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RINGED SEAL (*Pusa hispida hispida*): Arctic Stock

STOCK DEFINITION AND GEOGRAPHIC RANGE

Ringed seals (*Pusa hispida*) have a circumpolar distribution and are found in all seasonally ice-covered seas of the Northern Hemisphere as well as in certain freshwater lakes (King 1983). Most taxonomists currently recognize five subspecies of ringed seals: *P. h. hispida* in the Arctic Ocean and Bering Sea; *P. h. ochotensis* in the Sea of Okhotsk and northern Sea of Japan; *P. h. botnica* in the northern Baltic Sea; *P. h. lagodensis* in Lake Ladoga, Russia; and *P. h. saimensis* in Lake Saimaa, Finland. Morphologically, the Baltic and Okhotsk subspecies are fairly well differentiated from the Arctic subspecies (Ognev 1935, Müller-Wille 1969, Rice 1998) and the Ladoga and Saimaa subspecies differ significantly from each other and from the Baltic subspecies (Müller-Wille 1969, Hyvärinen and Nieminen 1990, Amano et al. 2002). Genetic analyses support isolation of the lake-inhabiting populations (Palo 2003, Palo et al. 2003, Valtonen et al. 2012). Lack of differentiation between the Baltic and the Arctic subspecies may reflect recurrent gene flow (Martinez-Bakker et al. 2013) but is more likely due to retention of high diversity within the relatively large effective population size of the Baltic subspecies since separation from the Arctic subspecies (Nyman et al. 2014). Widespread mixing within the Arctic subspecies is the likely explanation for its high diversity and apparent lack of population structure (Palo et al. 2001, Davis et al. 2008, Kelly et al. 2009, Martinez-Bakker et al. 2013). Differences in body size, morphology, growth rates, and/or diet between Arctic ringed seals in shorefast versus pack ice have been taken as evidence of separate breeding populations in some locations (McLaren 1958, Fedoseev 1975, Finley et al. 1983). This has not been thoroughly examined, however, and the taxonomic status and population structure of the Arctic subspecies remain unresolved (Berta and Churchill 2012). The stock, therefore, may be as large as the entire *P. h. hispida* subspecies range. This stock assessment considers only the portion of the stock found within U.S. waters bounded by the U.S. Exclusive Economic Zone (EEZ; Fig. 1), because the relevant stock assessment data on abundance and human-caused mortality and serious injury are generally not available for the broader range of the stock or even for waters adjacent to the U.S. EEZ.

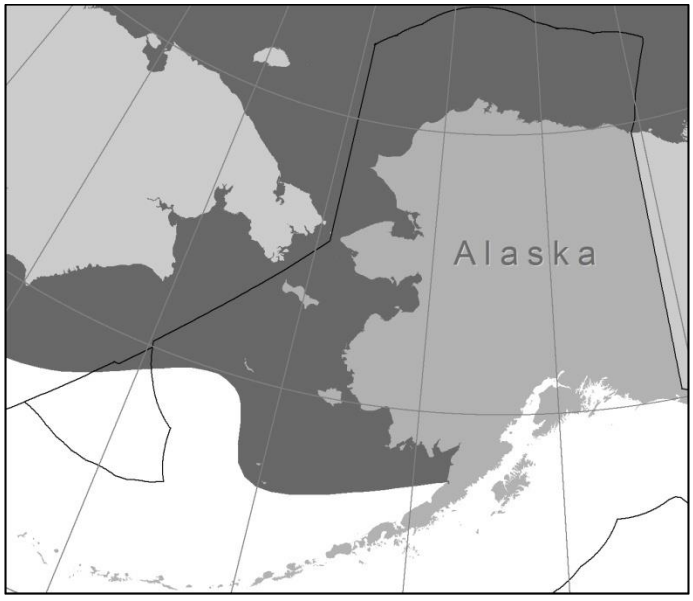

Figure 1. The Arctic ringed seal stock is defined as the population of the Arctic subspecies (*P. h. hispida*). This stock assessment considers only the portion of the stock occurring in U.S. waters (i.e., the U.S. Exclusive Economic Zone delineated by a black line). The dark shaded area shows the approximate winter distribution of the Arctic ringed seal stock around Alaska.

Throughout their range, ringed seals have an affinity for ice-covered waters and are well adapted to occupying both shorefast and pack ice (Kelly 1988). They remain with the ice most of the year and use it as a platform for pupping and nursing in late winter to early spring, for molting in late spring to early summer, and for resting at other times of the year. Arctic ringed seals rarely come ashore in the Arctic, although they have been observed during summer months resting on land in the White Sea (Lukin et al. 2006) and, recently, in a fjord system in Svalbard (Lydersen et al. 2017). In Alaska waters, during winter and early spring when sea ice is at its maximal extent, ringed seals are abundant in the northern Bering Sea, Norton and Kotzebue Sounds, and throughout the Chukchi and Beaufort seas. They occur as far south as Bristol Bay in years of extensive ice coverage but generally are not abundant south of Norton Sound except in nearshore areas (Frost 1985). However, surveys conducted in the Bering Sea in the spring of 2012 and 2013 documented numerous ringed seals in both nearshore and offshore habitat extending south of Norton Sound (79 FR 73010, 9 December 2014). Although details of their seasonal movements have not been adequately documented, most ringed seals that winter in the Bering, Chukchi, and Beaufort seas are

thought to migrate north in the spring as the seasonal ice melts and retreats (Burns 1970, Kelly et al. 2010b) and spend summers in the pack ice of the northern Chukchi and Beaufort seas, as well as on nearshore ice remnants in the Beaufort Sea (Frost 1985, Kelly et al. 2010b). During summer, ringed seals range hundreds to thousands of kilometers to forage along ice edges or in highly productive open-water areas (Harwood and Stirling 1992, Freitas et al. 2008, Kelly et al. 2010b, Harwood et al. 2015). With the onset of freeze-up in the fall, ringed seal movements become increasingly restricted. Seals that have summered in the Beaufort Sea are thought to move west and south with the advancing ice pack, with many seals dispersing throughout the Chukchi and Bering seas while some remain in the Beaufort Sea (Frost and Lowry 1984, Crawford et al. 2012, Harwood et al. 2012). Some adult ringed seals return to the same small home ranges they occupied during the previous winter (Kelly et al. 2010b).

POPULATION SIZE

Although a reliable population estimate for the entire stock is not available, survey methods have been developed and applied to substantial portions of the stock's range in U.S. waters. In the spring of 2012 and 2013, U.S. and Russian researchers conducted aerial abundance and distribution surveys over the entire ice-covered portions of the Bering Sea (Moreland et al. 2013). Conn et al. (2014), using a sub-sample of the data collected from the U.S. portion of the Bering Sea in 2012, calculated an abundance estimate of 171,418 ringed seals (95% CI: 141,588-201,090). This estimate did not account for availability bias due to seals in the water at the time of the surveys and did not include ringed seals in the shorefast ice zone, which were surveyed using a different trackline design that will require a separate analysis. Thus, the actual number of ringed seals in the U.S. portion of the Bering Sea is likely much higher, perhaps by a factor of two or more. Researchers expect to provide a population estimate, corrected for availability bias, for the entire U.S. portion of the ringed seal stock once the final Bering Sea results are combined with the results from spring surveys of the Chukchi Sea (conducted in 2016) and Beaufort Sea (planned for 2020).

Minimum Population Estimate

A minimum population estimate (N_{MIN}) for the entire U.S. portion of the stock cannot be determined because reliable abundance estimates are not yet available for the Chukchi and Beaufort seas. Using the 2012 Bering Sea density estimate by Conn et al. (2014), however, we are able to calculate an N_{MIN} of 158,507 ringed seals in the U.S. Bering Sea. The N_{MIN} for a stock is usually calculated using Equation 1 from the potential biological removal (PBR) guidelines (NMFS 2016): $N_{MIN} = N/\exp(0.842\times[\ln(1+[CV(N)]^2)]^{½})$, which approximates the 20th percentile of a distribution that is assumed to be log-normal. However, the abundance estimate based on Conn et al. (2014) was calculated using a Bayesian hierarchical framework, so we used the 20th percentile of the posterior distribution of abundance estimates as a more direct estimator of N_{MIN} than Equation 1. This N_{MIN} is negatively biased as an estimator of the Arctic ringed seal stock, and even the U.S. portion of the stock, because the estimate is based solely on the Bering Sea and, therefore, doesn't include the many ringed seals that inhabit the Chukchi and Beaufort seas (e.g., Kelly et al. 2010a, Laidre et al. 2015) and because the Conn et al. (2014) study did not adjust densities for seals in the water (not detectable by the surveys).

Current Population Trend

Reliable data on trends in population abundance for the Arctic stock of ringed seals or the portion of the stock within U.S. waters are not available.

CURRENT AND MAXIMUM NET PRODUCTIVITY RATES

A reliable estimate of the maximum net productivity rate (R_{MAX}) is not available for the Arctic stock of ringed seals or any portion of the stock within U.S. waters. Until additional data become available, the default pinniped maximum theoretical net productivity rate of 12% will be used for this stock (NMFS 2016).

POTENTIAL BIOLOGICAL REMOVAL

PBR is defined as the product of the minimum population estimate, one-half the maximum theoretical net productivity rate, and a recovery factor: $PBR = N_{MIN} \times 0.5R_{MAX} \times F_R$. The recovery factor ($F_R$) for this stock is 0.5, the value for pinniped stocks listed as threatened under the Endangered Species Act (ESA) (NMFS 2016). Using the negatively biased N_{MIN} for ringed seals in the U.S. portion of the Arctic stock, PBR is 4,755 seals (158,507 × 0.06 × 0.5). This PBR is negatively biased because of its dependence on the negatively biased N_{MIN} estimate.

ANNUAL HUMAN-CAUSED MORTALITY AND SERIOUS INJURY

Information for each human-caused mortality, serious injury, and non-serious injury reported for NMFS-managed Alaska marine mammals between 2014 and 2018 is listed, by marine mammal stock, in Young et al. (2020); however, only the mortality and serious injury data are included in the Stock Assessment Reports. The minimum estimated mean annual level of human-caused mortality and serious injury for the portion of the Arctic ringed seal stock in U.S. waters between 2014 and 2018 is 6,459 seals: 5 in U.S. commercial fisheries, 6,454 in the Alaska Native subsistence harvest (average statewide harvest, including struck and lost animals, in 2015, based on a recently published analysis (Nelson et al. 2019) that is higher and likely more accurate than previous estimates but also revealed stable or decreasing trends in harvest numbers; see below), 0.2 in marine debris, and 0.2 incidental to Marine Mammal Protection Act (MMPA)-authorized research. Additional potential threats most likely to result in direct human-caused mortality or serious injury of this stock include the increased potential for oil spills due to an increase in vessel traffic in Alaska waters (with changes in sea-ice coverage).

Fisheries Information

Information for federally-managed and state-managed U.S. commercial fisheries in Alaska waters is available in Appendix 3 of the Alaska Stock Assessment Reports (observer coverage) and in the NMFS List of Fisheries (LOF) and the fact sheets linked to fishery names in the LOF (observer coverage and reported incidental takes of marine mammals: https://www.fisheries.noaa.gov/national/marine-mammal-protection/marine-mammal-protection-act-list-fisheries, accessed December 2020).

Between 2014 and 2018, incidental mortality and serious injury of ringed seals in U.S. waters was reported in two of the federally-managed U.S. commercial fisheries in Alaska monitored for incidental mortality and serious injury by fisheries observers: the Bering Sea/Aleutian Islands flatfish trawl and Bering Sea/Aleutian Islands pollock trawl fisheries (Table 1; Breiwick 2013; MML, unpubl. data). Based on observer data from 2014 to 2018, the minimum average annual rate of mortality and serious injury incidental to U.S. commercial fishing operations is 4.8 ringed seals.

One ringed seal mortality resulting from entanglement in unidentified commercial gear in U.S. waters was reported to the NMFS Alaska Region marine mammal stranding network in 2017 (Young et al. 2020), resulting in a mean annual mortality and serious injury rate of 0.2 ringed seals between 2014 and 2018 (Table 3). This mortality and serious injury estimate results from an actual count of verified human-caused deaths and serious injuries and is a minimum because not all entangled animals strand nor are all stranded animals found, reported, or have the cause of death determined.

Table 1. Summary of incidental mortality and serious injury of Arctic ringed seals in U.S. waters due to U.S. commercial fisheries between 2014 and 2018 and calculation of the mean annual mortality and serious injury rate (Breiwick 2013; MML, unpubl. data). Methods for calculating percent observer coverage are described in Appendix 3 of the Alaska Stock Assessment Reports.

Fishery name	Years	Data type	Percent observer coverage	Observed mortality	Estimated mortality (CV)	Mean estimated annual mortality
Bering Sea/Aleutian Is. flatfish trawl	2014 2015 2016 2017 2018	obs data	100 100 99 100 100	0 1 0 8 14	0 1 (0.05) 0 8.0 (0.01) 14 (0.02)	4.6 (CV = 0.01)
Bering Sea/Aleutian Is. pollock trawl	2017	obs data	100	1[a]	N/A	0.2 (CV = N/A)
Minimum total estimated annual mortality						4.8 (CV = 0.01)

[a]This seal was discovered during a vessel offload. Because it could not be associated with a haul number, it was not included in the bycatch estimate for the fishery.

Alaska Native Subsistence/Harvest Information

NMFS signed an agreement with the Ice Seal Committee (ISC; 2006) to co-manage Alaska ice seal populations. This co-management agreement promotes full and equal participation by Alaska Natives in decisions affecting the subsistence management of ice seals (to the maximum extent allowed by law) as a tool for conserving

ice seal populations in Alaska (https://www.fisheries.noaa.gov/alaska/marine-mammal-protection/co-management-marine-mammals-alaska, accessed December 2020).

Ringed seals are an important resource for Alaska Native subsistence hunters. Approximately 64 coastal communities in Alaska, from Bristol Bay to the Beaufort Sea, harvest ice seals (ISC 2019). The ISC, as co-managers with NMFS, recognizes the importance of harvest information and has collected it since 2008. Annual household survey results compiled in a statewide harvest report include historical ice seal harvest information from 1960 to 2017 (Quakenbush et al. 2011, ISC 2019). To estimate the recent subsistence harvest of ice seals, Nelson et al. (2019) used ice seal harvest survey data collected from 1992 to 2014 for 41 of 55 communities that regularly hunt ice seals, as well as the per capita removal estimates (based on the 2015 human population) from the surveyed communities, to estimate the average regional and statewide subsistence harvest (Table 2). The best statewide estimate of the average number of ringed seals harvested in 2015, including struck and lost animals, is 6,454 seals (Nelson et al. 2019). The authors also found stable or decreasing trends in the annual numbers of ice seals harvested (Nelson et al. 2019).

Table 2. Average regional and statewide subsistence harvest (including struck and lost animals) of Arctic ringed seals in 2015 (Nelson et al. 2019). See Figure 1 in Nelson et al. (2019) for a list of the communities in each region.

Region	Average harvest (including struck and lost animals)
North Slope Borough	1,146
Maniilaq	493
Kawerak	2,287
Association of Village Council Presidents	2,484
Bristol Bay Native Association	44
Statewide total	6,454

Other Mortality

Reports to the NMFS Alaska Region marine mammal stranding network of ringed seals entangled in marine debris or with injuries caused by other types of human interaction are another source of mortality and serious injury data. These mortality and serious injury estimates result from an actual count of verified human-caused deaths and serious injuries and are minimums because not all entangled animals strand nor are all stranded animals found, reported, or have the cause of death determined. One ringed seal mortality due to entanglement in marine debris in U.S. waters was reported in 2017, resulting in a mean annual mortality and serious injury rate of 0.2 ringed seals between 2014 and 2018 (Table 3; Young et al. 2020).

Ringed seal mortality due to gunshot wounds reported to the NMFS Alaska Region stranding network (Young et al. 2020) is presumed to be animals struck and lost in the Alaska Native subsistence hunt and, therefore, is not included in the mean annual mortality and serious injury rate for 2014 to 2018.

Mortality and serious injury may occasionally occur incidental to marine mammal research activities authorized under MMPA permits issued to a variety of government, academic, and other research organizations. Between 2014 and 2018, there was one report, in 2016, of a mortality incidental to research on the Arctic stock of ringed seals (Table 3; Young et al. 2020), resulting in a mean annual mortality and serious injury rate of 0.2 ringed seals.

In 2011, NMFS and the U.S. Fish and Wildlife Service declared an Unusual Mortality Event (UME) for pinnipeds in the Bering and Chukchi seas, due to the unusual number of sick or dead seals and walruses discovered with skin lesions, bald patches, and other symptoms. The UME occurred from 1 May 2011 to 31 December 2016 and primarily affected ice seals, including ringed seals, bearded seals, ribbon seals, and spotted seals. The investigation concluded that the skin and hair symptoms were signs of a molt abnormality; however, no infectious disease agent or environmental cause for the UME symptoms and mortality was identified (https://www.fisheries.noaa.gov/national/marine-life-distress/active-and-closed-unusual-mortality-events, accessed December 2020). Patchy baldness and delayed molt, however, continue to be observed in limited numbers (<20 per year) of harvested and beachcast ringed seals, bearded seals, ribbon seals, and spotted seals in Alaska.

Since 1 June 2018, elevated numbers of ice seal strandings have occurred in the Bering and Chukchi seas in Alaska and NMFS declared a UME for bearded seals, ringed seals, and spotted seals from 1 June 2018 to present in the Bering and Chukchi seas (https://www.fisheries.noaa.gov/national/marine-life-distress/active-and-closed-unusual-mortality-events, accessed December 2020). As of 31 July 2020, 298 ice seal strandings of all age classes have been reported, including 88 bearded seals, 72 ringed seals, 49 spotted seals, and 89 unidentified seals. A subset

of seals has been sampled for genetics and harmful algal bloom exposure and a few have had histopathology samples collected.

Table 3. Summary of Arctic ringed seal mortality and serious injury in U.S. waters, by year and type, reported to the NMFS Alaska Region marine mammal stranding network and NMFS Office of Protected Resources between 2014 and 2018 (Young et al. 2020). Animals that were disentangled and released with non-serious injuries have been excluded from this table.

Cause of injury	2014	2015	2016	2017	2018	Mean annual mortality
Entangled in unidentified commercial gear	0	0	0	1	0	0.2
Entangled in marine debris	0	0	0	1	0	0.2
Incidental to MMPA-authorized research	0	0	1	0	0	0.2
Total in commercial fisheries						0.2
Total in marine debris						0.2
Total incidental to MMPA-authorized research						0.2

STATUS OF STOCK

On 28 December 2012, NMFS listed the Arctic ringed seal subspecies (*P. h. hispida*), which corresponds to the Arctic stock of ringed seals, as threatened under the ESA (77 FR 76706). The primary concern for this population is the ongoing and anticipated loss of sea ice and snow cover resulting from climate change, which is expected to pose a significant threat to the persistence of these seals in the foreseeable future (based on projections through the end of the 21st century; Kelly et al. 2010a). Because of its threatened status under the ESA, this stock is designated as depleted under the MMPA and is classified as a strategic stock. The best estimate of the mean annual level of human-caused mortality and serious injury in the U.S. waters portion of the stock is 6,459 ringed seals, which is greater than the negatively biased PBR of 4,755 seals. However, because this exceedance of PBR stems from an unrealistically low N_{MIN}, it should not be taken as indicative of a risk to this stock. The PBR was obtained from an N_{MIN} that is known to be an extreme underestimate of the abundance in the U.S. waters of the Bering Sea, which in turn is just a portion of the Arctic ringed seal stock in U.S. waters, and the best estimate of human-caused mortality and serious injury is for the entire U.S. portion of the stock, including, for example, Alaska Native subsistence takes in the Chukchi and Beaufort seas. Previous estimates from the U.S. waters of the Chukchi Sea (Bengtson et al. 2005) and results from a recent (2016) NOAA survey of those waters indicate that there are several hundreds of thousands of ringed seals in that region that are not included in N_{MIN} because the former results are outdated and the latter have not yet been published. Furthermore, ringed seals are known to remain abundant in the U.S. waters of the Beaufort Sea (which are also not included in N_{MIN}) based, for example, on hunter reports to the ISC and NOAA test surveys conducted in 2019. NMFS believes with high confidence that the number of ringed seals in Alaska waters greatly exceeds the number of individuals that would be required for the current take to balance the PBR (i.e., N_{MIN} × Mortality and Serious Injury / PBR = 215,310 individuals). Therefore, the apparent exceedance of PBR in this case reflects inadequacy in the abundance estimates, rather than an indication of excessive take. The minimum estimated mean annual rate of U.S. commercial fishery-related mortality and serious injury (5 seals) is less than 10% of the negatively biased PBR (10% of PBR = 476) and, therefore, can be considered insignificant and approaching a zero mortality and serious injury rate. Population trends and status of this stock relative to its Optimum Sustainable Population are unknown.

There are key uncertainties in the assessment of the Arctic stock of ringed seals. Abundance and mortality and serious injury estimates are not available for the vast majority of the stock's range. Within U.S. waters, where abundance estimates are being developed and data are currently available on mortality and serious injury in commercial fisheries and the Alaska Native subsistence harvest, key abundance estimates for the Beaufort and Chukchi seas are not yet available. The negatively biased N_{MIN} used here, based on a 2012 Bering Sea density estimate from Conn et al. (2014), was calculated using only a sub-sample of the data and is likely to be an underestimate for the U.S. waters of the Bering Sea because of availability bias. Also, it represents just a portion of the population of ringed seals in U.S. waters and is, therefore, not very reliable for comparison with mortality and serious injury numbers for the entire U.S. portion of the stock. Based on the best available information, ringed seals are likely to be highly sensitive to climate change.

HABITAT CONCERNS

The main concern about the conservation status of ringed seals is long-term habitat loss and modification resulting from climate change (77 FR 76706, 28 December 2012). Laidre et al. (2008) concluded that on a worldwide basis ringed seals were likely to be highly sensitive to climate change based on an analysis of various life-history features that could be affected by climate.

Climate models consistently project substantial reductions in sea ice and on-ice snow depths (Kelly et al. 2010a, Hezel et al. 2012). Ringed seals excavate subnivean lairs (snow caves) in drifts over their breathing holes in the ice, in which they rest, give birth, and nurse their pups for 5-9 weeks during late winter and spring (Chapskii 1940, McLaren 1958, Smith and Stirling 1975). Substantial data indicate high pup mortality due to hypothermia and predation as a consequence of inadequate snow cover (e.g., Kumlien 1879, Lukin and Potelov 1978, Lydersen and Smith 1989, Smith and Lydersen 1991, Hammill and Smith 1991, Stirling and Smith 2004). Decreases in ice, and especially on-ice snow depths, are expected to lead to increased juvenile mortality from premature weaning, hypothermia, and predation (Kelly et al. 2010a). Changes in the ringed seal's habitat will be rapid relative to their generation time and, thereby, will limit adaptive responses (Kelly et al. 2010a).

A second major concern, driven primarily by the production of carbon dioxide (CO_2) emissions, is the modification of habitat by ocean acidification, which may alter prey populations and other important aspects of the marine ecosystem. Ocean acidification, a result of increased CO_2 in the atmosphere, may affect ringed seal survival and recruitment through disruption of trophic regimes that are dependent on calcifying organisms. The nature and timing of such impacts are extremely uncertain. As discussed by Kelly et al. (2010a), changes in ringed seal prey, anticipated in response to ocean warming and loss of sea ice, have the potential for negative impacts, but the possibilities are complex. Ecosystem responses may have very long lags as they propagate through trophic webs. Because of ringed seals' apparent dietary flexibility, this threat may be of less immediate concern than the threats from sea-ice degradation.

Additional habitat concerns include the potential effects from increased shipping (particularly in the Bering Strait), such as disturbance from vessel traffic and the potential for oil spills.

CITATIONS

Amano, M., A. Hayano, and N. Miyazaki. 2002. Geographic variation in the skull of the ringed seal, *Pusa hispida*. J. Mammal. 83:370-380.

Bengtson, J. L., L. M. Hiruki-Raring, M. A. Simpkins, and P. L. Boveng. 2005. Ringed and bearded seal densities in the eastern Chukchi Sea, 1999-2000. Polar Biol. 28:833-845.

Berta, A., and M. Churchill. 2012. Pinniped taxonomy: review of currently recognized species and subspecies, and evidence used for their description. Mammal Rev. 42:207-234.

Breiwick, J. M. 2013. North Pacific marine mammal bycatch estimation methodology and results, 2007-2011. U.S. Dep. Commer., NOAA Tech. Memo. NMFS-AFSC-260, 40 p.

Burns, J. J. 1970. Remarks on the distribution and natural history of pagophilic pinnipeds in the Bering and Chukchi seas. J. Mammal. 51:445-454.

Chapskii, K. K. 1940. The ringed seal of western seas of the Soviet Arctic (The morphological characteristic, biology and hunting production), p. 147. *In* N. A. Smirnov (ed.), Proceedings of the Arctic Scientific Research Institute, Chief Administration of the Northern Sea Route. Izd. Glavsevmorputi, Leningrad, Moscow. (Translated from Russian by the Fisheries Research Board of Canada, Ottawa, Canada, Translation Series No. 1665, 147 p.)

Conn, P. B., J. M. Ver Hoef, B. T. McClintock, E. E. Moreland, J. M. London, M. F. Cameron, S. P. Dahle, and P. L. Boveng. 2014. Estimating multispecies abundance using automated detection systems: ice-associated seals in the Bering Sea. Methods Ecol. Evol. 5:1280-1293. DOI: dx.doi.org/10.1111/2041-210X.12127 .

Crawford, J. A., K. J. Frost, L. T. Quakenbush, and A. Whiting. 2012. Different habitat use strategies by subadult and adult ringed seals (*Phoca hispida*) in the Bering and Chukchi seas. Polar Biol. 35:241-255.

Davis, C. S., I. Stirling, C. Strobeck, and D. W. Coltman. 2008. Population structure of ice-breeding seals. Mol. Biol. 17:3078-3094.

Fedoseev, G. A. 1975. Ecotypes of the ringed seal (*Pusa hispida* Schreber, 1777) and their reproductive capabilities. Biology of the Seal. Proceedings of a Symposium held in Guelph, 14-17 August 1972. Rapports et Proces-verbaux des Réunions. Conseil International pour l'Éxploration de la Mer. 169:156-160.

Finley, K. J., G. W. Miller, R. A. Davis, and W. R. Koski. 1983. A distinctive large breeding population of ringed seals (*Phoca hispida*) inhabiting the Baffin Bay pack ice. Arctic 36:162-173.

Freitas, C., K. M. Kovacs, R. A. Ims, M. A. Fedak, and C. Lydersen. 2008. Ringed seal post-moulting movement tactics and habitat selection. Oecologia 155:193-204.

Frost, K. J. 1985. The ringed seal (*Phoca hispida*), p. 79-87. *In* J. J. Burns, K. J. Frost, and L. F. Lowry (eds.), Marine Mammal Species Accounts. Alaska Department of Fish and Game, Juneau, AK.

Frost, K. J., and L. F. Lowry. 1984. Trophic relationships of vertebrate consumers in the Alaskan Beaufort Sea, p. 381-401. *In* P. W. Barnes, D. M. Schell, and E. Reimnitz (eds.), The Alaskan Beaufort Sea: Ecosystems and Environments. Academic Press, Inc., New York, NY.

Hammill, M. O., and T. G. Smith. 1991. The role of predation in the ecology of the ringed seal in Barrow Strait, Northwest Territories, Canada. Mar. Mammal Sci. 7:123-135.

Harwood, L. A., and I. Stirling. 1992. Distribution of ringed seals in the southeastern Beaufort Sea during late summer. Can. J. Zool. 70(5):891-900.

Harwood, L. A., T. G. Smith, and J. C. Auld. 2012. Fall migration of ringed seals (*Phoca hispida*) through the Beaufort and Chukchi seas, 2001-02. Arctic 65:35-44.

Harwood, L. A., T. G. Smith, J. C. Auld, H. Melling, and D. J. Yurkowski. 2015. Seasonal movements and diving of ringed seals, *Pusa hispida*, in the western Canadian Arctic, 1999-2001 and 2010-11. Arctic 68(2):193-209.

Hezel, P. J., X. Zhang, C. M. Bitz, B. P. Kelly, and F. Massonnet. 2012. Projected decline in spring snow depth on Arctic sea ice caused by progressively later autumn open ocean freeze-up this century. Geophys. Res. Lett. 39:L17505.

Hyvärinen, H., and M. Nieminen. 1990. Differentiation of the ringed seal in the Baltic Sea, Lake Ladoga and Lake Saimaa. Finnish Game Res. 47:21-27.

Ice Seal Committee (ISC). 2019. The subsistence harvest of ice seals in Alaska – a compilation of existing information, 1960-2017. 86 p. Available online: http://www.north-slope.org/departments/wildlife-management/co-management-organizations/ice-seal-committee . Accessed December 2020.

Kelly, B. P. 1988. Ringed seal, *Phoca hispida*, p. 57-75. *In* J. W. Lentfer (ed.), Selected Marine Mammals of Alaska: Species Accounts with Research and Management Recommendations. Marine Mammal Commission, Washington, DC.

Kelly, B. P., M. Ponce, D. A. Tallmon, B. J. Swanson, and S. K. Sell. 2009. Genetic diversity of ringed seals sampled at breeding sites; implications for population structure and sensitivity to sea ice loss. University of Alaska Southeast, North Pacific Research Board 631 Final Report. 28 p.

Kelly, B. P., J. L. Bengtson, P. L. Boveng, M. F. Cameron, S. P. Dahle, J. K. Jansen, E. A. Logerwell, J. E. Overland, C. L. Sabine, G. T. Waring, and J. M. Wilder. 2010a. Status review of the ringed seal (*Phoca hispida*). U.S. Dep. Commer., NOAA Tech. Memo. NMFS-AFSC-212, 250 p.

Kelly, B. P., O. H. Badajos, M. Kunnasranta, J. R. Moran, M. Martinez-Bakker, D. Wartzok, and P. Boveng. 2010b. Seasonal home ranges and fidelity to breeding sites among ringed seals. Polar Biol. 33:1095-1109.

King, J. E. 1983. Seals of the World. 2nd edition. British Museum (Natural History), London. 240 p.

Kumlien, L. 1879. Mammals, p. 55-61. *In* Contributions to the Natural History of Arctic America Made in Connection with the Howgate Polar Expedition 1877-78. Government Printing Office, Washington, DC.

Laidre, K. L., I. Stirling, L. F. Lowry, Ø. Wiig, M. P. Heide-Jørgensen, and S. H. Ferguson. 2008. Quantifying the sensitivity of arctic marine mammals to climate-induced habitat change. Ecol. Appl. 18(2):S97-S125.

Laidre, K., H. Stern, K. M. Kovacs, L. Lowry, S. E. Moore, E. V. Regehr, S. H. Ferguson, Ø. Wiig, P. Boveng, R. P. Angliss, E. W. Born, D. Litovka, L. Quakenbush, C. Lydersen, D. Vongraven, and F. Ugarte. 2015. Arctic marine mammal population status, sea ice habitat loss, and conservation recommendations for the 21st century. Conservation Biology 29:724-737.

Lukin, L. R., and V. A. Potelov. 1978. Living conditions and distribution of ringed seal in the White Sea in the winter. Soviet J. Mar. Biol. 4:684-690.

Lukin, L. P., G. N. Ognetov, and N. S. Boiko. 2006. Ecology of the ringed seal in the White Sea. UrO RAN, Ekaterinburg, Russia. 165 p. (Translated from Russian by the Baltic Fund for Nature (BFN), State University of St. Petersburg, Russia.)

Lydersen, C., and T. G. Smith. 1989. Avian predation on ringed seal *Phoca hispida* pups. Polar Biol. 9:489-490.

Lydersen, C., J. Vaquie-Garcia, E. Lydersen, G. N. Christensen, and K. M. Kovacs. 2017. Novel terrestrial haul-out behaviour by ringed seals (*Pusa hispida*) in Svalbard, in association with harbour seals (*Phoca vitulina*). Polar Res. 36, 1374124. DOI: dx.doi.org/10.1080/17518369.2017.1374124 .

Martinez-Bakker, M. E., S. K. Sell, B. J. Swanson, B. P. Kelly, and D. A. Tallmon. 2013. Combined genetic and telemetry data reveal high rates of gene flow, migration, and long-distance dispersal potential in Arctic ringed seals (*Pusa hispida*). PLoS ONE 8:e77125.

McLaren, I. A. 1958. The biology of the ringed seal (*Phoca hispida* Schreber) in the eastern Canadian Arctic. Bull. Fish. Res. Board Can. 118:97.

Moreland, E., M. Cameron, and P. Boveng. 2013. Bering Okhotsk Seal Surveys (BOSS), joint U.S.-Russian aerial surveys for ice-associated seals, 2012-13. Alaska Fisheries Science Center Quarterly Report (July-August-September 2013):1-6.

Müller-Wille, L. L. 1969. Biometrical comparison of four populations of *Phoca hispida* Schreb. in the Baltic and White seas and lakes Ladoga and Saimaa. Commentationes Biologicae Societas Scientiarum Fennica 31:1-12.

National Marine Fisheries Service (NMFS). 2016. Guidelines for preparing stock assessment reports pursuant to the 1994 amendments to the Marine Mammal Protection Act. 23 p. Available online: https://www.fisheries.noaa.gov/national/marine-mammal-protection/guidelines-assessing-marine-mammal-stocks . Accessed December 2020.

Nelson, M. A., L. T. Quakenbush, B. D. Taras, and Ice Seal Committee. 2019. Subsistence harvest of ringed, bearded, spotted, and ribbon seals in Alaska is sustainable. Endang. Species Res. 40:1-16. DOI: dx.doi.org/10.3354/esr00973 .

Nyman, T., M. Valtonen, J. Aspi, M. Ruokonen, M. Kunnasranta, and J. U. Palo. 2014. Demographic histories and genetic diversities of Fennoscandian marine and landlocked ringed seal subspecies. Ecol. Evol. 4:3420-3434.

Ognev, S. I. 1935. Mammals of the U.S.S.R. and Adjacent Countries. Vol. 3. Carnivora. Glavpushnina NKVT, Moscow, Russia. 641 p. (Translated from Russian by the Israel Program for Scientific Translations, Jerusalem, Israel. 741 p.)

Palo, J. 2003. Genetic diversity and phylogeography of landlocked seals. Dissertation. University of Helsinki, Helsinki, Finland. 29 p.

Palo, J. U., H. S. Mäkinen, E. Helle, O. Stenman, and R. Väinölä. 2001. Microsatellite variation in ringed seals (*Phoca hispida*): genetic structure and history of the Baltic Sea population. Heredity 86:609-617.

Palo, J. U., H. Hyvärinen, E. Helle, H. S. Mäkinen, and R. Väinölä. 2003. Postglacial loss of microsatellite variation in the landlocked Lake Saimaa ringed seal. Conserv. Genet. 4:117-128.

Quakenbush, L., J. Citta, and J. Crawford. 2011. Biology of the ringed seal (*Phoca hispida*) in Alaska, 1960–2010. Final Report to NMFS. Arctic Marine Mammal Program, Alaska Department of Fish and Game, Fairbanks, AK. 72 p.

Rice, D. W. 1998. Marine Mammals of the World: Systematics and Distribution. Society for Marine Mammalogy, Lawrence, KS. 231 p.

Smith, T. G., and C. Lydersen. 1991. Availability of suitable land-fast ice and predation as factors limiting ringed seal populations, *Phoca hispida*, in Svalbard. Polar Res. 10:585-594.

Smith, T. G., and I. Stirling. 1975. The breeding habitat of the ringed seal (*Phoca hispida*). The birth lair and associated structures. Can. J. Zool. 53:1297-1305.

Stirling, I., and T. G. Smith. 2004. Implications of warm temperatures, and an unusual rain event for the survival of ringed seals on the coast of southeastern Baffin Island. Arctic 57:59-67.

Valtonen, M., J. Palo, M. Ruokonen, M. Kunnasranta, and T. Nyman. 2012. Spatial and temporal variation in genetic diversity of an endangered freshwater seal. Conserv. Genet. 13:1231-1245.

Young, N. C., B. J. Delean, V. T. Helker, J. C. Freed, M. M. Muto, K. Savage, S. Teerlink, L. A. Jemison, K. Wilkinson, and J. Jannot. 2020. Human-caused mortality and injury of NMFS-managed Alaska marine mammal stocks, 2014-2018. U.S. Dep. Commer., NOAA Tech. Memo. NMFS-AFSC-413, 142 p.