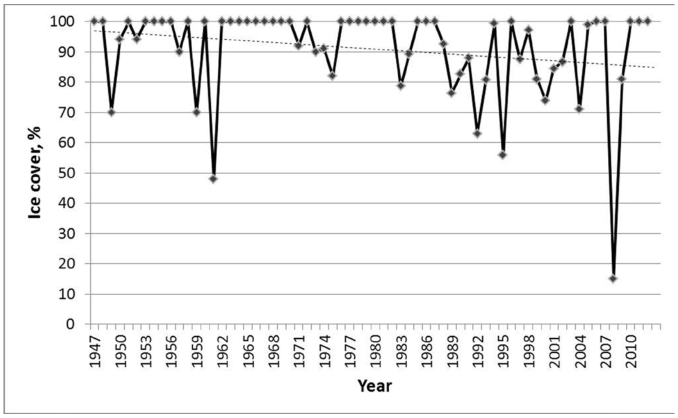

FIG. 5. Ice coverage (%) of Lake Ladoga in 1947–2012. Data from 1947 to 1982 are based on Usachev et al., 1985; estimates for 1983–2002 are based on the annual sum of negative temperatures for the Lake Ladoga area (I.S. Trukhanova, unpubl. data); and 2003–12 data from Lance Modis Aqua, http://rapidfire.sci.gsfc.nasa.gov.

higher mobility for foraging trips. In colder winters, animals “choose” preferable areas in relation to environmental characteristics and might even have an opportunity to maintain comfort distances from other individuals on the ice.

The primary factor for the seals in any season is prey availability (Smith, 1987), though this is among the most difficult variables to assess directly. Because of constraints on long-distance movements during the ice season (discussed above), the ability to catch fish close to wintering sites becomes extremely important. The data available on fish biomass distribution (Rumyantsev, 2002) show a possible correlation between seal habitat use in winter and concentration of fish species such as European smelt (*Osmerus eperlanus*), vendace (*Coregonus albula*), and European whitefish (*Coregonus lavaretus* spp.). To test this hypothesis and quantify these relationships, however, we require additional data and a more dedicated study.

Among marine mammals, ice-associated seal species are among the most vulnerable to climate warming, at both global and regional scales, suffering from compounded habitat loss and changes in prey abundance (Laidre et al., 2008; Kovacs et al., 2011). Among the ice-associated seals, the landlocked species, such as the Caspian seal, the Baikal seal (*Phoca sibirica*), and the Ladoga and Saimaa ringed seal subspecies, are additionally limited by the constraints to dispersal or range-shifting that are intrinsic to landlocked bodies of water. The ringed seal in Lake Ladoga lives at the very southern edge of the global range of the ringed seal species, and therefore it is particularly vulnerable to shifts in the temperature regime, especially during the most critical stages of its life cycle. The lake is not completely covered with ice every winter (Usachev et al., 1985). Since 1947, maximum ice coverage has been trending negatively at an average rate of 0.18% less ice per year (Fig. 5, linear regression $p = 0.066$): it has attained 100% of the lake in only 36 of the 60 years, with a decreasing probability of total coverage (binomial GLM of probability 100% coverage against year: $\beta = -0.028$, $p = 0.038$). Note that the maximum ice extent reached a historical low of 15% relatively recently, in 2008 (Fig. 5).

Light ice conditions, limited area of breeding habitat, and early breakup may lead to a decline in pup survival due to a higher number of stranded pups (Smith and Harwood, 2001; Alekseev et al., 2012) and greater exposure of pups to predation (Jüssi et al., 2008). The combined effects of diminished ice conditions and extensive fishing activity on the lake in winter and spring might have a cumulative impact on the ringed seal birth rate. Despite current positive trends in population size, a changing ice regime and increasing fishing activity may put this subspecies at risk. On the basis of these considerations and the results of our analyses, we believe that areas with limited access for fishermen and other anthropogenic disturbances such as the Nizhnesvirskiy Strict Nature Reserve area and the restricted military zone that covers a large portion of the western shore between 60.4˚ and 60.8˚ N (Fig. 1) will be critical for conserving the population of Lake Ladoga seals.

There is an urgent need to assess the condition of Ladoga fish stocks (a variable we could not include in the model), to clarify fish species distribution, and to identify sustainable levels of fishing effort, both commercial and recreational. Population monitoring of seals, including number estimation, satellite tracking, and diet studies, should be performed on a regular basis. Ice conditions in any given year may ultimately be used to predict seal distribution and thus allow protection of breeding winter habitats. Further, understanding of the seals’ seasonal movements, distribution patterns, and responses to increased anthropogenic pressures are also important to ensure conservation of the subspecies.

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